Glycogen metabolites and meat quality in feed-restricted re-fed beef heifers

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Yambayamba, E. S. K., Aalhus, J. L., Price, M. A. and Jones, S. D. M. 1996. **Glycogen metabolites and meat quality in feed-restricted re-fed beef heifers.** Can. J. Anim. Sci. **76**: 517–522. Twenty-four Hereford crossbred heifers weighing 222 kg (22 kg SD) and aged 226 d (13 d SD) on day 0 were used to investigate the effects of feed restriction (period 1) followed by realimentation (period 2) on hepatic and longissimus muscle glycogen metabolites and meat quality. The heifers were randomly assigned in equal numbers to either ad libitum feeding (ADLIB) or maintenance feeding for 92 d followed by realimentation (REST), and serially slaughtered over a wide range of liveweights (200-460 kg). The concentrations of glycogen, its metabolites, and the total glucidic potential (GP) were determined from portions of the caudate lobe of the liver and the longissimus lumborum (LL) muscle. Meat quality assessment of the longissimus thoracis (LT) was done by objective means. Hepatic glycogen concentration was lower ($P = 0.05$) in REST than in ADLIB heifers, and GP tended to show a similar pattern ($P = 0.07$). There were no significant differences in the concentrations of glycogen or its metabolites in the LL of REST compared with ADLIB heifers. However, the heifers slaughtered during period 1 had lower muscle glycogen ($P = 0.04$) and higher lactate ($P < 0.01$) concentrations than those slaughtered during period 2. REST heifers had lighter slaughter weights resulting in smaller ribeye areas ($P = 0.03$), lower intramuscular fat concentration ($P < 0.01$) and higher moisture content ($P < 0.01$). Independent of slaughter weight, REST heifers had higher drip loss ($P = 0.05$) and lower L * ($P = 0.01$) than ADLIB heifers. These results suggest that feed restriction affects hepatic glycogen reserves and also has minor effects on meat quality traits in beef heifers. However, there was no indication that meat from REST heifers had severe quality defects such as DFD (dark, firm, dry) meat.

Key words: Feed restriction, realimentation, longissimus muscle, liver, glucidic potential, meat quality

Yambayamba, E. S. K., Aalhus, J. L., Price, M. A. et Jones, S. D. M. 1996. **Rapport entre métabolites du glycogène et qualité de la viande chez des génisses à viande exposées à un cycle de rationnement-alimentation à volanté.** Can. J. Anim. Sci. **76**: 517–522. Nous avons examiner chez 24 génisses Hereford croisées, d'un poids initial de 222 kg (ET 22 kg) et d'un âge moyen de 226 j (± 13 j), les effets d'une phase de rationnement (phase 1) suivie par une phase d'alimentation à volonté (phase 2), sur les métabolites du glycogène présents dans le foie et dans le muscle longissimus lumborum ainsi que sur la qualité de la viande. Les génisses étaient affectées au hasard, en nombre égal, soit à un régime alimentaire à volonté (ADLIB), ou à un régime d'entretien pendant 92 j suivi d'un retour à l'alimentation à volonté (REST). Les bêtes étaient abattues en série à partir du PC de 200 jusqu'à celui de 460 kg. Les concentrations de glycogène et de ses métabolites, ainsi que le potentiel glucidique total (PG) étaient déterminés sur des portions du lobule de Spiegl du foie et du muscle longissimus lumborum (LL). En outre, l'appréciation qualitative de la viande du longissimus thoracis était faite par méthode objective. La concentration du glycogène dans le foie était plus basse ($P < 0,05$) chez les génisses au régime ADLIB, le PG suivant une évolution analogue ($P < 0,07$). Dans le LL, on n'observait pas de différence significative entre les deux régimes relativement aux concentrations de glycogène ou de ses métabolites. Les génisses abattues dans la phase 1 avaient moins de glycogène ($P = 0,04$) et plus de lactate ($P < 0,01$) dans le muscle que celles abattues dans la phase 2. Les bêtes au régime REST pesaient moins à l'abattage et présentaient une noix de côte plus petite ($P = 0,03$), une moindre concentration de gras intramusculaire ($P < 0,01$) et une plus forte teneur en eau de la viande ($P < 0,01$) que les génisses ADLIB. Indépendamment du poids à l'abattage, leur viande avait des pertes d'égouttage plus élevées ($P = 0,05$) et une valeur L* plus basse ($P = 0,01$). Il ressort de ces observations que le rationnement temporaire influe sur les réserves en glycogène du foie et ne produit que des effets bénins sur la qualité de la viande, rien de comparable en fait au grave défaut de la viande DFD (viande noire).

