

Effects of growth potential and growth path on tenderness of beef longissimus muscle from bulls and steers¹

R. W. Purchas^{*2}, D. L. Burnham[†], and S. T. Morris[†]

^{*}Institute of Food, Nutrition, and Human Health and [†]Institute of Veterinary, Animal, and Biomedical Sciences, Massey University, Palmerston North, New Zealand

ABSTRACT: The influence of growth potential or growth path on the tenderness of the longissimus muscle was investigated using 117 Angus and Angus-cross bulls and steers raised on pasture over two successive years. Growth rate for a period of 100 d from a weight of about 200 kg was used to identify the faster-growing two-thirds of cattle within the gender groups, half of which were grown fast to a slaughter weight of 530 kg at 16 to 18 mo of age (the Fast group), whereas the other half were restricted in growth (the Restricted group) so they attained a similar final weight as the slower-growing third (the Slow group) at about 26 mo of age. The Restricted group was included to determine whether the tougher meat expected from the Slow group relative to the Fast group (based on previous results) was due to the greater age of the Slow group or to their slower early growth rate. Beef from the Fast group was tenderer than that from both the Slow and Restricted groups based on sensory panels ($P < 0.05$) and objective measures ($P < 0.05$), indicating that the early growth-

rate potential was less important than the differences in age or the patterns of growth for the Slow and Restricted groups. Improved tenderness for the Fast group was associated with more intramuscular fat ($P < 0.05$) and higher myofibrillar fragmentation indexes ($P < 0.05$). Patterns of tenderness differences between treatment groups were similar for bulls and steers, but beef from bulls was tougher ($P < 0.001$) than that from steers. The more tender beef from steers was associated with a slightly lower ultimate pH ($P < 0.001$), higher myofibrillar fragmentation indexes ($P < 0.001$), and more intramuscular fat ($P < 0.001$). Ultimate pH affected beef tenderness ($P < 0.01$), but adjustments to a constant pH did not decrease differences between treatment and gender groups. The higher growth rates ($P < 0.01$) and leaner carcasses ($P < 0.01$) of bulls compared with steers were consistent with other studies. Increases in age of 8 to 10 mo may be associated with less tender beef for cattle finished on pasture, and beef from bulls is likely to be less tender than that from steers.

Key Words: Age Differences, Beef cattle, Meat Quality, Tenderness

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Introduction

The tenderness of beef has been identified as a quality characteristic that is closely related to the overall acceptability of beef (Chambers and Bowers, 1993) and that is often the cause of consumer dissatisfaction with beef quality. The tenderness of a piece of beef at the time of consumption is a complex characteristic that is determined by a range of intrinsic determinants within the muscle, many of which can be influenced, not only by the genetic makeup and age of the animal, but also by

many external factors. These may act during animal growth, during the preslaughter period, during the post-mortem period both before and after rigor mortis, and during cooking (Harper, 1999; Ferguson et al., 2001). Previous work has shown that spring-born cattle raised and finished on mixed pastures (primarily *Lolium perenne* and *Trifolium repens*) produce more tender beef if they are slaughtered before their second winter at an age of 15 to 18 mo than cattle from the same population that are kept through the winter and subsequent spring and slaughtered at 24 to 28 mo of age (Purchas and Grant, 1995; Purchas et al., 1997). However, in these studies, the younger group of cattle were those that were heavier at that time, so it was not possible to determine whether the beef was more tender because they were younger or because they had grown faster to that age. Therefore, the objective of the present experiment was to distinguish between these possibilities by having a third group of cattle that were faster growing, but which

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²Correspondence: Private Bag 11 222 (phone: 64-6-350-4336; fax: 64-6-350-5657; E-mail: R.Purchas@massey.ac.nz).

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were nutritionally restricted so that they reached the target slaughter weight at the same age as the slower-growing group. There was an equal number of bulls and steers within the three treatment groups in order to investigate further the inconsistent effects of castration on beef tenderness (Purchas, 1991).

Materials and Methods

Animals and Treatments

Bulls and steers ($n = 117$) used in this experiment were spring-born in either 1996 (Lot 1; Hereford-Angus cross cattle from one farm, $n = 60$) or 1997 (Lot 2; Angus cattle from a second farm, $n = 57$). The two farms were chosen because they each had compact calving periods and because at least 80 male calves were available for animal selection. Selection took place at approximately 2 mo of age to provide groups of 60 that were moderately even in terms of weight. Birth weights and dates of birth were not recorded. Half of each lot was selected at random to be castrated at an age of about 2 mo, and cattle were transferred from the commercial farms of birth to a Massey University research unit immediately after weaning at an age of about 5 mo. After a 2-wk acclimation period, growth rates were measured over test periods of 100 and 108 d for Lots 1 and 2, respectively, so cattle could be sorted within lot and gender into the slower-growing third (the Slow group) and the faster-growing two-thirds. Within the faster-growing group, half were allotted randomly to the Fast group and the remainder comprised the Restricted group. Subsequent nutritional management was such that animals of the Fast group were slaughtered at an age of 16 to 18 mo. Animals in the Slow and Restricted groups were slaughtered an average of 269 d later at an age of 24 to 28 mo. Steers were slaughtered an average of 38 d later than the bulls in order to reduce differences in mean carcass weights. The cattle were grazed on mixed pastures comprised primarily of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) at all times, with some pasture hay being supplied during periods of pasture shortage during the winter. No hay was fed during the 3 mo prior to slaughter. The different growth patterns required by the experimental design were achieved by providing the treatment groups with varying amounts of similar pastures rather than by providing pastures that differed in quality.

Slaughter and Meat Sample Collection

On the day of slaughter for each group, cattle were removed from pasture at approximately 0800 and trucked 20 km to a meat plant where preslaughter handling, washing, percussion stunning, exsanguination, and dressing followed normal commercial procedures, including low-voltage electrical stimulation (30 s with 14.28 pulses of $7.5 \text{ ms} \cdot \text{s}^{-1}$ and a peak voltage of 90 V) immediately after exsanguination. The period off feed

prior to reaching the meat plant was approximately 2 h and the holding time at the plant was either 4 or 28 h, with a random half within each lot by treatment by gender group being allocated to each holding-time class. There were five animals within each (lot \times gender \times treatment \times holding time) subgroup, except for three cells that contained four animals each.

During the period prior to the carcasses entering the chiller, the number of erupted permanent incisor teeth was recorded, and for each side, the length from the distal end of the tarsal bones to the midpoint of the cranial edge of the first rib (carcass length), and the length from the caudal edge of the cut pelvic bone to the midpoint of the cranial edge of the first rib (body length) were measured. In addition, the kidney plus pelvic (channel) fat from each side was removed and weighed. The liver (without gall bladder) and heart (after removal from the pericardium) were also weighed. Additionally, a sample of 1,800 to 2,000 g of the longissimus muscle (LM) was excised between the 6th and 12th ribs of the right side immediately prior to chilling.

