I. Project Title: Biochemical Characterization of Superior Quality Pork

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II. Abstract:

Our objective was to determine if superior pork water-holding capacity and color are associated with: 1) altered capacity of enzymes that control the rate of glycolysis and acid accumulation, 2) the amount of glycogen stored in muscle (glycolytic potential, which influences ultimate pH or acidity), and/or 3) an increase in the proportion of red muscle fibers. Three high meat quality-indexing Berkshire sires and four high cutability Yorkshire sires were used to artificially inseminate F_1 Yorkshire-Landrace sows. Sixteen Berkshire-sired and sixteen Yorkshire-sired progeny were raised under uniform conditions at the Michigan State University Swine Farm. Pigs were harvested at a commercial abattoir on two days. Carcass weights did not differ by breed, but carcasses from Yorkshire-sired pigs were leaner, yielded more pounds of fat-free lean, produced heavier hams and trimmed loins, but lighter bellies than carcasses from Berkshire-sired pigs ($P<.05$). Loin muscle protein, fat and dry matter content did not differ between breed groups. Berkshire progeny tended to have lower loin muscle glycogen content and glycolytic potential ($P<0.10$) and had higher loin muscle pH (less acidic) at 180 min and 24 h postmortem ($P<.05$). However, capacity of glycolytic enzymes, phosphofructokinase and pyruvate kinase, did not differ between breed groups.

Loin chops from Berkshire-sired pigs had higher subjective loin color and marbling scores, and lower (darker) Minolta CIE L* values on d 1 postmortem ($P<.05$), but did not differ from Yorkshire progeny in total muscle heme pigment concentration. Additionally, myosin heavy chain isoform distribution, which is related to muscle fiber type, did not differ between breed groups. A harvest day by breed interaction existed for loin muscle temperature at 20 min postmortem, drip loss and water loss measured by the filter paper method ($P<.05$). Yorkshire progeny had higher 20 min loin muscle temperatures and over twice the water loss measured by the suspension drip method and the filter paper method on the second harvest day when compared to the first harvest day. It is also interesting to note that on harvest day 2, myosin heavy chain isoforms IIa and IIx/b were correlated to 20 min pH (.61 and -.64, respectively; $P<.02$), 24 h pH (.61 and -.57, respectively; $P<.03$) and drip loss (-.51 and .54, respectively; $P<.06$). Vacuum packaged loin sections from Berkshire-sired pigs had less fluid loss when stored at 4°C for 7 d ($P<.003$), but both breed groups exhibited similar loin chop tenderness. Our data suggest that breed differences in color and water-holding capacity were not explained by differences in total

heme pigment concentration, glycolytic enzyme capacity, or the distribution of myosin heavy chain isoforms, but were associated with the rate and extent of pH decline.

III. Introduction

Pork products provide society with high quality, nutritious and palatable food. The rate and extent of biochemical reactions that occur in skeletal muscle of pigs prior to, and immediately following slaughter, have a dramatic impact on the quality of pork produced. Pale, soft and exudative (PSE) pork is a critical quality and economic concern. Although tremendous research efforts have been made to more effectively understand the mechanism(s) that cause inferior pork color and water-holding capacity, little progress has been made in improving pork quality over the last 30 years (Cassens, 2000). While research attention has been focused on characterization and prevention of pork quality problems, little research has focused on the mechanism(s) responsible for producing superior quality pork. The 1995 Terminal Sire Line National Genetic Evaluation Program (NGEP) measured 25 meat quality traits and identified Berkshire progeny as having superior pork color and water-holding capacity. Additionally, records of 1991-1999 National Barrow Show Sire Progeny Tests (NBS) established that Berkshire progeny had the highest ultimate pH, lowest Hunter L* values and lowest drip loss. On the other hand, NGEP and the NBS data have established that Berkshire progeny are generally slower growing, fatter and lighter muscled than other genetic lines. For these reasons, Berkshires have not been commercially accepted in the U.S. and thus their use in research has been limited. Nevertheless, understanding the biochemical mechanisms responsible for superior pork quality in Berkshire progeny may lead to new approaches to improve the quality and consistency of pork from all breeds of swine.