Mots clés: Rationnement, remise à l'alimentation à volonté muscle longissimus, foie potentiel glucidique, qualité de la viande

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GP is the sum of glycogen and its major metabolites from anaerobic glycolysis (glucose, glucose-6-phosphate, and lactate). In tissues such as postmortem muscle, where glycogen is labile, GP is a useful indication of the total energy available to the tissue. Among other things, GP has been related to the ultimate pH of meat (Guignot et al. 1992), with glycogen level being the main determinant of the pH (Warris et al. 1989). Glycogen depletion during the handling of cattle prior to slaughter can lead to an elevated ultimate pH and DFD meat. Thus a low GP at slaughter is indicative of a high likelihood of DFD.

While preslaughter handling is perhaps the most signifi-

Abbreviations: ADLIB, ad libitum; **DFD**, dark firm, dry; **DM**, dry matter; **GP**, glucidic potential; **G-6-P**, glucose-6-phosphate; **LL**, longissimus lumborum; **LT**, longissimus thoracis; **REA**, rib eye area; **REST**, maintenance feeding followed by realimentation

cant factor influencing DFD, feeding level may have some influence on meat quality; in a study by Crouse et al. (1984) fasting bulls for 4 d led to depletion of skeletal muscle glycogen (Crouse et al. 1984). Unlike skeletal muscle, the liver responds rapidly to nutrition; for example feed restriction has been associated with depletion of hepatic glycogen content in dairy cows (Drackley et al. 1991; Veenhuizen et al. 1991) and rapid liver weight loss in beef cattle (Jones et al. 1988).

The objective of the present study was to investigate the effects of a maintenance ration followed by realimentation on the glucidic potential of liver and skeletal muscle, and on meat quality in Hereford crossbred heifers.

Table 1. Composition of experimental diet (as fed)

Ingredient	Diet composition (g kg^{-1})
Barley	754.5
Alfalfa grass hay	200.0
Canola meal	30.0
Calcium carbonate	8.0
Fortified salt	5.0
Vitamin ADE	2.5
Calculated nutrient composition	
DM %	89.0
Crude protein, % of DM	12.86
DE, MJ kg^{-1} of DM	13.79

MATERIALS AND METHODS

Animals and Feeding

As part of a larger study (Yambayamba et al. 1996), 24 Hereford crossbred heifers weighing 222 kg (22 kg SD) and aged 226 d (13 d SD) on day 0 were used in the present experiment. The heifers were born in the spring of 1992 at the University of Alberta Ranch, Kinsella. They were randomly assigned to two treatments: 12 to ADLIB and 12 REST. During the period of adjustment to the experimental diet (Table 1), all the heifers were fed to appetite (ad libitum) and fresh water was always available.

At the beginning of the experiment, the ADLIB heifers continued on ad libitum feeding while the REST heifers were switched to a maintenance ration. The period during which REST heifers were restricted was designated period 1 and the period of realimentation was designated period 2. The heifers were all fed once daily at about 09:00 h, and the remaining feed from the ADLIB pens was removed and weighed before fresh feed was provided. The heifers were weighed weekly for the first 6 wk and thereafter every 2 wk. On day 92 of the experiment, the REST heifers were introduced to ad libitum feeding by increasing the ration by 400 g $head^{-1}$ d^{-1} until they were being offered feed in excess of appetite. This process took 2–3 wk.

