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Doctoral Dissertation

Maiju Pesonen

Luke

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Doctoral programme in the Sustainable Use of Renewable Natural Resources
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# Abstract

Maiju Pesonen

Beef production in Finland is mostly based on dairy breeds. However, the decrease in the dairy cattle population observed in recent years threatens to reduce the level of beef production. Therefore the beef production chain is making heavy investments in suckler cow production. Although the number of beef cows has increased by 20% over the last 10 years in Finland, there is a clear discrepancy between the demand for and supply of domestic beef. Consequently, slaughterhouse pricing favours heavy carcasses and the average carcass weights of slaughtered animals have increased in recent years. The current situation is challenging because the carcass fatness generally increases with higher carcass weights, and in Finland consumers generally favour low-fat products in beef markets.

There is a paucity of information on the effects of the breed on the performance, carcass characteristics and meat quality of beef breed bulls raised to heavy carcass weights, which is a typical Finnish practice. Therefore, the first aim of this thesis was to evaluate the growth performance, carcass traits and meat quality of different beef breeds in the Finnish beef cattle population. The second aim was to evaluate the potential for improvement of carcass and meat quality traits through crossbreeding compared to purebred animals. The third objective was to evaluate carcass fat scores in relation to carcass weights in different breed groups. In addition, the effects of the proportion of concentrates and rapeseed meal (RSM) supplementation on animal performance, carcass characteristics and meat quality parameters were determined for Hereford (Hf) and Charolais (Ch) bulls. To achieve these aims five experiments were carried out.

The objectives of the first experiment, in which Hf and Ch bulls were offered grass silage-based diets, were to determine the effects on the performance, carcass traits and meat quality of the proportion of concentrate in the diet, and the inclusion of RSM in a barley-based concentrate. The two concentrate proportions were 200 and 500 g/kg of dry matter fed with or without RSM. The Ch bulls tended to achieve higher gains, produce less fat, had a higher percentage of meat for highly priced joints and had a lower degree of marbling in their meat compared to the Hf bulls. The dry matter and energy intake, growth performance and carcass conformation improved with increasing concentrate levels. Rapeseed meal supplementation had only limited effects on the performance, carcass traits or meat quality.

The objective of the second experiment was to study performance and meat quality of purebred Hf and Ch bulls and Hf × Ch crossbred bulls which were offered grass silage-grain-based rations and raised to heavy carcass weights. The average slaughter age for all breeds was 565 days and the mean carcass weights for Hf, Hf × Ch and Ch bulls were 414, 476 and 507 kg, respectively. The Ch bulls tended to achieve higher weight gains, produced less fat and had a higher percentage of valuable cuts compared to the Hf bulls. The breed group had no significant effects on the beef flavour, but the tenderness and juiciness were better in the meat of the Hf bulls than that of the Ch bulls. The crossbred Hf × Ch bulls produced heavier and better conformed carcasses compared to pure Hf bulls, which indicates that this type of crossbreeding can enhance beef production under the conditions studied.

The objective of the third experiment was to study the performance, carcass traits and meat quality of purebred Aberdeen Angus (Ab) and Limousin (Li) bulls and Ab × Li crossbred bulls. The average slaughter age for all breeds was 540 days and the mean carcass weights for the Ab, Ab × Li and Li bulls were 391, 399 and 439 kg, respectively. The Li bulls tended to achieve a higher conformation score, produced less fat and had a higher percentage of valuable cuts compared to the Ab bulls. The crossbred Ab × Li bulls produced better conformed carcasses and a higher share of the rounds compared to the pure Ab bulls.

The objective of the fourth experiment was to determine the growth and carcass traits of beef breed bulls and heifers. The data collected from Finnish slaughterhouses included observations of 6 323 and 2 385 Hf (bulls and heifers, respectively), 4 421 and 1 794 Ch, 4 335 and 1 951 Li, 4 068 and 1 692 Ab, 2 151 and 774 Simmental (Si), 344 and 147 Blonde d'Aquitaine (Ba) animals. For estimating valuable cuttings, a separate dataset including 1 112 bulls and 260 heifers in total was also collected. The later maturing, Continental breeds seemed to reach higher carcass gains, produce less fat and have more valuable cuts than the earlier maturing British breeds. The later maturing beef breeds tended to have carcass traits that suit the Finnish beef production system well.

The objective of the fifth experiment was to study the potential for improvement in the gain and carcass traits through Ab × beef breed crossbreeding compared to purebred Ab bulls and through Hereford Hf × beef breed crossbreeding compared to purebred Hf bulls. The data included observations of 8 800 purebred Ab bulls plus Ab × beef breed crosses and 11 815 purebred Hf bulls plus Hf × beef breed crosses. Crossbreeding improved carcass gains and traits compared to purebred Ab and Hf bulls, and production traits improved more by using Continental breeds compared to British breeds.

Overall, Continental breeds tended to have carcass traits that suit the Finnish beef production system well under the current Finnish feeding management approach. On the other hand, British breeds produced more intramuscular fat in the meat and had a higher sensory quality compared to Continental breeds. The carcass traits of British breeds can be enhanced for the current market demand by crossbreeding British breed dams with Continental breeds. The grass silage-grain-based diet suited beef breeds well for growing and finishing diets. The concentrate level can be reduced for British breeds. Continental breeds will benefit from increased concentrate levels in the diet. Protein supplementation does not add any substantial advantages to the diet. Using protein supplements will increase the environmental impacts of beef production.

Keywords: beef production, beef bulls, beef breeds, growth performance, carcass characteristics, meat quality

# Tiivistelmä

Maiju Pesonen

Suomalainen naudanlihantuotanto perustuu maitorotuiseen eläinainekseen. Viime vuosina tapahtunut lypsylehmien lukumäärän väheneminen on vähentänyt naudanlihantuotantoon ohjautuvaa eläinmäärää. Tämän vuoksi suomalainen lihateollisuus on pyrkinyt tavoitteellisesti lisäämään emolehmien lukumäärää, joka onkin lisääntynyt noin 20 % viimeisten 10 vuoden aikana. Tästä huolimatta kotimaista naudanlihaa ei pystytä tuottamaan kulutusta vastaavasti ja vajetta joudutaan paikkaamaan tuontilihalla. Vallitsevan tilanteen seurauksena suomalaiset lihatalot ovat hinnoittelulla ohjanneet naudanlihantuottajia nostamaan nautojen teuraspainoa. Nykyinen tilanne on haasteellinen, koska ruhojen rasvaisuus yleensä lisääntyy teuraspainojen lisääntymisen seurauksena ja suomalaiset kuluttajat puolestaan suosivat vähärasvaisia lihatuotteita.

Työn ensimmäisenä tavoitteena oli tutkia eri lihanautarotujen vaikutuksia kasvuun sekä ruhon ja lihan laatuun, kun eläimet teurastetaan suomalaisiin tuotanto-olosuhteisiin tyypillisissä korkeissa teuraspainoissa. Toisena tavoitteena oli selvittää mahdollisuuksia parantaa tuotantotuloksia ja lihan laatua risteytysten avulla. Kolmas tavoite oli kartoittaa ruhojen rasvoittumista suhteessa teuraspainoon eri liharoduilla. Lisäksi selvitettiin ruokinnan väkirehutason ja valkuaislisän vaikutuksia kasvuun sekä ruhon ja lihan laatuun hereford (hf) ja charolais (ch) sonneilla.

Ensimmäinen osakoe toteutettiin hf- ja ch-rotuisilla sonneilla ja kokeen tavoitteena oli tutkia väkirehutason ja rypsilisän vaikutuksia eläintuotokseen ja lihan laatuun. Kokeen kaksi väkirehutasoa olivat 200 ja 500 g/kg ruokinnan kuiva-aineesta. Molemmilla väkirehutasolla puolet sonneista sai väkirehuna ohraa ja toinen puoli lisäksi rypsirouhetta valkuaislisänä. Ch-sonnit kasvoivat paremmin, niiden ruhot olivat vähärasvaisempia ja niillä arvopalojen osuus leikkuusaannosta oli suurempi hf-sonneihin verrattuna. Toisaalta ch-sonnien liha oli vähemmän marmoroitunutta hf-sonneihin verrattuna. Dieetin väkirehuosuuden lisääminen lisäsi sonnien kuiva-aineen syöntiä, energian saantia, kasvua sekä ruhojen lihakkuutta. Rypsilisä ei vaikuttanut merkitsevästi sonnien kasvu- ja teurasominaisuuksiin eikä lihan laatuun.

Toisen osakokeen tavoitteena oli tutkia hf-, ch- ja hf × ch –risteytyssonnien tuotanto-, teuras- ja lihan laatuominaisuuksia kasvatettaessa eläimet suuriin teuraspainoihin nurmisäilörehuun ja rehuviljaan pohjautuvalla ruokinnalla. Keskimääräinen teurasikä kaikille roduille oli 565 vuorokautta ja toteutuneet teuraspainot hf-, hf × ch- ja ch-sonneille olivat 414, 476 ja 507 kg. Hereford-sonneihin verrattuna ch-sonnit kasvoivat paremmin ja niiden ruhot sisälsivät enemmän arvopaloja ja vähemmän rasvaa. Rotu ei vaikuttanut ulkofileen makuun, mutta hf-sonnien ulkofile sai aistinvaraisessa arvioinnissa paremmat pisteet mureudessa ja mehukkuudessa ch-sonneihin verrattuna. Hf × ch-risteytyssonnit tuottivat painavampia ja paremmin luokittuneita ruhoja kuin puhdasrotuiset hf-sonnit, joten tämän

tyyppisellä risteytyksellä voidaan tehostaa tuotantoa vastaavan tyyppisissä tuotanto-olosuhteissa.

Kolmannen osakokeen tavoitteena oli tutkia Aberdeen angus- (ab), limousin- (li) ja ab × li –risteytyssonnien tuotanto-, teuras- ja lihan laatuominaisuuksia kasvatettaessa eläimet suuriin teuraspainoihin nurmisäilörehu-rehuviljapohjaisella ruokinnalla. Keskimääräinen teurasikä kaikille roduille oli 540 vuorokautta ja toteutuneet teuraspainot ab, ab × li ja li sonneille olivat 391, 399 ja 439 kg. Angus-sonneihin verrattuna li-sonnit tuottivat paremmin luokittuneita ruhoja, jotka sisälsivät enemmän arvopaloja ja vähemmän rasvaa. Angus × li -risteytyssonnit tuottivat paremmin luokittuvia ruhoja puhdasrotuisiin ab-sonneihin verrattuna, joten tämän tyyppisellä risteytyksella voidaan tehostaa tuotantoa vastaavissa tuotanto-olosuhteissa.

Neljännen osakokeen tavoitteena oli tutkia liharotuisten sonnien ja hiehojen kasvu- ja teurasominaisuuksia valtakunnallisen teurasdatan perusteella. Data-aineisto sisälsi yhteensä 6 323 ja 2 385 hf-sonnia ja hiehoa, 4 421 ja 1 794 ch-sonnia ja hiehoa, 4 335 ja 1 951 li-sonnia ja hiehoa, 4 068 ja 1 692 Ab-sonnia ja hiehoa, 2151 ja 774 simmental-sonnia (si) ja hiehoa sekä 344 and 147 blonde d’Aquitaine-sonnia (ba) ja hiehoa. Isojen mannermaisten liharotujen nettokasvut olivat aineistossa paremmat ja ne tuottivat ruhossaan enemmän arvopaloja ja vähemmän rasvaa keskikokoisiin brittiläisiin rotuihin verrattuna. Isot liharodut vaikuttivat tuottavan ruhoja, jotka sopivat teurasominaisuuksiltaan hyvin Suomen markkinoille.

Viidennen osakokeen tavoitteena oli selvittää Suomessa teurastettujen liharotuisten risteytysnautojen kasvu- ja teurasominaisuuksia laajan data-aineiston pohjalta. Angus-sonnien osalta vertailtiin puhtaiksi luokiteltujen ab-eläinten kasvu- ja teurastuloksia ab × hf-, ab × li-, ab × ch-, ab × si- ja ab × ba-risteytyseläimiin. Vastaavat vertailut tehtiin puhtaille hf-sonneille. Risteytys paransi kasvutuloksia ja ruhon laatuominaisuuksia puhtaisiin ab- ja hf-sonneihin verrattuna. Tuotanto-ominaisuudet paranivat eniten käytettäessä risteytyksessä pääterotujen (ch, li, si, ba) sonneja.

Yhteenvetona voidaan todeta, että isot liharodut tuottavat tyypillisessä suomalaisessa tuotantojärjestelmässä ruhoja, jotka sopivat teurasominaisuuksiltaan hyvin Suomessa vallitsevaan markkinatilanteeseen. Toisaalta keskikokoisten brittiläisten rotujen liha oli tutkimuksissa marmoroituneempaa ja se sai paremmat aistinvaraiset arviot kuin isojen rotujen liha. Keskikokoisten rotujen ruhon laatuominaisuuksia voidaan ohjata vallitsevaan markkinatilanteeseen sopivammaksi risteyttämällä keskikokoisten rotujen emot pääterodun sonnilla. Pääterodun sonnit hyötyvät keskikokoista rotua enemmän dieetin väkirehutason nostamisesta. Valkuaislisällä ei saavuteta mitään erityistä hyötyä liharotuisten nautojen loppukasvatuksessa. Sen sijaan valkuaislisän käytöstä luopuminen on tehokas keino vähentää sonnan ja virtsan kautta tapahtuvaa typen eritystä.

Avainsanat: naudanlihantuotanto, liharotu, sonni, kasvu, ruhon laatu, lihan laatu

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# List of original publications

This thesis is based on the following publications:

I Pesonen, M., Honkavaara, M., Kämäräinen, H., Tolonen, T., Jaakkola, M., Virtanen, V. & Huuskonen, A. 2013. Effects of concentrate level and rapeseed meal supplementation on performance, carcass characteristics, meat quality and valuable cuts of Hereford and Charolais bulls offered grass silage-barley-based rations. Agricultural and Food Science 22: 151–167.

II Pesonen, M., Honkavaara, M. & Huuskonen, A. 2013. Production, carcass and meat quality traits of Hereford, Charolais and Hereford × Charolais bulls offered grass silage-grain-based rations and slaughtered at high carcass weights. Acta Agriculturae Scandinavica, Section A – Animal Science 63: 28–38.

III Pesonen, M., Honkavaara, M. & Huuskonen, A. 2012. Effect of breed on production, carcass traits and meat quality of Aberdeen Angus, Limousin and Aberdeen Angus × Limousin bulls offered a grass silage-grain-based diet. Agricultural and Food Science 21: 361–369.

IV Pesonen, M. & Huuskonen, A. 2015. Production, carcass characteristics and valuable cuts of beef breed bulls and heifers in Finnish beef cattle population. Agricultural and Food Science 24: 164–172.

