

Performance, carcass and meat quality traits of grazing cattle with different exit velocity

M. M. Della Rosa^{A,B}, E. Pavan^{B,C,E}, S. Maresca^D, M. Spetter^B and F. Ramiro^B

^AConsejo Nacional de Investigaciones Científicas y Técnicas CONICET, Av. Rivadavia 1917 (C1033AAJ), Ciudad Autónoma de Buenos Aires, Argentina.

^BFacultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata, Ruta Nac. 226, km 73.5, (7620) Balcarce, Argentina.

^CEstación Experimental Agropecuaria Balcarce, Instituto Nacional de Tecnología Agropecuaria, Ruta Nac. 226, km 73.5, (7620) Balcarce, Argentina.

^DEstación Experimental Cuenca del Salado, Instituto Nacional de Tecnología Agropecuaria, Av. Belgrano 416, (7203) Rauch, Argentina.

^ECorresponding author. Email: pavan.enrique@inta.gob.ar

Abstract. To evaluate the effect of grazing cattle temperament on performance, as well as carcass and meat quality traits, exit velocity (EV) was assessed throughout two production cycles (PC1, $n = 38$ and PC2, $n = 52$). Individual EV determinations were assessed throughout each PC and then 100-days period averages were calculated for each animal. Animals were ranked based on their EV (EV-RANK) in the first 100-days period as SLOW, FAST and MEDIUM. The EV decreased from weaning to slaughter in FAST and MEDIUM ($P < 0.05$); but did not change in SLOW ($P > 0.10$). Initial liveweight was lowest in FAST and highest in MEDIUM ($P = 0.03$). DM intake ($P = 0.08$) and average daily gain ($P = 0.94$) were not affected by EV-RANK, but carcass subcutaneous fat thickness was lowest in FAST and highest in MEDIUM ($P = 0.02$). *Longissimus* muscle colour and shear-force were not affected by EV-RANK ($P > 0.05$), but muscle glycogen content at slaughter was higher in MEDIUM than in SLOW or FAST ($P = 0.047$). No EV-RANK effects were observed in the present study on meat colour and shear-force. However, its effects on subcutaneous fat thickness and muscle glycogen could result in low meat quality of temperamental cattle under more stressful handling situations.

Additional keywords: colour, glycogen, shear-force, subcutaneous fat.

Received 26 January 2018, accepted 31 October 2018, published online 4 December 2018

Introduction

Animal temperament can be defined as its behavioural response to stressful events. Temperamental cattle seem to adapt to new environments reducing their responsiveness to its stressor factors (Francisco *et al.* 2015; Lockwood *et al.* 2015; Ceballos *et al.* 2018); however, different studies reviewed by Haskell *et al.* (2014) demonstrated that these animals may have lower productivity affecting weaning weights, post-weaning growing rate, pregnancy rate, a diminished immunological system, or poorer meat quality. Still, most of these studies, which sought the relationship between animal temperament and meat quality, were performed using concentrate-finished *Bos indicus* cattle. This relationship was weaker (Cafe *et al.* 2011) or not significant (King *et al.* 2006; Turner *et al.* 2011) when it was assessed in concentrate-finished *Bos taurus* compared with *Bos indicus*.

Stressor events stimulate a rapid muscle glycogen catabolism that then requires several days to recover its original level. A depletion of muscle glycogen at slaughter in response to pre-slaughter stressor events would result in higher ultimate pH, which is associated with darker and tougher meats.

As cattle on forage-based diets have lower basal muscle glycogen content than those on concentrate-based diets (Immonen *et al.* 2000) and require longer periods to recover the original levels after being exposed to stressors events (McVeigh *et al.* 1982), the likelihood to obtain darker and tougher meats with temperamental cattle may be greater.

Besides, animal temperament has been associated with the rate of post mortem muscle pH decline. Faster muscle pH decline (King *et al.* 2006) and greater blood and muscle lactate concentrations immediately after slaughter (Coombes *et al.* 2014) were observed in more reactive concentrate-fed cattle, suggesting that glycogen was mobilised immediately before slaughter in this type of cattle. In contrast, Cafe *et al.* (2011) remarked that as exit velocity (EV) increased, the rate of pH decline decreased and meat shear-force increased. In their study, EV was negatively associated with subcutaneous fat thickness, a fact which may have contributed to greater muscle shortening due to lower muscle temperature at *rigor*. In addition, lower muscle temperature at *rigor* has been suggested to decrease meat lightness and brightness (Hughes

et al. 2018). Therefore, reduced fatness in temperamental cattle could also increase the likelihood to obtain darker and tougher meats in forage-fed cattle because they are leaner than concentrate-fed cattle.

The main objective of the present study was to evaluate the effect of Angus cattle temperament, which was measured as EV, on performance, as well as on carcass and meat quality traits when reared and finished on a grazing system.

Materials and methods

Animals were handled and managed in accordance with Argentinian national recommendations for animal handling and those of the National Institute for Agricultural Technology (INTA, Instituto Nacional de Tecnología Agropecuaria).

Animals handle and diets

A total of 90 calves were evaluated in two consecutive rearing and fattening production cycles. Calves for both cycles were obtained from the same cow-herd that was artificially inseminated at a fixed time. Twenty-three male and 15 female calves were used in the first production cycle (PC1) and 24 males and 28 females in the second production cycle (PC2). The cow-calf pairs were managed in an extensive rangeland-based system until weaning.

At weaning, calves were transported to the fattening system (200 km) and were reared until finishing on a pasture-based system. Animals were managed under a daily rotational grazing system on 5.5 ha of a tall fescue (*Fescue arundinacea* cv. Royal Q), white (*Trifolium repens* cv. Goliath) and red clover (*Trifolium pratense* cv. Star Fire) pasture, and 4 ha of tall fescue (*Fescue arundinacea* cv. Flecha) and lucerne (*Medicago sativa*) pasture. The instantaneous stocking rate was, on average, 500 animals per hectare. At the start of the study, pastures were on their second year of production. During periods of low pasture growth, a whole-plant corn silage was supplemented to a maximum of 1% liveweight (LW, DM basis). Cattle were slaughtered in a commercial slaughter house when their average LW reached 470 kg.

Bodyweight

Every 21 days (0800–0900 hours), animals were driven (3000 m) from their paddock to the working chute, where individual bodyweight and EV were recorded. Individual average daily gain (ADG) was estimated as a function of LW on days of the production cycle. Prior to shipping, animals were weighed at 0800 hours after 16 h of feed withdrawal (Shrunk LW). At 1200 animals were shipped 200 km to a commercial slaughter house where they were harvested overnight.

Exit velocity

Animal temperament was assessed by measuring EV as described by Curley *et al.* (2006). Briefly, two infrared sensors (REA COW, Paraná, Entre Rios, Argentina) were used to determine the time required for an individual animal to cover a distance of 1.83 m after its exit from the scale box. The EV (m/s) was calculated as the ratio between the distance and the time required.

Exit velocity was assessed after weighing, except on rainy days or when animals received special handling or treatments, i.e. vaccinations. Therefore, EV was assessed 15 times during PC1 and 20 times during PC2. The use of an average of EV substantially improves reliability of the trait compared with the use of a single determination (Burrow and Corbet 2000). Individual determinations of EV performed within periods of 100 days (PERIOD) were averaged throughout each production cycle. Therefore, six new variables were obtained with the individual average of EV determinations made within the first 100 days (EV_{0–100d}), the second 100 days (EV_{101–200d}), and so forth until the sixth 100 days (EV_{501–600d}). As cattle reached their slaughter weight within the fifth period (EV_{401–500d}) in the first production cycle and within the sixth period (EV_{501–600d}) in the second production cycle, five and six EV averages were estimated per animal, respectively, in each production cycle.

