



Beef carcasses with larger eye muscle areas, lower ossification scores and improved nutrition have a lower incidence of dark cutting

P. McGilchrist^{a,b,*}, C.L. Alston^c, G.E. Gardner^{a,b}, K.L. Thomson^d, D.W. Pethick^{a,b}

^a Australian Cooperative Research Centre for Beef Genetic Technologies, U.N.E., Armidale, N.S.W. 2351, Australia

^b School of Veterinary & Biomedical Science, Murdoch University, Murdoch, WA 6150, Australia

^c School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD 4001, Australia

^d Department of Agriculture & Food of Western Australia, South Perth, WA 6151, Australia

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ABSTRACT

This study evaluated the effect of eye muscle area (EMA), ossification, carcass weight, marbling and rib fat depth on the incidence of dark cutting ($\text{pH}_u > 5.7$) using routinely collected Meat Standards Australia (MSA) data. Data was obtained from 204,072 carcasses at a Western Australian processor between 2002 and 2008. Binomial data of pH_u compliance was analysed using a logit model in a Bayesian framework. Increasing eye muscle area from 40 to 80 cm^2 , increased pH_u compliance by around 14% ($P < 0.001$) in carcasses less than 350 kg. As carcass weight increased from 150 kg to 220 kg, compliance increased by 13% ($P < 0.001$) and younger cattle with lower ossification were also 7% more compliant ($P < 0.001$). As rib fat depth increased from 0 to 20 mm, pH_u compliance increased by around 10% ($P < 0.001$) yet marbling had no effect on dark cutting. Increasing musculature and growth combined with good nutrition will minimise dark cutting beef in Australia.

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1. Introduction

Dark cutting in beef carcasses is one of the largest problems affecting meat quality world-wide. Dark cutting is caused by muscle glycogen levels below about 60 $\mu\text{mol/g}$ at slaughter (Tarrant, 1989), which results in low lactate production post-mortem and subsequent high ultimate pH (pH_u). Meat Standards Australia (MSA) stipulate that carcasses must have a pH_u less than 5.71 in order to be eligible for grading (Thompson, 2002). Meat from carcasses with a pH_u greater than 5.7 has a darker colour, shorter shelf life, bland flavour, variable tenderness and it resists cooking, thus impacting on degree of doneness (Ferguson et al., 2001; Purchas & Aungsupakorn, 1993; Thompson, 2002). The colour of meat is the primary tool used by consumers to predict quality (Hendrick, Aberle, Forrest, Judge, & Merkel, 1994), therefore dark cutting severely affects purchasing decisions. In 2009, MSA graded 1,157,781 cattle in Australia and 5.45% had a pH_u greater than 5.7 (MSA, 2010). Due to its effect on quality, beef producers are commonly penalised around \$AUS0.50 per kg carcass weight for carcasses with a pH_u greater than 5.7. This penalty equates to a cost of around \$7.09 per animal graded under MSA in 2009 to producers alone, calculated using the average carcass weight of 260 kg.

Muscle glycogen at slaughter is a function of resting muscle glycogen 'on-farm' minus the quantity of glycogen loss due to stressors during the pre-slaughter period. Thus animals with low resting glycogen concentrations, which undergo similar pre-slaughter stress, are more susceptible to dark cutting. Considerable research over the past few decades has increased knowledge of the causes of dark cutting, enabling beef producers to put in place best management practices to minimise its incidence. However, there are still commonly variations in pH_u within a herd from the same pre-slaughter environment causing some to be dark, firm and dry, which may be attributed to intrinsic physiological differences between animals.

One cause of this physiological variability may be associated with the extent of muscle expression in individual animals and the resultant possible change in muscle fibre types. Selection for increased muscling is known to cause a shift in muscle fibre type, increasing the proportion of fast glycolytic type IIX myofibres (Wegner et al., 2000), while younger cattle also express greater proportions of fast glycolytic type IIX myofibres (Brandstetter, Picard, & Geay, 1998). Shift in fibre type proportions is likely to lead to metabolic changes in muscle, as has been shown by McGilchrist, Pethick, Bonny, Greenwood, and Gardner (2011a, 2011b) and Martin, McGilchrist, Thompson, and Gardner (2011) who demonstrated that more muscular cattle and lambs are more responsive to insulin, less responsive to adrenaline and had a higher storage of muscle glycogen (McGilchrist et al., 2011a). Therefore younger cattle and more muscular cattle are both likely to have increased glycogen at slaughter and a reduced incidence of dark cutting syndrome.

* Corresponding author at: School of Veterinary and Biomedical Science, Murdoch University, South St Murdoch, 6150 WA, Australia. Tel.: +61 893606199 (office), +61 419986056 (mobile); fax: +61 893606628.

E-mail address: p.mcgilchrist@murdoch.edu.au (P. McGilchrist).

