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41 increased. Numerous significant correlations were found among variables. Carcass weight is
42 associated with all the collagen and texture variables. Correlation coefficients among texture
43 and collagen variables were statistically significant and these correlation coefficients were in
44 general higher for solubility percentage than for total collagen content, highlighting the
45 importance of the solubility of collagen rather than total collagen in determining meat textural
46 properties.

47

48 **Keywords:** beef, breed, connective, sensory, texture.

49

50 **Practical applications**

51

52 To differentiate a product in the market, it is necessary to define its characteristics.
53 Differentiation allows increasing the added value of products and, therefore, income of the
54 farmers. In addition, it guarantees to the consumers that the product they purchase has the
55 intrinsic and extrinsic quality features that they seek. For consumers, beef texture is one of the
56 most important quality attributes sought, therefore studying factors that can affect beef texture is
57 a major interest for the industry.

58

59 **1. Introduction**

60

61 Beef production is an important sector in the livestock industry in the European Union (EU).
62 Local systems of beef production in the EU have a variety of characteristics, including several
63 breeds, feeding systems and age or weight at slaughter. The current agricultural policy of the
64 EU (https://europa.eu/european-union/topics/agriculture_en) aims to foster a new direction in
65 the meat production industry, increasing the diversification of agricultural production and the
66 promotion of specific products related to meat quality. In recent years, consumer perceptions of
67 meat quality have changed, and consumers have become more interested in factors beyond
68 sensory meat quality, that is, extrinsic qualities are becoming more important for consumers in
69 developed countries (Brunso *et al.*, 2004; Verbeke *et al.*, 2010). In this sense, Chamorro *et al.*
70 (2012) reported that consumers' purchasing decisions were based less on price, external
71 appearance and origin and more on third-party certification of quality. In the context of EU, the
72 main quality labels for meat or meat products are Protected Designation of Origin (PDO) and
73 Protected Geographical Indication (PGI) Local and non-specialized beef breeds raised under
74 traditional systems are usually covered under these EU labels, but also many other breeds have
75 their own quality brands, such as Charolais, Limousine and Aberdeen Angus.

76

77 Meat quality characteristics are affected by various pre- and post-slaughter factors. Among
78 them, the production system is of major importance, because a production system is essentially
79 the combination of the animals' breed, sex, age, diet, environment and handling.

79

80 This study was a part of a large project examining several carcass and meat characteristics
of 10 local Spanish and French beef breeds raised within their typical production systems.

81 Previous papers have described the carcass quality (Piedrafita *et al.*, 2003b) and some
82 instrumental and sensory meat characteristics (Gil *et al.*, 2001b; Serra *et al.*, 2004a; Serra *et al.*,
83 2008a) of these breeds. Thus, the aim of the present study was to examine the texture, collagen
84 and sensory variables of meat from animals that were raised in their respective breed-
85 production systems.

86

87 **2. Materials and methods**

88

89 *2.1. Animals*

90

91 A total of 712 young bulls from ten breeds were used in this study: Asturiana de los Valles
92 (AV, $n=70$), Bruna dels Pirineus (BP, $n=67$), Casina (CAS, $n=70$), Morucha (MO, $n=70$),
93 Avileña-Negra Ibérica (NE, $n=70$), Pirenaica (PI, $n=55$), Retinta (RE, $n=68$), Aubrac (AU, $n=78$),
94 Gasconne (GA, $n=82$) and Salers (SA, $n=82$). Young bulls were slaughtered locally at EU-
95 licensed commercial abattoirs. Slaughter age ranged from 443 days of age to 552 days for
96 Spanish breeds and from 610 days to 753 days for French breeds. The average slaughter
97 weight was breed-specific, and depended on the degree of maturity and local market
98 requirements. Additional details regarding breed characteristics, growth, slaughter conditions
99 and carcass traits are available in Piedrafita *et al.* (2003b).