V Pesonen, M. & Huuskonen, A. 2020. Carcass gain, carcass characteristics and valuable cuts of purebred Angus and Hereford bulls versus crossbreds of Angus and Hereford with different beef breeds. Manuscript.



The publications are referred to in the text by their Roman numerals.

All experiments were conducted at the Natural Resources Institute Finland (Luke; formerly MTT Agrifood Research Finland).

# Contribution

The contributions of all the authors to the original articles of this thesis are presented in the following table:

| | I | II | III | IV | V |
|---|---|---|---|---|---|
| Planning the experimentation | MP, AH, MH, HK, VV | MP, AH, MH | MP, AH, MH | MP, AH | MP, AH |
| Data analysis | MP, AH, TT, MJ | MP, AH | MP, AH | MP, AH | MP, AH |
| Calculating and interpreting the results | MP, AH, HK | MP, AH | MP, AH | MP, AH | MP, AH |
| Manuscript preparation | MP, AH, MH, TT, MJ, VV | MP, AH, MH | MP, AH, MH | MP, AH | MP, AH |

MP = Maiju Pesonen, AH = Arto Huuskonen, MH = Markku Honkavaara, HK = Helena Kämäräinen, TT = Tiina Tolonen, MJ = Mari Jaakkola, VV = Vesa Virtanen

# Abbreviations

| | |
|---|---|
| AAT | Amino acids absorbed from the small intestine |
| Ab | Aberdeen angus |
| AIA | Acid insoluble ash |
| ATP | Adenosine triphosphate |
| Ba | Blonde d'Aquitaine |
| Ch | Charolais |
| CLA | Conjugated linoleic acid |
| CP | Crude protein |
| FAME | Fatty acid methyl ester |
| DM | Dry matter |
| DMI | Dry matter intake |
| DOM | Digestible organic matter |
| D value | Digestible organic matter in dry matter |
| Hf | Hereford |
| HCW | Hot carcass weight |
| iNDF | Indigestible neutral detergent fibre |
| IMF | Intramuscular fat |
| L | Low concentrate proportion (200 g/kg dry matter) |
| Li | Limousin |
| LM | *Longissimus* muscle |
| LW | Live weight |
| LWG | Live weight gain |

| | |
|---|---|
| M | Medium concentrate proportion (500 g/kg dry matter) |
| ME | Metabolizable energy |
| MUFA | Monounsaturated fatty acids |
| NDF | Neutral detergent fibre |
| OM | Organic matter |
| PBV | Protein balance in the rumen |
| PUFA | Polyunsaturated fatty acids |
| RDP | Rumen-degradable protein |
| REA | Rib eye area |
| RSM | Rapeseed meal |
| RSM- | Feeding without rapeseed meal supplementation |
| RSM+ | Feeding with rapeseed meal supplementation |
| SFA | Saturated fatty acids |
| SEM | Standard error of the mean |
| Si | Simmental |
| SR | Substitution rate |
| TMR | Total mixed ration |
| WBSF | Warner-Bratzler shear force |
| WHC | Water holding capacity |
| WSC | Water soluble carbohydrates |
| YG | Yield grade |

# Contents

# 1. Introduction

## 1.1. Beef production in Finland

### 1.1.1. Production and consumption

In 2019 there were 857 700 bovines on 9 900 farms in Finland (Luke 2019). In 2017 about 3 350 farms specialized in beef production which is less than 7% of all farms (Niemi & Väre 2018). In 2017 the total amount of beef produced in Finland was 85 million kilograms. The most beef was produced in the North Ostrobothnia and North Savo areas (Luke 2019). The beef consumption in Finland amounted to 106 million kilograms, and on average 19.2 kilograms per capita of beef was consumed (Niemi & Väre 2018). Of the total consumption, 24% comprised imported beef (Niemi & Väre 2018).

Beef production in Finland is mostly based on dairy breeds (Niemi & Väre 2018). On average 80% of the produced beef is of dairy breed origin and only 20% is either from beef breeds or crossbred beef animals. However, the decrease in the dairy cattle population observed in recent years threatens to reduce the level of beef production. The number of dairy cows has decreased from 364 000 (2000) to 262 000 (2019) in 19 years in Finland (Luke 2019). Therefore the beef production chain is attempting to make heavy investments on suckler cow production. The number of beef cows has more than doubled during the 2000s (Niemi & Väre 2018) and there were 60 096 beef cows on 2 162 farms in 2019 (Luke 2019). The average number of beef cows per farm was 28.

Although the number of beef cows has increased by 20% over the last 10 years in Finland (Luke 2019) there is a clear discrepancy between the demand for and supply of domestic beef. While the beef cow herd has increased, it is not sufficient to offset the fall in the dairy cow numbers. Consequently, slaughterhouse pricing favours heavy carcasses and the average carcass weights of slaughtered animals have increased in recent years. In 2017, the average carcass weight (including both dairy and beef breeds) for bulls was 351 kg, while for heifers it was 246 kg and for cows it was 288 kg (Niemi & Väre 2018), while in 1996 the corresponding figures were 275, 204 and 230 kg (Niemi & Alhsted 2014), respectively. The number of bovines slaughtered in 2017 was 274 000, of which 50% were bulls, 30% were cows and 20% were heifers.

Beef cattle producers in Finland can be classified as cow-calf operations or grower or finisher operations (Figure 1). The farms can be fully specialized with one production line, but combinations are also common. The cow-calf or beef cow farms are either seedstock or commercial herds. The grower operations grow mainly dairy breed calves both male and female. The finishing farms are specialized in growing cattle up to slaughter maturity.

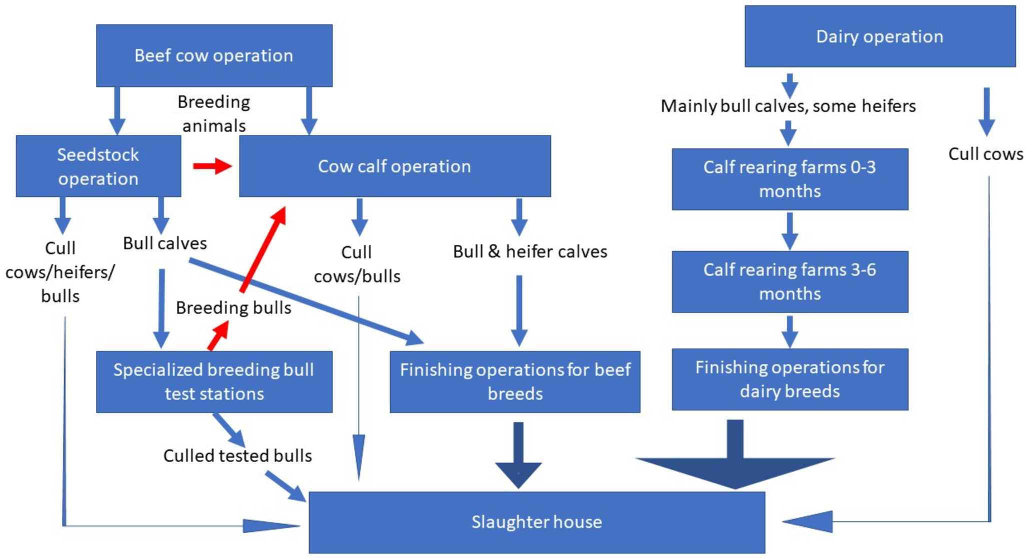


**Figure 1.** The beef production system in Finland. A schematic flow of cattle in the Finnish beef production chain.

The seedstock herds primarily use purebred animals for breeding purposes. Additionally, seedstock herds must take part in the breeding evaluation system. Breeding indexes are counted only for herds which have enlisted in the national breeding scheme. The animals must be weighed at birth, and then at 200 and 365 days of age. In 2017 only 13.5% of the beef cow farms took part in the national breeding evaluation system (Sirkko 2018).

Seedstock producers can grow their animals to market age on the same premises or calves can be sold to a specialized farm for auction marketing. Mainly bull calves are sold to specialized farms after weaning. The female calves are often kept on the farm for further growing. The best female animals are grown as replacement animals and the poorer are sold for slaughter. Seedstock producers use artificial insemination and embryo transplantation for introducing new breeding lines and genetics to the breeding population. Semen and embryos are mainly imported from abroad. In addition, the breeding herds use stud bulls for natural breeding. The main target of the seedstock producers should be to produce and introduce new, profitable genetics to the market. The genetics should produce the best outcome as well grown calves and good quality carcasses for the commercial cow-calf and finisher operations (Tauriainen 2006).

Commercial cow-calf farms produce calves that are targeted towards beef production. In Finland over 80% of the cow-calf farms sell their calves at weaning. The age of the marketed calves is 237 days on average (Susanna Vehkaoja, A-Farmers Ltd., personal communication). The cow-calf farms utilize the genetics which the seedstock have generated. Crossbreeding is used to add value to the sold animals. Terminal breed sired calves are higher priced than maternal breed sired calves (Price listings: A-Farmers Ltd., HKScan Ltd.).

The growing operations are operated in two different stages (Figure 1). In the first stage the animals are under four months of age. In the second stage they are from four months to 6–8 months of age. After the growing stage the animals are finished in a finishing operation, where the animals are grown from the age of six months to 16–19 months of age (Tauriainen 2006).

Basically there are two types of finishing operations (Figure 1). The farms are specialized either in dairy or beef breeds. Farms that have both dairy and beef breed bulls are not very common. Additionally, farms that have specialized only heifer finishing are rare. Heifers are usually grown on the same farms with the bulls. Commonly they are placed in separate buildings.

### 1.1.2. Feeding

Grass silage is the most common forage used in growing cattle diets in temperate regions (Phillips 2010). Additionally, in Finland most of the forage fed to growing and finishing cattle are traditionally based on ensiled mixtures of different grasses such as timothy (*Phleum pratense*), meadow fescue (*Festuca pratensis*), and red clover (*Trifolium pratense*). In general, the energy content of grass silage is higher than that of other silage when cut in the early maturity stage. The energy supply to a ruminant from grass silage is primarily influenced by altering the cutting date of the grass crop (Rinne 2000).

The most common cereal grain fed to beef cattle in Finland is barley (*Hordeum vulgare*) (Huuskonen et al. 2007). Oats (*Avena Sativa*) can be also fed to growing animals instead of barley without any major effects on the animals' performance (Huuskonen 2009a). In Finland, rapeseed meal (RSM) is the most important protein feed used in concentrates for cattle (Huuskonen 2009b). Many beef producers use protein supplements with grass silage-grain based feed in Finland even though the price of RSM is high compared to grain or forage and feeding supplementary protein increases the N and P excretion into manure (Klopfenstein & Erickson 2002, Huuskonen 2009a, Huuskonen et al. 2014a). The concentrate proportion in Finnish growing cattle diets is commonly around 400–600 g/kg dry matter (DM). Total mixed ration (TMR) feeding is the most common way of supplying the diet to growing cattle (Tauriainen 2006).

Feeding growing cattle is commonly practiced using two types of diets: forage- or grain-based diets. These practices can be combined depending on the availability of feed resources, as well as the purpose of the production system and the nutritive characteristics of the feed. Generally, forage-based diets provide more protein, while grain-based diets provide more energy (Ponnampalam et al. 2016). Although feedlot finishing is a standard practice in many countries with high grain diets, there is clear evidence that finishing on forage-based diets may provide benefits and offers a worthy alternative producing healthier beef (Vahnami et al. 2015, Huuskonen et al. 2016a,b). There are several points which should be considered when converting plant and other feed resources to animal products. Firstly, there should be a benefit for the producer and processor. Secondly, the product, in this case beef, should meet consumer needs in terms of human health (e.g. low fat, high protein) and eating quality (flavour, taste and tenderness). In some markets, the later has received increasing attention (Scollan et al. 2006, Daley et al. 2010).

The effects of both the concentrate level and protein supplementation have been extensively studied in growing cattle diets. It is established that good quality silage can support high levels of performance with moderate concentrate supplementation (200-400 g/kg DM) (e.g. Huuskonen et al. 2007, Randby et al. 2010). Silage digestibility is one of the most important factors when using grass-silage-based diets. Keady et al. (2013) concluded that overall each 10 g/kg increase in grass silage digestibility increases the carcass gain by 24 g/d. Each 10 g/kg decline in the digestibility of grass silage requires an additional 0.4 kg DM concentrate daily to sustain performance in finishing cattle (Keady et al. 2013).

Proteins in feed can be classified as complete or incomplete depending on their amino acid availability. Optimizing the dietary protein in animal production is essential to maximize the muscle productivity (Ponnampalam et al. 2016). In growing animals improved muscle gains are accompanied by an increase in both whole body (Lobley 1993) and muscle protein synthesis (Dawson et al. 1991). The influence of dietary protein on animal performance is always interrelated with the energy content of the diet. Ruminants obtain a significant amount of protein from forage (Ponnampalam et al. 2016). If the nutritive characteristic of the forage is inadequate or the production potential of the animals is high, producers tend to feed protein-rich concentrates to match the nutrient requirement of the animals (Dixon & Stockdale 1999, Huuskonen 2009a). With dairy bulls it has been concluded that concentrates with a higher protein concentration than barley grain is not needed when the animals are fed high- or medium-digestibility and restrictively fermented grass silage and barley-based concentrate (Huuskonen et al. 2007, 2008, Huuskonen 2009a, 2011).

### 1.1.3. Beef breeds

In total, 12 beef breeds are currently kept in Finland, and Aberdeen Angus (Ab), Blonde d'Aquitaine (Ba), Charolais (Ch), Hereford (Hf), Limousin (Li) and Simmental (Si) are the six most common breeds. Beef breeds can be classified by their growth rate in two different classes so that Ab and Hf are classified as early maturing and Ba, Ch, Li and Si as late maturing breeds (Phillips 2010).

Black hided, naturally polled Ab cattle are recognized for their moderate size, early puberty and maturation (Phillips 2010). Ab cattle are often noted to have good fleshing ability, meaning that they put weight and subcutaneous fat on easily without as much feed energy compared to some other breeds. They can produce carcasses with an average size at a relatively short 15–16 months slaughter age. Additionally they often produce more intramuscular fat (IMF) than other beef breeds in Europe (Phillips 2010). The Ab breed animals in Finnish beef production account for around 18% of the beef breeds (Finnish Food Authority 2019).

Hereford cattle have reddish-brown bodies with distinctive white faces, bellies and switches. They are known for their quiet dispositions and hardiness (Phillips 2010). The Hf breed matures relatively early and can produce average size carcasses with a relatively good amount of subcutaneous fat. They can be finished off at pasture at about 18 months of age (Phillips 2010). The Hf breed animals in Finnish beef production account for around 23% of the beef breeds (Finnish Food Authority 2019).

