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Effects of Grazing or Exercise in the Middle of the Fattening Period on the Growth and Carcass Traits of Japanese Shorthorn Steers

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Abstract

The effects of grazing or exercise in the middle of the fattening period on the growth and carcass traits of Japanese Shorthorn (JS) steers were investigated. JS steers were assigned to three groups: G (grazed), E (exercised), and B (barn-kept cattle). In the treatment period, group G was kept in the pasture, while groups B and E were confined to individual pens indoors at night, and stayed in a paddock during the day. In addition, group E was made to walk 4.0 km in the evening, five days a week. After the treatment, all the steers were housed and kept the same way as group B. The steers were slaughtered at 24 - 25 months of age. Group G exhibited a lower average daily gain (ADG) than groups B and E during the treatment period. Conversely, group G showed significantly higher ADG than the other two groups during the post-treatment period. Carcass weight for group G was smaller than those for the non-grazed counterparts. Groups G and E exhibited larger ($p < 0.05$) proportions of liver and spleen weights to live weight than those of group B. Group G also showed larger proportions of *biceps femoris* and *quadriceps femoris* muscles to carcass weight than those of group B. Group G exhibited a smaller ratio of fat and a larger ratio of muscle in the transverse section of the sixth rib, respectively, than those of group B. These results suggest that grazing or exercise in the middle of the fattening period affect growth in the late fattening period, and the carcass traits of JS steers even after being kept indoors for more than half a year.

Discipline: Animal industry
Additional key words: training course, liver, spleen, *biceps femoris* muscle, *quadriceps femoris* muscle

Introduction

In the Japanese beef industry, it is becoming more important to raise cattle using more domestic feed resources, so as to raise the feed self-sufficiency rate. Grazing is one effective way of utilizing domestic forage resources. Currently, the fattening of cattle in the pasture is not common in the Japanese beef industry. The reasons for using this practice are the slower growth of grazing cattle compared to those kept indoors and given concentrates (Keane and Drennan 2008), and the lower evaluation of beef produced with a forage-based diet in terms of beef color, tenderness and flavor (Davis et al. 1981, Hedrick et al. 1983, Imura et al. 2008). Therefore, it is worth developing proper methods of producing good quality beef for consumers by incorporating grazing in the fattening period.

Grazing is naturally accompanied by the spontaneous movement of cattle, and can be regarded as exercise. Although the quantity and quality of pasture grasses are important factors affecting beef quality (Gatellier et al. 2005, Julie et al. 2006, Petron et al. 2007), the effect of such exercise should not be ignored.

The purpose of the study is to investigate the effects of grazing or exercise in the middle of the fattening period on growth and carcass traits. The treadmill is a major tool used in studies concerning the effect of exercise on muscle

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biology (Aalhus et al. 1991, Apple et al. 1994, Aoki et al. 2007). As we were unable to use a treadmill, however, we selected an alternative method of making cattle walk a training course as exercise.

Materials and methods

1. Authorization of the study and ethical guidelines

The experimental scheme of this study was authorized by the Committee of Animal Experiments, Tohoku Agricultural Research Center (TARC), National Agriculture and Food Research Organization (NARO). All procedures including feeding, exercise and sacrificing were performed as per "The Guidelines for Experimental Animal Handling," TARC/NARO.

2. Experimental cattle

The experiment was repeated over the course of three consecutive years, and a total of 21 JS steers were used. Treatments were performed from the beginning of June to the end of September (16 weeks) every year. The age of steers at the beginning of treatment was 14-15 months, which corresponded to the beginning of the middle period of fattening for JS steers. The cattle were assigned to three treatment groups: G (grazed), E (exercised) and B (barn-kept cattle) (Table 1).

Table 1. Assignment of the experimental cattle

Groups (Treatments)	Year 1st	Year 2nd	Year 3rd	Total
Group G (Grazed)	2	3	3	8
Group E (Exercised)	2	2	2	6
Group B (Barn-kept cattle)	2	2	3	7
Total	6	7	8	21

3. Treatments

Group G steers were kept in the grasslands at TARC during the treatment period. In the first year, an old pasture (ca. 37,400 m^2) developed more than twenty years ago was used, and is located far from the cattle barn. The steers spent time in the pasture with another JS herd consisting of 10-15 cows and their spring-born calves, which was not related to this study. In the second and third years, another pasture was prepared next to the barn (Fig. 1), which had been renewed before the second year. The pasture was equally divided by a simple electric fence into three areas, with the cattle sequentially moving to the next area depending on pasture conditions. No supplemental feed other than mineral salt was fed to group G throughout the treatment period every year.