100

101 *2.2. Muscle sampling and analysis*

102

103 Details about the meat sampling method can be found in Gil *et al.* (2001a), Serra *et al.*
104 (2004a) and Serra *et al.* (2004b). Briefly, at 24 h post-mortem, the pH was measured on the
105 *Longissimus thoracis* muscle at the 5th rib. Next, the *Longissimus thoracis* muscle from the 6th
106 through 11th ribs was excised and the following variables were measured: concentration of the
107 haem pigment (Hornsey, 1956), dry matter (ISO 1442), water holding capacity (Grau and
108 Hamm, 1953), chemical intramuscular fat content (ISO 1443), crude protein quantification (ISO
109 937), determination of myosin heavy chain 1, lactate dehydrogenase (LDH) and isocitrate
110 dehydrogenase (ICDH) activities and colour measurements.

111

112 Additionally, a 3.5-thick chop from the 8th rib was used for calculating the total and soluble
113 collagen (Bonnet and Kopp, 1984). The sample for total collagen was immediately frozen, while
114 the sample for the soluble collagen was first hydrolysed and then frozen (Kopp and Bonnet,
115 1982). The percentage of soluble collagen was calculated as the difference between the
116 amount of total collagen and the amount of insoluble collagen left as a residue from the
117 solubilization process. Since the collagen quantification method presents high inter-assay
118 variability we carried out four repeated measurements by sample to increase measurements
119 accuracy (Listrat and Hocquette, 2004). Next, a 3.5-cm-thick steak from the 9th rib was vacuum
120 packed, kept at 4°C and aged for 14 days; thereafter, the steak was frozen at -18°C for texture
analysis. For the texture analysis, the steaks were thawed inside their plastic bags in tap water

121 for 4 hours until reaching an internal temperature of 15-17°C. Each steak was then cut
122 transversally into two halves to be used in an analysis of either cooked or raw meat. For the
123 cooked meat analysis, the meat was vacuum packed and cooked in a water bath at 75°C until
124 the internal temperature reached 70°C. Temperature was monitored using a Jenway 2000
125 thermometer (Cole-Parmer, Staffordshire, UK). Stress (N/cm²) and yield (N/cm²) were recorded
126 using a Warner-Bratzler (WB) device. The texture of the raw meat was analysed using a
127 modified compression device that avoids transversal elongation of the sample (Lepetit and
128 Culioli, 1994). For both the raw and cooked meat samples, a 1cm² cross-section was cut with
129 the muscles fibres parallel to the longitudinal axis of the sample. All texture measurements were
130 taken using an Instron 4301 (Illinois Tool Works Inc., Norwood, Massachusetts, US). The stress
131 was assessed when the device was no longer able to descend further, that is, when the sample
132 had been compressed to its full height (i.e., maximum rate of compression), and at 20% and
133 80% of this maximum compression (N/cm²).

134 For the sensory analysis, a 2-cm steak was sampled at the 10th-11th ribs. As in the texture
135 analysis, samples were vacuum packed and kept at 4°C and aged for 14 days, then frozen and
136 kept at -18°C. The freezing period was always less than 6 months. To assess the sensory
137 characteristics, the samples were defrosted in tap water for 4 hours until they reached an
138 internal temperature of 17-19°C. The samples were then analysed by teams in three different
139 laboratories: Zaragoza (Spain) analysed AV, CAS, PI and RE; Monells (Spain) analysed NE, BP
140 and MO; and Villers Bocage (France) analysed AU, GA and SA . The meat was cooked in
141 aluminium foil on a double plate grill in Zaragoza and Villers Bocage and in an oven in Monells.
142 The samples were cooked until they reached an internal temperature of 55°C in Villers Bocage
143 and 70°C in Zaragoza and Monells. Then, each steak was trimmed of any external connective
144 tissue, cut into 2-cm² samples, wrapped in labelled aluminium foil and stored for approximately
145 5 min at 60°C in warm pans until they were tasted. Samples were randomly served to trained
146 ten-member sensory panels in Monells and Villers Bocage and to a trained eleven-member
147 sensory panel in Zaragoza. Members of the panels were seated in individual booths under red
148 lighting to mask differences in meat colour. The panellists assessed tenderness, juiciness, beef
149 flavour intensity and overall appraisal using a non-structured ten-point scale. The experiment
150 was carried out following a balanced design (ISO-8586). In addition, cooking losses were
151 calculated as the difference in weight before and after cooking. More details for the panel in
152 Monells are available in Serra *et al.* (2008a).

