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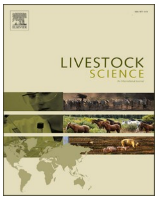

Sire breed has a larger impact on sensory and technological meat quality than dam breed in beef-on-dairy heifers reared on forage and semi-natural grasslands

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HIGHLIGHTS

- Beef-on-dairy heifers grazing semi-natural grasslands can produce high-quality beef.
- Angus crossbreeds produced beef of higher quality than Charolais crossbreeds.
- Beef-on-dairy from Holstein and Swedish Red-and-White have comparable meat quality.
- Moderately high feeding intensity resulted in higher intramuscular fat concentrations.
- Charolais heifers reared at low feeding intensity delivered the poorest meat quality.

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ABSTRACT

The aim of this study was to evaluate the meat quality of beef-on-dairy heifers from Holstein or Swedish Red-and-White dams sired by Angus or Charolais bulls reared on forage and semi-natural grasslands. Production systems with moderately high and low feeding intensities were compared, where animals grazed for one or two summers and were slaughtered at 20 or 27 months of age, respectively. Meat quality of crossbred heifers from Holstein and Swedish Red-and-White dams was comparable in *M. longissimus lumborum* (LL) and differed in pH, yellowness and Warner-Bratzler shear force (WBSF) in *M. semimembranosus* (SM) with Swedish Red-and-White being less tough. Compared with LL from Charolais crossbreeds, LL from Angus was redder and had lower WBSF, higher intramuscular fat concentration (IMF%), a more pronounced metallic flavour and a more pronounced umami taste. Meat quality of SM did not differ between Angus and Charolais crossbreeds. Generally, the production system with moderately high feeding intensity resulted in less tough beef that was lighter and less red and had higher IMF%. Consequently, beef from Charolais crossbreeds reared at a low feeding intensity exhibited the poorest meat quality with the lowest IMF% in LL (2.80 and 3.77 % for Holstein and Swedish Red-and-White, respectively). Nevertheless, crossbreeds did not differ in sensory meat quality. Generally, meat quality of beef-on-dairy heifers reared on forage and semi-natural grasslands was high, and while Angus crossbreeds delivered high-quality beef from both feeding intensities, Charolais crossbreeds are better suited for the moderately high feeding intensity, when aiming for high meat quality.

1. Introduction

The use of dairy × beef crossbreeding (beef-on-dairy), has increased globally the past decades. In Sweden, most dairy cows are still bred with bulls of the same breed, but in the past decade, insemination with semen from beef breeds has increased fourfold, rising from 4.2 % to 18.3 % (Sverige, 2023). In contrast to purebred beef breeds, beef-on-dairy share the carbon footprint from maintenance of dams with the concomitant

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dairy production, whereas the carbon footprint from production of beef breeds is solely attributed to the meat production (de Vries et al., 2015; Puillet et al., 2014). Moreover, beef-on-dairy offspring are more efficient than purebred dairy offspring in terms of feed efficiency, carcass weight, carcass conformation and meat yield, which is associated with increased beef production income (Bittante et al., 2021; Vestergaard et al., 2019). Due to their higher potential in carcass conformation and thus carcass price, most male calves in Sweden are intensively reared as intact bulls in indoor systems (Holmström et al., 2021). In contrast, heifers are known for their lower growth potential, but higher meat quality compared with bulls and steers, at least under intensive rearing conditions (Bittante et al., 2018; Pogorzelska-Przybyłek et al., 2021; Vestergaard et al., 2019). Moreover, heifers are easier to manage than bulls for beef production in free-range systems, and they pose fewer safety risks for visitors in grasslands with public access, favouring heifers in beef production systems with grazing.

To this point, the potential of extensive rearing of beef-on-dairy on semi-natural grasslands has already been evaluated (Hessle et al., 2011, 2007a, 2007b; Hessle et al., 2019; Holmström et al., 2021; Niemela et al., 2008), but so far the meat quality of such crossbreeds is barely explored (Fraser et al., 2009, 2007; Turner et al., 2011), especially for heifers. In general, low-energy intakes are often associated with leaner carcasses and tougher meat (Garmyn et al., 2010), and a study from Sweden confirms that animals on semi-natural grasslands are less profitable than animals reared indoors (Holmström et al., 2021). However, as semi-natural grassland is the most endangered habitat in Sweden, extensive grazing here plays a crucial role in preserving biodiversity by preventing habitat and species losses (Eriksson, 2022; Toräng and Jacobson, 2019). Traditionally, beef is reared either at low intensity grazing for two summers, or under moderately high conditions grazing for one summer. Hence, a comparison of meat quality from beef-on-dairy heifers with one or two grazing periods extensively reared on semi-natural grasslands and roughage is both relevant and of importance.

This study provides a Nordic perspective, investigating four crossbreeds between the two most common dairy breeds and two common beef breeds in Sweden (Sverige, 2023). These are Swedish Holstein (HOL) and Swedish Red-and-White (SRB), crossed with Charolais (CHA) and Angus (ANG), a late and an early maturing beef breed, respectively (Davis et al., 2019; Sinclair et al., 2001). The aim of this study was to investigate the impact of these dam and sire breeds as well as low or moderately high feeding intensities on the meat quality of beef-on-dairy from heifers reared on forage and semi-natural grasslands.

