Meat and Muscle Biology™

Expression of beef- versus dairy-type in crossbred beef × dairy cattle does not impact shape, eating quality, or color of strip loin steaks[1]

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Abstract: Phenotypic expression of dairy influence often carries negative implications in beef production; thus, considerable variation in expression of beef- versus dairy-type might adversely affect value of crossbred beef × dairy cattle. This study evaluated effects of phenotype in crossbred beef × dairy cattle, specifically that associated with beef- versus dairy-type, on meat quality. Effects were blocked within commercial feedlot pens because cattle within a pen were contemporaries for sex, age, management, and source. On their harvest date, 592 Angus or [Simmental × Angus] × Holstein cattle from 9 pens were assessed by 3 expert evaluators. Scores for muscling and frame size were used to categorize and subset cattle in a pen into 4 phenotype groups: (1) fully dairy-type, (2) partially dairy-type, (3) partially beef-type, and (4) fully beef-type. Strip loin steaks were obtained from selected cattle ($n = 82$ to 84 per group) and evaluated for descriptive sensory attributes, shear force, pH, color at retail display, steak dimensions, muscle fiber type, and fatty acid composition. Data were tested for fixed effects of phenotype group with random effects of pen. Despite distinct expression of visual beef- versus dairy-type among cattle sampled, phenotype groups were largely not different ($P > 0.05$) in shape, sensory attributes, color, or biochemical properties of strip loin steaks. Other body regions, separate from the loin, were likely responsible for differences in live animal muscling. Additional research is needed on effects of sire breed, individual sire, and management strategies on meat quality in beef × dairy crossbreds. Complementarity of beef breeds and sires to produce more profitable beef-type cattle from the beef × dairy mating system should not be expected to negatively influence meat quality. Marketing programs rooted in production of consistent and premium products may benefit from including beef from beef × dairy crossbreds.

Introduction

A major proportion of dairy-influenced fed cattle slaughtered in the United States has recently shifted towards beef × dairy crossbreds (and away from straightbred Holsteins) because of growth in crossbreeding beef breed sires to dairy breed cows, commonly termed "beef-on-dairy" (McWhorter et al., 2020; NAAB, 2021). Mating cattle breeds that are highly unrelated has been reported to increase heterozygosity and uniformity in resulting progeny for a variety of traits when compared to mating breeds that are more closely related (Weaber and Spangler, 2013). Gregory et al. (1995) demonstrated that crossbred cattle populations exhibit similar coefficients of variation for carcass and meat traits compared to their contributing parental purebreds. According to these principles, the beef × dairy crossbred population should exhibit similar, if not greater, consistency in many traits, including those related to meat production, when compared to the population of their contributing parent breeds.

University extension programs, genetics suppliers, feedlot operators, and beef packers have recently voiced concerns about considerable variation in visual expression of phenotype, or beef- versus dairy-type, in crossbred beef × dairy cattle, even within contemporary groups (Halfman and Sterry, 2019; Jaborek, 2021). Expression of dairy-type has often carried negative implications in beef production because of its association with inferior red meat yield, excessive prevalence of liver abscesses, dark colored meat, and irregularly shaped beef products (Faustman and Cassens, 1991; Schaefer, 2005; Amachawadi and Nagaraja, 2016). As such, many US Department of Agriculture (USDA) certified programs explicitly exclude animals with phenotypic expression of dairy influence (USDA Agricultural Marketing Service, 2021). Through complementarity of beef and dairy breeds, beef × dairy crossbreds may not exhibit the full extent of negative consequences associated with dairy influence in beef production (Weaber and Spangler, 2013; Berry et al., 2018). Variation in expression of beef- versus dairy-type within beef × dairy crossbreds, however, may contribute to meaningful differences that influence cattle value.

Beef from dairy-influenced cattle, including beef × dairy crossbreds, has demonstrated greater tenderness and flavor to beef from cattle without influence of dairy breeding, perhaps because of a difference between breed types in muscle fiber type composition (O'Quinn et al., 2016; Picard and Gagaoua, 2020; Frink, 2021). Moreover, Frink (2021) showed that steaks from beef × dairy crossbreds were more stable in color at retail display and more symmetrical in shape than steaks from straightbred dairy cattle. The positive influence of dairy breeding on eating quality traits in beef × dairy crossbreds, without a sacrifice to color or steak shape, may prove efficacious for the inclusion of products from beef × dairy crossbreds into quality-driven branded programs if the product is deemed consistent. Variation in expression of beef- versus dairy-type might suggest inconsistency in expected performance of beef products, such that beef from dairy-type crossbreds might perform differently than beef from beef-type crossbreds. A similar concept was shown by Sherbeck et al. (1996) in crossbred Brahman × Hereford cattle, where expression of *Bos indicus* phenotype detrimentally affected eating quality attributes like tenderness, even within cattle of equal Brahman breeding. Thus, this study evaluated the influence of phenotype, specifically that associated with beef- versus dairy-type, in crossbred beef × dairy cattle on meat traits, including steak shape, eating quality, and color at retail display, and biochemical factors that influence these traits, including muscle fiber type and fatty acid composition.

Materials and Methods

Animal handling procedures complied with standards published in the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (Federation of Animal Science Societies, 2020).

Cattle description

Crossbred beef × dairy cattle were placed at a commercial feedlot in southwest Kansas between July and September 2020. When available, cattle sire and dam identity was provided by a commercial genetics company and a dairy recordkeeping system. Cattle were resulting progeny of approximately 20 different Angus or Simmental × Angus sires and a contemporary set of Holstein cows from 3 large commercial dairies (greater than 5,000 cows each) under the same ownership. To a degree, such variability among sires used to breed a contemporary set of cows minimized individual effects of sire and dam in the study. Cattle arrived at the feedlot in 9 shipments (approximately 70 cattle each), with cattle from each shipment being of the same sex (6 groups of steers, 3 groups of heifers), same calf ranch source, similar calf management, and similar age (born within 30 d of each other). Cattle within a shipment were assigned to the same pen for the duration of the finishing period, such that cattle within a pen were fed the same diet and endured the same weather events. Cattle within a pen were harvested at an endpoint of constant days on feed, which was determined from a proprietary endpoint projection system (Performance Cattle Company LLC, Amarillo, TX) using body weight and linear body measurements. Between pens, a total of 592 cattle were harvested at an average of 180 days on feed (range 146 to 213 days on feed). Because cattle within a pen were contemporaries for sex, age, management, and source, the blocking effect of pen was used to assess study effects of interest (beef-versus dairy-type).

Visual assessment

Five experienced livestock evaluators (cumulative evaluation experience of greater than 80 years) collaboratively developed a scoring system for the beef × dairy crossbred population. Muscling and frame size

were traits used to characterize expression of beef-versus dairy-type, which was described as the visual phenotype in this study. Muscling was defined as thickness in relation to skeletal size (volume of muscle; muscle-to-bone ratio) and evaluated independent from degree of fatness. Muscling scores were anchored and assigned descriptions: 1 = narrow, light muscled, representative of dairy-type muscling, and 9 = thick, heavy muscled, representative of beef-type muscling. Frame size was defined as skeletal size in relation to age. Frame size scores were anchored and assigned descriptions: 1 = large skeletal size, representative of dairy-type frame, and 9 = moderate skeletal size, representative of beef-type frame.

Definitions for muscling and frame size employed in this study were similar to definitions provided for the assignment of USDA grades in feeder cattle (USDA, 2000). Despite differences in assessment of slaughter cattle compared to feeder cattle, the application of muscling in this study was similar to USDA (2000); however, the application of frame size in this study was different from USDA (2000). In the assignment of USDA feeder cattle grades, frame size is explicitly evaluated independent from muscling and is used to predict carcass fatness and the ability to achieve a US Choice grade (USDA, 2000). At equal muscling, larger framed animals require a greater body weight to achieve an equal level of fatness as smaller framed animals (Tatum et al., 1986a). During the development of a scoring system to assess beef- versus dairy-type in this study, evaluators noted a relatively strong correlation between muscling and frame size in the beef × dairy crossbred population (especially those cattle influenced by the Holstein breed). It was suggested that larger framed beef × dairy cattle might be similar in weight to smaller framed beef × dairy cattle because of differences in muscle. Hence, because cattle in this study were evaluated at a constant age, the application of frame size was strictly related to skeletal size and independent from weight, unlike the application of frame size described in USDA (2000).

A panel of 3 expert evaluators (participants in development of the scoring system) scored cattle within each pen on their date of harvest. For calibration purposes, evaluators verbally discussed and agreed upon a muscling score and frame size score for each of the first 10 cattle processed in a pen. After calibration, each evaluator independently assessed muscling and frame size for each animal in a pen. Muscling and frame size scores, averaged between panel members for each animal, were summed to develop a visual phenotype score: 2 = light muscled, large framed,

representative of dairy-type; and 18 = heavy muscled, moderate framed, representative of beef-type. Cattle that were scored 5 or more units different for muscling and frame size were removed from the study because their phenotype was not representative of study objectives within the Holstein-influenced crossbred population.