153

154 2.3. Statistical analysis

155

156 Animals in this experiment were raised in their typical production-systems, which have
157 differences in slaughter age and maturity. Therefore, a generalized linear model (GLM) with
158 breed-production system (denoted as breed hereafter) as a fixed effect and carcass weight as a
159 covariate was used for the analyses of the collagen measures, texture variables and sensory
160 variables. For the sensory variables and cooking losses, the GLM analysis was conducted for

161 each laboratory separately, because the sensory analysis methodology was different at each
162 laboratory. Least square means and standard errors were computed. Means were corrected for
163 a carcass weight of 327.42 kg. Differences between breeds were assessed with significance
164 based on Bonferroni adjustment to address multiple comparisons. Bivariate Pearson's
165 correlation coefficient was calculated including texture variables, collagen variables and cooking
166 losses with significance based on Bonferroni adjustment to address multiple comparisons. All
167 analyses were performed with the SPSS 15.0 (SPSS Inc., Chicago, US).

168

169 **3. Results**

170

171 *3.1. Summary of published results*

172

173 Previous studies showed relevant differences in carcass and meat quality traits among the
174 analysed breeds. According to those studies, all of the variables related to carcass and meat
175 quality were affected by breed. The animals slaughtered in Spain weighed between 444 and
176 551 kg., whereas the animals slaughtered in France weighed between 610 and 750 kg. The
177 daily weight gain ranged from 1.03 to 1.65 kg/day. Even across the wide range of carcass
178 weights studied, the general relationships among carcass traits were confirmed. Animals with
179 the best conformation were also leaner than less conformed animals, whereas long carcasses
180 tended to be associated with poor conformation and fatness. Bone content was negatively
181 correlated with carcass conformation and muscle content. RE and NE breeds were
182 distinguished from the other breeds by their high intra-muscular fat content. The meat from non-
183 specialized beef breeds was more oxidative. In terms of meat colour, AV, PI and NE had the
184 palest meats, CAS and MO had the reddest and darkest meats, and BP had an intermediate
185 colour. Meat colour was affected by the muscle biochemical traits since positive correlations
186 between MHC-1 and haem pigment content were observed for most of the breeds,
187 and haem pigment contents were correlated positively to a* and C* in most breeds.

188

189

190 *3.2. Collagen and texture variables*

191

192 Means, standard errors and p-values for the effect of breed on collagen and texture
193 variables are presented in Table 1. A significant effect of the breed was observed for all the
194 variables. In addition, all the measured variables showed a large amount of variation within
195 breeds. The coefficient of variation for the total collagen content was 21% but variability for
196 solubility percentage reached 48%. For variables related to texture, variability was 44% for
197 stress, 47% for yield, 22% for compression load, 29% for compression at 20% and 23% for
198 compression at 80%.

199

200

CAS and GA had lower values of total collagen than the rest of the breeds. Although GA
and the other French breeds had the lowest values of collagen solubility (from 12.1% to 13.8%),

201 CAS had high values for collagen solubility (40.9%). It was not statistically different from AV, PI,
202 RE or BP. MO and NE had intermediate solubility percentage values (32.5%).

203 Stress varied from 36 N/cm² in CAS to 44 N/cm² in SA, whereas yield, which measures the
204 limit of elasticity of the sample (Lepetit and Culioli, 1994), ranged from 22 N/cm² in SA to 46
205 N/cm² in AV. In the raw meat samples, compression stress was lower in BP and SA than in the
206 rest of the breeds, whereas compression stress at 80% ranged from 35 N/cm² in AV to 40
207 N/cm² in SA.