The level of whole body adiposity as measured by rib fat depth and MSA marbling score are generally negatively correlated with muscularity. More muscular animals have higher muscle to fat ratio (O'Rourke et al., 2009; Perry, Yeates, & McKiernan, 1993) and have more stress responsive adipose tissue to adrenaline (McGilchrist et al., 2011a), which partially explains the leanness of these animals. This indicates that under stressful conditions pre-slaughter, high muscled cattle utilise adipose tissue for energy production to a greater extent than low muscled cattle. However, there is no evidence to suggest that quantity of adipose tissue has any effect on glycogen storage at slaughter.

This paper investigates what variance in pH_u can be explained by carcass phenotype measurements recorded by MSA. It was hypothesised that more muscular animals with a larger eye muscle area and younger animals with a low ossification score will have a reduced incidence of dark cutting, while there will be no effect of MSA marbling or rib fat depth on average pH_u .

2. Materials and methods

Since 1996 MSA has identified critical control points from the production, processing, value adding and cooking sectors of the beef supply chain in Australia that impact on eating quality and combined these into the MSA grading system (Thompson, 2002). This paper describes the analysis of MSA data from a Western Australian meat processor. The data set contained individual carcass measurements for 204,071 carcasses graded under MSA between February 2002 and December 2008.

2.1. Producer and processor requirements

Producers and processors must comply with a set of conditions aimed at reducing pre-slaughter stress and optimizing processing conditions to be eligible to grade carcasses under the MSA grading system. A producer must declare on the national vendor declaration the *Bos indicus* percentage and if the cattle can be classed as milk fed vealer. The cattle can be sourced from saleyards however cattle must not be mixed in lairage and also must be harvested the day after dispatch (Thompson, 2002). The carcasses must also be dressed according to AUS-MEAT standard specifications (AUS-MEAT, 1998).

2.2. Carcass measurements

In order to generate an individual palatability score for each carcass, carcass measurements are required for the MSA prediction model. Carcass measurements are taken by graders accredited with both MSA grading and AUS-MEAT chiller assessment (MLA, 2006). The carcass measurements include:

- Gender (steer/heifer)
- Hump height is measured in gradients of 5 mm and is primarily used to verify the tropical breed content declared on the vendor declaration (MLA, 2006).
- Fat colour is determined from the intermuscular fat lateral to the rib eye muscle. It is assessed on the chilled carcass and scored against the AUS-MEAT fat colour reference standards (AUS-MEAT, 2005) – this is not an MSA requirement but is recorded by the abattoir.
- Meat colour is the predominant colour of the rib eye muscle (*longissimus thoracis et lumborum*). It is measured on the chilled carcass at the bloomed rib eye muscle face and is scored against AUS-MEAT colour reference standards (AUS-MEAT, 2005). Meat colour has a scale of 1 to 7, with carcasses in the range of 1B to 3 acceptable for MSA.
- MSA marbling score is a measure of the fat deposited between individual fibres in the rib eye muscle ranging from 100 to 1100 in increments of 10. Marbling is assessed at the quartering site of the

chilled carcass and is calculated by evaluating the amount, piece size and distribution of marbling in comparison to the MSA reference standards (AUS-MEAT, 2005; MLA, 2006; Romans, Costello, Carlson, Greaser, & Jones, 1994).

- Rib fat depth is the depth of subcutaneous fat in millimeters. It is measured at the quartering site in the chilled carcass approximately 75% of the way along the rib eye muscle (AUS-MEAT, 2005).
- Ossification score is measured following the guidelines from the United States Department of Agriculture (Romans et al., 1994). Ossification provides a scale between 100 and 590 in increments of 10 for MSA which is an assessment of physiological age of a bovine carcass. It is a measure of the calcification in the spinous processes in the sacral, lumbar and thoracic vertebrae (AUS-MEAT, 2005).
- Ultimate pH (pH_u) and loin temperature is measured in the rib eye muscle (*longissimus thoracis et lumborum*) of the chilled carcass at the quartering site approximately 20 h post-mortem. Temperature and pH are measured using an MSA approved TPS MC-80 or TPS WP-80M pH Meter (TPS Pty Ltd., Springwood, Brisbane, Qld, 4127, Australia). pH and temperature probes should be inserted into the muscle in close proximity to each other with enough time allowed for reading to be stabilised. MSA grading cannot commence if the loin temperature is above 12 °C (AUS-MEAT, 2005).
- Hot standard carcass weight (HSCW) – measured at the end of the slaughter chain in kilograms with carcasses dressed to AUS-MEAT carcass standards (AUS-MEAT, 2005)
- Eye muscle area (EMA) is measured using the AUS-MEAT EMA standard grid as the number of square centimetres of *longissimus thoracis et lumborum* at the quartering site (AUS-MEAT, 2005) – this is not an MSA requirement but is recorded by the abattoir.