Dry matter intake determination

When animals reached 300 kg, individual DM intake (DMI) and *in vivo* apparent DM digestibility were estimated by using chromium sesquioxide (Cr₂O₃) as an external marker, and indigestible neutral detergent fibre as an internal marker of the digesta (Lippke *et al.* 1986). In PC1, due to the reduced growth of the pasture, animals were individually supplemented with whole-plant corn silage and wheat-brans and their supplement DMI measured by weight difference. However, no supplementation was required in PC2. Chromium sesquioxide was individually dosed daily throughout 15 days. Faecal samples were collected twice a day (0800 hours and 1500 hours) from each animal for the last 5 days of the Cr₂O₃ dosing period. Concurrent with the faecal collection period, hand-plucked pasture and corn silage samples were taken daily, then pooled and frozen at –25°C for subsequent analyses.

Pasture, supplement and faecal samples were dried (48 h at 60°C) for DM determination, ground by using a Wiley mill (model 4, Thomas Scientific, Swedesboro, NJ, USA) equipped with a 1-mm screen, and analysed for neutral detergent fibre (NDF), acid detergent fibre (ADF) and indigestible NDF. Neutral detergent fibre and ADF were sequentially determined by using an Ankom 200 fibre extractor (Ankom Technologies, Fairport, NY, USA) according to the method of Van Soest *et al.* (1991). Indigestible NDF was determined by incubating samples for 288 h in the rumen of a ruminal fistulated steer with *ad libitum* access to water and grass hay before their NDF determination (Huhtanen and Kukkonen 1995). Crude protein concentration was determined in samples of both pasture and supplement with the combustion method by using a Leco FP-2000 N analyzer (Leco Corp., St Joseph, MI, USA). Chromium concentration was analysed in the faecal samples according to Czarnocki *et al.* (1961). Forage DMI and dietary DM and NDF *in vivo* apparent digestibility was calculated based on faecal output and indigestibility (Pavan *et al.* 2007).

Slaughter and sample collection

According to the standard procedure of the commercial slaughter house (inspected by the SENASA, National Service for Agrifood Health and Quality), after arrival, animals were

kept in lairage pens with feed withdraw and free access to fresh water until the following morning (0800 hours), when they were harvested.

At harvest, hot carcass weight (HCW) was registered; both muscle pH and temperature were recorded at 3 h (pH@3h and Temp@3h, respectively) and at 24 h post mortem (pH@24h and Temp@24h). Determinations were performed in the *Longissimus thoracis* muscle (LT) between the 12th and 13th ribs from the carcass left side by using a portable pH-meter (model 850081, SperScientific, Scottsdale, AZ, USA) with two penetration probes, one measuring temperature and the other, type-13 (Testo, Lenzkirch, Germany), measuring pH.

After pH@24h was recorded, the 9–12th rib loin block was obtained from carcass left side by cutting perpendicular to the long axis of the *Longissimus* muscle in the joints of the 8–9th and 12–13th dorsal vertebrae and parallel to the external end of the LT. On the cut performed between the 12–13th dorsal vertebrae, subcutaneous fat thickness, ribeye area (REA) were measured.

Meat colour

After ribbing between the 12th and 13th ribs *Longissimus* muscle, colourimetric parameters (L^* , a^* , b^* -values) were recorded on the exposed area with 30 min of blooming and then adjusted to a 90-min blooming period according to Wulf and Wise (1999). Readings were performed with a Minolta CR-310 (Minolta Corp, Ramsey, NJ, USA) with a 50-mm-diameter measuring area, a 10° standard observer and using a D65 illuminant. Values for L^* (measures lightness; greater L^* indicates a lighter colour), a^* (measures redness; greater a^* value indicates a redder colour), and b^* (measures yellowness; greater b^* value indicates a deeper yellow colour) were recorded in six positions averaged for each carcass. The instrument was calibrated by using the white ceramic disk provided by the manufacturer.

Loin composition

Approximately 48 h after harvest, the 9–11th rib section of each carcass was obtained and weighed. Then the subcutaneous fat and LT were removed and weighed. The remaining rib section was dissected into lean trim, inter-muscle fat, and bone, and weighed. The lean trim and a 2-cm-thick steak from the caudal side of the LT were ground for total lipid determination (see *Total lipid content*). Lean trim and LT lipids weights were subtracted from their whole weights to estimate total fat-free lean tissues in the 9–11th rib section and were added to the subcutaneous and inter-muscular fat weights to obtain total fat content.

Warner-Bratzler shear-force (WBSF)

The LT muscle from the 9th to 11th rib section was cut into four 2.5-cm-thick steaks for WBSF evaluation. Three steaks were vacuum-packaged and cooled (2°C) until they reached 3, 7 and 14 days *post-mortem*, and then were frozen (-25°C) for later analysis. The other steaks were vacuum-packaged and frozen immediately.

Warner-Bratzler shear-force analysis was conducted according to AMSA (2016) guidelines. Steaks were thawed at 4°C for 12 h

and cooked on preheated open heart electric grill (Farberware, Bronx, NY, USA) to an internal temperature of 71°C . Internal temperature from each steak was monitored by using a digital thermometer (Scanning thermometer, Digi-Sense, Eutech Instrument Pte. Ltd., Singapore). Steaks were cooled at 4°C for 1 h before six 1.27-cm-diameter cores were removed from each steak parallel to the muscle fibre orientation. Cores were sheared at right angles to the fibre direction by using a WBSF machine (G-R Manufacturing, Manhattan, KS, USA) with a digital dynamometer coupled.

Total lipid content

Prior to total lipid determinations, samples from the LT muscle and from lean trimmings were lyophilised (Labconco; Kansas, MI, USA). Total lipid content was determined by using a soxhlet extractor system with chloroform-methanol 4:1 (Novakofski *et al.* 1989).

Glycogen content

In accordance with Pighin *et al.* (2013), total muscle glycogen content at slaughter was calculated based on residual glucose and lactic acid determinations in LT samples obtained 48 h postmortem and immediately stored at -20°C . Residual glucose was extracted after taking the following steps: 1.5 g of muscle was homogenised (Ultraturrax, IKA, Staufen, Germany) with 20 mL of 2 N HCl at 4°C , for 45 min of acid hydrolysis at 4°C . Then, the samples were centrifuged at 3500g for 15 min at 4°C . The supernatants were filtered (Whatman No. 1) and incubated at 90°C in a water bath for 2 h and neutralised with 2 N NaOH. Glucose concentrations were determined by colourimetric assay, measured at 505 nm (spectrophotometer Genesys 10S, Thermo Fisher Scientific, Madison, WI, USA). A commercial kit (Wiener Laboratory – GOD/POD; Rosario, Argentina) was used for these determinations. The quantified glucose included free glucose, glucose as the product of glycogen hydrolysis and glucose 6-phosphate (Pighin *et al.* 2013).