208

209 *3.3. Sensory variables*

210

211 Table 2 shows the results of the GLM analyses completed by each laboratory for the
212 sensory data. At the Villers Bocage laboratory, no significant differences were found in the
213 sensory attributes among the French breeds ($p>0.05$). At the Zaragoza laboratory, only
214 tenderness was influenced by the breed ($p=0.039$). At the Monells laboratory, all variables
215 differed among breeds ($p<0.01$). Conversely, there was no significant breed effect on cooking
216 losses in the Zaragoza laboratory nor in the Monells laboratory, whereas in the Villers Bocage
217 laboratory, there were highly significant differences ($p<0.0001$) in cooking losses among the
218 French breeds. Oven cooking resulted in greater cooking losses than grill cooking: meat cooked
219 in an oven (BP, NE and MO breeds) had an average cooking loss of 24%, whereas meat
220 cooked on a grill had average losses of only 8 and 14% when the internal temperature reached
221 70°C and 55°C, respectively. Variability in the data was similar for the Zaragoza and Monells
222 laboratories (from 13 to 27%) and slightly lower for the Villers Bocage laboratory (from 8 to
223 19%).

224

225 *3.4. Pearson Correlations*

226

227 There were some significant correlations between collagen and texture variables (Table 3).
228 Carcass weight influenced all of the variables, and because of that, carcass weight was
229 included as a covariate in the models. The percentage of soluble collagen had a stronger
230 correlation with textural variables than the total collagen content, which highlights that collagen
231 solubility, rather than the total amount of collagen, is important in defining the textural quality of
232 meat. The Warner-Bratzler test variables were closely correlated, and the compression
233 variables were closely correlated, but weak relationships were observed between the Warner-
234 Bratzler and the compression test variables.

235

236 **4. Discussion**

237

238 *4.1. Collagen and texture variables*

239

240 The total collagen content values reported herein were similar to those reported by Campo
241 *et al.* (2000b) in several Spanish breeds (from 2.3 mg/g to 4.7 mg/g), and by Christensen *et al.*
242 (2011b) in several European breeds (approximately 3.5 mg/g). The breed effect on collagen
243 characteristics agrees with previous studies completed by several authors (Jeremiah and
244 Martin, 1982; Campo *et al.*, 2000b; Christensen *et al.*, 2011a). Differences in the production
245 systems may explain breed-specific differences in these other studies. In central and northern
246 Europe, cattle feeding is based on grazing in natural pastures that are supplemented with
247 concentrate and/or high quality forage (silage, hay) at the end of fattening period. Alternatively,
248 in the European Mediterranean regions, cattle are primarily raised on concentrate ad libitum and
249 cereal straw throughout the fattening period. Feed with higher energy value was related to
250 decreased total collagen content because of the higher protein deposition diluting the collagen
251 content (Archile-Contreras *et al.*, 2010). It should be noted that the slaughter criterion used in
252 this study was the degree of maturity, which implies differences in the chronological age at
253 slaughter (Piedrafita *et al.*, 2003a), because animals were raised in their typical production
254 system. Blanco *et al.* (2011) reported that the relationship between collagen content and age
255 follows a quadratic relationship, where collagen content is higher at birth and at puberty than
256 during the growing period.

257 Our solubility percentage values were higher than those found by other authors in several
258 European breeds (Seideman, 1986; Christensen *et al.*, 2005; Christensen *et al.*, 2011b; Moran
259 *et al.*, 2017) but similar to those reported by Campo *et al.* (2000c) and Panea *et al.* (1999) in
260 Spanish breeds. French breeds had much lower collagen solubility than the rest of the breeds.
261 Schreurs *et al.* (2008) published a meta-analysis including 33 different experiments carried out
262 in French breeds and found an average solubility percentage of 19.35%, but they reported
263 values of 12.8% and 12.7% in the Aubrac and Salers breeds, respectively. However, the effect
264 of the solubilization method on the solubility percentage should be considered when comparing
265 these studies, as it is widely accepted that the duration and temperature of the solubilization
266 method affect the results (Kopp, 1971). Many authors use a 77°/75 min procedure (Crouse *et al.*
267 *et al.*, 1985; Seideman, 1986), while we used a 90°/2 hours procedure, following the method
268 described by Bonnet and Kopp (1984). Alternatively, the percentage of soluble collagen also
269 depends on the pH of Ringer's solutions (Latorre *et al.*, 2016) and solubility is higher at when
270 the pH of Ringer's solution is 5.6 than when the pH of Ringer's solution it is 7.4. The pH of the
271 solution used in the current project was 7.5. Finally, there would be an overestimation of
272 collagen solubility when the samples are solubilized before freezing (Jeremiah and Martin,
273 1982).

