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Meat Science

Influence of finishing systems on sensory characteristics and the mechanisms regulating tenderness formation in the *longissimus lumborum* of bison bulls

Lydia M. O'Sullivan[†,‖], Clay J. Newton[†,#], Keith R. Underwood[†], Judson K. Grubbs[†], Christina E. Bakker[†], Thu Dinh[‡], Carter Kruse[$], and Amanda D. Blair[†,1]

[†]Department of Animal Science, South Dakota State University, Brookings, SD 57007, USA
[‡]Tyson Foods, Springdale, AR 72762, USA
[$]Turner Institute of EcoAgriculture, Bozeman, MT 59718, USA
[‖]Present address: Murray State University, Murray, KY 42071, USA
[#]Present address: Agricultural Utilization Research Institute, Crookston, MN 56716, USA
[1]Corresponding author: amanda.blair@sdstate.edu

ABSTRACT

The objective of this study was to characterize the influence of finishing system on the sensory characteristics and mechanisms of tenderness formation in the *longissimus lumborum* (striploin) of bison bulls. Bison bulls (n = 196) were randomly assigned to one of two finishing treatments at approximately 25 mo of age: 1) Grain-finished (n = 98; placed in an open lot with ad libitum access to prairie hay, alfalfa hay, and whole shell corn prior to slaughter) or 2) Grass-finished (n = 98; bulls allowed to graze native pasture until slaughter). Bulls were harvested at approximately 30 mo of age and striploins were collected. Ultimate pH was recorded, and striploins were fabricated into steaks for assessment of sensory characteristics by consumer and trained sensory panels (steaks aged 14 d), and analysis of Warner-Bratzler shear force (WBSF; steaks aged 4, 7, 14 or 21 d). Additional steaks were aged for 14 d for determination of collagen content and sarcomere length. Proteolysis of desmin and troponin-T was evaluated on samples aged for 4, 7, 14, or 21 d. Consumer panel results indicate that grain-finished steaks had higher ratings for overall liking ($P = 0.04$) and flavor liking ($P < 0.01$) whereas off-flavor intensity was increased ($P < 0.01$) for grass-finished steaks compared to grain-finished steaks. Trained panelists indicated that grass-finished bison steaks had increased ($P < 0.01$) aroma and flavor intensities compared to grain-finished bison steaks and "ammonia, metallic, and gamey flavors" were associated with the grass-finished treatment. Warner-Bratzler shear force was affected by the interaction of finishing treatment with aging period ($P < 0.01$). Steaks from the grain-finished bulls became more tender ($P \leq 0.02$) as aging time increased from 4 d to 14 d, whereas WBSF of steaks from grass-finished bulls did not differ ($P \geq 0.10$) during this period. Steaks from grass-finished bulls were more tender ($P \leq 0.01$) than steaks from grain-finished bulls at 4 d and 7 d but treatments were similar ($P \geq 0.61$) at 14 and 21 d. Samples from grass-finished bulls had less ($P < 0.01$) intact desmin compared to grain-finished bulls. This study demonstrates that finishing system influences sensory attributes of steaks from bison bulls and highlights the role of proteolysis as the primary mechanism regulating tenderization of bison.

LAY SUMMARY

This study investigated the influence of finishing systems (grain- or grass-finishing) on sensory characteristics and tenderness attributes of bison strip loin steaks. The experiment compared bulls finished on native rangeland or in a pen-finishing system with free choice access to grain. Bulls were harvested and samples collected from the loin muscle to evaluate the influence of finishing systems on sensory characteristics and the mechanisms that influence tenderness (sarcomere length, collagen content, and the degradation of proteins caused by aging). Grain finished bison bulls produced steaks that had more favorable ratings for flavor liking indicating that consumer panelists preferred the flavor of grain-finished steaks. Steaks from grass-finished bulls were more tender than steaks from grain-finished bulls when aged for 4 or 7 d, however by day 14 there was no difference between treatments and consumer panelists did not detect a difference in tenderness of steaks aged for 14 d. This improvement in tenderness at early aging periods appears to be related to increased degradation of structural proteins early postmortem, suggesting differences in the aging process between the two finishing systems. This study provides some of the first evidence evaluating mechanisms of tenderness formation in bison.

Key Words: bison, finishing system, proteolysis, sensory, tenderness

INTRODUCTION

Bison production and demand for bison meat products have grown in recent years (Galbraith et al., 2014; USDA-NASS, 2024). Approximately 75,000 bison were harvested under federal inspection in 2023 in the United States (USDA-AMS, 2024). Of all bison harvested, bison bulls represent the greatest proportion of this slaughter mix (USDA-AMS, 2024). It is common in the bison industry for males to remain intact (not castrated) and bulls typically finish at a heavier weight compared to bison heifers (Rutley et al., 2003). Additionally, both grain- and grass-finishing systems are commonly utilized for bison production (Anderson & Feist, 2015). Previous

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research has demonstrated that production systems can influence carcass characteristics of bison heifers. Janssen et al. (2021) reported grain-finished bison heifers had heavier hot carcass weights, as well as increased dressing percentages, larger ribeye areas, greater backfat thickness, and increased marbling scores compared to grass-finished heifers. Janssen et al. (2021) also reported that finishing treatment did not influence consumer sensory ratings, however steaks from the grain-finished system produced more tender steaks as evaluated by Warner-Bratzler shear force (WBSF). Research investigating the impact of finishing system on sensory responses and tenderness of steaks from bison bulls is lacking. Further, it is unclear what mechanism may be responsible for tenderness differences in bison steaks.