2. Materials and methods

2.1. Experimental design and animal management

Sourcing and rearing of the heifers used in the present study were described by Hessle et al. (2024). Briefly, the study included 72 beef-on-dairy heifers from Swedish Holstein (HOL) and Swedish Red-and-White (SRB), crossed with Charolais (CHA) and Angus (ANG) bulls with 18 individuals of each crossbreed (ANG × SRB, ANG × HOL, CHA × SRB and CHA × HOL). The heifer calves entered the experimental stations at 11–14 weeks of age. Half of the calves from each crossbreed were allocated to one of the two production systems, moderately high (H) or low (L) indoor feed intensity, coupled with grazing on semi-natural grasslands. Heifers in production system H were born between April and August 2020 and assigned a moderately high feed intensity during two indoor periods with an intermediate grazing period (May 5 to September 1, 2021) and were slaughtered at an average age of 613 ± 7 days from December 15, 2021, to April 20, 2022. Heifers in production system L were born between June and October 2019 and assigned a low feed intensity during three indoor periods with two intermediate grazing periods (May 6 to October 23, 2020, and May 5, 2021, to eight weeks before their individual day of slaughter, i.e. from August 3 to November 17, 2021). Heifers in production system L were slaughtered at an average age of 824 ± 5 days from September 29, 2021, to January 12, 2022.

During grazing periods, all heifers were kept in one group, rotating among four enclosures every 7-14 days. The pasture consisted of permanent semi-natural grasslands of 19.5 ha in 2020 and 37.3 ha in 2021, with approximately 20 % dry, 60 % mesic, and 20 % wet areas. During indoor periods, the heifers were fed ad libitum receiving total mixed rations consisting of grass-clover silage, rolled barley, rolled peas, and rapeseed meal. The feed composition for each pen was adjusted when the average liveweight of the two lightest heifers in the pen reached the minimum weight for a next step of decrease in the protein/energy ratio according to the Swedish recommendations (Spörndly, 2003). For L heifers, grass clover silage was fed ad libitum as the sole feed from 225 kg until slaughter, whereas 80 % grass clover silage and 20 % rolled barley was fed to H heifers during the final indoor period. Feed values and chemical composition of the experimental diets and pastures can be seen in detail in Hessle et al. (2024). In these two production systems, the average carcass weights for Angus and Charolais crossbreeds were 323 kg and 350 kg, respectively in system H and 351 kg and 369 kg, respectively in system L.

2.2. Slaughter and sampling

Heifers were slaughtered individually as they reached their target age. They were transported 31 km to the commercial abattoir (Skövde Slakteri, Skövde, Sweden) and slaughtered within 2 h of arrival by stunning with a captive bolt, followed by bleeding. Post slaughter the carcasses were hung by Achilles suspension and divided along the vertebral column. A Mettler Toledo Seven2Go pro mobile pH-meter equipped with a spearhead glass electrode (Mettler Toledo, Columbus, Ohio, USA) standardized using commercial pH buffers of 4.01 and 7.01, was applied to the left side of the carcass in *M. longissimus lumborum* (LL) between the 10th and 11thrib to measure pH 24 h *post-mortem*. Finally, the carcasses were shock cooled at +2 °C for approximately 3.5 hours and then kept at +4.5 °C.

Two days *post-mortem*, the carcasses were split into the fore- and hindquarters between the 10th and 11th ribs. From the left hindquarters, LL, and *M. semimembranosus* (SM) was removed by an experienced butcher for meat quality analyses. SM was cut to an approximate size of 10 × 12 cm with a horizontal cut removing the distal part of the muscle and two vertical cuts narrowing the size to 10 cm in width. Ultimate pH was measured in the cranial end of LL and the distal end of SM, after which slices were cut from the same ends of both muscles in the following order: 1 cm slice (vacuum packed and frozen at -20 °C for later determination of intramuscular fat concentration (IMF%)), 1 cm slice (for colour analysis), 7–8 cm slice (vacuum packed and stored at 4 °C until 7 days *post-mortem*, and then frozen at -20 °C for later determination of cooking loss and Warner-Bratzler shear force (WBSF)). Additionally, a 12–15 cm sample of LL was removed from 56 carcasses for sensory analyses (vacuum packed and stored at 4 °C until 7 days *post-mortem*, and then frozen at -20 °C). The frozen samples for cooking loss, WBSF and IMF% were shipped on ice to the meat laboratory at Aarhus University, Denmark and the frozen samples for sensory analyses were shipped on ice to Kristianstad University, Sweden.

2.3. pH and colour

Ultimate pH and colour were measured 48 h *post-mortem* on the carving/boning line at the abattoir. pH_{48h} was measured in duplicates with the same type of pH meter as the one used for pH_{24h} (see above). Colour was measured after 60 min of blooming (Caldwell et al., 2017) at five sites per slice with a CM-600d spectrophotometer (Konica Minolta, Osaka, Japan), calibrated against a white tile provided by the manufacturer ($L^* = 97{,}38$, $a^* = -0{,}16$ and $b^* = -0{,}03$). The average CIE 1976 values (L^*, lightness; a^*, redness; b^*, yellowness) were recorded.