Lactate was determined following the procedure described by Neath *et al.* (2007) with modifications. Briefly, 3 g of muscle was placed in a test tube containing 1.5 N perchloric acid solution. After adding 5 mL of hot distilled water (90°C), samples were held at 90°C for 2 min into a stirred water bath; then, they were incubated at 4°C for 45 min and filtered. The filtrate obtained was neutralised with NaOH (2 M) and muscle lactate concentration was determined by measured absorbance at 550 nm (spectrophotometer – Thermo Fisher Scientific) by using a Randox kit LAC (Randox Laboratories Ltd, Crumlin, Co. Antrim, UK). Lactate concentration was expressed as μmol lactate per g of fresh tissue.

Total glycogen content in the LT was then estimated as the sum of the total glucose and half of the lactate content in each sample.

Total and insoluble collagen content

Total collagen content on LT muscle was estimated by determining hydroxyproline concentration through the use of the rapid procedure described by Bergman and Loxley (1963). *Longissimus thoracis* muscle insoluble collagen content was

determined according to a procedure adapted from Hill (1966). In short, it consisted of two steps hydrolysis: thermal and acidic. The first hydrolysis was performed by heating samples in a water bath at 77°C for 70 min. Then, after centrifuging the samples at 6000g for 10 min at 2°C, the second hydrolysis was performed by adding 5 N HCl and incubating the samples in an oven at 110°C for 12 h. Hydroxyproline concentration was determined by colourimetric assay and converted to collagen by using the 7.25-factor (Cross *et al.* 1973).

Sarcomere length

The helium-neon laser diffraction method described by Cross *et al.* (1981) was used for sarcomere length evaluation on LT muscle samples. The sarcomere length value from each sample was the average of 10 readings.

Myofibrillar fragmentation index

Myofibrillar fragmentation index (MFI) was determined in the LT samples according to Hopkins *et al.* (2004), with minor modifications. Loin samples were cut parallel to the myofibres and mixed with buffer solution (0.1 M KCl, 1 mM EDTA (disodium), 1 mM sodium azide (NaN₃) and 25 mM potassium phosphate (7 mM KH₂PO₄ and 18 mM K₂HPO₄), by using a homogeniser (Ultraturrax, IKA, Staufen, Germany) at 15 000 rpm for 30 s. The homogenised samples were filtered and centrifuged at 1000g for 10 min at 2°C. The process was repeated twice to obtain the protein extract before determining their concentration on Epoch Microplate Spectrophotometer equipped with a reader type (No. 257878; Biotek; Vernon Hills, IL, USA).

Protein extract aliquots, i.e. duplicate samples, were diluted with buffer to reach the final concentration of 0.5 mg/mL. Absorbance was measured at 562 nm with a spectrophotometer (Visible Spectrophotometer SP 2000). Readings were multiplied by 150 to obtain an index of myofibrillar fragmentation.

Calculations and statistical analyses

The consistency of EV throughout each production cycle was evaluated by Pearson correlations analysis by using individual EV averages calculated for each period of 100 days.

Then, animals from each production cycle were ranked based on their initial EV (EV_{0–100d}); the animals were grouped as follows: cattle slower than 1 s.d. from the mean EV on EV_{0–100d} were classified as SLOW, those faster than 1 s.d. from the mean as FAST, and all other cattle as MEDIUM.

The effects of EV-RANK (SLOW, MEDIUM and FAST) on the EV throughout each production cycle were evaluated by using a linear mixed model including SEX, EV-RANK and PERIOD as main fixed effects; PERIOD was included as a repeated-measured over animal within EV-RANK. The model also included the interaction of main fixed effects. The structure of covariance was modelled by using the type = unstructured option of the 'repeated' statement of the MIXED procedure of SAS, when significant ($P < 0.05$) interactions were opened by using slide option of the LSMEAN statement.

To assess EV-RANK effects on the different performance, carcass and meat quality variables were evaluated by using

the PROC MIXED procedure of SAS and Satterthwaite approximation. The model statement contained the effect of EV-RANK, SEX, production cycle (PC) and all possible interactions. To allow variances between EV-RANK × SEX × PC to differ, the GROUP = option on the REPEATED statement was used. Results were reported as least square means ± standard error of the mean (Lsmeans ± s.e.m.). When detected, EV-RANK differences were separated by using the PDIFF option on the LSMEAN statement when F -test was significant. Significance was set at $P \leq 0.05$, with $P > 0.10$ and $P \leq 0.10$ considered to reflect tendencies. Results are reported according to EV-RANK effects when no interaction was significant or according to the highest order of significant interaction.

The procedure GLMSELECT of SAS was used to select independent classification variables (EV-RANK, SEX and PC) and their interaction, in addition to performance (initial LW, average daily gain), carcass (HCW, FT, REA, LT fat) and meat quality (pH@3h, temp@3h, pH@24h, sarcomere length, MFI, total collagen content, proportion of insoluble collagen) variables to be included in the model to predict LT muscle colour and shear-force after 3, 7 and 14 days of aging. A stepwise method for testing potential independent variables with an entry P -value of 0.10 and a P -value of 0.05 to remain in the model was used. The Mallows' C(p) statistic was specified in the model options as the method for choosing the best model.

Results and discussion

Prior to presenting and discussing the effects observed in animal temperament on performance, as well as carcass and meat quality traits, individual and EV-RANK EV evolution throughout the study is briefly analysed.

Exit velocity variation throughout the study

In both production cycles, significant positive Pearson correlations were obtained between the averages EV of the different 100-days periods; these positive correlations were attained even between the EV averages of the initial (EV_{1–100d}) and those of the pre-slaughter periods (EV_{401–500d} or EV_{501–600d} in the first or second production cycle, respectively; Table 1).

When evaluating the EV throughout each production cycle for the three EV-RANK groups, an interaction effect was observed ($P < 0.05$; Figs 1, 2). In both production cycles, when EV differed between EV-RANK ($P < 0.05$), EV was highest in FAST and lowest in SLOW. In addition, EV differences were observed ($P < 0.05$) in FAST and MEDIUM, but not in SLOW ($P > 0.10$) when comparing PERIOD within each EV-RANK. The trends observed in both, FAST and MEDIUM, showed a tendency to reduction of EV as days in both production cycles increased.

In agreement with Cafe *et al.* (2011), our results suggest that the average of EV assessments during the first 100 days after weaning were consistent throughout the production system. Hence, cattle with greater EV at the beginning had also greater EV at the end. In addition, as observed by Francisco *et al.* (2015) and Lockwood *et al.* (2015), changes in EV throughout the production cycle were not constant for the different EV ranks (EV-RANK × PERIOD). When exposed

Table 1. Mean, standard deviation (s.d.) and Pearson correlation coefficients between exit velocity (EV) averages every 100-days periods for cattle

Values above the diagonal correspond to the first production cycle (PC1; $n = 38$) and values below the diagonal to second production cycle (PC2; $n = 52$). *, $P < 0.05$. **, $P < 0.01$. ***, $P < 0.001$