Pale, soft and exudative pork is associated with a rapid postmortem glycolytic rate that causes a rapid pH decline (acidification) while muscle temperature is still high (Briskey, 1964). Two major regulatory points in glycolysis are the steps catalyzed by the enzymes, phosphofructokinase and pyruvate kinase. The capacity of these enzymes and their relationship to glycolytic rate in muscle of Berkshire-sired pigs has not been compared to other breeds. Berkshire-sired pigs have higher ultimate muscle pH (less acidic) than many other breeds (NPPC, 1995). Higher ultimate pH is undoubtedly related to improved color and water-holding capacity associated with this breed. These effects may be due to decreased protein denaturation and/or increased net protein charge, which enable better interaction of muscle proteins with water. It is not known if the higher ultimate pH of Berkshire-sired pigs is due to decreased glycogen storage, improved buffering capacity of the muscle, or an unidentified mechanism.

Glycogen storage, glycolytic rate and muscle color are associated with different muscle fiber types. White muscle fibers are characterized by being fast-twitch (based on myosin ATPase activity), glycolytic (based on capacity to utilize glycogen as an energy source), and light in color (due to low myoglobin content). The extent to which fiber type influences superior color and water-holding capacity in Berkshire-sired pigs has not been determined. We hypothesized that superior pork color and water-holding capacity observed in Berkshire-sired pigs was due to decreased muscle glycolytic rate and reduced glycogen storage, and that these changes result from an increase in the proportion of red/slow muscle fibers.

IV. Objectives:

Our objective was to determine if superior pork water-holding capacity and color are associated with: 1) altered activity of glycolytic enzymes that control the rate of glycogen conversion to lactic acid, 2) amount of glycogen stored in muscle (glycolytic potential, which

influences ultimate lactic acid accumulation or pH), and/or 3) an increase in the proportion of red muscle fibers.

V. Procedures:

Experimental Groups. Three high meat quality-indexing Berkshire sires and four high cutability Yorkshire sires were used to artificially inseminate F_1 Yorkshire-Landrace sows maintained at the Michigan State University (MSU) Swine Teaching and Research Farm. Progeny were raised in uniform conditions at MSU facilities.

Carcass Traits. Eight pigs from each breed group were harvested at a commercial abattoir on two harvest dates (n=32 pigs total). Carcass weights were recorded prior to chilling. At 24 h postmortem, loin muscle area, 10^{th} rib and last rib fat thickness were determined according to current NPPC guidelines (NPPC, 2000). The right side of each carcass was fabricated into wholesale cuts, which were subsequently trimmed and weighed. The right loin from each carcass was transported to the MSU Meat Laboratory for subsequent analysis.

Meat Quality Traits. At 20, 45, 180 min and 24 h postmortem, *longissimus* muscle temperature and pH were measured adjacent to the last rib. Temperature was measured using a hand held temperature probe (Model Number 33032, Atkins Technical Inc., Gainesville, FL) and pH was measured using a portable pH meter equipped with a puncture-type pH electrode (Model 1140, Mettler-Toledo, Woburn, MA). At 20 min postmortem, *longissimus* muscle samples were removed midway between the last rib and the cranial edge of the ilium on the left side of the carcass. These samples were cut into 0.5 cm^3 pieces, frozen in liquid nitrogen, and stored at -80°C.