Slaughter and Tissue Collection

The heifers were randomly allocated to slaughter dates, with two heifers being slaughtered from each treatment on each occasion (Fig. 1) over a wide range of liveweights (200 to 460 kg). Animals were transported 130 km to a research abattoir, held overnight in lairage with free access to water, and slaughtered the following morning in the normal commercial manner. Within 5 min following exsanguination, a small muscle sample (40–50 g) was obtained from the 3rd–4th lumbar region of the LL, using a 20-mm-diameter stainless steel corer. The sample was immediately frozen in liquid nitrogen (–70°C) and stored at –35°C until analyzed. A liver sample (50–100 g) from the caudate lobe was obtained approximately 20 min postmortem, and immediately frozen in liquid nitrogen and stored at –35°C for later analysis.

Assessment of Meat Quality

Temperature and pH were measured in the LT at a muscle depth of approximately 3 cm between the 10th and 11th ribs on both sides of each carcass at 45 min postmortem prior to entering the cooler, using a Corning Model 4 pH/temperature meter (Corning Glass Works, Medfield, MA) equipped with an Ingold spear-type electrode (Ingold Messtechnik AG, Urdorf, Switzerland). The carcasses were chilled in the commercial manner at 2°C for 24 h.

After 24 h, carcass side weights were recorded to determine cooler shrink losses, and pH and temperature were again measured between the 10th and 11th ribs. The carcass sides were split at the Canadian grade site (between the 12th and 13th ribs) and the surface was allowed to "bloom" for 15–20 min. Three meat color measurements [CIE L* (brightness), a* (red-green axis) and b* (yellow-blue axis) values (Commission Internationale de l'Eclairage 1976)] were made at the grade site surface using a Chroma Meter II (Minolta Canada Inc., Mississauga, ON) and the results were averaged. REA at the 12th rib was traced and the tracings were placed on a Kurta digitizing tablet (Kurta Corp., Phoenix, AZ) for the calculation of muscle area.

Twenty-four hours post-slaughter, a steak was cut from the LT muscle samples and placed in a styrofoam steak tray overwrapped with an oxygen permeable film and stored for 5 d at 2°C for determination of drip loss. The remaining portions of the muscle samples were stored in polythene bags at 2°C for 5 d. After 5 d another steak was cut from each of the muscle samples and ultimate pH was recorded. Final objective Chroma Meter II color readings were recorded prior to cooking the steak to an internal temperature of 72°C (monitored with an electronic temperature probe; Technoterm 1100, Germany) in saline in an 80°C water bath. After chilling the steaks overnight to 2°C, three 19-mm cores were sheared on an Instron 4301 Material Testing System (Burlington, ON). The remainder of the muscle was ground once, and duplicate subsamples were taken for moisture determination by weight difference following 24 h in a drying oven. Intramuscular fat was determined on the dried samples using a Soxtec apparatus (ether extraction).

Determination of Muscle and Hepatic Glucidic Potential

Glycogen and its metabolites were extracted from frozen liver and muscle samples by first pulverizing the sample with a chilled (–70°C) mortar and pestle using liquid nitrogen to keep the sample frozen. About 1 g of the crushed sample was weighed into a 15-mL disposable, conical cen-

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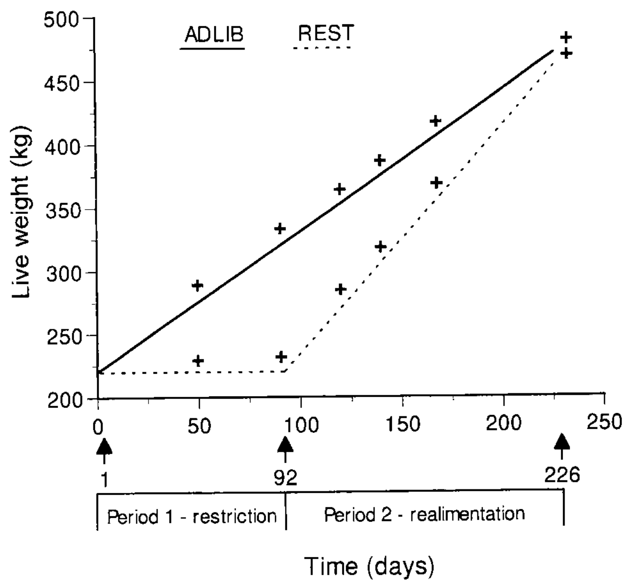

Fig. 1. Schematic design of experiment. + indicates slaughter of two heifers.