	Mean	s.d.	EV _{0–100 d}	EV _{101–200 d}	EV _{201–300 d}	EV _{301–400 d}	EV _{401–500 d}
Mean	–	–	2.85	2.59	2.91	2.24	1.70
s.d.	–	–	0.70	0.68	1.55	0.84	0.53
EV _{0–100d}	2.58	0.83	–	0.72***	0.47**	0.47**	0.53**
EV _{101–200d}	2.50	0.86	0.52***	–	0.40*	0.24	0.34*
EV _{201–300d}	2.74	1.26	0.41**	0.57***	–	0.73***	0.52***
EV _{301–400d}	2.52	0.89	0.52***	0.58***	0.73***	–	0.54***
EV _{401–500d}	2.16	0.72	0.47***	0.57***	0.62***	0.74***	–
EV _{501–600d}	1.85	0.55	0.32*	0.50***	0.54***	0.60***	0.83***

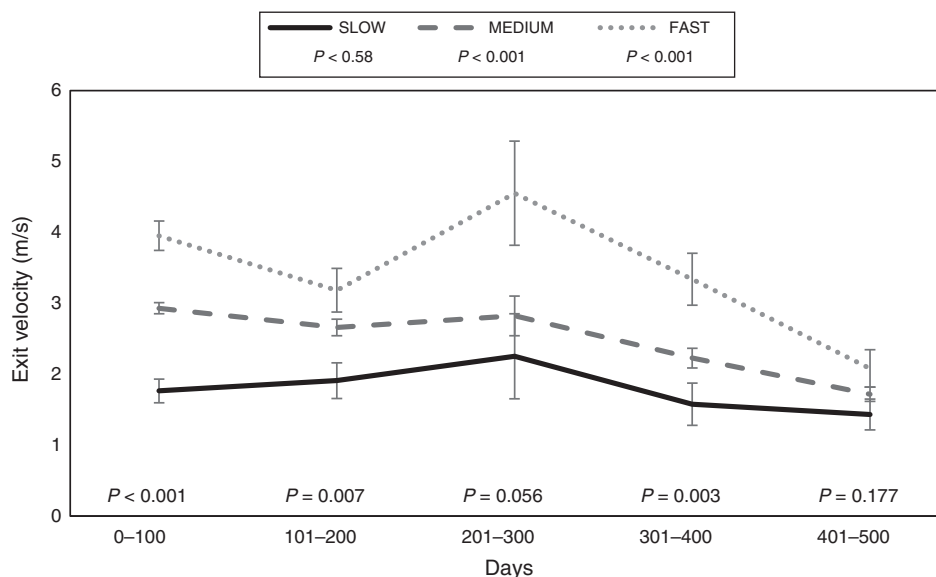


Fig. 1. Least-squares means for exit velocity averages throughout the first production cycle for each exit velocity ranking (EV-RANK). Cattle slower than 1 s.d. from the mean exit velocity on EV_{0–100d} (2.86 ± 0.68 m/s) were classified as SLOW ($n = 5$), those faster than 1 s.d. from the mean as FAST ($n = 5$), and all other cattle as average (MEDIUM; $n = 28$). SEX, $P = 0.64$; EV-RANK, $P < 0.001$; PERIOD, $P < 0.001$; EV-RANK \times PERIOD, $P < 0.001$.

to a new environment, temperamental animals, with a higher EV, are more reactive than calmer ones, but they become less reactive as they adjust to the new conditions, and the differences between calm and temperamental tend to disappear. Our results support the observation of Ceballos *et al.* (2018) that more reactive cattle also get used to handlers in semi-intensive grazing systems. Based on the habituation of animals to new environments, Lockwood *et al.* (2015) suggested that cattle's true temperament has to be assessed when animals are exposed to a new environment or to new handlers; which in our study was at weaning. Although animals got used to the study environment, it is expected that cattle expressed their different temperaments when exposed to the new environment, i.e. shipping and slaughter house lairage pens, before slaughter.

A greater standard deviation was observed for the exit velocities assessed in the third period of both production cycles, suggesting that not all animals had the same ability

to habituate to the new environment (Behrends *et al.* 2009). The greater variation observed in the third period cannot be explained through differences in individual animal handling routine. Within each production cycle, all received a similar handling quality and frequency during the experiment and for the EV determinations.

Effect of EV-RANK on performance

Initial bodyweight was lower in FAST than in MEDIUM, and intermediate in SLOW ($P = 0.027$; Table 2). Nonetheless, no differences were observed between EV-RANK for final and shrunk bodyweight ($P = 0.167$ and $P = 0.191$, respectively), or for ADG ($P = 0.973$). A trend ($P = 0.080$) was observed towards a lower total DM intake (kg/day) in FAST rather than in SLOW and MEDIUM; but no EV-RANK differences were observed ($P = 0.757$) for DM intake as proportion of LW

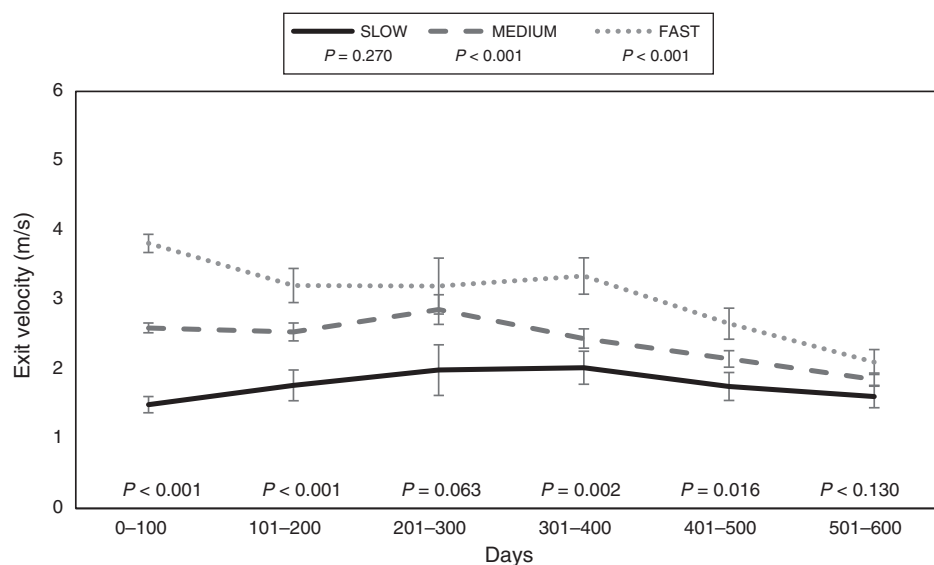


Fig. 2. Least-squares means for exit velocity averages throughout the second production cycle for each exit velocity ranking (EV RANK). Cattle slower than 1 s.d. from the mean exit velocity on EV_{0-100d} (2.58 ± 0.83 m/s) were classified as SLOW ($n = 10$), those faster than 1 s.d. from the mean as FAST of 3 ($n = 9$), and all other cattle as MEDIUM ($n = 33$). SEX, $P = 0.118$; EV-RANK, $P < 0.001$; PERIOD, $P < 0.001$; EV-RANK \times PERIOD, $P < 0.001$.