Adjacent to the third lumbar vertebra, a 2.54-cm thick loin chop was removed at 24 h postmortem for determination of proximate analysis and water-holding capacity. Duplicate 10 g samples from this chop were used to determine water-holding capacity by high-speed centrifugation (40,000 x **g** for 30 min; Honikel and Hamm, 1994). Immediately posterior to this sample, two 2.54-cm thick loin chops were removed, allowed to bloom 15 min and used to determine subjective color and marbling according to current NPPC guidelines (NPPC, 2000) and firmness on a 5 point scale (1= soft and 5 = very firm). These chops were also used for objective color measurement (CIELab L*, a*, b*, D_{65}, 2° standard observer and 50 mm-diameter measuring area) with a Minolta chromameter (CR-310 series; Ramsey, NJ) and drip loss by the suspension method from 24 to 48 h postmortem (Honikel and Hamm, 1994). The cut surface of the remaining loin section (~520 g) was used to measure exudate by the filter paper test (NPPC, 2000), except that duplicate Whatman® #3, 4.25 cm diameter circles were used. This section was vacuum packaged at 24 h postmortem in Cryovac shrink bags using a Mutli Vac machine (Koch, Type AG 800) and held at 4°C until day 7 postmortem. The difference between d 7 and 24 h weight was divided by 24 h weight and expressed as percent purge. Loin chop tenderness was determined by Warner-Bratzler shear force of 1.27 cm diameter cores from duplicate chops aged 7 d, then cooked to 71ºC.

Proximate Analysis. Longissimus samples used for the proximate analysis were obtained at 24 h postmortem and frozen at –20°C until analysis was conducted. These samples were milled with dry ice. Carbon dioxide was allowed to evaporate for two days at –20°C. Moisture content was measured by air-drying (AOAC Method 950.46B). Total fat was determined using the Soxtec Fat

Analyzer (Tecator, Höganäs, Sweden; AOAC Method 991.36 Solvent Extraction Method) and crude protein was determined using combustion method 992.15 (AOAC, 1995; Leco FP-2000, Leco Corp., St Joseph, MI).

Glycolytic Potential. All biochemical analyses were conducted on *longissimus* muscle samples collected at 20 min postmortem. *Longissimus* samples (2 g) were homogenized in 10 mL of 0.6 N perchloric acid with a Polytron (Brinkman, Westbury, NY) at setting 4 for two 30 sec bursts. Three 200 μL aliquots were obtained and 1 mL of amyloglucosidase (AMG) was added to each aliquot for quantification of glucose from glycogen, glucose-6-phosphate and free glucose as described by Dalrymple and Hamm (1973). The remainder of the homogenate was centrifuged at 40,000 x g for 20 min at 4°C in a RC-5 superspeed centrifuge (Sorvall). The supernatant was not treated with AMG and was used for determination of lactate, free glucose and glucose-6-phosphate. Amyloglucosidase, glucose-6-phosphate dehydrogenase, and assay kits for quantification of glucose and lactate were purchased from Sigma Chemical Co. (St. Louis, MO). Glucose, lactate, free glucose and glucose-6-phosphate assays were adapted to a 96-well microtiter plate format. For each assay, 10 μL extracted sample and 190 μL of glucose reagent or lactate reagent were added to each well. All samples were assayed in duplicate and absorbance was measured at 340 nm on a VERSAmax™ plate reader (Sunnyvale, CA). Glyocolytic potential was calculated by 2([glycogen] + [glucose] + [glucose-6-phosphate]) + [lactate] and is expressed as μmoles of lactate equivalents/g tissue. Glucose-6-phosphate was subtracted from the amount of glucose measured on the non-AMG treated supernatant to determine free glucose. Glycogen was calculated by subtracting the amount of free glucose and glucose-6-phospate from the total amount of glucose equivalents (AMG treated sample).

Glycolytic Enzyme Analysis. For quantification of pyruvate kinase capacity, 1 g LM samples frozen at 20 min postmortem were homogenized in 10 volumes of ice-cold buffer (75 mM KCl, 10 mM KH_2PO_4, 2 mM $MgCl_2$, 2 mM EGTA, pH 7.0, containing 50 mM NaF, 2 mM phenylmethylsulfonyl fluoride (PMSF), and 6 mg/L of leupeptin). Samples were homogenized on ice using a Polytron (Brinkman, Westbury, NY) for 2 x 20 sec bursts (setting 4). Homogenates were fractionated by centrifugation at 10,000 x **g** for 15 minutes. Supernatant fluids were saved and pellets were suspended in 10 mL of extraction buffer and centrifuged again at 10,000 x **g** for 15 min. The two supernatant fluids were combined. In preliminary experiments, we found that the sarcoplasmic fraction (supernatant) contained >95 % of the PK activity (data not shown). Thus, the sarcoplasmic fraction was used for quantification of PK activity.

