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1 **Biochemical and organoleptic characteristics of muscle from early and late**
2 **maturing bulls in different production systems**

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13 **Short title**

14 **Effect of breed type and diet on bull beef quality**

15

16 **Abstract**

17 In grass based beef production systems (PS), early maturing breed types (EM) may be
18 preferable to late maturing breed types (LM) in achieving adequate fat cover.
19 Biochemical and organoleptic characteristics of muscle from suckler bulls were
20 investigated in EM and LM (n = 28/breed) assigned to one of two PS [*ad libitum*
21 concentrates and grass silage to slaughter (C) or *ad libitum* silage plus 2 kg concentrate
22 daily during winter followed by 99 days at pasture and then an indoor finishing period on
23 C (GSPC)] in a 2 breed type × 2 PS factorial arrangement of treatments. Bulls were
24 managed to have a common target carcass weight of 380 kg. Intramuscular fat (IMF)
25 content was higher ($P < 0.05$) for EM than LM, and for C than GSPC bulls. Collagen
26 solubility was higher ($P < 0.05$) for C than GSPC bulls. Lactate dehydrogenase (LDH)
27 and phosphofructokinase activities were higher ($P < 0.05$) for LM than EM. Isocitrate
28 dehydrogenase activity and the Type I myosin heavy chain (MyHC) proportion were
29 higher ($P < 0.05$) for EM than LM. The LDH activity and the Type IIX MyHC proportion
30 were higher ($P < 0.05$) for C than GSPC bulls. Sensory ratings for tenderness and
31 juiciness were higher ($P < 0.01$) for beef from EM than LM while sensory ratings for
32 tenderness, flavour liking and overall liking were higher ($P < 0.001$) for C than for GSPC
33 bulls. Differences in sensory quality were largely eliminated when adjusted for IMF.
34 Overall, carcass fat scores, IMF and sensory scores were higher in EM than LM and in
35 C than GSPC bulls but most differences in sensory quality could be attributed to
36 differences in IMF.

37 **Key words:** beef, breed type, diet, sensory, intramuscular fat

38 **Implications**

39 In countries like Ireland, where grazed grass is abundantly available, inclusion of grass
40 silage followed by a period of grazed grass, prior to finishing on a high energy
41 concentrate diet, decreases production costs in late maturing suckler bull production
42 systems but the bulls may not meet the market-specific requirements in terms of
43 carcass fat cover. It may be more appropriate, therefore, to rear early maturing breed
44 types in such production systems as the bulls have higher carcass fat scores and
45 marbling fat, and yield a more tender and juicier beef.

46 **Introduction**

47 In Ireland, late maturing breed types (LM) account for 85% of the suckler beef herd
48 while the remaining 15% are early maturing breed types (EM) (McGee, 2012).
49 Traditionally, the male beef cattle population was dominated by steers, but more
50 recently the proportion of bulls has increased as steers are less efficient in nutrient
51 utilization than bulls when reared similarly (O'Riordan *et al.*, 2011). However, producing
52 beef from suckler bulls, which usually involves provision of a high concentrate ration for
53 a prolonged period, is usually less profitable because of the higher cost of concentrates
54 compared to grass silage or grazed grass diets (Finneran *et al.*, 2011). Incorporating a
55 grazing period prior to finishing on a concentrate diet has been shown to reduce the
56 production costs of LM suckler bulls (O'Riordan *et al.*, 2011) with little impact on eating
57 quality of the beef (Mezgebo *et al.*, 2016).

58 However, while it is economically viable to incorporate a grazing period in the LM
59 suckler bull production system (PS), the bulls may not meet the market requirements in
60 terms of adequate carcass fat cover at a particular carcass weight (O'Riordan *et al.*,
61 2011). Carcass fat cover and colour are important parameters for the beef industry as
62 they influence the quality and consumer acceptability of beef (Moloney and Richardson,
63 2013). Even though LM predominate in the suckler herds in Ireland, EM may be more
64 suitable for a grass-based PS because when managed to a particular slaughter weight
65 and/or age, EM have a higher genetic potential to deposit fat than LM (Keane, 2011).

66 Recently, the influence, on beef quality characteristics, of incorporating a grazing period
67 prior to indoor finishing on a concentrate diet in the LM suckler bull PS was evaluated

68 (Mezgebo *et al.*, 2016). However, to our knowledge, little is known about the effect of
69 incorporating a grazing period in EM suckler bull PS on the quality of the beef.
70 Therefore, the aim of this study was to determine the influences of breed maturity and
71 inclusion of a period of grazed grass in a suckler bull PS on the compositional,
72 biochemical and organoleptic characteristics of beef. It was hypothesised that LM could
73 be replaced by EM, to achieve adequate fat cover and product quality specifications, in
74 a suckler bull beef PS.