Table 2. Animal performance and carcass characteristics of grazing heifers and steers ranked by their average exit velocity during their first 100 days period on the system

Values within a row with different letters differ significantly at $P < 0.05$. EV-RANK, SLOW, cattle slower than one standard deviation (s.d.) from the mean exit velocity during the first 100 days of evaluation; FAST, faster than one s.d. from the mean, and MEDIUM, all other cattle; LW, liveweight; ADG, average daily weight; DMI, dry matter intake; HCW, hot carcass weight; FT, fat thickness; REA, rib eye area; LT, *Longissimus thoracis*. No interaction were detected ($P > 0.05$)

	Exit velocity RANK (EV-RANK)			Production cycle (PC)		<i>P</i> -value	
	SLOW	MEDIUM	FAST	1	2	EV-RANK	PC
LW (kg)							
Initial	162 \pm 6.0	168 \pm 3.8	151 \pm 4.9	167 \pm 5.0	153 \pm 2.4	0.027	0.018
Final	467 \pm 12.9	483 \pm 5.6	460 \pm 11.7	457 \pm 9.0	483 \pm 8.1	0.167	0.039
Final shrunk	449 \pm 12.8	462 \pm 5.4	439 \pm 12.8	443 \pm 9.5	456 \pm 8.0	0.191	0.277
ADG	0.53 \pm 0.01	0.54 \pm 0.01	0.54 \pm 0.02	0.58 \pm 0.01	0.49 \pm 0.01	0.937	<0.001
DMI							
kg DM	10.2 \pm 0.28	10.5 \pm 0.21	9.7 \pm 0.29	10.2 \pm 0.19	10.1 \pm 0.24	0.080	0.779
% of LW	2.8 \pm 0.08	2.8 \pm 0.05	2.7 \pm 0.07	2.8 \pm 0.06	2.7 \pm 0.04	0.750	0.145
HCW (kg)	243 \pm 7.8	251 \pm 3.1	237 \pm 8.5	242 \pm 6.4	245 \pm 4.8	0.225	0.709
Carcass yield (%)	54.1 \pm 0.36	54.5 \pm 0.25	54.1 \pm 0.60	54.7 \pm 0.40	53.7 \pm 0.28	0.627	0.065
FT (mm)	4.0 \pm 0.61ab	4.8 \pm 0.34a	3.3 \pm 0.39b	3.6 \pm 0.42	4.4 \pm 0.34	0.020	0.138
REA (cm ²)	56.6 \pm 1.96	54.9 \pm 0.58	53.5 \pm 1.58	59.6 \pm 1.50	50.4 \pm 0.84	0.476	<0.001
LT fat (g/100 g) ^A	2.4 \pm 0.27	2.4 \pm 0.15	2.0 \pm 0.44	2.2 \pm 0.32	2.4 \pm 0.18	0.707	0.683
Block composition ^B (%)							
Lean	55.5 \pm 2.3	57.0 \pm 0.4	58.7 \pm 1.6	56.3 \pm 1.8	57.8 \pm 0.5	0.475	0.421
Fat	14.5 \pm 1.0	16.2 \pm 0.5	14.1 \pm 1.0	14.8 \pm 0.8	15.2 \pm 0.6	0.099	0.724
Bone	27.7 \pm 0.6	26.9 \pm 0.3	29.0 \pm 1.3	28.7 \pm 0.9	27.0 \pm 0.4	0.200	0.090

^Ag/100 g of fresh tissue.

^BComposition 9–11th rib section.

(% LW). Lower initial LW in excitable rather than in calm cattle was also observed by Francisco *et al.* (2012) when evaluating, as in the present study, cattle coming from extensive rangeland-based cow-calf systems. In their study, these differences in LW

were not associated with animal age at weaning and, based on a previous study (Cooke 2014), they suggest, that they should neither be attributed to temperament of the dam. In contrast to our observations, initial differences in LW were still evident

at slaughter in the study of Francisco *et al.* (2012). As in both studies ADG did not differ between EV-RANK groups, the longer period ranging from weaning to slaughter in our study (18 and 20 month vs 8–9 month) could have blurred the initial differences in LW. Others (Petherick *et al.* 2002; Cafe *et al.* 2011; Francisco *et al.* 2015) observed that cattle with greater EV had lower ADG. Petherick *et al.* (2002) and Francisco *et al.* (2015) observed that the lower ADG in more excitable cattle was obtained despite similar intakes. Petherick *et al.* (2002) suggested that the lower ADG, as well as the lower feed efficiency observed in more excitable cattle, could be attributed to a greater expenditure of energy caused by being in a state of high arousal. Conversely, Cafe *et al.* (2011) observed that differences in ADG were associated with concomitant differences in DMI and concluded that animal temperament plays a major role in controlling feed intake and time spent eating, although it has a lesser effect on feed efficiency. Supporting this last hypothesis, the lower DM intake (kg/day) observed in FAST rather than in the other EV-RANK was not associated with differences in ADG, but with a still lower LW at the moment of intake determination (similar intake as % LW).

Effect of EV-RANK on carcass quality

No EV-RANK effect ($P > 0.10$) was observed on hot carcass weight, carcass yield, rib eye area, or LT lipid content, but on subcutaneous fat thickness ($P = 0.020$). Subcutaneous fat thickness was lowest in FAST and highest in MEDIUM; whereas in SLOW it was intermediate not differing from any

of the other two EV-RANK. In agreement with this, total fat proportion of the 9–11th rib block tended to be highest in MEDIUM ($P \geq 0.099$).

Some observations were made about different responses, namely carcasses from more temperamental cattle had lower rib eye area (Behrends *et al.* 2009), lower marbling and muscle lipid content (Francisco *et al.* 2015) or, as in the present study, lower subcutaneous fat thickness (Cafe *et al.* 2011). The different responses between studies could be associated to overall temperament differences between the herd use in each study, to dietary differences or both. Cafe *et al.* (2011) reported a weaker relationship between temperament and carcass traits in Angus rather than in Brahman cattle; King *et al.* (2006) and Francisco *et al.* (2012) did not observe any association in Angus or Angus \times Hereford cattle. However, the ability to express the potential for muscle and fat accumulation is reduced in forage- rather than in concentrate-fed cattle when slaughtering at similar weights (Duckett *et al.* 2007, 2013).

According to Cafe *et al.* (2011) the lower subcutaneous fat thickness observed in cattle with greater EV was a consequence of their lower bodyweight at slaughter, but that was not the case in our study, where lower subcutaneous fat thickness and similar body or hot carcass weights were observed. Francisco *et al.* (2015) suggested that the lower marbling and total muscle lipid content in carcasses from feedlot-finished cattle ranked as more excitable were associated with higher cortisol and lower serum insulin concentration. However, insulin concentration affects intramuscular (i.m.) fat accretion in cattle fed on high-concentrate diets, but not high-forage diets (Rhoades *et al.* 2007). In the latter, greater insulin

Table 3. Meat quality characteristics of the *Longissimus thoracis* (LT) from grazing heifers and steers ranked by their exit velocity in two production cycles

Values within a row with different letters differ significantly at $P < 0.05$. EV-RANK, SLOW, cattle slower than one standard deviation (s.d.) from the mean exit velocity during the first 100 days of evaluation; FAST, faster than 1 s.d. from the mean, and MEDIUM, all other cattle; Temp@3h, temperature at 3 h post mortem; pH@3h, pH 3 h post mortem; pH@24h, pH 24 h post mortem; WBSF, Warner-Bratzler shear-force; TC, total collagen; IC, insoluble collagen; MFI, myofibrillar degradation index; SL, sarcomere length. No interactions were detected ($P > 0.05$)