2.4. Warner–Bratzler shear force and cooking loss

Warner-Bratzler shear force samples were thawed in one layer at 5 °C for 1 or 2 days (LL and SM respectively). Samples were first cut to size (5 × 4 × 8 cm), weighed, vacuum packed, and heat treated in circulating water (10 min at 4 °C, 60 min at 62 °C, and 30 min at 4 °C). Fifteen samples were randomly selected for each heating batch. Samples were then rinsed with water, blotted dry with clean paper towels, and weighed again to determine the cooking loss, defined as the percentage weight loss of the samples after cooking relative to prior cooking. Four 1-cm slices were cut from each sample on an electric food slicer, and two 1-cm-wide strips were cut from each slice parallel to the muscle fibres to yield eight replicates (size 4 × 1 × 1 cm) per sample. Two of the eight replicates were omitted based on a process of selective evaluation of sample homogeneity considering fibre direction, dimensions, and appearance of connective tissue. The remaining six replicates were analysed on the TMS-Pro-Texture Analyser equipped with a 1000 N load cell (Food Technology Corporation, Sterling, Virginia, USA). The analysis was carried out at a speed of 48 mm/min using a square Warner-Bratzler shear blade (11 mm wide, 15 mm tall, 1.2 mm thick) for shearing of the meat strips across the fibres. The mean maximum force of replicates was recorded.

2.5. Chemical intramuscular fat concentration

Samples (40–50 g) for IMF analyses were thawed for 2 h at room temperature or overnight at 5 °C. The intermuscular fat and visible connective tissue were removed and discarded, and the meat slices were cut into smaller pieces and homogenized in a small food processor. A subsample of 9.5 ± 0.5 g was weighed from each sample, and IMF was extracted using a combination of the closed system apparatuses HYDROTHERM (ISO 8262-1 Weibull-Berntrop gravimetric method) and SOXTHERM® (rapid soxhlet extraction) according to the procedure described by Gerhardt (C. Gerhardt GmbH & Co. KG, Königswinter, Germany). The sample IMF% was determined from the amount of fat extracted relative to the sample weight.

2.6. Sensory analysis

2.6.1. Sample preparation

Samples weighing approximately 1000 g (mean ± SD 1013 ± 123 g) were thawed for 48 h at 4 °C, heat treated in circulating water at 63 °C for four hours to an internal temperature of 61.9 °C ± SD 0.9 °C and left to rest for 90 min. In preparation for sensory analysis, the samples were cut into 7 mm slices using a commercial meat slicer and trimmed into rectangular pieces measuring 20 × 30 × 7 mm. One slice per sample was placed in tree-digit coded petri dishes and held at 55 °C for approximately 30 min before served to the panellists in a randomised serving order. Samples were evaluated in triplicate meaning that each panellist was presented to and tested all animals three times.

2.6.2. Sensory evaluation

Sensory evaluation was performed using descriptive analysis (Stone and Sidel, 2004). Training and evaluation were carried out using an analytical panel of six panellists who were selected and trained according to ISO 3972:2011, SS-EN ISO 8586:2014 in a sensory laboratory at Kristianstad University, equipped according to SS-EN ISO 8589:2010. Across two training sessions lasting 2 h each, the panel, that had previous experience in sensory analysis of beef, started by individually developing descriptions of sensory attributes categorized as appearance, odour, texture, and flavour of the meat. In the next step, the panel leader led a discussion during which consensus was developed regarding the evaluation of selected attributes (Table 1). For training, four samples from animals representing large quality variations were used to expose the panellists to different types of beef within the range of the experimental setup. The intensity of selected attributes was collectively evaluated by the panel using a line scale ranging from 0 to 100 with indented anchors placed at 10 and 90. Cucumber, wheat wafers and water were chosen by the panel for optimal cleansing of the palate. After training, the intensity of the selected attributes was evaluated by the panellists individually across ten testing sessions and days, 5–6 samples per day. The samples were kept together, so that during one testing session, the same sample (animal) was evaluated in triplicate while the serving order was randomized over the total number of samples tested on that same day. The mean values of replicates, obtained from each panellist, were recorded. In total 56 heifers were evaluated, including seven heifers from each combination of production system, sire breed and dam breed, with the exclusion of individuals with the highest and lowest carcass weights in each group.

Table 1
List of sensory terms with definitions derived for sensory profiling of beef from beef-on-dairy heifers reared on forage and semi-natural grasslands.

Category	Attribute	Definition
Appearance	Redness-A (weak-strong)	Red colour of non-denatured myoglobin
	Lightness-A (light-dark)	Deepness of colour related to muscle fibre composition
	Fibre structure-A (fine-coarse)	The width of exposed muscle fibres
Odour	Stable-O (weak-pronounced)	A combined sensation of silage, ammonia, and staleness
	Metal-O (weak-pronounced)	Metallic aromatic, closely related to the smell of iron and blood
Flavour (after mastication, 3 chews)	Metal-F (weak-pronounced)	Iron and blood
Taste (after mastication, 3 chews)	Umami-T (weak-pronounced)	A meaty taste closely related to sodium glutamate
	Saltiness-T (weak-pronounced)	The taste of sodium chloride;
	Acidity-T (weak-pronounced)	The taste of sourness, lactic acid
	Sweetness-T (weak-pronounced)	Sweet taste related to sucrose
Texture hand (after 3 draws with a table knife)	Resistance to cutting-TH (tender-tough)	The force needed to penetrate the meat using a table knife across the fibres
Texture mouth (after mastication, 3 chews)	Juiciness -TM (little- much)	Perceived succulence of the meat
	Crumbliness-TM (little –much)	Disintegration during mastication
	Chewiness-TM (low-high)	Resistance to mastication, higher intensity means tougher meat