2.3. Data analysed

From February 2002 till December 2008, there were 204,071 carcasses graded at the processing plant and 8.75% had a pH_u greater than 5.7. The numbers of carcasses graded from each year are given in Table 1 along with descriptive statistics for HSCW, EMA, ossification, rib fat and MSA marbling. The numbers graded in 2002 are the smallest as MSA grading did not commence in full until late February that year, while in 2008, the numbers graded almost doubled on the previous year due to company policy to increase throughput. Average ossification over each year has decreased slightly, indicating the animals are younger at slaughter. Both EMA and MSA marbling have increased since 2002, while rib fat depth has averaged between 8 and 11 mm and is assumed to reflect the differences in animal nutrition between years.

2.4. Statistical analysis

Data was analysed in two ways, firstly to assess the impact of variables on mean pH_u (mean pH_u analysis), and secondly to assess the impact on pH_u compliance rate.

2.5. Mean pH_u analysis

The effect of variables on pH_u was analysed using a linear mixed effects model which can be represented by

$$pH = X\beta + Zu + \varepsilon$$

where X represents the design matrix of fixed effects, β are the coefficients of the fixed effects, Z is the design matrix for the random effects and u are the random effect coefficients, with ε representing the random error term.

Table 1
Within year descriptive statistics for the number of carcasses graded and means $\pm$ standard deviations for hot standard carcass weight (HSCW), eye muscle area (EMA), ossification (Oss), rib fat and MSA marbling (MSAMarb) with minimum and maximum values in brackets.

Year	No. graded	HSCW (kg)	EMA (cm ²)	Oss (100–590)	Rib fat (mm)	MSAMarb (100–1100)
2002	17,043	257 $\pm$ 34.12 (136; 597)	65.7 $\pm$ 8.3 (32; 150)	154.9 $\pm$ 19.15 (100; 400)	8.0 $\pm$ 3.46 (0; 56)	234.7 $\pm$ 80.64 (110; 650)
2003	15,220	240 $\pm$ 42.42 (112; 658)	64.76 $\pm$ 7.56 (30; 150)	145.7 $\pm$ 19.35 (100; 410)	7.5 $\pm$ 3.16 (0; 56)	274.0 $\pm$ 70.32 (110; 860)
2004	28,633	261 $\pm$ 52.02 (105; 533)	67.23 $\pm$ 7.15 (30; 150)	152.4 $\pm$ 22.99 (100; 500)	10.1 $\pm$ 4.68 (0; 60)	313.1 $\pm$ 57.53 (120; 880)
2005	25,727	251 $\pm$ 46.43 (101; 498)	68.13 $\pm$ 7.03 (30; 150)	146.9 $\pm$ 21.89 (100; 480)	9.5 $\pm$ 5.06 (0; 60)	293.1 $\pm$ 55.45 (100; 940)
2006	26,944	244 $\pm$ 51.5 (127; 673)	69.28 $\pm$ 8.55 (30; 150)	146 $\pm$ 20.05 (100; 320)	10.3 $\pm$ 4.88 (0; 41)	295.7 $\pm$ 70.89 (120; 990)
2007	36,026	256 $\pm$ 69.31 (112; 588)	71.17 $\pm$ 10.68 (30; 150)	149.7 $\pm$ 20.56 (100; 430)	10.9 $\pm$ 5.32 (0; 58)	326.5 $\pm$ 64.11 (100; 1050)
2008	54,477	239 $\pm$ 33.82 (117; 464)	69.69 $\pm$ 7.96 (30; 150)	138.5 $\pm$ 13.78 (100; 500)	8.2 $\pm$ 3.14 (0; 58)	327.4 $\pm$ 38.31 (130; 1100)

2.6. Compliance assessment

Carcass compliance for pH_u less than 5.7 was also analysed. Within this model, the probability of a carcass complying ($Y_i = 0$) or failing ($Y_i = 1$) can be represented by:

$$\text{prob}(Y_i = 0) = p_i \text{ and } \text{prob}(Y_i = 1) = 1 - p_i.$$

The model is represented as:

$$\text{logit}(p) = X\beta + Zu + \varepsilon$$

where logit is the usual canonical link (McCulloch & Nelder, 1989) for binomial data. β represents the fixed effects in the model, u the random effects, and ε is the random error.

For both the mean pH_u and compliance models, the variance structure of the model can be represented as:

$$\begin{bmatrix} \beta \\ u \\ \varepsilon \end{bmatrix} = N \left(\begin{bmatrix} \beta_0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} B & 0 & 0 \\ 0 & G & 0 \\ 0 & 0 & R \end{bmatrix} \right)$$

with the random, fixed and error terms being treated as independent.