Extensive research in the meat industry has identified three mechanisms that regulate tenderness: collagen content and extent of cross-linking, sarcomere length, and proteolysis of myofibrillar proteins (Koohmaraie et al., 2002; Rhee et al., 2004; Hopkins & Geesink, 2009). Collagen content is responsible for background toughness in meat, which is a baseline threshold that cannot be reversed by postmortem aging (Purslow, 2005). Li et al. (2022) indicated that both connective tissue content and solubility can impact tenderness of beef. Increased total collagen and mature collagen crosslinks can result in increased toughness, whereas increases in soluble collagen benefit tenderness. Sarcomeres are the functional unit of muscle and shorter sarcomeres post rigor typically result in increased meat toughness and reduced water-holding capacity (Huff-Lonergan et al., 2010; Ertbjerg & Puolanne, 2017). Proteolysis of myofibrillar proteins is credited for changes in skeletal muscle associated with meat tenderization during aging (Koohmaraie, 1992). However, there is limited research investigating the influence of finishing systems on these mechanisms that regulate tenderness in bison. Therefore, the objectives of this study were to characterize the influence of finishing system (grain-finished vs. grass-finished) on the sensory characteristics of steaks from bison bulls and evaluate the mechanisms of tenderness formation in the *longissimus lumborum* of bison bulls.

MATERIALS AND METHODS

Animals and Sample Collection

Bison bulls (n = 196) from a common source were allowed to graze native pasture in the Sandhills Ecoregion of Nebraska under free-range conditions from weaning until assignment to finishing treatments. When bulls were approximately 25 mo of age (mean body weight = 308 ± 3.0 kg), they were randomly assigned to one of two finishing treatments: 1) Grain-finished (n = 98; placed in an open lot with ad libitum access to prairie hay, alfalfa hay, and whole shell corn for 146 d prior to slaughter) and 2) Grass-finished (n = 98; bulls continued to graze native pasture for 146 d prior to slaughter). Details of typical plant composition of these pastures, finishing methods, and facilities are described by van Vliet et al. (2023). At approximately 30 mo of age, all bulls were transported (~608 km) to a commercial harvest facility and harvested over 2 d. On the first day of slaughter, 50 grain-finished bulls and 49 grass-finished bulls were slaughtered. On the second day, 48 grain-finished bulls and 49 grass-finished bulls were slaughtered. After an approximately 20-h chilling period, carcasses were ribbed between the 12th and 13th rib. A subsample (n = 30 per finishing system; 15 carcasses closest to the average hot carcass weight per treatment per slaughter day) was selected and transported to a commercial fabrication facility. A boneless strip loin was obtained from both sides of each subsampled carcass, vacuum packaged, and transported in a refrigerated trailer back to the South Dakota State University Meat laboratory for steak fabrication and further analysis.

Strip Loin Fabrication and pH Measurement

Samples arrived at the South Dakota State University Meat Laboratory at 2 or 3 d postmortem. Strip loins were trimmed to remove all subcutaneous fat and fabricated into 2.54-cm-thick steaks beginning at the anterior end of the strip loin. Steaks were trimmed of accessory muscles and all analyses were conducted on the *m. longissimus lumborum*. From the strip loin of the right side of the carcass, the first steak was aged for 4 d at 4 °C then frozen for evaluation of collagen content. The second steak was designated for a trained sensory panel and the third steak was designated for a consumer sensory panel. The second and third steaks were aged for 14 d at 4 °C then frozen. The fourth steak was divided into quadrants and each quadrant was assigned to age for 4, 7, 14, or 21 d for analysis of proteolysis using Western blotting techniques.

From the left strip loin of the carcass, the first steak was aged for 4 d at 4 °C and then frozen for determination of sarcomere length. The second through fifth steaks were designated for Warner-Bratzler shear force (WBSF) analysis and aged for 4, 7, 14, or 21 d, respectively, at 4 °C then frozen prior to shear force analysis. Ultimate pH was measured on the posterior end of the strip loin prior to fabrication using a hand-held pH meter (Thermo-Scientific Orion Star, Beverly, MA, Model #A221 and Star A321 Portable pH probe).

Consumer Sensory Panel

A consumer sensory panel was conducted at the University of Minnesota Sensory Laboratory to evaluate subjective sensory characteristics of grain- and grass-finished bison strip loin steaks. Random participants (n = 82) were recruited from the student and staff population of the University of Minnesota. Qualified participants were 18 y or older, had no food allergies or sensitivities, were willing to consume bison meat, and must have consumed any type of meat at least once a year. Participants were compensated $10.00 for their time. The University of Minnesota's Institutional Review Board approved all recruiting and experimental procedures (IRB #6792). Sample steaks were aged 14 d and kept in frozen storage conditions (~10 mo) prior to analysis. Frozen steaks were delivered under refrigeration to the University of Minnesota and individual steaks were removed from vacuum packaging, wrapped in aluminum foil and placed on trays labeled with each sample's unique 3-digit code. The trays were then stored in a refrigerator to allow steaks to thaw prior to cooking and serving to panelists the following day. On the day of testing, steaks were removed from the refrigerator, placed on metal sheet pans, and cooked in an electric oven set at 204 °C until they reached an internal temperature of 71 °C (approximately 30 min). After cooking, the steaks were allowed to rest for 10 min. Once rested a sample cutter was used to portion each steak into 1 cm x 1 cm x 2.5 cm cuboids. Cuboids were placed into a porcelain double-broiler labeled with the sample's respective three-digit code. The water in the lower part of each double-broiler was maintained

at approximately 60 °C. Before being served, two steak pieces were placed in 4-ounce foam cups (Dart Container Corporation, Mason, WI) labeled with the three-digit code for each sample, covered with a plastic lid, placed on a serving tray, and held inside a proofing cabinet (Win-Holt NSF ETL, Syosset, NY Model #NHPL-1836C) with a humidity setting of 9 and temperature setting of 54 °C—60 °C. Each participant received two cuboids of bison steak per treatment and were provided with distilled water. The order in which the participants tasted the samples was balanced for position and carryover effects using a Williams Latin square design (Lucas, 1957). For each sample, participants were instructed to "open the lid of the sample part-way, sniff the sample, and rate your liking of the sample's overall aroma by placing a mark on the scale below." After rating aroma liking, participants were instructed to "eat one bison piece and rate it for the following attributes by placing a mark on each of the scales below." The attributes included overall liking, aroma liking, flavor liking, and texture liking. Next participants were instructed to "eat the second bison piece and rate the following attributes." The attributes included juiciness intensity, toughness intensity, meat flavor intensity, and off-flavor intensity. During testing, all liking ratings were made on a -100 to 100-point labeled affective magnitude scale with the left most end labeled "Greatest Imaginable Dislike" and the right most end labeled "Greatest Imaginable Like." All intensity ratings were made on modified 51-point labeled magnitude scales with marks from left to right labeled "None," "Barely Detectable," "Slight," "Moderate," "Very," and "Extreme."