Basically, groups B and E were kept in the same manner. Both were confined in individual pens (ca. 5.85 m^2) in the barn (Fig. 2). In the daytime (from 9:00 a.m. to 1:30 p.m.), both groups stayed as one herd in the outdoor paddock neighboring the barn for barn management. After being rehoused in the pens at 1:30 p.m., both groups were fed commercial concentrate (89% dry matter (DM), 13% crude protein (CP) and 73% total digestible nutrients (TDN)/raw matter (RM)) at a rate of 1.4% of live weight. And they freely accessed timothy hay silage produced at TARC (50% DM, 7% CP /RM and 32% TDN/RM, estimated values from Standard Tables of Feed Composition in Japan, 2009).

In addition, group E was made to walk three laps around the training course each day (1.3 km circuit, 4.0 km total distance, Figs. 1 and 2). The walking began at 4:20 p.m. to avoid the hot midday conditions. The average walking time was 55 min. (ca. 4.4 km/h walking speed). The exercise was undertaken five days a week over the duration of the experiment.

4. Number of steps

In the third year, the numbers of steps taken by the cattle were monitored throughout the treatment period to evaluate their activity levels. A remote-counting pedometer system was prepared ("Gyu-Ho" made by Comtec, Miyazaki, Japan), and a pedometer with a transmitter was firmly attached to the metacarpus of one of the forelegs with a nylon band (Fig. 2). The data from the pedometer was occasionally received via a local antenna mounted on the cattle barn and accumulated on a personal computer.

5. Keeping steers in the post-treatment period

At the end of the treatment, group G steers were housed in individual pens in the barn. All steers were fed the concentrate at a rate of 1.6% of live weight per day and timothy silage *ad libitum* from October to next April (designated as the "post-treatment period" lasting 28-30 weeks, varying by individuals). Although the paddock was covered with snow from December to March, all the steers spent time as a herd in the paddock from 9:00 a.m. to 1:30 p.m. as in the summer season.

6. Monitoring of feed intake

In the treatment period, feed residue for groups E and B was recorded daily to calculate the true feed intake. The forage intake for group G in the pasture could not be monitored. In the post-treatment period, the feed intake of all steers was monitored daily until slaughter. The feed intake data at 28 weeks from the start of the post-treatment period was adopted for further analyses due to different lengths of the post-treatment period that varied by individuals (28-30 weeks).

