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Selection for growth rate at pasture in Angus cattle results in heavier cattle that eat more in the feedlot

R. M. Herd[A,B,*], V. H. Oddy[A,B], P. F. Arthur[C] and M. B. McDonagh[D]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
R. M. Herd
NSW Department of Primary Industries, Livestock Industry Centre, Armidale, NSW 2351, Australia
Email: robert.herd@dpi.nsw.gov.au

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ABSTRACT

Context. Selection for growth rate has received considerable attention in beef cattle but the evidence for an improvement in the efficiency of feed conversion is equivocal. **Aim.** To examine whether feed efficiency by beef cattle finished in a feedlot had been changed in response to divergence selection for growth rate. **Methods.** The Angus cattle used came from three lines of cattle selected for over five generations for fast growth rate to yearling age (High-line), slow growth (Low-line), or from an unselected Control-line. Over sequential years, a cohort of steers, then of heifers and then of steers, representative of the lines, were measured for feedlot performance, and carcase- and meat-quality traits. The animals were fed a high-energy feedlot ration and after an adjustment period they underwent a performance test of at least 70 days of duration. After slaughter, muscle samples were taken for subsequent measurement of the components of the endogenous calpain proteolytic enzyme system. Their carcasses underwent a standard chiller assessment and meat samples were taken after 1 day and 14 days (steers) or 17 days (heifers) for objective measurement of tenderness. **Key results.** Cattle from the High-line grew 48% faster ($P < 0.05$), and ate 48% more feed ($P < 0.05$) than did those from the Low-line, but had similar ($P > 0.05$) feed conversion ratio and residual feed intake. There were no differences between the High-line and Low-line in the visual meat-quality attributes of meat colour, fat colour and marbling, and no differences in the objective measurements of tenderness and connective-tissue toughness. There was no evidence of a selection response in the circulating concentrations of the metabolites and hormones measured, nor in the endogenous calpain proteolytic enzyme system in muscle. **Conclusions.** The superior growth demonstrated by the High-line cattle over the feedlot test was accompanied by a higher feed intake, with no evidence for an improvement in feed efficiency. **Implications.** Selection for growth rate is a powerful tool to alter animal performance but the beef industry needs to be cognisant of the proportional increase in feed requirement from breeding bigger animals.

Keywords: ADG, calpain, calpastatin, FCR, meat quality, RFI, tenderness, weight.

Introduction

Selection for growth rate has received considerable attention as a means to improve the efficiency of beef production (Barlow 1984). The evidence that selection for growth rate in cattle is accompanied by an improvement in the efficiency of feed conversion is equivocal (Herd *et al.* 1991). Since that time, the authors are aware of only two published experiments with beef cattle (Morris *et al.* 1992; Koch *et al.* 2004) on the consequences of selection for weight on feed intake of growing animals and both experiments provide evidence of no improvement in feed conversion. The increase in cow size, and presumably in feed costs for the cow herd accompanying selection for growth, led Barlow (1984) to question whether growth selection would lead to a net benefit in whole-herd efficiency and profitability. Studies on Angus cows from lines divergently selected for growth rate from birth to yearling age have shown that, compared with cows in the low-growth line, the correlated increase in cow size in the high-growth line was accompanied by an increase in feed required for maintenance of liveweight and increase in feed consumed by the cow/calf

unit over an annual production cycle, with no improvement in the efficiency of feed use (Herd 1995; Herd and Oddy 2023).

Protein turnover in the tissues of farm animals is an energetically expensive process (Lobley 2003) and variation in protein turnover in response to level of nutrition and between genotypes is known (Lobley 1998). Variation in protein turnover has been shown to accompany genetic selection for growth and other traits in domestic animals (Oddy 1999) and these differences may, in part, account for the response to selection. Thus, for example, Oddy *et al.* (1998) reported that in Angus steers from lines divergently selected for growth rate, the difference in oxygen consumption accompanying divergence in protein turnover could explain up to 70% of the difference in growth when they were fed at 1.6 times their expected maintenance requirement. About half the variation in protein degradation measured *in vivo* can be accounted for by the activity of the calpain system (Oddy *et al.* 2001). The calpain system comprises endogenous proteases (calpains), which are considered as the primary candidates for muscle protein degradation postmortem, and with their endogenous inhibitor, calpastatin, contribute to the meat tenderisation process during aging (Bhat *et al.* 2018).

The aim of this experiment was to measure the response to divergent selection for yearling growth rate on the growth, feed intake, feed efficiency, carcase and meat tenderness attributes in Angus cattle fed for slaughter under feedlot conditions. Further, aspects of the physiological basis of the growth response from differences in the endogenous calpain proteolytic enzyme system in muscle, differences in the concentration in blood of four metabolic markers, and any differential responses to implantation with a mixed anabolic hormonal growth promotant (HGP) were also determined. The Angus cattle came from closed lines that had been divergently selected for over five generations for the single trait of growth rate at pasture and differed by 34% in yearling weight. The animals used represented a random sample of the progeny in the lines managed under identical conditions and observed differences between the selection lines reported herein can be considered to be principally a response to genetic selection (Parnell *et al.* 1997).

Materials and methods

Animals and their management

Animals were bred at the NSW Department of Primaries Research Centres at Trangie, New South Wales (NSW), and Glen Innes, NSW, under approvals from their Animal Care and Ethics Committees. Management and measurements on cattle in the research feedlot were made under approvals of the University of New England Animal Ethics Committee.