Sample selection

Visual phenotype scores were used to categorize and identify a subset of cattle from each pen with the greatest variability in beef- versus dairy-type for collection of meat sample (Figure 1). Mean and standard deviation of visual phenotype scores were calculated for each pen. Within a pen, cattle were categorized into 4 phenotype groups: (1) fully dairy-type, with a visual phenotype score less than 1 negative standard deviation from the mean; (2) partially dairy-type, with a visual phenotype score greater than 1 negative standard deviation from the mean but less than the mean; (3) partially beef-type, with a visual phenotype score greater than the mean but less than 1 positive standard deviation from the mean; and (4) fully beef-type, with a visual phenotype score greater than 1 positive standard deviation from the mean. All cattle from either the fully dairy-type group or the fully beef-type group—whichever had less—were selected for inclusion in the study. Cattle from each of the remaining 3 phenotype groups were randomly selected in a quantity equal to the lesser number of cattle in the fully dairy-type group or the fully beef-type group. Cattle were selected within phenotype groups to minimize individual sire effects as much as possible, such that a certain phenotype group was not comprised of a single sire more than another. A total of 333 cattle ($n = 82$ to 84 per phenotype group; $n_{[n]} = 8$ to 11 per phenotype group within each of 9 pens) were selected for inclusion in the study.

Harvest and sample collection

All cattle in a pen were transported to a commercial harvest facility operating under USDA federal inspection and harvested on the same day as visual assessment. Tag transfer was performed to maintain live animal identity with carcass identity. Carcasses were electrically stimulated and then chilled for approximately 30 h. Cattle were selected, according to their visual phenotype score, at the time of carcass grading. Selected carcasses were assigned an experimental identification number. An approximately 6.4-cm-long section of anterior strip loin (Institutional Meat Purchase

Figure 1. Crossbred beef × dairy steers that represent distinct phenotype groups: (A) fully dairy-type, (B) partially dairy-type, (C) partially beef-type, and (D) fully beef-type.

Specifications #180; NAMP, 2010) was removed from both sides of each selected carcass. From cattle ($n_1 = 10$ to 17 per phenotype group) in the first 2 pens harvested, the remainder of the whole strip loin (untrimmed) from one carcass side was collected for whole strip loin steak dimension analysis. Strip loin sections (and whole strip loins) from each carcass were transported at 0°C to 4°C to the Gordon W. Davis Meat Laboratory (Lubbock, TX).

Sample processing and pH determination

Strip loin sections were processed between 60 and 96 h postmortem. An approximately 1.3-cm-thick slice was cut from the posterior end of one strip loin section from each carcass and trimmed, such that only *longissimus lumborum* remained. The lateral third of each slice was allocated for immunohistochemical analysis and pH determination. Remaining identified strip loin sections were separately vacuum packaged and placed in dark storage at 2°C to 4°C.

From each slice designated for immunohistochemical analysis, samples (prepared in duplicate to minimize sample loss from cryodamage during freezing) were excised parallel to muscle fiber orientation and relatively free from intramuscular fat. Each sample was embedded in optimum cutting temperature clear sectioning compound (VWR International, Radnor, PA) in a mold and immediately frozen in a 2-methyl-butane bath chilled with dry ice. Frozen molds were identified and stored at −80°C for further analysis.

From remaining tissue of each slice, pH was determined in duplicate. Two grams of sample was added to 18 mL of double distilled, deionized water in a 50 mL conical tube and homogenized (Model 225318 VirTisShear, The VirTis Co., Inc., Gardiner, NY). A calibrated pH meter fitted with a glass electrode (Model 14703; Denver Instrument, Bohemia, NY) was used to determine pH, and values were averaged between duplicate samples.

Steak fabrication and imaging

At 14 d postmortem, a strip loin section from each carcass was fabricated, in anterior to posterior direction, to obtain a 2.54-cm-thick steak designated for shear force (steak number 1) and a 2.54-cm-thick steak designated for sensory evaluation (steak number 2). From cattle ($n_2 = 38$ to 40 per phenotype group) in 4 pens across 2 different harvest times, the alternate strip loin section (not fabricated into shear force or sensory steaks) was fabricated into a 2.54-cm-thick steak designated for retail color display. Approximately 150 g of tissue (*longissimus lumborum* only) remaining from a strip loin section of each carcass was allocated for determination of fatty acid composition. External fat on all steaks was trimmed to approximately 0.3 cm thick. Steaks designated for shear force and sensory evaluation were imaged before packaging using a digital single-lens reflex camera (Model D7100, Nikon Corp., Ayutthaya, Thailand) equipped with a fixed-zoom lens (Model DXSWMVREDIF, Nikon Corp.)

mounted to a tripod directly above each steak. A ruler with known measurements was placed adjacent to each steak at a level of approximately 2.54 cm (steak thickness) in each image. Steaks designated for shear force and sensory evaluation were vacuum packaged, frozen in single layers, and stored at −20°C. Tissue allocated for determination of fatty acid composition was vacuum packaged and stored at −80°C. Steaks designated for retail color display remained fresh for immediate retail display.

At 28 d postmortem, whole strip loins (with anterior sections removed) were fabricated into 2.54-cm-thick steaks in an anterior (steak number 3) to posterior (steak number varied depending on strip loin length) direction and identified with their steak number. Steaks remained untrimmed and were imaged using the same methods described for steak numbers 1 and 2. Steaks imaged for whole strip loin steak dimension analysis were not retained for further analysis.

Retail color display

Color of strip loin steaks was assessed according to AMSA (2012). After fabrication, steaks assigned to retail color display were placed (cut surface side up) on soaker pads in white 4S Styrofoam trays and over-wrapped with polyvinyl chloride film (MAPAC L; oxygen transmission rate $= 21,700$ cm^3 of O^2 per m^2 per 24 h; Borden Packaging and Industrial Products, North Andover, MA). Trays were placed under continuous fluorescent lighting (mean: 1,900 lux, standard deviation: 297 lux; high-output bulbs with a color temperature of 3,500 K and a color rendering index of 70) at 1.8°C (standard deviation: 2.8°C) in coffin-style retail cases.

Color was evaluated when steaks were placed in the case (0 h) and every subsequent 12 h for 144 h. A 12-member panel was trained during 3 sessions before color evaluations began to identify color attributes in study-representative samples. Panelists were required to achieve a total error score less than 70 on the Farnsworth-Munsell 100-Hue Test (X-Rite, Grand Rapids, MI) on their first attempt to qualify for participation in the study. At each evaluation timepoint, 6 panelists evaluated the predominant lean color (at least 12.9 cm^2 of contiguous lean) of each steak for redness and brightness, as well as external fat color and percent lean discoloration, on an anchored, continuous 100-point line scale. Panelists recorded their responses on a digital survey (Qualtrics Surveys, Provo, UT) using a tablet (iPad, Apple, Inc., Cupertino, CA). Responses were averaged between panelists for each sample.

At each color evaluation timepoint, lean color was objectively assessed using a spectrophotometer (MiniScan XE Plus, Model MSXP-4500C, HunterLab, Reston, VA) with Illuminant A, a 10° observer angle, and a 2.54 cm aperture. The spectrophotometer was calibrated using black and white tiles before measurements were taken at each timepoint. Measurements of $L*$ (black to white), $a*$ (green to red), and $b*$ (blue to yellow) were averaged between 3 different locations on each steak at each timepoint.

Steak dimensions

Digital images of strip loin steaks were processed using an image analysis software (Fiji Image J) capable of measuring individual pixel size. A line of 7.6 cm (distance known from the ruler placed in each image) was measured on the image, and its corresponding length in pixels was entered into the scaling feature of the software. From steak numbers 1 and 2, *longissimus* muscle of each steak was measured for area, length (maximum), and width at 50% and 88% of length (from medial to lateral direction). From steaks fabricated from whole strip loins, *longissimus lumborum* and *gluteus medius* (when present) were measured together for the same measurements taken on steak numbers 1 and 2. Additionally, from steaks of whole strip loins, subcutaneous fat depth at 75% of length (from medial to lateral direction) was measured. To reduce technician measurement error, images of steak numbers 1 and 2 were measured by 2 different technicians, and images of steaks fabricated from whole strip loins were measured by 3 different technicians. Measurements were averaged between technicians. Lateral steak angle (in angle degrees) from width at 50% to width at 88% was calculated using the equation below, where $L =$ length, $W_{50} =$ width at 50%, and $W_{88} =$ width at 88%.

$$Lateral\ steak\ angle = \frac{\left(sin^{-1}\frac{(0.88-0.50)\times L}{\sqrt{(W_{50}-W_{88})^2+((0.88-0.50)\times L)^2}}\right)\times 180}{\pi}$$

Steak cooking procedures

Steaks for trained sensory evaluation and shear force were tempered for 24 to 48 h at 2°C to an internal temperature of 0°C to 4°C at the time of cooking. Groups of steaks (4 at a time for sensory analysis; 6 at a time for shear force analysis) were singly layered and cooked on a grill grate (Model SCC WE 61 E; Rational, Landsberg am Lech, Germany) centrally located in a combi-oven (Model SCC WE 61 E; Rational) at 204°C, 0% relative humidity, and default

fan speed. Steak temperature was monitored in the cooking process using an oven core temperature probe (Model SCC WE 61 E; Rational) placed in the geometric center of a steak representative of the cooking group for size and shape. Steaks were removed from the oven to target a peak internal temperature of 71°C. Peak internal temperature was measured in the geometric center of each steak using a calibrated type K thermocouple thermometer (AccuTuff 340, model 34040, Cooper-Atkins Corporation, Middlefield, CT) and recorded.