After overnight chilling of the carcass at 1 to 3°C (18 to 24 h postmortem), the cross-sectional area of the LM at a transverse cut between ribs 12 and 13 was traced, and the area subsequently measured using a digital planimeter (Placom KP-90N, Tokyo, Japan). The fat thickness over this muscle at the same site between ribs 12 and 13 and at two-thirds of the muscle width from its medial edge was measured. The left femur bone was collected during fabrication, and after having muscle and fat remnants removed, its weight and maximal length were recorded as an indication of skeletal development.

Laboratory Methods

Muscle samples collected within 90 min postmortem were held at 12 to 15°C for 24 h to avoid any cold-shortening. These were then aged at 2 to 4°C for a further 6 d before being divided into an 800-g anterior portion for sensory evaluation, which was vacuum-packed prior to freezing at -30°C, and a posterior portion (~1,000 g), which was packaged and frozen at -20°C until objective measures of tenderness and other meat quality characteristics could be made. After thawing the latter sample overnight at 2 to 3°C, two 25-mm thick steaks were cut for assessment of Warner-Bratzler shear force and Meat Industry Research Institute of New Zealand (MIRINZ) force score after cooking at 70°C for 90 min (Purchas and Aungsupakorn, 1993). A third 25-mm thick steak was cooked at 60°C for 60 min for assessment of compression parameters. At the time of preparing these steaks, uncooked samples were set aside for the evaluation of meat color, muscle pH, myofibrillar fragmentation index, sarcomere length, muscle fiber diameter, and intramuscular fat.

For the Warner-Bratzler and MIRINZ tenderometer measurements, six 13-mm² cores were prepared from each steak in such a way as to ensure that shears were made across the fibers. Measurements with a Warner-

Bratzler device (crosshead speed of $230 \text{ mm}\cdot\text{min}^{-1}$; G-R Electric Mfg. Co., Manhattan, KS) fitted with a square blade and a 30-kg load cell as described by Purchas and Aungsupakorn (1993), were made at about one-third the distance along each core. Parameters recorded were total work done (WB-WD), initial yield (WB-IY), and peak force (WB-PF) (Purchas and Aungsupakorn, 1993). The remaining two-thirds of each core was then trimmed to a $10 \times 10 \text{ mm}$ cross section and assessed with the MIRINZ tenderometer (Smith-Biolab, Ltd., Auckland, NZ) for a force score (Macfarlane and Marer, 1966).

An Instron compression device was used to measure hardness (Harris, 1976) as the force required to drive a $10 \times 10 \text{ mm}$ square-faced flat-ended plunger (at a crosshead speed of $100 \text{ mm}\cdot\text{min}^{-1}$) 8 mm into a sample of meat cooked at 60°C for 60 min with a cross section across the fibers of $10 \times 10 \text{ mm}$, as described by Peachey et al. (2002).

Muscle pH was measured in an homogenate of 2 g of LM in 10 mL of 5 mM iodoacetate and 150 mM KCl (Bendall, 1973). Sarcomere length was measured by laser diffraction (Bouton et al., 1973). Meat color was assessed with a Minolta Chromameter (CR-200, 8 mm measured area diameter, standard illuminant C, white tile calibration; Ramsey, NJ) following exposure of a cut surface to air for at least 30 min. Measurements of intramuscular fat by Soxhlet extraction and expressed juice by the filter paper press method were as described by Purchas and Aungsupakorn (1993). Measurements of myofibrillar fragmentation index (MFI%) by a filtration method based on that of Johnson et al. (1990) were carried out as outlined by Purchas et al. (1997). The MFI% procedure included a drying step so that values ranged from 78 (when no fragments passed through the filter) to 100 (when all fragments passed through). Muscle fiber diameter was measured on the same slides that were prepared for sarcomere length assessment. The diameter of 13 fibers that extended as single fibers from the edge of the preparation on the slide were measured for each sample using an eye-piece micrometer fitted to a microscope at $100\times$.

Sensory evaluation was by a trained panel of 11 people, each of whom evaluated three steaks from each animal over two series of 15 sittings with 12 samples being evaluated by each panelist at each sitting. Details of sensory panel procedures, including the training protocol, were reported by Peachey et al. (2002). Characteristics evaluated on 100-mm unstructured line scales included initial juiciness, hardness, cohesiveness, toughness, chewiness, and overall juiciness as described by Peachey et al. (2002).

Statistical Analysis

Statistical analyses were performed using the GLM procedure of SAS (SAS Inst., Inc., Cary, NC). The main model was a $3 \times 2 \times 2 \times 2$ factorial with three treatments (Fast, Restricted, and Slow), two lots (yr 1 and yr 2), two genders (bulls and steers), and two holding times at the

meat plant (4 or 28 h). Covariates fitted before the main effects in the models included carcass weight for composition characteristics, and ultimate pH for meat quality characteristics. All two-way interactions between the main effects and between the main effects and covariates (when present) were evaluated, but were not retained in the model if they were not significant ($P < 0.05$).

Data from the sensory panels were initially analyzed using the raw data to derive least squares means for each animal, and then these means were used in subsequent analyses to evaluate the significance of the main effects and the relationships between sensory characteristics and other measurements (Peachey et al., 2002). The design used to determine which samples to present to panelists at a particular sitting, and the sequence in which the samples were presented, permitted the effects of different panelists and sequences to be adjusted for in the first analysis. A session effect could not be taken out because all panelists received samples from the same 12 animals at the same sitting. Animal and session effects were not confounded, however, because each panelist evaluated three samples from each animal in different sessions, and different combinations of animals were used at each sitting.

Results and Discussion

Differences between the two lots were sometimes statistically significant, but are not reported here (except for growth rates) because it was not possible to separate the effects of different years, different farms of origin, and different breed makeup.

On-Farm Performance

Growth rates for bulls and steers within the three treatment groups are shown separately for Lot 1 and Lot 2 in Table 1 over four periods. Growth rates during the initial "test period" were used to allocate animals to treatment groups as described above. During the differential-feeding period up to the time when the first animals from the Fast group were slaughtered, the Fast group was given access to more pasture than the other two groups so that they could be slaughtered before their second winter. The final two periods, with only the Restricted and Slow groups present (Table 1), were up to the time when the first of the animals in those groups were slaughtered. This period included an initial period of slow growth over the winter followed by a period of faster growth during the spring leading up to slaughter.