A long-term experiment based on divergent selection for daily gain in liveweight (LW) at pasture from birth to 1 year of age commenced in 1974 at Trangie (NSW, Australia). A base herd of Angus cattle was subsampled to form an unselected Control line, and the remainder divergently selected on the basis of average daily gain from birth to 1 year of age to create a high growth-rate line (High-line) and a low growth-rate line (Low-line (Parnell *et al.* 1997)). After over five generations, selection within the growth-rate lines was relaxed in 1992, at which time cattle in the High-line differed in yearling weight over the Low-line by approximately 34% (Arthur *et al.* 1997). The Trangie herd was split into three and cattle representative of each line moved to Glen Innes, NSW, and to Victoria, as described in Parnell *et al.* (1994). The lines remained closed and were maintained without further intentional selection for growth rate.

At Glen Innes, females within each selection line were subdivided into three groups and single-sire mated to sires supplied from the Trangie herd, with different sires used each year. Cattle born across 3 years were available to this experiment and within each selection line the cattle used were the progeny of nine sires. The followng three cohorts of cattle were formed for this study: Cohort 1 being steers born in the spring of 1993; Cohort 2 being heifers born in 1994; and Cohort 3 being steers born in 1995. They were weaned at approximately 7 months of age and grown on improved pastures, near Armidale, NSW, until feedlot entry. For each cohort, the cattle for feedlot evaluation were chosen from within each line after the available animals were ranked by sire and on LW taken just prior to feedlot entry.

Cohort 1 steers were grown on pasture until 19 months of age and, in April 1995, were moved into the research feedlot for a feed-efficiency evaluation. They were fed for 100 days on finisher ration, with their individual feed intake and gain in LW recorded over the final 87 days of the feedlot performance test. The Cohort 2 heifers were 16 months old when they were inducted into the feedlot in January 1996. They were fed for 97 days on finisher ration, with their individual feed intake and gain in LW recorded over the final 88 days of the performance test. Within each line, the heifers were ranked on their age and every second heifer received a HGP implant on Day 0 of the performance test. The implant used was a mixed anabolic HGP (Revalor®-h; Coopers Animal Health, Australia) formulated for beef heifers to contain 200 mg trenbolone acetate and 20 mg oestradiol in pelleted form for insertion under the skin of the ear. It is claimed to improve weight gain and feed conversion through increased deposition of lean meat tissue (https://www.coopersanimalhealth.com.au/product/revalorh/, verified 8 August 2023). The expected period of efficacy was 90 days according to the manufacturer. Cohort 3 steers were 12 months old when they were inducted into the feedlot in November 1996. They were fed for 156 days on finisher ration, with their individual feed intake and gain in LW recorded over the final 70 days of the performance test. Trait definitions and their abbreviations are given in Table 1.

Table 1. Trait definitions.

Trait name	Abbreviation	Unit	Definition
Liveweight	LW	kg	Full, not fasted, animal weight
Average daily gain	ADG	kg/day	Daily gain in LW calculated from regression of fortnightly LWs against day-of-test
Start of test LW	STWT	kg	Weight at start of feedlot test calculated from regression for ADG
End of test LW	ENDWT	kg	Weight at end of feedlot test calculated from regression for ADG
Dry-matter intake	DMI	kg/day	Daily feed dry-matter (DM) intake over the test
Feed conversion ratio	FCR	kg/kg	DMI divided by ADG
Residual feed intake	RFI	kg/day	Residual from regression of DMI against metabolic mid-test LW and ADG
Rib fat depth	RIBFAT	mm	Subcutaneous fat thickness at the 12/13th rib
Rump fat depth	RUMPFAT	cm	Subcutaneous fat thickness at the p8 rump site
Eye-muscle area	EMA	cm^2	Sectional area of the *M. longissimus dorsi* at the 12/13th rib
Carcase weight	Carcase-WT	kg	Weight of the carcase after 24 h in chiller
Dressing percentage	Dressing-%	%	Carcase-WT/ENDWT, expressed as a percentage
Marbling score	MbSc	units	Scale 0 nil visible to 12 abundant
Shear force	SF	kg	A measure of myofibrillar toughness
Compression	COMP	kg	A measure of connective tissue toughness
Calpastatin	Calp	units/g	Endogenous inhibitor of caplains
micro-calpain	μ-Cal	units/g	Endogenous protease in muscle
milli-calpain	m-Cal	units/g	Endogenous protease in muscle
Ratio of μ-Cal to Calp	μ-Cal:Calp		μ-Cal divided by Calp

Feedlot management and performance tests

Feedlot performance tests were conducted in the 'Tullimba' Research Feedlot, about 50 km west of Armidale, NSW, and operated by the University of New England. Across the years of this experiment, management of cattle, rations offered and measurement of their performance in the feedlot followed standardised procedures described in Upton *et al.* (2001). Cattle were trucked to the feedlot and held overnight in receival yards, with hay and water provided. Next day they were inducted following standard procedures in place at the feedlot. Initially, all animals within a cohort were fed together from a feedlot bunk on a starter ration (typically: 40% grain content; 7 days), then an intermediate ration (60% grain content; 7 days) and finally a finisher ration. The finisher ration contained (on fresh-weight basis) 75–79% rolled barley, 10% hammer-milled sorghum hay, 4% monensin (molasses mix containing urea), vitamins and minerals; Molafos®, Ridley Corporation, Wacol, Qld, Australia), 5% cottonseed meal pellets, 1% fine ground limestone, 0.5% sulfate of ammonia and 0.5% sodium bicarbonate. Final composition of the finisher ration was managed to provide a total mixed ration of about 89% dry matter (DM), 11 MJ of metabolisable energy and 14% crude protein/kg DM.