75 **Materials and methods**

76 *Animals and management*

77 As part of a larger study described by Marren *et al.* (2013), 28 spring-born (mean birth
78 date 30 March) EM (Aberdeen Angus and Hereford sired calves) and 28 spring-born
79 (mean birth date 8 March) LM (Charolais and Limousin sired calves) weaned suckler
80 bulls were purchased at livestock markets in Ireland at approximately 8 months of age,
81 acclimatised to slatted floor accommodation and offered grass silage *ad libitum* plus 2
82 kg/head/day of a barley-based concentrate. Bulls were randomly assigned (1
83 December) within breed maturity to a two breed types (B) × two PS factorial
84 arrangement of treatments, balanced for sire breed and initial weight. The two PS were:
85 (1) *ad libitum* concentrates (870 g/kg rolled barley, 60 g/kg soya bean meal, 50 g/kg
86 molasses and 20 g/kg minerals/vitamins) plus *ad libitum* grass silage (GS) (dry matter
87 digestibility 700 g/kg) (C), and (2) GS plus 2 kg concentrate daily during the winter (123
88 day duration) followed by 99 days at pasture and then an indoor finishing period on C
89 (GSPC). Bulls were slaughtered at a commercial slaughter plant (Kepak Group, Clonee,
90 Co. Meath, Ireland) on reaching a mean live weight estimated to achieve a target
91 carcass weight of 380 kg. The study was carried out under license from the Irish
92 Government and with the approval of Teagasc, the Agricultural and Food Development
93 Authority.

94 *Carcass grading and muscle tissue collection*

95 Post slaughter, carcasses were weighed and graded for conformation according to the
96 EU Beef Carcass Classification Scheme as described in Mezgebo *et al.* (2016). At 1 h
97 post-slaughter, a sample (*ca.* 20 g) of *longissimus thoracis* (LT) muscle tissue was
98 taken (from 9th rib), snap frozen in liquid nitrogen and maintained at -80°C for muscle
99 metabolic enzyme activity and muscle typing analyses.

100 *Muscle pH and temperature measurement*

101 Muscle pH was measured at 2, 3.5, 5 and 48 h post-mortem by making a scalpel
102 incision in the muscle at the 10th rib and inserting a glass electrode (Model EC-2010-06,
103 Amagross Electrodes Ltd., Westport, Co. Mayo, Ireland) attached to a portable pH
104 meter (Model no. 250A, Orion Research Inc., Boston, MA) approximately 4.0 cm into

105 the muscle. The temperature was recorded simultaneously and used to make a
106 temperature compensated pH measurement.

107 *Fat and muscle colour measurements*

108 A detailed procedure is given in Mezgebo *et al.* (2016). Briefly, at 48 h post-mortem,
109 carcasses were cut at the 5/6th rib interface prior to subcutaneous fat and muscle colour
110 measurements. Subcutaneous fat colour (i.e. *L*, *a*, *b* colour coordinates) was measured
111 using a Miniscan XE Plus (Hunter Associates Laboratory Inc., Reston, VA, USA) at two
112 positions: (1) the lower round/rump region and (2) 13th rib region. Chroma/saturation (*C*)
113 and hue angle (*h*[°]) values were calculated from the '*a*' and '*b*' values. For muscle colour
114 measurement, the cut surface of the muscle was first allowed to bloom for 1 h. Muscle
115 colour grade was also subjectively assessed on the chilled carcass using Meat
116 Standards Australia colour sticks (Anon, 2005). A portion of LT muscle (13 cm in length,
117 from the 10th rib region) was excised, vacuum packed, aged for 14 days at 2°C, and
118 finally frozen and stored at -18°C prior to compositional, collagen and sensory analysis.

119 *Proximate composition, collagen content and sensory analyses*

120 Moisture, intramuscular fat (IMF) and protein contents of the LT muscle were
121 determined using the SMART System 5 microwave moisture drying oven, NMR SMART
122 Trac rapid fat analyser (CEM Corporation, Matthews, NC, USA) and LECO FP328
123 (LECO Corp., St. Joseph, MI, USA) protein analyser, respectively (AOAC, 1990).
124 Collagen content (i.e. total and soluble) was determined by quantitative determination of
125 hydroxyproline by a colorimetric reaction (Kolar, 1990). Sensory analysis was carried
126 out using a 10-person trained taste panel who had been selected for their sensory
127 acuity, a detailed procedure is given in Mezgebo *et al.* (2016).