274 Kopp (1971) stated that collagen solubility in males reaches its maximum at 13 months of
275 age and subsequently decreases until the animals reach 19 months of age. This fact could
276 partly explain the differences between the Spanish and French breeds because the French
277 animals were older at slaughter. Additionally, as the age of the animal increases, collagen forms
278 thermally stable, mature crosslinks that cause a decrease in collagen solubility (Judge and
279 Aberle, 1982; Horgan *et al.*, 1991; Bosselmann *et al.*, 1995). Some discussions can be found in

280 the literature concerning diet effects on collagen solubility. One study found that high-energy
281 diets promoted the turnover of newly synthesized soluble collagen (Therkildsen *et al.*, 2011),
282 while Archile-Contreras *et al.* (2010) reported that heat-soluble collagen was lower in corn-fed
283 cattle than in cattle finished on alfalfa pasture. Cox *et al.* (2006) concluded that the finishing diet
284 (grain vs. forage) did not affect insoluble or soluble collagen. Additionally, Damergi *et al.* (1998)
285 suggested that daily weight gain was an important factor in determining collagen characteristics.
286 As explained, we worked with animals which differed in age at maturity, since every breed was
287 raised within their typical production systems. As a consequence, slaughter ages ranged from 364
288 days to 541 days in Spanish breeds and from 61 days to 753 days in French breeds. Therefore, our
289 results suggest that collagen solubility might be the best parameter for detecting differences
290 among breed types when the animals are of similar age. Alternatively, different breeds could be
291 at different maturity stages at the same or similar chronological age and this could influence the
292 crosslinking degree of the collagen (Kopp, 1971; Damergi *et al.*, 1998). Consequently, these
293 differences in maturity may partially explain variation in the thermal properties of intramuscular
294 collagen.

295 All the texture variables were similar to those reported in the literature for animals of similar
296 characteristics (Campo *et al.*, 1999; Campo *et al.*, 2000a; Macie *et al.*, 2000; Monsón *et al.*,
297 2003; Monson *et al.*, 2004; Oliván *et al.*, 2004; Sanudo *et al.*, 2004; Olleta *et al.*, 2005; Panea *et al.*,
298 2010a; Christensen *et al.*, 2011a; Panea *et al.*, 2011; Barahona *et al.*, 2016). Some authors
299 reported a lack of breed or production system effect on texture variables (Vieira *et al.*, 2006;
300 Marino *et al.*, 2011; Guerrero *et al.*, 2013), whereas other authors found such an effect (Sañudo
301 *et al.*, 2004; Christensen *et al.*, 2011b; Panea *et al.*, 2016). Campo *et al.* (2000b) suggested that
302 the meat textural characteristics were defined by breed purpose, but in the present study, the
303 textural characteristics did not follow a clear pattern in the ten European breeds we tested. Two
304 non-specialized breeds, Casina and Avileña, had the lowest values for stress, and they were
305 not different from the Bruna or PI breeds, two breeds raised specifically for meat. In addition,
306 the French breeds had the lowest values for yield, but the Salers breed, a hardy breed, had the
307 same values for stress as the Asturiana, a double-muscle breed. We expected that yield,
308 which measures the limit of elasticity of the sample, would be related to connective tissue, but
309 the relationship was not significant (Table 3).