After approximately 1 week of being group-fed on the finisher ration, cattle within a cohort were divided into groups of 8–10 animals and each group was placed in a separate feedlot yard containing an automated self-feeder, which measured feed intake by individual animals (described in Bindon (2001)). Group size and number of groups were dictated by the number of animals available to be tested and the number of pens available with feed-intake recorders. Each group contained a representative subsample of cattle from each of the selection lines, achieved by ranking animals by sire and final LW at pasture. Self-feeders were replenished once daily and feed was available *ad libitum*. Each animal wore an electronic eartag that facilitated its identification as it entered the feeder and the weight of feed consumed at each meal by each animal was electronically recorded. Daily intakes by cattle were monitored by feedlot staff and the few animals judged to have an unacceptably low intake from the self-feeders, either before or during the performance test, were removed and fed separately, and their data were not used in this study. Cattle were weighed at the start of their test and then fortnightly, without fasting.

At the end of their performance test, a blood sample for metabolic markers was collected from each animal by tail venepuncture into evacuated tubes containing EDTA anticoagulant, stored in an insulated box above ice, centrifuged in the lab within 6 h of collection and the plasma was stored at −14°C for subsequent analyses. The cattle were scanned using an Aloka 500 ultrasound scanner (Medtel, Sydney, NSW, Australia), and the inbuilt callipers of the scanner were used to measure subcutaneous fat thickness at the 12/13th rib site (RIBFAT) and the Australian P8 rump site (RUMPFAT), and the cross-sectional area of the *M. longissimus dorsi*

('eye-muscle area'; EMA) at the 12/13th rib. The same accredited ultrasound scanner was used throughout the experiment.

Carcase and meat samples

Two to four days after the final weighing at the end of the performance tests, the animals were trucked to a commercial abattoir and slaughtered, the morning after an overnight curfew without feed but with water available. For Cohorts 1 and 3, electrical stimulation was not applied to the carcases. For Cohort 2, electrical stimulation (200 milliamps, peak voltage 45 V, 40 s) was inadvertently switched on for the first 36 bodies. The remainder, consisting of 10 HGP-treated animals from the High ($N = 2$), Control ($N = 5$) and Low ($N = 3$) lines were not stimulated. Within 1 h of death, muscle samples were removed by coring from the left-side *M. longissimus dorsi* between the 11th and 12th ribs and frozen in liquid nitrogen for later separation of the calpain-system proteins. Carcasses were weighed and stored at 1°C overnight. Next day, the *M. longissimus dorsi* was cut between the 12th and 13th ribs and scored by an accredited assessor for marble score (scale: 0, nil visible; to 12, abundant), meat colour (scale: 1, light; to 9, dark) and fat colour (scale: 0, white; to 9, yellowish). For objective measurements of meat quality, the *M. longissimus dorsi* anterior to the 13th rib was taken from the left side of each carcass and divided into two. Each piece was individually vacuum packaged. The cranial portion of half the samples from animals from each selection line and the caudal portion from the others was frozen (−20°C) at 1 day postmortem. The reminder caudal and cranial portions were vacuum packed and stored chilled (1°C) until Day 14 postmortem for the steers born in 1995, and Day 17 for the heifers, and then frozen. Meat samples from the 1993-born steers were not retained beyond 1 day.

Laboratory analyses

Metabolic markers

Total plasma protein (g/L), albumen (g/L), urea (mmol/L) and insulin (mg/L) in plasma were assayed as described in Richardson *et al.* (2004). Total plasma protein and albumen were used as markers for protein metabolism. Urea was chosen as a marker for protein degradation, with higher concentration being used as evidence of greater protein turnover. Insulin has multiple roles, including inhibiting lipolysis and stimulating lipogenesis in fat and increasing muscle protein synthesis and decreasing proteolysis. The justification of the use of these markers to detect differences in metabolic processes is discussed in Richardson and Herd (2004) and Richardson *et al.* (2004).

Meat-tenderness measurements

In addition to chiller-assessment measurements described above, shear force (myofibrillar toughness) and compression (connective-tissue toughness) values were determined on thawed meat samples following the methods of Bouton *et al.* (1975) and as described in McDonagh *et al.* (2001). Briefly, samples were thawed and cooked in individual plastic bags in a 70°C water bath for 60 min, then stored overnight at 1°C before analysis. Textural measurements were made on a Lloyd Instruments LRX Materials Testing Machine fitted with a 500N load cell (Lloyd Instruments Ltd, Hampshire, UK), and the mean of six measurements was recorded for shear force and compression. All objective meat-quality measurements were performed at the Meat Science Laboratory at the University of New England, Armidale, NSW, Australia.

Separation and functional assay of calpain-system proteins

Within 2 weeks of storage at −80°C, 5 g of trimmed and diced lean muscle was prepared for separation of calpastatin, m-calpain and μ-calpain, following the procedure described by Koohmaraie (1990), with modifications described in McDonagh *et al.* (2001). Proteolytic activity of the calpains was determined using casein as a substrate and the inhibitory activity of calpastatin was determined by titration against a fixed amount of m-calpain activity.