	Exit velocity RANK (EV-RANK)			Production cycle (PC)		<i>P</i> -value	
	SLOW	MEDIUM	FAST	1	2	EV-RANK	PC
Glycogen ($\mu\text{mol/g}$)	57.9 \pm 2.00b	62.7 \pm 1.33a	58.1 \pm 1.69b	65.0 \pm 1.73	54.2 \pm 0.91	0.047	<0.001
pH@3h	6.75 \pm 0.08	6.67 \pm 0.04	6.82 \pm 0.05	6.82 \pm 0.05	6.68 \pm 0.05	0.083	0.040
Temp@3h ($^{\circ}\text{C}$)	20.9 \pm 0.37	21.5 \pm 0.25	21.2 \pm 0.54	23.3 \pm 0.29	19.1 \pm 0.36	0.426	<0.001
pH@24h	5.72 \pm 0.04	5.67 \pm 0.02	5.75 \pm 0.04	5.61 \pm 0.02	5.82 \pm 0.03	0.209	<0.001
Temp@24h ($^{\circ}\text{C}$)	5.0 \pm 0.09	4.8 \pm 0.07	4.8 \pm 0.17	4.8 \pm 0.11	4.9 \pm 0.08	0.456	0.316
	<i>Colour LT</i>						
L*-value	34.8 \pm 1.26	33.3 \pm 0.59	33.3 \pm 1.28	34.6 \pm 1.01	33.0 \pm 0.75	0.613	0.570
a*-value	17.2 \pm 0.75	17.9 \pm 0.35	16.9 \pm 0.76	16.6 \pm 0.60	18.0 \pm 0.45	0.690	0.021
b*-value	13.9 \pm 0.63	13.6 \pm 0.30	13.0 \pm 0.64	13.3 \pm 0.51	13.7 \pm 0.38	0.586	0.185
	<i>WBSF (kgf)</i>						
3 days	5.5 \pm 0.42	5.6 \pm 0.19	6.7 \pm 0.60	6.5 \pm 0.43	5.4 \pm 0.27	0.212	0.038
7 days	4.7 \pm 0.33	4.6 \pm 0.14	5.3 \pm 0.47	5.8 \pm 0.36	4.0 \pm 0.15	0.359	<0.001
14 days	3.9 \pm 0.27	4.0 \pm 0.17	4.1 \pm 0.16	4.6 \pm 0.19	3.5 \pm 0.14	0.691	<0.001
TC (mg/100 g) ^A	4.13 \pm 0.20	4.67 \pm 0.18	4.51 \pm 0.34	4.58 \pm 0.15	4.30 \pm 0.25	0.144	0.339
IC (%)	55.3 \pm 5.6	55.4 \pm 2.7	60.0 \pm 4.1	58.8 \pm 3.5	55.0 \pm 3.5	0.632	0.454
MFI	47 \pm 3.1	50 \pm 1.5	51 \pm 2.3	48 \pm 2.4	51 \pm 1.4	0.666	0.200
SL (μm)	1.86 \pm 0.03	1.84 \pm 0.01	1.80 \pm 0.03	1.80 \pm 0.02	1.86 \pm 0.02	0.389	0.085

^Amg/100 g of fresh tissue.

concentration would marginally increase subcutaneous fat accretion by increasing production of the reduced form of nicotinamide adenine dinucleotide phosphate (NADPH) through the pentose pathway and acetate incorporation into fatty acid (Rhoades *et al.* 2009). This may partially explain why in the present study, lower subcutaneous fat but similar i.m. lipid content was observed in more excitable cattle.

Effect of EV-RANK on meat quality

Considering that (a) in previous studies only weak or non-existent relationships were observed between animal temperament and meat quality when evaluated in concentrate-fed Angus cattle, (b) forage-fed cattle had lower degree of fatness and muscle glycogen content than concentrate-fed cattle, it was hypothesised that such a relationship would be observed in Angus cattle when fed on a forage diet.

Increasing subcutaneous fat thickness up to 7 or 8 mm would improve meat tenderness (Tatum *et al.* 1982) and meat colour (Page *et al.* 2001). This would be related to a reduction of muscle temperature decline during the onset of rigor that would reduce sarcomere shortening (Hopkins *et al.* 2014) and promote light scattering (Hughes *et al.* 2018). Even so, in the present study, differences in subcutaneous fat thickness between EV-RANK below the proposed threshold were not associated with differences in LT shear-force ($P > 0.212$) or colour ($P > 0.586$; Table 3). The lack of EV-RANK effects observed in LT shear-force and colour are in agreement with their similar post mortem pH and temperature decline (pH@3h, $P = 0.083$ and Temp@3h, $P = 0.212$) and sarcomere length ($P = 0.389$).

The lack of shear-force and colour differences observed between EV-RANK in the present study are also supported by their similar pH@24h ($P = 0.209$), collagen content ($P = 0.144$), MFI ($P = 0.666$), and muscle total lipid content ($P = 0.707$). Similar pH@24h was obtained between EV-RANK despite their differences in muscle glycogen content ($P = 0.047$), which was greater in MEDIUM than in SLOW or FAST. This would indicate that, even in the more temperamental animals, stress was sufficiently reduced to avoid reaching slaughter with muscle glycogen reserves below the threshold level (45–57 $\mu\text{mol per g}$) that would increase meat ultimate pH (Ferguson and Warner 2008). Nonetheless, the differences in muscle glycogen content suggests that, despite not having observed meat colour and shear-force differences, temperament increases the likelihood of obtaining darker and tougher meats if animals are exposed to stressor factors.

Explanatory variables for meat shear-force and colour

Our results from the regression analysis indicates that sarcomere length explained part of the variation observed in LT shear-force when aged for 3, 7 or 14 days and also the variation observed in meat colour parameters (Table 4). The positive relationship between colour and length of sarcomeres could be due to structural changes. According to Yao (2016), the less the sarcomeres overlap, the more light is reflected, a fact which results in higher colourimetric readings. Looser structures would also increase oxygen diffusion and subsequent oxygenation of myoglobin, promoting the formation of oxymyoglobin

Table 4. Equations for predicting *Longissimus thoracis* (LT) colour and Warner-Bratzler shear-force (kg) after 3, 7 or 14 days of aging from classification variables (SEX, PRODUCTIVE CYCLE and EV-RANK) and performance, carcass and meat quality independent variables

SL, sarcomere length; Gly, muscle glycogen content at slaughter; Gly², squared muscle glycogen content at slaughter; PC1, effect of productive cycle; LT fat, *Longissimus thoracis* fat content; REA, rib eye area; FT, subcutaneous fat thickness; HCW, hot carcass weight; RMSE, root mean square error; WBSF 3 days, Warner-Bratzler shear-force at 3 days of aging; WBSF 7 days, Warner-Bratzler shear-force at 7 days of aging; WBSF 14 days, Warner-Bratzler shear-force 14 days of aging; SL, sarcomere length; Temp@3h, temperature at 3 h post mortem; pH@3h, pH at 24 h post mortem. *, $P < 0.10$. **, $P < 0.05$. ***, $P < 0.01$