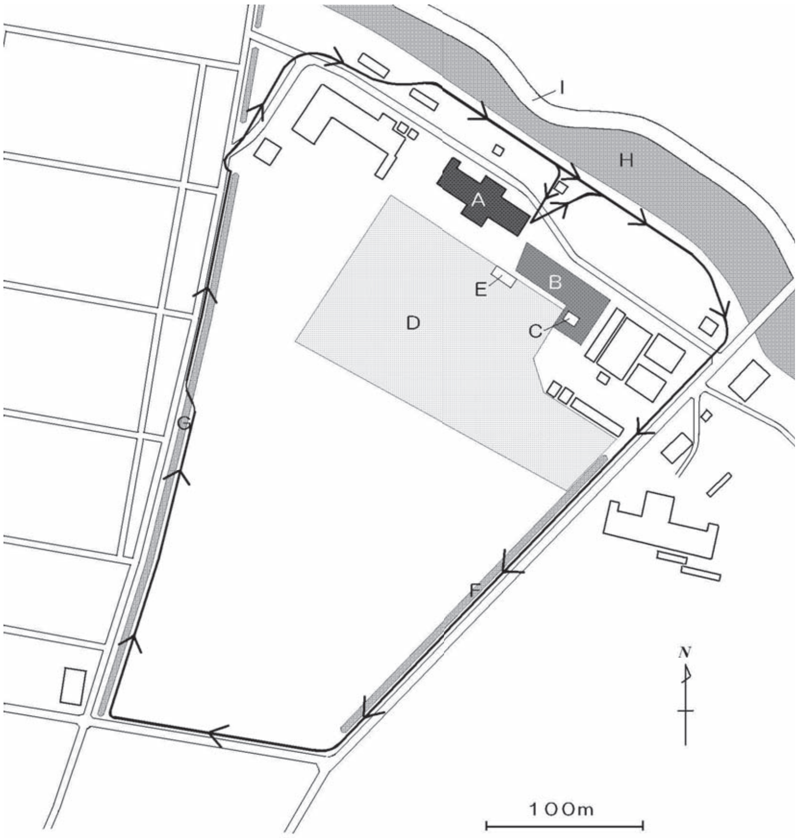

Fig. 1. Schematic illustration of the facilities and exercise course

(A) cattle barn, (B) outdoor paddock (ca. 1,300 m^2), (C) temporary sunshade with a shading textile, (D) pasture used in the 2nd and 3rd years (ca. 15,500 m^2), (E) roofed lot with water point and mineral salt setting for grazing steers, (F and G) rows of larch and red pine trees, respectively, which provided sunshade for the exercised steers, (H) thicket that separates the area of TARC and public road (I). The walking course is indicated by bold lines with arrowheads.

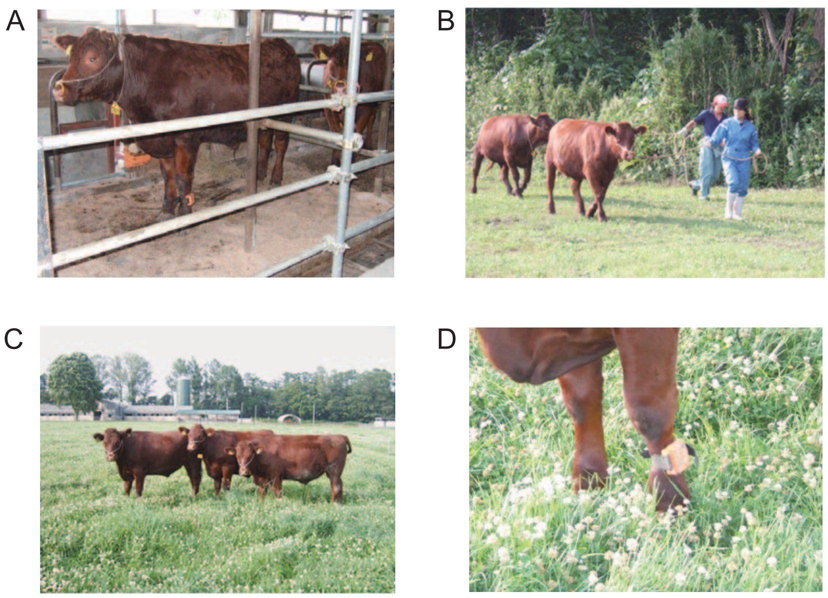

Fig. 2. The treatments for each group

(A) group B steers housed in individual pens in the barn, (B) group E steers undergoing exercise, (C) group G steers in the pasture, (D) remote pedometer attached to the left foreleg of the steer.

Table 2. Live weight gain of the experimental steers [1]

	n	Age at the start of treatment (day)		Age at slaughter (day)		Live weight at the start of treatment (kg)		Live weight at the end of treatment (kg)		Live weight at slaughter (kg)		ADG[2] in the treatment period (kg)		ADG in the post-treatment period (kg)		Overall ADG[3] (kg)	
		LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
Groups [4]																	
G	8	433.3	2.2	750.2	2.5	421.1	9.1	497.2^{b}	7.8	688.2	12.9	0.68^{b}	0.04	0.96^{a}	0.04	0.86	0.03
E	6	436.5	2.5	752.7	2.9	432.7	10.3	535.0^{a}	8.9	714.7	14.7	0.92^{a}	0.04	0.88^{b}	0.04	0.89	0.03
B	7	434.4	2.4	749.5	2.7	440.9	9.7	545.8^{a}	8.4	708.7	13.8	0.94^{a}	0.04	0.80^{b}	0.04	0.85	0.03
Year [5]																	
1st	6	429.8^{a}	2.5	742.3^{b}	2.9	446.8^{a}	10.3	521.0	8.9	683.0	14.7	0.66^{a}	0.04	0.81	0.04	0.76^{b}	0.03
2nd	7	432.2^{a}	2.4	748.4^{b}	2.7	442.8^{a}	9.7	541.8	8.4	721.0	13.8	0.89^{b}	0.04	0.90	0.04	0.90^{a}	0.03
3rd	8	442.1^{b}	2.2	761.6^{a}	2.5	405.1^{b}	9.1	515.2	7.8	707.6	12.9	0.98^{b}	0.04	0.93	0.04	0.95^{a}	0.03
Interaction Groups * Year		NS[6]		NS		NS		NS		NS		p<0.01		NS		NS	

[1] Values are expressed as least-squares means (LSM) and standard errors (SE).
[2] ADG: Average daily gain.
[3] ADG from the beginning of treatment to slaughter.
[4] Values with a different superscript in a column differ between the groups at the 5% level.
[5] Values with a different superscript in a column differ between the years at the 5% level.
[6] NS: non-significant.