2.7. Statistics

Data handling and editing were performed in the statistical software R version 4.0.5 (R Core Team, 2022). The linear mixed model (lmer from package lme4) was used to analyse the influence of the two different production systems, the two different sire breeds and the two different dam breeds and their interaction on the technological meat quality traits and sensory evaluations (Bates et al., 2015). The model employed on technological meat quality traits was as follows:

$$y_{ijk} = age + \mathrm{PEN} + \mathrm{dam}_i + \mathrm{sire}_j + ps_k + \mathrm{dam}_i * \mathrm{sire}_j + \mathrm{dam}_i * \mathrm{ps}_k + \mathrm{sire}_j * \mathrm{ps}_k + \mathrm{dam}_i * \mathrm{sire}_j * \mathrm{ps}_k + e_{ijk}$$

where y_{ijk} is the vector of meat quality observations on the heifers, described by the fixed effect (dam_i) of the i'th dam breed (i = HOL, SRB), $sire_j$ is the fixed effect of the j'th sire breed (j = ANG, CHA), ps_k is the fixed effect of the k'th production system ($k = H$, L), and all interactions between these three fixed effects, as well as the covariate effect of age defined as the deviation from raw mean within each production system k (*age*), PEN is included as a random effect (1-12), and e_{ijk} is the residual effect. The model employed on sensory evaluations was as follows:

$$y_{ijk} = age + PEN + PANELLIST + dam_i + sire_j + ps_k + dam_i * sire_j + dam_i * ps_k + sire_j * ps_k + dam_i * sire_j * ps_k + e_{ijk}$$

where PANELLIST is the random effect of panellist (1-6), and the remaining variables follow the description above. The inclusion of random effect of analysis day was tested but omitted in the model due to minimal impact.

Performance on meat quality traits was estimated by Type II Wald chi-square tests conducted for the linear mixed models using the Anova function, from package car (Fox and Weisberg, 2019). Differences were considered statistically significant when $P < 0.05$. The emmeans package was used to generate least-squares means (LSmeans) and standard error of the mean (SEM) for all response variables (Lenth, 2023). Group differences were tested for significance with Tukey–Kramer method for a family of eight estimates at 0.05 significance level using the cld function, from package multcomp (Hothorn et al., 2008). Pearson correlations between IMF% and duration of grazing and indoor periods prior to slaughter were calculated using the cor function of the base R environment (R Core Team, 2022).

3. Results

The technological meat quality differs between production system H and L of both LL (Table 2) and SM (Table 3). Generally, beef from production system L had higher pH_{24h}, pH_{48h}, was darker, redder, had higher WBSF (not significant in SM) and lower IMF%. In LL, beef from ANG crossbreeds had lower pH_{24h}, was redder, had lower WBSF and higher IMF% compared with beef from CHA crossbreeds. For SM, there were no significant effects of sire breed on any of the technological meat quality traits. In SM, HOL crossbreeds produced meat with higher pH_{48h}, lower yellowness, and higher WBSF compared with SRB crossbreeds, whereas there were no significant effects of dam breed on any of the technological meat quality traits in LL, however, there were a significant interaction between dam breed and feeding intensity on pH_{24h}, pH_{48h} and lightness. This means that beef from HOL crossbreeds had darker meat than beef from SRB crossbreeds in production system H, and vice versa for production system L. Furthermore, there was a significant interaction between feeding intensity, sire breed and dam breed for WBSF in LL and for yellowness in SM. This was expressed as trends where LL from ANG crossbreeds in production system H had the lowest WBSF and CHA × HOL in production system L had the highest WBSF. For SM yellowness, the significant three-way interaction introduces more complexity to the relationships between groups of heifers, however the b^* values lie within a narrow range without expected impact for the consumer. Beef from LL did not differ between groups on yellowness, and for both LL and SM, the meat did not differ between groups on cooking loss.

Statistical tests found no relationship between IMF% and duration of indoor period prior to slaughter in production system H, as well as no relationship between IMF% and duration of grazing period prior to the standardized eight weeks indoor prior to slaughter in production system L (Pearson correlation coefficients 0.01 and 0.18 respectively).

The production systems H and L are also distinguishable in the sensory analysis of LL (Table 4), especially on appearance and texture, as well as metal flavour and acidity. The sensory panel evaluated the beef from production system L as redder and darker with a coarser fibre structure (appearance) than beef from production system H. Furthermore, it had more resistance to cutting, higher chewiness, more intense metallic flavour, and less acidulous taste than beef from production system H. The sire breeds differentiate on flavour and taste characteristics, with beef from ANG crossbreeds having a more intense metallic flavour and umami taste than beef from CHA crossbreeds. Finally, there is a significant effect of dam breed on acidity, with beef from SRB crossbreeds being evaluated with more acidulous taste than beef from HOL crossbreeds. There are also some interactions between dam breed and feeding intensity on crumbliness and chewiness, indicating a more pronounced crumbliness and lower chewiness in HOL compared to SRB from production system H.

4. Discussion

4.1. Effects of feeding intensity on meat quality

The results showed that meat quality differed between the two production systems with 20 months old crossbreeds reared on

Table 2
Technological meat quality of *M. longissimus lumborum* from heifers with the effects of feeding intensity (moderately high and low), sire breed (Angus and Charolais) and dam breed (HOL—Swedish Holstein; SRB—Swedish Red-and-White). Results are presented as least-squares means, standard error of the mean (SEM) with *P*-values.