310

311 4.2. Sensory variables and cooking losses

312

313 The sensory attributes of the analysed breeds fell within the range described by most
314 authors (Campo *et al.*, 1998; Campo *et al.*, 1999; Ciria *et al.*, 2000; Gorraiz *et al.*, 2002; Olleta
315 *et al.*, 2006; Serra *et al.*, 2008a; Serra *et al.*, 2008b; Panea *et al.*, 2011; Guerrero *et al.*, 2013;
316 Gagaoua *et al.*, 2016). In the literature, there is not a clear consensus about a breed effect on
317 the sensory quality of meat. Campo *et al.* (1999) reported that sensory variables are influenced
318 by breed purpose, whereas Panea (2002) did not find differences in tenderness, juiciness or
319 overall appraisal of the meat from several European breeds whose meat was aged for 14 days.

320 Similarly, Monson et al. (2005) found no significant differences in odour intensity in the meat
321 from Spanish Holstein, Parda de Montaña, Limousin and Blonde d'Aquitaine breeds whose
322 meat was aged for different lengths of time. Consequently, Monson et al. (2005) concluded that
323 longer ageing times reduced between-breed variability in sensory variables. In the current
324 experiment, the meat was aged for 14 days.

325 Comparison between laboratories are difficult in sensory analysis. Gagaoua et al. (2016) in
326 an inter- laboratory study with different types of animals and two endpoint temperatures, found
327 that tenderness and juiciness scores were lower at the higher internal end-point cooking
328 temperature, independent of the sensory protocol used whereas the endpoint temperature
329 effect on beef flavour depended on lab conditions. Nevertheless, in the current experiment,
330 inter-laboratory comparison was not possible because each laboratory worked only at one
331 endpoint temperature.

332 The cooking losses we found were similar to those reported by other authors in breeds with
333 similar characteristics (Panea, 2002; Panea *et al.*, 2010a; Panea *et al.*, 2011). Cooking losses
334 are important because they explain part of the variation in juiciness and because they influence
335 meat appearance (Aaslyng *et al.*, 2003). Significant differences in cooking losses were
336 observed between the three French breeds sampled. Conversely, there were no significant
337 differences in cooking losses among the Spanish breeds, which agrees with the absence of a
338 breed effect on cooking losses described by several authors (Panea, 2002; Aviles *et al.*, 2015).
339 In this study, the cooking method influenced cooking losses. Panea *et al.* (2008) reported that
340 cooking losses were greater for grilling than for a water bath. When examining four different
341 cooking methods, Turp (2016) reported a significant effect of cooking method on meatball
342 cooking losses. Pathare and Roskilly (2016) provided a good review of the influence of the
343 cooking method and temperature on cooking losses. It is well known that different cooking
344 techniques, the duration of cooking and core temperatures have a large effect on the physical
345 properties of the meat and its eating quality (Combes *et al.*, 2003). Temperature influences the
346 rate and extent of changes in protein structure, whereas the method of heat transfer (air, steam
347 or contact) affects sensory perception (Bejerholm and Aaslyng, 2003). The changes that occur
348 during cooking affect both the myofibrillar and connective tissues: heat solubilizes collagen,
349 which causes tenderization of the meat but also denatures the myofibrillar proteins, resulting in
350 an increase in toughness of the meat (Obuz *et al.*, 2003).

351

352

353 *4.3. Pearson's Correlations*

354

355 High correlation coefficients were detected among the Warner-Bratzler variables and
356 among the compression variables, as has been described in the literature (Ngapo *et al.*, 2002;
357 Panea *et al.*, 2010a). It is common to find a lack of correlations between the Warner-Bratzler
358 and compression variables, as we observed in this study. As noted by Panea *et al.* (2010b), this
359 absence of correlations is commonly due to differences in the sample preparation, since the