128 *Muscle metabolic enzyme activity and muscle contractile and metabolic type*

129 Glycolytic enzyme activities (lactate dehydrogenase (LDH) and phosphofructokinase
130 (PFK)) and oxidative enzyme activities (isocitrate dehydrogenase (ICDH), citrate
131 synthase (CS) and cytochrome *c* oxidase (COX)) were quantified
132 spectrophotometrically according to Jurie *et al.* (2006). Muscle typing was assessed by
133 determination of relative proportions of myosin heavy chains (MyHC) isoforms types I,

134 IIA and IIX using high-resolution mini-gel electrophoresis as described by Picard *et al.*
135 (2011).

136 *Statistical analysis*

137 Data were subjected to analysis of variance using the General Linear Model procedure
138 of SPSS (IBM SPSS Statistics Version 20) where the B, PS and their interaction were
139 regarded as fixed factors. For data relating to sensory analysis, assessor and session
140 effects were also included as fixed factors. The sensory data were also analysed using
141 IMF as an overall linear covariate. Means were considered significant at $P < 0.05$.

142 **Results**

143 *Production and carcass traits*

144 Production, carcass and subcutaneous fat colour data are presented in Table 1. There
145 was an interaction ($P < 0.001$) between B and PS with respect to age at slaughter.
146 Thus for C bulls, age at slaughter was higher for EM than for LM, but for GSPC bulls,
147 age at slaughter was similar for EM and LM. The ADG indoor (i.e. during finishing on
148 the concentrate diet) was lower ($P < 0.001$) for C than for GSPC. There was an
149 interaction ($P < 0.05$) between B and PS with respect to ADG overall. Thus for C bulls,
150 ADG overall was lower for EM than for LM, but for GSPC bulls, ADG overall was
151 similar for EM and LM. Conformation score was lower ($P < 0.001$) for EM than for LM.
152 There was an interaction ($P < 0.001$) between B and PS with respect to fat score. Thus
153 for C bulls, fat score was similar for EM and LM, but for GSPC bulls, fat score was
154 higher for EM than for LM. Subcutaneous fat 'L' and 'b' values were higher ($P < 0.05$)
155 for EM than for LM, and for C than for GSPC. 'h^o' value was higher ($P < 0.05$) for C
156 than for GSPC bulls.

157 *Muscle pH, temperature, colour, proximate composition and collagen data*

158 Muscle pH, temperature, colour, proximate composition and collagen data are
159 presented in Table 2. At 2 h post-mortem, muscle pH was higher for EM than for LM (P
160 < 0.001), and for C than for GSPC ($P < 0.01$). There was an interaction ($P < 0.05$)
161 between B and PS with respect to pH at 3.5 h post-mortem. Thus for EM, pH at 3.5 h
162 was higher for C than for GSPC, but for LM, pH at 3.5 h was similar for C and GSPC.
163 There was an interaction ($P < 0.01$) between B and PS with respect to pH at 5 h post-
164 mortem. Thus for C bulls, pH at 5 h was higher for EM than for LM, but for GSPC bulls,
165 pH at 5 h was lower for EM than for LM. There was an interaction ($P < 0.05$) between B
166 and PS with respect to ultimate pH (pH_u), i.e. 48 h post-mortem. Thus for C bulls, pH_u
167 was similar for EM and LM, but for GSPC bulls, pH_u was higher for EM than for LM.
168 There was an interaction ($P < 0.001$) between B and PS with respect to muscle
169 temperature at 2 h post-mortem. Thus for C bulls, muscle temperature at 2 h was lower
170 for EM than for LM, but for GSPC bulls, muscle temperature at 2 h was higher for EM
171 than for LM. At 3.5 h post-mortem, muscle temperature was higher ($P < 0.001$) for EM
172 than for LM. There was an interaction between B and PS with respect to muscle

173 temperature at 5 h post-mortem. Thus for C bulls, muscle temperature at 5 h post-
174 mortem was similar for EM and LM, but for GSPC bulls, muscle temperature at 5 h post-
175 mortem was higher ($P < 0.01$) for EM than for LM. At 48 h post-mortem, muscle
176 temperature was higher ($P < 0.001$) for C than for GSPC.

177 For muscle colour, 'L' value was higher ($P < 0.001$) for C than for GSPC, and 'a' value
178 was higher ($P < 0.001$) for GSPC than for C. There was an interaction ($P < 0.05$)
179 between B and PS with respect to 'b', 'C' and 'h^o' values. Thus for C bulls, 'b', 'C' and
180 'h^o' values were lower for EM than for LM, but for GSPC bulls, 'b', 'C' and 'h^o' values
181 were similar for EM and LM. Muscle colour grade was higher ($P < 0.05$) for GSPC than
182 for C. The IMF content was higher ($P < 0.001$) for EM than for LM, and for C than for
183 GSPC. Moisture content was higher for LM than for EM ($P < 0.001$), and for GSPC than
184 for C ($P < 0.05$). Total collagen was higher ($P < 0.05$) for EM than for LM. There was an
185 interaction ($P < 0.05$) between B and PS with respect to percentage of soluble collagen.
186 Thus for C bulls, percentage of soluble collagen was higher for EM than for LM, but for
187 GSPC bulls, percentage of soluble collagen was similar for EM and LM.