Three strains of cattle comprise the Ba breed. These are the Garonnais strain, the Quercy, and the Blonde des Pyrenees (Dudouet 2010). Blonde d'Aquitaine are light cream or white coloured cattle and are known for their good growth with an excellent feed conversion ratio. The beef production level of the Ba breed is high. The breed produces carcasses with a high percentage of lean meat with minimum or no subcutaneous fat (Dudouet 2010). The average daily gain for Ba breed bulls in intensive feeding systems between 6–12 months of age is 1 400–1 500 g/d. The recommended slaughter age for Ba bulls is 14–16 months in French production system (Dudouet 2010). The Ba suits crossbreeding with other beef breeds or with dairy breeds particularly well (Dudouet 2010, Huuskonen et al. 2014b). The number of Ba breed animals in Finnish beef production is around 5% of the beef breeds nationwide (Finnish Food Authority 2019). The Ba animals are mainly crossbred cattle either with other beef breeds or dairy breeds in Finland.

Charolais cattle are solid white or cream coloured, large framed animals with heavy muscling (Phillips 2010). Their skin is light brown some resistance against sunburn. The Ch breed is known for its rapid growth rate, even though they are slower to mature than the other beef breeds. They produce large and lean carcasses. This breed is an efficient converter of high-energy feed into beef. The potential to grow to a large size suits modern beef industry demands. They are most suited to fattening with some supplementary feed (Dudouet 2010, Phillips 2010). The average daily gain for Ch bulls in intensive feeding systems between 6–12 months of age is 1 450–1 550 g/d. The recommended slaughter age for bulls is 14–16 months in French production systems (Dudouet 2010). The number of Ch breed cattle in Finland is around 14% of the beef breeds (Finnish Food Authority 2019).

Limousin cattle are reddish-brown, heavily muscular and light boned animals (Phillips 2010). This breed can produce lean carcasses with a low level of subcutaneous fat in a variety of environments while growing rapidly and utilizing feed efficiently (Dudouet 2010, Phillips 2010). Limousin cattle are smaller than the other major continental breeds. They are particularly suited as a crossing sire as the calves are relatively small at birth and there are very few calving difficulties (Phillips 2010). The average daily gain for Li breed bulls in intensive feeding systems between 6–12 months of age is 1 400–1 500 g/d. The recommended slaughter age for Li bulls is 14–16 months in French production systems and Li carcasses fulfil the French meat industry demands well. The sensory quality of Li beef is best when animals are slaughtered between 9–10 months of age. Limousin beef is particularly known for its tenderness (Dudouet 2010). The Li breed in Finland accounts around 15% of the beef breeds (Finnish Food Authority 2019).

Simmental is one of the most popular dual-purpose cattle breeds for milk and meat production (Phillips 2010). The Si is recognized as the heaviest milker of all commonly used beef breeds. The high milk production ability results in large calves at weaning. The growth continues as the animals mature allowing Si animals to produce large and lean carcasses (Phillips 2010). Simmental breed cattle in Finland account for around 12% of the beef breeds (Finnish Food Authority 2019). There are also several other beef breeds in Finland such as Dexter, Galloway, Highland Cattle, Texas Longhorn and Piemontese. The number of animals in these breeds is relatively low (Finnish Food Authority 2019).

The choice for a breed depends not only on the growth performance and carcass characteristics but also on the other aspects affecting the beef production. Maximizing the profit potential in beef production usually requires matching the genetic potential of the animals with the available resources. The genetic potential of milk yields differs between breeds and greatly influences several important production traits, e.g. calf performance, dams' nutritional needs and rebreeding rates (Mallinckrodt et al. 1993). The maternal ability of beef cows has been shown to be a critical component of pre-weaning growth in their calves (Fiss & Wilton 1993, Mallinckrodt et al. 1993). The weaning weight affects the profit potential of the beef herd, especially when selling beef calves (Miller et al. 1999).

British beef breeds (Ab and Hf) and their crossbreeds are often used as dam breeds in beef production. Their hardiness, robustness and good maternal ability have been shown in numerous experimental settings, especially in challenging production environments (Nuñez-Dominguez et al. 1991, Davis et al. 1994, Arango et al. 2002). British beef breed cows tend to be lighter, their diet energy demand is less, and their body condition score is more stable than breeds of European Continental origin (Ch, Li, Si, Ba) (Freetly et al. 2001, Arango et al. 2002). In addition, the lifetime productivity measured by the number of matings per cow, calves weaned per cow and calf weight weaned per cow was significantly higher for Ab × Hf crossbred dams than for other straight breeds or crossbreds in extensive cow-calf production systems (Davis et al. 1994). Additionally, Nuñez-Dominguez et al. (1991) reported positive breed effects for Ab and Hf breeds and their crosses for calf survival rates and the durability of dam dentation. Davis et al. (1994) concluded that for northern range production systems, breed groups of a moderate mature size and moderate milk production were more profitable than more extreme types for growth and milk production. However, the demand for high carcass weights in Finland is pronounced, and early maturing British breeds create challenges when aiming for heavy and lean carcasses.

### 1.1.4. Crossbreeding

The reason for crossbreeding different breeds or lines is to compliment breed traits to achieve an efficient and applicable set of traits for a particular use. Heterosis is a beneficial result of crossbreeding different breeds. Heterosis is expressed especially in less heritable traits such as fertility (Gregory & Cundiff 1980, Gregory et al. 1992, Legarra et al. 2007). Heterosis is expressed in more challenging environments and when breeds of different biological types are crossed compared to two breeds within the same biological group (Herring 2014).

The foundation of a crossbreeding programme should be the choice of parental breeds or types. It should be taken into account that the heritability traits differ and the level of heterosis is expressed differently in different traits (Herring 2014). There are distinct advantages that crossbreeding strategies offer over purebred strategies: 1) the ability to blend desirable breed characteristics, 2) the more desirable performance of crossbred animals relative to the average of the purebred parental types (heterosis or hybrid vigour) and 3) the ability to use specialized sire or dam parental types, referred to as complementary (Herring 2014). In meat production, reasons for crossbreeding include crossing of breeds or specialized sire and dam lines that are of high genetic merit in different traits to increase the efficiency of a production system (Mortimer & Przybylski 2016). Enhancing production traits in beef producing animals can include more suitable carcass traits (Herring 2014) or/and better beef quality (Mortimer & Przybylski 2016). The expected gain to be achieved in growth traits is 4–10% more growth and on average 5% gain in carcass traits (Lawrence et al. 2012).

Crossbreeding systems are referred to as terminal, continuous, rotational and combination systems (Herring 2014). The cross is a terminal when no replacements are produced as the progeny is genetically different from both parental types. Terminal systems have the potential to produce the highest possible levels of heterosis and the maximum potential to utilize specialized parental types. Rotational systems use two or more parental types. Rotational systems can be used for replacement heifer production (Herring 2014).

The early maturing British breeds are particularly useful for finishing on grass. These breeds are found in all areas of the world with extensive grassland production systems. During the course of the twentieth century, it has become increasingly common to feed cattle on cereal grains, particularly maize and barley, in feedlots (Price 2017). The moderately to high propensity of British cattle to fatten meant that their carcasses were either too fat at the appropriate weight or too light at the appropriate fat level. Larger bodied, more heavily muscled and lower propensity to fatten Continental breeds can be used to enhance the growth potential, feed efficiency and carcass traits when increasing the concentrate proportion of the diet and aiming for higher carcass weights (Price 2017).

There are no statistics available on the level of systematic crossbreeding in Finland. The slaughterhouses recommend production herds to use crossbreeding as an effective production level enhancing tool. The recommended crossbreeding system is rotational crossbreeding for maternal breeds e.g. Ab, Hf or Si for crossbred dam cows. Terminal breed sires e.g. Ch or Li are used for two or three crossbred dams to get three breed crosses for efficient growth and good quality carcass production (Vehkaoja et al. 2007).

## 1.1.5. Challenges in carcass and meat quality

The carcass composition largely determines the carcass value. A high proportion of muscle with an optimum level of fat dictated by local consumer preferences represents a superior carcass. The current situation in Finland is challenging because carcass fatness generally increases with a higher carcass weight (Keane & Allen 1998) and market demand in Finland concerning carcass fat is different from beef markets where marbled beef is favoured (Herva et al. 2011). In Finland, consumers generally favour low-fat products in beef markets. Over the years the beef industry has stated that optimally two thirds of the carcasses would have a EUROP fat score of 2 and one third a EUROP fat score of 3 (Herva 2015). Lean carcasses are favoured for setting prices. There are penalties for carcasses under 320 kg with fat scores 3–5 and carcasses over 320 kg with fat scores 4–5 (Herva 2015). Up to 2018 carcasses had been classified in Finland for their fat cover degree using the EUROP classification range from 1 to 5 (1: low, 2: slight, 3: average, 4: high, 5: very high). From 2019 onwards each level of the fat cover scale was subdivided into three sub-classes (e.g. 3+, 3, 3-).

Differences between individual beef breeds in growth performance and carcass traits have been extensively evaluated in multiple earlier studies for example by Bartoň et al. (2006), Bureš et al. (2006), Cuvelier et al. (2006a,b), Alberti et al. (2008) and Kaminiecki et al. (2009) to mention a few. In addition, numerous research reports have been published comparing the performance of different sire breeds in crossbreeding trials for example in Great Britain (Kempster et al. 1982, 1988), Scandinavia (Aass & Vangen 1998), the Czech Republic (Šubrt et al. 1999, Polách et al. 2004) and the USA (Koch et al. 1982, Wheeler et al. 1996). However, the number of experimental animals is often limited when growth and carcass characteristics of different breed groups are compared. There is also a paucity of information on the effects of breed and crossbreeding on the performance, carcass traits and meat quality of beef breed bulls raised to heavy carcass weights with grass silage-grain-based rations, which is a typical practice in Finnish production systems.

In Finland, the solution chosen to maintain beef output has been to increase carcass weights. However, increasing carcass weights with the current breed distribution is not desirable. Beef carcasses are already adequately fat or over-fat at existing carcass weights (Herva et al. 2011). It has also been stated that increased carcass size and reduced carcass numbers have the potential to increase sustainability by producing a greater amount of beef using the same amount of resources (Bunting 2015). However, the biological fact is that feed efficiency in beef production decreases with prolonged growing periods due to increased maintenance energy requirements and increased fatness (e.g. Manni et al. 2013, Herring 2014). One approach to increase carcass weights without a subsequent increase in fatness could be a change in the breed distribution. Increasing the animal size has been the method used to combat reduced cattle numbers also in the USA (Kay 2012). Nevertheless, high carcass weights are challenging for beef markets because the valuable cut size becomes inadequately large (Leick et al. 2012, Maples et al. 2016, Boykin et al. 2017).

The beef industry is facing a changing marketplace, with evolving consumer demands and competition from emerging and alternative sources of protein (Bonny et al. 2015). The beef industry must become more consumer-focused, moving away from a commodity type product, traded solely on price (Bonny et al. 2018). A consumer's eating experience is one of the biggest determinants of repeat purchase intent. Repeat purchases are vital to maintaining and growing the market share for the beef industry (Morgan et al. 1991). Inconsistent product quality may negatively affect beef demand and returns for the beef industry (Schroeder & Mark 2000). The risk of consumers having negative eating experiences with beef is moderately high in Europe (Bonny et al. 2017a). Bonny et al. (2017b) found that the chances of consumers having unsatisfactory eating experiences was 26%, though this varied by cut and cooking method. Consumers' surveys have suggested that there is willingness to pay for better quality beef (Bonny et al. 2017a). The European carcass classification system does not have a relationship with eating quality (Guzek et al. 2013, Bonny et al. 2016). There would be a beneficial effect on the production chain profitability if the beef eating quality would be considered in the beef pricing (Bonny et al. 2018).

The beef eating quality is influenced by the gender of the animal (Boccard et al. 1979, Seideman et al. 1989, Chriki et al. 2013). In the European Union bulls are an important production class (De Roest 2015). Bulls have been demonstrated to have a slightly lower eating quality compared to females after correction to other carcass measurements (Bonny et al. 2016). British breeds have been shown to enhance the tenderness traits over the Continental breeds under carefully controlled conditions (Wheeler et al. 2005). However, these stated comparisons in meat tenderness and eating quality are difficult to interpret. The differences in eating quality between breeds are generally not significant if the animals are slaughtered at the same physiological stage of maturity, aging and if the processing is carried out similarly (Renand 1988, Dransfield et al. 2003).

Meat eating quality traits are moderate to low heritable traits. Hocquette et al. (2006) reported heritability coefficients ($h^2$) of 0.24, 0.11 and 0.09 for tenderness, juiciness and flavour scores, respectively. Phenotypic traits such as IMF, carcass weight and ossification scores have a large impact on the palatability score in the Australian MSA-system. The carcass weight and ossification score combined together form a proxy for the growth rate (Watson et al. 2008). The growth rate and IMF have higher heritability ($h^2$ 0.25 and 0.50, respectively) compared to straight meat-eating quality traits (Shackelford et al. 1994). However, selection on the bases of IMF should consider the carcass fatness. There is a positive genetic correlation between marbling and carcass fatness (Hocquette et al. 2006). New genomic tools might provide solutions for enhancing meat eating quality equally despite the breed effect (Picard et al. 2015). Eating quality can be improved indirectly through targeted breeding programmes but they should be carefully planned for specific markets.

## 1.2. Objectives and hypotheses of the study

There is a paucity of information on the effects of breed on the performance, carcass characteristics and meat quality traits of beef breed bulls raised to heavy carcass weights on grass silage-based diets, which is a typical Finnish practice. Therefore, the first objective of this thesis was to evaluate growth performance, carcass traits and meat quality of different beef breeds in Finnish beef cattle population. The second objective was to evaluate the potential for improvement of carcass and meat quality traits through crossbreeding compared to purebred beef breed animals. The third objective was to evaluate carcass fat scores in relation to carcass weights in different breed groups. In addition, the effects of concentrate proportion and RSM supplementation on animal performance, carcass characteristics and meat quality parameters were determined when Hf and Ch bulls were slaughtered at typical Finnish carcass weights on grass silage-based diet.

It was hypothesized that:

1. The later maturing Continental beef breeds would have a higher growth performance, produce less fat and have more valuable cuts compared to the earlier maturing British breeds.
2. The crossbred British × Continental bulls have a higher growth rate and they produce better conformed carcasses with a higher proportion of valuable cuts compared to purebred British bulls, so this type of crossbreeding can enhance beef production under typical Finnish production conditions.
3. Continental breeds are classified in lower fat score classes compared to British breeds of the same carcass weight. By using Continental breed bulls it is possible to achieve 400–500 kg carcass weights with EUROP fat scores of 2–3.
4. British breeds produce more IMF into the meat and produce higher eating quality meat compared to the Continental breeds.
5. Using British × Continental crossbreeding improves the meat eating quality compared to purebred Continental breeds.
6. The growth performance and carcass conformation of beef breed bulls will improve with increasing concentrate levels on grass silage-based diets.
7. The concentrate level has only minor effects on meat quality in a grass silage-based diet.
8. There is no benefit of using RSM supplementation for growing beef bulls fed a typical Finnish grass silage-barley-based diet.