Feeding intensity (FI)	High				Low				SEM	*P*-values[1]		
Sire breed (S)	Angus		Charolais		Angus		Charolais					
Dam breed (D)	HOL	SRB	HOL	SRB	HOL	SRB	HOL	SRB		FI	S	D
n	9	9	9	9	9	9	9	9	—	—	—	—
pH_{24h}[2]	5.49^{ab}	5.47^{ab}	5.53^{ab}	5.53^{ab}	5.46^{a}	5.59^{b}	5.59^{ab}	5.61^{b}	0.03	0.014	0.007	0.104
pH_{48h}[2]	5.39^{ab}	5.40^{abc}	5.37^{a}	5.39^{ab}	5.48^{e}	5.42^{bcd}	5.45^{de}	5.44^{cde}	0.01	<0.001	0.362	0.153
L^*[3]	31.0^{abcd}	32.1^{cd}	31.5^{bcd}	32.7^{d}	28.4^{abc}	28.0^{ab}	28.0^{ab}	27.4^{a}	0.8	<0.001	0.958	0.411
a^*[3]	15.1^{abc}	14.8^{abc}	14.2^{ab}	13.8^{a}	16.5^{cd}	17.2^{d}	16.0^{bcd}	16.0^{bcd}	0.4	<0.001	0.003	0.882
b^*[3]	15.6	16.2	15.9	15.4	15.9	16.8	15.1	15.6	0.5	0.810	0.068	0.249
Cooking loss (%)	15.1	15.3	15.8	16.2	14.9	15.4	16.2	17.0	0.8	0.697	0.051	0.297
WBSF (N)[4]	38.0^{a}	34.9^{a}	40.1^{a}	41.9^{ab}	43.3^{ab}	45.3^{ab}	56.4^{b}	43.3^{ab}	3.2	<0.001	0.010	0.247
IMF (%)[5]	6.37^{bc}	7.28^{c}	3.96^{ab}	4.04^{ab}	5.27^{abc}	5.14^{abc}	2.80^{a}	3.77^{ab}	0.67	0.012	<0.001	0.326

[1] Interactions not shown: Significant interaction between FI × D for pH24h ($P = 0.045$), pH48h ($P < 0.001$) and L^* ($P = 0.031$). Significant interaction between FI × S × D for WBSF ($P = 0.019$).

[2] pH was measured at the 11thrib 24 h and 48 h *post-mortem*.

[3] L^* (lightness), a^* (redness), b^* (yellowness) measured on CIE 1976 $L^*a^*b^*$ scale.

[4] Warner-Bratzler shear force, peak force.

[5] Intramuscular fat concentration assessed by chemical analysis.

[a-e] Values within a row with different superscripts differ significantly at $P < 0.05$.

Table 3
Technological meat quality of *M. semimembranosus* from heifers with the effects of feeding intensity (moderately high and low), sire breed (Angus and Charolais) and dam breed (HOL—Swedish Holstein; SRB—Swedish Red-and-White). Results are presented as least-squares means, standard error of the mean (SEM) with *P*-values.

Feeding intensity (FI)	High				Low				SEM	*P*-values[1]		
Sire breed (S)	Angus		Charolais		Angus		Charolais					
Dam breed (D)	HOL	SRB	HOL	SRB	HOL	SRB	HOL	SRB		FI	S	D
n	9	9	9	9	9	9	9	9	—	—	—	—
pH_{48h}[2]	5.40^{a}	5.39^{a}	5.40^{a}	5.40^{a}	5.42^{ab}	5.41^{ab}	5.45^{b}	5.42^{ab}	0.01	<0.001	0.272	0.030
L^*[3]	32.3^{abc}	34.2^{c}	33.9^{bc}	34.4^{c}	29.6^{a}	30.0^{ab}	31.0^{abc}	31.1^{abc}	0.8	<0.001	0.113	0.124
a^*[3]	18.7^{ab}	19.5^{ab}	19.7^{ab}	18.5^{a}	20.9^{ab}	21.4^{b}	20.0^{ab}	20.8^{ab}	0.6	<0.001	0.392	0.488
b^*[3]	18.9	20.8	20.5	19.6	20.3	21.1	19.5	20.9	0.7	0.386	0.817	0.021
Cooking loss (%)	16.1	16.8	18.1	18.1	18.3	17.1	18.8	17.6	0.8	0.271	0.065	0.486
WBSF (N)[4]	48.7^{ab}	44.4^{a}	52.6^{ab}	49.4^{ab}	53.6^{ab}	49.7^{ab}	55.9^{b}	48.7^{ab}	2.4	0.062	0.152	0.003
IMF (%)[5]	2.13	3.28	1.95	1.80	1.73	1.89	1.70	1.83	0.41	0.007	0.059	0.246

[1] Interactions not shown. Significant interaction between FI × S × D for b^* ($P = 0.013$).
[2] pH was measured in the centre of the muscle 48 h *post-mortem*.
[3] L^* (lightness), a^* (redness), b^* (yellowness) measured on CIE 1976 $L^*a^*b^*$ scale.
[4] Warner-Bratzler shear force, peak force.
[5] Intramuscular fat concentration assessed by chemical analysis.
$^{a-c}$ Values within a row with different superscripts differ significantly at $P < 0.05$.

Table 4
Sensory analysis of *M. longissimus lumborum* with the effects of feeding intensity (moderately high and low), sire breed (Angus and Charolais) and dam breed (HOL—Swedish Holstein; SRB—Swedish Red-and-White). Attributes were evaluated on intensity scales ranging from 0 to 100, and are presented as least-squares means, standard error of the mean (SEM) with *P*-values.