Trained sensory evaluation

Trained sensory evaluation of strip loin steaks was conducted at Texas Tech University. Panelists were trained to identify and quantify attributes associated with beef according to the lexicon developed by Adhikari et al. (2011) and the *Research Guidelines for Cookery, Sensory Evaluation, and Instrumental Tenderness Measurements of Meat* (AMSA, 2016; Table 1). A continuous 100-point line scale (0 = tough, dry, not present; 100 = tender, juicy, extremely intense) was adapted and used to quantify attributes: tenderness, juiciness, beef flavor identity, browned, roasted, metallic, fat-like, sour, oxidized, liver-like,

umami, and buttery. Upon training, discriminative triangle tests were used to qualify a pool of 12 trained panelists for sensory evaluation.

After peak internal steak temperature was measured, each steak was held on a cooling rack in an electric, insulated food transport box (Model UPCH400110, Cambro Manufacturing Company, Huntington Beach, CA) maintained at 55°C until serving. Cooked steaks were served to panelists within 15 min of their removal from the oven. Each of 28 panel sessions consisted of 3 steaks from each phenotype group (12 steaks total per session). Moreover, steaks from cattle within the same pen were served within a panel session to maintain the block effect of the pen. Steaks from each phenotype group were fed in a random and different order for each panel session. No panelist served on more than 2 panel sessions per day, and a minimum of 1 h existed between the end of a session and the start of another. Panelists were seated in individual cubicles in a dark room under red incandescent lighting. Distilled water, apple juice, and unsalted saltine crackers were supplied as palate cleansers. Immediately before serving, cooked steaks were trimmed of any remaining external fat and connective tissue and cut into cubes (1 cm × 1 cm × steak thickness). Each panelist received 3 cubes for evaluation.

Table 1. Sensory attributes, descriptors, and anchors on a 100-point continuous line scale[1] used for trained sensory analysis adapted from Adhikari et al. (2011)

Attribute	Description	Anchor
Tenderness	Amount of force required to masticate a piece of meat	Beef shank cooked to 71°C = 45 Select strip steak cooked to 71°C = 60 Tenderloin steak cooked to 71°C = 95
Juiciness	Amount of juice released from the product during mastication (average of initial first 5 chews and sustained last 5 chews)	Select strip steak cooked to 82°C = 35 Select strip steak cooked to 58°C = 75
Beef flavor identity	Flavor associated with cooked beef; basic meaty flavor of unseasoned beef broth	Swanson's beef broth = 35 80% lean ground beef = 45 Beef brisket cooked to 71°C = 75
Browned	Flavor associated with grilled beef; caramelized	Beef suet (broiled) = 60
Roasted	Flavor associated with roasted beef	80% lean ground chuck = 70
Metallic	Impression of slightly oxidized metal, such as iron, copper, and silver spoons	0.10% potassium chloride solution = 10 Select strip steak = 30 Dole canned pineapple juice = 40
Fat-like	Aromatics associated with cooked animal fat	Hillshire Farms Lit'l beef smokies = 45 Beef suet = 80
Umami	Flat, salty, somewhat brothy; taste of glutamate, salts of amino acids and other molecules called nucleotides	0.035% accent flavor enhancer solution = 50 (flavor)
Sour	Fundamental taste factor associated with citric acid	0.015% citric acid solution = 10 0.050% citric acid solution = 25
Oxidized	Aromatics commonly associated with oxidized fat and oils; cardboard, painty, varnish, and fishy	Microwaved Wesson vegetable oil (3 min at high) = 45 Microwaved Wesson vegetable oil (5 min at high) = 60
Liver-like	Aromatics associated with cooked organ meat/liver	Beef liver (broiled) = 50
Buttery	Sweet, dairy-like aromatic associated with natural butter	Land O'Lakes unsalted butter tasted = 40 (flavor and aroma)

[1]Attributes were scored using a 100-point scale: 0 = very tough, very dry, and not present; 100 = very tender, very juicy, and very intense.

A warm-up sample representative of the study sample (beef × dairy strip loin steak cooked using the same procedures) was independently evaluated by each panelist, and attributes of this sample were verbally discussed by the project leader before each panel as an additional method to calibrate panelists. Study samples were evaluated every 3.5 to 4 min by 6 panelists per session. Panelist responses were recorded on an electronic ballot generated by an online survey software (Qualtrics Surveys) using a tablet (iPad, Apple, Inc.). Intensity ratings for each attribute were averaged among panelists for each sample.

Shear force

Strip loin steaks assigned to shear force from cattle in the same pen were sheared on the same day to maintain the block effect of the pen. Warner-Bratzler shear force (WBSF) and slice shear force (SSF) measurements were obtained from every steak using procedures described by Lorenzen et al. (2010). Steaks were cooked in groups of similar weight, size, and shape. Within 1 to 2 min of recording peak internal temperature, the lateral end of each cooked steak was squared, and a slice (1 cm thick × 5 cm long) was removed parallel to muscle fibers. This slice was sheared perpendicular to muscle fibers, using an SSF machine (Tallgrass Solutions, Inc., Manhattan, KS) equipped with a flat, blunt-end blade (crosshead speed: 500 mm/min, load capacity: 50 kg), resulting in a single peak SSF measurement for each steak. Remaining steak portions were equilibrated to room temperature (22°C) or below, and 4 to 6 cores (1.2 cm diameter) were removed parallel to muscle fibers. Each core was sheared perpendicular to muscle fibers using a WBSF machine (Tallgrass Solutions, Inc.) fitted with a Warner-Bratzler shear head (crosshead speed: 225 mm/min, load cell capacity: 50 kg). Peak shear force of each core was recorded, and resulting values were averaged to obtain a single WBSF measurement for each steak.

Muscle fiber type determination

Muscle fiber cross-sectional area and myosin heavy chain (MHC) isoforms of *longissimus lumborum* muscle were determined by procedures similar to Hergenreder et al. (2016). Samples embedded in frozen section compound were removed from −80°C and thawed at −20°C approximately 24 h before sectioning. After removing molds, 10-μm-thick cross-sections were cut perpendicular to the muscle fibers at −20°C using a Leica CM1950 cryostat (Leica Biosystems, Deer Park, IL). Five sections per sample were mounted onto positively charged glass slides (Superfrost Plus, VWR International). Slides were stored at −20°C.

Immunohistochemical staining began with thawing slides to 22°C and outlining each slide with a PAP pen (VWR International). Cross-sections were fixed in 4% paraformaldehyde in phosphate-buffered saline (PBS; ThermoFisher Scientific, Waltham, MA) at pH 7.4 for 10 min at 22°C. Slides were washed 3 times for 5 min each in fresh PBS at pH 7.4. Blocking solution consisted of 5% horse serum (Gibco, Waltham, MA), 2% bovine serum albumin (MP Biomedical, Solon, OH), and 0.2% Triton × −100 (Fisher Scientific, Waltham, MA) in PBS at pH 7.4; 400 μL of blocking solution was added to each slide and incubated for 30 min at 22°C to prevent nonspecific antibody binding.

Primary antibody solution consisted of blocking solution and 1:100 alpha dystrophin, rabbit polyclonal (Thermo Scientific, Waltham, MA); 1:100 anti-MHC-Type-I, mouse IgG2b (BAD5; Developmental Studies Hybridoma Bank, University of Iowa, Iowa City, IA); 1:75 anti-MHC, mouse IgG1 (BF-35; DSHB); 400 μL of primary antibody solution was added to each slide and incubated for 1 h at 22°C. Slides were washed 3 times for 5 min each in fresh PBS at pH 7.4. Secondary antibody solution consisted of blocking solution and 1:1,000 goat anti-rabbit, IgG, Alexa-Flour 488 (Invitrogen); 1:1,000 goat anti-mouse, IgG2b, Alexa-Flour 546 (Invitrogen); 1:1,000 goat anti-mouse, IgG1, Alexa-Flour 633 (Invitrogen); 400 μL of secondary antibody solution was added to each slide in the dark before incubation for 30 min at 22°C. Slides were washed 3 times for 5 min each in fresh PBS. Slides were covered with 4 drops of ProLong Gold with DAPI mounting media (Life Technologies, Carlsbad, CA) and thin glass coverslips (VWR International). Slides were cured for a minimum 24 h at 4°C in the dark.