The expected faster growth shown by the bulls was more marked during the test period (a 21% advantage for both lots) than in the second period (14% for Lot 1 and 18% for Lot 2) or the final period (7% for Lot 1 and 8% for Lot 2). Furthermore, during the test period, the slowest-growing third grew at 74% the rate of the faster-growing two-thirds, but during subsequent periods, differences in growth rate were a reflection of the amount of pasture provided in order to keep them on the planned

Table 1. Least squares means for growth rates of bulls and steers for Lots 1 and 2 over four sequential periods

Item	Bulls ^a			Steers ^a			RSD ^b	P-value		
	Fast	Restr	Slow	Fast	Restr	Slow		B/S ^c	FRS ^c	Int ^c
Test period, kg·d ⁻¹										
Lot 1 (100 d)	0.67 ^x	0.69 ^x	0.53 ^y	0.55 ^y	0.58 ^y	0.42 ^z	0.06	***	***	NS
Lot 2 (108 d)	0.62 ^x	0.62 ^x	0.43 ^{yz}	0.49 ^y	0.50 ^y	0.37 ^z	0.06	***	***	NS
Differential feeding period with all three groups, kg·d ⁻¹										
Lot 1 (224 d)	1.29 ^x	0.79 ^z	0.72 ^z	1.09 ^y	0.70 ^z	0.66 ^z	0.10	***	***	†
Lot 2 (217 d)	1.16 ^x	0.56 ^z	0.54 ^z	0.95 ^z	0.48 ^z	0.49 ^z	0.08	***	***	**
Two periods with Restricted and Slow groups only, kg·d ⁻¹										
Lot 1										
Winter (210 d)		0.15 ^x	0.16 ^x	—	0.19 ^x	0.13 ^x	0.10	NS	NS	NS
Spring (63 d)		0.82 ^{yz}	1.51 ^x	—	0.78 ^z	1.30 ^{xy}	0.43	NS	***	NS
Lot 2										
Winter (202 d)	—	0.21 ^x	0.19 ^x	—	0.24 ^x	0.24 ^x	0.10	NS	NS	NS
Spring (65 d)	—	1.54 ^y	2.14 ^x	—	1.37 ^y	1.64 ^y	0.23	***	***	*

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bRSD = residual standard deviation.

^cB/S = bull/steer; FRS = Fast, Restricted, and Slow groups; Int = interaction term.

^{x,y,z}Within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

growth paths. There was a significant interaction between castration status and treatment for Lot 2 during the differential feeding period ($P < 0.01$) (Table 1) due to the difference between bulls and steers being greater within the Fast group than within the Restricted and Slow groups.

Withers heights did not differ significantly between the treatment groups when values were adjusted to the same live weight, but weight-adjusted withers heights were greater for steers than bulls ($P < 0.001$) at the three older ages when they were measured (Figure 1). These results are consistent with those of Brannang (1971), who showed that the long bones of bulls were shorter than those of steers, possibly due to the action of testosterone on the epiphyseal growth plate.

Composition Characteristics

Despite the fact that steers were slaughtered an average of 38 d later than the bulls, their mean carcass weight was 18.3 kg less (Table 2). There were no ($P > 0.10$) carcass weight differences between the three growth-pattern groups. Weight-adjusted dressing percentages were slightly higher ($P < 0.10$) for bulls than steers, as has been reported in some other studies (Field, 1971; Purchas and Grant, 1995), and were higher ($P < 0.05$) for the Fast group than for the Slow or Restricted groups, probably because of higher ($P < 0.05$) levels of fatness (Table 3).

Weight-adjusted body length and carcass length did not differ ($P > 0.10$) between bulls and steers, but the ratios of body length to carcass length and femur bone

length were less ($P < 0.001$) for bulls, suggesting that the higher levels of testosterone may have limited the

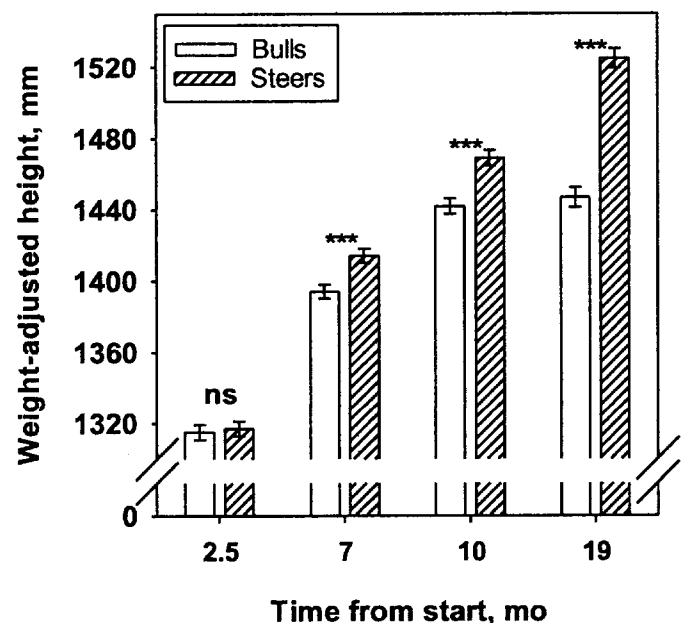


Figure 1. Weight-adjusted withers height (means \pm SE) was significantly greater for steers than bulls in three out of four measurements. Measurement times are relative to the start of the trial. At the start, the cattle weighed about 200 kg. This trait did not differ significantly between the growth-pattern groups. (***) $P < 0.001$; ns, $P > 0.05$.

Table 2. Least squares means for carcass weight and carcass weight-adjusted values for carcass and noncarcass characteristics of bulls and steers that were grown along three different growth paths

Item	Castration status			Growth pattern ^a			Carcass weight ^b	R ² , % (RSD) ^c
	Bull	Steer	Effect	Fast	Restr.	Slow		
Number of cattle	58	59		39	39	39		
Carcass weight, kg	283.2	264.9	***	280.7 ^y	269.7 ^y	271.8 ^y	—	23 (24.4)
Dressing, %	55.1	54.6	†	56.0 ^y	54.0 ^z	54.7 ^z	***	54 (1.5)
Carcass length (CL), mm	2,059	2,076	NS	2,034 ^z	2,092 ^y	2,077 ^y	***	53 (41)
Body length (BL), mm ^d	1,477	1,476	NS	1,459 ^z	1,492 ^y	1,479 ^y	***	53 (31)
BL/CL	0.717	0.711	***	0.717 ^y	0.714 ^{yz}	0.712 ^z	**	27 (0.008)
Femur length, mm	399	410	***	397 ^z	410 ^y	406 ^y	***	41 (10)
Heart weight, kg	1.91	1.84	*	1.86 ^y	1.87 ^y	1.90 ^y	***	51 (0.16)
Liver weight, kg	6.37	6.68	†	5.95 ^z	6.75 ^y	6.87 ^y	***	40 (0.66)

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bSignificance of the carcass weight effect when carcass weight was fitted as a covariate.

^cR² = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dBody length = carcass length less the length of the hind leg.

^{y,z}Within the three growth patterns and within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

length of long bones such as the femur (Brannang, 1971). Cattle in the Fast group had shorter ($P < 0.05$) carcasses, bodies, and femur bones relative to the older cattle in the Restricted and Slow groups when compared at the same weight (Table 2). Such effects have been shown previously (Purchas and Grant, 1995) and reflect the fact that cattle tend to continue to grow in frame size even when overall body growth has been restricted by lower levels of nutrition. Differences between groups in the weights of heart and liver were small, but hearts were heavier ($P < 0.05$) for bulls than steers, and the Fast-group cattle had lighter livers than animals in the Slow and Restricted groups ($P < 0.001$).

Teeth eruption patterns at the time of slaughter (results not shown) revealed no clear differences between

the bulls and steers. All animals in the Fast group and 23.1% of those in the Restricted and Slow groups had no permanent incisors erupted at the time of slaughter, which indicates that the different tenderness of beef from cattle in these groups could not have been predicted satisfactorily on the basis of teeth eruption patterns if the age of the animals was not known.