Trained Sensory Panel

Eleven sensory panelists were recruited from the Animal Science Department at South Dakota State University and trained to evaluate tenderness, juiciness, aroma, and bison flavor intensity of strip loin steaks. Panelists were trained and sensory evaluations were performed according to American Meat Science Association (AMSA) training guidelines with modification appropriate for this study (AMSA, 2016). Steaks designated for evaluation by trained panelists were aged 14 d and kept in frozen storage conditions (~10 mo) prior to analysis. Steaks were cooked on an electric clamshell grill (George Foreman, Model #GRP1060B, Middleton, WI) to a target peak internal temperature of 71 °C. Internal temperature was monitored using a digital thermometer (Cooper-Atkins Aqua Tuff NSF Series, Middlefield, CT, Model #41-983430-5) placed near the geometric center of each steak. After cooking, steaks were held at 63 °C in a warming oven (MetroHM2000, Wilkes-Barre, PA). Approximately 15 min prior to sensory evaluation, steaks were portioned into 1 cm x 1 cm x 2.5 cm cuboids. Two cuboids were placed into a pre-labeled lidded 2-ounce plastic cup and returned to the warming oven until they were served to panelists. Panelists evaluated the attributes on an anchored unmarked line scale with the far-left point indicating extremely tender, extremely juicy, no aroma, or extremely bland bison flavor and the far-right point representing extremely tough, extremely dry, extreme aroma, or extremely intense bison flavor. Nine samples were evaluated in each session, and one session was held per day, for a total of 8 sessions. Sample evaluations were alternated by treatment to reduce first and last order bias. Panelists were secluded by partitioned booths with red lighting and separated from the steak preparation area.

Warner-Bratzler Shear Force and Cook Loss

Frozen steaks were thawed for 24 h at 4 °C before cooking and weighed prior to cooking. Steaks were cooked on an electric clamshell grill (George Forman 9 Serving Classic Plate Grill, Model #GR2144P, Middleton, WI) to an internal temperature of 71 °C. Internal temperature was monitored using a digital thermometer (Cooper-Atkins Aqua Tuff NSF Series, Middlefield, CT, Model #41-983430-5) placed near the geometric center of each steak. After cooking, all steaks were cooled for 24 h at 4 °C. Steaks were allowed to warm to room temperature before they were reweighed to determine cook loss; reported as a percentage of the raw weight using the following equation: [(raw weight—cooked weight) / raw weight] × 100. After weighing, 5 cores (1.27-cm in diameter) were removed parallel to the muscle fiber orientation and sheared once perpendicular to the muscle fiber orientation. A texture analyzer (Shimadzu Scientific Instruments Inc., Lenexa, KS, Model #30825535050) with a Warner-Bratzler attachment was used to determine the peak force required to shear each core. Peak force was recorded, and an average shear force peak value was reported for each steak (AMSA, 2016).

Protein Extraction

Frozen samples were allowed to thaw slightly and were prepared for protein extraction by slicing into small pieces, snap frozen in liquid nitrogen, and powdered for 30 sec in stainless steel blender cups (Waring Products Division, New Hartford, CT, Model SS 110) until they achieved a uniform consistency. Powdered samples were stored in 7.62 x 12.7 cm sample bags (Fisher, Hanover Park, IL) at –20 °C until further analysis. Powdered samples were used to create protein samples for gel electrophoresis and Western blots using methods by Melody et al. (2004) with several modifications. Following powdering, 0.60 g of each sample were weighed out and homogenized using a 30 mL Potter-Elvenjen Tissue Grinder attached to an overhead stirrer (Heidolph, Schwabach, Germany, Model RZR1) in 10 mL of whole muscle buffer (2% Sodium Dodecyl Sulfate [SDS], 10 mM Sodium Phosphate, pH 7.0) to extract myofibrillar proteins. Homogenized samples were centrifuged for 15 min at 1,500 x *g* at 25 °C. Protein concentrations of the supernatant were determined in duplicate by diluting samples with a 1:20 dilution in double distilled deionized water. A Lowry protein assay (RC/DC Protein Assay Kit, Bio-Rad Laboratories, Hercules, CA) was used to determine protein concentrations. The protein assay was analyzed using a spectrophotometer at 750 nm wavelength (SpectraMax 190; Molecular Devices, Sunnyvale, CA). The associated spectrophotometer software (SoftMax Pro 6, version 6.2.1, Molecular Devices) was used to evaluate protein concentrations compared to a standard curve. Protein gel samples were prepared with a final sample concentration of 4 mg/mL and stored at –20 °C. Prior to Western blot analysis, load checks were conducted using 15% sodium dodecyl sulfate polyacrylamide separating gels (SDS-PAGE; acrylamide: N-N'-bis-methylene acrylamide = 100:1, 0.1% SDS, 0.05% TEMED, 0.5% Ammonium Persulfate [APS], and 0.375 M Tris HCl, pH 8.8) with 5% stacking gels (acrylamide: N-N'-bis-methylene acrylamide = 100:1, 0.1% SDS, 0.125% TEMED, 0.075% APS, and 0.125 M Tris HCl, pH 6.8) to ensure proper dilution of each sample. Gels were run using a mini gel electrophoresis unit (Model SE-260; Hoefer

Scientific, Holliston, MA) at 120 v for 390 v h. Gels were stained using Coomassie blue (40% Methanol, 7% Glacial Acetic Acid, 53% ddH_2O, 0.1% Coomassie brilliant blue R-250) for 24 h. Gels were destained using 40% methanol and 7% glacial acetic acid. Protein profiles were visually analyzed for similarities across samples (FlourChem M multiflour imaging system; Protein Simple, Santa Clara, CA) using auto-exposed white light.