Feeding intensity (FI)	High				Low				SEM	*P*-values[1]		
Sire breed (S)	Angus		Charolais		Angus		Charolais					
Dam breed (D)	HOL	SRB	HOL	SRB	HOL	SRB	HOL	SRB		FI	S	D
n	7	7	7	7	7	7	7	7	—	—	—	—
Odour												
Stable-O	48.4	50.0	49.2	49.7	42.8	51.4	46.3	50.3	7.6	0.374	0.757	0.086
Metal-O	48.7	48.0	46.4	46.5	47.3	50.2	44.9	46.4	7.3	0.926	0.111	0.084
Appearance												
Redness-A	41.9^{ab}	40.4^{ab}	36.7^{a}	39.7^{ab}	63.7^{c}	62.3^{c}	62.3^{c}	54.6^{bc}	4.4	<0.001	0.153	0.076
Lightness-A	42.2^{abc}	38.8^{abc}	33.1^{a}	36.6^{ab}	54.3^{bc}	54.5^{c}	54.4^{c}	48.8^{abc}	5.1	<0.001	0.161	0.226
Fiber structure-A	45.8	44.0	45.0	46.7	50.1	52.6	47.3	45.6	3.8	0.039	0.281	0.959
Texture hand												
Resistance to cutting-TH	23.0^{a}	34.0^{abcd}	28.7^{ab}	32.5^{abc}	48.7^{cd}	50.4^{d}	48.2^{cd}	44.0^{bcd}	5.5	<0.001	0.763	0.383
Texture mouth												
Juiciness-TM	51.2	47.1	57.0	50.2	51.9	47.0	47.2	49.8	5.8	0.440	0.466	0.201
Crumbliness-TM	50.8^{d}	40.6^{bcd}	44.3^{cd}	39.1^{abcd}	32.9^{abc}	29.4^{ab}	29.3^{a}	35.0^{abc}	5.9	<0.001	0.373	0.271
Chewiness-TM	32.1^{a}	43.1^{ab}	36.7^{ab}	42.9^{ab}	61.4^{b}	61.7^{b}	61.3^{b}	57.5^{ab}	7.0	<0.001	0.959	0.333
Flavour												
Metal-F	55.0	57.3	54.0	54.1	61.4	61.5	57.7	54.6	6.3	0.016	0.017	0.695
Taste												
Umami-T	55.6	55.2	54.8	54.6	56.5	55.8	52.3	54.8	9.2	0.927	0.032	0.323
Saltiness-T	16.0	16.2	16.4	16.6	15.2	15.8	16.1	16.4	2.2	0.303	0.204	0.129
Acidity-T	22.9	23.6	22.2	23.8	20.0	21.6	21.3	22.0	3.7	0.004	0.731	0.033
Sweetness-T	14.4	13.6	14.5	13.2	13.9	12.9	13.2	13.5	2.8	0.196	0.855	0.180

[1] Interactions not shown. Significant interaction FI × D for chewiness ($P = 0.026$) and crumbliness ($P = 0.014$). Significant interaction S × D for crumbliness ($P = 0.020$).
$^{a-d}$ Values within a row with different superscripts differ significantly at $P < 0.05$.

moderately high feeding intensity during two indoor periods with an intermediate grazing period of 4 months on semi-natural grasslands (production system H) and 27 months old crossbreeds reared on low feeding intensity during three indoor periods with two intermediate grazing periods on semi-natural grasslands of 5.5 and 3 to 6.5 months respectively (production system L). Colour measurements and sensory analyses on redness and lightness agree that beef from production system L is redder and darker. The darker and redder colour of beef from L heifers may be explained by the age differences between L and H heifers, as myoglobin concentration and activities of cytochrome oxidase and succinic dehydrogenase increases with age, enhancing aerobic metabolism leading to a change from a white to a red muscle type (Renerre, 1990). It has previously been hypothesized that grazing animals have more myoglobin than animals reared indoors, due to increased physical activity pre-slaughter (French et al., 2000). However, since all heifers in this study were housed indoors for a minimum of eight weeks prior to slaughter, this is likely not applicable. Also, French et al. (2000) found no significant differences in colour traits of raw meat between steers assigned to five different treatments with varying portions of concentrate and grass-based feeding and slaughtered at the same age. This further indicates that age may be the strongest colour determinant in our study.

The higher pH_{24h} and pH_{48h} of beef from production system L in both muscles suggests a lower glycogen reserve in the muscles at slaughter and lower *post-mortem* production of lactic acid compared with crossbreeds in production system H. This is a rational explanation considering the differences in finishing between the two production systems (100 % silage in L and 80 % silage plus 20 % rolled barley in H). The higher pH might also partly explain the higher WBSF, resistance to cutting and higher chewiness in LL from heifers in production system L, as shear force has been shown to increase with increasing ultimate pH from pH 5.4 to pH 6.0 (Lomiwes et al., 2014). This relationship between WBSF and ultimate pH was also seen in a study on grazing bulls and steers (Purchas et al., 2002). Turner et al. (2011) did not find any difference in WBSF 1 day *post-mortem* between animals assigned to different feeding intensities, and French et al. (2000) saw no differences between the diet groups in WBSF and cooking loss 7 days *post-mortem*. However, 2 days *post-mortem*, the diet group with the highest proportion of concentrate had lower WBSF than the remaining diet groups with no differences in cooking loss (French et al., 2000). This is consistent with our findings, suggesting that extended ageing could have reduced or eliminated the differences in WBSF between different rearing conditions in our study. According to Belew et al. (2003), the WBSF values in our study categorizes the LL beef from production system H as “tender” (31.38 – 38.25 N) and “intermediate” (38.25 – 45.11 N), whereas beef from production system L is categorized as “intermediate” and “tough” (> 45.11 N). This may be related to a presumed higher average daily gain (ADG) in heifers from production system H. Previous research found a negative correlation between ADG and WBSF of LL, i.e., higher ADG resulted in lower WBSF (Therkildsen et al., 2002).