Results relating to the fatness and muscling of the cattle after adjustment to a common carcass weight are given in Table 3. As expected, steers were fatter ($P < 0.001$) than bulls at the same carcass weight for all measures of fatness, and they had smaller ($P < 0.01$) LM areas, but there was no castration effect on femur bone weight. The Fast group of cattle was fatter than the other two groups in terms of kidney and pelvic fat weight

Table 3. Least-squares means for carcass weight-adjusted composition characteristics for bulls and steers that were grown along three different growth paths

Item	Castration status			Growth pattern ^a			Carcass weight ^b	R ² , % (RSD) ^c
	Bull	Steer	Effect	Fast	Restr.	Slow		
Kidney and pelvic fat, kg	2.48	5.43	***	5.52 ^y	2.94 ^z	3.40 ^z	*	75 (1.13)
Fat thickness at rib 12, mm	1.76	5.61	***	4.73 ^y	2.99 ^z	3.34 ^z	NS	71 (1.34)
Intramuscular fat, %	0.74	2.45	***	2.02 ^y	1.40 ^z	1.38 ^z	**	54 (0.85)
LM area, cm ^{2d}	77.3	73.3	**	75.0 ^y	75.1 ^y	75.8 ^y	***	41 (6.7)
Femur weight, g	2,371	2,421	NS	2,339 ^z	2,463 ^y	2,385 ^z	***	49 (139)

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bSignificance of the carcass weight effect when carcass weight was fitted as a covariate.

^cR² = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dLongissimus muscle area between ribs 12 and 13.

^{y,z}Within the three growth patterns and within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 4. Least squares means for pH-adjusted evaluations by a trained sensory panel of juiciness and tenderness characteristics of longissimus muscle from bulls and steers that were grown along three different growth paths

Item	Castration status			Growth pattern ^a			pH effect (lin, qua) ^b	R ² , % (RSD) ^c
	Bull	Steer	Effect	Fast	Restr.	Slow		
Initial juiciness ^d	4.19	4.70	***	4.52 ^y	4.42 ^y	4.40 ^y	†, NS	39 (0.60)
Hardness	5.98	4.76	***	4.90 ^z	5.55 ^y	5.65 ^y	*** **	57 (0.70)
Cohesiveness	6.03	4.51	***	4.70 ^z	5.50 ^y	5.61 ^y	* **	53 (0.88)
Toughness	5.84	4.14	***	4.36 ^z	5.27 ^y	5.33 ^y	** ***	55 (0.97)
Chewiness	6.46	4.79	***	5.05 ^z	5.85 ^y	5.69 ^y	** ***	56 (0.91)
Overall juiciness	4.60	4.80	*	4.69 ^y	4.72 ^y	4.68 ^y	NS, NS	49 (0.40)

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bSignificance of the ultimate-pH effect when it was fitted as a covariate with linear (lin) and quadratic (qua) terms.

^cR² = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dAll characteristics were assessed on scales of 10, where for initial and overall juiciness, 0 = not juicy and 10 = very juicy, for hardness, 0 = soft and 10 = hard, for cohesiveness, 0 = not cohesive and 10 = very cohesive, for toughness, 0 = tender and 10 = tough, and for chewiness, 0 = not chewy and 10 = very chewy.

^{y,z}Within the three growth patterns and within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

($P < 0.05$), fat thickness ($P < 0.05$), and intramuscular fat level ($P < 0.05$) (Table 3), and had significantly lighter ($P < 0.05$) femur bones at the same carcass weight. Longissimus muscle areas did not differ ($P > 0.10$) between the growth-pattern groups. There are numerous reports of cattle being less fat at a common carcass weight when they have undergone a period of restricted feeding prior to being finished; although in some studies, it is difficult to separate the effects of growth pattern from the effects of different diets. Carstens et al. (1991) found that Angus-Hereford cross steers that had been through a period of restricted growth prior to finishing were less fat (24 vs 32% empty body fat) than a nonrestricted group of the same final weight. Purchas and Grant (1995) demonstrated that cattle from the same initial population that were slaughtered at 20 mo were fatter than those slaughtered at 28 mo after adjustments were made for differences in carcass weight. Steen and Kilpatrick (1995) reported that cattle finished on a ration of grass silage and concentrates offered ad libitum grew faster and had greater fat depths at the same carcass weight (+35% for bulls and +14% for steers) than cattle fed at a rate of 80% ad libitum. Short et al. (1999) found that steers of several crosses placed on a high-concentrate finishing diet at 6 mo of age had fat depths and marbling scores approximately double those for cattle placed on-feed at 12 mo of age, when comparisons were made at a carcass weight of about 250 kg.

Sensory and Objective Measures of Beef Tenderness

Results using both subjective and objective measurements were very consistent in showing that beef from bulls was tougher ($P < 0.01$) than that from steers (Tables 4 and 5). Sensory evaluation of the four aspects of tough-

ness assessed (hardness, cohesiveness, toughness, and chewiness) were higher ($P < 0.001$) for the bull beef (Table 4). In addition, bull beef was assessed as being less juicy ($P < 0.05$), particularly in terms of initial juiciness, which may be attributable in part to the fact that intramuscular fat levels were only about 30% of those for steer beef. Juiciness was included in the sensory analysis because it has been shown to be an integral component of the sensory perception of meat texture (Mathoniere et al., 2000).

Objective measures of tenderness also showed that the beef from bulls was tougher than that from steers, with higher ($P < 0.001$) forces being required for the Warner-Bratzler device, the MIRINZ tenderometer, and the Instron compression measurements (Table 5). Multiple objective measures were employed because different components of tenderness were measured by the different devices. For example, the difference between WB-PF and WB-IY has been shown to be indicative of the connective tissue contribution to tenderness (Beilken et al., 1986), and the Instron compression measures should have been indicative of connective tissue characteristics because of the lower cooking temperature and a shorter cooking time, as well as the nature of the measurement (Eikelenboom et al., 1998). The fact that the difference for the compression measures was at least as great as for other measures of tenderness, indicates that collagen differences may have been involved in toughness differences between beef from bulls and steers, as has been suggested in other studies (Dikeman et al., 1986; Bosselmann et al., 1995).

Ultimate pH as a linear and quadratic term was included as a covariate for all the characteristics shown in Tables 4 and 5 because it had a significant effect on

most of the characteristics. The nature of the relationship with measures of tenderness was similar to that reported elsewhere (e.g., Purchas and Aungsupakorn, 1993) with maximal toughness at a pH of around 6.0. When ultimate pH was left out of the model, the coefficients of determination (R^2) were significantly reduced, but the nature and significance of differences between the groups remained essentially the same.

Differences between the three growth-pattern groups for measures of beef tenderness were smaller than the differences between bulls and steers, but generally, beef from the Fast group was more tender than that from the Slow and Restricted groups based on sensory scores (Table 4) and objective measures (Table 5). In some cases (WB-IY, WB-WD, and MIRINZ force score), the Restricted group was not significantly different from either of the other groups. Unlike the bull/steer comparison, growth pattern did not affect the Instron compression parameters (Table 5) or measures of sensory juiciness (Table 4). Interactions between growth pattern and castration status were not significant. Means within the subgroups for two measures of tenderness (Figure 2) illustrate how the Fast group bulls produced beef that was not significantly tougher than beef from steers of the Slow or Restricted groups.

