ABSTRACT A total of 42 F1 Red Angus progeny from sires divergent in maintenance energy (ME\textsubscript{M}) EPD were analyzed to determine whether selecting for sire ME\textsubscript{M} would alter end-product meat quality. Data from animals were grouped based on the divergence of the ME\textsubscript{M} EPD of their sire from the Red Angus Association-reported breed average and defined as either high or low, the assumption being that high-ME\textsubscript{M} cattle are less efficient because their maintenance requirements represent a larger proportion of their dietary intake. Steer progeny (n = 7) from the high group produced bottom round steaks with a greater a* (redness) color value (P = 0.02) after 5 d in a simulated retail display when compared with bottom round steaks from the low group (n = 18). Bottom round steaks from the high group had a greater b* (yellowness) color value at d 1 (P = 0.03) and d 5 (P = 0.01) of retail display. Samples from the biceps femoris were taken at 12 mo (from both steers and heifers) and 15 mo (from steers only) of age for fiber type proportion analysis. At 12 mo of age, steers from the low group had more type I fibers (P = 0.02), whereas steers from the high group had more type IIb fibers (P = 0.01). Furthermore, samples from steers in the low group at 15 mo had more type I fibers (P = 0.02), and steers from the high group maintained more type IIb fibers (P = 0.02). No changes in fiber type proportions were observed between the high- and low-ME\textsubscript{M} EPD heifers (n = 17). Relative mRNA abundance of genes involved in the synthesis, storage, and breakdown of glycogen were analyzed as a variable important for meat quality, but no statistical differences were observed. At 12 mo age, glycogenin (glyc) was negatively correlated with the proportion of type Ia fibers (r = −0.32 and P = 0.12) as well as with the proportion of type IIb fibers (r = −0.42 and P = 0.03) in the biceps femoris of the steers. In samples taken from the biceps femoris at 15 mo age, glyc was negatively correlated with the proportion of type Ia fibers (r = −0.42 and P = 0.03) in the steers. This indicates that relative mRNA expression of glyc may serve as a marker of muscle glycogen storage capacity in steers. Thus, selection for efficient Red Angus beef cattle based on sire ME\textsubscript{M} EPD does not adversely affect meat quality in F1 progeny, based on the variables assessed in this study. Furthermore, selection for progeny from low-ME\textsubscript{M} EPD sires may improve fresh meat quality within Red Angus beef cattle.

Keywords: bovine, color stability, glycogen, maintenance energy, meat quality, muscle fiber type

INTRODUCTION

Costs of raising beef cattle across the world are increasing, assuming no changes in fixed costs. Feed costs represent the largest single cost associated with production (Arthur et al., 2001; Johnson et al., 2003). As feed costs rise, identification of animals with improved efficiency has become an important selection criterion for producers. The maintenance energy (ME\textsubscript{M}) requirement of an animal is the energy required to sustain their body tissues with no net changes in body tissue. In cattle, approximately 73% of total ME within cattle is ME\textsubscript{M}, and 60 to 65% of the total feed used by the herd is for maintenance (Arthur et al., 2001; Johnson et al., 2003). Selection for low ME\textsubscript{M} is attractive because it is a moderately heritable trait that potentially increases energy available for growth (Hotovy et al., 1991). However, it is important that genetic selection for efficiency does not negatively alter the quality of the end-product.
Skeletal muscle becomes meat through predictable metabolic changes within the muscle postmortem. Changes in the substrates present in the muscle at the time of harvest alter these processes and ultimately affect meat quality. At least 3 different muscle fiber types (type I, type IIa, and type IIb) are found within the skeletal muscle of cattle, each of which differs in its metabolic properties, including catabolic and anabolic attributes. Type I fibers are smaller in diameter and utilize substrates aerobically, whereas type IIb fibers are larger in diameter and metabolize substrates anaerobically; type IIa fibers are intermediate (Kirchofer et al., 2002). These innate differences in the biochemical and biophysical properties of muscle fibers directly contribute to postmortem metabolism within the meat and ultimately determine end-product quality. The objective of this study was to investigate the end-product quality of progeny from sires divergent for ME$_M$ EPD.

**MATERIALS AND METHODS**

All animal procedures were reviewed and approved by the Institutional Animal Care and Use Committee as required by federal law and University of Idaho policy.