# 2. Materials and methods

The data for this thesis derives from one experiment that was performed in the experimental barn of the Natural Resources Institute Finland (Luke, previously MTT Agrifood Research Finland) (publication I) and two experiments that were conducted on the affiliated farm of Luke (publications II and III). In addition, extensive data material used for studying growth performance, carcass traits and valuable cuts was collected from four Finnish slaughterhouses (publications IV and V). The experimental procedures are described in detail in publications I–V. A short summary is presented here.

## 2.1. Housing, animals, diets and experimental designs

In the first experiment (I) the bulls were placed in an insulated barn in adjacent tie-stalls and fed individually. In experiments II and III the bulls were housed in pens in an uninsulated barn with straw bedding.

The first experiment was performed in 2008–2011 and included three feeding trials. The objectives of this experiment with growing Hf and Ch bulls were to determine the effects on animal performance, carcass characteristics, valuable cuts, meat quality parameters and fatty acid composition of the *Longissimus muscle* (LM) of (1) the proportion of concentrate in the diet, and (2) the inclusion of RSM in the barley-based concentrate fed in TMR when animals are slaughtered at typical Finnish carcass weights. The first trial started in December 2008, the second in January 2010 and the third in January 2011. The three feeding trials comprised 48 purebred Hf bulls and 48 purebred Ch bulls in total. The diet *in vivo* digestibility, animal performance (intake and gain) and carcass characteristics (carcass weight, dressing proportion, conformation score and fat score) were determined in all three trials. The meat quality parameters and valuable cuts were measured in the second and third trial. All the animals had an initial live weight (LW) 306±97.9 kg (Hf) and 333±63.1 kg (Ch) on average and were spring-born calves purchased from commercial suckler herds. During the feeding experiment the bulls were fed a TMR *ad libitum*. Both Hf and Ch bulls were randomly allotted to the experimental feeding treatments. The two concentrate proportions were 200 (L) and 500 (M) g/kg DM, fed without RSM (RSM−) or with RSM (RSM+). The concentrate used was rolled barley. Rapeseed meal was given so that the crude protein (CP) content of the concentrate was raised to 160 g/kg DM in the RSM+ diets. Therefore the amount of RSM supplement depended on the CP content of the barley which was measured by chemical analyses. In the RSM− diets the average CP content of the concentrate was 126 g/kg DM, so the content increased 27% with RSM supplementation.

The second experiment (II) was performed in 2009–2010. The objective of this experiment was to study the growth, carcass characteristics, valuable cuts and meat quality parameters of purebred Hf and Ch bulls and Hf × Ch crossbred bulls, and to evaluate the potential for improvement in the carcass and meat quality through this type of crossbreeding compared to purebred Hf bulls. In total, the experiment included 8 Hf bulls, 8 Ch bulls and 8 Hf × Ch crossbred bulls. All animals had an initial LW of 254±27.9 kg (Hf), 289±67.4 (Hf × Ch) and 312±50.3 kg (Ch) and were spring-born calves purchased from commercial suckler herds. The animals were offered grass silage *ad libitum* and a mixture of rolled barley and oats (1:1 on DM basis). The target for the average concentrate level during the experiment was 400 g/kg DM.

The third experiment (III) was performed in 2010–2011. The objective of this experiment was to study the growth, carcass characteristics, valuable cuts and meat quality parameters of purebred Ab and Li bulls and Ab × Li crossbred bulls, and to evaluate the potential for improvement in the carcass and meat quality through this type of crossbreeding compared to purebred Ab bulls. In total the experiment included 8 Ab bulls, 8 Li bulls and 8 Ab × Li crossbred bulls. The animals had an initial LW of 285±38.0 kg (Ab), 276±36.8 (Ab × Li) and 325±18.7 kg (Li) and were spring-born calves purchased from commercial suckler herds. The animals were fed in the same manner as in the second experiment. In addition, in experiments I–III the daily concentrate ration included 150 g of a mineral mixture (150 g/head/day). Additionally, a weekly vitamin mixture of 50 g/animal was given.

In experiment IV the main objective was to study the growth and carcass traits of beef breed bulls and heifers in Finnish beef cattle population. The second objective was to evaluate the carcass fat score in relation to the carcass weight in different breed groups. Data collected from Finnish slaughterhouses included observations of 6 323 and 2 385 Hf (bulls and heifers, respectively), 4 421 and 1 794 Ch, 4 335 and 1 951 Li, 4 068 and 1 692 Ab, 2 151 and 774 Si, 344 and 147 Ba animals. For estimating valuable cuttings, a separate dataset including in total 1 112 bulls and 260 heifers was also collected.

In experiment V the objective was to study the potential for improvement in the growth and carcass characteristics through Ab × beef breed crossbreeding compared to purebred Ab bulls and through Hf × beef breed crossbreeding compared to purebred Hf bulls. The data collected from Finnish slaughterhouses included observations of 8 800 purebred Ab bulls plus Ab × beef breed crosses and 11 815 purebred Hf bulls plus Hf × beef breed crosses. For estimating valuable cuttings, a separate dataset including 771 bulls in total was also collected. A summary of experiments I–V is presented in Table 1.

**Table 1.** Summary of the experiments I-V.

| Paper | Number of animals | Breed / sex | Carcass weight, kg | Slaughter age, d | Diet |
|---|---|---|---|---|---|
| I | 11 | Hf / bulls | 375 | 551 | L RSM- |
| I | 12 | Hf / bulls | 383 | 550 | L RSM+ |
| I | 12 | Hf / bulls | 382 | 505 | M RSM- |
| I | 11 | Hf / bulls | 402 | 522 | M RSM+ |
| I | 11 | Ch / bulls | 406 | 531 | L RSM- |
| I | 12 | Ch / bulls | 418 | 537 | L RSM+ |
| I | 11 | Ch / bulls | 438 | 501 | M RSM- |
| I | 10 | Ch / bulls | 439 | 494 | M RSM + |
| II | 8 | Hf / bulls | 414 | 561 | Grass silage *ad libitum* + rolled barley and oats |
| II | 8 | Hf × Ch / bulls | 476 | 568 | |
| II | 8 | Ch / bulls | 507 | 569 | |
| III | 8 | Ab / bulls | 391 | 526 | Grass silage *ad libitum* + rolled barley and oats |
| III | 8 | Ab × Li / bulls | 399 | 547 | |
| III | 8 | Li / bulls | 439 | 561 | |
| IV | 4 068 | Ab / bulls | 368 | 571 | Data collected from Finnish slaughterhouses, diet information not available |
| IV | 344 | Ba / bulls | 393 | 570 | |
| IV | 4 421 | Ch / bulls | 413 | 552 | |
| IV | 6 323 | Hf / bulls | 368 | 572 | |
| IV | 4 335 | Li / bulls | 391 | 571 | |
| IV | 2 152 | Si / bulls | 402 | 565 | |
| IV | 1 692 | Ab / heifers | 233 | 458 | |
| IV | 147 | Ba / heifers | 252 | 475 | |
| IV | 1 794 | Ch / heifers | 255 | 451 | |
| IV | 2 385 | Hf / heifers | 232 | 465 | |
| IV | 1 951 | Li / heifers | 250 | 469 | |
| IV | 774 | Si / heifers | 244 | 453 | |
| V | 4 068 | Ab / bulls | 368 | 571 | Data collected from Finnish slaughterhouses, diet information not available |
| V | 6 323 | Hf / bulls | 368 | 572 | |
| V | 127 | Ab × Ba / bulls | 384 | 572 | |
| V | 1 018 | Ab × Ch / bulls | 400 | 567 | |
| V | 1 483 | Ab × Hf / bulls | 384 | 571 | |
| V | 1 299 | Ab × Li / bulls | 383 | 572 | |
| V | 805 | Ab × Si / bulls | 396 | 566 | |
| V | 240 | Hf × Ba / bulls | 383 | 572 | |
| V | 1 392 | Hf × Ch / bulls | 402 | 565 | |
| V | 1 344 | Hf × Li / bulls | 387 | 574 | |
| V | 1 033 | Hf × Si / bulls | 393 | 570 | |

L = low concentrate proportion (200 g/kg DM); M = medium concentrate proportion (500 g/kg DM); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

## 2.2. Experimental measurements and calculations (I-III)

In experiments I-III silage samples were analysed for DM, ash, CP, neutral detergent fibre (NDF), digestible organic matter (DOM) in DM (D value) and fermentation quality (pH, water-soluble carbohydrates (WSC), lactic and formic acids, volatile fatty acids, soluble and ammonia-N content of N). In addition, ether extract, indigestible NDF (iNDF) and starch were analysed in I. Concentrate samples were analysed for DM, ash, CP and NDF in I-III. Additionally, ether extract, iNDF and starch were analysed in I. The methods of analysis are described in detail in publications I-III. In experiment I, the diet digestibility was estimated using acid insoluble ash (AIA) as an internal marker (Van Keulen & Young 1977). In experiments I-III the metabolizable energy (ME) concentrations as well as the values of amino acids absorbed from the small intestine (AAT) and the protein balance in the rumen (PBV) were calculated according to Finnish Feed Tables (Luke 2020) and are described in detail in publications I-III.

In experiments I-III the animals were weighed on two consecutive days at the beginning of the experiment and before slaughter. The live weight gain (LWG) was calculated as the difference between the means of initial and final weights. The dressing proportion, carcass conformation and carcass fat scores were determined according to the EUROP classification (EC 2006).

Meat quality measurements were taken in experiments I-III. After classification, the carcasses were chilled overnight below 7 °C. One day after slaughter the right side of carcasses were commercially cut. Primal cuts included the forequarter, back, side and round. The right side of each carcass was cut into valuable cuts [outside round (*Musculus semitendinosus*), inside round (*Musculus semimembranosus*), corner round (*Musculus quadriceps femoris*), roast beef (*Musculus gluteus medius*), tenderloin (*Musculus psoas major*), loin (*Musculus longissimus lumborum*) and entrecote (*Musculus longissimus thoracis*)], subcutaneous fat and bones.

The marbling score of entrecote (at the 7th rib) and loin (at the 1st lumbar vertebra) were evaluated using a six-point scale (0=devoid to 5=abundant). The pH-value of the loin was measured with a Knick 651 instrument with an Inlab Solid electrode (Mettler Toledo) at the level of the 1st lumbar vertebra. The meat colour of the loin was measured after a bloom time of half an hour with a Minolta Cr-200 handheld chroma meter (Minolta Camera Co., Ltd., Osaka, Japan).

During cutting, a 2 kg loin sample was taken and vacuum packed. These samples were sent to the Finnish Meat Research Institute for further analyses. The total ageing time of the samples was 8 days at 4 °C. Thereafter the samples were analysed for drip loss, moisture, protein and fat concentrations, Warner-Bratzler shear force and for tenderness, juiciness and beef flavour (sensory analysis) using standard methods which are described in detail in publications I-III. In experiment I fatty acids were extracted from the loin samples according to a slightly modified AOAC standard method (AOAC 2002).

## 2.3. Slaughter datasets and analysis (IV-V)

The dataset used for studying the growth and carcass characteristics was collected from four Finnish slaughterhouses (Atria Ltd., Seinäjoki, Finland; HK-Agri Ltd., Turku, Finland; Saarioinen Lihanjalostus Ltd., Tampere, Finland, and Snellman Lihanjalostus Ltd., Pietarsaari, Finland). These slaughterhouses are major meat companies in Finland, which, as a part of their business operations, transfer calves from dairy farms, or suckler cow herds, to co-operating farms for fattening prior to slaughter. The raw slaughter data for each animal included an individual animal identification number on the ear tag, date of birth, date of slaughter, sex, carcass weight, carcass conformation score (EUROP) and carcass fat score (EUROP). Identities of breeds (dam and sire breed) were collected from the National Animal Identification Register for Cattle (ProAgria Agricultural Data Processing Centre, Vantaa, Finland). The slaughtering data and identities of breeds for individual animals were linked through individual animal identification numbers.

In experiment IV all purebred Ab, Ba, Ch, Hf, Li and Si bulls aged 365–730 days old and heifers aged 240–600 days old which were slaughtered by the above-mentioned slaughterhouses during 2009–2011 were selected for the study. In experiment V all purebred Ab and Hf bulls as well Ab × beef breed and Hf × beef breed crossbred bulls aged 365–730 days old and slaughtered by the above-mentioned slaughterhouses in 2009–2011 were selected for the study. In all the slaughterhouses the carcasses were weighed hot after slaughter and the cold carcass weight was estimated as 0.98 of the hot carcass weight. The carcasses were classified for conformation and fatness using the EUROP quality classification (EC 2006).

The birth weight assumptions used in the calculations were adopted from Åkerlind et al. (2011). The birth carcass weight was assumed to be 0.4 × birth weight since the same value is used by Atria Ltd. in their daily extension work (Herva et al. 2009, 2011). An estimated daily carcass gain was calculated by subtracting the birth carcass weight from the reported slaughter weight and dividing the result by the age at slaughter.

For estimating valuable cuttings for the studied breeds a separate sub-dataset was collected during 2010–2011 from Snellman Lihanjalostus Ltd. In addition to the above-mentioned variables, this dataset also included information on commercial cuttings. After classification, the carcasses were chilled overnight below 7 °C. On the day after slaughter the carcasses were commercially cut. Each carcass was cut into valuable cuts [outside round (*Musculus semitendinosus*), inside round (*Musculus semimembranosus*), corner round (*Musculus quadriceps femoris*), roast beef (*Musculus gluteus medius*), tenderloin (*Musculus psoas major*) and loin (*Musculus longissimus*)] and tallow (subcutaneous fat). All these cuttings were weighed automatically in the slaughter line and their yields were expressed as percentages of the cold carcass weight (0.98 × hot carcass weight, 50 min *post-mortem*).

## 2.4. Statistical procedures

The statistical analyses were performed using the SAS/MIXED (I, II, IV, V) and SAS/GLM (III) procedures (SAS 1999). Using the SAS/GLM procedure, the error term for each comparison had to be defined by the user as well as when the standard error of the mean (SEM) was calculated. The results were expressed as least square means with the SEM. The normality of residuals was checked for each analysis using graphical methods including a box plot and scatter plot of residuals and fitted values. In experiment I the results were analysed for all three trials (the results of meat quality and valuable cuts were analysed for two trials). For parameters that were measured several times per individual (loin samples for their shear force and the sensory analysis in experiments I, II and III) all repeated measures on an animal were summarized, and the average was used for the statistics (one single value per animal). The data collected from Finnish slaughterhouses (IV, V) was analysed, so that the effect of the slaughterhouse location was not taken into consideration in the final statistical model because the effect was quantitatively minimal and of no importance from a practical point of view. In all publications *P*-values less than 0.05 were reported as statistically significant. In addition, when a *P*-value of around 0.10 was obtained it was discussed in the text.