All slides were sealed and imaged within 48 h of curing using 200× magnification of an inverted fluorescence microscope (Nikon Eclipse, Ti-E; Nikon Instruments, Inc., Mellville, NY) with an ultraviolet light source (Intensilight C-HGFIE; Nikon Instruments, Inc.) and a CoolSNAP ES2 monochrome camera (Teledyne Photometrics, Tucson, AZ). Images were artificially colored and analyzed using NIS-Elements imaging software (Nikon Instruments, Inc.). Five independent images were captured from cryosections of each slide. All MHC Type-I, Type-IIA, and Type-IIX muscle fibers were counted and measured for cross-sectional area. Images deemed unacceptable in quality, primarily because of cryodamage to sample, were not counted. Average cross-sectional area and average

proportion of cross-sectional area of each MHC isoform were calculated for each sample.

Fatty acid composition

Frozen tissue (*longissimus lumborum* muscle; approximately 150 g) designated for determination of fatty acid composition (in vacuum package) was thawed in ice water for approximately 1 min to allow portioning by hand into small pieces. Tissue pieces were flash frozen using liquid nitrogen, transferred to a blender (NutriBullet LEAN, Pacoima, CA), ground into a fine powder, and stored in an individual bag at −80°C.

Fatty acid methyl esters (FAME) were prepared by the method described by O'Fallon et al. (2007). In a glass Pyrex tube, 1 g of raw ground meat homogenate, 1 mL internal standard solution of tridecanoic acid (0.5 mg/mL in methanol; Nu-Chek Prep T-135; Elysian, MN), 0.7 mL 10 N potassium hydroxide, and 5.3 mL methanol were added, and contents were sealed with a polypropylene lined screw cap. Tubes were incubated in a 55°C water bath for 1.5 h and hand-shaken every 20 min. Tubes were cooled in an ice water bath for 20 min, mixed with 0.58 mL 24 N sulfuric acid, and incubated again in a 55°C water bath for 1.5 h (hand-shaking every 20 min). To extract FAME, 3 mL hexane was mixed with tube contents in a vortex for 5 min, and tube contents were separated on a centrifuge at $2,385 \times g$ for 5 min. From the hexane layer of tube contents, 300 μL of FAME in hexane was transferred into an amber, fixed insert screw vial (Agilent Technologies 5188-6592; Santa Clara, CA) and sealed with 9 mm silicone septa in a screw cap (ALWSCI Technologies C0000146; Shaoxing, China). Vials were stored at −80°C until FAME separation and quantification with gas chromatography (GC).

From an injection of 1 μL of sample at a 50:1 split ratio with hydrogen as a carrier gas (2.4 mL/min), FAME were separated on an HP-88 capillary column (100 m × 250 μm × 0.2 μm; Agilent Technologies) using a GC system equipped with a flame ionization detector (Agilent Technologies 7890A). For each sample, oven temperature remained 35°C for 2 min, then increased 4°C/min to 170°C and remained 170°C for 4 min, and then increased 3.5°C/min and remained 240°C for 2 min. The injector and detector were operated at 250°C. Fatty acids were identified based on similarity of their retention times with reference standards (Nu-Chek Prep, GLC 463). Fatty acid concentrations were calculated relative to initial wet sample weight (milligrams/grams) and expressed as percentage of total lipid fraction in the sample. Total percentage of saturated, monounsaturated, and polyunsaturated fatty acids were calculated for each sample.

Statistical analysis

Data were analyzed using R statistical software, version 4.1.2 (R Core Team, 2021). Data for each trait measured on beef from cattle (experimental unit; $n =$ 82 to 84 per phenotype group; $n_{[n]} = 8$ to 11 per phenotype group within each of 9 pens) were visually assessed for normality using boxplots and histograms before analysis. Because they exhibited non-normal distributions, sensory attributes of sour, metallic, oxidized, and liver-like were square root transformed to meet test assumptions. For fatty acid analysis, samples were removed that contained a percentage value greater than 5 standard deviations away (positive or negative) from the mean value for an individual fatty acid. Values with such an extreme deviance in fatty acid composition were attributed to instrument error and not the sample itself; thus, removal of these outliers provided for data that more appropriately met statistical test assumptions. From whole strip loins collected on a subset of carcasses, only measurements from steak numbers 3 to 12 (in addition to steak numbers 1 and 2 from all carcasses) were analyzed.

The lmer function from the lme4 package (Bates et al., 2015) was used to fit a restricted maximum likelihood–based, mixed model for all attributes. To account for the randomized complete block design of the study, models for all variables were fit with pen (block) as a random effect. Residuals and fitted values from each model were plotted to assess model assumptions for homogeneity of variance. Effects from all models, except those for sensory attributes, were tested with an analysis of variance (ANOVA) using the anova function from the lmerTest package (Kuznetsova et al., 2017) with Kenward-Roger approximation of denominator degrees of freedom. When effects were significant, group means were separated with Tukey adjusted pairwise comparisons and Kenward-Roger approximation of denominator degrees of freedom using the emmeans function from the emmeans package (Lenth, 2018). Significance of effects and pairwise comparisons was established at $\alpha \leq 0.05$.

Shear force values, pH, cross-sectional areas of each MHC isoform, proportions of cross-sectional area of each MHC isoform, and fatty acid compositions were modeled (fixed effect: phenotype group; random effect: pen). Respective peak internal cooked temperature was included as a covariate (fixed effect) in models for shear force. Dimensions of steaks from

anterior strip loin regions (steak numbers 1 and 2) were modeled and analyzed separately from dimensions of steaks from whole strip loins (steak numbers 3 to 12) from a subset of cattle ($n_1 = 10$ to 17 per phenotype group). Steak area measurements were modeled with repeated measures (fixed effects: phenotype group and phenotype group-steak number interaction; random effects: experimental identity and pen), and total number of steaks produced was included as a covariate (fixed effect; model for steak numbers 3 to 12 only). Lateral steak angles were modeled with repeated measures (fixed effects: phenotype group, steak number, and phenotype group-steak number interaction; random effects: experimental identity and pen), and total number of steaks produced was included as a covariate (model for steak numbers 3 to 12 only). Fat depth at 75% was modeled with repeated measures (fixed effects: phenotype group, steak number, and phenotype group-steak number interaction; random effects: experimental identity and pen), and total number of steaks produced was included as a covariate. Measurements of instrumental and trained color from a subset of cattle ($n_2 = 38$ to 40 per phenotype group) were modeled with repeated measures (fixed effects: phenotype group, timepoint, and phenotype group-timepoint interaction; random effects: experimental identity and pen).

Sensory attributes were modeled (random effect: pen), with peak internal temperature included as a covariate (fixed effect). Residuals from sensory attributes were tested for the fixed effect of phenotype group using a discriminant function analysis to account for the multidimensionality of sensory evaluation (Foraker et al., 2020). Mahalanobis' distances were calculated to assess multivariate normality on each sample at a χ^2 critical value of 32.9 (df = 12, $P = 0.001$). Homogeneity of variance-covariance matrices was evaluated using Box's M test from the heplots package (Fox et al., 2018), where $\alpha < 0.001$ indicated heterogeneity (Tabachnick and Fidell, 2013). Multicollinearity was formally assessed by fitting a linear model to predict sample sequence with residuals from all sensory attributes; using the olsrr package condition indices greater than 30 at each eigen value were considered a violation (Hebbali, 2018). After evaluation of test assumptions, a linear model was fit to predict phenotype group from a combination of sensory attribute residuals. The candisc package was used to evaluate the canonical correlation of sensory attributes and phenotype group on each discriminant function (Friendly and Fox, 2017). Loadings and standardized coefficients for sensory attributes were assessed to determine the discriminating ability of each attribute.

Results and Discussion

This study was designed to evaluate meat quality and traits of economic relevance among 4 phenotype groups (fully beef-type, partially beef-type, partially dairy-type, and fully dairy-type) of crossbred beef × dairy cattle that, on average, differed in their expression of beef- versus dairy-type. Before cattle were categorized into phenotype groups, 12 animals were removed from the study because their muscling and frame size scores differed by 5 units or more (i.e., very beef-type for frame size but very dairy-type for muscling, or vice versa). Like most biological traits, expression of beef- versus dairy-type in this population exhibited a normal distribution; 68% of cattle were categorized into intermediate phenotype groups (partially dairy or beef-type). Hence, the population was subsampled to equally represent both intermediate and extreme (fully dairy or beef-type) phenotypes.

Scores for muscling, frame size, and ultimately phenotype served as numerical values to identify a categorical outcome of phenotype group, which was used to test for effect of beef- versus dairy-type. Reasonable justification could also be made to linearly regress each measured trait on phenotype score (as a continuous predictor), and this study probably contained sufficient sample size and range in phenotype scores to do so. However, cattle were categorized into phenotype groups that, in an industry setting, might have more practical meaning (at least in terminology) than a numerical phenotype score. Because phenotype groups progressed in a stepwise fashion, contrasts between only adjacent phenotype groups could have identified gradience in a trait, if it was linear in response. Yet, the greater influence of an extreme phenotype compared to all other phenotypes on a trait was considered; thus, all comparisons were made between phenotype groups using an ANOVA to protect from comparison-wise error. Using this technique, when an extreme phenotype (e.g., fully beef-type) was different from an opposite intermediate phenotype (e.g., partially dairy-type) but not directionally different (numerically or statistically) from the opposite extreme phenotype (e.g., fully dairy-type), a Type I error was likely committed. This study contained a large sample size and was designed to provide sufficient power to correctly identify differences, when they existed.