Derived traits

The average daily gain (ADG) in weight of each animal over the performance test period was modelled by linear regression of LW on test day and the regression equation parameters were used to calculate ADG, start-of-test weight (STWT) and end-of-test weight (ENDWT). The average of the computed start-of-test and end-of-test weights for an animal was used as the mid-test weight of an animal during the test and metabolic mid-test weight (MMWT) was calculated as $(\text{mid-test weight})^{0.73}$. To calculate RFI, a linear regression model of DMI on MMWT and ADG was performed with the residuals, representing the difference between actual (measured) DMI and that predicted from the model, saved as RFI for each animal. For the RFI calculation, the two cohorts of steers were modelled together, with cohort being fitted as a class variable. The GLM had an R^2 of 82%. The calculation of RFI for the heifers was performed separately and the GLM had an R^2 of 85%. Feed conversion ratio (FCR) was calculated as DMI divided by ADG. Days expected to be required to gain 100 kg of LW was computed as 100 kg/ADG. Feed required to gain 100 kg LW was computed as DMI times Days to gain 100 kg.

Data analyses

Data for traits were analysed using the general linear model (GLM) procedure of SAS (2022). Data for the two cohorts of steers were modelled together with cohort and selection line being fitted as class variables, plus their interaction. Data for the cohort of heifers, half of whom received the HGP implant, was modelled separately, with HGP-implant status and its

interaction with selection line included in the GLM. For the heifer cohort, the GLM for meat tenderness measurements and components of the calpain system also included whether electrical stimulation had been applied, nested within HGP status.

Results

Steers

The High-line steers were 42% heavier at the start of the feedlot test than were the Low-line steers, and grew 49% faster over the test period and were 43% heavier at the end of their test (Table 2). High-line steers ate 51% more feed per day but did not differ from the Low-line steers in FCR or RFI. Days expected to be required to gain 100 kg LW was 43 days shorter for the High-line than Low-line steers, but both lines required a similar amount of feed to achieve this same gain in LW, reflecting the lack of difference in FCR between the lines. The High-line steers had a greater depth of subcutaneous fat at the rib and rump sites, but when expressed relative to their ENDWT, the High-line steers had less subcutaneous fat at both sites than did the Low-line steers. The High-line steers had heavier carcase-WT than did the Low-line steers, but did not differ in dressing percentage. All Cohort 1 steers had the same meat colour score of 1C, whereas the Cohort 3 steers had meat colour scores of 1B (83%) and 1C (17%) with no obvious association with the selection line. All steers had a fat colour score of 0 (white). There was no difference in carcase MbSc between the selection lines.

There were no differences between the High-line and Low-line steers in the blood concentrations of the four metabolic markers analysed (Table 3). Shear force and compression values for meat did not differ between the High-line and Low-line steers, either in meat aged for 1 day or for 14 days, whereas values for both measures of tenderness were lower (more tender) after 14 days of ageing than after 1 day. The concentrations of the components of the calpain system measured in muscle taken just after death did not differ between the High-line and the Low-line steers.

Heifers ± HGP

The results for the selection lines in feedlot performance by heifers (Table 4) were consistent with those reported above for teers. In brief, the High-line heifers grew 48% faster than did the Low-line heifers, were 48% heavier at the end of their feedlot test, ate 45% more feed per day and did not differ in either measure of feed efficiency, i.e. FCR or RFI. Days

Table 2. Feedlot performance and carcase attributes of Angus steers born in 1993 and 1995 from lines divergently selected for high or low growth rate from birth to 1 year of age, or from an unselected control line.

Trait	Line			s.e.
	High	Control	Low	
Number of animals	27	23	26	
Start-of-test LW (kg)	468a	407b	330c	7
ADG (kg/day)	1.22a	1.12a	0.82b	0.05
End-of-test LW (kg)	561a	493b	393c	9
DMI (kg/day)	12.2a	10.0b	8.1c	0.3
FCR (kg/kg)	9.8a	9.3a	10.2a	0.5
RFI (kg/day)	0.22a	−0.27a	0.15a	0.23
Days to gain 100 kg	86a	97a	129b	6
DMI to gain 100 kg (kg)	981a	934a	1016a	46
RIBFAT (mm)	15.3a	15.7a	13.2b	0.6
RUMPFAT (mm)	16.9a	16.0a,b	14.5b	0.8
RIBFAT/ENDWT (mm/kg)	0.028a	0.032b	0.034b	0.001
RUMPFAT/ENDWT (mm/kg)	0.030a	0.033a,b	0.037b	0.002
EMA (cm^2)[A]	65.6a	66.4a	58.5b	1.6
Carcase-WT (kg)	296a	261b	209c	5
Dressing-%	52.7a	52.9a	52.3a	0.3
Carcase MbSc (units)	2.0a	2.0a	2.0a	0.2

Values are LS means. s.e., pooled standard error. See Table 1 for explanation of trait abbreviations.
Within Line, row means with different letters differ significantly (at $P = 0.05$).
[A]Steers born in 1993 did not have EMA records.

Table 3. Metabolic markers in blood taken at the end of feedlot tests and objective measurements of meat quality and calpain system activity in the *M. longissimus dorsi* of Angus steers born in 1993 and 1995 from lines divergently selected for high or low growth rate from birth to 1 year of age, or from an unselected control line.