360 Warner-Bratzler test is usually carried out with cooked meat, whereas the compression test is
361 usually carried out with raw meat. Panea *et al.* (2010b) demonstrated that the Warner-Bratzler
362 variables were highly correlated with the compression test variables when the samples were
363 prepared in the same manner. It was reported that the amount and properties of collagen are
364 important factors in determining the toughness of the meat (Cross *et al.*, 1973) but the
365 significance of the collagen influence on texture variables differs among studies. For example,
366 Torrescano *et al.* (2003) in a study with several muscles reported high correlation coefficients
367 between the Warner-Bratzler variables and collagen content and solubility. Alternatively, Chriki
368 *et al.* (2013) in a meta-analysis including several muscles of more than 500 animals reported
369 that WB shear was significantly correlated with insoluble collagen amount but not with total
370 collagen content. On the other hand, Christensen *et al.* (2011b) reported that total and insoluble
371 collagen content were significantly correlated with compression variables measured in raw but
372 not with WB shear independently of whether the meat was raw or cooked. In general, when
373 samples used in the analysis had marked differences in collagen amount or solubility, significant
374 correlations were found. However, when samples had low collagen content (Dransfield, 1977),
375 as m. *Longissimus thoracis et lumborum* (Listrat and Hocquette, 2004), no significant correlation
376 was found. This would explain the lack of significance in the current study.

377

378 **5. Conclusions**

379

380 From the current results, it can be concluded that the breed-production system is an
381 important factor contributing to the variation in both collagen and meat texture traits, whereas
382 sensory characteristics are less affected by the breed. All the variables examined had high
383 within-breed variability. These results suggest that collagen solubility might be the best
384 parameter to use for detecting differences among breeds when the animals are of similar age
385 and that differences in age at maturity are essential for explaining the thermal properties of
386 intramuscular collagen. Despite an effect of the breed-production system on the texture
387 variables, it was not possible to detect a relationship between the texture variables and breed-
388 aptitude or chronological age. The cooking method affected cooking losses, with oven cooking
389 resulting in greater cooking losses than grill cooking. As the temperature of the grill increased,
390 the cooking losses also increased. Because collagen, texture and sensory variables varied as a
391 function of carcass weight, including carcass weight in the models as a covariate is
392 recommended to accurately compare meat traits that may depend on carcass weight. The
393 percentage of collagen solubility was more strongly correlated with texture and sensory
394 variables than total collagen content, which highlights that solubility, rather than the total amount
395 of collagen, is important in defining meat textural and sensory quality. All Warner-Bratzler test
396 variables were closely correlated, as were the compression variables, but there were only weak
397 relationships between Warner-Bratzler and compression test variables. Weak or no correlations
398 were found between the collagen and texture variables. All of the sensory variables were
399 closely related to each other.

400

401 **Ethical Statements**

402

403 The authors declare that they do not have any conflict of interest. All procedures were approved
404 by the animal experimentation ethics committee of the Centro de Investigación y Tecnología
405 Agroalimentaria de Aragón (CITA). Written informed consent was obtained from all study
406 participants.

407

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409

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413

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415

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Table 1. Least square means, standard errors (s.e.) and p-values for the effect of breed-production system on collagen and texture variables in ten local European beef cattle breed-production systems.

	CAS	AV	NE	BP	MO	PI	RE	AU	GA	SA	s.e.	P-value
Total collagen (mg/g)	2.47 ^b	2.94 ^a	3.39 ^a	3.15 ^a	2.73 ^a	2.90 ^a	3.06 ^a	2.86 ^a	2.56 ^b	3.12 ^a	0.025	≤0.0001
Collagen solubility (%)	40.90 ^a	42.36 ^a	32.50 ^b	39.43 ^a	32.56 ^b	40.33 ^a	39.94 ^a	13.26 ^c	13.78 ^c	12.16 ^c	0.395	≤0.0001
Stress Warner-Bratzler (N/cm ²)	35.98 ^c	41.39 ^{ab}	36.87 ^c	39.42 ^{bc}	43.94 ^{ab}	38.10 ^{bc}	41.53 ^{ab}	37.43 ^{bc}	38.82 ^{bc}	44.29 ^a	0.488	≤0.0001
Yield Warner-Bratzler (N/cm ²)	37.93 ^{bc}	45.51 ^a	37.72 ^{bc}	41.85 ^{ab}	44.46 ^a	38.13 ^{bc}	44.92 ^a	21.84 ^d	34.03 ^c	21.60 ^d	0.624	≤0.0001
Compression load (N/cm ²)	62.86 ^{abc}	56.37 ^d	62.50 ^{abc}	58.82 ^{cd}	59.39 ^{bcd}	56.24 ^d	58.23 ^{cd}	68.37 ^{ab}	64.58 ^{abc}	69.07 ^a	0.600	≤0.0001
Compression stress at 20% (N/cm ²)	5.24 ^a	4.95 ^a	5.04 ^a	4.18 ^b	4.83 ^a	5.12 ^a	4.59 ^a	4.34 ^a	4.98 ^a	3.81 ^b	0.057	≤0.0001
Compression stress at 80% (N/cm ²)	38.77 ^a	34.59 ^b	38.41 ^a	37.35 ^a	34.90 ^b	35.50 ^b	35.82 ^a	39.85 ^a	35.41 ^b	40.18 ^a	0.362	0.002