**Animals**

Red Angus steers ($n = 25$) and heifers ($n = 17$) sired by bulls divergent for ME$_M$ EPD were used in this study. The F$_1$ progeny were grouped as either high ($n = 10$) or low ($n = 32$) based on the deviation of their sire from the Red Angus Association-reported breed average of 4. The ME$_M$ EPD values of the bulls ranged from 12 to $-9$, with a smaller number indicating a more efficient animal. The current estimates of the EPD accuracies as of October 2011 indicate that all are above 50% and range from 55 to 62%. Calves were produced through AI of bulls and raised at the University of Idaho Cummings Ranch (Salmon, ID) until weaning. Cows were from a mixed-breed commercial herd; all cows were located at the Cummings Ranch and were managed under similar conditions. Steer and heifer calves were transported from Salmon to the cattle-feeding barn located on the University of Idaho–Moscow campus meat science laboratory for aging and postslaughter processing. These samples were used for analyses of color, pH, Warner-Bratzler shear force, residual glycogen content, and lactate content. On d 9 postmortem, wholesale cuts were removed from the vacuum packages. The anterior end of the strip loin was prepared by removing a slice approximately 2 cm thick, perpendicular to the long axis of the LM. Subsequently, a 2.54-cm-thick steak was removed for analysis of color and instrumental tenderness. The ischiatic head (IMPS 171E) was removed from outside round flats to produce the trimmed flat (IMPS 171D). Bottom round steaks (2.54 cm thick) were cut lengthwise, perpendicular to muscle fibers. A portable pH meter (Model 1140, Mettler-Toledo, Woburn, MA) equipped with a puncture-type electrode was used to measure pH of steaks from the proximal region of the bottom round and anterior end of the strip loin. The pH meter was calibrated using standard pH 4.0 and 7.0 buffers chilled to 4°C. Steaks for retail display were packaged in white Styrofoam trays with an oxygen-permeable polyvinyl chloride overwrap (7500-3815, Koch Industries Inc., Wichita, KS) and allowed to bloom for at least 20 min. Two objective color measurements per steak were taken using a Hunter MiniScan EZ instrument (Hunter, Restin, VA). This instrument is equipped with a 25-mm-diameter measuring area and a 10° standard observer. The instrument was set to D$_{65}$ illuminant, and CIE L*, a*, and b* duplicate values taken from 2 different places on the steak were recorded. The scale for L* is from 0 (black) to 100 (white). Positive a* and b* values are red and yellow, respectively, and negative a* and b* values are green and blue, respectively. Calibration of the machine was carried out each day by measuring against black and white calibration tiles, as suggested by the manufacturer. Hue angle was calculated as tan$^{-1}$ a*/b* (Wheeler et al., 1996).

**Beef Quality Measurement**

Steers were slaughtered in May of 2009 at Washington Beef (Toppenish, WA). After processing, the vacuum-packaged bottom round [flat; Institutional Meat Purchase Specification (IMPS) 171B] and strip loin (IMPS 180) from the left side were purchased and transported to the University of Idaho–Moscow campus meat science laboratory for aging and postslaughter processing. These samples were used for analyses of color, pH, Warner-Bratzler shear force, residual glycogen content, and lactate content. On d 9 postmortem, wholesale cuts were removed from the vacuum packages. The anterior end of the strip loin was prepared by removing a slice approximately 2 cm thick, perpendicular to the long axis of the LM. Subsequently, a 2.54-cm-thick steak was removed for analysis of color and instrumental tenderness. The ischiatic head (IMPS 171E) was removed from outside round flats to produce the trimmed flat (IMPS 171D). Bottom round steaks (2.54 cm thick) were cut lengthwise, perpendicular to muscle fibers. A portable pH meter (Model 1140, Mettler-Toledo, Woburn, MA) equipped with a puncture-type electrode was used to measure pH of steaks from the proximal region of the bottom round and anterior end of the strip loin. The pH meter was calibrated using standard pH 4.0 and 7.0 buffers chilled to 4°C. Steaks for retail display were packaged in white Styrofoam trays with an oxygen-permeable polyvinyl chloride overwrap (7500-3815, Koch Industries Inc., Wichita, KS) and allowed to bloom for at least 20 min. Two objective color measurements per steak were taken using a Hunter MiniScan EZ instrument (Hunter, Restin, VA). This instrument is equipped with a 25-mm-diameter measuring area and a 10° standard observer. The instrument was set to D$_{65}$ illuminant, and CIE L*, a*, and b* duplicate values taken from 2 different places on the steak were recorded. The scale for L* is from 0 (black) to 100 (white). Positive a* and b* values are red and yellow, respectively, and negative a* and b* values are green and blue, respectively. Calibration of the machine was carried out each day by measuring against black and white calibration tiles, as suggested by the manufacturer. Hue angle was calculated as tan$^{-1}$ a*/b* (Wheeler et al., 1996).
All steaks were displayed in a glass retail display case (Model GDM-69, True Manufacturing Co., O’Fallon, MO) at 2°C. The display case was equipped with natural white mercury 40-W lights, and the average light intensity was 408 lx. Color, surface discoloration, and amount of browning were measured following American Meat Science Association guidelines (AMSA, 1991) by 2 evaluators on d 0, 1, 3, and 5 after being re-packaged for retail display. To avoid effects attributable to location, steaks were rotated after each measurement. On d 14 post-mortem, steaks were removed from the retail packaging, weighed, and cooked on open-hearth broilers to an internal temperature of 40°C, then turned and cooked to a final internal temperature of 71°C. Steaks were reweighed to determine cooking loss and allowed to cool to room temperature. Six cores (1.27 cm in diameter) were mechanically removed parallel to the muscle fiber orientation by using a drill-press-mounted coring device, and shear force was determined by shearing each core perpendicular to the muscle fiber by using a Warner-Bratzler shear machine (GR Manufacturing, Manhattan, KS).

Determination of Glycogen Content

Glycogen Extraction. Samples were ground using a supercooled mortar and pestle under liquid nitrogen. Twenty milligrams of frozen biceps femoris muscle tissue from samples taken at 12 and 50 mg of steak tissue frozen at 9 d postmortem (bottom round and strip loin) taken at 15 mo were used. Glycogen was extracted from the tissue using a modification of the method of Suzuki et al. (2001). Samples taken at 12 mo were diluted (1:5 with 0.2 M NaOAc; pH 4.8) to yield absorbance values within the linear range of the standard curve.

Relative Glycogen Determination. Total glycogen content was measured in samples of the biceps femoris taken at both 12 and 15 mo age, as well as the amount of residual glycogen present in the steak tissue (bottom round and strip loin), after aging and storage of the steaks. Glycogen content was quantified from each muscle sample by using a modified colorimetric method (Suzuki et al., 2001). Quantification of glucose, derived from total tissue glycogen, was measured at 340 nm by using an Evolution 300 UV-visible spectrophotometer (Thermo Scientific, Waltham, MA). All samples were quantified in duplicate.