Trait	Line			s.e.
	High	Control	Low	
Number of animals	27	23	26	
Total protein (g/L)	61.2a	62.2a	61.2a	1.1
Albumen (g/L)	32.0a	32.4a	32.6a	0.6
Urea (mmol/L)	6.01a	6.05a	5.71a	0.23
Insulin (mg/L)	3.19a	3.13a	3.01a	0.40
Day 1 shear force (kg)	4.12a	4.08a	4.23a	0.15
Day 14 shear force (kg)[A]	3.07a	2.95a	3.26a	0.18
Day 1 compression (kg)	1.53a	1.40b	1.51a,b	0.05
Day 14 compression (kg)[A]	1.29a	1.30a	1.39a	0.05
Calpastatin (units/g)	3.16a,c	3.35a,b	3.04c	0.09
μ-calpain (units/g)	1.62a	1.89a	1.73a	0.10
m-calpain (units/g)	2.65a	2.71a	2.63a	0.08
μ-Cal:Calp	0.51a	0.57a	0.56a	0.03

Values are LS-means. s.e., pooled standard error.
Within Line, row means with different letters differ signficantly (at $P = 0.05$).
[A]Steers born in 1993 did not have Day 14 meat samples.

Table 4. Feedlot performance and carcase attributes of Angus heifers born in 1994 from lines divergently selected for high or low growth rate from birth to 1 year of age, or from an unselected control line, with half of the heifers in each line receiving a HGP implant.

Trait	Line			s.e.	HGP implant			Line × HGP
	High	Control	Low		No	Yes	s.e.	
Number of animals	15	16	15		22	24		
STWT (kg)	359a	305b	242c	6	299d	304d	5	n.s.
ADG (kg/day)	1.55a	1.36b	1.05c	0.05	1.26d	1.39e	0.04	n.s.
ENDWT (kg)	495a	424b	335c	9	410d[A]	426e[A]	7	n.s.
DMI (kg/day)	11.6a	9.8b	8.0c	0.3	9.8d	9.8d	0.2	n.s.
FCR (kg/kg)	7.6a	7.3a	7.7a	0.3	7.9d	7.2e	0.2	n.s.
RFI (kg/day)	0.11a	−0.16a	0.05a	0.17	0.13d	−0.13d	0.14	n.s.
Days to gain 100 kg	66a	75b	98c	3	83d[B]	76e[B]	3	n.s.
DMI to gain 100 kg (kg)	760a	734a	772a	26	789d	722e	21	n.s.
RIBFAT (mm)	13.0a,b	13.9a	11.7b	0.6	12.6d	13.1d	0.5	n.s.
RUMPFAT (mm)	14.7a	15.7a	15.1a	0.7	14.7d	15.6d	0.6	n.s.
RIBFAT/ENDWT (mm/kg)	0.026a	0.033b	0.035b	0.001	0.031d	0.032d	0.001	n.s.
RUMPFAT/ENDWT (mm/kg)	0.030a	0.037b	0.045c	0.002	0.037d	0.038d	0.001	n.s.
EMA (cm^2)	64.6a	59.7d	51.9c	1.5	58.3d	59.2d	1.2	n.s.
Carcase-WT (kg)	260a	223b	174c	4	215d	223d	4	n.s.
Dressing-%	52.6a	52.7a	52.1a	0.3	52.5d	52.4d	0.2	$P < 0.05$
Carcase MbSc (units)	1.6a	1.6a	1.8a	02	1.6d	1.7d	0.2	n.s.

Values are LS-means. s.e., pooled standard error. See Table 1 for explanation of trait abbreviations.
Within Line, row means with different lower-case letters (a, b, c) differ significantly (at $P = 0.05$).
Within HGP implant, row means with different upper-case letters (d, e) differ significantly (at $P < 0.05$).
n.s., $P > 0.1$.
[A]Differ at $P = 0.1$.
[B]Differ at $P = 0.06$.

expected to be required by High-line heifers to gain 100 kg LW was 32 days shorter than that for the Low-line heifers, but both lines required a similar amount of feed to achieve this same gain in LW. Both the High-line and Low-line heifers had a similar depth of subcutaneous fat at the rib and rump sites, but when expressed relative to their ENDWT, the High-line heifers had less subcutaneous fat at both sites than did the Low-line heifers. The High-line heifers had a heavier carcase-WT than did the Low-line heifers, but did not differ in dressing-%. Most heifers (87%) had a meat colour score of 1B or 1C and the remaining (13%) scores from 2 to 4 (darker), with no obvious association with selection line, HGP status or electrical stimulation. All heifers had a fat colour score of 0 (white). There was no difference in carcase MbSc between the selection lines.

Heifers implanted with the HGP grew faster and were heavier (at $P = 0.1$) at the end of the feedlot test than were heifers not implanted. Implantation with the HGP did not change DMI, but did lower (improve) FCR but not RFI. Days required to gain 100 kg LW was shortened (at $P = 0.06$) by implantation and DMI required to gain 100 kg LW was lower, reflecting the improvement in FCR in implanted heifers. Non-implanted and implanted heifers had a similar depth of subcutaneous fat at the rib and rump sites, both actual and relative to their ENDWT, and similar carcase-WT, dressing-% and carcase MbSc. Except for dressing-%, there were no significant interactions of selection line with HGP-status for the other traits reported in Table 4, meaning that the anabolic effects of the implant were similar in the High and Low-line heifers. Treatment with the HGP reduced dressing-% by 1.5 units in the implanted compared with non-implanted High-line heifers, with no effect in the Control and Low-line animals.