Finally, the lower IMF% of both muscles from L heifers compared with H heifers indicate a stronger effect of the feeding intensity than of the slaughter age. Generally, IMF% is known to increase with age but energy intake and source is also important (Wang et al., 2019). Mialon et al. (2014) compared starch-rich and fibre-rich concentrate diets fed ad libitum to bulls slaughtered at the same age (17–18 months) and found a significantly higher IMF% in bulls fed the starch-rich diet compared with bulls fed the fibre-rich diet. Wang et al. (2019) compared three grain-based diets with high, medium, or low energy, and found that differences in IMF% between energy groups increased with increasing slaughter age of 20, 23 and 26 months. At the same time, their results show that IMF% in bulls assigned to the low energy diet slaughtered at 26 months, did not differ from IMF% in bulls assigned to the medium or high energy diets slaughtered at 20 months. Another study found a lower IMF% in grass-fed steers compared with concentrate-fed steers grown to similar slaughter weights (Purchas and Davies, 1974). These results are consistent with the findings of our study. Many studies have reported a negative correlation between IMF% and WBSF (Cafferky et al., 2019; Hoa et al., 2023; Lee and Choi, 2019). Therefore, it is speculated that the between-group-differences in LL WBSF 7 days *post-mortem*, are primarily determined by the differences in IMF%, as indicated by French et al. (2000), who found no disparities between groups in either IMF% or WBSF at the same *post-mortem* time point. This could also explain the absence of significance in SM WBSF with remarkably lower IMF%.

In contrast to our findings on sensory quality, other studies found no significant differences on flavour or texture attributes between animal groups of different feeding intensities at either similar slaughter ages or similar slaughter weights (Bidner et al., 1986; Fraser et al., 2007; French et al., 2000). As reviewed by e.g. Poveda-Arteaga et al. (2023), older animals are associated with more oxidative muscle fibres, with higher myoglobin and iron levels, resulting in darker muscles. Increasing the slaughter age in cattle has also been shown to give a higher proportion of red oxidative fibres that grows at a faster pace than the glycolytic ones (Jurie et al., 2005). Thus, age differences between animals from the two production systems may be important in explaining that the sensory panel evaluated the appearance of the meat from production system L as redder and darker with a more coarse fibre structure than that from production system H. The age factor may also play a role in the findings of a more intense metallic flavour and less acidulous taste in meat from the older animals in system L as compared to that from production system H.

4.2. *Effects of sire and dam breeds on meat quality*

The differences in meat quality between crossbreeds were less dominating than the differences between feeding intensities, yet they existed. Curiously, sire breed was only significant on technological meat quality traits of LL, and dam breed was only significant on technological meat quality traits of SM. Yet, both sire breed and dam breed had significant effects on some sensory attributes in LL. The results suggest that differences between sire breeds are more pronounced than differences between dam breeds only differing on ultimate pH, yellowness and WBSF in SM and LL acidity. This implies that differences between crossbreeds in the economically valuable LL muscle are minimal. Nevertheless, these findings are valuable as research on meat quality in SRB is scarce. Previous studies showed that crossbred steers from ANG and Hereford dams sired by SRB and Friesian bulls performed similarly on WBSF and sensory tenderness, juiciness, and beef flavour intensity in *M. longissimus thoracis* (Wheeler et al., 2004). Another research project on meat quality of young purebred Danish Red and Holstein bulls revealed no significant differences between breeds on ultimate pH, colour traits, WBSF, sensory tenderness, juiciness, beef flavour, or off flavour in *M. longissimus thoracis* (Christensen et al., 2011; Conanec et al., 2021; Ripoll et al., 2018). It is important to note that SRB and Danish Red are not directly comparable, however, they are to some extent genetically related (Averdunk, 2002; Zhou et al., 2014).

Regarding the impacts of sire breed on meat quality, LL from ANG crossbreeds was redder, had lower WBSF, higher IMF% and a more intense umami taste than LL from CHA crossbreeds, indicating superior meat quality characteristics. The difference in redness was also reported by Ripoll et al. (2018), who demonstrated that young purebred ANG bulls had darker and redder meat than purebred CHA bulls. They also found that beef from purebred CHA exhibited higher metmyoglobin concentrations, which is the oxidized brown state of myoglobin with lower redness (Corlett et al., 2021). This might explain the difference in redness in our study, but metmyoglobin determination or oxidation analyses are needed to confirm this hypothesis. However, as ANG was associated with a more intense metallic flavour in the sensory analysis, it is more likely caused by a higher myoglobin content in these crossbreeds (England et al., 2017; Jeong et al., 2009). We did not observe significant differences in lightness between the crossbreeds. This lack of differentiation is likely due to the higher slaughter age, which may have reduced the impact of early- vs. late-maturity characteristics of ANG and CHA seen in previous studies (20–27 months in our study vs. 14–15 months in the study by Ripoll et al. (2018)). Moreover, crossbreeding with HOL and SRB may have contributed to a reduction in sire breed effects. Like lightness, ultimate pH did not differ between crossbreeds, which is consistent with previous findings on purebred ANG and CHA (Chambaz et al., 2003; Christensen et al., 2011; Sinclair et al., 2001).