Determination of Lactate Content

Lactate content was determined using 50 mg of frozen steak tissue (bottom round and strip loin), according to the procedure of the BioVision lactate assay kit (K607100, BioVision, Mountain View, CA). Lactate content was quantified by fluorometric detection (excitation 535 nm, and emission 590 nm) of duplicate samples using a BioTek Synergy 2 plate reader (BioTek, Winooski, VT) and was based on comparison with standard curves. Lactate content is expressed as nanomoles of lactate per milligram of wet tissue weight.

RNA Isolation and Quantification, and cDNA synthesis

Total RNA was extracted from biceps femoris samples using TRIzol reagent (Invitrogen, Carlsbad, CA) according to the manufacturer’s protocol. Isolates of RNA were quantified using a Nanodrop ND-1000 UV-visible spectrophotometer (Nanodrop Technologies, Wilmington, DE). Total RNA integrity was assessed using 1.5% denaturing formaldehyde agarose gel electrophoresis. All samples (2 μg) were treated with deoxyribonuclease (Ambion, Foster City, CA) before cDNA synthesis by using a high-capacity cDNA reverse-transcription kit (Applied Biosystems, Foster City, CA).

Quantitative Real-Time PCR

Real-time PCR quantification of mRNA was determined using the Taqman MGB primer/probe system. Primer express 3.0 software (Applied Biosystems) was used to design the primers and probes for all genes (Table 1). An ABI 7500 fast real-time PCR system (Applied Biosystems) was used to detect relative mRNA expression of glycogen synthase 1 (gys1), glycogen synthase 2 (gys2), glycogenin (glyc), and glycogen phosphorylase (glyp) in each muscle sample (Chapalamadugu et al., 2009).

Fiber Type Proportions within the Biceps Femoris

Biceps femoris samples, mounted perpendicular to fibers on cork, were cryosectioned (10 μm thick) and used for histochemical fiber type staining. Serially sectioned samples were stained using a succinate dehydrogenase stain and a myosin adenosine triphosphatase stain at 3 different pH values, 2 acidic and 1 basic, using modified protocols described previously (Pearse et al., 1968; Brooke and Kaiser, 1970; Picard et al., 1998). Images were taken using a Nikon 80i microscope with NIS-BR elements software (Nikon, Melville, NY). At least 3 different captured images were printed in color and used for fiber-type counting. A minimum of 250 fibers per image were counted. Fiber types present in each image were counted and the number of fibers of type I, IIa, or IIb are reported as percentages of the total fibers. Representative serial images can be observed in Figure 1.
Figure 1. Representative fiber type-staining images of 10-μm skeletal muscle serial sections. A) Myosin adenosine triphosphatase, pH 4.3; B) myosin adenosine triphosphatase, pH 4.6; C) myosin adenosine triphosphatase, pH 9.4; D) succinate dehydrogenase. Representative fiber type labeling was overlaid on the images before counting to illustrate fiber type identification.

Table 1. Primer and probe sequences used in real-time PCR

<table>
<thead>
<tr>
<th>Gene</th>
<th>Accession number</th>
<th>Primers and TaqMan probe sequences, 5’–3’</th>
</tr>
</thead>
<tbody>
<tr>
<td>18S</td>
<td>AF243428</td>
<td>FP: CCACGCGGAGATTTGAGCAAT</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RP: GCAGCCCGGACATCTAA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TP: ACAGGCTGATGACCC</td>
</tr>
<tr>
<td>Glycogen synthase 1 (gys1)</td>
<td>NM_001024515</td>
<td>FP: AAGTGCGCAGATCTACA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RP: TCCCCGGTCACCTGTGTC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TP: AGTGCAGACGAA</td>
</tr>
<tr>
<td>Glycogen synthase 2 (gys2)</td>
<td>XM_617616.3</td>
<td>FP: TCAGAACACTGCCCCATTGC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RP: AGATACCGCCCGAAGCTG</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TP: CAATCTTACCCACCCACG</td>
</tr>
<tr>
<td>Glycogen phosphorylase (glyp)</td>
<td>NM_175786.2</td>
<td>FP: CCAGGCCCTCCCCGCTCA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RP: TCCCCGAGAGATCATTATGT</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TP: ATTTGACCAACGCACCC</td>
</tr>
<tr>
<td>Glycogenin (glyc)</td>
<td>NM_001045867.1</td>
<td>FP: GCAGATACCTGTTCAGCAAAT</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RP: GGTGCACGACAATTC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TP: TCGACGATTCCTTTTCAGAGAGA</td>
</tr>
</tbody>
</table>

1Forward primer (FP), reverse primer (RP), and Taqman probe (TP) sequences were indices along with GenBank accession number for the genes analyzed by using the Taqman primer/probe system of real-time PCR (Applied Biosystems, Foster City, CA).

Statistical Analyses

Statistical analysis of the data was completed using SAS software (SAS Inst. Inc., Cary, NC). A 2-sample t-test was performed to identify the mean significant differences in gene expression, glycogen content, lactate content, ultimate pH, Warner-Bratzler shear force values, Hunter color scores, and fiber type proportions. Animals were grouped according to the ME_M EPD of their sire. For categorization based on ME_M EPD of the sire, F1 progeny from sires were grouped as either high or low based on deviation of sire ME_M EPD from the breed average provided by the Red Angus Association of America (Denton, TX). Gene expression analysis using quantitative real-time PCR was performed using the relative threshold cycle (ΔCt) values of each of the can-
didate genes with that of the matched 18S rRNA values. Gene expression threshold cycle values were analyzed in duplicate. A $P$-value of $\leq 0.05$ was considered statistically significant using a 1-tailed $t$-test, whereas a $P$-value $\leq 0.10$ was considered a trend in the data. Correlations were determined using Pearson correlations.