Implanted heifers had higher concentrations of total protein in their blood than did heifers without an implant (Table 5). There were no effects of implant status on the concentrations in blood of the other three metabolic markers analysed. Shear force in meat after 1 day of ageing was unaffected by implant status, but although shear force declined between 1 day and 17 days, it declined less (towards being less tender) in the HGP-treated heifers. Treatment with the HGP resulted in an increase in shear force across both 1 day and 17 days of ageing in the High-line heifers (implanted: 5.06 ± 0.28 kg vs non-implanted: 4.27 ± 0.23 kg), with an effect in the Control and Low-line animals only evident at 17 days. Compression values for meat after 1 day were higher (less tender) for

Table 5. Metabolic markers in blood taken at the end of feedlot tests and objective measurements of meat quality and calpain system activity in the *M. longissimus dorsi* of Angus heifers born in 1994 from lines divergently selected for high or low growth rate from birth to 1 year of age, or from an unselected control line, with half of the heifers in each line receiving a HGP implant, and either electrically stimulated or not.

Trait	Line			s.e.	HGP implant			Line × HGP	Electrical stimulation		
	High	Control	Low		No	Yes	s.e.		No	Yes	s.e.
Number of animals	15	16	15		22	24			36	10	
Total protein (g/L)	72.6a	69.7a	69.6a	1.3	69.1c[A]	72.1d[A]	1.1	n.s.	n.a.		
Albumen (g/L)	35.2a	34.8a,b	34.0b	0.4	34.7c	34.6c	0.3	n.s.	n.a.		
Urea (mmol/L)	8.0a,b	8.7a	7.8b	0.3	8.0c	8.3c	0.2	n.s.	n.a.		
Insulin (mg/L)	5.3a	3.6b	5.5a	0.6	4.5c	5.0c	0.5	n.s.	n.a.		
Day 1 SF (kg)	4.67a	4.88a	4.75a	0.16	4.63c	4.89c	0.13	n.s.	5.30e	4.46f	0.19
Day 17 SF (kg)	3.21a	3.57a	3.38a	0.35	3.06c	3.72d	0.10	$P < 0.05$	4.23e	3.22f	0.14
Day 1 compression (kg)	1.57a	1.48a	1.59a	0.05	1.44c	1.59d	0.04	n.s.	1.44e	1.60e	0.06
Day 17 compression (kg)	1.28a	1.37a	1.41a	0.04	1.29c	1.41d	0.04	n.s.	1.46e	1.36e	0.06
Calpastatin (units/g)	5.62a	5.26a,b	4.93b	0.16	4.77c	5.77d	0.13	n.s.	5.83e	5.71e	0.19
μ-Calpain (units/g)	2.34a	1.89a	1.92a	0.16	2.00c	2.10c	0.13	n.s.	2.42e	1.79f	0.19
m-Calpain (units/g)	4.24a	3.86a	3.92a	0.18	3.94c	4.07c	0.15	n.s.	3.94e	3.98e	0.21
μ-Cal:Calp	0.43a	0.37a	0.40a	0.03	0.43c	0.37c	0.03	n.s.	0.41e	0.32e	0.04

Values are LS-means. See Table 1 for explanation of trait abbreviations. s.e., pooled standard error.
Within Line, row means with different letters (a, b) differ significantly (at $P = 0.05$).
Within HGP implant, row means with different letters (c, d) differ significantly (at $P = 0.05$).
Within Electrical stimulation, row means with different letters (e, f) differ signficantly (at $P = 0.05$).
n.a., not applicable.
n.s. $P > 0.1$.
[A]Differ at $P = 0.05$.

implanted heifers, and although they declined between 1 day and 17 days, compression values were still higher for implanted heifers than for non-implanted heifers at 17 days. The concentration of calpastatin in muscle after death was higher in the High-line heifers, whereas the concentrations of the two calpains, and the ratio of μ-calpain to calpastatin, did not differ between the selection lines. The concentration of calpastatin in muscle was higher in the implanted heifers than in the non-implanted heifers. The concentrations of the two calpains, and the ratio of μ-calpain to calpastatin, was not affected by implant status. Except for shear force at 17 days, there were no significant interactions of selection line with HGP status for the other traits reported in Table 5, meaning that the effects of the implant were similar in the High-line and Low-line heifers. Electrical stimulation reduced μ-calpain activity but did not appear to have any effect on the other components of the calpain system. Electrical stimulation reduced shear force at 1 day and 17 days postmortem but appeared to have no effect on compression values.

Discussion

Divergent selection for growth rate at pasture produced consistent changes in feed intake and growth rate in the two cohorts of steers and the cohort of heifers fed for slaughter under commercial feedlot conditions. The High-line cattle were more than 40-% heavier at the end of the feedlot performance test than were Low-line cattle, accompanied by a proportional increase in feed consumed, and with no improvement in the efficiency of feed conversion (FCR) or in feed intake independent of LW and gain (RFI). In other words, after more than five generations of genetic selection, the superior growth was driven by increased feed intake rather than increased efficiency of feed use. In a different feeding experiment with younger, yearling-age steers from these growth-rate lines, Herd *et al.* (1991) also concluded that divergent selection had produced different-sized animals whose ability to convert feed to gain in LW had not been altered.