Within 2 h of muscle homogenization, pyruvate kinase activity was measured using a coupled enzyme assay described by Schwagele et al. (1996) and adapted so that it could be performed in a 96-well microtiter plate. Activity was measured at 22°C by following the oxidation of NADH to NAD^+ at 340 nm on a VERSAmax plate reader (Molecular Devices, Sunnyvale, CA). Assays performed in the absence of substrate (PEP) contained less than 1% of sample activity, demonstrating that conversion of NADH to NAD^+ was coupled to PK activity. Pyruvate kinase activity (μmole/min·g^{-1} muscle) was determined using V_{max} calculated from a linear decrease in absorbance for 60 sec (measurements taken at 15 sec intervals) using SOFTmax PRO software (Molecular Devices, Sunnyvale, CA). Samples were assayed in triplicate and the intra-assay coefficient of variation was <4%.

For quantification of phosphofructokinase capacity, samples (1 g) were homogenized in 10 volumes of ice-cold buffer (50 mM Tris-HCl, 10 mM KH_2PO_4, 2 mM $MgCl_2$, 2 mM EGTA, pH

7.8, containing 50 mM NaF, 30 mM 2-mercaptoethanol, 2 mM PMSF and 6 mg/L leupeptin) for 2 x 20 sec bursts. An aliquot of crude homogenate was assayed within 45 min of muscle homogenization using a modification of the coupled enzyme assay described by Krause and Wegener (1996). Assay reagent consisted of 30 mM Tris (pH 8.0), 50 mM KCl, 2 mM $MgCl_2$, 10 mM NaH_2PO_4, 1 mM AMP, 5 mM fructose-6-phosphate, 1 mM fructose-2,6-phosphate, 0.4 mM NADH, 2 mM adenosine triphosphate (ATP), 1 U/mL aldolase, 6 U/mL glycerol-3-phosphate dehydrogenase, 10 U/mL triose-phosphate isomerase and 10 µL of a 1:4 dilution of the crude homogenate. Activity was measured at 22°C by following the oxidation of NADH to NAD^+ at 340 nm for 180 sec (measurements taken at 15 sec intervals). Negative control assays with no fructose-6-phosphate were performed for each sample and the V_{max} from control assays were subtracted from the V_{max} for assays performed with substrate. The total activity is expressed as µmole/min·g^{-1} muscle. Chemicals used in muscle extraction and enzyme assays were purchased from Sigma Chemical Company (St. Louis, MO).

Myosin Heavy Chain Analysis. The washed pellet (myofibrillar component) remaining from pyruvate kinase extraction (above) was suspended in 10 mL of buffer (same as homogenization buffer except NaF, PMSF and leupeptin were omitted). A 0.75 mL aliquot of the suspension was removed and was diluted with 0.75 mL of 2X sample loading buffer (125 m*M* Tris, 4% SDS, 20% glycerol, pH 6.8) without 2-mercaptoethanol. This diluted aliquot was heated at 50ºC for 20 min and samples were mixed by inversion every 5 min. Samples were then heated to 95ºC for 3 min then centrifuged at 14,000 x ***g*** at 22ºC for 20 min to remove insoluble material. Samples were stored at -20ºC until analyzed. Protein concentrations were determined by using BCA Protein Assay (Pierce, Rockford, IL). Samples were mixed with 2X sample loading buffer containing 10% mercaptoethanol. Myosin heavy chain isoform distribution (IIa, IIx/IIb, and I) was determined by SDS-PAGE using 8% (50:1) polyacrylamide resolving gels with 4% (50:1) stacking gels using a Mini-Protean II PAGE gel system (BIORAD) as described by Talmadge and Roy (1993). Sample proteins (0.75 µg protein in 10 µL per lane) were electrophoretically separated at 150 V for 3 h and 70 V for 21 h at 4ºC. Upper and lower buffers were changed after 3 h. Proteins were stained with Coomassie blue to allow visualization. Gel images were acquired using a BIO-RAD gel documentation system and protein bands were analyzed using Quantity One 4.1.0 software (BIO-RAD).