These results indicate that the greater tenderness of beef from cattle aged 16 to 18 mo (the Fast group), relative to cattle taken through a second winter to an age of 24 to 28 mo (the Restricted and Slow groups), was due to the lower age of the former cattle or to their different growth patterns and levels of nutrition rather than to the fact that their early growth rates were slower. From these results, it is not possible to distinguish between the

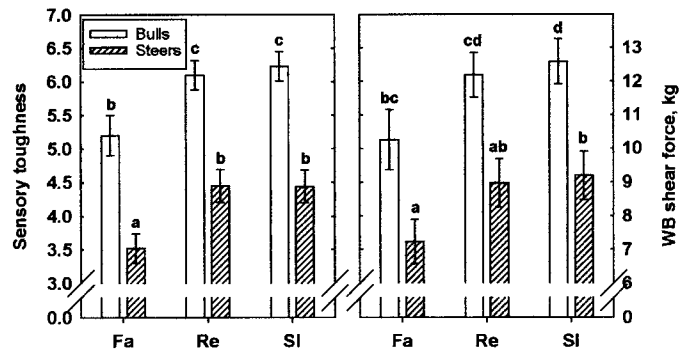


Figure 2. Least squares means (\pm SE) showing the effects of treatment (Fa = Fast group, Re = Restricted group, Sl = Slow group) and castration status on the tenderness of the longissimus muscle as assessed by sensory panel toughness (0 = tender, 10 = tough) (left graph) or shear force values using a Warner-Bratzler shear device fitted with a square blade (right graph). Within either graph, bars without a common letter above them differ significantly ($P < 0.05$).

effects of the different growth patterns and the different ages. The term growth pattern as used here encompasses several variables, including different levels of nutrition, the pattern of growth rate changes, and different seasons of the year at the time of slaughter.

Other Quality-Related Characteristics

Beef from Bulls and Steers. Ultimate pH values were higher ($P < 0.001$) for bulls than steers (Table 6), but the

Table 5. Least squares means for pH-adjusted objective measures of the tenderness of cooked longissimus muscle from bulls and steers that were grown along three different growth paths

Item	Castration status			Growth pattern ^a			pH effect (lin, qua) ^b	R^2 , % (RSD) ^c
	Bull	Steer	Effect	Fast	Restr.	Slow		
Warner-Bratzler shear parameters ^d								
WB-PF, kg	11.68	8.46	***	8.74 ^y	10.58 ^x	10.89 ^x	NS ***	39 (2.90)
WB-IY, kg	9.65	7.06	***	7.35 ^y	8.63 ^{xy}	9.08 ^x	NS ***	35 (2.60)
WB-WD, kg	3.50	2.78	***	2.87 ^y	3.15 ^{xy}	3.38 ^x	NS ***	34 (0.80)
PF-IY, kg	2.04	1.40	***	1.40 ^y	1.95 ^x	1.81 ^x	* ***	41 (0.65)
PF/WD	3.32	3.05	***	3.03 ^z	3.33 ^x	3.19 ^y	NS **	58 (0.21)
MIRINZ force score, kg	7.45	5.28	***	5.45 ^y	6.67 ^{xy}	6.96 ^x	NS ***	40 (2.13)
Instron compression parameters								
Maximum force, N	110.7	68.8	***	82.5 ^x	93.8 ^x	92.9 ^x	* *	48 (24.0)
Force at 8 mm, N	93.0	62.4	***	90.4 ^x	82.0 ^x	80.6 ^x	NS *	39 (21.0)
Work done to 8 mm, J	0.44	0.29	***	0.37 ^x	0.37 ^x	0.35 ^x	NS †	43 (0.09)

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bSignificance of the ultimate-pH effect when it was fitted as a covariate with linear (lin) and quadratic (qua) terms.

^c R^2 = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dWB-PF = Warner-Bratzler (WB) peak force; WB-IY = WB initial yield; WB-WD = WB work done in terms of the average of values making up the force-deformation curve; PF-IY = peak force minus initial yield; PF/WD = peak force relative to work done.

^{x,y,z} Within the three growth patterns and within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

difference of 0.19 pH units was smaller than for some previous studies. Purchas and Grant (1995), for example, reported mean values of 5.64 and 6.07 for Friesian-cross steers and bulls, respectively. The higher ($P < 0.05$) ultimate pH for the Fast group relative to the Slow and Restricted groups (Table 6) was largely attributable to a particularly large difference between bulls and steers in the Fast group (5.88 for bulls vs 5.50 for steers), giving rise to a significant bull/steer \times growth pattern interaction for ultimate pH ($P < 0.01$). All characteristics in Table 6, except MFI%, were significantly affected by ultimate pH and were, therefore, adjusted to a common ultimate pH. This gave models with a better fit (higher R^2 values), and including adjustments for ultimate pH had minimal effects on the size or significance of differences between castration groups or growth-pattern groups for measures of tenderness or most other quality characteristics. This contrasts with the results of Purchas and Aungsupakorn (1990), where differences between bulls and steers for several quality characteristics changed when adjustments for ultimate pH were made; but in that study, the group difference in mean pH was much larger.

The nature of the relationships between ultimate pH and quality characteristics were consistent with those reported previously (Purchas et al., 1999), in that higher ultimate pH values were associated with lower values for color parameters (overall linear correlations [r] of -0.62 , -0.56 , and -0.69 , for L^* , a^* and b^* , respectively), shorter sarcomere lengths ($r = -0.32$), slightly higher fiber diameters ($r = +0.19$), and higher water-holding

capacity ($r = -0.63$, -0.28 , and -0.60 for expressed juice, cooking loss at 60°C , and cooking loss at 70°C , respectively). The low positive relationship between pH and fiber diameter reflects the shorter sarcomeres at higher pH values.

Beef from bulls and steers did not differ with respect to pH-adjusted lightness (L^*), but beef from steers was redder ($P < 0.001$) and more yellow ($P < 0.001$) than beef from bulls. When values were not adjusted to constant pH, L^* values were also lower for bulls (35.0 vs 36.8, $P < 0.01$). The lower MFI% values were consistent with studies showing lower proteolytic enzyme activity in muscle from bulls (Morgan et al., 1993; Thompson et al., 1996). The lower water-holding capacity of bull beef after adjustment for pH differences may partially explain the lower levels of tenderness for beef from bulls relative to that from steers. Lower pH-adjusted levels of cooking loss have been reported previously for beef from bulls (Dikeman et al., 1986; Purchas et al., 1997), whereas differences between beef from bulls and steers for cooking losses and expressed juice values were not significant when data were not adjusted for pH (data not shown). Similar results have been reported previously by Purchas and Aungsupakorn (1993) and Purchas and Grant (1995).