Evidence that selection for growth rate improves feed efficiency from a number of breeding experiments with beef cattle is equivocal argued Herd *et al.* (1991) and part of the reason might be the differences in maturity when comparisons of selection-line animals are made at the same age. The protein and fat contents of LW-gain change as animals grow, are known to differ between sexes and genotypes, and to change an animal's predicted feed requirement (see, for example, Freer *et al.* 2007). Thus cattle with the same ADG but with different protein and fat contents in that gain could be expected to have different feed requirements, which for the same ADG, would change FCR. Variation in

body composition is also known to be a contributor, among many, to variation in feed efficiency measured as RFI (Herd *et al.* 2019). In the feeding experiment with yearling-age animals reported by Herd *et al.* (1991), steers from the high and low growth-rate selection-lines had a similar percentage of body fat, indicative of having attained a similar degree of maturity at yearling age. In the present experiment, the High-line animals had a greater depth of RIBFAT and RUMPFAT than did the Low-line animals, but when divided by LW, both measures of fat were less in the High-line animals. Measurements of subcutaneous fat are taken in one dimension only for what is a multi-dimensional structure and subcutaneous fat is only one of several fat depots that make up total body fat. In a serial slaughter experiment with steers from the high and low growth-rate lines, Perry and Arthur (2000) found no difference between the lines in the pattern of growth of the different body components (dissected weight of muscle, bone, fat and viscera), as a proportion of empty bodyweight, from weaning age to 45 months of age. In the present experiment, the animals tested within each cohort were being compared at the same age and, within a cohort, were likely to be at a similar maturity of body composition, which may explain the lack of an observed difference in FCR between the lines. In experiments with cows from the growth-rate lines, Herd and Oddy (2023) reported an improvement in feed efficiency (as kilograms of cow weight gain plus calf weaning weight/(total cow + calf DMI)) in the High-line animals, and Herd (1995) found that High-line cows were more efficient in maintaining LW than were their Low-line counterparts. In both experiments, these differences in measures of efficiency were associated with differences in body composition that emerged well after the age of selection, with body fat content being greater in High-line than in Low-line cows, and when compared on an energy basis calculated from body composition, the differences in efficiency between the selection lines were no longer significant.

Since Herd *et al.* (1991), the authors are aware of only two published experiments with beef cattle on the consequences of selection for weight on feed intake of growing animals (Morris *et al.* 1992; Koch *et al.* 2004), and both have provided evidence of no improvement in feed conversion. Selection for increased yearling or 18-month LW in Angus cattle was effective in increasing LW compared with a control line, and when feed intake by growing bulls was measured after 18 months of age, it was found to have increased in proportion to the LW and thereby provided evidence of no improvement in feed conversion (Morris *et al.* 1992). In the second experiment, Koch *et al.* (2004) reported that, compared with an unselected control line, selection for weaning weight or yearling weight in Hereford cattle was effective in increasing LW at the same slaughter age, with a non-significant increase in feed intake and gain:feed ratio. When compared over a weight-constant interval, both weight selection lines required fewer days of feeding to achieve the target gain in LW, with less feed required and an improvement in the gain:feed ratio. In the current experiment, when compared over a weight-constant interval, the High-line animals also required fewer days to achieve the target gain in LW than did the Low-line animals, but without a statistically significant reduction in feed required. The evidence from these selection experiments supports the hypothesis that superior growth is driven by increased feed intake.

Differences in protein turnover in hind-limb muscle between the Trangie growth-rate selection lines were reported by Oddy *et al.* (1998), with lower rates of protein turnover measured in the High-line animals, which they concluded could provide a mechanistic basis for the between-line difference in growth rate and might be expected to contribute to an improvement in feed conversion in the High-line animals. An improvement in nitrogen-use efficiency by the cow–calf unit in the High-line compared with the Low-line reported by Herd and Oddy (2023) is also consistent with a difference in protein turnover. No differences between the High-line and Low-line steers in the concentrations in blood of the four metabolic markers analysed were detected, and in the heifers only albumen and urea concentrations differed and were higher in the High-line animals. Albumen was used as a marker for protein metabolism and urea as a marker for protein degradation, with higher concentrations being evidence of greater protein turnover, making these results for High-line heifers contrary to those from isotopic flux studies in steers reported by Oddy *et al.* (1998). In yearling-age steers from these selection lines, no differences in blood concentrations of growth hormone, insulin or insulin-like growth factor-1 (IGF1) were detected between the selection lines (Speck *et al.* 1990). However, blood concentration of growth hormone was negatively correlated, and insulin positively correlated, with dietary energy intake, which provided evidence for their involvement with metabolic processes. For Trangie animals at pasture, no differences between High and Low selection lines in IGF1 blood concentrations were detected between birth and weaning (Ferns *et al.* 1996) and during post-weaning growth (Herd 1992). Blood concentration of IGF1 and its associations with LW and feed efficiency (measured as RFI) are known (Moore *et al.* 2005; Jeyaruban *et al.* 2009), but appear to not be a driver of divergence in the Trangie growth-rate selection lines. Implantation of half the heifers with a HGP resulted in an increase in total protein in blood and no change in the other three metabolites measured. The lack of an interaction between selection line and HGP-implant status provided evidence that the HGP was having a similar effect on the endocrine axis within each selection line. Together the above results provided evidence that no differences in the circulating concentrations of the hormones measured (insulin, growth hormone and IGF1) were associated with the difference in growth rate between the selection lines.