Parameters were estimated using a Bayesian analysis, with prior distributions for the unknown parameters taken to be:

$$\begin{aligned} \pi(\beta_0) &\sim N(0, 10) \\ \pi(u|G) &\sim N(0, G) \\ \pi(\varepsilon|R) &\sim N(0, R) \\ \pi(G) &\sim IW(5, 2) \\ \pi(R) &\sim IW(1, 1). \end{aligned}$$

The purpose of the prior distribution is to define knowledge of the parameters before collection of data, or base the priors on previous experimental data collection, hence making the model an accumulation of existing knowledge and new data. In this case, minimal prior information about the parameters was available, so vague priors which

summarise the known likely range of the parameters were used. Representations of these densities for β_0 , G and R are given in Fig. 1.

The chosen prior distributions are from conjugate families, meaning that using Bayes' rule, the product of the likelihood and the prior will result in a distribution from the same family. This in turn allows the estimation of the parameters using the Monte Carlo Markov Chain (MCMC) technique known as the Gibbs sampler, which updates parameters individually using their full conditional distribution. This is advantageous, as the joint distribution of the unknown parameters is difficult to sample directly, however, the full conditional distributions are from known densities, and as such, are relatively easy to sample.

For the analysis of mean pH_u, only significant fixed terms ($P < 0.05$) were retained. These included HSCW, EMA, ossification, MSA marbling, rib fat, loin temperature at time of grading, season (Summer, Autumn, Winter, Spring), gender (male castrates or female), finishing system (sourced from an Australian Lot Feeders Association accredited feedlot or otherwise cattle were assumed to be grass fed), tropical breed content (percentage of *bos indicus* from 0 to 100%), lot size (from 1 to 188) and the interaction between finishing system and season. HSCW was also divided into two groups of less than and greater than 350 kg, given that preliminary data analysis suggested that the linear impact of HSCW was greater in carcasses which were < 350 kg. These two HSCW categories (representing heavy and light animals) were interacted with rib fat, EMA, ossification, and MSA marbling. MSA grader, producer, year (from 2002 to 2008) and the interaction between season and year were included in the model as random terms. Exactly the same fixed terms were then used in the logit analysis to assess pH_u compliance, irrespective of significance.

The Gibbs sampler was run for 100,000 iterations, with a burn-in of 25,000 iterations and a thinning of 100. The large burn-in was used to allow the MCMC chain to settle due to the vague priors and starting values. Thinning was used to reduce the auto-correlation in the MCMC chains from which the parameters are estimated. The models were fitted using the package MCMCglmm (Hadfield, 2010) in the R statistical analysis software (R Development Core Team, 2008).

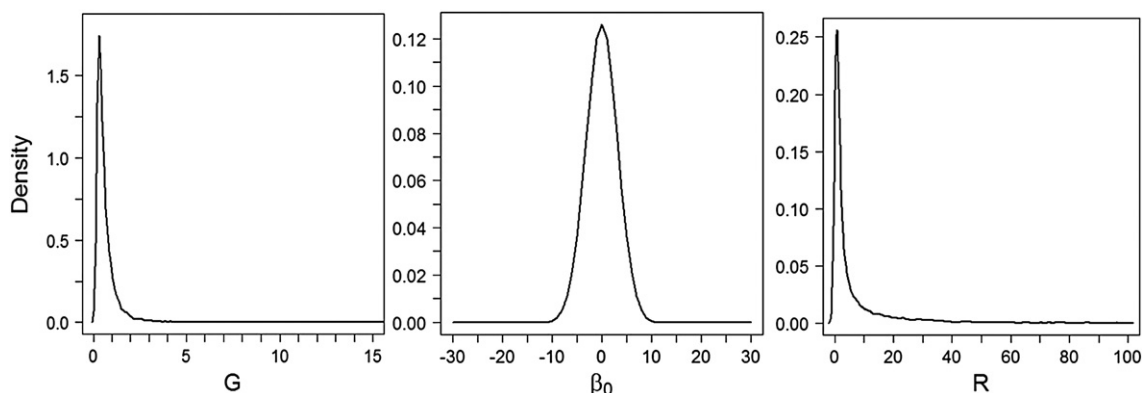


Fig. 1. Representation of the prior distribution densities for G , β_0 and R .

The probability of non-compliance can be visualised using the schematic back transformation of the logit scale in Fig. 2. An overall coefficient value ($X\beta$) of zero represents 50% probability of having a pH_u greater than 5.7, and as values become more negative, the probability of non-compliance decreases. Fig. 2 probabilities of having a $pH_u > 5.7$ are calculated using the back-transformation

$$Prob(pH_u > 5.7) = \frac{e^{X\beta}}{1 + e^{X\beta}}$$

where X is the design matrix of fixed effects and β are the estimated model coefficients.

2.7. Results interpretation

The effects of each parameter in the logit model are stated in Table 2 as mean estimates, for example -0.006847 for HSCW. To estimate the probability of having a $pH_u > 5.7$, -0.006847 is multiplied by the positive value of HSCW, which implies that the heavier the carcass, the lower the probability of non-compliance when back transformed on the logit scale (Fig. 2). Whereas, the parameter estimate for male castrates was positive (0.118139), implying that carcasses from male castrates are more likely to have a value of $pH_u > 5.7$ than the female carcasses in the model. However, as the data are naturally unbalanced, care must be taken when viewing the coefficients in isolation.