trifuge tube. While in the ice bath, 5 mL of 0.6 N cold perchloric acid was added to the tube and the sample was homogenized with a Polytron homogenizer (Kinematica GmbH, Switzerland) for 45 s. An aliquot of the homogenate (0.2 mL) was pipetted into a centrifuge tube for the amyloglucosidase procedure described by Dalrymple and Hamm (1973). The remaining homogenate was centrifuged (3000 × g) for 20 min at 2°C, following which the supernatant was decanted into a 15-mL centrifuge tube. The extracts were then neutralized as described by Dalrymple and Hamm (1973) except that the supernatant was not filtered but centrifuged as above. The neutralized extract was stored at 0°C until assayed for glucose, lactate, and glucose-6-phosphate (G-6-P). All spectrophotometric readings were performed at 340 nm on a Pharmacia Ultrospec III spectrophotometer (Cambridge, UK).

Glycogen and Metabolite Assays

Since the assay for glycogen required a glucose blank (perchloric acid extract) from the same sample, both glycogen and glucose were determined using the same glucose blank. The assays were performed as described by Keppler and Decker (1974) using the homogenate incubated with amyloglucosidase (for glycogen) and the supernatant from the perchloric acid extraction assay (for glucose). Liver samples required an additional 1:5 dilution for the glucose assay.

The lactate assay was performed as described by Gutmann and Wahlefeld (1974) using the supernatant from the perchloric acid extraction. In some cases it was necessary to dilute the supernatant (usually 1:10) with neutralized perchloric acid (0.6 N neutralized to a methyl orange end point with 5.4 N KOH) to obtain absorbency readings in acceptable ranges (i.e., < 1.000). These dilutions were accounted for in the calculations. The G-6-P assay was performed as described by Lang and Michal (1974) using the

Table 2. Hepatic concentrations of glycogen, its metabolites, the glucidic potential (μmol g^{-1}) and the glycogen:lactate ratio in ADLIB and REST heifers

Metabolite	ADLIB (n = 12)	REST (n = 12)	SEM	P
Glycogen	138.20	110.84	9.41	0.05
Glucose	88.10	80.90	5.93	0.40
Lactate	14.12	12.13	0.91	0.14
Glucose-6-phosphate	0.024	0.022	0.012	0.91
Glucidic potential	233.39	197.83	13.35	0.07
Glycogen:Lactate ratio	20.19	18.87	1.96	0.64

Table 3. Concentrations of glycogen, its metabolites, the glucidic potential (μmol g^{-1}) and the glycogen:lactate ratio in the LL of heifers during the feed restriction and realimentation periods

Metabolite	Period 1 restriction period (n = 8)	Period 2 realimentation period (n = 16)	P
Glycogen	54.98 ± 7.91	76.68 ± 5.59	0.04
Glucose	1.05 ± 0.15	0.73 ± 0.11	0.10
Lactate	30.18 ± 3.34	15.66 ± 2.36	< 0.01
Glucose-6-phosphate	0.074 ± 0.106	0.304 ± 0.075	0.09
Glucidic potential	71.20 ± 7.21	85.54 ± 5.10	0.12
Glycogen:Lactate ratio	4.63 ± 1.93	11.47 ± 1.37	< 0.01

supernatant from the perchloric acid extraction except that fructose 6-phosphate was not assayed after completion of the G-6-P assay.

Statistical Analysis

Glucidic potential was calculated using the formula:

$$GP = ([\text{glycogen}] + [\text{glucose}] + [\text{G-6-P}] + 1/2[\text{lactate}])$$

expressed in μmol glucose equivalent g^{-1} of fresh tissue. Prior to averaging CIE a* and b* values were converted to hue angle (Hab = arctan [b*/a*]) and chroma (Cab = [a*2 + b*2]$^{0.5}$). Both the glucidic potential and meat quality data were analyzed using a model that combined the slaughter dates within each period. A two-way analysis of variance using the GLM procedure (SAS Institute, Inc. 1990) was done to assess treatment and period effects and their interaction. The model used in the analysis was:

$$Y_{ijk} = \mu + T_i + P_j + TP_{ij} + \varepsilon_{k(ij)}$$

where Y_{ijk} = glucidic or meat quality trait, T_i = nutritional treatment, P_j = period of slaughter, TP_{ij} = nutritional treatment × period interaction, and $\varepsilon_{k(ij)}$ = random error term. Linear contrasts with one degree of freedom were used for means separation ($P < 0.05$). The above model was re-run with slaughter weight as a covariate to distinguish the effects of treatment and period from those of slaughter weight on the meat quality characteristics.