Gel Electrophoresis Western Blot Analysis

A 10% SDS-PAGE gel was used for quantification of intact desmin and a 15% SDS-PAGE gel was used for intact troponin-T with 5% stacking gels. Forty µg of protein sample (4, 7, 14, and 21 d postmortem) was loaded onto gels and allowed to run at 120 v for 24 v h. A reference sample containing protein representing 48 samples (6 samples per treatment for each of four aging days) was included on each blot for analysis. After the completion of electrophoresis, gels were transferred to a polyvinylidene difluoride (PVDF Transfer Membrane, Thermo Fisher Scientific, Asheville, NC) membrane with a pore size of 0.45 µm using a TE-22 transfer unit (Hoefer Scientific, Holliston, MA) at 135 v h. The membrane was emersed in transfer buffer (24 mM Tris, 186 mM Glycine, and 15% Methanol) at 4 °C using a refrigerated water bath (IsoTemp, Model #6200 R28; Thermo Fisher Scientific, Asheville, NC). After the transfer was complete membranes were blocked in phosphate-buffered saline (PBS)-Tween (66mM Sodium phosphate, 0.1 M NaCl, and 0.1% Tween-20) mixed with 5% nonfat dry milk and incubated for 1 h at room temperature (22 °C). Primary antibody concentrations were diluted in PBS-Tween and added to each blot for incubation overnight at 4 °C. The following concentrations were used: desmin [1:80,000 polyclonal rabbit anti-desmin antibody; courtesy of the Lonergan Lab at Iowa State University (Huff-Lonergan et al., 1996)] and troponin-T (1:15,000 JLT-12 goat anti-mouse; Sigma, St. Louis, MO). After overnight incubation with the primary antibodies, blots were warmed to room temperature for one h and then washed 3 times in PBS-Tween for 10-min intervals. Following the final wash, a secondary antibody prepared in PBS-Tween was applied to each membrane for 1 h. The following concentrations were used: desmin (1:20,000 goat anti-rabbit horseradish peroxidase; product #31460, Thermo Fischer Scientific, Asheville, NC) and troponin-T (1:20,000 goat anti-mouse horseradish peroxidase; product #31430, Thermo Fischer Scientific, Asheville, NC). After secondary antibody incubation, blots were triple washed in PBS-Tween for 10-min intervals. Blots were developed using an enhanced chemiluminescence (ECL) Prime detection kit (GE Healthcare, Lafayette, CO). Images were collected using the imaging system described above. Alpha View SA Software (Protein Simple; San Jose, CA) was used for visualization and quantification of the disappearance of the 55 kDa intact desmin band, the 35 kDa (band 1) and 33 kDa (band 2) of intact troponin-T. Intact desmin and intact troponin-T were analyzed as the ratio to the internal reference standard used across all western blots to control variation.

Collagen Analysis

Samples designated for collagen analysis were powdered as described above to produce a homogenous sample. Heat soluble collagen was extracted from 1g of powdered raw meat samples in 5 mL of deionized water at 77 °C for 1 hr. The heat soluble collagen extract was cooled on ice, centrifuged at 3,000 x *g* for 10 min at 4 °C, and separated from the meat pellets (insoluble collagen fraction). Norvaline was introduced into both heat soluble and insoluble fractions as internal standards and either 12-N HCl (concentrated, for heat soluble) or 6-N HCl (for insoluble) was added. Acidified heat soluble and insoluble fractions were placed in a drying oven at 100 °C for 16 h. A volume of 50 µL of heat soluble hydrolysate and 5 µL of hydrolysates were neutralized with the same volume of 6N NaOH and were diluted in deionized water to a total volume of 1 mL. The neutralized solutions were centrifuged at 10,000 x *g* for 5 min at room temperature. A volume of 200 µL of the neutralized, diluted solutions were reacted with propyl chloroformate in chloroform, sodium hydroxide, and n-propanol, as described by (Kaspar et al., 2008). The amino acid derivatives were extracted in isooctane for gas chromatography-mass spectrometry determination. Amino acid derivatives were injected into an inlet of an Agilent 7890A GC system coupled to an Agilent 5975C inert XL MSD with a triple-axis mass detector, an Agilent 7693 series autosampler, and a capillary column (Zebron EZ-AAA 10 m x 0.25 mm; Phenomenex®, Santa Clara, CA, USA). The inlet was operated at 250 °C and had a 1:15 split ratio. The helium carrier gas was at 1 mL/min constant flow rate. The temperatures of the transfer line, ion source, and quadrupole were 310, 240, and 180 °C, respectively. The oven was programmed initially at 110 °C and increased to 320 °C within 11 min. The solvent delay was 1.30 min. The mass spectrometer was operated in selected ion monitoring mode and the target and qualifier ions were selected according to the mass spectra of authentic standards. Amino acids were quantified using an internal calibration method with authentic amino acid standards (Phenomenex®, Santa Clara, CA, USA). The collagen content (heat soluble or insoluble, mg/g) was calculated by multiplying the hydroxyproline concentration by a factor of 7.52 (heat soluble) or 7.25 (insoluble) (Cross et al., 1973).

Sarcomere Length Determination

Myofibrils were isolated from a strip loin steak according to the procedures described by Weaver et al. (2008). Approximately 2.5 g of muscle was minced and homogenized in 20 mL of rigor buffer [RB; 75 mM KCl, 10 mM Imidazole, 2 mM $MgCl_2$, 2 mM ethylene glycol-bis(2-aminoethylether)-*N,N,N',N'*,-tetraacetic acid (EGTA), and 1 mM NaN_3] for two 10 sec bursts using an digital IKA T25 Ultra-Turrax homogenizer (Model T25 DS1, IKA Works, Inc., Wilmington, NC). Homogenized samples were brought to 35 mL using RB and centrifuged at 1,000 x *g* for 10 min at 4 °C. The supernatant was decanted, and the remaining pellet was homogenized in 20 mL of RB for a short 10-sec burst at medium speed. Samples were brought to 35 mL using RB and centrifuged again at 1,000 x *g* for 10 min at 4 °C. The supernatant was decanted, and the remaining pellet was re-suspended in 35 mL of RB by vigorously shaking. Samples were centrifuged a third time at 1,000 x *g* for 10 min at 4 °C. The supernatant was decanted, and the pellet was re-suspended in 20 mL of RB plus 20 µL of 0.1 mM phenylmethylsulfonyl fluoride by shaking vigorously.