A clear explanation of why the beef from bulls was less tender than that from steers in this study was not apparent, but the lower proteolytic activity, slightly higher ultimate pH, lower levels of intramuscular fat, higher cooking losses, and possibly a greater contribution of connective tissue components may all have contrib-

Table 6. Least squares means for ultimate pH and other pH-adjusted quality measurements made on longissimus muscle of bulls and steers grown along three different growth paths

Item	Castration status			Growth pattern ^a			pH effect (lin, qua) ^b	R^2 , % (RSD) ^c
	Bull	Steer	Effect	Fast	Restr.	Slow		
Ultimate meat pH	5.66	5.47	***	5.69 ^y	5.49 ^z	5.51 ^z	—	46 (0.18)
Color Parameters								
L^* (Lightness)	35.6	36.3	ns	35.4 ^y	36.3 ^y	36.1 ^y	*** **	49 (1.7)
a^* (Redness)	13.3	14.5	***	15.3 ^y	13.4 ^z	12.9 ^z	*** NS	64 (1.3)
b^* (Yellowness)	5.1	6.0	***	5.92 ^y	5.45 ^{yz}	5.29 ^z	*** **	66 (0.9)
MFI% ^d	87.9	95.8	***	94.1 ^y	90.7 ^z	90.8 ^z	NS NS	56 (4.4)
Sarcomere length, μm	1.76	1.75	ns	1.78 ^y	1.74 ^y	1.74 ^y	*** *	25 (0.09)
Fiber diameter, μm	70.4	64.9	**	68.5 ^y	68.4 ^y	66.1 ^y	** †	58 (8.0)
Expressed juice, $\text{cm}^2 \cdot \text{g}^{-1}$	40.5	39.7	*	40.0 ^y	40.7 ^y	39.6 ^y	*** **	57 (2.4)
Cooking loss at 60°C , %	15.8	14.6	**	14.1 ^y	16.0 ^y	15.4 ^y	*** **	65 (3.1)
Cooking loss at 70°C , %	27.7	26.4	***	25.8 ^z	27.8 ^y	27.6 ^y	*** **	73 (2.2)

^aFast = fast growth pattern; Restr. = animals with the potential for fast growth that were restricted to grow at a similar rate to the Slow group; Slow = slow growth pattern.

^bSignificance of the ultimate-pH effect when it was fitted as a covariate with linear (lin) and quadratic (qua) terms.

^c R^2 = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dMFI% = myofibrillar fragmentation index.

^{y,z}Within the three growth patterns and within a row, means without a common superscript letter differ ($P < 0.05$).

NS = $P > 0.10$.

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

uted. Comparisons of the tenderness of beef from bulls and steers have been reported many times with the results being highly variable, as noted in reviews by Field (1971), Seideman et al. (1982), and Purchas (1991). The tenderness difference reported here was larger than that in most previous studies, and although it is supported by some other reports (Crouse et al., 1983; Gregory et al., 1983; Dikeman et al., 1986), it also needs to be considered alongside many other studies where significant differences have not been detected (Woodhams and Trower, 1965; Dransfield et al., 1984; Purchas and Grant, 1995). Clear explanations for the basis of these variable results would be of value when seeking ways to produce beef of consistently high quality from bulls.

Growth-Pattern Effects. Color differences between the three growth-pattern groups were small (Table 6), with no difference in lightness, but with the Fast group producing beef that was slightly redder and more yellow ($P < 0.05$) after an adjustment for differences in ultimate pH. Beef from the Fast group also had a significantly higher MFI% ($P < 0.05$), suggesting that proteolytic activity was greater, which could go some way to explaining the higher tenderness scores. There were no differences ($P > 0.10$) in sarcomere length or fiber diameter, and measures of water-holding capacity were similar ($P > 0.10$), except that cooking loss at 70°C was lower ($P < 0.05$) for the Fast group than the Slow and Restricted groups. Overall, there was no single characteristic that stood out as being responsible for the greater tenderness of beef from the Fast group for both bulls and steers (Figure 2), and it seems likely that the difference may have been the net effect of a number of factors, including higher MFI% and intramuscular fat level, lower cooking loss, and possibly, differences in the nature of the collagen that were not measured directly in this study. The fact that there was little difference in the tenderness of beef between the Restricted and Slow groups indicates that their lower tenderness relative to the Fast group was primarily due to their greater age and/or to the different growth paths.

Clear reductions in beef tenderness have been reported when wide ranges in age have been considered (Hiner and Hankins, 1950 [2.5 to 67 mo of age]; Tuma et al., 1962 [18 mo to 90 mo of age]), and especially when muscles with a high connective tissue content are considered (Shorthose and Harris, 1990), apparently largely due to increases in collagen cross-linking (Goll et al., 1964; Nishimura et al., 1999). Over shorter age ranges, such as those involved in the current trial (8 to 10 mo), there have been reports of increases, decreases, and no change in measures of tenderness. Thus, Jacobson and Fenton (1956) reported that tenderness of beef from Holstein heifers decreased as age increased from 11 to 20 mo, and Field et al. (1966) showed that beef was tougher for bulls aged 600 to 699 d relative to those aged 300 to 399 d, but was more tender for steers and heifers of similar ages. No significant difference in tenderness was noted between cattle aged 12 or 24 mo by Dikeman et al. (1986) or by Gullet et al. (1996), but Short et al. (1999) showed

that tenderness improved with increased time on feed (and therefore increased age), particularly for cattle that entered the feedlot at 12 mo of age. Vestergaard et al. (2000) reported that beef from bulls raised in an extensive system to 14 mo was less tender than beef from bulls raised intensively to the same weight by 11 mo. Muir et al. (2001) reported that pasture-fed steers that had undergone a period of slow growth over winter yielded beef that was less tender than that from control cattle that had grown faster and were therefore younger at slaughter. Oddy et al. (2001), in reviewing the effect of patterns of growth, concluded that there was good evidence that growth patterns could influence beef tenderness, but that the exact nature of the effects could not be accurately predicted. They did note, however, that high rates of growth leading up to slaughter, as was the case for all groups in the current trial (Table 1), were generally associated with reduced toughness. Sinclair et al. (2001), on the other hand, concluded that there was limited scope for improving beef eating quality by increasing growth rate through higher levels of nutrition.

Holding-Time Effects

Cattle held at the meat plant for an extra 24 h had lower carcass weights ($P < 0.01$) (Table 7), which was probably due to a decrease in gut contents (Kirton et al., 1972). This was reflected in a lower ($P < 0.001$) dressing percentage based on live weight at the time of slaughter for the 4-h hold group. Dressing percentage based on live weight prior to trucking, however, was higher ($P < 0.001$) for the 4-h hold group, indicating that some of the weight lost over the extra 24 h of holding time was carcass weight. For a 500-kg animal, this decrease in dressing-out percentage would represent a decrease of 6.9 kg in carcass weight. The suggestion by these results that significant carcass weight losses may occur after fasting times of 30 h or less, is in agreement with some other studies (Raikes and Tilley, 1975; Jones et al., 1990; Purchas, 1992), but not with others (Carr et al., 1971; Kirton et al., 1972), where longer periods off feed have been needed before carcass weight losses have been detected.