188 *Muscle metabolic enzyme activity and muscle contractile and metabolic type*

189 Muscle metabolic enzyme activity and MyHC proportion data are presented in Table 3.
190 When enzyme activity was expressed as $\mu\text{mol}/\text{min}$ per g of tissue, LDH activity was
191 higher for LM than for EM ($P < 0.001$), and for C than for GSPC bulls ($P < 0.05$); PFK
192 activity was higher ($P < 0.05$) for LM than for EM; ICDH activity was higher ($P < 0.01$)
193 for EM than for LM and COX activity tended to be higher ($P < 0.07$) for EM than for LM.
194 When enzyme activity was expressed as $\mu\text{mol}/\text{min}$ per g of protein, similar trends were
195 observed although significance ($P < 0.05$) was only reached in the case of the breed
196 type effects on LDH and ICDH activities. Type I MyHC proportion was higher ($P <$
197 0.001) for EM than for LM. Type IIX MyHC proportion was higher ($P < 0.05$) for C than
198 for GSPC.

199 *Sensory characteristics*

200 Muscle sensory data are presented in Table 4. Tenderness, flavour liking and overall
201 liking were higher ($P < 0.001$) for C than for GSPC. Tenderness and juiciness were
202 higher ($P < 0.01$) for EM than for LM. Ease of cutting ($P < 0.001$) and cleanness of cut

203 ($P < 0.05$) were higher for C than for GSPC. Clean cut was higher ($P < 0.05$) for EM
204 than for LM. Toughness (both during in-bite and eating) was higher for GSPC than for C
205 ($P < 0.001$), and for LM than EM ($P < 0.05$). Juiciness (during in-bite) was higher for C
206 than for GSPC ($P < 0.01$), and for EM than for LM ($P < 0.001$). Sponginess was higher
207 ($P < 0.001$) for C than for GSPC. Moisture, greasiness and pulpiness (both during
208 eating and residual), dissolubility, ease of swallow and mouthfeel were higher ($P < 0.05$)
209 for C than GSPC, and for EM than LM. Chewiness, fibrousness and residual particles
210 were higher ($P < 0.05$) for GSPC than for C. When the sensory data were analysed
211 using IMF as a covariate, only beefy flavour was lower ($P < 0.05$) and moisture and
212 pulpiness (during eating) were higher ($P < 0.05$) for EM than for LM (mean values of
213 4.39 vs 4.59, 50.8 vs 46.9 and 55.8 vs 52.0 for beefy flavour, moisture and pulpiness
214 respectively). Ease of swallow was higher ($P < 0.05$) for C than GSPC (mean values of
215 60.0 vs 54.7).

216 **Discussion**

217 The bulls were slaughtered on reaching a mean group live weight estimated to achieve
218 a target carcass weight of 380 kg which is required by some markets (Bord Bia, 2011).
219 To reach the same target carcass weight, the LM bulls reared in the C PS grew faster
220 generally (i.e. higher ADG overall), reached the desired live weight earlier and therefore
221 were slaughtered at a younger age compared to that of EM bulls on the same PS. This
222 confirms that LM are better converters of a high energy diet to carcass weight (Keane,
223 2011). However, when reared on the GSPC system, both breed types grew at a slower
224 rate overall and took longer to reach the target live weight. Prior to slaughter (i.e.
225 finishing period), the GSPC bulls grew faster compared to C bulls. The higher growth
226 rate prior to slaughter for the GSPC bulls suggests compensatory growth during the
227 indoor period as they had received a low energy diets (i.e. grass at pasture) prior to the
228 finishing period compared to C bulls (Hornick *et al.*, 2000).

229 When managed to the same carcass weight, carcasses from LM are characterised by
230 having relatively more muscle and less fat compared to carcasses from EM (O'Riordan
231 *et al.*, 2011, Keane, 2011). In the present study, the better carcass conformation of the
232 LM bulls compared to the EM bulls can be attributed to a higher degree of muscularity in
233 the LM carcasses. Fat score, which is a measure of subcutaneous fat thickness or
234 degree of finish, was similar between EM and LM in the C group possibly because of
235 rapid growth due to the high energy diet of the C diet. However, in the GSPC bulls,
236 carcasses of the LM were leaner even though both breed types were finished on the
237 same concentrate diet. In this case, it appears that during the concentrate finishing
238 period the LM were physiologically 'younger' and therefore were depositing less fat than
239 the physiologically 'older' EM (Warriss, 2010). With regard to subcutaneous fat colour,
240 the higher lightness of fat from EM compared to LM, and for C compared to GSPC bulls
241 may be attributed to the higher fat scores (i.e. subcutaneous fat thickness over the
242 muscle) of the carcasses of EM and C groups. Fat yellowness, often associated with
243 grass diets due to accumulation of carotenoids (Dunne *et al.*, 2006), and reported to
244 negatively influence consumer acceptability (Cornforth, 1994), was unexpectedly higher
245 for C bulls compared to GSPC bulls. However, although differences in fat yellowness
246 due to B and PS were significant ($P < 0.05$), values were numerically quite similar,

247 suggesting that these colour differences would probably not be perceived by
248 consumers. In the case of PS this may be attributed to the similarity in diets in the
249 immediate pre-slaughter period.