Sarcomere length was determined using the methods described by Mohrhauser et al., 2011 with modifications. Isolated myofibrils were diluted with water 1:50 and a 175 µL aliquot of suspended myofibrils was immediately affixed

Table 1. Least square means for the effect of finishing system[1] on pH, proteolysis of intact desmin and troponin-T, collagen content, and sarcomere length of bison bulls

Attribute	GRAIN	GRASS	SEM[2]	*P*-value[3]
Ultimate pH[4]	5.68	5.65	0.013	0.14
Intact Desmin (55 kDa)[5]	1.09	0.90	0.036	<0.01
Intact Troponin-T band 1 (35 kDa)[5]	1.08	1.06	0.161	0.91
Intact Troponin-T band 2 (33 kDa)[5]	1.62	2.24	0.367	0.10
Insoluble collagen, mg/g	2.14	2.05	0.072	0.39
Heat soluble collagen, mg/g	0.30	0.22	0.053	0.31
Total collagen, mg/g	2.44	2.27	0.088	0.19
Sarcomere length, µm	1.27	1.25	0.014	0.45

[1]Treatments: GRAIN = bison bulls (n = 98) backgrounded on grass and finished for 130 days with ad libitum access to grass hay, alfalfa, and a corn prior to slaughter. GRASS = bison bulls (n = 98) remained on pasture until slaughter.
[2]Standard error of the mean.
[3]Probability of difference among least square means.
[4]Ultimate pH was measured at either 2- or 3-days postmortem from grain- (n = 30) and grass- (n = 30) finished strip loins.
[5]Expressed as a ratio to an internal standard.

onto a microscope slide using centrifugation at 140 x *g* at 25 °C (Cytofuge 2, Model M801-22, Westwood, MA). Slides were dried for one h in an oven at 37 °C. One hundred-fifty µL of monoclonal anti-α-actinin (sarcomeric) antibody (#MA1-22863, Thermo Fisher Scientific, Asheville, NC) diluted 1:5000 with RB was placed onto each slide, and slides were then incubated for one h in an oven at 37 °C. Slides were rinsed twice (2.5 min per wash) with RB and allowed to completely air dry at room temperature. One hundred-fifty µL of donkey anti-mouse fluorescein isothiocyanate conjugated secondary antibody (#715-095-150, Jackson Immuno Research, West Grove, PA) diluted 1:100 with RB was applied to each slide and incubated for one h in an oven at 37 °C to allow for visualization of the Z-lines. Following incubation with secondary antibody slides remained in the dark. Slides were rinsed twice with RB (2.5 min per wash) and then rinsed with ddH_2O for 2.5 min and allowed to air dry at room temperature. Twenty µL of mounting media [75 mM KCl, 10 mM Tris pH 8.5, 2 mM EGTA, 2 mM $MgCl_2$, 2 mM NaN_3, 9.25 mM phenylenediamine; and 75% (vol/vol) glycerol] was added to each slide and a coverslip was applied. Coverslips were sealed with nail polish and air dried overnight in the dark. The distance between fluorescently labeled Z-lines was measured directly using a microscope (BX53, Olympus, Waltham, MA) equipped with a fluorescence filter at 40x magnification. Images were captured and the distance between Z-lines of 5 sarcomeres was measured across 10 myofibrils per sample using ImageJ2 software and the average sarcomere length was recorded.

Statistical Analysis

Muscle pH, collagen content, and sarcomere length were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC, v 9.4) for the main effect of finishing system. To evaluate the influence of finishing system on WBSF, cook loss, and postmortem proteolysis samples were subjected to different postmortem aging periods before freezing and data were analyzed as repeated measures using the compound symmetry covariance structure for the main effects of finishing treatment, aging day, and their interaction; peak temperature was included as a covariate for WBSF and cook loss. Consumer and trained sensory data were analyzed in the GLIMMIX procedure of SAS for the main effects of finishing system and panelist was included as a random effect. Least squares means were separated with the PDIFF option. Carcass served as the experimental unit for all assays. Statistical significance was assumed at an alpha level of < 0.05

RESULTS AND DISCUSSION

The influence of finishing system on carcass characteristics, proximate composition, and fatty acid profile of the animals in this study are described by Newton et al. (2024).

Influence of Finishing System on Ultimate pH

Finishing system did not influence ($P = 0.14$; Table 1) the ultimate pH of bison strip loins. Janssen et al. (2021) also reported that finishing system did not influencing the ultimate pH of strip loins from bison heifers. Additionally, two studies comparing beef cattle finished on a forage diet in a grazing system to cattle finished on a concentrate diet in a feedlot system also reported no difference in ultimate muscle pH between finishing treatments (French et al., 2001; Chail et al., 2016), indicating limited influence of diet on muscle pH.

Influence of Finishing Treatment on Sensory Responses

Consumer sensory results are presented in Table 2. Consumers were asked to rate bison samples for liking and intensity of various attributes. Grain-finished steaks had higher overall liking ($P = 0.04$) and flavor liking ($P < 0.01$) ratings indicating panelists preferred the grain-finished steaks compared to grass-finished steaks. Increased flavor liking in grain-finished steaks could be correlated to increased marbling scores in grain-finished carcasses as reported by Newton et al. (2024). Intramuscular fat, or marbling, positively influences sensory traits of meat including flavor, juiciness, and tenderness (Hocquette et al., 2010; Van Elswyk & McNeill, 2014; Frank et al., 2016). Aroma liking was also higher for grain-finished steaks ($P < 0.05$) compared to grass-finished steaks. Koch et al. (1995) concluded bison steaks had increased off-flavors compared to beef. The off-flavors in the bison steaks were described as "intense ammonia, metallic, and gamey flavor" (Koch et al., 1995). Larick et al. (2008) utilized a trained

Table 2. Least square means for the effect of finishing system[1] on subjective meat quality attributes of strip loin steaks from bison bulls rated by a consumer sensory panel