By design, crossbred beef × dairy cattle categorized into each of the 4 phenotype groups were scored very differently for beef- versus dairy-type using the described scoring system, and a full range of phenotype scores were represented in this study (Figure 2).

Variation in phenotype scores within each group can be attributed to variation between pens (e.g., sex, placement weight, and days on feed), which was accounted in analyses. Despite visual differences in beef- versus dairy-type among the cattle sampled, traits in *longissimus lumborum* important for meat performance were largely not different between phenotype groups.

Differences in live expression of muscling between phenotype groups of crossbred beef × dairy cattle suggested that muscle size and shape might also be different in meat cuts prone to large variation in shape, like strip loin steaks. However, differences in steak size and shape, when identified, were not as profound in magnitude as what might be expected (Figure 3). Phenotype group and the interaction of phenotype group and steak number had no effect ($P \geq 0.09$) on steak area measurement at steak numbers 1 and 2 or steak numbers 3 to 12. The numerical difference in mean steak area between groups at steak numbers 1 and 2 was not more than 4.1 cm^2. Area measurements of steak numbers 3 to 12 were numerically and consistently greater in beef-type (partially or fully) crossbreds versus dairy-type (partially or fully) crossbreds, with the mean difference in area between phenotype groups being greater than 6 cm^2 at
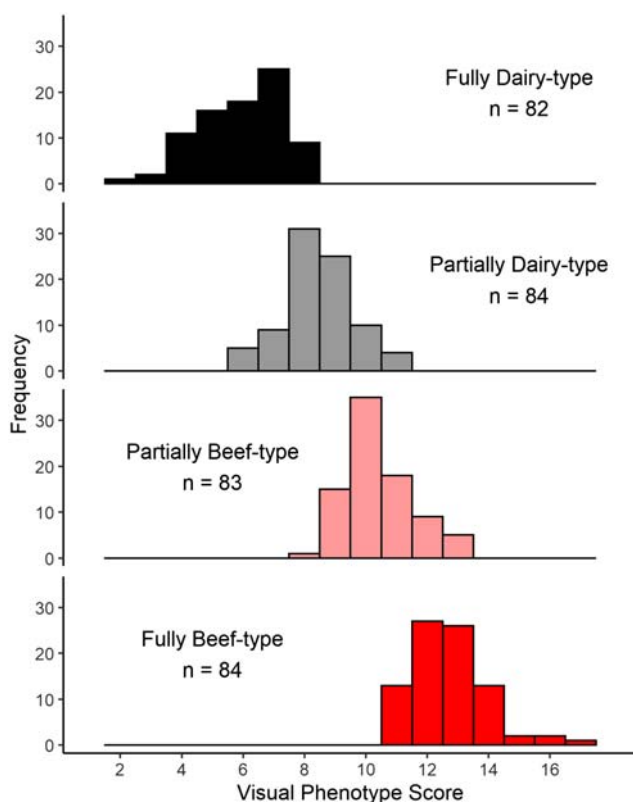

Figure 2. Distributions of visual phenotype scores (muscling score plus frame size score; unadjusted for pen effects) of crossbred beef × dairy cattle. Phenotype group was designated from the mean and standard deviation of these scores within each of 9 feedlot pens.

some steak numbers. A larger sample size (here, only a subset of cattle was represented in steak numbers 3 to 12) might better characterize muscle shape in posterior regions of strip loins between beef × dairy crossbreds with different expression of beef- versus dairy-type. Lateral steak angle was also not influenced by phenotype group ($P \geq 0.40$) or the interaction of phenotype group and steak number ($P \geq 0.06$), suggesting that large differences in steak angularity do not exist in the beef × dairy crossbred population. These results were surprising given the large differences in live animal expression of muscling and suggested that muscling in other body regions, separate from the loin, may have been responsible for differences in live animal muscling and thickness assessed by expert evaluators.

Some retailers and foodservice distributors have reported that, because of differences in steak size and angularity, dairy steaks have been undesirable to sell alongside conventional beef steaks. However, minimal research exists on the influence of steak shape to consumer purchasing decisions and that which does conflicts with many industry perceptions. Steger (2014) showed low correlations between consumer rankings and measurements of strip loin steaks from Holsteins and conventional beef cattle, and Thonney et al. (1991) demonstrated that experienced retail meat managers could not distinguish between ribeye steaks of Holstein and Simmental × Angus cattle. While the influence of steak shape on retail sales is unclear, strip loin steaks from Holstein cattle have been measured with a smaller total surface area and greater angularity in lateral steak regions when compared to conventional beef cattle (Steger, 2014). Concerns of steak shape and angularity, at least in anterior portions of the strip loin, seem to be less pronounced in beef × dairy crossbreds, such that steak shape from beef × dairy crossbreds and conventional beef cattle has been similar (Frink, 2021). Additional research is needed to evaluate more posterior regions of the strip loin, such as the "saddle region," in dairy-influenced cattle populations.

Fat depth at 75% length from steak numbers 3 to 12 was greater ($P < 0.05$) in fully beef-type crossbreds than partially dairy-type crossbreds. Because cattle within a pen were slaughtered at an endpoint of constant days on feed, differences in subcutaneous fat deposition over the strip loin may have suggested slight differences in maturing rate or fat deposition (e.g., subcutaneous versus other depots, like internal) between phenotype groups. Greater subcutaneous fat deposition has been shown in earlier maturing, more moderately framed cattle populations (Berg and Butterfield, 1976; Tatum et al., 1986b).
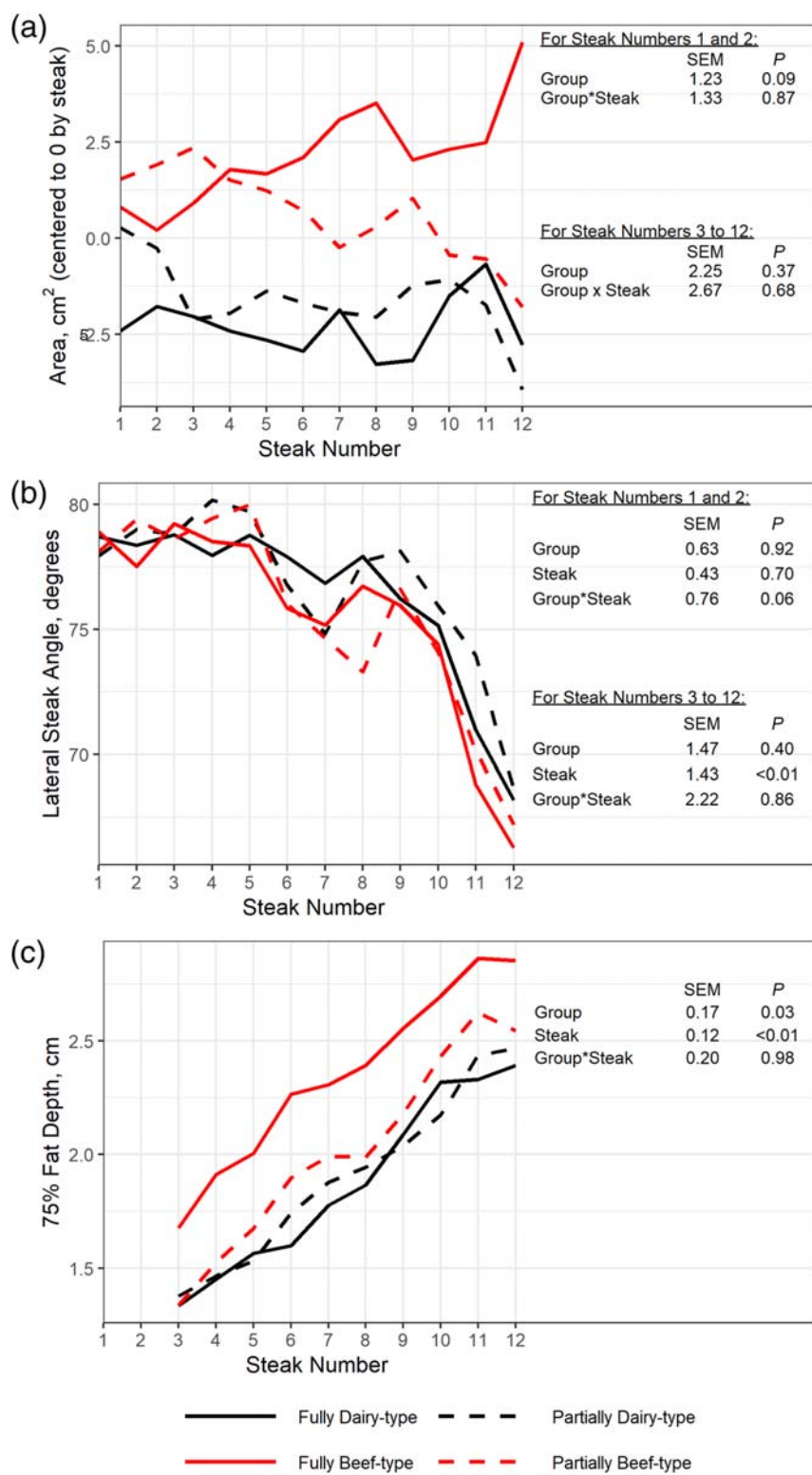
Figure 3. Area, lateral steak angle, and 75% fat depth of strip loin steaks (1 = most anterior, 12 = most posterior) from crossbred beef × dairy cattle (for steaks 1 and 2: n = 82 to 84 per group; for steaks 3 to 12: n_1 = 10 to 17 per group) with different visual phenotypes (SEM = standard error of the means, pooled).