Total Heme Pigment Quantification. Total heme pigments were quantified as described by Warriss (1979), with slight modifications. Two g of *longissimus* muscle (collected 24 h postmortem and stored at -80ºC) were homogenized in 10 mL of 0.04 M sodium phosphate buffer pH 6.8. Samples were homogenized on ice using a Polytron (Brinkman, Westbury, NY) for 2 x 20 sec bursts (setting 4). Homogenized samples were held at 4ºC for 1 h, then centrifuged at 6500 x ***g*** for 10 min at 4ºC. A 5 mL aliquot of supernatant fluid was removed and 0.5 mL of a solution containing 6.6 mM potassium ferricyanide and 8.8 mM sodium cyanide was added. Samples were clarified by centrifugation at 30,000 x ***g*** for 1 h at 4ºC. Absorbance of the supernatant fluid at 540 nm was measured. Total heme pigment concentration was expressed as mg of total pigment/g of tissue and was calculated as outlined by Fleming et al. (1960). We attempted to specifically quantify myoglobin using an ELISA designed for quantification of human myoglobin (ALPCO Diagnostics, Windham, NH). This assay utilizes polyclonal antibodies. Despite 93% homology between human and porcine myoglobin, the assay failed to detect porcine myoglobin from skeletal

muscle extracts at concentrations calculated to be within or above the limits of the assay for human myoglobin.

Statistical Analysis. Statistical analysis was conducted by using the mixed procedure of SAS (1998). For carcass and meat quality traits, gender, breed group and harvest date were included in the model statement. Interactions for gender by breed group, harvest date by breed group and gender by harvest date were also evaluated. Breed group least squares means and standard errors of the means are reported for carcass and meat quality traits. Harvest date by breed group interactions existed ($P<0.05$) for loin muscle area, 20 min temperature, 24 h temperature, 24 h drip loss and exudate measured by the filter paper method. No interactions were observed for gender by breed group or harvest date. Traits with a harvest date by breed interaction were plotted graphically to determine the causes for the interactions.

VI. Results:

Yorkshire-sired pigs used in this study had less backfat and produced more pounds of fat-free lean than Berkshire-sired pigs at similar carcass weights (Table 1). A harvest date by breed interaction existed for loin muscle area (LMA) and this is attributed to Yorkshire-sired pigs on the second harvest day having larger LMA than Yorkshire-sired pigs on the first harvest day. Carcasses of Yorkshire-sired pigs also produced heavier loins and hams, but lighter bellies than carcasses of Berkshire-sired pigs (Table 2). Carcasses of Yorkshire-sired pigs exhibited higher loin muscle temperatures at 20 min postmortem than carcasses of Berkshire-sired pigs on the second harvest day, resulting in a harvest day by sire-breed interaction (Table 3). Overall, loin muscle from Berkshire-sired pigs had a higher pH (less acidic) at 180 min postmortem, indicating a slower rate of pH decline. Ultimate meat pH measured at 24 h postmortem was also slightly higher in loin muscle from Berkshire-sired pigs (Table 3).

Loin chops from Berkshire- and Yorkshire-sired pigs had similar proportions of dry matter, protein and fat (Table 4). Chops from Berkshire-sired pigs were darker in color based on both subjective and objective (Minolta CIE L* values) measures, and appeared to have more marbling (Table 4). Total heme pigment did not differ between sire-breeds (Table 4). Therefore, differences in visual lightness of chops between sire-breeds are not explained by differences in total pigment, although total pigment was correlated to Minolta a* (redness; $r = .61$). A harvest date by breed interaction existed for drip loss and water loss measured by the filter paper method (Table 5). This interaction is caused by a disproportionate increase in fluid loss from loin muscle of Yorkshire-sired carcasses on the second harvest day. It seems likely that this increased fluid loss is associated with the elevated muscle temperature of Yorkshire-sired pigs on harvest day 2. The reason for the elevated postmortem muscle temperature on day 2 is unclear, as all pigs were handled in a similar fashion on both harvest days. Berkshire-sired pigs also had less fluid loss from vacuum packaged loin sections stored at 4ºC for 7 d (Table 5). Loin chop tenderness was similar for both sire-groups.