**RESULTS AND DISCUSSIONS**

Sire ME$_M$ EPD as a determinant for efficiency selection has not been completely characterized with respect to its effect on muscle and meat parameters that influence end-product quality. Beef quality is determined by multiple factors, including appearance, molecular metabolism, cooking, and eating characteristics (Bass et al., 2008). Conversion of beef muscle to meat is the result of a series of changes in metabolism within the muscle postslaughter, as well as the transition from aerobic metabolism to anaerobic metabolism. Postslaughter muscle uses glycogen reserves, creating lactic acid as an accumulating byproduct (Scanga et al., 1998). Lactic acid accumulation reduces the muscle pH, triggering changes in structural proteins within the muscle, which is an important process toward the transition of muscle to meat (Immonen et al., 2000). Importantly, the relative fiber type composition of the different muscles determines the predominant metabolic properties of the muscle as a whole (Peter et al., 1972; Ozawa et al., 2000). Therefore, fiber type composition influences the conversion of muscle to meat and ultimately meat quality (Klont et al., 1998; Brocks et al., 2000; Kirchofer et al., 2002; Ryu and Kim, 2005). As cattle mature, they tend to accrue more type IIb fibers at the expense of type I and type IIa fibers (Wegner et al., 2000). Type IIb fibers tend to store greater amounts of glycogen (Immonen et al., 2000). In the context of F$_1$ progeny sired by high- and low-ME$_M$ EPD bulls, we characterized the relative fiber type proportions, fiber type transition from 12 to 15 mo, meat color, color stability, glycogen content, lactate accumulation, glycogen storage, and utilization genes and tenderness.

**Fiber Type**

Fiber type analysis of all animals ($n = 42$) at 12 mo age when grouped by sire ME$_M$ EPD did not show statistical differences between the high and low calves sired by bulls divergent in ME$_M$ EPD (data not shown). However, animals from the low-ME$_M$ EPD group tended to have more type I fibers ($P = 0.07$), whereas animals from the high group tended to have more type IIb fibers ($P = 0.06$; data not shown). When heifers were analyzed separately, no statistical difference was observed between the 2 groups (data not shown). In contrast, when steers at 12 mo age were analyzed, the low-ME$_M$ EPD group had more type I fibers ($P = 0.02$) and the high-ME$_M$ EPD sired group had more type IIb fibers ($P = 0.01$; Figure 2). No significant differences were observed in the proportion of type IIa fibers between the 2 groups of steers. Muscle fiber types in the 15 mo steers samples demonstrated that the low-ME$_M$ EPD-sired group had more type I fibers ($P = 0.02$), whereas the high-ME$_M$ EPD-sired group had more type IIb fibers ($P = 0.02$; Figure 2).

The fiber type percentage at 12 mo of age relative to the percentage at 15 mo of age in the same steers was quantified as a representation of the rate of maturational associated fiber type transition. No statistical differences were found between the low- and high-ME$_M$ EPD-sired groups (Figure 3). However, it is important to note that the observed changes in fiber type followed trends seen in previous studies (Johnston et al., 1975; Wegner et al.,

![Figure 2. Proportions of each fiber type, represented as percentages within the biceps femoris of the progeny grouped by high and low sire maintenance energy (ME$_M$) EPD. *$P \leq 0.05$; **$P \leq 0.01$. Steers (high: $n = 7$; low: $n = 18$). Error bars represent the SEM.](image)

![Figure 3. Changes in fiber type proportion of the biceps femoris within the steers based on progeny sire maintenance energy (ME$_M$) EPD. Dashed lines indicate type IIb fibers, dotted lines indicate type IIa fibers, and solid lines indicate type I fibers. Solid black markers represent animals from the high group ($n = 7$), and open markers indicate animals from the low group ($n = 18$). Error bars represent the SEM.](image)
As the steers aged, they tended to accrue more type IIb fibers at the expense of type I fibers in the biceps femoris muscle. The proportions of type IIa fibers remained relatively constant, as shown by the lack of slope in the line. Although not statistically significant, steers from the high group tended to accrue more type IIb fibers at the expense of type I fibers, whereas this process was not as pronounced in the low group (Figure 3). An increased proportion of type I fibers has been associated with an improvement in fresh meat quality, which suggests that selection for low-ME<sub>M</sub> EPD animals may yield a greater quality end product.