250 The extent of post-mortem pH decline in a muscle depends on the glycogen
251 concentration at slaughter which in turn depends on the animal's physical activity,
252 nutrition and/or stress prior to slaughter (Klont and Lambooy, 1995; Warriss, 2010). In
253 the present study, the influence of pre-slaughter physical activity and stress on muscle
254 glycogen level would likely be minimal as the bulls were finished indoors and therefore
255 were familiar with pre-slaughter handling; in addition the animals were carefully
256 managed during transport and lairage. However, early post-mortem (i.e. 2, 3.5 and 5 h),
257 a lower pH was recorded in the muscle from GSPC bulls compared to C bulls. This may
258 be related to the higher growth rate of GSPC bulls during the finishing period compared
259 to C bulls, whereby muscle is believed to become more glycolytic during periods of
260 compensatory growth (Brandstetter et al., 1998). Similarly, a higher pH_u (i.e. pH at 48 h
261 post-mortem) was recorded in the muscle from EM breed types than LM breed types;
262 however, there was an interaction between B and PS whereby the difference was
263 observed in GSPC bulls and not in C bulls. The lower pH_u for LM GSPC bulls could
264 possibly reflect a higher muscle glycolytic potential as LM breed types are often
265 characterised by an accelerated lean tissue growth compared to EM breed types when
266 reared similarly (Hocquette *et al.*, 1998), in this case to a similar carcass weight. In
267 agreement, glycolytic enzyme activity (LDH and PFK) were higher in muscle from LM
268 breed types, as discussed further below. The higher muscle temperature at 3.5 h post-
269 mortem for EM than LM bulls, and at 5 and 48 h post-mortem for C than GSPC bulls is
270 most probably related to the carcass fat score as carcasses from EM and C groups had
271 higher fatness scores than LM and GSPC groups, respectively. This is due to the fact
272 that carcasses with a thicker fat cover cool more slowly than carcasses with a thinner fat
273 cover (Warriss, 2010).

274 With regard to muscle colour, the lower lightness, higher redness, colour saturation and
275 muscle colour grade (i.e. the higher the value, the darker the muscle) for the GSPC
276 bulls could be explained by the higher age at slaughter (15.9 vs 18.5 months for C vs
277 GSPC, respectively) as muscle tissue becomes darker and redder with increasing

278 slaughter age (Dunne *et al.*, 2006). The lower proportion of Type IIX MyHC, a
279 characteristic of white muscles, for the GSPC bulls could also be responsible for the
280 lower lightness of their LT muscle (Henckel *et al.*, 1997). The darker muscle from GSPC
281 compared to C bulls could also be related to the physical activity during the pasture
282 feeding period (Priolo *et al.*, 2001). However, it should be mentioned that the post-
283 mortem pH profile of each muscle was within an acceptable pH range (Warriss, 2010),
284 and thus meat from either group could not be considered to have experienced the 'dark
285 cutting beef' condition.

286 The higher IMF content for EM compared to LM may be related to the intrinsic variations
287 in the physiology of the animals (Oddy *et al.*, 2001) whereby at a similar live weight, the
288 EM bulls were physiologically 'older' and therefore were depositing more IMF than the
289 LM bulls, which were 'younger' physiologically, and therefore were depositing less IMF.
290 The higher IMF content for C bulls reflects the higher energy content of the concentrate
291 diet through out their life (Oddy *et al.*, 2001). The lower collagen solubility for GSPC
292 bulls may be related to the greater age at slaughter (Blanco *et al.*, 2013) and lower IMF
293 content (Nishimura, 2015) as an increase in slaughter age increases the proportion of
294 mature collagen crosslinks which in turn leads to a decrease in solubility of the collagen
295 (McCormick, 1994).

296 The higher glycolytic enzyme activities (LDH and PFK) for LM could be related to the
297 higher overall growth rate of these bulls as an increase in growth rate early in life (i.e.
298 period of rapid growth from one to 12 months) and further growing stage until sexual
299 maturity is associated with an increase in muscle LDH activity (i.e. glycolytic
300 metabolism) and a decrease in ICDH activity (i.e. oxidative metabolism) (Jurie *et al.*,
301 1995). A similar explanation could be offered for the tendency towards lower oxidative
302 enzyme activities ($P < 0.07$) of ICDH and COX, marker enzymes for tricarboxylic acid
303 cycle and mitochondrial electron transport respectively, and lower proportion of slow
304 twitch Type I oxidative MyHC in the muscle from LM. The higher LDH activity (per g of
305 tissue) and proportion of Type IIX (fast twitch glycolytic) MyHC for C bulls could be
306 explained by the higher overall growth rate which is mainly attributed to the continued
307 provision of concentrate diet which in turn results in a more glycolytic muscular
308 metabolism (Brandstetter *et al.*, 1998, Cassar-Malek *et al.*, 2004). In addition, such

