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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, International Business Machines (IBM)
139 Corporation, Armonk, NY, USA) where the B, PS and their interaction were regarded as
140 fixed factors. For data relating to sensory analysis, assessor and session effects were
141 also included as fixed factors. The sensory data were also analysed using IMF as an
142 overall linear covariate. Means were considered significant at $P < 0.05$.

143 **Results**

144 *Production and carcass traits*

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

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

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

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

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

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

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

200 *Sensory characteristics*

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

204 ($P < 0.05$) were higher for C than for GSPC. Clean cut was higher ($P < 0.05$) for EM
205 than for LM. Toughness (both during in-bite and eating) was higher for GSPC than for C
206 ($P < 0.001$), and for LM than EM ($P < 0.05$). Juiciness (during in-bite) was higher for C
207 than for GSPC ($P < 0.01$), and for EM than for LM ($P < 0.001$). Sponginess was higher
208 ($P < 0.001$) for C than for GSPC. Moisture, greasiness and pulpiness (both during
209 eating and residual), dissolubility, ease of swallow and mouthfeel were higher ($P < 0.05$)
210 for C than GSPC, and for EM than LM. Chewiness, fibrousness and residual particles
211 were higher ($P < 0.05$) for GSPC than for C. When the sensory data were analysed
212 using IMF as a covariate, only beefy flavour was lower ($P < 0.05$) and moisture and
213 pulpiness (during eating) were higher ($P < 0.05$) for EM than for LM (mean values of
214 4.39 vs 4.59, 50.8 vs 46.9 and 55.8 vs 52.0 for beefy flavour, moisture and pulpiness
215 respectively). Ease of swallow was higher ($P < 0.05$) for C than GSPC (mean values of
216 60.0 vs 54.7).

217 **Discussion**

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

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

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

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

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

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

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

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

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

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

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

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

358 **Conclusion**

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

368

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473 **Table 1** Production, carcass and subcutaneous fat colour data of bulls from two breed
 474 types (B) (EM = early maturing, LM = late maturing), raised on two production systems
 475 (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		*	

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

477 ² Average daily live weight gain

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

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

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

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

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

486 **Table 2** Post-mortem pH and temperature, colour, proximate composition and collagen
 487 content of longissimus thoracis muscle from bulls from two breed types (B) (EM = early
 488 maturing, LM = late maturing), raised on two production systems (PS) (C = concentrate,
 489 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		***	***

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

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

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

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

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

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

502 COX: cytochrome c oxidase; CS: citrate synthase

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

504 **P* < 0.05, ***P* < 0.01, ****P* < 0.001

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

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