**Color of the Bottom Round**

Color of bottom round steaks was measured on d 0, 1, 3, and 5 of simulated retail display. Day 0 simulates the day the product would first be viewed by the consumer. The color and appearance of the fresh product has been characterized as the largest deciding factor in whether a customer will purchase a cut of beef at retail (Dunsing, 1959; Jeremiah et al., 1972; Kropf, 1980). Once the product is placed on retail display, discoloration can occur. The more stable the color of a product, the more potential it has to be selected by a consumer, thus making it more marketable (Wheeler et al., 1996). The L* (lightness) of bottom round steaks did not differ in F<sub>1</sub> progeny of sires divergent for ME<sub>M</sub> EPD (Figure 4). The a* (redness) values were greater in the bottom round steaks produced from steer progeny of high-ME<sub>M</sub> EPD sires with a tendency on d 3 (P = 0.07) and a difference on d 5 (P = 0.02) of retail display (Figure 4). This would indicate that steer progeny of high-ME<sub>M</sub> EPD sires produced bottom round steaks that maintained a red color throughout display more than those produced from steer progeny of sires with a low-ME<sub>M</sub> EPD. The b* (yellowness) color values were greater in steaks from steer progeny of the high-ME<sub>M</sub> EPD sire group on d 1 (P = 0.03) and 5 (P = 0.01; Figure 4). No difference was observed between b* values of the steaks on d 3, although the same patterns were observed without reaching significance. However, on d 0 the pattern was inconsistent but did not reach statistical significance. Analysis of the hue angle of the steaks over the 5-d retail display simulation showed no significant differences between the bottom round steaks from steer progeny of sires divergent for ME<sub>M</sub> EPD (Figure 5). Although, on d 5 (P = 0.09), the hue angle values of steaks from steer progeny of the high-ME<sub>M</sub> EPD sire group tended to be greater. The hue angle calculation determines the amount of true red present, indicating that the steer progeny from a high-ME<sub>M</sub> EPD sire produced bottom round steaks that tended to show a more true red color. The amounts of browning and surface discoloration of the steaks were also measured using a visual scale over the 5-d simulated retail display, and again no significant differences were observed among the steaks when grouped by sire ME<sub>M</sub> EPD (data not shown).

![Figure 4](image_url) Hunter color values of the bottom round steaks over 5 d in retail display. The L* score measured lightness on a scale of 0 to 100, with 0 being the lightest; the a* score measured the amount of red vs. green, with red being a positive number and green being a negative number; and the b* score measured the amount of yellow vs. blue, with yellow being a positive number and blue being a negative number. Steaks were packaged in a Styrofoam tray with an oxygen-permeable overwrap and placed in a retail display cabinet under uniform lighting for 5 d. Day 0 represents color after steaks were cut from vacuum-packaged wholesale cuts on d 9 postmortem and allowed to bloom. *P < 0.05. Significant markings indicate a difference between high (n = 7) and low (n = 18) sire maintenance energy (ME<sub>M</sub>) EPD groups on each day. Error bars represent the SEM.
Although no panel studies were performed to determine consumer preference of the steaks, several studies have shown that consumers typically prefer an end product that is bright red in color (Carpenter et al., 2001; Rogers et al., 2010). The differences between the steaks after the aging process were significant in terms of their instrumental color values; however, the differences were relatively small and thus not likely to adversely affect marketing of the final product.

**Color in the Strip Loin**

Color evaluation of the strip loin steaks over a 5-d simulated retail display was performed in a manner similar to that of the bottom round steaks. Analysis of the L* value on d 0 \((P = 0.07)\) and 3 \((P = 0.09)\) showed that steaks from steer progeny of the high-ME EPD sire group tended to be lighter in color (data not shown). On d 0, the a* value suggests that steaks from steer progeny of the low-ME EPD sire group were more red in color \((P = 0.02)\) although there was no difference in the values on d 1, 3, and 5 (data not shown). No difference in the b* values between the 2 groups was observed on any of the days (data not shown). The hue angle of the strip loin steaks was also calculated; however, no significant was difference seen between strip loin steaks produced from steers based on sire ME EPD (Fig. 5).

**Glycogen Content**

Analyses of muscle glycogen content from all animals sampled at 12 mo (heifers and steers), all heifers, and all steers grouped based on the ME EPD of their sire were not statistically different (Table 2). Residual glycogen in neither the bottom round nor strip loin steaks from steers was different when data were grouped based on sire ME EPD. (Table 3) However, glycogen content was correlated with some other variables measured in the current study. When muscle samples collected from the steers at 12 mo were analyzed, biceps femoris glycogen content was negatively correlated with the percentage of type I fibers \((r = -0.43; P = 0.03; \text{Table 4})\). Type I fibers primarily function in an oxidative manner, and as such, do not need to store large quantities of glycogen. Muscle glycogen content in the steers was also correlated with the number of type IIa fibers \((r = 0.03; P = 0.05; \text{Table 4})\). Similarly, muscle glycogen tended to be correlated with the number of type IIb fibers \((r = 0.29; P = 0.06; \text{Table 4})\) in the steers. Type IIa fibers function in both an oxidative and glycolytic manner, whereas type IIb fibers function only in a glycolytic manner. The greater concentration of glycogen in these glycolytic fiber types is consistent with how these fibers function because glycogen and glucose derived from the muscle are the main energy substrates. A similar observation was made when data from the premortem heifers and the premortem steers were analyzed separately, perhaps validating this observation. Although a study conducted by Kim et al. (2000) suggests that fiber type composition is not closely associated with glycogen content and the rate of postmortem glycolysis, data from the present study suggest that these 2 factors are associated. Our findings may differ from those in the study conducted by Kim et al. (2000) because they looked at a different breed of cattle (intact male Korean native cattle). Kim et al. (2000) also analyzed the LM and psoas major muscles, neither of which was fiber typed in the present study. The muscle analyzed for fiber type in this study, the biceps femoris,

**Figure 5.** Hue angle within both the bottom round and strip loin steaks from the steers over 5 d of simulated retail display. Hue angle was calculated as \(\tan^{-1} \frac{a^*}{b^*}\) (Wheeler et al., 1996); the hue angle represents the amount of true red. After blooming, steaks were aged in a Styrofoam tray with an oxygen-permeable overwrap in a fluorescent retail display cabinet, with each steak provided similar amounts of lighting. Day 0 represents color after 9 d of aging, followed by fabrication and a blooming period. No data presented in this figure reached statistical significance. However, on d 3 \((P = 0.12)\) and d 5 \((P = 0.09)\), the hue angle tended to be less in the animals from the low-maintenance energy (ME) EPD group \((n = 18)\) compared with the high-ME EPD group \((n = 7)\). Error bars represent the SEM.
is a mixed fiber type muscle that was accessible for pre-mortem and postmortem sampling, and as such, may be more useful than other muscle types in elucidating the relationship between fiber type transition, postmortem glycolysis, and the ultimate effect on product quality.