Dependent variable	Regression coefficients										Regression statistics			
	Intercept	SL	pH@3h	pH@24h	Gly	Gly ²	PC1	LT fat	REA	FT	Temp@3h	HCW	RMSE	Adj-R ²
WBSF 3 days	14.16	-5.72***	1.44***	-1.34**	-	-	-	-	-	-	-	-	1.37	0.28
WBSF 7 days	0.52	-3.11***	1.18***	-	0.03**	-	0.68**	-	-	-	-	-	1.01	0.42
WBSF 14 days	8.39***	-4.09***	-	-	0.03***	-	-	0.03**	-	-	-	-	0.92	0.40
L*-value	55.79***	8.71**	-	-6.26**	-	-	-	-	-	0.42**	-	-	4.05	0.20
a*-value	31.57***	7.43***	-	-4.31	-	-	-	-	0.30**	-0.20*	-	-	2.47	0.21
b*-value	20.23***	7.20***	-1.47**	-1.91**	-	-	-	-	0.20*	-	-	-	1.92	0.29
SL	2.05***	-	-0.05**	-	-	-	-	-	-	0.013**	-	-	0.10	0.13
Temp@3h	11.62***	-	-	-	-	-	3.30***	0.12***	0.30***	-	-	-	1.73	0.65
pH@3h	6.26***	-	-	-	-	-	-	0.01**	-0.03**	-	-	-	0.297	0.08
pH@24h	7.83***	-	-	-	-0.05***	0.0003***	-0.08**	-	-	-	-0.001*	-	0.147	0.45

(Ertbjerg and Puolanne 2017). In regard to shear-force, short sarcomeres hinder the contact of myofibrils with proteolytic enzymes, and therefore a decrease in the aging effect occurs (Hwang *et al.* 2004; Weaver *et al.* 2009).

In addition, and in agreement with the literature (Thompson *et al.* 2006), we observed that sarcomere length was reduced as rate of pH decline decreases (greater pH@3h) and as cooling rate increases (lower Temp@3h; Adj- $R^2 = 0.13$). These rates changed according to carcass REA and s.c. fat thickness (Adj- $R^2 = 0.08$ and Adj- $R^2 = 0.69$, respectively). Overall, our results suggest that any management strategy that can be implemented to increase subcutaneous fat thickness, rib eye area or both in grazing-finished cattle with less than 7–8 mm of subcutaneous fat thickness would contribute to improve meat quality. Selecting animals with higher subcutaneous fat thickness or REA could be one potential strategy to ensure high EV cattle meat quality in grazing systems.

Conclusions

No differences in EV between more temperamental and calmer Angus were observed at the end of the fattening period and before slaughter. Common practices carried out in a semi-intensive grazing system could foster habituation of more reactive animals.

Although in this study, performance and meat quality were hardly affected or not affected at all by cattle temperament, the low carcass fatness and muscle glycogen content at slaughter in temperamental animals would increase the risk of defects on meat under inappropriate animal handling before slaughter.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This study was funded by the Instituto Nacional de Tecnología Agropecuaria (INTA, PNPA-1126024) and the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT- PICT 2010–018). This publication is presented as a partial requirement for the first author to obtain a Doctor Degree at Universidad Nacional de Mar del Plata, Argentina.

References

AMSA (2016) 'Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of meat.' (American Meat Science Association: Champaign, IL)

Behrends SM, Miller RK, Rouquette FM, Randel RD, Warrington BG, Forbes TDA, Welsh TH, Lippke H, Behrends JM, Carstens GE, Holloway JW (2009) Relationship of temperament, growth, carcass characteristics and tenderness in beef steers. *Meat Science* **81**, 433–438. doi:10.1016/j.meatsci.2008.09.003

Bergman I, Loxley R (1963) Two improved and simplified methods for the spectrophotometric determination of hydroxyproline. *Analytical Chemistry* **35**, 1961–1965. doi:10.1021/ac60205a053

Burrow HM, Corbet NJ (2000) Genetic and environmental factors affecting temperament of zebu and zebu-derived beef cattle grazed at pasture in the tropics. *Australian Journal of Agricultural Research* **51**, 155–162. doi:10.1071/AR99053

Café LM, Robinson DL, Ferguson DM, McIntyre BL, Geesink GH, Greenwood PL (2011) Cattle temperament: persistence of assessments and associations with productivity, efficiency, carcass and meat quality

traits1. *Journal of Animal Science* **89**, 1452–1465. doi:10.2527/jas.2010-3304

Ceballos MC, Góis KCR, Sant'Anna AC, da Costa MJRP (2018) Frequent handling of grazing beef cattle maintained under the rotational stocking method improves temperament over time. *Animal Production Science* **58**, 307–313. doi:10.1071/AN16025

Cooke RF (2014) BILL E. KUNKLE INTERDISCIPLINARY BEEF SYMPOSIUM: Temperament and acclimation to human handling influence growth, health, and reproductive responses in *Bos taurus* and *Bos indicus* cattle. *Journal of Animal Science* **92**, 5325–5333. doi:10.2527/jas.2014-8017

Coombes SV, Gardner GE, Pethick DW, McGilchrist P (2014) The impact of beef cattle temperament assessed using flight speed on muscle glycogen, muscle lactate and plasma lactate concentrations at slaughter. *Meat Science* **98**, 815–821. doi:10.1016/j.meatsci.2014.06.029

Cross HR, Carpenter ZL, Smith GC (1973) Effects of intramuscular collagen and elastin on bovine muscle tenderness. *Journal of Food Science* **38**, 998–1003. doi:10.1111/j.1365-2621.1973.tb02133.x

Cross HR, West RL, Dutton TR (1981) Comparison of methods for measuring sarcomere length in beef semitendinosus muscle. *Meat Science* **5**, 261–266. doi:10.1016/0309-1740(81)90016-4

Curley KO Jr, Paschal JC, Welsh TH, Randel RD (2006) Technical note: Exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls. *Journal of Animal Science* **84**, 3100–3103. doi:10.2527/jas.2006-055

Czarnocki J, Sibbald IR, Evans EV (1961) The determination of chromic oxide in samples of feed and excreta by acid digestion and spectrophotometry. *Canadian Journal of Animal Science* **41**, 167–179. doi:10.4141/cjas61-024

Duckett SK, Neel JPS, Sonon RN Jr, Fontenot JP, Clapham WM, Scaglia G, Sonon RN Jr, Fontenot JP, Clapham WM, Scaglia G (2007) Effects of winter stocker growth rate and finishing system on: II. Ninth tenth eleventh-rib composition, muscle color, and palatability. *Journal of Animal Science* **85**, 2691–2698. doi:10.2527/jas.2006-734

Duckett SK, Neel JPS, Lewis RM, Fontenot JP, Clapham WM (2013) Effects of forage species or concentrate finishing on animal performance, carcass and meat quality. *Journal of Animal Science* **91**, 1454–1467. doi:10.2527/jas.2012-5914

Ertbjerg P, Puolanne E (2017) Muscle structure, sarcomere length and influences on meat quality: A review. *Meat Science* **132**, 139–152. doi:10.1016/j.meatsci.2017.04.261

Ferguson DM, Warner RD (2008) Have we underestimated the impact of pre-slaughter stress on meat quality in ruminants? *Meat Science* **80**, 12–19. doi:10.1016/j.meatsci.2008.05.004

Francisco CL, Cooke RF, Marques RS, Mills RR, Bohnert DW (2012) Effects of temperament and acclimation to handling on feedlot performance of *Bos taurus* feeder cattle originated from a rangeland-based cow-calf system1. *Journal of Animal Science* **90**, 5067–5077. doi:10.2527/jas.2012-5447

Francisco CL, Resende FD, Benatti JMB, Castilhos AM, Cooke RF, Jorge AM (2015) Impacts of temperament on Nelore cattle: physiological responses, feedlot performance, and carcass characteristics. *Journal of Animal Science* **93**, 5419–5429. doi:10.2527/jas.2015-9411