# 3. Results and discussion

## 3.1. Effects of breed

### 3.1.1. Growth performance and slaughter age

In all experiments I-V, the Continental breeds (Ba, Ch, Li, Si) were observed to be superior in growth performance compared to British breeds (Ab, Hf) (Figure 2), which is in agreement with several previous experiments (Gregory et al. 1994, Wulf et al. 1996, Barton & Pleasants 1997, Crump et al. 1997, Laborde et al. 2001, Sami et al. 2004, Alberti et al. 2008, Williams et al. 2010). Different biological types of breed differ in their size and composition in the foetal period of life (Mao et al. 2008). This difference in the breeds continues till the later period of an animal's production. The different breeds differ in their growth rates and size at maturity. Thus, marketing animals at a constant LW results in animals slaughtered at various stages of growth and carcass composition (Lawrence et al. 2012). The same type of variability is also possible within a breed but may not have the same degree of extremes (Herring 2014).

In I the LWG and carcass weight gains of the Ch bulls were 10 and 22% higher than those of the Hf bulls, respectively. Similarly in II purebred Ch bulls had 14 and 28% higher LWG and carcass gains compared to purebred Hf bulls, respectively. The higher growth capacity of the Ch breed compared to the Hf breed has been demonstrated previously in numerous studies (e.g. Gregory et al. 1994, Aass and Vangen 1998, Jakubec et al. 2003, Schenkel et al. 2004, Krupa et al. 2005, Bartoň et al. 2006).

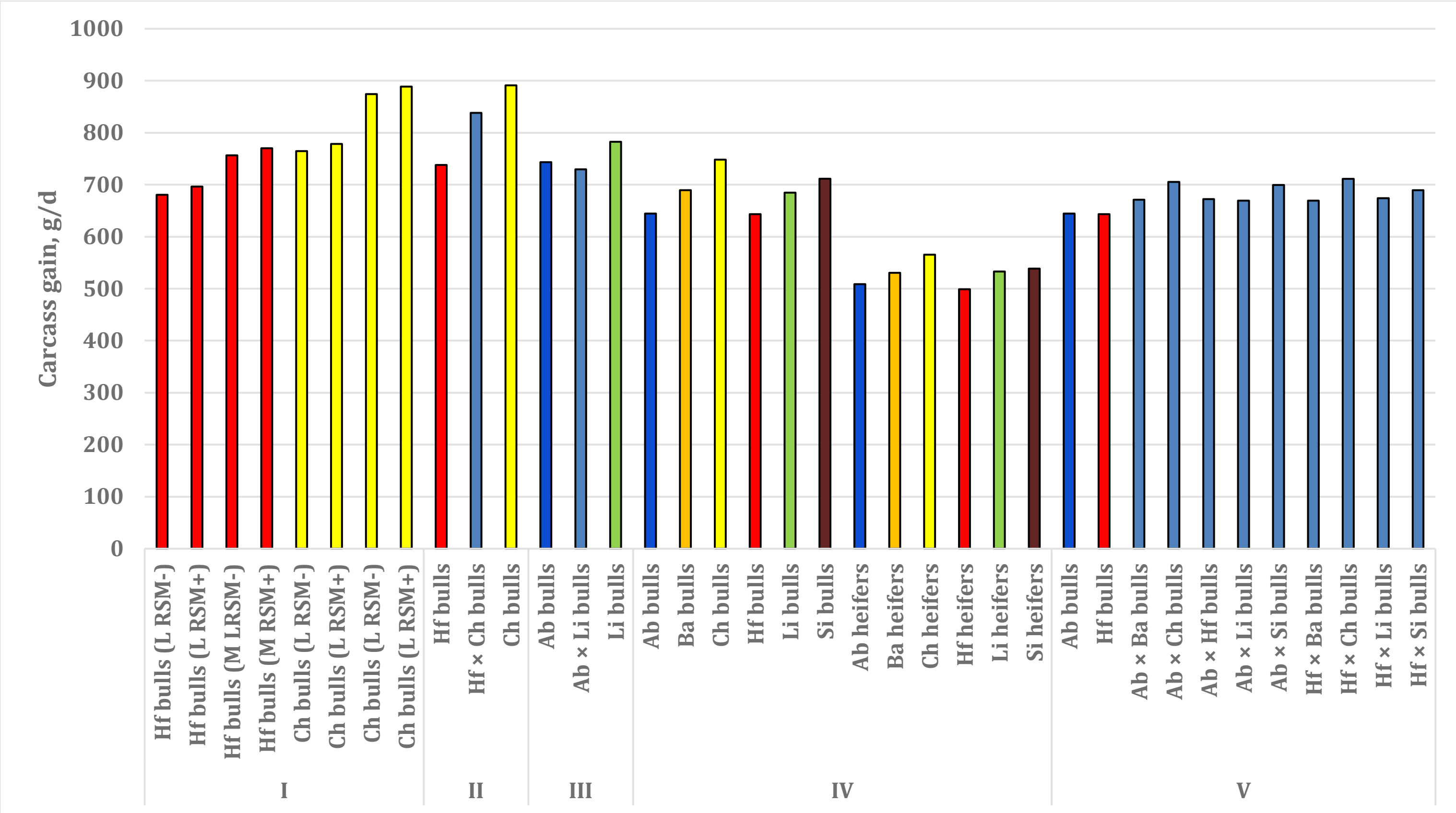


**Figure 2.** Carcass gain (g/d) of the experimental animals in I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

In III there was no difference in LWG between Ab and Li bulls, but the carcass gain of the Li bulls was 7.5% higher than that of the Ab bulls. Previously, Cuvelier et al. (2006a) reported no difference in LWG between Ab and Li bulls fattened with a sugar-beet pulp or cereal-based diet and slaughtered at the age of 530 days. In contrast, Alberti et al. (2008) observed that the LWG of Ab bulls was superior compared to Li bulls (1.97 vs. 1.46 kg/d) when both breeds were slaughtered at the age of 428 days and offered a high concentrate diet. Furthermore, Chambaz et al. (2003) found that Ab steers reared until they reached the same IMF content had a higher growth rate compared to Li steers.

In IV the carcass gain of the Continental breeds was significantly higher than that of the British breeds (Figure 2). Angus and Hf bulls had the lowest (619 and 618 g/d, respectively) and the Ch bulls had the highest (724 g/d) average daily carcass gain (IV). Ba and Li bulls grew 7%, Si bulls 11% and Ch bulls 17% faster compared to British breeds. The carcass gain of the Si bulls was 4% and Ch bulls 9% higher than that of the Li bulls. Furthermore, Ch bulls grew 6% faster compared to Si bulls. Although Continental breeds have been observed to achieve superior growth performance in numerous previously mentioned experiments, contradictory observations have also been made. For example, Chambaz et al. (2003), Bartoň et al. (2006) and Holló et al. (2012) reported similar or higher carcass gains for British breeds compared to late maturing Continental breeds. Furthermore, some studies have reported no difference in LWG between late maturing Si and early maturing Hf (Mandell et al. 1998, Laborde et al. 2001) or Ab (Myers et al. 1999) on high grain diets.

In most regions, the value of cattle used for beef production is highly related to their weight and the weight relative to age in young and growing animals (Herring 2014). The animal adult size correlates highly with growth performance. Good growth means fewer days on feed and more profitable production. In I-V there were no meaningful differences in the slaughter age between the different breeds (Figure 3). Instead, the slaughter age was on average 105 days lower for heifers than for bulls. In IV earlier maturing Ab and Hf bulls had the same or a higher slaughter age and a clearly lower slaughter weight compared to Continental bulls. The slaughter age of Ab and Hf bulls in IV was contrary to some previous studies in which different breeds and cattle types were slaughtered at a similar endpoint, e.g. back fat thickness (Gregory et al. 1994), IMF content (Chambaz et al. 2003) or slaughter weight (Holló et al. 2012). In these studies, earlier maturing breeds reached the slaughter endpoint earlier than the late maturing breeds. In Finland Ab and Hf animals are slaughtered at heavy carcass weights due to the falling supply of domestic beef and due to a pricing scheme that favours heavier animals (Herva et al. 2011). The breed characteristics at the slaughter age is not utilized in the Finnish beef production system (Huuskonen & Pesonen 2017).

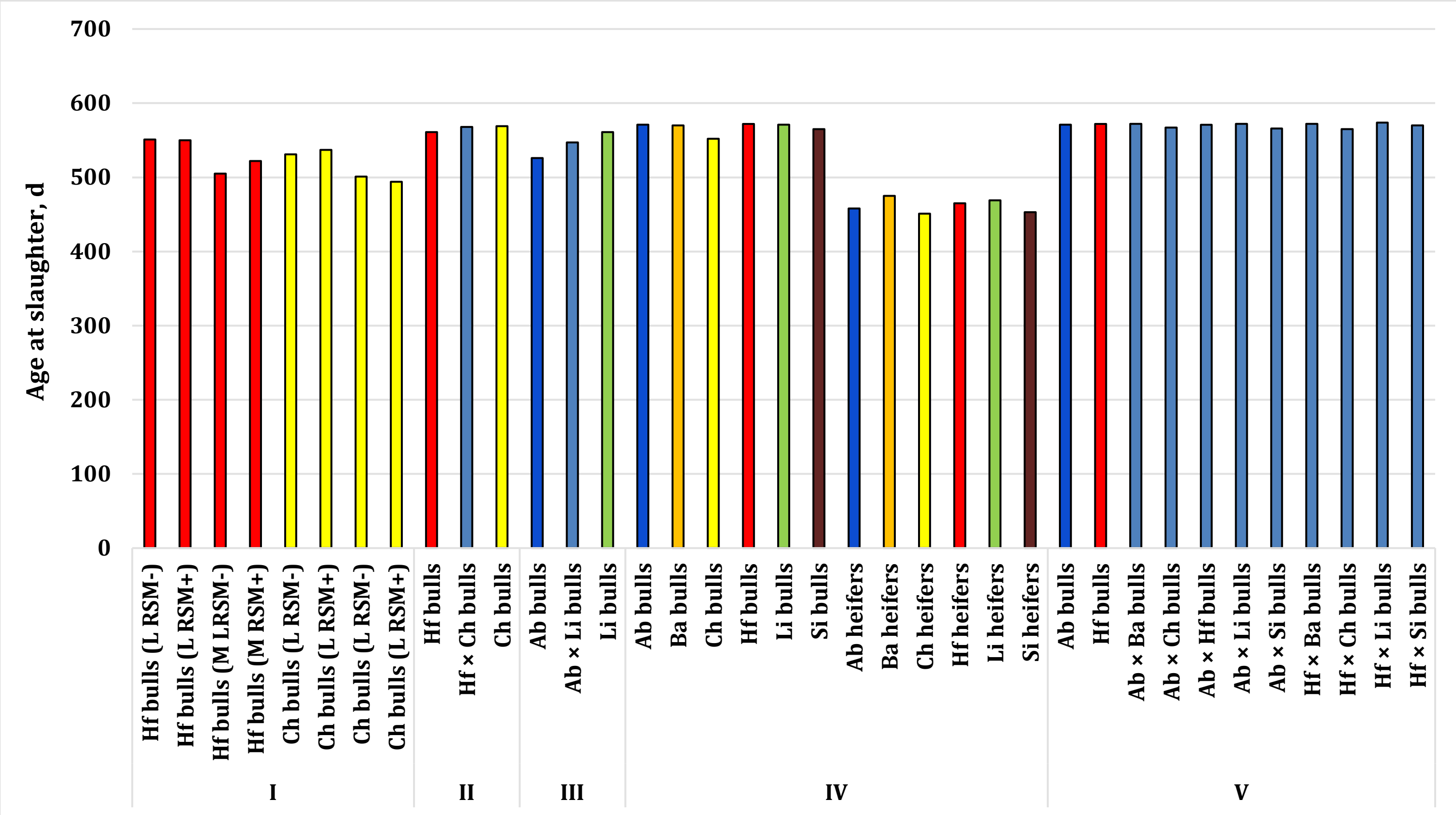


**Figure 3.** Age at slaughter (days) in I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

Generally, late maturing Continental breeds have needed more days on feed to reach same back fat thickness than early maturing British breeds in several studies (e.g. Chambaz et al. 2003, Rios-Utrera et al. 2006, Williams et al. 2010). When high grain finishing diets and adjusted back fat end points were used, late maturing Li animals needed 102 days longer feeding period compared to Ab animals (Vanderwert et al. 1985). Mandell et al. (1998) observed that Si animals required 67 more days on feed to achieve the same back fat end point than Hf animals. Laborde et al. (2001) got similar results and reported that Si steers needed 71 days more on feed than Red Ab steers to reach the same target level of back fat thickness.

In II Ch crossbreeding enhanced the growth performance by 18% compared to purebred Hf bulls, but in III Li crossbreeding had no significant effect on the growth performance compared to purebred Ab bulls (Figure 2). In V crossbreeding Ab and Hf with Continental breeds enhanced carcass gains on average by 6.5% compared to purebred Ab and Hf bulls. The average carcass gain improved most with Ch and Si crosses (Figure 4). Consistent with these results, Ch and Si breeds have been observed to enhance growth rates in crossbreeding in previous studies by Andersen et al. (1977) and Cundiff et al. (1986). Additionally, Williams et al. (2010) concluded that Ch had the most positive and British breeds the most negative effect on post weaning growth. A similar trend was found by Legarra et al. (2007), although in that case Si had the most positive effect. Mainly due to heterosis, crossbreeding British breeds between each other also increased their growth performance significantly (V). Generally, crossbreeding is expected to enhance growth by 4–10% (Dillard et al. 1980, Lawrence et al. 2012). Williams et al. (2012) observed that crossbreeding British × British breeds enhanced the growth performance by 6.3%, British × Continental breeds by 7.9% and Continental × Continental breeds by 9.1% compared to pure breeds. Recently, Huuskonen & Pesonen (2017) reported that Si × Ba crossbreeding enhanced growth by 3% and Si × Ch by 6% compared to purebred Si bulls.

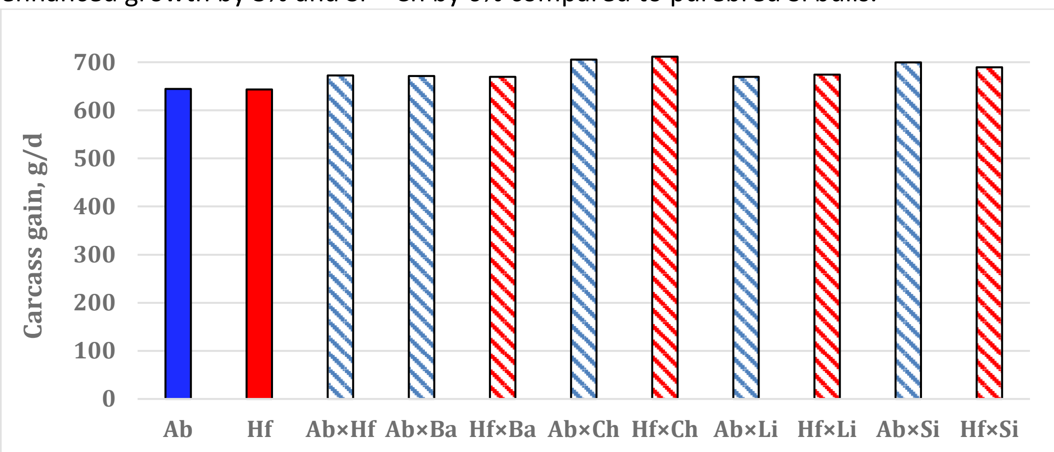


**Figure 4.** Growth performance enhancement of bulls in crossbreeding (V). Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental.