**Lactate Content**

Lactate content was measured in both the bottom round and strip loin steaks. Lactate is the anaerobic product of glycogen metabolism. This metabolic waste is generally cleared by the intact circulatory system in the live animal; however, lactate remains and accumulates in the postmortem muscle (Immonen et al., 2000). No differences in lactate content were observed among any of the groups studied (Table 3). As previously stated, no change was observed in the amount of glycogen present in the muscle either before or after harvest, indicating that as long as metabolism proceeds normally in the muscles postmortem, there should not be a change in the amount of lactate present. Although it was hypothesized that the amounts of lactate and glycogen would be different between steers from sires divergent in MEₐ EPD values, because changes in fiber type proportions were seen, no quantifiable differences were observed in this study.

**Final pH of the Steaks**

No significant differences were observed in final pH values, taken 9 d after slaughter, of either bottom round or strip loin steaks, when the data were analyzed based on sire MEM EPD (Table 3). Detrimental effects to the end-product quality, such as dark-cutting beef, occur when the final pH of the meat is above 5.8 (Scanga et al., 1998; Immonen et al., 2000). None of the values recorded in this study was above 5.8, and all fit within the normal range, defined as 5.50 to 5.75. However, other studies have found that postmortem pH declines more quickly in animals that possess more type IIb fibers because they typically contain more glycogen (Kim et al., 2000). The rate of pH decline within the steaks analyzed in this study was not characterized because the only pH measurement was final pH. Although no measurable difference was observed between the groups, this suggests that selection for more efficient cattle may not alter the final pH of the end product and, as such, has no detrimental effect on end-product quality, which is the favorable result.

<table>
<thead>
<tr>
<th>Sire</th>
<th>MEM EPD¹</th>
<th>Glycogen content, μg/mg</th>
<th>gys1, ΔCt</th>
<th>glyp, ΔCt</th>
<th>glyc, ΔCt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heifers, 12 mo</td>
<td></td>
<td>0.99</td>
<td>0.30</td>
<td>0.69</td>
<td>0.57</td>
</tr>
<tr>
<td>High (n = 3)</td>
<td>1.46 ± 0.22</td>
<td>−9.06 ± 0.14</td>
<td>−6.18 ± 2.27</td>
<td>−7.79 ± 0.29</td>
<td></td>
</tr>
<tr>
<td>Low (n = 14)</td>
<td>1.46 ± 0.06</td>
<td>−9.45 ± 0.16</td>
<td>−5.11 ± 0.30</td>
<td>−8.11 ± 0.25</td>
<td></td>
</tr>
<tr>
<td>Steers, 12 mo</td>
<td></td>
<td>0.98</td>
<td>0.68</td>
<td>0.76</td>
<td>0.65</td>
</tr>
<tr>
<td>High (n = 7)</td>
<td>1.43 ± 0.19</td>
<td>−9.28 ± 0.27</td>
<td>−5.87 ± 0.87</td>
<td>−7.99 ± 0.38</td>
<td></td>
</tr>
<tr>
<td>Low (n = 18)</td>
<td>1.44 ± 0.11</td>
<td>−9.41 ± 0.18</td>
<td>−6.00 ± 0.43</td>
<td>−7.84 ± 0.15</td>
<td></td>
</tr>
<tr>
<td>Steers and heifers, 12 mo</td>
<td></td>
<td>0.97</td>
<td>0.37</td>
<td>0.53</td>
<td>0.93</td>
</tr>
<tr>
<td>High (n = 10)</td>
<td>1.44 ± 0.14</td>
<td>−9.21 ± 0.19</td>
<td>−5.96 ± 0.84</td>
<td>−7.93 ± 0.27</td>
<td></td>
</tr>
<tr>
<td>Low (n = 32)</td>
<td>1.45 ± 0.06</td>
<td>−9.43 ± 0.12</td>
<td>−5.39 ± 0.27</td>
<td>−7.96 ± 0.14</td>
<td></td>
</tr>
<tr>
<td>Steers, 15 mo</td>
<td>0.43</td>
<td>0.56</td>
<td>0.64</td>
<td>0.79</td>
<td></td>
</tr>
<tr>
<td>High (n = 7)</td>
<td>0.94 ± 0.16</td>
<td>−5.07 ± 3.95</td>
<td>−4.19 ± 0.35</td>
<td>−7.72 ± 0.20</td>
<td></td>
</tr>
<tr>
<td>Low (n = 18)</td>
<td>1.09 ± 0.10</td>
<td>−8.82 ± 0.09</td>
<td>−4.38 ± 0.21</td>
<td>−7.14 ± 0.11</td>
<td></td>
</tr>
</tbody>
</table>

¹MEₐ = maintenance energy; gys1 = glycogen synthase 1; glyp = glycogen phosphorylase; glyc = glycogenin; ΔCt = relative threshold cycle.