Chambaz et al. (2003) investigated purebred ANG and CHA fattened to an IMF% of 3.25 % (slaughter age 381 days and 513 days for ANG and CHA, respectively) and saw no differences between breeds on pH, colour traits or WBSF. This highlights that animals of the same percentage of adult live weight exhibit greater similarity in meat quality than animals slaughtered at the same age, which is attributed to variations in the maturity levels of different breeds. Interestingly, Chambaz et al. (2003) found a significantly higher cooking loss ($P < 0.001$) in purebred ANG compared with purebred CHA, which approached statistical significance in our study ($P = 0.051$) with a higher cooking loss in CHA compared with ANG. Again, this deviation from the Chambaz et al. (2003) study is explained by the breed maturity effects and dam crossbreeding effects. Nonetheless, our observations align well with expectations of positive correlation between cooking loss and WBSF, implying that higher cooking losses results in tougher meat (Cafferky et al., 2019).

Previous studies on purebred ANG and CHA have shown mixed results regarding the relationship between these breeds and WBSF. Chambaz et al. (2003) and Sinclair et al. (2001) found no significant difference in instrumental texture between breeds when steers were reared to the same IMF% or slaughtered at the same age, respectively. In contrast, Christensen et al. (2011) found a higher WBSF in young purebred ANG compared with young purebred CHA bulls 10 days *post-mortem*. In our study, ANG had lower WBSF than CHA and according to Belew et al. (2003), LL was categorized as tender to intermediate, whereas LL from CHA crossbreeds was categorized as intermediate to tough. This aligns with the notion that early maturing breeds are better suited to extensive systems, while late maturing breeds are more appropriate for intensive systems (Keane and Drennan, 2008). The observed relationship between breeds on WBSF fit the expected negative correlation with IMF% (Lee and Choi, 2019), as ANG crossbreeds had higher IMF% than CHA crossbreeds. This finding is consistent with previous literature, reporting higher IMF% in purebred ANG bulls than purebred CHA bulls of 15 months (Christensen et al., 2011).

Intramuscular fat concentration is known as a strong predictor of eating quality and correlates positively with juiciness, tenderness, flavour, and overall acceptability (Cheng et al., 2015; Corbin et al., 2015; Frank et al., 2016; Savell et al., 1987). Nevertheless, neither juiciness nor the attributes related to texture were significantly different between ANG and CHA crossbreeds. However, Sinclair et al. (2001) reported higher juiciness, beef flavour and overall acceptability of LL from purebred ANG steers compared with LL from purebred CHA steers, with no differentiation on sensory tenderness. Interestingly, Chambaz et al. (2003), who compared purebred steers fattened to 3.25 % IMF, saw no effects of breed on sensory tenderness, flavour intensity or preference, but found that CHA had higher juiciness than ANG. Our results deviate from these findings, possibly due to crossbreeding and the fact that our animals are heifers, whereas the references focus on purebred steers. Our results suggest that CHA and ANG has similar potentials for high meat quality production when sufficiently finished/fattened. In fact, previous research proposes a plateau of 3 % as the minimum amount of IMF to achieve acceptable consumer satisfaction (Miller, 2014; Savell and Cross, 1986). Given that nearly all heifers in our study met or exceeded this threshold, the limited differentiation in sensory quality between ANG and CHA crossbreeds is not surprising.

5. Conclusion

Beef-on-dairy heifers reared on forage and semi-natural grasslands with one or two grazing seasons can deliver high quality beef. Beef from heifers reared under moderately high feeding intensity was less tough and had higher IMF% but was lighter and less red compared with heifers reared under low feed intensity. Beef from ANG crossbreeds was redder with lower WBSF and higher IMF% than CHA. These characteristics are generally associated with superior meat quality. Notably, beef from CHA crossbreeds in production system L was of considerably lower quality, compared to the better-performing ANG crossbreeds and CHA crossbreeds in production system H. While sire breeds differed on some important meat quality traits, meat quality of HOL and SRB crossbreeds was comparable.

6. Implications

This research project provided a Nordic perspective of beef production based on grazing semi-natural grasslands during the summer season and compared offspring from two Swedish dairy breeds. Our results and the production results presented by Hessle et al. (2024) revealed that beef-on-dairy heifers are relevant in extensive beef production systems based on semi-natural grasslands regardless of dam breed, which had minimal impact on final carcass and meat quality. The choice of sire breed may depend on the feeding intensity during winter as Angus, being an early maturing breed, can deliver beef with more intramuscular fat and lower Warner-Bratzler shear force than Charolais in production systems with low as well as moderately high feeding intensities including two or one grazing seasons, respectively. Beef from the production system with low feeding intensity, may require longer ageing time to deliver a similar texture. Finally, it is worth considering the positive impact on environmental impact from the shorter life span of the production system with moderately high feeding intensity, and the positive impact from the two grazing seasons on biodiversity in the production system with low feeding intensity. Yet, the number of grazing seasons depends on the time of birth for the individual heifer. Calves in the average Swedish dairy herd is born continuously through the year (Sverige, 2023). Hence, the optimal production system for a single herd or single heifer groups must be chosen on a farm level.

CRediT authorship contribution statement

Fie F. Drachmann: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Viktoria Olsson:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Karin Wallin:** Writing – review & editing, Methodology, Investigation. **Nicolai F.H. Jensen:** Writing – review & editing, Investigation. **Anders H. Karlsson:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Margrethe Therkildsen:** Writing – review & editing, Supervision, Project administration, Investigation.

Declaration of competing interest

None.

Ethical statement

The protocol and execution of the study was approved by the Ethics Committee on Animal Experiments in Gothenburg, Sweden (ID number 002530).

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