309 higher glycolytic metabolism in muscle could also be associated with the longer
310 concentrate finishing period of the C group compared to GSPC group (i.e. concentrate
311 finishing period of 98 and 71 d for GSPC and 258 and 201 d for C bulls of EM and LM
312 respectively). Even though grazing on pasture is associated with an increase in
313 oxidative metabolism of muscle mainly due to higher physical activity (Therkildsen *et al.*,
314 1998), the C and GSPC groups had similar oxidative enzyme activities. However, this
315 was not unexpected as all bulls were finished indoors on the same concentrate diets for
316 at least 71 days. In the present study, the fast twitch Type IIB glycolytic muscle MyHC
317 was expressed in only 6 bulls (1 in EM of C, none in EM of GSPC, 1 in LM of C and 4 in
318 LM of GSPC bulls, data not shown) in contrast to a study by Picard and Cassar-Malek
319 (2009) in a Blonde d'Aquitaine (a French beef breed) in which Type IIB MyHC was
320 usually identified.

321 The effect of PS on sensory characteristics was in agreement with Mezgebo *et al.*
322 (2016). The higher tenderness scores for C bulls may be related to their younger age at
323 slaughter (Bures and Barton, 2012), higher IMF (Thompson, 2004) and collagen
324 solubility (Cross *et al.*, 1973). A similar explanation could be given for the higher
325 sensory ratings for ease of cutting, cleanness of cut, juiciness (in-bite), sponginess,
326 moisture, greasiness, pulpiness, dissolubility, ease of swallow and mouthfeel, and lower
327 ratings in toughness, chewiness, fibrousness and residual particles for C bulls
328 compared to GSPC bulls. The contribution of IMF to these differences was shown by
329 the lack of significant differences in sensory ratings (except for ease of swallow)
330 between PS when the data were adjusted for IMF. In addition, the higher LDH activity
331 for the C bulls compared to GSPC bulls could also be linked to the higher tenderness
332 ratings of the C bulls, as an increase in glycolytic characteristics of a muscle often leads
333 to an increase in eating quality of meat mainly by accelerating the post-mortem
334 tenderization process of the muscle (Maltin *et al.*, 2001). The sensory analysis also
335 showed that the sensory data ratings were internally consistent, especially for
336 tenderness, i.e. higher tenderness score (during the basic taste) was consistent with the
337 lower toughness scores (both during in-bite and eating). Even though all bulls were
338 finished indoors, the lower flavour liking and overall liking ratings of beef from GSPC
339 bulls could possibly be associated with the inclusion of grass diet prior to the finishing

340 period as beef from pasture based systems is often reported to be less preferred by
341 consumers (Griebenow *et al.*, 1997).

342 The higher sensory ratings in tenderness and juiciness, and associated higher scores in
343 cleanness of cut, moisture, greasiness, pulpiness, dissolubility, ease of swallow and
344 mouthfeel, and lower scores in toughness for EM could be related to their higher
345 carcass fat cover and IMF content compared to LM. Similar findings were reported by
346 Sinclair *et al.* (2001) in beef from Aberdeen-Angus and Charolais breeds. In the current
347 study, beef from LM was rated to be lower in tenderness, juiciness and related sensory
348 quality attributes compared to beef from EM even though the LM were younger at
349 slaughter. In addition, LM muscle had higher glycolytic (LDH and PFK) and lower
350 oxidative (ICDH and COX) metabolic enzyme activities and lower Type I MyHC
351 proportion than EM, and an increase in glycolytic (Maltin *et al.*, 2001) and decrease in
352 oxidative (Monin and Ouali, 1991) characteristics of a muscle can lead to superior
353 eating quality in meat. When IMF was included as a covariate in the sensory data
354 analysis, most of the observed differences disappeared, confirming that IMF content
355 was the major contributor to differences in meat tenderness and juiciness between EM
356 and LM breeds (Sinclair *et al.*, 2001).

357 **Conclusion**

358 When managed to a similar carcass weight EM were older at slaughter, had higher
359 carcass fat scores and IMF content and produced beef that was rated more tender and
360 juicier by trained sensory panellists than LM. Furthermore, C bulls were younger at
361 slaughter, had higher carcass fat scores, IMF and soluble collagen content and
362 produced beef rated more highly by a trained sensory panel than GSPC bulls. While
363 variations in sensory characteristics due to breed maturity and dietary inclusion of grass
364 silage followed by pasture exist, IMF contributed to much of the variation and it remains
365 to be established whether or not the differences would be perceptible to untrained
366 consumers.