The credible intervals (CI) in Table 2 are the 95% cut-off for values in the MCMC chain. If zero is not contained in the 95% CI, then this effect is significant at the 5% level. Additionally, a p-value was calculated which is the proportion of values in the MCMC that are greater than zero, if the estimated parameter is negative, and vice versa. This provides a level of confidence in the significance of the effect of a parameter in the model.

To represent the effect of the significant parameters, a method of conveying these results was established. To account for the wide range and unbalanced data that existed for most parameters, the mean estimated probability for each data point was calculated from the respective model, and then the mean response for each variable was predicted using the non-parametric method of loess smoothing to average over the values of the other variables in the data set. Due to the restriction of computing power for a data set this large, fitting the loess function for all data points using the standard R package was unachievable on a standard PC. To obtain mean estimates and standard error of this mean, a simulation study was conducted. In this study, 1000 carcasses from the data set were chosen randomly and

the loess estimate of the mean over the range of the chosen elements was calculated. This was repeated 5000 times in order to obtain a mean of these responses and its standard error. These are the means and standard error lines displayed in the graphs in the results section.

3. Results

3.1. Animal phenotype effects on pH_u

Carcass weight had a significant effect on mean pH_u and pH_u compliance ($P < 0.0001$, Table 2). The proportion of carcasses with a $pH_u > 5.7$ decreased in a curvilinear fashion from around 18% to 5% as HSCW increased from 150 kg to around 220 kg. Beyond this point, the proportion of $pH_u > 5.7$ continued to decrease, but at a slower rate (Fig. 3).

Eye muscle area when adjusted for HSCW had an effect on mean pH_u and carcass compliance for pH_u ($P < 0.0001$, Table 2). In lighter carcasses (< 350 kg) the effect of EMA was greater than in heavy carcasses, as shown by the significant interaction between the two terms in the model ($P < 0.0001$, Table 2). In the light carcasses (< 350 kg), as EMA increased from 40 to 80 cm², the proportion of non-compliant carcasses with a $pH_u > 5.7$ decreased from around 22% to 6%, while in heavy carcasses the non-compliance level dropped from around 8% to 3% as EMA increased from 50 to 80 cm² (Fig. 4). There were minimal improvements in pH_u compliance in both light and heavy carcasses as EMA increased above around 85 cm².

Rib fat levels had a significant effect on both non-compliance ($pH_u > 5.7$) and mean pH_u ($P < 0.0001$, Table 2). As rib fat depth increased from 0 to 20 mm, the proportion of non-compliant carcasses with a $pH_u > 5.7$ decreased from around 14% to 4% (Fig. 5). There were no further improvements in pH_u compliance as rib fat depth increased above 25 mm (Fig. 5).

Ossification had a significant effect on mean pH_u and pH_u compliance of carcasses ($P < 0.0001$, Table 2). In lighter carcasses (< 350 kg), pH_u non-compliance increased from around 6% to 20% as ossification score increased from 100 to 300 (Fig. 6) with the biggest increases occurring at ossifications scores above 200. While in heavy carcasses, non-compliance increased from around 0% to 7% across the same range of ossification scores.

Meat Standards Australia marbling score had a significant impact on mean pH_u ($P < 0.05$, Table 2), however there was no significant impact of MSA marbling on pH_u compliance. As MSA marbling increased by 100 points, mean pH_u decreased by 0.0034 pH units (Table 2).

4. Discussion

4.1. Effect of muscling

More muscular cattle with larger EMA's had a lower incidence of dark cutting syndrome, supporting our initial hypothesis. A reduction in the incidence of dark cutting in high muscled cattle complements the other advantages of muscular cattle like increased retail beef yield (O'Rourke et al., 2009) and processing efficiency. This is a very important finding for the beef industry as it demonstrates that beef producers can actively select for more muscular cattle with the knowledge that it will not increase the incidence of dark cutting carcasses. As shown in Fig. 4, the effect of muscling approached a plateau beyond an EMA of around 70 cm², which would suggest that producers should breed animals to have an EMA greater than this size to ensure a reduced incidence of dark cutting syndrome. This value of 70 cm² is around 5 cm² larger than the average EMA measured in this data set, thus it is an achievable goal if producers utilise sires that have an estimated breeding value for EMA higher than the average. Producers can also evaluate their current position by viewing

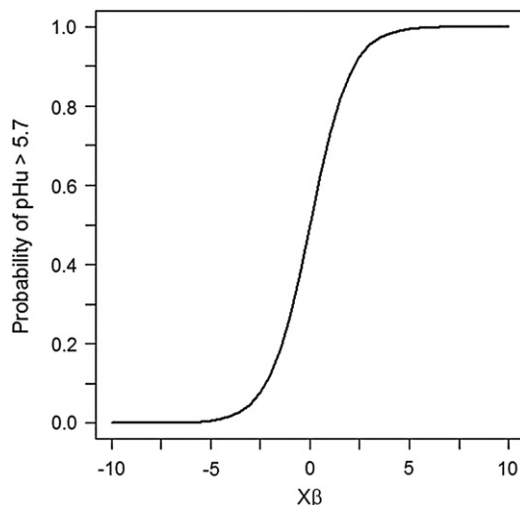


Fig. 2. Probability of non-compliance is given by the back transform of the logit function used in the generalised linear model analysis.