RESULTS AND DISCUSSION

In almost all cases, there were no significant treatment × period interactions. Treatment and period main effects have been presented where significant.

Hepatic Glucidic Potential

There was an overall treatment effect on liver glycogen concentration ($P = 0.05$) and GP ($P = 0.07$), with livers of REST heifers having a lower concentration than those of ADLIB heifers (Table 2). The liver is known to be highly responsive to nutritional changes (Goss 1978) and it was therefore not surprising to observe a lower glycogen and GP in REST heifers. Veenhuizen et al. (1991) who restricted dairy cows to 20% of ad libitum feeding observed a significant decrease in the glycogen liver content within 5 d; the values reached nearly zero by day 35. Similar results have been reported in rats (Calder and Geddes 1992) where, after 40 h of fasting, liver glycogen concentration was decreased by 95%. Minnassian et al. (1994) also reported that liver glycogen stores were depleted in rats faster for 24 or 48 h, although there was a rebound of the glycogen stores in rats fasted for longer periods.

There were no significant effects on hepatic glucose, G-6-P or lactate and their values were low despite collecting the samples 20 min postmortem. The low values, particularly for lactate, reflect the limited anaerobic capacity of the liver in the postmortem period.

Muscle Glucidic Potential

There was no significant treatment effect or treatment × period interaction on the concentrations of glycogen or any of its metabolites. However, there was a significant period effect ($P < 0.05$) on muscle glycogen, lactate, and the glycogen:lactate ratio, and a suggestion of significance ($P < 0.15$) for glucose, G-6-P, and GP (Table 3). The lower muscle glycogen concentration in the heifers slaughtered during period 1 compared with those slaughtered during period 2 could partly be due to the effect of feed restriction of REST heifers, although there was no significant treatment effect per se. Skeletal muscle glycogen reserves in cattle have been reported to be depleted during either feed restriction (McVeigh and Tarrant 1982) or fasting (Crouse et al. 1984). Similarly, Calder and Geddes (1992) reported a decrease of up to 55% in skeletal muscle glycogen concentration in rats that were fasted for 40 h.

A higher lactate concentration ($P < 0.01$) was associated with the lower glycogen concentration during period 1; glucose concentration also tended to be higher ($P = 0.10$) while G-6-P concentration tended to be lower ($P = 0.09$) in this period. The higher breakdown of glycogen associated with higher muscle concentrations of lactate, glucose, and G-6-P is in agreement with similar observations in pigs (Klont and Lambooy 1995). It is evident from the present data that glycogen breakdown in these heifers was more rapid than in those slaughtered during period 2, suggesting preslaughter stress in the former. In particular, the high lactate concentration and the significantly lower ($P < 0.01$) glycogen to lactate ratio in these heifers were indicators of preslaughter stress. However, it is not known what caused the stress although lighter-weight, younger animals may be more stress susceptible than heavier, older animals.

Although the actual effect of feed restriction on muscle glycogen is difficult to determine due to stress affecting the concentrations of glycogen, the suggestion of a lower GP ($P = 0.12$) in period 1 indicates that the REST heifers may have a reduced glycogen content. Lighter weight animals may also have lower glycogen reserves; hence a reduced GP would be observed. Conversely the higher GP during period 2 may reflect the recovery of glycogen in REST heifers. McVeigh and Tarrant (1982) observed that following refeeding of their heifers, glycogen content increased slowly, reaching 17.5% above the control value by day 25.

At any rate, changes in the muscle glycolytic metabolites have been used previously as indicators of meat quality (Henckel et al. 1992). A low GP at slaughter is indicative of prolonged stress prior to slaughter and the possible development of DFD. In contrast, a low glycogen-to-lactate ratio immediately post-slaughter is indicative of stress during slaughter.