**Final pH of the Steaks**

No significant differences were observed in final pH values, taken 9 d after slaughter, of either bottom round or strip loin steaks, when the data were analyzed based on sire MEₐ EPD (Table 3). Detrimental effects to the end-product quality, such as dark-cutting beef, occur when the final pH of the meat is above 5.8 (Scanga et al., 1998; Immonen et al., 2000). None of the values recorded in this study was above 5.8, and all fit within the normal range, defined as 5.50 to 5.75. However, other studies have found that postmortem pH declines more quickly in animals that possess more type IIb fibers because they typically contain more glycogen (Kim et al., 2000). The rate of pH decline within the steaks analyzed in this study was not characterized because the only pH measurement was final pH. Although no measurable difference was observed between the groups, this suggests that selection for more efficient cattle may not alter the final pH of the end product and, as such, has no detrimental effect on end-product quality, which is the favorable result.

<table>
<thead>
<tr>
<th>Sire</th>
<th>MEM EPD¹</th>
<th>Residual glycogen, μg/mg</th>
<th>Residual lactate, nmol/mg</th>
<th>Final pH, 9 d postmortem</th>
<th>Warner-Bratzler shear force, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom round</td>
<td></td>
<td>0.07</td>
<td>0.75</td>
<td>0.75</td>
<td>0.55</td>
</tr>
<tr>
<td>High</td>
<td>0.23 ± 0.02</td>
<td>0.45 ± 0.06</td>
<td>5.62 ± 0.05</td>
<td>3.77 ± 0.34</td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.28 ± 0.02</td>
<td>0.47 ± 0.03</td>
<td>5.64 ± 0.04</td>
<td>3.51 ± 0.23</td>
<td></td>
</tr>
<tr>
<td>Strip loin</td>
<td>0.29</td>
<td>0.23</td>
<td>0.84</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>0.22 ± 0.03</td>
<td>0.16 ± 0.02</td>
<td>5.57 ± 0.02</td>
<td>2.48 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.18 ± 0.02</td>
<td>0.20 ± 0.02</td>
<td>5.57 ± 0.01</td>
<td>2.60 ± 0.10</td>
<td></td>
</tr>
</tbody>
</table>

¹High (n = 7); low (n = 18).
**Warner-Bratzler Shear Force**

Warner-Bratzler shear force values were recorded for both the bottom round and strip loin steaks after aging for 14 d. No differences were observed in Warner-Bratzler shear force between bottom round and strip loin steaks from steer progeny of sires divergent for ME$_M$ EPD (Table 3). Average Warner-Bratzler shear force values for strip loin steaks were less than 4, signifying variable across all animals, regardless of group (Table 2). Data from this study suggest that the expression of genes gys1 and II, glyc, or glyp. No significant differences were detected in expression of the candidate genes when calves were separated by their sex and grouped based on the ME$_M$ EPD value of their sire (Table 2). No significant differences were observed in relative mRNA expression of the genes studied from biceps femoris samples collected at 15 mo age. However, it should be noted that examination of the SE in the assay of glyp expression showed that expression of this gene was highly variable across all animals, regardless of group (Table 2). Data from this study suggest that the expression of glyc may be used to determine the glycogen storage capacity of skeletal muscle in steers. This was concluded as glyc is involved in the synthesis of glycogen from glucose molecules for storage in both skeletal muscle and liver. The glyc attaches to the first glycogen residues and serves as a template for subsequent glycogen branch formation. These data are supported by correlations relating glyc expression and fiber type proportion within the steers.

**Quantification of Muscle Gene Expression**

When all animals (high n = 10; low n = 32) were analyzed using samples taken at 12 mo age, no significant difference was observed in the mRNA expression of the genes gys1 and II, glyc, or glyp. No significant differences were detected in expression of the candidate genes when calves were separated by their sex and grouped based on the ME$_M$ EPD value of their sire (Table 2). No significant differences were observed in relative mRNA expression of the genes studied from biceps femoris samples collected at 15 mo age. However, it should be noted that examination of the SE in the assay of glyp expression showed that expression of this gene was highly variable across all animals, regardless of group (Table 2). Data from this study suggest that the expression of glyc may be used to determine the glycogen storage capacity of skeletal muscle in steers. This was concluded as glyc is involved in the synthesis of glycogen from glucose molecules for storage in both skeletal muscle and liver. The glyc attaches to the first glycogen residues and serves as a template for subsequent glycogen branch formation. These data are supported by correlations relating glyc expression and fiber type proportion within the steers.

**Correlations between Gene Expression and Fiber Type Percentages**

In the present study, the correlation between fiber type and glyc in biceps femoris samples taken from the steers at both 12 and 15 mo age parallels the predicted physiological model within the animal. In muscle tissue collected from steers at 12 mo age, gys1 and type Iib fiber percentage were negatively correlated (r = −0.42 and P = 0.03; Table 4), which was expected. However, no correlation was observed between glyc and glycolgen content within the muscle of the steers. In the samples collected from the steers at 15 mo of age, glyc and type Ila fiber proportion were also negatively correlated (r = −0.42 and P = 0.03; Table 4) Thus, it appears that glyc gene expression may be a useful marker of glycolgen storage capacity in skeletal muscle of steers. Of course, a larger number of animals will be required to determine the true value of this measure.

We report that in the samples taken at 12 and 15 mo, steers selected from a sire with a low-ME$_M$ EPD had significantly more type I fibers and, inversely, significantly fewer type Iib fibers than steers selected from a sire with a high-ME$_M$ EPD. Unexpectedly, no correlations were found between the fiber type and the amount of lactate or the final pH of the steaks, nor was there a relationship between glycogen content and the amount of lactate present in the steak or the ultimate pH. It is worth noting that the majority of the correlations between these data trended in the expected manner but did not reach statistical significance.