7. Slaughter and carcass dismantling

All the cattle were slaughtered in April at 24-25 months of age in the experimental slaughterhouse at TARC. The weights of body parts (e.g., head, legs, skin) and organs (i.e., heart, liver, spleen) were recorded. The carcass was split into right and left half carcasses, and then kept in a chilling room at 2ºC. The right carcass was sold to packers and the left carcass was dismantled two days after slaughter. The carcass was split into primal cuts (i.e., forequarter, rib plate and flank, loin, full round) following the Japanese standard method. The transverse section containing the whole sixth rib was separated from the forequarter and dissected into bone, muscle and fat to estimate the whole carcass bone/muscle/fat ratios (Oliván et al. 2001). The individual muscles in the loin and round were separated and weighed.

8. Statistical analyses

All statistical analyses were conducted using the SAS GLM procedure by incorporating the treatment groups and experimental years as independent variables, and with their interaction also being added to the structural model. Multiple comparisons were adjusted by using the Tukey-Kramer method.

Results

1. Live weight gain

Group G steers exhibited a significantly smaller average daily gain (ADG) during the treatment period than that of the non-grazed counterparts, especially in the first year in the old pasture. Group E cattle showed slightly slower growth than group B in that period. Conversely, group G exhibited the largest ADG in the post-experiment period, while group B showed the smallest ADG in the same period. The live weight at slaughter did not significantly differ among the three groups. The interaction between groups and years was significant for ADG in the treatment period, due to much lower ADG for group G in that period in the first year (Table 2).

2. Feed intake

Group E ingested a significantly smaller amount of forage than group B in the treatment period. Overall TDN intake in the treatment period did not differ between the two groups. In the post-treatment period, group G exhibited a larger forage intake than the other groups (G vs. E, $p < 0.05$). In contrast, group G tended to show a smaller concentrate intake compared to the other two groups (G vs. E, $p < 0.1$). Group G required significantly smaller TDN per 1 kg live weight gain than group B ($p < 0.05$) in the post-treatment period (Table 3).

3. Number of steps

In the third year, the numbers of steps taken on weekdays were ca. 13,500, 12,000 and 6,100 per day for groups G, E and B, respectively. The differences among all three groups were significant ($p < 0.05$). Group E steers took ca. 5,000 steps for exercise on weekdays (data not shown). On Saturday and Sunday, the numbers of steps taken by groups G, E and B were ca. 13,700, 7,200 and 6,100, respectively. Group E walked a little more than group B in the paddock

Table 3. Feed intake and feed efficiency of the steers [1]