Trained sensory evaluation of beef from beef × dairy crossbreds indicated that expression of beef- versus dairy-type had no influence on sensory ratings for any specific attribute. By using a discriminant function analysis rather than more traditional univariate techniques, all sensory attributes (as residuals after

accounting for study design) were assessed in a single analysis, just as a trained panelist assessed all attributes of a sample at the same time. Consequently, this multivariate technique resulted in fewer comparisons between phenotype groups and reduced the opportunity for Type I error compared to a univariate technique. Three discriminant functions (linear combinations of all sensory attributes) were calculated to predict membership of samples to a phenotype group. The first discriminant function accounted for 68.8% of variation in individual scores, but this function was not correlated ($R^2 = 0.08$; $P = 0.27$) to phenotype group membership (Figure 4). Because they account for variation orthogonal to previous function(s), successive functions also did not ($P > 0.93$) explain differences between phenotype groups. Loadings and standardized coefficients suggested that notes of buttery, liver-like, and sour contributed to the greatest variability between phenotype groups; however, because the first discriminant function was not significant, the contribution of these notes to phenotype group differences was negligible (Table 2). Means (and standard errors of means) for measurements of other traits related to eating quality, including WBSF values (2.66 to 2.78 ± 0.116 kg), SSF values (12.7 to 13.4 ± 0.31 kg), and pH (5.43 to 5.44 ± 0.018), were also not different ($P \geq 0.30$) between phenotype groups. Lastly, mean marbling amount was equal across phenotype groups (not published in this manuscript). Marbling amount has known effects on the sensory

Table 2. Loadings and standardized coefficients[1] on the first discriminant function of ratings for sensory attributes evaluated by trained panelists in strip loin steaks from crossbred beef × dairy cattle

Item	Loadings	Standardized coefficients
Sensory attribute		
Beef flavor identity	0.10	0.62
Browned	−0.11	−0.22
Buttery	−0.40	−0.75
Fat-like	−0.27	−0.01
Juiciness	0.04	0.39
Liver-like	−0.47	−0.56
Metallic	−0.16	−0.29
Oxidized	0.00	−0.05
Roasted	−0.11	−0.16
Sour	−0.38	−0.48
Tenderness	−0.19	−0.22
Umami	−0.25	−0.32
Canonical R^2	0.08	
Eigen value	0.09	
P value (H_0: canonical $R^2 = 0$)	0.27	

[1]Loading indicates the relationship between a variable and discriminant function, and standardized coefficient indicates unique contribution of a variable to a function.

experience and, if different between phenotype groups, could have confounded results of this study (Emerson et al., 2013).
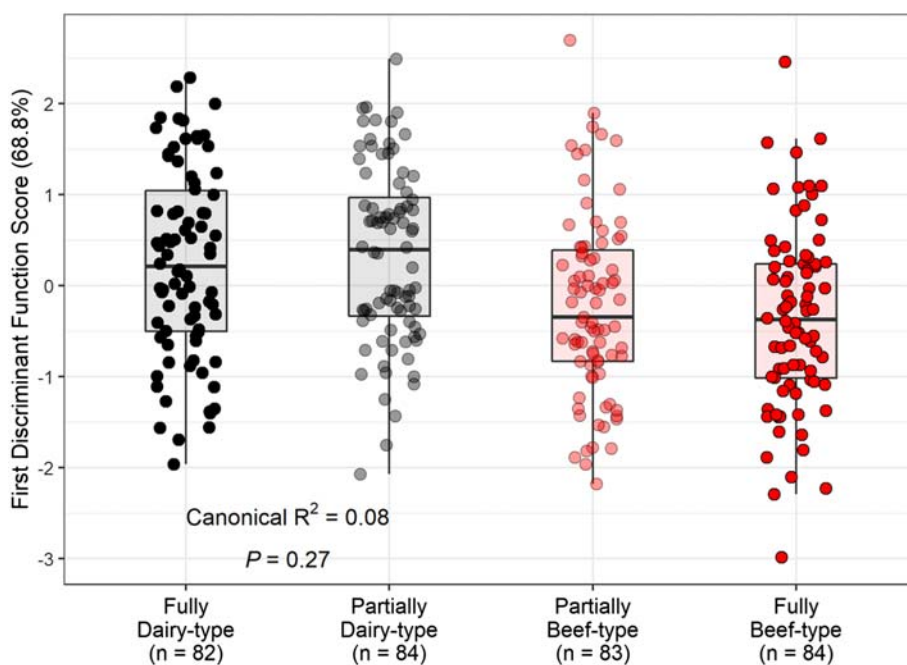

Figure 4. Scores on the first discriminant function of trained panelist sensory ratings for 12 attributes of strip loin steaks from crossbred beef × dairy cattle. (H_0: canonical correlation between all sensory attributes and phenotype group of given function is 0.)

Beef products sampled from the population of beef × dairy crossbreds represented in this study performed with consistency in eating quality and superiority for tenderness, specifically. Shear force values were compared to USDA thresholds for beef product tenderness claims (ASTM, 2011). Based on their WBSF and SSF values, greater than 98% and 86% of strip loin steaks (when aged 14 d postmortem, frozen, thawed, and cooked) from beef × dairy crossbreds in this study were eligible for the USDA Certified Tender and Very Tender claims, respectively. Greater tenderness in beef from beef × dairy crossbreds compared to beef without influence of dairy breeding was previously demonstrated by Frink (2021). Thus, opportunities may exist for marketing beef from crossbred beef × dairy cattle in programs centered around eating quality and consistency.

Consumers have been shown to discriminate against beef that contains 20% or more lean surface area discoloration (Hood and Allen, 1971). Consequently, economic losses to the US beef industry associated with discolored cuts have been estimated at more than $1 billion annually (Smith et al., 2000). Strip loin steaks in this study reached 20% lean surface area discoloration between 84 and 96 h of retail display, which was similar to the rate of discoloration in beef × dairy steaks shown by Frink (2021). Beef from dairy cattle

has been reported as darker in color with a faster discoloration rate than beef from conventional beef cattle (Faustman and Cassens, 1991; Page et al., 2001; Frink, 2021). These deleterious color properties in dairy cattle have not been shown in beef × dairy crossbreds (Frink, 2021), and this study demonstrated consistent color performance across beef × dairy crossbreds with different expression of beef- versus dairy-type. Visual and instrumental assessments of retail display color (Figures 5 and 6, respectively) in strip loin steaks were not affected by phenotype group ($P \geq 0.20$) or the interaction of phenotype group and time ($P \geq 0.82$).