Type I fibers typically have the smallest cross-sectional area; type Ila are of intermediate size and type Iib have the largest diameter (Johnston et al., 1975). Because of the differences in diameter size between the different fiber types, fiber type has been shown to affect tenderness within steaks. Muscles with larger mean fiber size yield tougher meat than muscles with smaller fibers (Karlsson et al., 1993; Maltin et al., 1997). Type Iib fibers have been shown to be negatively correlated with Warner-Bratzler shear force values, indicating that a greater proportion of type Iib fibers may produce a

**Table 4. Correlation values of fiber type relative to glycogen or genes associated with glycogen storage and utilization**

<table>
<thead>
<tr>
<th>Item</th>
<th>Type I fiber, %</th>
<th>Type Ila fiber, %</th>
<th>Type Iib fiber, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glycogen content, μg/mg</td>
<td>−0.43 0.03</td>
<td>0.31 0.05</td>
<td>0.29 0.06</td>
</tr>
<tr>
<td>gys1, ΔCt</td>
<td>−0.01 0.97</td>
<td>−0.20 0.35</td>
<td>0.05 0.82</td>
</tr>
<tr>
<td>glyp, ΔCt</td>
<td>−0.01 0.95</td>
<td>0.39 0.05</td>
<td>−0.10 0.64</td>
</tr>
<tr>
<td>glyc, ΔCt</td>
<td>−0.10 0.65</td>
<td>0.32 0.12</td>
<td>−0.42 0.03</td>
</tr>
</tbody>
</table>

1 $gys1 = $glycogen synthase 1; $glyp = $glycogen phosphorylase; $glyc = $glycogenin; ΔCt = relative threshold cycle.
Warner-Bratzler shear force values in the bottom round were analyzed in this study. Wegner et al. (2000) found that steers based on HCW when grouped by sire ME_M EPD (P = 0.91). The differences in fiber type proportions seen in this study are not due to an indirect selection for mature size through the selection of animals for ME_M (data not shown). Our study determined that selection for efficient cattle based on the sire ME_M EPD did not significantly affect the Warner-Bratzler shear force values in the bottom round or the strip loin. Therefore, selection for efficient cattle did not affect the tenderness of the end product, which is the desirable outcome. Of further interest is the fact that the average Warner-Bratzler shear force values of all the steaks in all the different groupings were, on a numeric basis, relatively tender (Hildrum et al., 2009). Because this was true, fiber type may not have affected the Warner-Bratzler shear force tenderness score in this study as much as originally anticipated.

Previous studies have demonstrated a relationship between fiber type proportions within the muscle and coloration of the meat. Type Iib fibers have also been shown to be more prone to discoloration and to complete the aging process faster (Klont et al., 1998). An increased proportion of type Iib fibers has also been shown to produce meat that is paler in color (Wegner et al., 2000). Most important, our study indicated that steaks from progeny of a sire with a high ME_M EPD value had greater Hunter a* and b* color values in the bottom round steaks after 5 d in a simulated retail display case. Analysis of the color values of the 5-d simulated retail display period showed that the steaks from the strip loin had increased color stability when compared with the bottom round steaks. Further, the bottom round steaks from steers of a sire with a high-ME_M EPD appeared to have better color stability over the 5-d retail display period. Our results differed from previous studies because the steaks from sires with a high-ME_M EPD value had a greater proportion of type Iib fibers and were more red in color. Previous studies have shown that an increased proportion of type Iib fibers produces steaks that are paler in color (Wegner et al., 2000). A paler color can be attributed to differences in both the L* and a* values. The study conducted by Wegner et al. (2000) differs from ours in the fact that different breeds of cattle were analyzed in this study. Wegner et al. (2000) found that steaks from different breeds vary in their color, and an extreme example of an increased proportion of type Iib fibers, the Belgian Blue, was used to make this statement. Additionally, many other factors besides muscle fiber type that alter the color of a steak, such as myoglobin content, were not measured in this study. Further analysis needs to be completed on selection for efficient animals based on their sire ME_M EPD in terms of the different physiological factors that are known to affect end-product color. Type I fibers have been shown to contain more calpains (Klont et al., 1998). An increased proportion of calpains is associated with improved end-product tenderness because these proteins are responsible for much of the protein breakdown during the conversion of muscle to meat. Given that greater proportions of type I and type Ila fibers have been associated with improved meat quality, it was important to characterize muscle fiber type in our sample population selected based on sire ME_M. In this context, we found that animals selected from a sire with a low-ME_M value had significantly more type I fibers and, inversely, significantly fewer type Iib fibers in samples taken from the biceps femoris both pre- and postmortem. These data indicate that selecting for efficient cattle does not create any detrimental effects in terms of fiber type and may actually improve the end-product quality, if quality is based on fiber type proportions. Most important, when all the measures of meat quality characterized in this study are compiled, there is evidence that selecting for efficient Red Angus beef cattle based on sire ME_M EPD values should not negatively affect end-product quality, and efficient animals may produce a product of greater quality.

Implications

As modern beef production changes with increasing feed costs, there is a need for selection of more efficient animals. However, it is imperative that selection for efficient animals does not negatively affect end-product quality. In the present study, we have demonstrated that selection for efficient Red Angus cattle based on ME_M EPD does not negatively affect end-product quality, based on the variables measured. Furthermore, selecting for efficient Red Angus beef cattle may improve fresh meat quality as related to differences observed in fiber type proportions.

LITERATURE CITED