CAS- Asturiana de las Montañas, AV- Asturiana de los Valles, PI- Pirenaica, RE- Retinta, BP- Bruna dels Pirineus, MO- Morucha, NE- Avileña-Negra Ibérica, AU- Aubrac, GA- Gasconne, SA- Salers. Different superscripts in the same row indicate statistically significant differences (p<0.05) among breeds. Corrected carcass weight = 327.42 kg.

Table 2. Least square means, standard errors (s.e.) and p-values for the effect of breed-production system on sensory variables in ten local European beef cattle breed-production systems. Generalized linear models (GLM) were completed independently for each laboratory.

Laboratory	Zaragoza						Monells					Villers Bocage				
Cooking method	Grill						Oven					Grill				
Cooking temperature	70°C						70°C					55°C				
Breed	CAS	AV	PI	RE	P-value	s.e.	BP	NE	MO	P-value	s.e.	AU	GA	SA	P-value	s.e.
Tenderness	6.12 ^{ab}	6.03 ^b	6.54 ^a	6.01 ^{ab}	0.039	0.062	4.56 ^a	5.35 ^b	4.69 ^a	≤0.0001	0.054	5.93	6.49	6.17	0.163	0.065
Juiciness	4.92	5.18	4.92	5.14	0.360	0.065	4.37 ^{ab}	4.43 ^b	3.99 ^a	0.003	0.053	6.25	6.15	6.20	0.856	0.037
Beef flavour	5.33	5.37	5.20	5.30	0.464	0.038	4.50 ^a	5.07 ^b	5.01 ^b	0.008	0.042	6.23	6.17	6.20	0.911	0.032
Overall appraisal	4.62	4.57	4.37	4.68	0.341	0.052	4.69 ^a	5.38 ^b	4.87 ^a	≤0.0001	0.044	6.01	6.31	6.19	0.630	0.050
Cooking losses	14.39	14.33	15.18	13.53	0.176	0.240	23.61	23.26	24.13	0.683	0.396	8.27 ^b	9.78 ^a	7.36 ^c	≤0.0001	0.090

CAS- Asturiana de las Montañas, AV- Asturiana de los Valles, PI- Pirenaica, RE- Retinta, BP- Bruna dels Pirineus, MO- Morucha, NE- Avileña-Negra Ibérica, AU- Aubrac, GA- Gasconne, SA- Salers. Different superscripts in the same row indicate statistically significant differences ($p < 0.05$) among breeds within each laboratory.

Table 3. Pearson bivariate correlation coefficients for texture variables, collagen variables and cooking losses in ten local European beef cattle breed-production systems. Only significant coefficients are shown. Correlation coefficients that were significant at $p < 0.05$ are shown in italics, all other correlation coefficients were significant at $p < 0.01$.

	Total collagen	Solubility percentage	Stress WB	Yield WB	Comp. load	Comp. 20%	Comp. 80%	Cooking losses
Carcass weight	-0.126	-0.621		-0.437	0.099	0.309	-0.007	-0.577
Total collagen		0.242				-0.127	0.139	0.159
Solubility percentage				0.377	-0.169	-0.174		0.406
Stress WB				0.605		0.166	-0.092	
Yield WB					<i>-0.088</i>			0.312
Compression load						0.205	0.677	<i>-0.098</i>
Compression 20%							0.276	-0.188