Table 4. Meat quality traits in ADLIB and REST heifers

Quality trait	ADLIB ($n = 12$)	REST ($n = 12$)	SEM	P^z	P^y
Slaughter weight (kg)	351	283	17	0.01	–
Ribeye area (cm^2)	57.4	47.2	3.10	0.03	0.93
Cooler shrink (%)	1.25	0.92	0.169	0.18	0.65
pH					
45 min	6.65	6.67	0.059	0.74	0.61
24 h	5.72	5.81	0.060	0.31	0.91
Ultimate	5.50	5.51	0.028	0.89	0.24
Temperature (°C)					
45 min	38.9	38.4	0.022	0.16	0.41
24 h	1.0	0.9	0.157	0.56	0.62
Minolta (24 h)					
L*	36.0	33.6	0.66	0.02	0.11
Hue (°)	22.0	20.2	1.18	0.30	0.94
Chroma	19.0	16.8	0.86	0.09	0.29
Minolta (ultimate)					
L*	39.7	38.2	0.456	0.04	0.01
Hue (°)	22.5	19.9	0.895	0.06	0.26
Chroma	20.5	19.4	0.671	0.27	0.25
Drip loss ($g\ kg^{-1}$)	19.4	25.2	1.563	0.02	0.05
Moisture ($g\ kg^{-1}$)	738.9	749.8	2.597	< 0.01	0.18
Intramuscular fat ($mg\ g^{-1}$)	103.0	61.1	9.54	< 0.01	0.14
Shear (kg)	8.64	9.83	0.708	0.25	0.31

[z]Significance of a treatment effect without slaughter weight as a covariate.
[y]Significance of a treatment effect with slaughter weight as a covariate.

Meat Quality

Slaughter weight was almost 70 kg lower in REST than ADLIB heifers ($P = 0.01$; Table 4). As a result the REA in REST heifers was smaller ($P = 0.03$) than in ADLIB heifers. Since the level of intramuscular fat is positively correlated with liveweight (Berg and Butterfield 1976), the lower intramuscular fat in REST compared with ADLIB heifers was expected. Intramuscular fat was inversely related to the moisture content which was higher ($P < 0.01$) in REST than in ADLIB heifers. Drip loss was also higher ($P = 0.02$) in REST than in ADLIB heifers, suggesting that increasing carcass weight and fatness may have been involved. The objective colour measurements indicated meat from REST heifers was a darker, more purple-red (lower L* and hue) than meat from ADLIB heifers.

When slaughter weight was used as a covariate, ultimate L* remained significantly lower ($P = 0.01$) and drip loss

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Table 5. Meat quality traits in heifers slaughtered during the feed restriction period and realimentation period

Quality trait	Period 1 restriction period (n = 8)	Period 2 realimentation period (n = 16)	P^z	P^y
Slaughter weight (kg)	248 ± 19.5	385 ± 13.8	< 0.01	–
Ribeye area (cm^2)	45.5 ± 3.6	59.1 ± 2.5	< 0.01	0.08
Cooler shrink (%)	0.92 ± 0.19	1.24 ± 1.14	0.19	0.09
pH				
45 min	6.60 ± 0.068	6.72 ± 0.048	0.15	0.59
24 h	5.91 ± 0.069	5.62 ± 0.049	< 0.01	0.48
Ultimate	5.45 ± 0.031	5.56 ± 0.025	0.01	0.79
Temperature (°C)				
45 min	38.1 ± 0.26	39.2 ± 0.18	< 0.01	0.15
24 h	0.7 ± 0.18	1.1 ± 0.13	0.11	0.67
Minolta (24 h)				
L*	35.3 ± 0.77	34.3 ± 0.54	0.30	0.19
Hue (°)	20.6 ± 1.37	21.6 ± 0.97	0.53	0.30
Chroma	18.0 ± 0.997	17.8 ± 0.705	0.83	0.51
Minolta (ultimate				
L*	39.6 ± 0.53	38.3 ± 0.37	0.05	0.93
Hue (°)	21.0 ± 1.03	21.4 ± 0.73	0.80	0.53
Chroma	19.9 ± 0.78	20.0 ± 0.54	0.89	0.64
Drip loss (g kg^{-1})	27.3 ± 1.80	17.3 ± 1.28	< 0.01	0.01
Moisture (g kg^{-1})	752 ± 3.0	736 ± 2.1	< 0.01	0.34
Intramuscular fat (mg g^{-1})	58.1 ± 11.0	106.0 ± 7.8	< 0.01	0.77
Shear (kg)	10.30 ± 0.82	8.18 ± 0.58	0.05	0.19