367

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475 **Table 1** Production, carcass and subcutaneous fat colour data of bulls from two breed
 476 types (B) (EM = early maturing, LM = late maturing), raised on two production systems
 477 (PS) (C = concentrate, GSPC = grass silage followed by pasture and then concentrate)

	B		EM		LM		Significance		
	PS	C	GSPC	C	GSPC	s.e.m	B	PS	B x PS
Finishing period (days) ¹		258	98	201	71				
Age at slaughter (months)		16.7 ^b	18.6 ^c	15.0 ^a	18.3 ^c	0.25	***	***	**
ADG ² finishing (kg/day)		1.35	2.09	1.50	2.06	0.081		***	
ADG overall (kg/day)		1.38 ^b	1.09 ^a	1.58 ^c	1.10 ^a	0.042	*	***	*
Slaughter weight (kg)		681	704	667	693	14.1			
Carcass weight (kg)		375	385	379	387	9.1			
Conformation score ³		8.3	8.7	9.9	9.7	0.36	***		
Fat score ⁴		8.3 ^b	8.3 ^b	8.4 ^b	6.6 ^a	0.26	***	***	***
Fat colour ⁵									
'L'		72.4	68.9	68.6	64.5	0.66	***	***	
'a'		9.1	9.5	8.8	9.3	0.50			
'b'		16.9	15.6	15.6	15.4	0.32	*	*	
'C'		19.3	18.3	17.9	18.0	0.46			
'h°'		62.0	58.9	61.1	58.9	1.16		*	

478 ¹ Days on *ad libitum* concentrates prior to slaughter

479 ² Average daily live weight gain

480 ³ Conformation classes E⁺ (highest) to P⁻ (lowest), (E⁺ is 15)

481 ⁴ Fat score classes 5⁺ (highest) to 1⁻ (lowest), (5⁺ is 15)

482 ⁵ Subcutaneous fat colour: 'L' = lightness, 0 (black) to 100 (white); 'a' = redness, +a (red) to -a
 483 (green); 'b' = yellowness, +b (yellow) to -b (blue); 'C' = chroma, higher 'C' values higher colour
 484 saturation; 'h°' = hue, 0/360° is red, 90° is yellow, 180° is green and 270° is blue colour

485 ^{a, b, c} means within rows (where interaction exists), assigned different superscripts differ
 486 significantly ($P < 0.05$)

487 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

488 **Table 2** Post-mortem pH and temperature, colour, proximate composition and collagen
 489 content of longissimus thoracis muscle from bulls from two breed types (B) (EM = early
 490 maturing, LM = late maturing), raised on two production systems (PS) (C = concentrate,
 491 GSPC = grass silage followed by pasture and then concentrate)

	B		EM		LM		s.e.m	Significance		
	PS		C	GSPC	C	GSPC		B	PS	B x PS
pH, post-mortem (h)										
2			6.59	6.47	6.45	6.28	0.054	***	**	
3.5			6.21 ^c	5.84 ^a	6.11 ^{bc}	5.97 ^{ab}	0.054		***	*
5			6.03 ^c	5.67 ^a	5.87 ^b	5.85 ^b	0.056		***	**
48			5.69 ^{ab}	5.74 ^b	5.68 ^{ab}	5.62 ^a	0.026	**		*
Temperature, post-mortem (h)										
2			33.1 ^a	35.1 ^b	35.3 ^b	32.4 ^a	0.55			***
3.5			29.1	29.5	28.1	27.3	0.48	***		
5			23.9 ^b	24.1 ^b	24.4 ^b	21.9 ^a	0.47		*	**
48			3.90	3.25	3.66	3.09	0.154		***	
Muscle colour ¹										
'L'			31.1	28.1	32.8	28.3	0.80		***	
'a'			19.8	21.6	20.5	21.2	0.30		***	
'b'			12.2 ^a	12.9 ^a	13.9 ^b	12.9 ^a	0.24	***		***
'C'			23.3 ^a	25.1 ^b	24.8 ^b	24.8 ^b	0.32		**	**
'h ^o '			31.7 ^a	30.8 ^a	34.2 ^b	31.4 ^a	0.50	***	***	*
Muscle colour grade ²										
			3.07	3.29	2.57	3.21	0.172		*	
Proximate composition (g/kg)										
Intramuscular fat			55.2	27.7	26.2	10.2	3.94	***	***	
Moisture			720	738	747	749	4.8	***	*	
Protein			229	233	229	231	2.7			
Ash			10.5	12.0	11.2	11.3	0.59			
Collagen content										
Total collagen (mg/g)			4.06	4.21	3.86	3.87	0.126	*		
Soluble collagen (%)			13.4 ^b	8.3 ^a	9.4 ^a	9.4 ^a	0.79		***	***