	n	Total concentrate intake (kg raw matter)		Total forage intake (kg raw matter)		Total dry matter intake (kg)		Forage ratio on dry matter basis		Overall TDN [2] intake (kg)		TDN ratio derived from forage		TDN required for 1-kg live weight gain (kg)	
Treatment period (16 weeks)															
Groups [3,4]		LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
E	6	745.5	17.9	761.3[b]	29.7	1040.3	20.0	0.36[b]	0.01	787.8	14.9	0.31[b]	0.01	7.8	0.3
B	7	724.2	16.9	871.1[a]	28.0	1075.7	18.8	0.40[a]	0.01	807.4	14.1	0.34[a]	0.01	7.8	0.3
Year [5]															
1st	4	757.9	21.9	610.6[b]	36.4	976.8[b]	24.5	0.31[b]	0.01	748.7[b]	18.3	0.26[b]	0.01	7.6	0.4
2nd	4	725.0	21.9	898.3[a]	36.4	1089.8[a]	24.5	0.41[a]	0.01	816.7[a]	18.3	0.35[a]	0.01	8.2	0.4
3rd	5	721.6	20.0	939.7[a]	33.2	1107.4[a]	22.3	0.42[a]	0.01	827.5[a]	16.7	0.36[a]	0.01	7.5	0.4
Interaction Groups * Year		NS [6]		NS		NS		NS		NS		NS		NS	
Post-treatment period (28 weeks)															
Groups [4]		LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE	LSM	SE
G	8	1471.9	32.3	1461.1[a]	59.6	2033.2	48.7	0.35[a]	0.01	1542.0	35.7	0.30[a]	0.01	7.2[b]	0.4
E	6	1591.2	36.7	1219.4[b]	67.6	2019.7	55.2	0.30[b]	0.01	1551.8	40.5	0.25[b]	0.01	8.0[ab]	0.4
B	7	1528.8	34.6	1266.7[ab]	63.7	1987.6	52.0	0.31[b]	0.01	1521.3	38.2	0.26[b]	0.01	8.8[a]	0.4
Year [5]															
1st	6	1475.6	36.7	1049.7[b]	67.6	1832.9[b]	55.2	0.28[c]	0.01	1413.1[b]	40.5	0.24[c]	0.01	8.2	0.4
2nd	7	1575.3	34.6	1340.3[a]	63.7	2065.5[a]	52.0	0.32[b]	0.01	1578.9[b]	38.2	0.27[b]	0.01	7.9	0.4
3rd	8	1540.8	32.3	1557.1[a]	59.6	2142.1[a]	48.7	0.36[a]	0.01	1623.1[b]	35.7	0.31[a]	0.01	7.8	0.4
Interaction Groups * Year		NS		NS		NS		NS		NS		NS		NS	

[1] Values are expressed as least-squares means (LSM) and standard errors (SE).
[2] TDN: total digestible nutrients.
[3] Feed intake for group G cattle could not be monitored; therefore, exercised cattle and barn-kept cattle were compared for the treatment period.
[4] Values with a different superscript in a column differ between the groups at the 5% level.
[5] Values with a different superscript in a column differ between the years at the 5% level.
[6] NS: non-significant.

Table 4. Average number of steps taken by the steers throughout the treatment period in the third year [1]

Groups	n	Monday-Friday [2]		Saturday and Sunday [3]		Overall	
		Mean	SD	Mean	SD	Mean	SD
G	3	13472 [a]	2771	13697 [a]	2661	13535 [a]	2738
E	2	12011 [b]	1889	7155 [b]	2016	10637 [b]	2915
B	3	6069 [c]	1771	6101 [c]	1796	6078 [c]	1775

[1] Values are expressed as means and standard deviations (SD). Values with a different superscript in a column differ at the 5% level.
[2] Group E was made to engage in exercise.
[3] Group E was treated the same way as the group S without exercise.

even on the weekend with no imposed exercise (Table 4).

4. Carcass traits

Hot carcass weight (HCW) for group G was the lightest (G vs. E, $p < 0.05$). Group E exhibited the largest liver and spleen weights among the three treatment groups (E vs. B, $p < 0.05$). Liver and spleen weights of group G were intermediate between those of the other two groups. Group B cattle showed significantly ($p < 0.05$) smaller liver and spleen proportions to slaughter weight than groups E and G (Table 5).

There were no individual muscles that showed significant differences in raw weights among the three groups. In contrast, group G cattle exhibited larger *biceps femoris* (BF) and *quadriceps femoris* (QF) muscle proportions to left-side cold carcass weight (CCW) than group B ($p < 0.05$). Group E showed intermediate values for the two muscle proportions to CCW. Group G exhibited the highest and lowest

Table 5. Weights of body parts and their percentage to live weight at slaughter [1]