Haskell MJ, Simm G, Turner SP (2014) Genetic selection for temperament traits in dairy and beef cattle. *Frontiers in Genetics* **5**, 1–18. doi:10.3389/fgene.2014.00368

Hill HF (1966) The solubility of intramuscular collagen content in meat animals of various ages. *Food Science* **31**, 161–166. doi:10.1111/j.1365-2621.1966.tb00472.x

Hopkins DL, Martin L, Gilmour AR (2004) The impact of homogenizer type and speed on the determination of myofibrillar fragmentation. *Meat Science* **67**, 705–710. doi:10.1016/j.meatsci.2004.01.011

- Hopkins DL, Ponnampalam EN, van de Ven RJ, Warner RD (2014) The effect of pH decline rate on the meat and eating quality of beef carcasses. *Animal Production Science* **54**, 407–413. doi:10.1071/AN12314
- Hughes J, Clarke F, Purslow P, Warner R (2018) A high rigor temperature, not sarcomere length, determines light scattering properties and muscle colour in beef *M. sternomandibularis* meat and muscle fibres. *Meat Science* **145**, 1–8. doi:10.1016/j.meatsci.2018.05.011
- Huhtanen P, Kukkonen U (1995) Comparison of methods, markers, sampling sites and models for estimating digesta passage kinetics in cattle fed at two levels of intake. *Animal Feed Science and Technology* **52**, 141–158. doi:10.1016/0377-8401(94)00699-A
- Hwang IH, Park BY, Cho SH, Lee JM (2004) Effects of muscle shortening and proteolysis on Warner-Bratzler shear force in beef longissimus and semitendinosus. *Meat Science* **68**, 497–505. <http://www.science-direct.com/science/article/B6T9G-4CHHR4K-4/2/ad5a46768a4a985b2f3462821d5c6a34>. doi:10.1016/j.meatsci.2004.04.002
- Immonen K, Ruusunen M, Hissa K, Puolanne E (2000) Bovine muscle glycogen concentration in relation to finishing diet, slaughter and ultimate pH. *Meat Science* **55**, 25–31. doi:10.1016/S0309-1740(99)00121-7
- King DA, Schuehle Pfeiffer CE, Randel RD, Welsh JTH, Oliphint RA, Baird BE, Curley JKO, Vann RC (2006) Influence of animal temperament and stress responsiveness on the carcass quality and beef tenderness of feedlot cattle. *Meat Science* **74**, 546–556. doi:10.1016/j.meatsci.2006.05.004
- Lippke H, Ellis WC, Jacobs BF (1986) Recovery of indigestible fiber from feces of sheep and cattle on forage diets. *Journal of Animal Science* **69**, 403–412.
- Lockwood SA, Kattesh HG, Krawczel PD, Kirkpatrick FD, Saxton AM, Rhinehart JD, Wilkerson JB (2015) Relationships among temperament, behavior, and growth during performance testing of bulls. *Journal of Animal Science* **93**, 5856–5862. doi:10.2527/jas.2015-9302
- McVeigh JM, Tarrant PV, Mc Veigh JM, Tarrant PV (1982) Glycogen content and repletion rates in beef muscle, effect of feeding and fasting. *The Journal of Nutrition* **112**, 1306–1314. doi:10.1093/jn/112.7.1306
- Neath KE, Del Barrio AN, Lapitan RM, Herrera JRV, Cruz LC, Fujihara T, Muroya S, Chikuni K, Hirabayashi M, Kanai Y (2007) Difference in tenderness and pH decline between water buffalo meat and beef during postmortem aging. *Meat Science* **75**, 499–505. doi:10.1016/j.meatsci.2006.08.016
- Novakofski J, Park S, Bechtel PJ, McKeith FK (1989) Composition of cooked pork chops: effect of removing subcutaneous fat before cooking. *Journal of Food Science* **54**, 15–17. doi:10.1111/j.1365-2621.1989.tb08556.x
- Page JK, Wulf DM, Schwotzer TR (2001) A survey of beef muscle color and pH. *Journal of Animal Science* **79**, 678–687. doi:10.2527/2001.793678x
- Pavan E, Duckett SK, Andrae JG (2007) Corn oil supplementation to steers grazing endophyte-free tall fescue. I. Effects on *in vivo* digestibility, performance, and carcass traits. *Journal of Animal Science* **85**, 1330–1339. doi:10.2527/jas.2006-623
- Petherick JC, Holroyd RG, Doogan VJ, Venus BK (2002) Productivity, carcass and meat quality of lot-fed *Bos indicus* cross steers grouped according to temperament. *Animal Production Science* **42**, 389–398. doi:10.1071/EA01084
- Pighin DG, Davies P, Grigioni G, Pazos AA, Ceconi I, Mendez D, Buffarini M, Sancho A, Gonzalez CB (2013) Effect of slaughter handling conditions and animal temperament on bovine meat quality markers. *Archivos de Zootecnia* **62**, 399–409. doi:10.4321/S0004-05922013000300008
- Rhoades RD, Sawyer JE, Chung KY, Schell ML, Lunt DK, Smith SB (2007) Effect of dietary energy source on *in vitro* substrate utilization and insulin sensitivity of muscle and adipose tissues of Angus and Wagyu steers. *Journal of Animal Science* **85**, 1719–1726. doi:10.2527/jas.2006-498
- Rhoades RD, Sawyer JE, Ponce CH, Lunt DK, Smith SB (2009) Substrate utilization and dose response to insulin by subcutaneous adipose tissue of Angus steers fed corn- or hay-based diets. *Journal of Animal Science* **87**, 2338–2345. doi:10.2527/jas.2008-1365
- Tatum JD, Smith GD, Carpenter ZL (1982) Interrelationships between marbling, subcutaneous fat thickness and cooked beef palatability. *Journal of Animal Science* **54**, 777–784. doi:10.2527/jas1982.544777x
- Thompson JM, Perry D, Daly B, Gardner GE, Johnston DJ, Pethick DW (2006) Genetic and environmental effects on the muscle structure response post-mortem. *Meat Science* **74**, 59–65. doi:10.1016/j.meatsci.2006.04.022
- Turner SP, Navajas EA, Hyslop JJ, Ross DW, Richardson RI, Prieto N, Bell M, Jack MC, Roehe R (2011) Associations between response to handling and growth and meat quality in frequently handled *Bos taurus* beef cattle. *Journal of Animal Science* **89**, 4239–4248. doi:10.2527/jas.2010-3790
- Van Soest PJ, Robertson JB, Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597. doi:10.3168/jds.S0022-0302(91)78551-2
- Weaver AD, Bowker BC, Gerrard DE (2009) Sarcomere length influences u-calpain-mediated proteolysis of bovine myofibrils. *Journal of Animal Science* **87**, 2096–2103. doi:10.2527/jas.2008-1317
- Wulf DM, Wise JW (1999) Measuring muscle color on beef carcasses using the L*a*b* color space. *Journal of Animal Science* **77**, 2418–2427. doi:10.2527/1999.7792418x
- Yao G (2016) Light propagation in meat and meat analog: theory and applications. 'Light scattering technology for food property, quality and safety assessment.' (Ed. R Lu) p. 483. (CRC Press, Taylor & Francis Group: Boca Raton, FL)

Handling editor: Joe Jacobs