Muscle fiber properties are often used to partially explain differences in more applied eating quality assessments, like sensory evaluation and shear force (Lefaucheur, 2010; Picard et al., 2020). Correspondingly, because no differences were shown between beef- versus dairy-type crossbreds in sensory, shear force, and color analyses, it was not surprising that immunohistochemical analyses also revealed no differences. Cross-sectional area and proportion of cross-sectional area for each MHC isoform (I, IIA, and IIX) were not different ($P \geq 0.12$) between phenotype groups (Figure 7). Often at an expense to eating quality traits, muscle from beef breeds of cattle has been shown to contain larger diameter muscle fibers
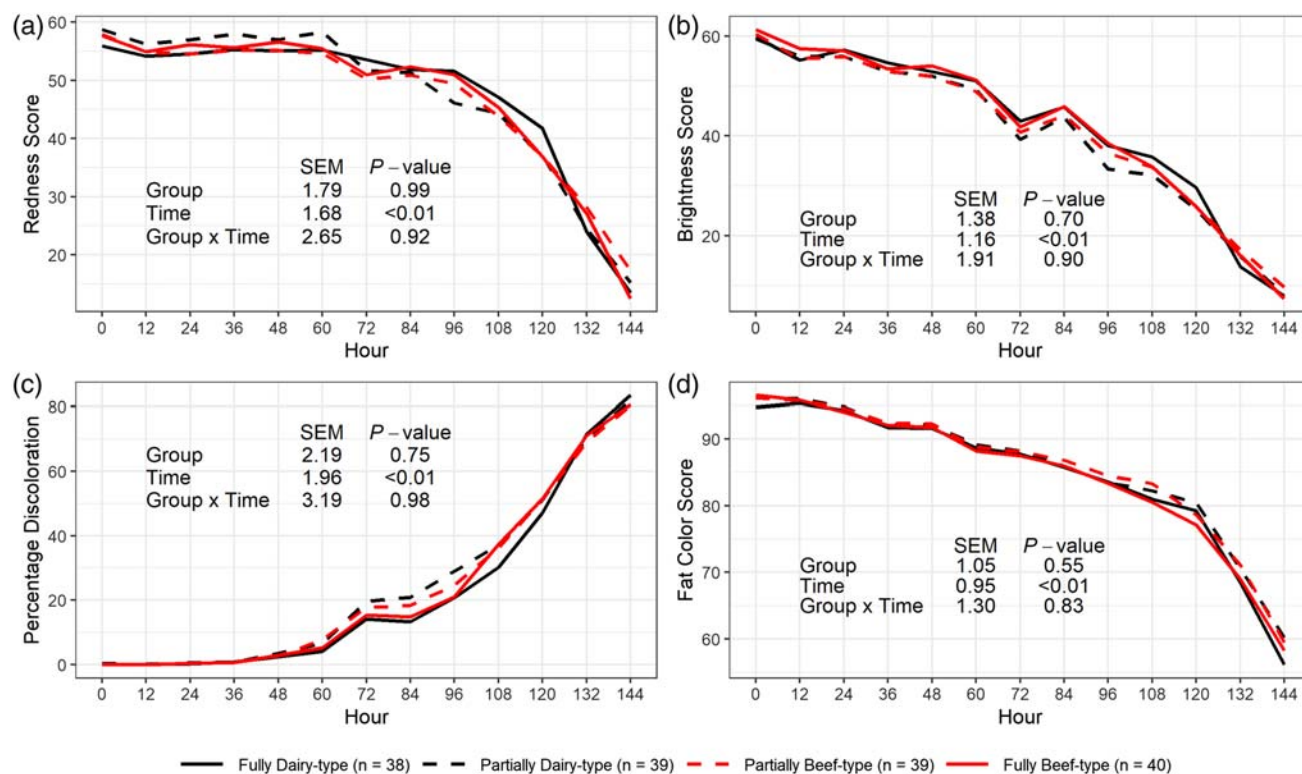

Figure 5. Trained panelist color ratings during retail display of strip loin steaks from crossbred beef × dairy cattle with different phenotypes (SEM: standard error of means, pooled).
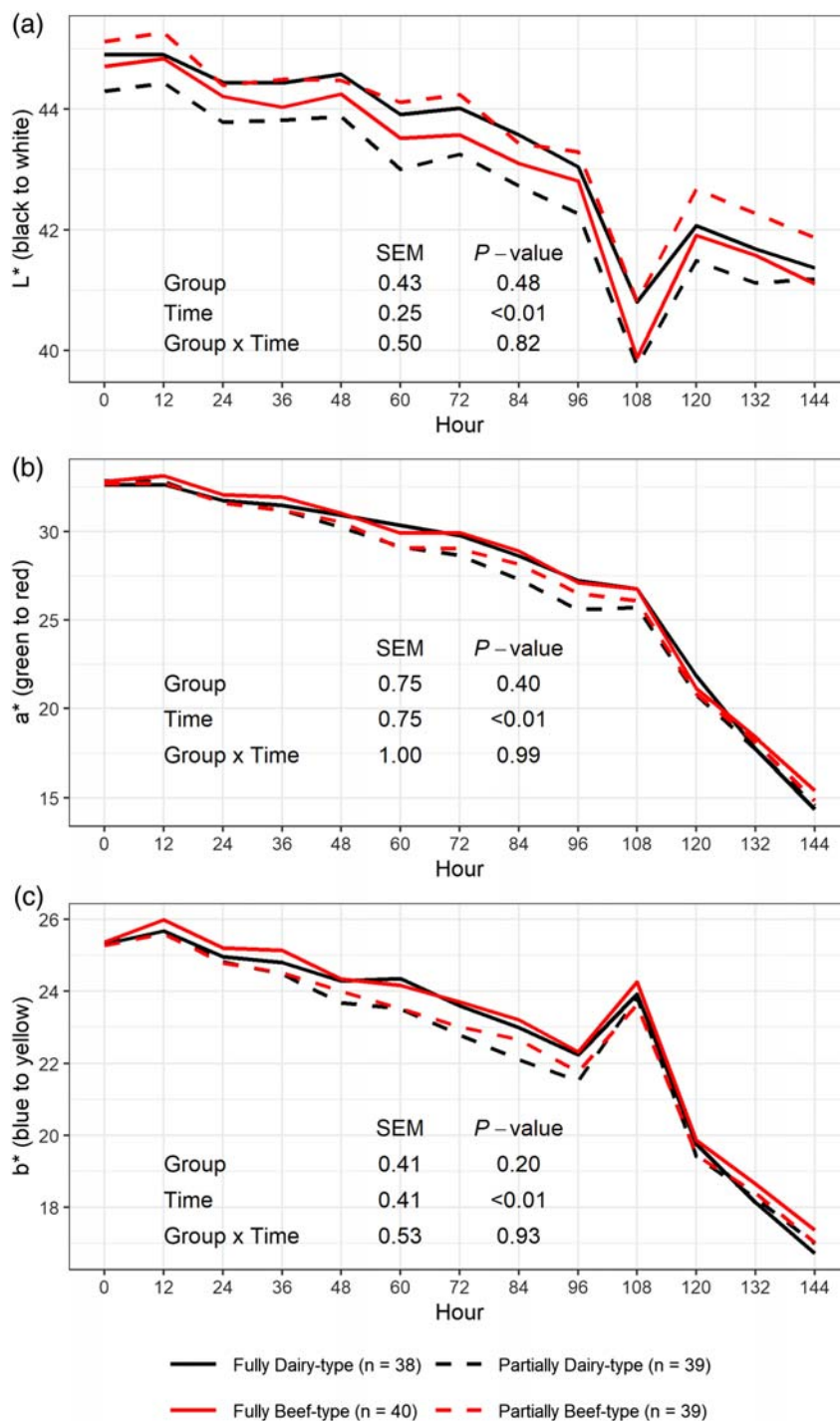
Figure 6. Instrumental color measurements during retail display of strip loin steaks from crossbred beef × dairy cattle with different phenotypes (SEM: standard error of means, pooled).

and a greater proportion of glycolytic fibers than muscle from dairy breeds because of greater selection pressure in beef breeds for muscle growth (Spindler and Mathias, 1980; Schreurs et al., 2008; Chriki et al., 2012). The results presented here only accounted for muscle fiber properties of the *longissimus* muscle. Because muscle fiber properties have differed between different growth types (e.g., breeds) of cattle,

differences in muscle fiber properties between phenotype groups may be more apparent in muscles other than *longissimus*.

Fatty acid composition of beef has been used to explain differences in sensory evaluation for flavor and has been linked to fiber type differences between beef and dairy breeds (Spindler and Mathias, 1980; Legako et al., 2015; O'Quinn et al., 2016;
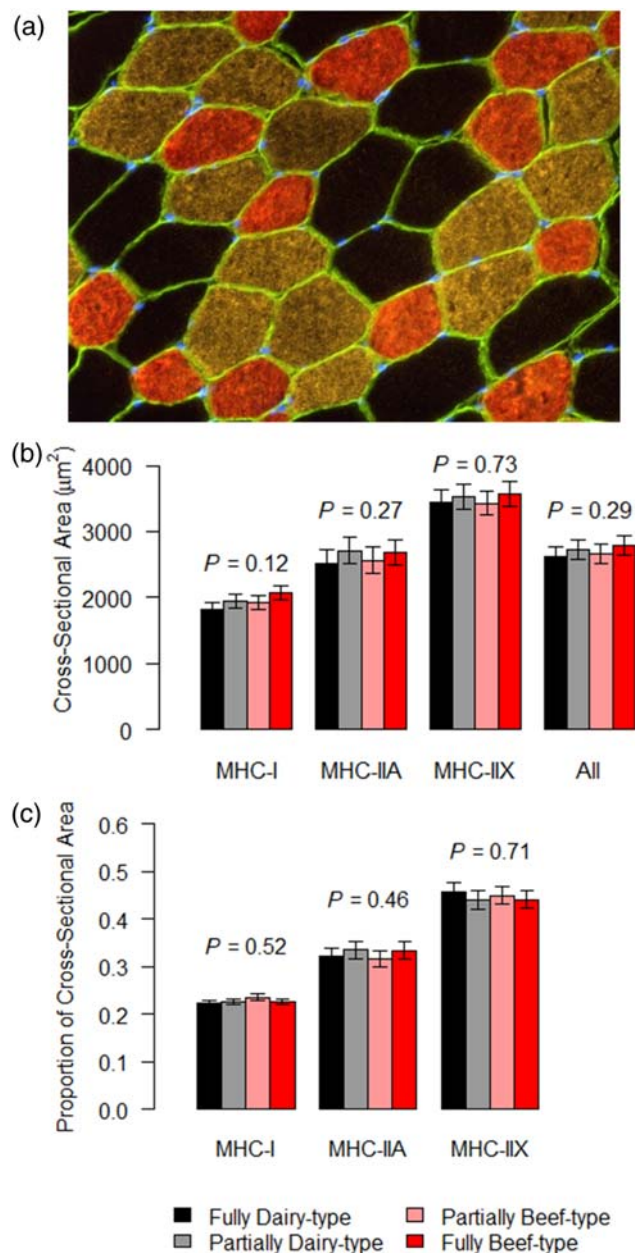
Figure 7. (A) Cross-sectional image of *longissimus* muscle stained by myosin heavy chain (MHC) isoform (red: MHC-I, yellow: MHC-IIA, black: MHC-IIX, green: cell membrane, blue: nuclei). Cross-sectional area (B) and proportion of cross-sectional area (C) of MHC isoforms of crossbred beef × dairy cattle with different phenotypes.