Raw weight (kg)	Group G (n=8) LSM	SE	Group E (n=6) LSM	SE	Group B (n=7) LSM	SE
Live weight at slaughter (SW)	688.2	12.9	714.7	14.7	708.7	13.8
Hot carcass weight (HCW)	435.9 [b]	7.2	466.3 [a]	8.1	457.4 [ab]	7.6
Head	20.7	0.3	20.5	0.3	20.6	0.3
Forefeet	5.8	0.2	5.7	0.2	6.1	0.2
Hind feet	4.9	0.3	5.6	0.4	5.8	0.3
Tail	2.1	0.1	2.1	0.1	2.2	0.1
Skin	48.9	1.3	49.1	1.4	48.7	1.4
Abdominal fat	11.7	1.0	13.1	1.1	12.4	1.1
Heart	2.6	0.1	2.6	0.1	2.6	0.1
Liver	7.5 [ab]	0.1	7.9 [a]	0.2	7.2 [b]	0.1
Spleen	1.8 [ab]	0.1	1.9 [a]	0.1	1.3 [b]	0.1
Ratios to SW (%)						
Dressing percentage [2]	63.37	0.52	65.25	0.59	64.55	0.56
Head	3.01	0.05	2.87	0.06	2.91	0.05
Forefeet	0.84	0.03	0.79	0.04	0.87	0.03
Hind feet	0.71	0.05	0.79	0.06	0.82	0.05
Tail	0.31	0.01	0.29	0.01	0.31	0.01
Skin	7.11	0.15	6.89	0.17	6.87	0.16
Abdominal fat	1.70	0.14	1.82	0.16	1.76	0.15
Heart	0.38	0.01	0.36	0.02	0.36	0.02
Liver	1.09 [a]	0.02	1.11 [a]	0.03	1.02 [b]	0.02
Spleen	0.27 [a]	0.01	0.27 [a]	0.02	0.18 [b]	0.01

[1] Values are expressed as least-squares means (LSM) and standard errors (SE). Values with a different superscript in a row weight differ at the 5% level between the groups.
[2] Dressing percentage = 100*HCW/SW.

muscle and fat percentages for the sixth rib section among the three groups, respectively. In contrast, group B showed the lowest and highest lean and fat percentages, respectively (Table 6).

Discussion

Grazing cattle generally tend to exhibit slower growth than those kept indoors (Ozutsumi and Okada 1981, Allingham et al. 1997, Keane and Drennan 2008). One possible reason for this tendency may be the extra energy expenditure caused by spontaneous movements in the pasture. A difference in nutritional conditions may also be a cause of slower growth. In this study, the feedstuffs were grasses in the pasture alone for group G, and concentrate with ensilaged hay for groups B and E. The forage itself might be the cause of a diminished growth rate. Saintz et al. (1995) reported that steers raised with a forage-based diet exhibited slower growth and leaner carcasses than those fed a concentrate-based diet under the same nutritional level. In addition, fresh grasses are abundant in n-3 family polyunsaturated fatty acids (PUFAs), and the ingested PUFAs may be accumulated in skeletal muscles. The n-3 PUFAs increase thermogenesis and decrease body fat deposition (Julie et al. 2006). The reason for the slower growth of group G steers during the treatment period might be the extra energy consumption that accompanies spontaneous movement with a lower nutritional level, combined with a higher heat increment with grass-derived PUFAs in skeletal muscles.

Contrary to the slower growth in the pasture, group G exhibited significantly larger ADG during the post-treatment period than group B. Such a growth pattern is recognized as “compensatory growth.” Such compensatory growth is widely observed in meat animals whose growth was previously restricted by a lower dietary level, and then are given high nutritional feed (Allingham et al. 1998, Therkildsen et al. 2008, Stolzenbach et al. 2009, Greenwood et al. 2009). Compensatory growth has also been observed in grazed cattle that are often subject to an under-nutritional level in the pasture, when the cattle are housed after grazing and re-alimented (Hersom et al. 2004a). One explanation for this phenomenon is that animals which are chronically fed at a low nutritional level eventually exhibit diminished basal metabolism mainly due to the decreased mass of visceral organs, including the liver and intestines that are metabolically active, and when such animals are re-alimented, they require less energy for live weight gain

Table 6. Weights of primal cuts, individual muscles, their ratios to cold carcass, and bone/muscle/fat ratios [1]