[z]Significance of a period effect without slaughter weight as a covariate.
[y]Significance of a period effect with slaughter weight as a covariate.

remained significantly higher (P = 0.05) in REST compared with ADLIB heifers. Thus the majority of meat quality traits were influenced more by the difference in slaughter weight caused by the dietary treatment than by the dietary treatment per se. There were neither significant treatment effects on muscle glycogen concentration nor 45 min, 24 h, and ultimate pH and temperature, hence the observed differences in L* and drip loss must arise from differences in intramuscular fat or subtle differences in cooling rates and rates of pH decline between the lighter-weight REST and heavier-weight ADLIB carcasses.

Time of slaughter had a larger effect on the meat quality traits than treatment (Table 5). As was the case with treatment, the lighter (P < 0.01) slaughter weights during period 1 were directly associated with smaller REA (P < 0.01) compared with those heifers slaughtered during period 2. Again these were associated with less intramuscular fat (P < 0.01), more moisture (P < 0.01), and a higher drip loss (P < 0.01) than the heavier slaughter weights (period 2). The heifers slaughtered during period 1 showed biochemical symptoms of stress at slaughter (lower glycogen:lactate ratio), which corresponded with a lower 24 h (P < 0.01) and ultimate pH (P = 0.01), a lighter muscle colour (higher ultimate L*; P = 0.05) and a higher shear value (P = 0.05).

The difference in the mean shear values (2.12 kg) would be detectable by the average consumer, and was probably due to the smaller, lighter carcasses in period 1 chilling more rapidly than the larger, heavier carcasses in period 2. The 45-min temperature in carcasses from period 1 was significantly lower (P < 0.01) than in carcasses from period 2. Merkel and Pearson (1975) suggested that even under conventional chilling methods, the major difference in tenderness between fat, higher-grading and thin, lower-grading beef is due to fat (including marbling) slowing down the rate of carcass cooling. Some researchers have attributed these effects to cold shortening although there is some doubt that cold shortening actually occurs in beef except in excised tissue (Aalhus et al. 1991). More recently, this phenomenon has been referred to as cold toughening and has been attributed to reduced activity of proteases at cooler temperatures (Marsh et al. 1987, 1988). However, smaller carcasses may have smaller muscle fibre diameters which could result in a higher proportion of connective tissue to myofibrillar proteins in the same cross sectional area as larger carcasses.

CONCLUSIONS

In conclusion, long periods of feed restriction in beef heifers had a greater effect on glycogen stores in the liver than in skeletal muscle, although skeletal muscle stores were confounded by preslaughter stress in the present study. Feed restriction also led to significant effects on meat quality traits including a higher drip loss, lower intramuscular fat, higher moisture and darker colour (lower L*). For the most part these effects were directly attributable to the significantly lower slaughter weight in REST compared with ADLIB animals. Hence, there was no indication from the longissimus muscle that feed restriction led to a greater incidence of meat quality defects such as DFD.

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Aalhus, J. L., Tong, A. K. W., Robertson, W. M. and Jones, S. D. M. 1991. The effect of rapid chilling on beef quality. Int. Congr. Meat Sci. Technol. **37**: 220–223.

Berg, R. T. and Butterfield, R. M. 1976. New concepts of cattle growth. University of Sydney Press, Sydney, Australia.

Calder, P. C. and Geddes, R. 1992. Heterogeneity of glycogen synthesis upon refeeding following starvation. Int. J. Biochem. **24**: 71–77.

Commission International de l'Eclairage. 1976. 18th session, London, England. Sept. 1975. CIE Publication 36.