Najar-Villarreal et al., 2019). Because phenotype group did not affect sensory evaluation or muscle fiber type, it was not surprising that phenotype group had a seemingly negligible effect on fatty acid composition (Table 3). Beef from fully dairy-type crossbreds contained the greatest ($P < 0.05$) percentage of 20:3 $n - 6$ (dihomo-gamma-linolenic acid) and 20:4 $n - 6$ (arachidonic acid) compared to all other phenotype groups. Further, fully dairy-type crossbreds contained a greater ($P < 0.05$) percentage of 18:2 $n - 6$ (linoleic

acid) and a lesser ($P < 0.05$) percentage of 17:0 (margaric acid) and 15:0 (pentadecylic acid) than partially beef-type crossbreds but, for these same fatty acids, were not different ($P > 0.05$) from the other 2 phenotype groups. These differences in individual fatty acids contributed to fully dairy-type crossbreds containing a greater ($P < 0.05$) total percentage of polyunsaturated fatty acids than partially beef-type crossbreds (but not different from the other 2 phenotype groups; $P > 0.05$). It is difficult to explain why the fully dairy-type group contained a different fatty acid profile than the partially beef-type group but not the fully beef-type group. As previously suggested about the categorization of samples and statistical analysis, this was likely more a result of Type I error than an effect of beef-type versus dairy-type expression. Nonetheless, total fat was not different ($P = 0.54$) between phenotype groups.

Objectives of this study were derived from the work of Sherbeck et al. (1996), where phenotypic expression of Brahman breeding was negatively related to tenderness. Few studies have evaluated effects of visual phenotype expression on meat quality in beef cattle, primarily because the genotype (usually breed composition, at a minimum) of the experimental sample in most studies was known, which is not often the case in a commercial industry setting. The few other investigations of phenotype expression effects on meat quality demonstrated similar results to this study. Dolezal et al. (1985) showed few meaningful differences in palatability traits between classes of feeder cattle with different frame sizes and muscle thicknesses. Additionally, cattle with different visual phenotypes, including those that contained up to 25% evidence of Brahman breeding, sampled in a commercial feedlot have produced beef with minimal differences in tenderness and flavor profiles (Hilton et al., 2004).

Discrepancies between studies relating cattle phenotype to meat quality might be explained by a difference in expression of genes influencing the phenotypes studied. In Sherbeck et al. (1996), phenotypic expression of Brahman breeding tended to be positively related with calpastatin activity. Elevated calpastatin activity, and its role in the calpain protease system, has been used to explain why beef from *B. indicus* cattle exhibits greater toughness than beef from *Bos taurus* cattle (Wheeler et al., 1990; Whipple et al., 1990; O'Connor et al., 1997; Pringle et al., 1997). Calpastatin expression has been associated with a few single nucleotide polymorphisms in well characterized genes, like *Calpain-1* and *Calpastatin*, which have also been related to conformation traits and body type likeability in beef cattle (Calkins et al., 1981; Raynaud et al.,

Table 3. Fatty acid composition (% of total fat) of raw strip loin steaks from crossbred beef × dairy cattle with different phenotypes

Item	Fully dairy-type	Partially dairy-type	Partially beef-type	Fully beef-type	SEM[1]	P value
Number of cattle	75	75	75	78		
Saturated, total	47.12	47.93	48.16	47.42	0.635	0.34
10:0	0.05	0.05	0.05	0.05	0.002	0.30
12:0	0.08	0.08	0.08	0.08	0.002	0.63
14:0	3.29	3.39	3.31	3.37	0.066	0.54
15:0	0.59[b]	0.62[ab]	0.64[a]	0.62[ab]	0.028	0.03
16:0	27.38	27.91	28.05	27.54	0.315	0.24
17:0	1.49[b]	1.54[ab]	1.62[a]	1.55[ab]	0.033	<0.01
18:0	13.99	14.10	14.20	13.96	0.376	0.89
19:0	0.06	0.05	0.05	0.05	0.002	0.18
20:0	0.15	0.15	0.14	0.15	0.005	0.17
22:0	0.02	0.02	0.02	0.02	0.002	0.24
24:0	0.01	0.01	0.01	0.01	0.001	0.29
Monounsaturated, total	46.29	45.98	46.03	46.59	0.551	0.62
13:1	0.08	0.07	0.07	0.08	0.025	0.25
14:1 *n* − 5	0.85	0.84	0.83	0.83	0.035	0.93
16:1 *trans*	0.11	0.12	0.12	0.11	0.016	0.87
16:1 *n* − 7	3.14	3.11	3.05	3.11	0.098	0.84
17:1	1.06	1.06	1.08	1.08	0.031	0.77
18:1 *trans*	6.67	7.22	6.68	6.96	0.236	0.07
18:1 *n* − 9	32.29	31.50	32.18	32.36	0.445	0.22
18:1 *n* − 7	1.56	1.54	1.52	1.55	0.038	0.71
19:1	0.04	0.04	0.04	0.04	0.002	0.07
20:1 *n* − 5	0.0	0.0	0.0	0.0	0.001	0.40
20:1 *n* − 8	0.09	0.09	0.09	0.10	0.002	0.55
20:1 *n* − 11	0.37	0.38	0.37	0.38	0.011	0.56
22:1	0.01	0.01	0.01	0.01	0.001	0.92
24:1 *n* − 9	0.0	0.0	0.0	0.0	<0.001	0.17
Polyunsaturated, total	6.59[a]	6.09[ab]	5.80[b]	5.99[ab]	0.277	0.03
18:2 *trans*	0.21	0.22	0.22	0.21	0.006	0.28
18:2 *n* − 6	4.53[a]	4.21[ab]	3.96[b]	4.15[ab]	0.190	0.03
18:3 *n* − 3	0.06	0.06	0.06	0.06	0.003	0.48
18:3 *n* − 6	0.17	0.17	0.17	0.17	0.003	0.84
20:2	0.06	0.06	0.06	0.06	0.003	0.27
20:3 *n* − 3	0.01	0.01	0.01	0.01	0.002	0.98
20:3 *n* − 6	0.25[a]	0.22[a]	0.22[a]	0.22[a]	0.012	0.05
20:4 *n* − 6	1.00[a]	0.85[b]	0.84[b]	0.83[b]	0.065	0.01
20:5	0.02	0.02	0.02	0.02	0.002	0.06
22:3	0.01	0.01	0.01	0.01	0.002	0.85
22:4	0.10	0.09	0.09	0.09	0.005	0.26
22:5 *n* − 3	0.14	0.12	0.12	0.12	0.007	0.09
22:6 *n* − 3	0.04	0.04	0.04	0.03	0.004	0.50
Total fat[2], % of sample	5.91	6.16	6.42	6.30	0.362	0.54

[1]Standard error of the means (SEM), pooled.

[2]Calculated as the sum of fatty acids, in grams, per 100 g of raw *longissimus* muscle tissue.

[a,b]Estimated marginal means in a row that do not share a common superscript are different (*P* < 0.05).

2005; White et al., 2005; Casas et al., 2006; Xiang et al., 2017; Leal-Gutiérrez et al., 2018). Therefore, it could be speculated that single nucleotide polymorphisms at a few genes (e.g., those controlling the calpain proteinase system) were responsible for results of Sherbeck et al. (1996).

Characteristics comprising the phenotypes evaluated in this study and other studies (Dolezal et al., 1985; Hilton et al., 2004) were likely controlled by many more genes, which has been hypothesized of complex quantitative traits that do not exhibit Mendelian inheritance (Fisher, 1919). It has been reported that skeletal type traits (many of which share similarity to the traits comprising beef- versus dairy-type in this study) are controlled by a very large number of single nucleotide polymorphisms with small effect—a phenomenon termed omnigenic (Boyle et al., 2017; Doyle et al., 2020). Thus, the many different genes, or combination of genes, controlling beef-versus dairy-type in crossbred beef × dairy cattle in this study were not likely the same genes, or combination of genes, controlling meat quality.

Conclusions

This study demonstrated that expression of beef-versus dairy-type in crossbred beef × dairy cattle does not meaningfully contribute to shape, eating quality, or color of strip loin steaks. Therefore, efforts that increase additive genetic effects from complementarity of beef breeds and individual beef sires to produce more beef-type cattle from the beef × dairy mating system will not negatively influence meat quality in beef from terminal beef × dairy progeny. Beef marketing programs rooted in the production of consistent and premium products may benefit from including beef from crossbred beef × dairy cattle.

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