Attribute[2]	GRAIN	GRASS	SEM[3]	*P*-value[4]
Overall liking	27.72	19.59	3.157	0.04
Flavor liking	27.34	14.94	3.262	< 0.01
Aroma liking	16.70	7.72	3.220	0.02
Texture liking	26.56	26.02	3.494	0.89
Toughness intensity	13.70	12.49	1.072	0.31
Juiciness intensity	11.04	14.30	1.226	0.02
Meat Flavor intensity	17.99	19.17	1.082	0.32
Off-flavor intensity	5.16	9.30	0.968	< 0.01

[1]Treatments: GRAIN = bison bulls (n = 98) backgrounded on grass and finished for 130 days with ad libitum access to grass hay, alfalfa, and a corn prior to slaughter. GRASS = bison bulls (n = 98) remained on pasture until slaughter.
[2]Liking ratings were made on a -100 to 100-point labeled affective magnitude scales, with the left most end labeled greatest imaginable disliking and the right most end labeled greatest imaginable liking. Intensity ratings were made on 0-51-point line scales with the left most ends labeled none and the right most end labeled extremely intense for off-flavor.
[3]Standard error of the mean.
[4]Probability of difference among least square means.

sensory panel to compare steaks from bison, *Bos taurus,* and *Bos indicus*. Bison samples revealed more off-flavors and aftertaste compared to both cattle species (Larick et al., 2008). Larick et al. (2008) suggested that flavor differences could be the result of increased polyunsaturated fatty acid (PUFA) content of bison. In the present study off-flavor intensity was increased ($P < 0.01$) for grass-finished steaks compared to grain-finished steaks. Newton et al. (2024) evaluated the steaks from this same study for fatty acid profile and reported in that steaks from grass-finished bison, had increased PUFA concentrations when expressed on a percentage of total lipids. In the present study juiciness intensity was increased ($P = 0.02$) for grass-finished steaks compared to grain-finished steaks. Newton et al. (2024) reported that steaks from grass-finished bison in this study had increased moisture content compared to steaks from grain-finished bison, which may contribute to improvements in juiciness ratings. Finishing treatment did not influence consumer ratings for texture liking ($P = 0.89$), toughness intensity ($P = 0.31$), or meat flavor ($P = 0.32$) intensity. The lack of difference between treatments for toughness intensity is supported by WBSF results that indicate treatments were similar ($P > 0.05$; Figure 1) at 14 d (steaks for the consumer sensory panel were also aged for 14 d). Similarly, Janssen et al. (2021) observed no differences in consumer panel ratings for overall liking, texture liking, toughness intensity, or juiciness intensity of steaks from bison heifers.

Trained sensory panel results are presented in Table 3. Trained panelists detected differences between treatment groups for aroma and flavor intensities. Grass-finished bison steaks had increased ($P < 0.01$) aroma and flavor intensities compared to grain-finished bison steaks. Panelists indicated intense "ammonia, metallic, and gamey flavors" associated with the grass-finished treatment, which may account for the off-flavors detected by the consumer panelists and improved 'liking' rating for grain-finished steaks. Koch et al. (1995) reported that similar off-flavors were detected in bison by a trained sensory panel when comparing bison and beef samples. No treatment differences were detected by trained panelists for juiciness ($P = 0.58$) or toughness ($P = 0.30$) intensity, which is supported by WBSF results as treatments were similar ($P > 0.05$; Figure 1) at 14 d.

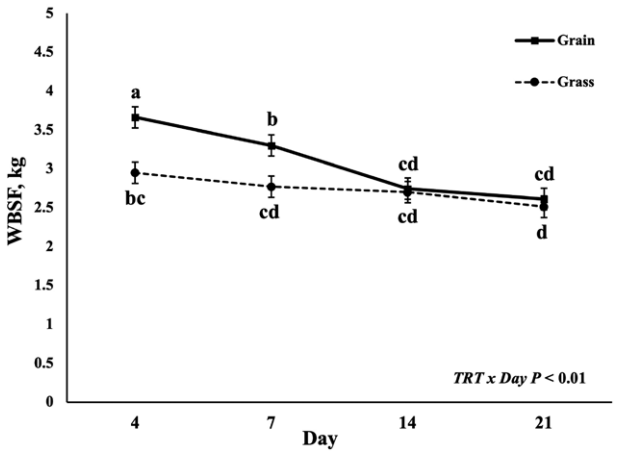

Figure 1. Least squares means for the interaction of finishing system and aging day on Warner-Bratzler shear force of strip loin steaks from grain- or grass-finished bison bulls. [abcd] Means lacking common superscripts differ $P < 0.01$.

Influence of Finishing System on Warner-Bratzler Shear Force and Cook Loss

Warner-Bratzler shear force was affected by the interaction of finishing treatment with aging period ($P < 0.01$; Figure 1). Steaks from the grain-finished bulls became more tender ($P \leq 0.02$) as aging time increased from 4 d to 14 d, whereas WBSF of steaks from grass-finished bulls did not differ ($P \geq 0.10$) during this period. Steaks from grass-finished bulls were more tender ($P \leq 0.01$) than steaks from grain-finished bulls at 4 d and 7 d but treatments were similar ($P \geq 0.61$) at 14 and 21 d. In contrast, Janssen et al. (2021) observed that steaks from grain-finished heifers were more tender than grass-finished steaks and WBSF of steaks from bison heifers in both treatments decreased with postmortem aging. Several studies in beef have also concluded that steaks from grass-fed beef were less tender than grain-finished steaks (Bowling et al., 1977; Brewer & Calkins, 2003; Van Elswyk & McNeill, 2014).