Table 2
Co-efficient estimates for the mean, 95% credible interval (CI) and P-values for fixed effects in the linear model of mean pH_u and generalised linear model of pH_u compliance. P-values represent the proportion of MCMC estimates that support significance.

	GLM model analysis of mean pH _u				Logit model analysis of pH _u compliance			
	Mean	2.5% CI	97.5% CI	P-value	Mean	2.5% CI	97.5% CI	P-value
Intercept	5.44	3.92	6.78	0	−2.09	−3.41	−0.744	0.0013
HSCW	−0.000146	−0.000237	−6.10E−05	0	−0.00685	−0.0126	−0.00195	0
EMA	−0.000534	−0.00084	−0.000233	7.00E−04	−0.0488	−0.0654	−0.0287	0
Ossification	0.000958	0.000763	0.00115	0	0.0284	0.0231	0.0343	0
Ossification ²	−1.00E−06	−2.00E−06	−1.00E−06	0	−4.70E−05	−6.50E−05	−3.00E−05	0
MSA marbling	−3.40E−05	−6.70E−05	−2.00E−06	0.018	0.000181	−0.00232	0.00204	0.419
Rib fat	−0.000743	−0.00124	−0.000219	0.004	−0.0554	−0.102	−0.0233	0
Sex – Male	0.00414	0.00248	0.0057	0	0.118	0.0789	0.159	0
Loin temperature	−0.00229	−0.00263	−0.00195	0	−0.0221	−0.031	−0.0113	0
Finishing system – feedlot	−0.0463	−0.0811	−0.0113	0.0067	−0.736	−1.017	−0.431	0
Tropical breed content	−0.000266	−0.000341	−0.000189	0	−0.00657	−0.00934	−0.00394	0
Lot size	−6.20E−05	−9.40E−05	−3.40E−05	0	−0.00192	−0.00281	−0.00105	0
Season – spring	0.0497	−0.730	0.847	0.44	0.148	−0.628	0.983	0.364
Season – summer	0.0408	−0.749	0.827	0.463	0.447	−0.349	1.23	0.13
Season – winter	0.0249	−0.818	0.841	0.481	−0.0744	−0.889	0.758	0.443
Season – spring: feedlot	0.00524	9.60E−05	0.0102	0.0227	0.0775	−0.0505	0.206	0.123
Season – summer: feedlot	−0.00962	−0.0154	−0.00383	0	−0.123	−0.318	0.0644	0.109
Season – winter: feedlot	0.000336	−0.00334	0.00387	0.42	0.0161	−0.0871	0.123	0.379
<i>Coefficient adjustments for carcasses <350 kg</i>								
HSCW <350 kg	−4.00E−05	−0.000126	5.00E−05	0.201	0.0013	−0.0039	0.00715	0.363
Rib fat: HSCW <350 kg	−0.000807	−0.00135	−0.000281	0.0027	0.00699	−0.0256	0.0553	0.359
EMA: HSCW <350 kg	−0.00049	−0.00079	−0.000183	0.002	0.021	0.00134	0.0369	0.02
MSA Marbling: HSCW <350 kg	9.50E−05	6.10E−05	0.00013	0	0.00113	−0.000795	0.00369	0.168
<i>Coefficient adjustments for carcasses >350 kg</i>								
Ossification: HSCW >350 kg	−5.90E−05	−0.000191	6.80E−05	0.1847	0.00945	0.00251	0.0159	0.0067

MSA feedback sheets which give EMA measurements, which will allow appropriate breeding decisions to be made.

These results suggests that more muscular cattle have higher muscle glycogen content at the time of slaughter resulting from either greater muscle glycogen concentration prior to the pre-slaughter period or less mobilisation of glycogen during the pre-slaughter period. McGilchrist et al. (2011b) has shown that Angus cattle selected for high muscling had increased whole body insulin responsiveness. This may enhance the uptake of glucose into muscle tissue in the post-prandial period and allow for an increased rate of glycogenesis, allowing these animals to have higher resting concentrations of

muscle glycogen (McGilchrist et al., 2011a). More muscular cattle may also mobilise less glycogen during the pre-slaughter period. The level of glycogenolysis during mustering, transport and lairage is largely due to the catabolic hormone adrenaline. Alternatively, McGilchrist et al. (2011a) and Martin et al. (2011) have shown that cattle and lambs selected for high muscling had muscle tissue that was less responsive to exogenous adrenaline, indicating that more muscular cattle may mobilise less glycogen during the stressful pre-slaughter period. Therefore both of these mechanisms may have contributed to the positive phenotypic association between EMA and muscle glycogen concentration.