	Group G (n=8)		Group E (n=6)		Group B (n=7)	
	LSM	SE	LSM	SE	LSM	SE
Raw weights (kg)						
Left-side cold carcass	214.0 [b]	3.7	228.9 [a]	4.2	226.5 [ab]	3.9
Primal cuts						
Forequarter	81.1	0.8	84.4	1.1	82.7	0.9
Loin	22.0	0.9	24.1	1.0	24.7	0.9
Rib plate and flank	37.5	1.3	41.6	1.5	40.4	1.4
Full round	59.4	1.6	62.4	1.8	63.0	1.7
Individual muscles						
Psoas major (PM)	2.9	0.3	2.4	0.3	2.5	0.3
Longissimus thorasis et lumborum (LTL) [2]	4.5	0.1	4.7	0.1	4.7	0.1
Biceps femoris (BF)	7.2	0.1	7.4	0.2	7.0	0.2
Quadriceps femoris (QF)	6.2	0.2	6.2	0.2	5.9	0.2
Gluteus medius and G. accessorius (GM+GA)	3.5	0.2	3.8	0.2	3.8	0.2
Semitendinosus (ST)	2.3	0.1	2.4	0.1	2.3	0.1
Semimembranosus (SM)	4.9	0.2	5.3	0.2	5.6	0.2
Adductor (AD)	1.8	0.1	1.7	0.2	1.5	0.2
Relative ratios to left-side cold carcass (%)						
Primal cuts						
Forequarter	37.93	0.44	37.68	0.58	36.49	0.47
Loin	10.28	0.38	10.52	0.43	10.88	0.40
Rib plate and flank	17.56	0.39	18.13	0.44	17.87	0.42
Full round	27.78	0.57	27.30	0.64	27.79	0.60
Individual muscles						
PM	1.34	0.11	1.02	0.12	1.10	0.11
LTL	1.76	0.16	2.06	0.18	2.06	0.17
BF	3.36 [a]	0.05	3.23 [ab]	0.06	3.11 [b]	0.06
QF	2.90 [a]	0.07	2.72 [ab]	0.08	2.61 [b]	0.08
GM+GA	1.63	0.07	1.66	0.08	1.67	0.07
ST	1.08	0.02	1.07	0.02	1.03	0.02
SM	2.28	0.09	2.34	0.10	2.45	0.11
AD	0.84	0.06	0.72	0.07	0.66	0.08
Bone/muscle/fat ratios [3] (%)						
Bone	15.7	0.6	13.9	0.7	14.2	0.7
Muscle	49.2 [a]	1.2	47.3 [ab]	1.3	43.0 [b]	1.3
Fat	33.1 [b]	1.2	36.8 [ab]	1.4	40.0 [a]	1.3

[1] Values are expressed as least-squares means (LSM) and standard errors (SE). Values with a different superscript in a row differ at the 5% level between the groups.
[2] From the 7th thoracic to the 2nd lumbar vertebra.
[3] The ratios for the transverse section containing the whole 6th rib.

and exhibit rapid growth (Hornick et al. 2000). However, this explanation may not be suitable for grazed animals, as grazed cattle exhibit an enlargement of visceral organs including the liver, spleen and gastrointestinal tract, as well as higher heat production when they are re-alimented (Ura et al. 1983, Sainz & Bentrey 1997, Hersom et al. 2004b). Visceral organs are the major sources of heat production and the enlarged visceral organs require more maintenance energy (Hersom et al. 2004b), which might lead to a decrease in growth efficiency for previously grazed cattle. Nevertheless, compensatory growth did occur in group G in the present study. It might be possible that some other unknown mechanisms had caused the growth pattern for group G in the post-treatment period.

Group G exhibited a smaller carcass weight, lower dressing percentage, less subcutaneous and intermuscular fat accumulation at slaughter than groups E and B, irrespective of compensatory growth in the post-treatment period. One reason would be that the grazed animals exhibit a shift in muscle energy metabolism from anaerobic glycolysis toward fatty acid oxidation (Aalhus & Price 1991, Julie et al. 2006). In this study, group G steers ingested the largest amount of timothy hay silage among the three treatment groups in the post-treatment period. As previously discussed, a forage-based diet causes more heat production in cattle than a grain-based diet. This is caused by the increase in fatty acid oxidation, resulting in less accretion of fat. In the transverse section of the sixth rib, group G showed significantly smaller and larger ratios for fat and muscle than group B, respectively, suggesting that the energy metabolism which had shifted toward oxidation in group G steers in the treatment period had been maintained through the post-treatment period. In terms of beef production, it seems unlikely that compensatory growth alone is sufficient to fully "compensate" for slower growth in the pasture.

We referred to Dunne et al. (2005), who made steers walk a 4.41 km course at an average speed of 5.2 km/h, six days a week for 18 weeks. In the present study, we made the steers walk a distance of 4.0 km, five days a week for 16 weeks. Therefore, the intensity of the exercise in this study was slightly less than that of Dunne et al. (2005).

There should be an argument over whether such imposed exercise of animals reflects their spontaneous movements in the grassland. Oudshoorn et al. (2008) reported that lactating dairy cows kept in the grassland (15,000 m^2) for nine hours during the day exhibited an average walking speed of 0.58 km/h and an average walking distance of ca. 5.8 km/day. We did not measure the walking speed of group G steers. However, it might be possible that group G moved much more slowly on average in the pasture than group E steers engaged in exercise (4.4 km/h).