For Continental heifers the growth performance was on average 7% higher than that of the British breed heifers (IV). The lowest daily carcass gain (468 g/d) was observed in Hf heifers. Ab heifers grew 2%, Ba, Li and Si heifers 8% and Ch heifers 15% faster compared to Hf heifers (IV). This is in agreement with previous work by Ulrick et al. (1991) when Continental crossbred heifers enhanced growth by 5% compared to Ab and Red Poll heifers. However, in more recent work Lambe et al. (2010) did not observe differences in growth performance between Ab and Li heifers.

In IV the carcass gain of beef breed heifers was 23% lower, on average, compared to bulls. Generally, the growth performance of heifers has been 13–21% lower than that of bulls when reared in similar production environments (Bureš & Bartoň 2012, Tagliapietra et al. 2018). Velik et al. (2008) observed that the daily carcass gain of Si × Ch crossbred heifers was only 8% lower than that of bulls.

### 3.1.2. Carcass weight

Continental breeds produced higher carcass weights compared to British breeds (I-V) (Figure 5). In I and II the carcass weights of Ch bulls were 13.6% and 18.3% higher than that of Hf bulls, respectively. This is in agreement with Bartoň et al. (2006) who observed that Ch bulls produced 16.4% higher carcass weight compared to Hf bulls. In III the carcass weight of Li bulls was 10.9% higher than that of Ab bulls. Previously, Alberti et al. (2008) concluded that the carcass weight of Li bulls was 6.7% higher than that of Ab bulls.

In IV carcass weights of the bulls ranged from 368 kg for Ab and Hf to 413 kg for Ch. In general, British breeds produce lighter carcasses than the Continental breeds (Wulf et al. 1996, Barton & Pleasants 1997, Hassen et al 1999, Šubrt & Divis 2002, Polách et al. 2004, Sami et al. 2004, Rios-Utrera et al. 2006, Bartoň et al. 2006, Alberti et al. 2008, Williams et al. 2010). Compared to British breeds continental breeds are known to be larger framed which is typically associated with heavier carcasses (Arango et al. 2002). When Ab was set as a control breed, Williams et al. (2010) observed that the carcass weight was -1.9 kg for Hf, +53.4 kg for Ch, +24.9 kg for Li and +35.5 kg for Si bulls. Similarly, Rios-Utrera et al. (2006) noted a trend for hot carcass weight (HCW) estimates from -10.2 kg for Hf to +33.6 kg for Si bulls using Ab as a control breed. Hassen et al. (1999) found that the HCW of Si bulls was 36.5 kg larger than that of Ab bulls. Laborde et al. (2001) reported that Si bulls had a 38% heavier HCW than Red Ab (405 vs. 294 kg) bulls at the same back fat end point.

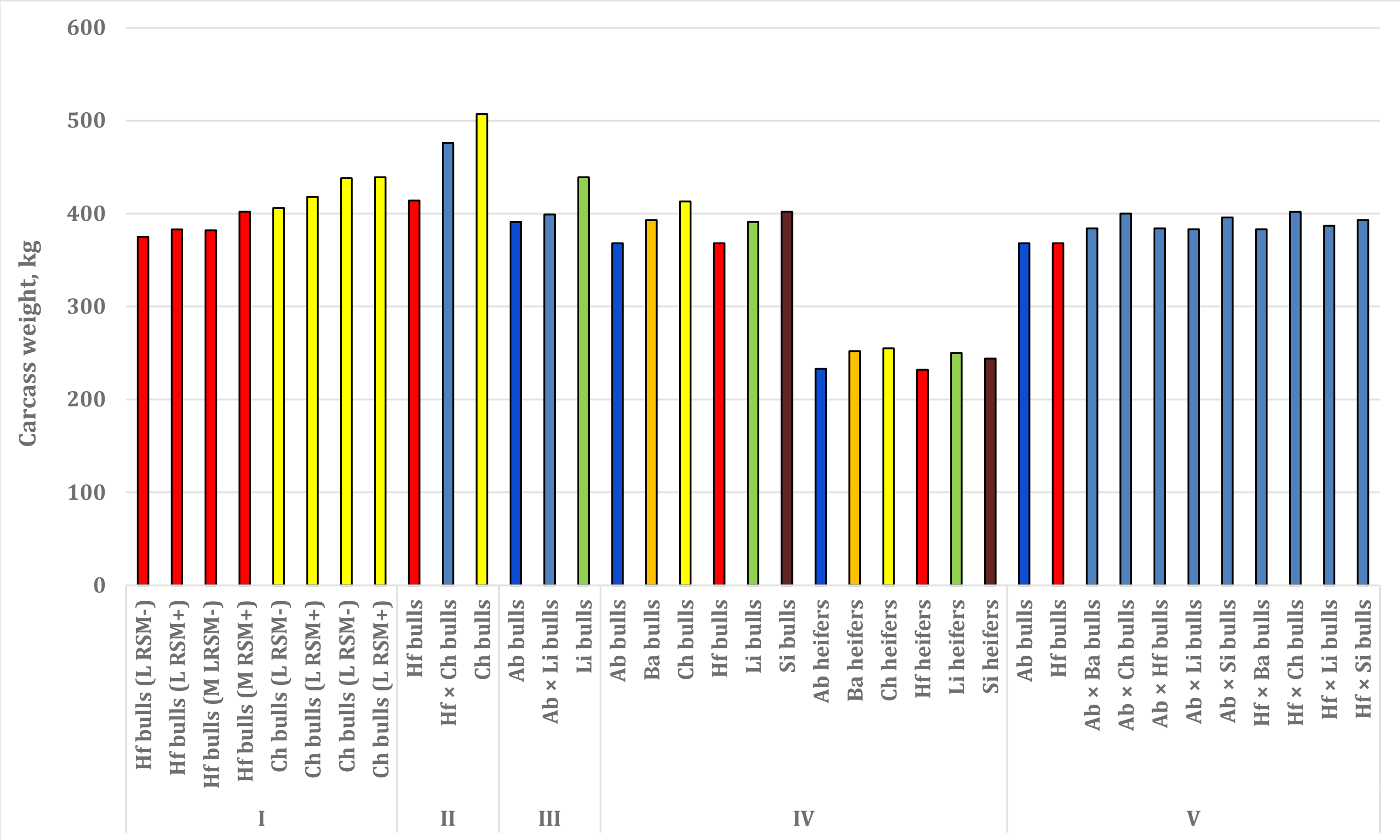


**Figure 5.** Carcass weights (kg) in experiments I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

The average carcass weight of the Ab and Hf bulls in V was 368 kg. Crossbreeding Ab and Hf with Continental breeds increased the carcass weight on average by 6% compared to purebred Ab and Hf bulls (Figure 5). Crossbreeding British breeds with other increased the carcass weight on average by 4%. In experiment II Ch crossbreeding increased the carcass weight by 15% compared to purebred Hf bulls. The corresponding positive effect of Continental breeds on the carcass weight has been previously demonstrated for example by Williams et al. (2010). In their study Ch breed increased carcass weight by 13.4%, Li by 6.2% and Si by 8.9%, but Hf had a 0.5% lover carcass weight compared to Ab breed.

In experiment III the average carcass weight of the Ab bulls was 391 kg and it was not significantly affected by Li crossbreeding. Generally, Li crossbreeding does not increase the carcass weight if the endpoint is determined to be similar (Chambaz et al. 2001, Alberti et al. 2008). Huuskonen & Pesonen (2017) observed that Si crossbreeding with Ba and Ch breeds increased carcass weights by 2.8%. In their study Si crossbreeding with Ab, Hf and Li reduced the carcass weight on average by 1.5%. Williams et al. (2010) demonstrated the crossbreeding effect of different breed combinations. In their study a British × British breed cross increased carcass weights by 10.3%, while a British × Continental breed cross increased them by 13.1% and a Continental × Continental breed cross increased them by 16.4%.

In IV the carcass weight of heifers ranged from 232 kg for Hf to 255 kg for Ch heifers. When Ab was used as a control breed the differences between the Ba, Ch, Hf, Li and Si breeds were +7.6, +8.6, -4.3, +6.8 and +4.5%, respectively (Figure 5). The differences between breeds were consistent with previous research (Rios-Utrera et al. 2006; Williams et al. 2010). Rios-Utrera et al. (2006) presented breed differences in adjusted fat thickness, different carcass weights and at an age constant when Ab was set as a control breed. At an age constant of 423.5 d Hf breed decreased their carcass weight by 3% while Ch, Li and Si breeds increased it by 9, 4 and 9%, respectively.

Generally, gender has a significant influence on the carcass weight. In IV heifers had a 37% lower carcass weight compared to bulls, on average. Previously, Bureš & Bartoň (2012) compared different fixed slaughter ages at 14 and 18 months with Ch × Si crossbred bulls and heifers. They observed that the carcass weight of heifers was 15% lower at the first endpoint and 9% lower at the second endpoint than that of bulls. Similar results were obtained by Velik et al. (2008) who reported that the difference in crossbred heifer vs. bull carcass weights was 13%. Hassen et al. (1999) found a similar (14%) difference between heifer and bull carcass weights. In IV the difference between bull and heifer carcass weights was higher than in previous studies (Hassen et al. 1999, Velik et al. 2008, Bureš & Bartoň 2012). This might be due to the fact that in IV there was no fixed endpoint for the carcass weights.

### 3.1.3. Dressing proportion

In I the Ch bulls had a 5.4% higher dressing proportion compared to the Hf bulls, while the corresponding difference between purebred Ch and Hf bulls was 7.6% in II (Figure 6). The lower dressing proportion of the Hf bulls can be partly explained by the lower average carcass weight compared to the Ch bulls because it is fairly well-established that the dressing proportion is increased by increasing the slaughter weight (e.g. Kempster et al. 1988). However, the body composition and dressing proportion of beef breeds is not only dependent on the carcass weight. The superiority of the Ch breed concerning the dressing proportion compared to the Hf breed has been reported in many earlier studies (Polách et al. 2004, Sochor et al. 2005, Wheeler et al. 2005, Bartoň et al. 2006, Rios-Utrera et al. 2006). For example, Bartoň et al. (2006) reported a 3.9% lower dressing proportion for Hf compared to Ch bulls. At the same carcass weight end point the dressing proportion for Ch bulls was 2.3% higher than for Hf bulls (Bartoň et al. 2006).

In III the dressing proportion of the pure Li bulls was 7.5% higher than that of pure Ab bulls (Figure 6), while the carcass weight of the Li bulls was 11% higher than that of Ab bulls. This observed difference between Ab and Li breeds in the dressing proportion is in line with previous observations by Bonaiti et al. (1988), Wulf et al. (1996), Barton & Pleasants (1997), Sinclair et al. (2001) and Cuvelier et al. (2006a). Correspondingly, Alberti et al. (2008) reported an almost 12% higher dressing proportion for Li bulls compared to Ab bulls, while Wheeler et al. (2005) observed that the dressing proportion for Li breed was on average 1.9% higher than for Ab breed at a constant carcass weight (Wheeler et al. 2005).

Heavy muscling increases the dressing proportion. Increased lean yields for late maturing vs. early maturing breeds have been found after constant times on feed (Gregory et al. 1994) or at a common back fat end point (Mandell et al. 1998). Laborde et al. (2001) found that the Si breed had a 7.7% greater lean yield percentage than Red Ab (569 vs. 528 g/kg). Wheeler et al. (2005) reported that Li sired steers had a higher dressing proportion than both British breeds and their crossbreeds. Corresponding results were also found by Rios-Utrera et al. (2006) and Papaleo Mazzucco et al. (2016). The dressing proportions reported by Papaleo Mazzucco et al. (2016) were 522 g/kg for Ab, 513 g/kg for Hf and 537 g/kg for Li crossbreds.

The effects of crossbreeding on the dressing proportion were evaluated in II and III. It was observed that Ch crossbreeding enhanced the dressing proportion compared to Hf purebreds by 6.1% (II) which was according to existing literature. Earlier, Wallace et al. (1966) and Cundiff (1970) reported on average an increase of 0.8–1.9% in the dressing proportion when crossbreeding Ab or Hf dams with Ch bulls compared to purebred British breeds.