492 ¹Muscle colour: 'L' = lightness, 0 (black) to 100 (white); 'a' = redness, +a (red) to -a (green); 'b'
 493 = yellowness, +b (yellow) to -b (blue); 'C' = chroma, higher 'C' values higher colour saturation;
 494 'h^o' = hue, 0/360° is red, 90° is yellow, 180° is green and 270° is blue colour

495 ²Muscle colour grades: 1 (extremely bright red) to 9 (extremely dark red)

496 ^{a, b, c} means within rows (where interaction exists), assigned different superscripts differ
 497 significantly ($P < 0.05$)

498 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

499 **Table 3** Metabolic enzyme activity and myosin heavy chains (MyHC) proportion of
 500 longissimus thoracis muscle from bulls from two breed types (B) (EM = early maturing,
 501 LM = late maturing), raised on two production systems (PS) (C = concentrate, GSPC =
 502 grass silage followed by pasture and then concentrate)

	B		EM		LM		Significance		
	PS	C	GSPC	C	GSPC	s.e.m	B	PS	B x PS
Metabolic enzyme activity ¹									
µmol/min per g of tissue									
LDH		936	838	999	969	26.5	***	*	
PFK		101	96	112	112	6.8	*		
ICDH		1.17	1.33	1.01	1.02	0.085	**		
COX		17.0	18.3	15.1	15.2	1.33	0.07		
CS		5.27	5.37	5.34	4.58	0.463			
µmol/min per g of protein									
LDH		4908	4350	5007	5478	275.9	*		
PFK		527	498	559	636	45.0	0.06		
ICDH		6.14	6.90	5.12	5.68	0.483	*		
COX		89.3	94.7	75.7	87.1	8.14			
CS		27.7	27.9	27.1	26.2	2.86			
Protein (mg/g of tissue)		191	193	200	186	4.7			
MyHC ² proportion (%)									
I		22.5	23.2	18.5	17.1	1.64	***		
IIA		45.1	48.8	38.6	46.8	3.35			
IIX		35.3	32.7	44.1	29.8	3.44			*

503 ¹LDH: lactate dehydrogenase; PFK: phosphofructokinase; ICDH: isocitrate dehydrogenase;

504 COX: cytochrome c oxidase; CS: citrate synthase

505 ²I: oxidative, IIA: oxido-glycolytic, IIX: glycolytic

506 **P* < 0.05, ***P* < 0.01, ****P* < 0.001

507 **Table 4** Sensory characteristics of of longissimus thoracis muscle from bulls from two
 508 breed types (B) (EM = early maturing, LM = late maturing), raised on two production
 509 systems (PS) (C = concentrate, GSPC = grass silage followed by pasture and then
 510 concentrate)

	B	EM		LM		s.e.m.	Significance		
	PS	C	GSPC	C	GSPC		B	PS	B x PS
<i>Basic tastes, scale 1 (least) - 8 (most)</i>									
Tenderness		4.81	4.50	4.63	4.20	0.093	**	***	
Juiciness		5.10	4.90	4.83	4.81	0.068	**		
Beefy flavour		4.54	4.41	4.55	4.51	0.060			
Abnormal flavour		2.30	2.50	2.30	2.42	0.074			
Flavour liking		5.45	5.02	5.46	5.10	0.081		***	
Overall liking		5.15	4.71	5.03	4.59	0.081		***	
<i>Specific sensory indicators, scale 0 (nil) - 100 (extreme)</i>									
<i>On-cut</i>									
Ease of cutting		55.7	49.6	53.5	46.7	1.34		***	
Cleanness of cut		59.2	56.8	56.6	53.9	1.20	*	*	
<i>In-bite</i>									
Toughness		43.1	48.8	45.5	54.9	1.35	**	***	
Crispness		25.3	26.1	24.3	25.6	1.08			
Juiciness		51.1	47.5	46.7	44.2	1.03	***	**	
Sponginess		29.9	26.9	28.6	25.5	0.87		***	
<i>Eating</i>									
Toughness		43.1	48.7	44.9	53.5	1.33	*	***	
Moisture		52.2	49.6	48.1	45.0	1.05	***	**	
Chewiness		40.9	47.1	42.6	49.0	1.42		***	
Greasiness		21.5	17.9	19.1	15.7	0.88	**	***	
Fibres		42.1	43.2	42.6	46.1	1.05		*	
Gristle		5.5	6.2	6.4	6.2	0.68			
Pulpy		57.5	54.9	52.7	50.2	1.08	***	**	
Dissolubility		51.5	46.3	49.6	43.0	1.31	*	***	
<i>Residual</i>									
Greasiness		21.5	18.2	18.4	15.4	0.93	**	***	
Ease of swallow		62.1	55.3	59.5	52.5	1.21	*	***	
Pulpy		56.7	54.4	51.9	48.2	1.12	***	**	
Particles		49.6	50.3	48.9	52.5	0.99		*	
Mouthfeel		57.0	54.5	52.2	49.8	0.99	***	*	

511 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$