It is unclear why grass-finishing differentially influenced tenderness of bison bulls and heifers, but it is possible that

Table 3. Least square means for the effect of finishing system[1] on subjective meat quality attributes of strip loin steaks from bison bulls rated by a trained sensory panel

Attribute[2]	GRAIN	GRASS	SEM[3]	*P*-value[4]
Aroma intensity	91.41	102.79	2.607	< 0.01
Flavor intensity	81.14	100.17	2.356	< 0.01
Toughness intensity	57.11	60.07	2.866	0.30
Juiciness intensity	65.66	67.36	3.084	0.58

[1]Treatments: GRAIN = bison bulls (n = 98) backgrounded on grass and finished for 130 days with ad libitum access to grass hay, alfalfa, and a corn prior to slaughter. GRASS = bison bulls (n = 98) remained on pasture until slaughter.
[2]Evaluated on an anchored unmarked line scale with the far-left point indicating extremely tender, extremely juicy, no aroma, or extremely bland bison flavor and the far-right point representing extremely tough, extremely dry, extreme aroma, or extremely intense bison flavor.
[3]Standard error of the mean.
[4]Probability of difference among least square means.

this is a result of proteolysis early postmortem. Steaks from grass-finished bulls had less ($P < 0.01$; Table 1) intact desmin compared to steaks from grain-finished bulls. This could be one possible explanation for the differences in WBSF results between this study and Janssen et al. (2021) however proteolysis was not evaluated by Janssen et al. (2021). Muscle protein turnover and rate of postmortem tenderization is highly related to calpastatin activity (Goll et al., 1998). Higher calpastatin activity decreases the rate of muscle protein turnover and is correlated with increased rate of skeletal muscle growth (Goll et al., 1998). Calpastatin is the inhibitor of calpain and is hence associated with a lower rate of postmortem tenderization (Goll et al., 1998). Calpastatin activity has not been evaluated in bison but differences in intact desmin and WBSF between treatments suggest that grain-finished bulls had increased calpastatin activity compared to grass-finished bulls.

Tenderness of meat improves during postmortem storage and has been heavily investigated in beef (Goll et al., 1964; Calkins & Seideman, 1988; Koohmaraie et al., 1988). Tenderization occurs relatively rapidly from 3 to 7 d postmortem and then slows with minimal improvements in tenderness of beef loins reported after 7 to 10 d (Parrish Jr et al., 1973; Huff-Lonergan et al., 1996). However, research investigating tenderization in bison is limited. Grain-finished bison steaks in the current study as well as Janssen et al. (2021) appear to follow similar postmortem aging patterns, whereas steaks from grass-finished bulls in the present study were initially very tender and did not experience a marked improvement over time.

In beef cattle, tenderness has been identified as a primary trait that impacts the overall eating experience (Savell et al., 1987, 1999; Miller et al., 1995). The role and value of this palatability trait has not been well characterized for bison consumers, however understanding the influence of different finishing systems on bison tenderness can support future work on bison palatability and possible marketing opportunities for bison products. For example, beef products that meet the American Society for Testing and Materials (ASTM-International, 2011) minimum tenderness threshold value can apply tenderness claims to their products. "USDA Tender" (WBSF ≤ 4.4 kg) or "USDA Very Tender" (WBSF ≤ 3.9 kg). Although these standards were developed for beef, bison steaks from both finishing systems in the present study were below 3.9 kg at 4 d postmortem, indicating a very tender product can be produced with minimal aging from bison bulls finished in either system.

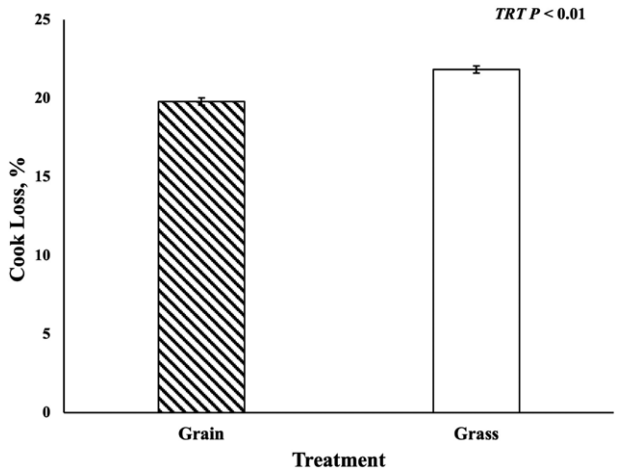

Figure 2. Least square means for the effect of finishing system on cook loss percentage of strip loin steaks from grain- or grass-finished bison bulls. [ab] Means lacking common superscripts differ $P < 0.01$.

No treatment by aging day interaction was observed for cook loss ($P = 0.88$). Steaks from grass-finished bison bulls had greater cook loss compared to steaks from grain-finished bison bulls ($P < 0.01$; Figure 2); however, aging day did not influence ($P = 0.12$) cook loss. These results are supported by the proximate analyses data for these same animals reported by Newton et al. (2024) indicating that steaks from grass-finished bison bulls had increased moisture content compared to grain-finished steaks (Newton et al., 2024). The increased moisture content of grass-finished steaks is likely contributing to increased cook loss percentage. Similar results were observed by Janssen et al. (2021) with steaks from grass-finished bison heifers yielding more cook loss compared to steaks from grain-finished heifers.

Influence of Finishing System on Postmortem Proteolysis

There was no treatment by aging day interaction for proteolysis of desmin ($P > 0.05$). Steaks from grass-finished bulls had less ($P < 0.01$; Table 1) intact desmin compared to steaks from grain-finished bison bulls indicating more postmortem degradation. These data are supported by the WBSF results that indicate grass-finished steaks are more tender at 4- and 7-d postmortem (Figure 1). Desmin is an intermediate filament protein and is important in maintaining the structural integrity of muscle cells (Huff-Lonergan et al., 1996). Desmin

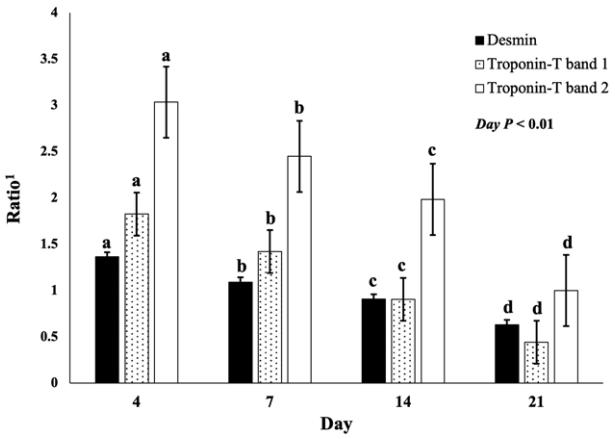

Figure 3. Least square means for the effect of aging day on proteolysis of intact desmin (55 kDa) and intact troponin-T (band 1; 35 kDa and band 2; 33 kDa) of strip loin steaks from grain- or grass-finished bison bulls. [1]Expressed as a ratio to an internal standard. [abcd] Within protein/band means lacking common superscripts differ among days $P < 0.01$.