The combination of low muscle pH at relatively high muscle temperature is known to have detrimental effects on pork color and water-holding capacity. Loin muscle that tended to have a higher temperature and lower muscle pH early postmortem produced paler and more exudative chops in this study. Differences in loin muscle pH between Berkshire- and Yorkshire-sired pigs were not related to overall differences in capacity of glycolytic enzymes or the distribution of myosin heavy chain isoforms between breeds (Table 6). It is interesting to note that on harvest day 2, myosin heavy chain isoforms IIa and IIx/b were correlated to 20 min pH (.61 and -.64,

respectively; P<.02), 24 h pH (.61 and -.57, respectively; P<.03) and drip loss (-.51 and .54, respectively; P<.06). Thus, it seems that relationships between myosin heavy chain isoform distribution and muscle pH or water-holding capacity may only be manifested on harvest days when environmental conditions are less favorable for optimum meat quality. Yorkshire-sired pigs tended to have muscle with higher glycolytic potential than muscle of Berkshire-sired pigs (Table 6). Differences in glycolytic potential are attributed to greater glycogen stores in muscle of Yorkshire pigs, and appear to explain the slightly lower ultimate pH (24 h postmortem) in Yorkshire-sired pigs. The observed differences in ultimate pH, although statistically significant, are small and seem unlikely to account for practical differences in pork quality.

In summary, Yorkshire-sired pigs were leaner, heavier muscled and produced more fat-free lean than Berkshire progeny. However, loin chops from Berkshire-sired pigs had more desirable color and better water-holding capacity, presumably due to a more gradual muscle pH decline within the first 180 min postmortem. Yorkshire-sired pigs and/or carcasses responded adversely to conditions on harvest day 2 that resulted in elevated loin muscle temperature and increased fluid loss. Differences in meat quality characteristics between sire-breeds do not appear to be associated with an increase in glycolytic enzyme capacity or the proportion of fast myosin isoforms, although a higher proportion of type IIb/x myosin isoforms may contribute to accelerated pH decline under less favorable antemortem or postmortem conditions. The differences in loin muscle temperature and pH observed between Berkshire- and Yorkshire-sired pigs are likely to be associated with muscle energy consumption, which is largely controlled by intracellular calcium partitioning. Our current research efforts will help decipher the relationship between the capacity of skeletal muscle to sequester intracellular calcium, the rate of muscle pH decline and pork quality in these pigs. Collectively, this information will allow development of strategies to 1) rapidly identify live hogs or carcasses that will be likely to produce superior quality pork, and 2) improve pork quality by manipulating biochemical events that determine pork quality.

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Table 1: Carcass Traits

Carcass Trait	Berkshire		Yorkshire		Probability Level*
	LS Means	SEM	LS Means	SEM	
Hot Carcass Weight (kg)	86.1	1.27	86.7	1.10	NS
Loin Muscle Area (cm^2)	37.6	1.03	43.2	0.88	HD X B (P<0.05)
Tenth Rib BF (mm)	23.3	1.00	18.0	0.90	(P<0.001)
Last Rib BF (mm)	26.4	1.15	23.5	0.99	(P=0.0503)
USDA Grade	2.20	0.22	1.60	0.19	(P<0.05)
Fat-Free Lean (kg)	42.5	0.74	46.0	0.64	(P<0.001)

*HD X B indicates a harvest date by breed group interaction.