Ultimate muscle pH was slightly higher ($P < 0.05$) for the group held for 28 h, and there was a significant holding time \times gender interaction for ultimate pH ($P < 0.05$), with the holding time having a greater effect on bulls (5.57 and 5.75 for holding times of 4 h and 28 h, respectively, $P < 0.05$) than steers (5.47 and 5.46 for holding times of 4 h and 28 h, respectively, $P > 0.10$). Previous studies have also indicated that preslaughter holding time has a greater effect on the ultimate pH of bulls than of steers (Purchas, 1992).

None of the pH-adjusted measures of beef tenderness, juiciness, or color differed between the two holding-time groups. Three of these measurements are given as examples in Table 7. Similar results were obtained for unadjusted values (data not shown). Beef from cattle held for the extra 24 h had lower ($P < 0.001$) expressed juice levels and lower ($P < 0.05$) cooking losses at 70°C when

Table 7. Least squares means for carcass and meat quality characteristics for cattle held at the meat plant for either 4 or 28 h prior to slaughter

	Holding time, h ^a		Effect	Covariate ^b	R ² , % (RSD) ^c
	4	28			
Number of cattle	59	58		—	—
Carcass weight, kg	281.2	267.0	**	—	23 (24.4)
Dressing-out percent (1) ^d	54.16	55.62	***	Carcass weight	54 (1.50)
Dressing-out percent (2) ^d	51.99	50.73	***	Carcass weight	69 (1.54)
Ultimate muscle pH	5.51	5.61	*	—	46 (0.18)
Sensory toughness	5.03	4.95	NS	Ultimate pH	55 (0.97)
Sensory overall juiciness	4.73	4.67	NS	Ultimate pH	49 (0.40)
WB-PF, kg ^e	10.03	10.11	NS	Ultimate pH	39 (2.90)
Expressed juice, cm ² ·g ⁻¹	41.1	39.1	***	Ultimate pH	57 (2.4)
Cooking loss at 60°C, %	15.8	14.6	NS	Ultimate pH	65 (3.1)
Cooking loss at 70°C, %	27.6	26.4	*	Ultimate pH	73 (2.2)

^aHolding times at the plant of 4 and 28 h correspond to times off feed of approximately 6 and 30 h, respectively.

^bInformation regarding the significance of the covariate effects is given in previous tables. Ultimate pH was fitted as a covariate with both linear and quadratic terms.

^cR² = coefficient of determination expressed as a percentage; RSD = residual standard deviation.

^dDressing-out percent (1) is based on live weights at the time of slaughter. Dressing-out percent (2) is based on full live weights prior to trucking.

^eWB-PF = Warner-Bratzler (WB) peak force.

NS = $P > 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

adjustments were made for differences in ultimate pH. The differences remained when adjustments for pH were not made (data not shown). These results are consistent with a loss of muscle water during the longer holding period, as was suggested by the studies of Jones et al. (1988).

Implications

This study sought to determine whether the greater tenderness of the longissimus muscle from cattle that reached a finished weight sooner was attributable mainly to their higher growth potential or their younger age at slaughter. The results, which were obtained by limiting the feed for a group with a high growth potential so they reached a slaughter weight at the same time as cattle with a lower growth potential, showed that tenderness of beef from this restricted group was lower than that of the fast-growing group and very similar to the slow group. This suggests that beef tenderness is determined more by the age at slaughter than by early growth rates, although in this study it was not possible to separate age effects from effects of different nutritional levels and seasons of slaughter. These growth-pattern effects on tenderness were similar for beef from steers and bulls, but beef from bulls was less tender than that from steers for all groups.

Literature Cited

Beilken, S. L., P. E. Bouton, and P. V. Harris. 1986. Some effects on the mechanical properties of meat produced by cooking at temperatures between 50° and 60°C. *J. Food Sci.* 51:791–796.

- Bendall, J. R. 1973. Postmortem changes in muscle. Pages 243–309 in *The Structure and Function of Muscle*. G. H. Bourne, ed. Academic Press, New York.
- Bouton, P. E., A. L. Fisher, P. V. Harris, and R. I. Baxter. 1973. A comparison of the effects of some post-slaughter treatments on the tenderness of beef. *J. Food Technol.* 8:39–49.
- Bosselmann, A., C. Moller, H. Steinhart, M. Kirchgessner, and F. J. Schwarz. 1995. Pyridinoline cross-links in bovine muscle collagen. *J. Food Sci.* 60:953–958.
- Brannang, E. 1971. Studies on monozygous cattle twins. XXIII. The effect of castration and age of castration on the development of single muscles, bones and special sex characters. Part II. *Swedish J. Agric. Res.* 1:69–78.
- Carr, T. R., D. M. Allan, and P. Phar. 1971. Effect of preslaughter fasting on bovine carcass yield and quality. *J. Anim. Sci.* 32:870–873.
- Carstens, G. E., D. E. Johnson, M. A. Ellenberger, and J. D. Tatum. 1991. Physical and chemical components of the empty body during compensatory growth in beef steers. *J. Anim. Sci.* 69:3251–3264.
- Chambers, E., IV, and J. R. Bowers. 1993. Consumer perception of sensory qualities in muscle foods. *Food Technol.* 47:116–120.
- Crouse, J. D., S. C. Seideman, and H. R. Cross. 1983. The effects of carcass electrical stimulation and cooler temperature on the quality and palatability of bull and steer beef. *J. Anim. Sci.* 56:81–90.
- Dikeman, M. E., G. B. Reddy, V. H. Arthaud, H. J. Tuma, R. M. Koch, R. W. Mandigo, and J. B. Axe. 1986. Longissimus muscle quality, palatability and connective tissue histological characteristics of bulls and steers fed different energy levels and slaughtered at four ages. *J. Anim. Sci.* 63:92–101.
- Dransfield, E., G. R. Nute, and M. A. Fancombe. 1984. Comparison of eating quality of bull and steer beef. *Anim. Prod.* 39:37–50.
- Eikelenboom, G., V. M. H. Barnier, A. H. Hoving-Bolink, F. J. M. Smulders, and J. Culioli. 1998. Effect of pelvic suspension and cooking temperature on the tenderness of electrically stimulated and aged beef, assessed with shear and compression tests. *Meat Sci.* 49:89–99.
- Ferguson, D. M., H. L. Bruce, J. M. Thompson, A. F. Egan, D. Perry, and W. R. Shorthose. 2001. Factors affecting beef palatability—farmgate to chilled carcass. *Aust. J. Exp. Agric.* 41:879–891.