The calpain system comprises endogenous proteases (calpains) that are considered the primary candidates for

muscle protein degradation initiated during the first 24 h postmortem, and their endogenous inhibitor, calpastatin (Bhat *et al.* 2018). Calpastatin is the more variable component of the calpain system and higher concentrations are associated with a decrease in muscle protein turnover and enhanced rate of growth of muscle in the intact animal (Goll *et al.* 1998). The concentrations of the components of the calpain system measured in muscle taken just after death did not differ between the High-line and the Low-line steers. In the heifer cohort, the concentrations of the two calpains, and the ratio of μ-calpain to calpastatin, did not differ between the selection lines. However, the concentration of calpastatin was higher in the High-line heifers and may have contributed to decreased protein turnover and enhanced muscle growth. The carcasses of most, but not all, heifers received electrical stimulation, which has previously been shown to result in early activation of the calpains, accelerated proteolysis of the muscle proteins and increased muscle tenderness in cattle (Kaur *et al.* 2021). In muscle of Swedish Red cattle, μ-calpain was activated earlier in electrically stimulated than in control bovine muscle, but the difference in activity in muscle samples taken immediately after slaughter was small, and there was no observable effect on m-calpain (Li *et al.* 2012). These results are consistent with those of the present experiment; that is, there was a small effect of electrical stimulation on μ-calpain and no apparent effect on the other components. There is no reason to expect that electrical stimulation had differential effects in the selection lines. Together, the results for the steers and heifers suggested that only the concentration of the calpain-inhibitor calpastatin may differ between the selection lines, but that the difference is small, as is its likely contribution of physiological driver of differences in protein turnover and growth.

Ageing is an effective and traditional way of improving tenderness and other characteristics of meat. The tenderisation effect of aging is primarily enzymatic in nature and involves activation of endogenous proteolytic enzymes that are responsible for degradation of muscle fibres, with the calpain system generally being identified as the main driver for most of the proteolysis and tenderisation process (Bhat *et al.* 2018). In the present experiment, ageing was effective in reducing shear force and compression values; however, as no differences between the selection lines were recorded in any of the meat-tenderness measurements made, the values provided no evidence for any between selection-line differences in activity of endogenous proteolytic enzymes, which would include the calpain system.

In the present experiment, half of the heifer cohort was implanted with a mixed anabolic HGP, which increased growth rate, without increasing feed intake, and decreased (improved) FCR, but not RFI. Treatment of HGP had little effect on body composition and carcase traits, although it did reduce dressing-% in the High-line animals. Differences in the inhibitory activity of calpastatin have been used to explain meat toughness resulting from the treatment of animals with various β-adrenergic agonists (Kretchmar *et al.* 1990; McDonagh *et al.* 1999). Consistent with this theory, HGP treatment increased concentrations of the calpain inhibitor, calpastatin, which had a detrimental effect on postmortem meat quality, with higher (less tender) values for shear force at 17 days and for compression at 1 day and 17 days. The lack of an interaction between selection line and HGP-implant status provided evidence that the HGP was having a similar effect on the endogenous proteolytic enzyme systems within each selection line.

Conclusions

Selection on growth rate remains a powerful tool to alter animal performance to meet-market specifications. After over five generations of divergent selection for growth rate on pasture, the High-line cattle grew faster in the feedlot and were over 40% heavier at slaughter. The superior growth demonstrated by the High-line cattle over the feedlot performance test was accompanied by a proportionally higher feed intake. There was no measurable improvement in feed conversion by the High-line over the Low-line cattle. There were no differences between the High-line and Low-line animals in the visual meat-quality attributes of meat colour, fat colour and marble score, and no differences in the objective measurements of tenderness and connective tissue toughness made in this study. There was no evidence of a selection response in the circulating concentrations of the hormones measured in this and other experiments with these selection lines, nor in endogenous proteolytic enzyme systems in muscle. Differences in protein turnover may be present between the selection lines but were not accompanied by measurable differences in concentrations of metabolic markers, in components of the calpain system, in meat tenderness or in feed efficiency. By way of contrast, divergent selection for feed efficiency, measured as RFI, has been shown to be accompanied by changes in all these traits and many more (McDonagh *et al.* 2001; Richardson and Herd 2004; Herd *et al.* 2019) and variation in RFI to have a complex physiological basis (Cantalapiedra-Hijar *et al.* 2018; Kenny *et al.* 2018). However, the correlated improvement in growth rate by High-line cattle in the feedlot can be expected to reduce the number of days of feeding required to grow to target market LWs, which may have economic benefits in terms of a higher throughput of animals in the feedlot, greater utilisation of feedlot infrastructure and labour, and in animals being younger when they reach market weight.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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Author affiliations

[A]NSW Department of Primary Industries, Livestock Industry Centre, Armidale, NSW 2351, Australia.

[B]Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia.

[C]NSW Department of Primary Industries, Elizabeth Macarthur Agricultural Institute, Menangle, NSW 2568, Australia.

[D]Australian Wagyu Association, Suite 6, 146 Marsh Street, Armidale, NSW 2350, Australia.