Table 2: Wholesale Cut Yields

Wholesale Cut	Berkshire		Yorkshire		Probability Level
	LS Means	SEM	LS Means	SEM	
Trimmed Loin (kg)	8.97	0.19	9.47	0.16	(P<0.05)
Ham (kg)	9.43	0.16	10.2	0.16	(P<0.01)
Boston Butt (kg)	4.09	0.12	4.21	0.10	NS
Picnic Shoulder (kg)	3.53	0.08	3.70	0.07	NS
Belly (kg)	5.83	0.12	5.35	0.10	(P<0.01)

Table 3: Loin Muscle Temperature and pH Decline

Trait	Berkshire		Yorkshire		Probability Level*
	LS Means	SEM	LS Means	SEM	
T20 min (^oC)	37.9	0.24	38.5	0.20	HD X B (P<0.05)
T45 min (^oC)	35.9	0.36	36.6	0.31	NS
T180 min (^oC)	24.7	0.56	24.5	0.48	NS
T24 hr (^oC)	4.47	0.08	4.40	0.07	HD X B (P<0.05)
pH20 min	6.5	0.06	6.4	0.05	NS
pH45 min	6.4	0.08	6.2	0.07	NS
pH180 min	6.0	0.09	5.8	0.08	(P<0.05)
pH24 hr	5.5	0.02	5.4	0.02	(P<0.02)

*HD X B indicates a harvest date by breed group interaction.

Table 4: Fresh Loin Chop Characteristics (Day 1 Postmortem)

Proximate Analysis	Berkshire		Yorkshire		Probability Level
	LS Means	SEM	LS Means	SEM	
Dry Matter (%)	26.9	0.22	26.4	0.19	NS
Protein (%)	23.2	0.16	23.4	0.14	NS
Fat (%)	2.72	0.27	2.29	0.23	NS

Subjective Quality Measures	LS Means	SEM	LS Means	SEM	Level
Color (1-6)	3.0	0.19	2.5	0.16	(P<0.05)
Marbling (1-10)	2.5	0.19	1.7	0.17	(P<0.01)
Firmness (1-5)	2.8	0.17	2.4	0.15	NS

Objective Color Measures	LS Means	SEM	LS Means	SEM	Level
Minolta L* Day 1	50.5	0.72	53.1	0.62	(P<0.01)
Minolta a* Day 1	16.2	0.31	15.6	0.27	NS
Minolta b* Day 1	10.1	0.29	11.1	0.25	(P<0.02)

Pigment Concentration	LS Means	SEM	LS Means	SEM	Level
Total Heme Pigment (mg/g)	0.89	0.03	0.85	0.03	NS

Table 5: *Longissimus* Muscle Water-Holding Capacity and Tenderness

Measures of Water Loss	Berkshire		Yorkshire		Probability Level*
	LS Means	SEM	LS Means	SEM	
Centrifuge WHC (%)	14.7	1.27	17.6	1.09	NS
Whatman Filter Paper (mg)	17.1	4.94	31.5	4.26	HD X B (P<0.05)
24 h Drip (%)	1.27	0.29	2.31	0.25	HD X B (P<0.05)
Day 7 Purge (%)	2.57	0.26	3.64	0.22	(P<0.01)
Warner-Bratzler Shear Force (kg)	3.1	0.34	3.2	0.49	NS

*HD X B indicates a harvest date by breed group interaction.

Table 6: Biochemical Characteristics of *Longissimus* Muscle

Glycogen Metabolism	Berkshire		Yorkshire		Probability Level
	LS Means	SEM	LS Means	SEM	
Glycolytic Potential (μmol Lac eq/g)	103.9	3.89	113.6	3.35	(P<0.06)
Glycogen (μmol/g)	31.5	1.86	35.6	1.60	(P<0.1)
Glucose-6-P (μmol/g)	4.37	0.92	3.34	0.79	NS
Lactate (μmol/g)	29.8	1.86	32.5	1.60	NS

Glycolytic Enzyme Capacity	LS Means	SEM	LS Means	SEM	Level
Phosphofructokinase (μmol/min/g)	132.7	5.18	132.3	4.46	NS
Pyruvate Kinase (μmol/min/g)	418.7	27.7	441.4	23.9	NS

Myosin Heavy Chain Isoforms	LS Means	SEM	LS Means	SEM	Level
Type I (% of Total MHC)	9.3	1.1	9.5	0.9	NS
Type IIA (%of Total MHC)	34.8	1.5	32.9	1.3	NS
Type IIB/X (% of Total MHC)	55.9	1.8	57.6	1.6	NS