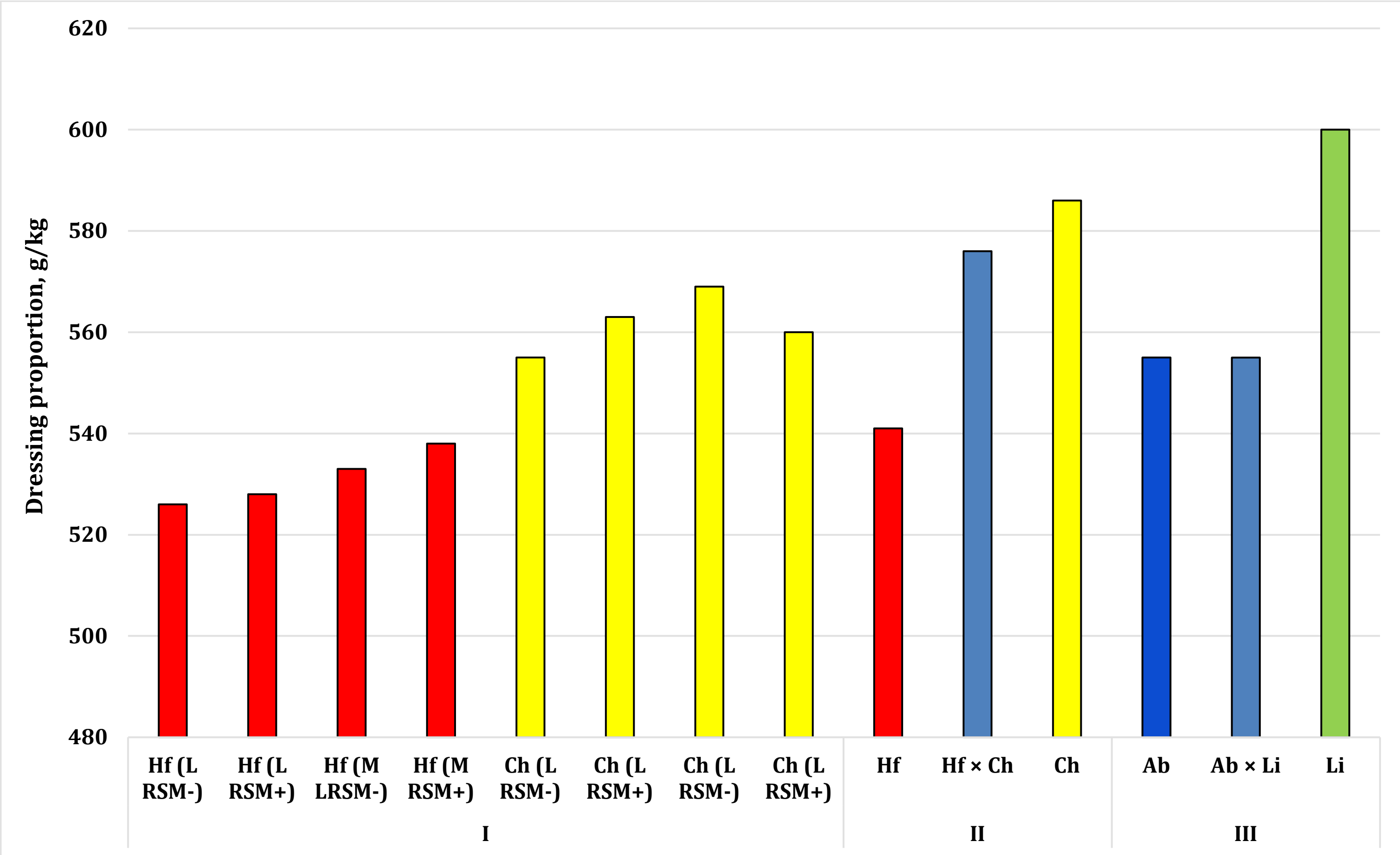


**Figure 6.** Dressing proportions (g/kg) of bulls in experiments I-III. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

In III Li crossbreeding did not have any effect on the dressing proportion compared to pure Ab bulls. This was most likely due to the relatively low number of the bulls in the experiment. Previously, the dressing proportion enhancing effect of crossbreeding was observed to be 0.3% for Hf bulls, 1.5% for Ch bulls and 2.2% for Li bulls when Ab was used as a control breed and the slaughter age was used as an endpoint of the study (Marshall 1994). Using Ab as a control breed Rios-Utrera et al. (2006) demonstrated that the dressing proportion was affected by different breeds as follows: Ch +6.7%, Hf -0.1%, Li +8.9% and Si +6.9%. Graham et al. (2009) reported that Li crossbreeding increased the dressing proportion compared to Ab sires chosen for high rib eye area (REA) by 3%, Ab sires chosen for REA and IMF by 2.9% and Ab sires chosen for IMF by 3.5%.

### 3.1.4. Carcass conformation

In I and II the conformation score for Ch bulls was 32 and 57% higher than for Hf bulls, respectively (Figure 7). In III the conformation score for Li bulls was 80% higher than that of Ab bulls. Previously Bartoň et al. (2006), Alberti et al. (2008) and Holló et al. (2012) also concluded that the EUROP conformation score is generally higher for Continental breeds compared to British breeds. However, Alberti et al. (2008) observed no significant difference in the conformation score between Ab and Li bulls which had been offered a concentrate-based diet. Bartoň et al. (2006) compared the carcass conformation scores of Ab, Ch, Hf and Si bulls. In their study Ch bulls had 14% and Si bulls 1.6% better conformed carcasses, respectively, compared to Ab bulls. Furthermore, Hf bulls achieved a 2% lower conformation score than Ab bulls. The difference in conformation score between Ch and Hf bulls was 16.4% in favour of Ch bulls (Bartoň et al. 2006).

In IV the conformation score was higher in late maturing Ba, Li, Si and Ch breeds compared to earlier maturing Ab and Hf breeds. In Ab, Hf and Si bulls 62–63% of carcasses were given a EUROP conformation score from 7 to 9, and the most common conformation score was 7 (23–33% of all observations). A conformation score of 9 or better was given for 22% of the Si carcasses but only 3% of the Ab and Hf carcasses (IV). Instead, for Ba, Ch and Li bulls, 43–53% of the carcasses conformed to a score of 9 or better. Considering the most common conformation scores (6–12) the average carcass weights of Ba and Li bulls were generally lower compared to Ab, Ch, Hf and Si bulls. In other words, Ba and Li bulls were classified better than other breeds for the same carcass weight. This is in agreement with earlier studies by Bartoň et al. (2006) and Holló et al. (2012) who reported significantly higher conformation scores for Ch and Si bulls in comparison to British breeds. In I–V the lower conformation scores of certain breeds, gender and crosses can be partly explained also by lower average slaughter weights. In general, carcass conformation increases with increasing carcass weight (Kempster et al. 1988).

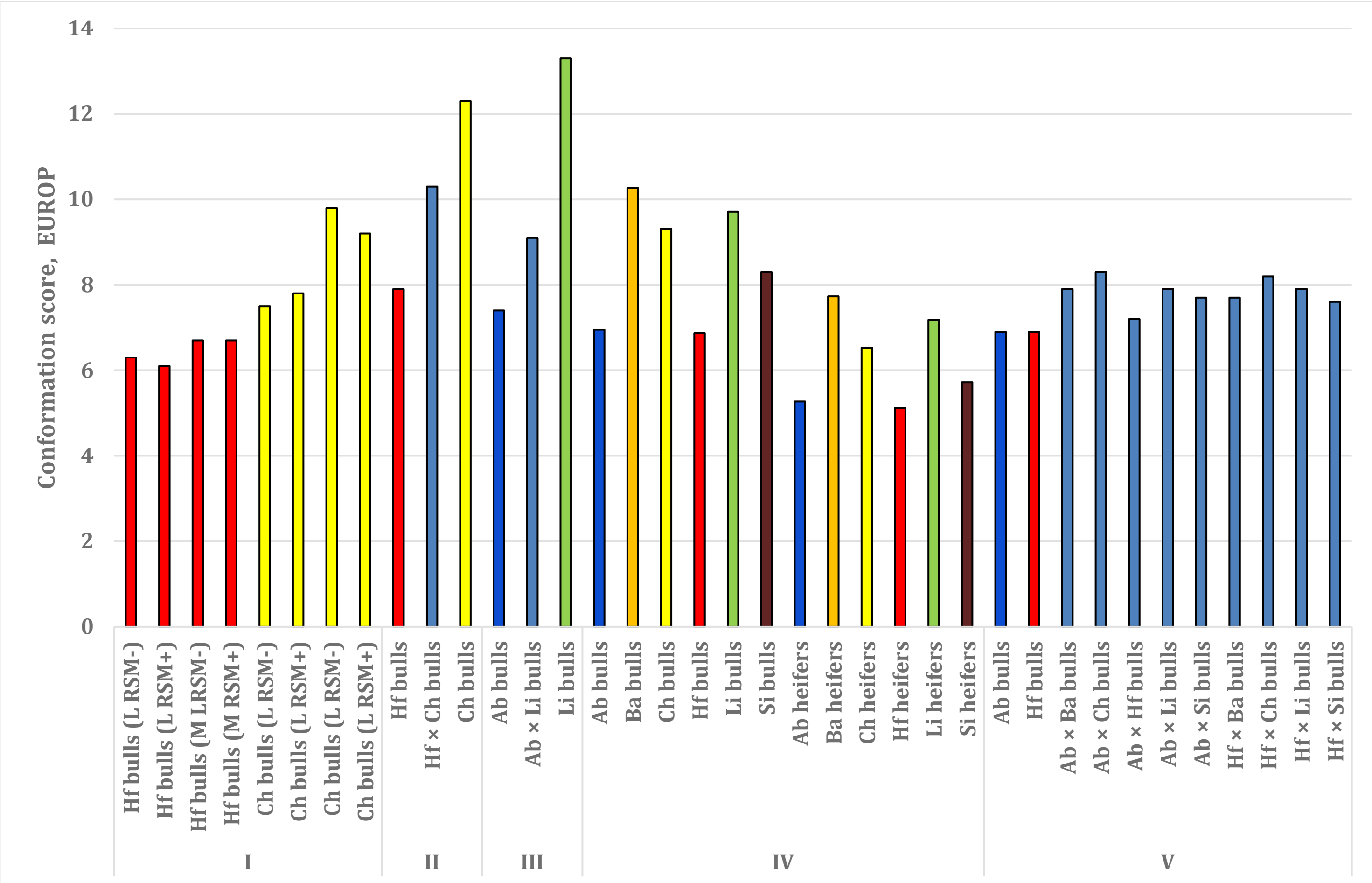


**Figure 7.** Carcass conformation score in experiments I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

In II crossbreeding Hf with Ch increased the conformation score by 30% compared to purebred Hf bulls. Correspondingly, Bartoň et al. (2007) demonstrated that the conformation score increased 14.7% compared to Hf purebred bulls when crossbreeding Hf and Ch breeds. Røbotten et al. (2002) perceived that Li crossbred bulls obtained higher scores for conformation than the Ab crossbred bulls, which is in accordance with the findings in III where the conformation scores of Ab × Li crosses were 23% higher than purebred Ab bulls. In V the EUROP conformation score of purebred Ab bulls was 6.9 and it improved the most with Continental crossbreeding (12–16%). British crossbreeding improved the conformation score by 4% compared to purebred Ab bulls. Similar results were obtained for the Hf crossbreeding (V) when conformation score was improved most (14–19%) by using Ch and Li crosses. These results are consistent with earlier observations concerning crossbreeding effects on conformation and yield grades (e.g. Rios-Utrera et al. 2006, Huuskonen & Pesonen 2017). Huuskonen & Pesonen (2017) reported that crossbreeding Si bulls with Continental Ba, Ch and Li breeds increased conformation score by 10, 2 and 7%, respectively, but crossbreeding with Ab and Hf breeds reduced the conformation scores by 7 and 8%.

The conformation scores for heifers ranged from 5.12 for Hf to 7.73 for Ba (IV). Generally the breed differences in yield and conformation remain the same despite the gender of the animal (Lawrence et al. 2012, Herring 2014). However, bulls are generally more muscular and therefore the EUROP conformation class is usually higher for bulls than heifers (Steen & Kilpatrick 1995, Link et al. 2007, Velik et al. 2008, Bureš et al. 2012) which was also the case in IV. Heifers have more meat in the rump and loin, and overall more meat in the hindquarters than bulls (Steen & Kilpatrick 1995, Link et al. 2007, Bureš et al. 2012). The enhanced muscularity in bulls and different distribution of muscle mass is due to sexual hormones especially testosterone (Lawrence et al. 2012). Bureš et al. (2012) examined crossbred beef bulls and heifers at two different slaughter ages. In their study the difference between bull and heifer conformation scores was 2.4% at 14 months slaughter age. At the later slaughter age at 18 months the difference in the conformation score increased to 12%. However, Tagliapietra et al. (2018) did not observe any differences in the conformation score between crossbred bulls and heifers. In IV the conformation score was on average 27% lower for heifers than bulls. The least difference in conformation score was observed for the Ab and Ba breeds and the most difference in Si bulls and heifers.

### 3.1.5. Carcass fat score

The higher fat deposition of British compared to Continental breeds was clearly demonstrated in all experiments I–V (Figure 8). In I the EUROP fat score for the Hf bulls was 55% higher than for Ch bulls, while the carcass weights were 380 and 420 kg, respectively. In II the fat score of the Hf bulls was 22% higher compared to the Ch bulls while the carcass weights were 414 and 507 kg. In III Li bulls had a 45% lower fat score compared to Ab bulls. In IV the fat score was the lowest for Ba bulls (1.75) and the highest for Ab bulls

(3.29). If Ab was used as a control breed the fat scores were depressed with Ba -1.54, Ch -1.04, Hf -0.04, Li -1.1 and Si -0.98 (IV). These observations are in line with previous results that British breeds tend to increase the carcass fat while Continental breeds are expected to produce leaner carcasses with lower fat cover (e.g. Chambaz et al. 2003, Bartoň et al. 2006, Alberti et al. 2008).

Increased fat yields in early maturing relative to late maturing cattle at constant times on feed have been reported previously by Gregory et al. (1994) and also when the data has been adjusted to a constant grade fat (Mandell et al. 1998). Williams et al. (2010) reported that Ab breed has the overall most positive effect for fat thickness. Johnson et al. (1988) observed a variation in subcutaneous fat thickness from 0.95 cm for British breed type bulls to 0.65 cm for Continental breed type bulls. The same tendency was observed by Hassen et al. (1999) who noted that Si bulls had an estimated subcutaneous fat thickness of 0.77 cm below than that of Ab bulls. At a fixed carcass weight of 386 kg Gregory et al. (1994) observed that Hf breed reduced the carcass fat thickness by -0.02 cm while the corresponding effects of Continental breeds ranged from -0.76 cm (Li) to -0.81 cm (Ch) when Ab was set as a control breed. Papaleo Mazzucco et al. (2016) concluded that Li and Li crossbreds are leaner breed types but also have greater nutritional requirements that might affect their back-fat thickness for finishing under grazing conditions. Higher carcass weights are often accompanied with increased fat scores (Keane & Allen 1998). In Finland, the aim is to produce over 400 kg carcass weights for beef breed bulls and over 250 kg for heifers, which leads to challenges with the carcass fat scores especially for British breed and heifer carcasses. Huuskonen et al. (2012) concluded that the optimum carcass weight interval for Ab and Hf bulls would be 360–380 kg according to biological and market limitations concerning fat deposition.