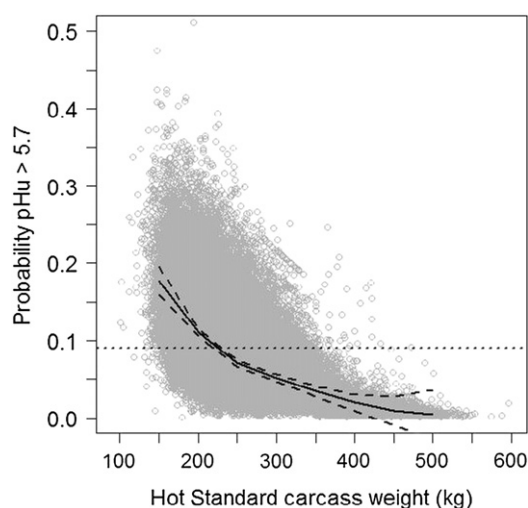


Fig. 3. Estimated mean (solid line) and standard deviation (dashed lines) for the effect of hot standard carcass weight on the probability of pH_u being greater than 5.7. Mean estimated probabilities of each raw data point are included to show the range of the data. The dotted line is the mean pH compliance rate of all carcasses.

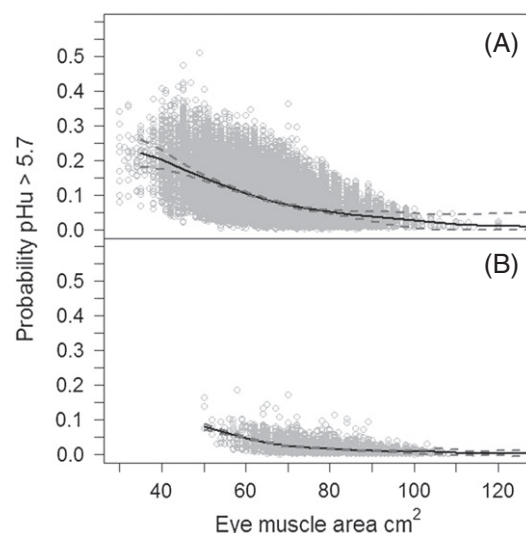


Fig. 4. Estimated mean (solid line) and standard error (dashed lines) for the effect of eye muscle area on pH_u compliance in carcasses <350 kg (A) and >350 kg (B). Mean estimated probabilities of each raw data point are included to show the range of the data.

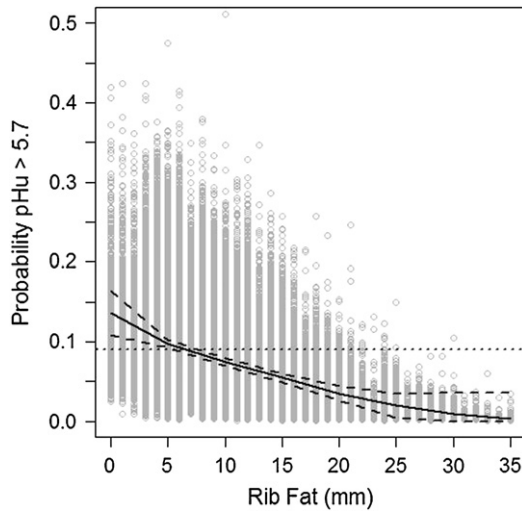


Fig. 5. Estimated mean (solid line) and standard errors (dashed lines) for the effect of rib fat depth on the probability of pH_u being greater than 5.7. Mean estimated probabilities of each raw data point are included to show the range of the data. The dotted line is the mean pH compliance rate of all carcasses.

4.2. Effect of rib fat depth and carcass weight

Carcasses with a higher depth of fat at the ribbing site had higher rate of pH_u compliance, contrary to our initial hypothesis that there would be no difference. Likewise heavier carcasses also had a higher rate of pH_u compliance. These two relationships are likely to be associated with better nutrition of the fatter and heavier cattle. The statistical model used attempted to capture the effect of nutrition through inclusion of finishing system and season within the model, however these terms are unlikely to have described all of the variance associated with improved nutrition. Cattle that have been supplemented or grain assisted through the finishing phase on non-Australian Lot Feeders Association registered feedlots were unable to be identified using the MSA database. Furthermore, the nutritional quality of pastures can vary greatly within seasons between years, and this variance may also have not been reflected adequately by the season and year terms in the model. Muscle glycogen