is located in the costamere, which is a structure located near the surface of muscle cells that functions to connect the myofibril to the sarcolemma (Craig & Pardo, 1983; Taylor et al., 1995). Research has identified that the costameres are extensively degraded within the first 24 h postmortem (Taylor et al., 1995). Desmin is routinely evaluated in studies regarding proteolysis of muscle fibers. To date no research has investigated postmortem protein degradation in bison or the influence of different finishing systems on this process. Additionally, the amount of intact desmin decreased over the aging period ($P < 0.01$; Figure 3), which was expected as desmin typically degrades during postmortem storage in other species (Koohmaraie et al., 1984; Huff-Lonergan et al., 1996).

There was no treatment by aging day interaction for proteolysis of intact troponin-T (band 1 or band 2, 35 kDa and 33 kDa, respectively; $P > 0.05$). Further, finishing treatment did not influence disappearance of band 1 ($P = 0.91$) or band 2 ($P = 0.10$; Table 1) of intact troponin-T. However, the amount of intact troponin-T at band 1 and 2 decreased over the aging period ($P < 0.01$; Figure 3). Troponin-T is a regulatory protein responsible for regulating contraction and research has concluded that this protein plays a very minimal role in maintaining myofibril structure (Huff-Lonergan et al., 1996; Koohmaraie et al., 2002; Weaver et al., 2008). While degradation of troponin-T will not cause the physical disruption of myofibers that is needed for tenderness development it is commonly used as an indicator of tenderization (Huff-Lonergan et al., 1996, 2010; Koohmaraie et al., 2002). Decreases in intact proteins, while never characterized in bison, was expected as myofibrillar proteins typically degrade during postmortem storage (Koohmaraie et al., 1984; Huff-Lonergan et al. 1996; Weaver et al., 2008).

Influence of Finishing System on Collagen Content and Solubility

Finishing system did not influence insoluble ($P = 0.39$), heat soluble ($P = 0.31$), or total ($P = 0.19$) collagen content of steaks from grain- and grass-finished bison carcasses. Studies investigating the influence of finishing system on collagen content in bison are lacking; however, one study in beef concluded that total collagen content and heat soluble collagen were decreased in *longissimus dorsi* samples of corn-fed steers compared to pasture fed steers (Archile-Contreras et al., 2010). While it was hypothesized that grain-finished bison would have decreased collagen content it is possible that finishing systems influence bison differently than beef.

Influence of Finishing System on Sarcomere Length

Finishing system did not influence ($P = 0.45$; Table 1) sarcomere length of bison strip loin samples. The length of a sarcomere is measured as the distance between two Z-lines (Aberle et al., 2012) and in resting muscle, the average sarcomere length is 2.5 µm (Cross et al., 1981; Weaver et al., 2009). Biochemical changes caused by proteolysis and postmortem metabolism are connected with sarcomere length in a very complex manner (Ertbjerg & Puolanne, 2017). Throughout a carcass, tension placed on individual muscle will vary resulting in variation in sarcomere length (Rhee et al., 2004). However, it does not appear that finishing system influences postmortem metabolism or muscle tension in bison carcasses to a degree that influenced sarcomere length.

To date, there is only one other study investigating sarcomere length of bison. Mickelson and Claus (2020) evaluated the impact of an early postmortem vascular rinse and chill system (Rinse and Chill®) on tenderness attributes of muscles from bison bulls and reported no difference in sarcomere length compared to conventional chilling. Sarcomere lengths in the present study were shorter than the sarcomere lengths reported by Mickelson and Claus (2020). Differences in sarcomere lengths between the two studies may be related to differences in fat thickness of carcasses, which could influence the rate of chilling and shortening of muscles. However, similar to results in beef (Rhee et al., 2004), there was little variation in the sarcomere length of the longissimus muscle.

CONCLUSIONS

This study indicates that sensory and tenderness of steaks from bison bulls are influenced by finishing system with grain-finished animals producing steaks that were more favorably rated for flavor, aroma, and overall liking by a consumer panel. The consumer panel indicated that steaks from grass-finished bulls had greater juiciness intensity, however they also detected more off-flavor intensity, which likely contributed to less favorable overall liking compared to grain-finished. The trained sensory panel also detected increased aroma and flavor intensity from grass-finished samples, and identified specific off-flavors as ammonia, metallic, and gamey flavors. The increased flavor and aroma intensities coupled with more intense off-flavors of the grass-finished steaks are likely contributing to the less favorable overall liking rating by consumers. While steaks from grass-finished bulls were objectively more tender at 4 and 7 d postmortem, these differences did not persist, and by 14 d postmortem no differences in tenderness were detectable by WBSF, consumer, or trained sensory panels. This study provides some of the first evidence that postmortem proteolysis is a primary mechanism regulating tenderization of bison and demonstrates that proteolytic degradation of bison is differentially influenced by finishing system.

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Author Contributions

Lydia M. O'Sullivan (Formal analysis, Investigation, Validation, Visualization, Writing—original draft), Clay J. Newton (Formal analysis, Investigation, Writing—review & editing), Keith Underwood (Investigation, Writing—review & editing), Judson Grubbs (Conceptualization, Investigation, Resources, Supervision, Writing—review & editing), Christina Bakker (Investigation, Writing—review & editing), Thu Dinh (Investigation, Methodology, Resources, Writing—review & editing), Carter Kruse (Conceptualization, Methodology, Project administration, Resources, Writing—review & editing), and Amanda Blair (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing—review & editing)

Conflict of Interest Statement

No potential conflict of interest is reported by L.M.O, C.J.N, K.R.U., J.K.G., C.E.B., T.D. or A.D.B. Turner Institute of Ecoagriculture provided funding and C.K. was involved in the conceptualization of the study but had no role in the collection, analysis or interpretation of the data.

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