Crouse, J. D., Smith, S. B. and Prior, R. L. 1984. Bovine muscle glycogen as affected by fasting and refeeding. J. Anim. Sci. **59**: 384–387.

Dalrymple, R. H. and Hamm, R. 1973. A method for the extraction of glycogen and metabolites from a single muscle sample. J. Food Technol. **8**: 439–444.

Drackley, J. K., Veenhuzein, J. J., Richard, M. J. and Young, J. W. 1991. Metabolic changes in blood and liver of dairy cows during either feed restriction or administration of 1,3-butanediol. J. Dairy Sci. **74**: 4254–4264.

Goss, R. J. 1978. The physiology of growth. Academic Press, Inc.,

New York, NY.
Guignot, F., Quilichini, Y., Renerre, M., Lacourt, A. and Monin, G. 1992. Relationship between muscle type and some traits influencing veal colour. J. Sci. Food Agric. **58**: 523–529.
Gutmann, I. and Wahlefeld, A. W. 1974. L-(+)-Lactate determination with lactate dehydrogenase and NAD. *In* H. U. Bergmeyer, ed. Methods of enzymatic analysis. Academic Press, Inc., New York, NY.
Henckel, P., Jorgensen, P. F. and Jensen, P. 1992. Glycogen content, buffering capacity and resting pH in live muscles of pigs of different halothane genotypes (a pilot project). Meat Sci. **32**: 131–138.
Jones, S. D. M., Schaefer, A. L. and Tong, A. K. W. 1992. The effects of fasting, electrolyte supplementation and electrical stimulation on carcass yield and meat quality in bulls. Can. J. Anim. Sci. **72**: 791–798.
Keppler, D. and Decker, K. 1974. Glycogen determination with amyloglucosidase. *In* H. U. Bergmeyer, ed. Methods of enzymatic analysis. Academic Press, Inc., New York, NY.
Klont, R. E. and Lambooy, E. 1995. Effects of preslaughter muscle exercise on muscle metabolism and meat quality studied in anesthetized pigs of different halothane genotypes. J. Anim. Sci. **73**: 96–107.
Lang, G. and Michal, G. 1974. D-glucose-6-phosphate and D-fructose-6-phosphate. *In* H. U. Bergmeyer, ed. Methods of enzymatic analysis. Academic Press, Inc., New York, NY.
Marsh, B. B., Ringkob, T. P., Russell, R. L., Swartz, D. R. and Pagel, L. A. 1987. Effects of early-postmortem glycolytic rate on beef tenderness. Meat Sci. **21**: 241–248.
Marsh, B. B., Russell, R. L., Swartz, D. R. and Ringkob, T. P. 1988. Electrical stimulation and meat texture: A reply to comments by E. Dransfield and D. J. Etherington. Meat Sci. **24**: 229–232.
McVeigh, J. M. and Tarrant, P. V. 1982. Glycogen content and repletion rates in beef muscle, effect of feeding and fasting. J. Nutr. **112**: 1306–1314.
Merkel, R. A. and Pearson, A. M. 1975. Slow chilling could produce tender beef from lean carcasses. Meat Industry Digest **21(5)**: 27, 62.
Minnassian, C., Ajzannay, A., Riou, J. P. and Mithieux, G. 1994. Investigation of the mechanism of glycogen rebound in the liver of 72-hr fasted rats. J. Biol. Chem. **269**: 16585–16588.
SAS Institute, Inc. 1990. SAS user's guide: Statistics Version 6.06 edition. SAS Institute Inc., Cary, NC.
Veenhuizen, J. J., Drackley, J. K., Richard, M. J., Sanderson, T. P., Miller, L. D. and Young, J. W. 1991. Metabolic changes in blood and liver during development and early treatment of experimental fatty liver and ketosis in cows. J. Dairy Sci. **74**: 4238–4253.
Warris, P. D., Bevis, E. A. and Ekins, P. J. 1989. The relationships between glycogen stores and muscle ultimate pH in commercially slaughtered pigs. Br. Vet. J. **145**: 378–383.
Yambayamba, E. S. K., Price, M. A. and Jones, S. D. M. 1996. Compensatory growth of carcass tissues and visceral organs in beef heifers. Livest. Prod. Sci. **46**: 19–32.

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