We anticipated that the number of steps taken per day by group E steers would be compatible with that taken by group G. However, group E showed a significantly smaller number of steps than group G on weekdays. Moreover, group G cattle exhibited frequent movements in the pasture even at midnight in contrast to those of group E that spent the night in individual pens (data not shown). The results imply that the moving patterns for groups G and E were quite different from each other, and that the imposed exercise alone was not sufficient to simulate movement of the grazing steers.

Dunne et al. (2005) reported that the exercised steers exhibited slower growth than the non-exercised counterparts. The same tendency was observed in this study. In the treatment period, the overall TDN intake did not differ between the two groups. However, group E ingested a significantly smaller amount of forage than group B steers, indicating that group E depended more on concentrate for their nutrients than group B. One possible reason is that the extra energy expenditure caused by the exercise might have made group E steers prefer concentrate to forage as an energy source for a rapid recovery. The growth pattern for group E in the post-treatment period was not compensatory, since ADG in the post-treatment period for group E was smaller than in the treatment period, although the preference for concentrate by group E continued in the post-treatment period.

Group B exhibited the smallest ADG in the post-treatment period and the lowest feed efficiency in the same period among the three groups. And group B displayed the largest and smallest ratios for fat and lean, respectively, in the transverse section of the 6th rib among the groups. One possible reason is that the behavioral activity of group B was lowest in the treatment period, resulting in diminished basal metabolism and body composition with a liability to accumulate more fat compared to groups G and E.

We observed larger proportions of the liver and spleen to the live weight at slaughter in groups G and E. Sainz and Bentley (1997) reported that growth-compensated steers showed larger liver weight and a higher protein/DNA ratio in the liver than growth-uninterrupted steers, and the authors attribute the results to the increase in dry matter intake (DMI) and enlarged liver cell size in the compensated steers. In contrast, Julie et al. (2006) observed no significant difference in liver weight between exercised and non-exercised steers. Rather the same authors commented that a higher intake of intestine-digestible protein would result in increased liver mass. It is likely that the exercise or grazing in the treatment period affected liver enlargement during the post-treatment period in this study. However, total DMI in the post-experimental period did not differ statistically among the three groups. Another reason would explain this phenomenon.

Sainz and Bentley (1997) observed a larger spleen weight in steers that were fed forage in the growing phase and then re-alimented with concentrate in the fattening phase, compared with steers fed concentrate *ad libitum* throughout the growing and fattening phases. Mader et al. (2009) reported that a positive relation exists between the spleen proportion per body weight and the gain/feed ratio ($p < 0.05$). However, both articles did not discuss what caused the enlarged spleens. In mammals, the spleen serves the role of not only removing old blood components and unwanted materials by filtration and immune phagocytosis, but also reserving erythrocytes for aerobic exercise (Otto et al. 1995). Spontaneous movement accompanying grazing or exercise would cause an increase in oxygen demand in various organs, leading to the requirement for a larger blood reservoir. The steers in groups G and E might have adapted to the treatments through enlargement of the spleen via such a role.

Aalhus & Price (1991) observed larger round muscles, namely *semimembranosus*, *semitendinosus*, *vastus lateralis* (a component of QF) and *gastrocnemius* for exercised sheep as compared to non-exercised control sheep. In the present study, the proportions of BF and QF to CCW at slaughter were significantly larger for group G than for group B, suggesting that grazing influenced the development of these muscles. However, the effect of exercise on the round muscle proportions to CCW was not clear, as group E did not exhibit significant differences in the composition of those muscles in comparison to group B. It seems that the impact of exercise alone on muscle composition at slaughter was weaker than that of grazing in the present study.

Conclusion

The present study showed the significant effects of grazing or imposed exercise in the middle of the fattening period on cattle growth and feed intake as compared to barn-kept cattle. The treatments also influenced the organ mass and carcass conformation even after keeping the cattle in a barn for more than six months of the post-treatment period. The results might help researchers develop a system to produce beef that incorporates grazing with a diminished amount of concentrate in comparison to the conventional fattening system, thereby leading to lower feed costs in beef production. Further investigation will be required to elucidate the mechanisms accompanying grazing that would yield differences in beef quality for producing lean beef with consumer-acceptable quality.

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