- Field, R. A. 1971. Effect of castration on meat quality and quantity. *J. Anim. Sci.* 32:849–858.
- Field, R. A., G. E. Nelms, and G. E. Schoonover. 1966. Effects of age, marbling, and sex on palatability of beef. *J. Anim. Sci.* 25:360–366.
- Goll, D. E., W. G. Hoekstra, and R. W. Bray. 1964. Age-associated changes in bovine muscle connective tissue. *J. Food Sci.* 24:615–621.
- Gregory, K. E., S. C. Seideman, and J. J. Ford. 1983. Effects of late castration, zeranol, and breed group on composition and palatability characteristics of longissimus muscle of bovine males. *J. Anim. Sci.* 56:781–786.
- Gullet, E. A., S. Buttenham, and T. Hore. 1996. Effect of age and cut on consistency of tenderness and leanness of beef. *Food Qual. Pref.* 7:37–45.
- Harper, G. S. 1999. Trends in skeletal muscle biology and the understanding of toughness in beef. *Aust. J. Agric. Res.* 50:1105–1129.
- Harris, P. V. 1976. Structural and other aspects of meat tenderness. *J. Texture Stud.* 7:49–63.
- Hiner, R. L., and O. G. Hankins. 1950. The tenderness of beef in relation to different muscles and age in the animal. *J. Anim. Sci.* 9:347–373.
- Jacobson, M. J., and F. Fenton. 1956. Effects of three levels of nutrition and age of animal on the quality of beef. I. Palatability, cooking data, moisture, fat, and nitrogen. *Food Res.* 21:415–426.
- Johnson, M. H., C. R. Calkins, R. D. Huffman, D. D. Johnson, and D. D. Hargrave. 1990. Differences in cathepsin B + L and calcium-dependent protease activities among breed type and their relationship to beef tenderness. *J. Anim. Sci.* 68:2371–2379.
- Jones, S. D. M., A. L. Schaefer, W. M. Robertson, and B. C. Vincent. 1990. The effects of withholding feed and water on carcass shrinkage and meat quality in beef cattle. *Meat Sci.* 28:131–139.
- Jones, S. D. M., A. L. Schaefer, A. K. W. Tong, and B. C. Vincent. 1988. The effects of fasting and transportation on beef cattle. 2. Body component changes, carcass composition and meat quality. *Livest. Prod. Sci.* 20:25–35.
- Kirton, A. H., D. J. Paterson, and D. M. Duganzich. 1972. Effect of pre-slaughter starvation in cattle. *J. Anim. Sci.* 34:555–559.
- Macfarlane, P. G., and J. M. Marer. 1966. An apparatus for determining the tenderness of meat. *Food Technol.* 20:134–135.
- Mathoniere, C., L. Mioche, E. Dransfield, and J. Culioli. 2000. Meat texture characterisation: comparison of chewing patterns, sensory and mechanical measures. *J. Texture Stud.* 31:183–203.
- Morgan, J. B., T. L. Wheeler, M. Koohmaraie, J. W. Savell, and J. D. Crouse. 1993. Meat tenderness and the calpain proteolytic system in longissimus muscle of young bulls and steers. *J. Anim. Sci.* 71:1471–1476.
- Muir, P. D., N. B. Smith, P. M. Dobbie, D. R. Smith, and M. D. Bown. 2001. Effects of growth path on beef quality in 18-month-old Angus and South Devon \times Angus pasture-fed steers. *Anim. Sci.* 72:297–308.
- Nishimura, T., A. Hattori, and K. Takahashi. 1999. Structural changes in intramuscular connective tissue during the fattening of Japanese Black cattle: Effect of marbling on beef tenderization. *J. Anim. Sci.* 77:93–104.
- Oddy, V. H., G. S. Harper, P. L. Greenwood, and M. B. McDonagh. 2001. Nutritional and developmental effects on the intrinsic properties of muscles as they relate to the eating quality of beef. *Aust. J. Exp. Agric.* 41:921–942.
- Peachey, B. M., R. W. Purchas, and L. M. Duizer. 2002. Relationships between sensory and objective measures of meat tenderness on *m. longissimus thoracis* from bulls and steers. *Meat Sci.* 60:211–218.
- Purchas, R. W. 1991. Effect of sex and castration on growth and composition. Pages 203–254 in *Growth Regulation in Farm Animals. Advances in Meat Research*, Vol. 7. A. M. Pearson and T. R. Dutson, ed. Elsevier, London.
- Purchas, R. W. 1992. Does reducing pre-slaughter holding time to four hours decrease the incidence of dark-cutting beef? *Proc. 27th Meat Ind. Res. Conf.*, Hamilton, NZ 27:107–114.
- Purchas, R. W., and R. Aungsupakorn. 1993. Further investigations into the relationship between ultimate pH and tenderness for beef samples from bulls and steers. *Meat Sci.* 34:163–178.
- Purchas, R. W., and D. A. Grant. 1995. Liveweight gain and carcass characteristics of bulls and steers farmed on hill country. *N. Z. J. Agric. Res.* 38:131–142.
- Purchas, R. W., D. G. Hartley, Y. Xun, and D. A. Grant. 1997. An evaluation of the growth performance, carcass characteristics, and meat quality of Sahiwal-Friesian cross bulls. *N. Z. J. Agric. Res.* 40:497–506.
- Purchas, R. W., X. Yan, and D. G. Hartley. 1999. The influence of a period of ageing on the relationship between ultimate pH and shear values of beef *m. longissimus thoracis*. *Meat Sci.* 51:135–141.
- Raikes, R., and D. S. Tilley. 1975. Weight loss of fed steers during marketing. *Am. J. Agric. Econ.* 57:83–89.
- Seideman, S. C., H. R. Cross, R. R. Oltjen, and B. D. Schanbacher. 1982. Utilization of the intact male for red meat production: A review. *J. Anim. Sci.* 55:826–840.
- Short, R. E., E. E. Grings, M. D. MacNeil, R. K. Heitschmidt, C. B. Williams, and G. L. Bennett. 1999. Effects of sire growth potential, growing-finishing strategy, and time on feed on performance, composition, and efficiency of steers. *J. Anim. Sci.* 77:2406–2417.
- Shorthose, W. R., and P. V. Harris. 1990. Effect of animal age on the tenderness of selected beef muscles. *J. Food Sci.* 55:1–8.
- Sinclair, K. D., G. E. Lobley, G. W. Horgan, D. J. Kyle, A. D. Porter, K. R. Matthews, C. C. Warkup, and C. A. Maltin. 2001. Factors influencing beef eating quality. 1. Effects of nutritional regimen and genotype on organoleptic properties and instrumental texture. *Anim. Sci.* 72:269–277.
- Steen, R. W. J., and D. J. Kilpatrick. 1995. Effects of plane of nutrition on slaughter weight on the carcass composition of serially slaughtered bulls, steers and heifers of three breed crosses. *Livest. Prod. Sci.* 43:205–213.
- Thompson, B. C., P. M. Dobbie, N. J. Simmons, K. Singh, and P. A. Speck. 1996. Differences in the post mortem kinetics of the calpain system in meat from bulls and steers. *Proc. N. Z. Soc. Anim. Prod.* 56:195–197.
- Tuma, H. J., R. L. Henrickson, D. F. Stephens, and R. Moore. 1962. Influence of marbling and animal age on factors associated with beef quality. *J. Anim. Sci.* 21:848–851.
- Vestergaard, M., M. Therkildsen, P. Henckel, L. R. Jensen, H. R. Andersen, and K. Sejrsen. 2000. Influence of feeding intensity, grazing and finishing feeding on meat and eating quality of young bulls and the relationship between muscle fiber characteristics, fiber fragmentation and meat tenderness. *Meat Sci.* 54:187–195.
- Woodhams, P. R., and S. J. Trower. 1965. Palatability characteristics of rib steaks from Aberdeen Angus Steers and bulls. *N. Z. J. Agric. Res.* 8:921–926.