concentrations can range from 60 to 130 $\mu\text{mol/g}$ (Crouse, Smith, & Prior, 1984; McVeigh & Tarrant, 1982; Pethick, Rowe, & McIntyre, 1994) depending on the diet and rearing conditions, with high concentrations shown in cattle on high metabolisable energy grain rations (Gardner, McIntyre, Tudor, & Pethick, 2001; Pethick et al., 1994). As such these animals would have high glycogen concentrations prior to mustering, transport and lairage, decreasing the likelihood that glycogen levels will be depleted to less than 60 $\mu\text{mol/g}$ which would cause dark, firm, dry beef (Ferguson et al., 2001; Tarrant, 1989) with a pH_u higher than 5.7. Knee, Cummins, Walker, and Warner (2004) also demonstrated that glycogen levels were highly correlated with the metabolisable energy content of pasture, thus muscle glycogen was highest during spring and lowest during winter in Victoria. Therefore animals with more rib fat and heavier cattle can be assumed to have received better nutrition in the months leading up to slaughter, allowing for high muscle glycogen concentrations.

4.3. Effect of ossification

Carcasses with lower ossification scores had a lower incidence of dark cutting beef, aligning with our initial hypothesis. Lower ossification scores in cattle at the same HSCW indicate a more rapid growth rate throughout life. Growth rate in cattle is increased by good nutrition and previous work by Gardner et al. (2001) and Pethick et al. (1994) has demonstrated that animals on high energy rations have higher muscle glycogen concentrations, which would reduce the incidence of dark cutting in these carcasses. Our results, showing that faster growing cattle with lower ossification had improved pH_u compliance, align well with these previous findings.

Another possibility is that the effect of ossification on pH_u compliance was possibly associated with a shift in muscle fibre type as the animals aged. The largest difference in pH_u compliance existed in carcasses with an ossification score of above 175. Younger cattle have a greater proportion of glycolytic type IIX myofibres (Brandstetter et al., 1998) which have been shown to have higher expression of glucose transporter-protein (GLUT4) than in oxidative muscles in cattle (Hocquette et al., 1995). This may increase the uptake of glucose into the muscle because glucose transport is the rate-limiting step in insulin-stimulated glucose utilisation in muscle cells across most species (Hocquette et al., 1995; Ziel, Venkatesan, & Davidson, 1988; Zierler, 1999), which will in-turn increase glycogenesis. Younger cattle may also be less responsive to stress in the pre-slaughter period as they have a lower proportion of type I myofibres (Brandstetter et al., 1998). Muscle with a higher proportion of oxidative type I myofibres had an increased density of β_2 -adrenoreceptors and increased glycogenolysis in rats (Martin, Murphree, & Saffitz, 1989). This proposed mechanism is supported by Martin et al. (2011), which demonstrated that the muscle tissue of older sheep was more responsive to adrenaline than that of younger lambs. Thus glycogenolysis may be reduced in younger cattle in the pre-slaughter period.

5. Conclusion

Phenotypic measurements of beef carcasses taken at the time of grading for MSA explain differences in animal physiology which have effects on pH_u . More muscular cattle with larger EMA had higher levels of pH_u compliance, which could be associated with increased insulin responsiveness and reduced adrenaline responsiveness in more muscular cattle, increasing muscle glycogen at slaughter. Cattle with increased subcutaneous fat depth at the quartering site also had higher pH_u compliance, which may be due to improved nutrition and greater nutrient availability for both lipogenesis and glycogenesis, ultimately increasing accretion of muscle glycogen and fat. Heavier cattle also had increased pH_u compliance which is likely to be associated with the better nutrition and growth. pH_u compliance of carcasses

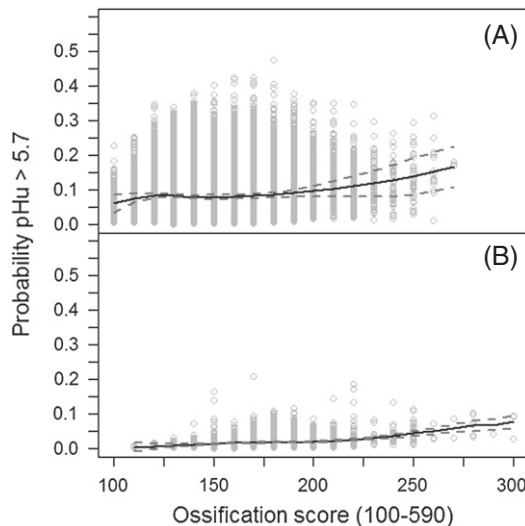


Fig. 6. Estimated means (solid line) and standard errors (dashed lines) for the effect of ossification on pH_u compliance in light carcasses <350 kg (A) and in heavy carcasses >350 kg (B). Mean estimated probabilities of each raw data point are included to show the range of the data.

decreased as ossification or age increased, possibly reflecting a shift in muscle fibre type. Furthermore, there was no affect of marbling on pH_u compliance.

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