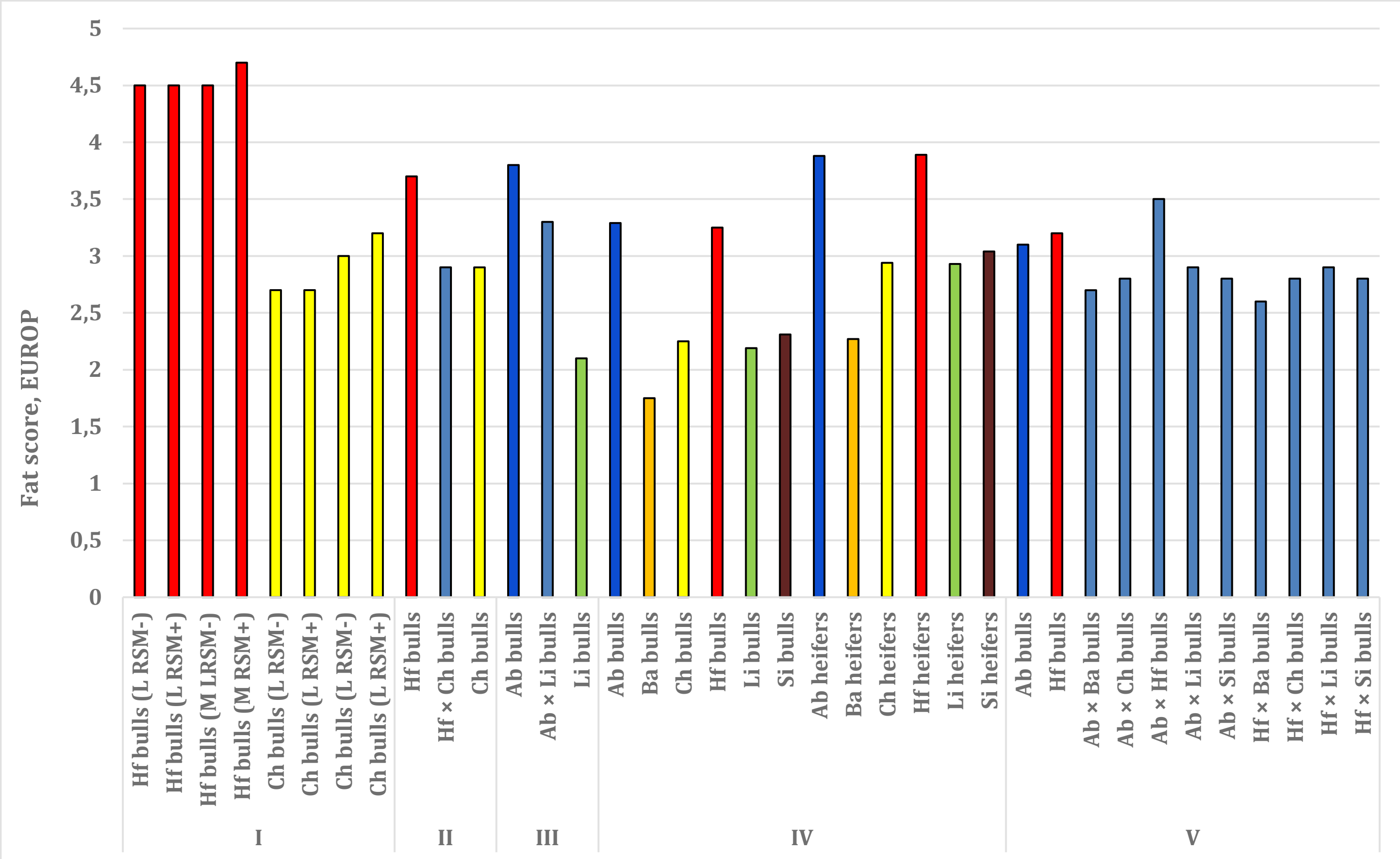


**Figure 8.** Carcass fat score in experiments I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

The number of bulls in different EUROP fat scores indicate the probability of a certain breed reaching a certain fat score (Figure 9). In IV the most common fat score for Ba, Ch, Li and Si bulls was 2 including 52–58% of all observations within the breed group. For Ab and Hf bulls fat scores of 3 were more frequent than fat scores of 2, being 40–41%. Thirty-two percent of Ab and Hf bulls were given a fat score of 4, while this was observed for only 2–5% of the other breeds. Furthermore, 8–9% of Ab and Hf bulls, but less than 1% for other breed groups were given a fat score of 5. Previously, Schenkel et al. (2004) reported with purebred beef bulls that Ba bulls showed the least back fat thickness, followed by Li, Ch and Si bulls when breed differences for growth and body composition traits were observed in Ontario bull test stations from 1991 to 2000. In that data Hf bulls had the highest and Ab bulls the second highest level of back fat thickness. These results are consistent with Finnish slaughterhouse data (IV).

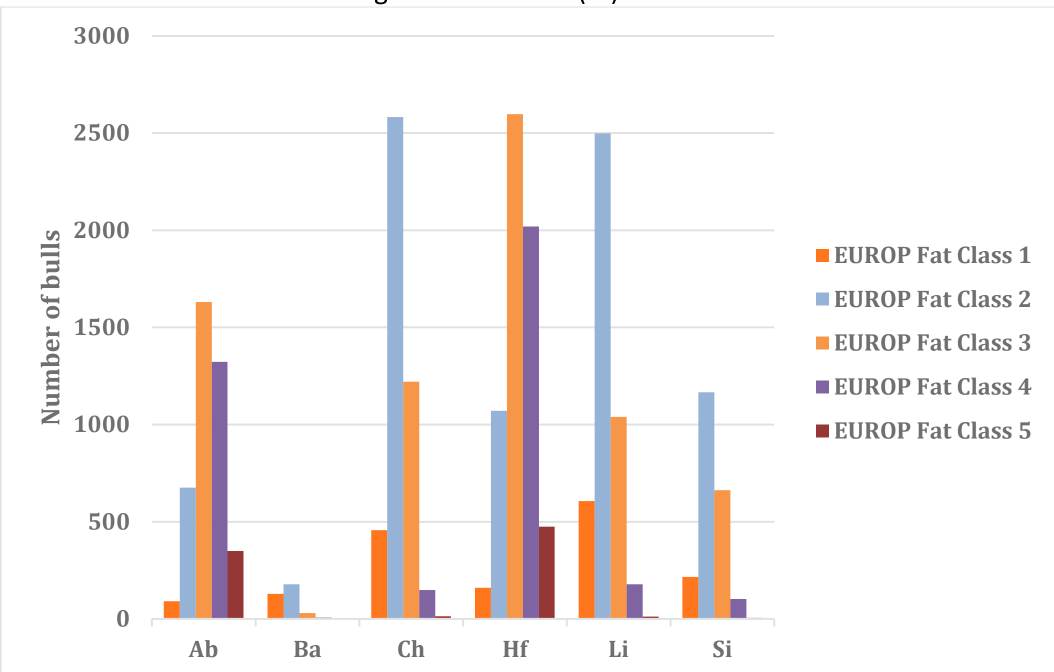


**Figure 9.** EUROP fat score distributions of bulls in experiment IV. Ab = Aberdeen angus; Ba = Blonde d’Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental.

The average carcass weight of Continental breed bulls in different fat score classes was higher than that of the British breeds (IV) (Figure 10). For example, for a fat score of 3 the average carcass weights were 12–18% higher for Ba, Ch, Li and Si bulls compared to Ab and Hf bulls. According to present data, Ab and Hf bulls would obtain a carcass fat score of 3 at a carcass weight of ca. 366–369 kg and late maturing Continental breed bulls would do so at a carcass weight of ca. 412–435 kg. The current target for the Finnish beef industry is to achieve a fat score of 3 or 3+ for beef breed bulls (personal communication 2019 Atria Ltd., HKScan Ltd.). According to this data, the desired carcass weight range should be breed-specific as follows: Ab 366–385 kg, Ba 412–430 kg, Ch 435–455 kg, Hf

369–390 kg, Li 412–430 kg and Si 424–445 (Figure 10). However, according to II, even up to 500 kg carcass weights with fat score of 3 are possible for Ch bulls.

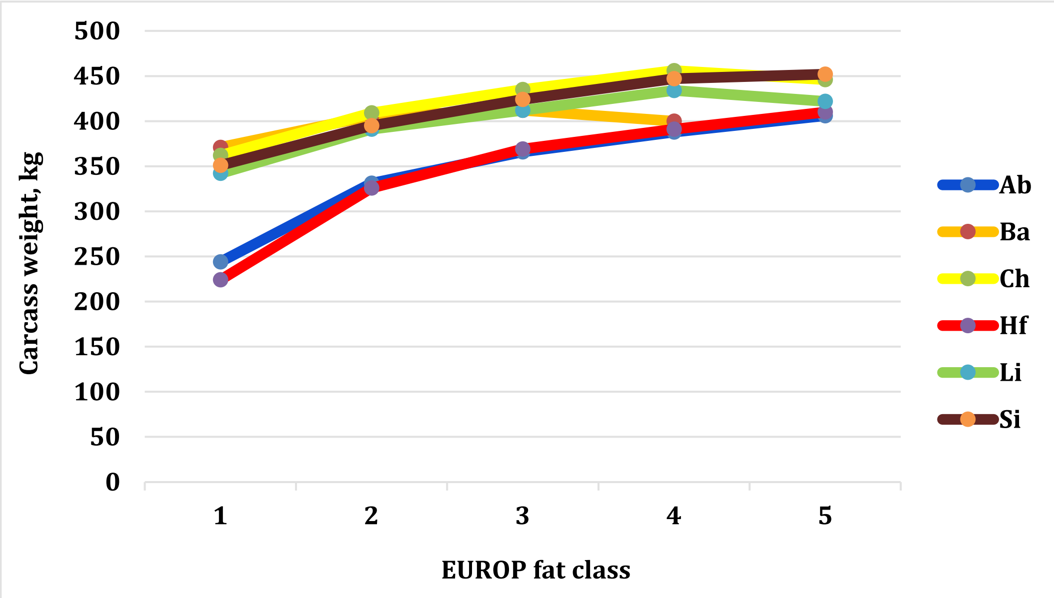


**Figure 10.** EUROP fat score and carcass weight of bulls in experiment IV. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental.

Crossbreeding has an impact on carcass fat distribution and accumulation. In II crossbreeding Ch with Hf breed reduced the EUROP fat scores by 22% compared to pure Hf bulls. However, the effect of Ab × Li crossbreeding compared to pure Ab bulls on the fat score was not statistically significant in III although the fat score numerically decreased by using Ab × Li crossbreeding. In V the Continental crossbreds of Ab × Ba, Ab × Ch, Ab × Li and Ab × Si had 12–18% lower fat scores compared to purebred Ab bulls. Similarly Continental crossbreeding reduced the fat score 9–19% compared to purebred Hf bulls (V). According to Williams et al. (2010) British × Continental crossbreeding reduced the fat thickness by 2% compared to pure bred British breeds (Williams et al. 2010). Rios-Utrera et al. (2006) examined the crossbreeding effect on fat thickness at a constant slaughter age, and the breed effects were shown using Ab as a control breed. Crossbreeding with Hf breed increased the fat thickness by 0.3% while Ch, Li and Si crossbreeding reduced the fat thickness by 24, 33 and 22%, respectively. Bartoň et al. (2007) reported that Hf × Ch crossbreeding reduced the fat thickness by 10% compared to purebred Hf bulls. Huuskonen & Pesonen (2017) observed that the carcass fat scores of Si × Ab, Si × Hf and Si × Li bulls were 22, 22 and 4% higher than that of purebred Si bulls, respectively.

In IV the fat score of heifers was 15–25% higher than that of bulls. Gender affects the composition and the maturity of the animal because of endogenous sex hormones (Lawrence et al. 2012). Bulls (intact males) produce leaner carcasses than heifers. Females reach maturity earlier than males. The fat accumulation in females at the same maturity is 38–42% higher than that of the bulls (Lawrence et al. 2012). The EUROP fat score is based on an external fatness assessment (Herring 2014). In general, the fat score is 17–26% higher for heifers compared to bulls at a similar slaughter age (Velik et al. 2008, Bureš et al. 2012, Tagliapietra et al. 2018). Bureš et al. (2012) examined crossbred bulls and heifers at two different ages. At the first end point at 14 months of age the carcass fatness of heifers was 9% higher, but the internal fat proportion was 37% higher than that of the bulls. At the second endpoint the corresponding fat score difference was 17% and the internal fat proportion difference was 46% (Bureš et al. 2012).

In IV the fat score was the lowest for Ba (2.27) heifers and highest for Ab (3.88) and Hf (3.89) heifers. The breed trend was similar compared to bulls in IV. If Ab was used as a control breed the fat score differences were -1.61 (Ba), -0.94 (Ch), +0.01 (Hf), -0.95 (Li) and –0.84 (Si). For heifers, the most common fat score for Ba breed was 2 including 48% of observations (IV). For Ch, Li and Si heifers the most common was fat score was 3, including 41–51% of observations (Figure 11). Instead, for Ab and Hf heifers the most common fat class was 4, including 41–43% of observations. In addition, 27–28% of Ab and Hf heifers, but only 1–3% of Continental breeds had a fat score of 5. The fat score distribution by breed was the same as for the bulls Continental breeds having a lower fat score compared to the British breeds (IV).

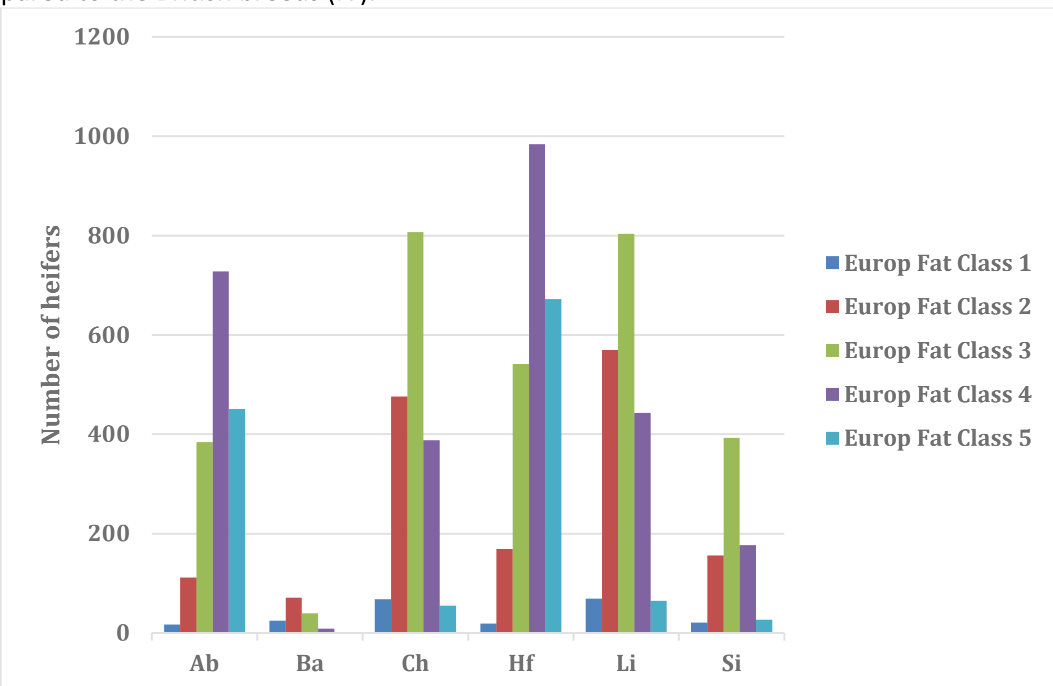


**Figure 11.** EUROP fat score distribution of heifers in experiment IV. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental.

The average carcass weight of Continental breed heifers in different fat score classes was higher than that of the British breeds (Figure 12). For a fat score of 3 the average carcass weights were 30–56 kg higher for Ba, Ch, Li and Si heifers and 3 kg lower for Hf compared to Ab heifers. The current target fat score for the Finnish beef industry is 3+ for beef breed heifers (personal communication 2019 Atria Ltd., HKScan Ltd.). According to this data, the slaughter weight range should be breed-specific as follows: Ab 220–230 kg, Ba >270 kg, Ch 260–280 kg, Hf 215–230 kg, Li 250–270 kg and Si 250–265 kg.

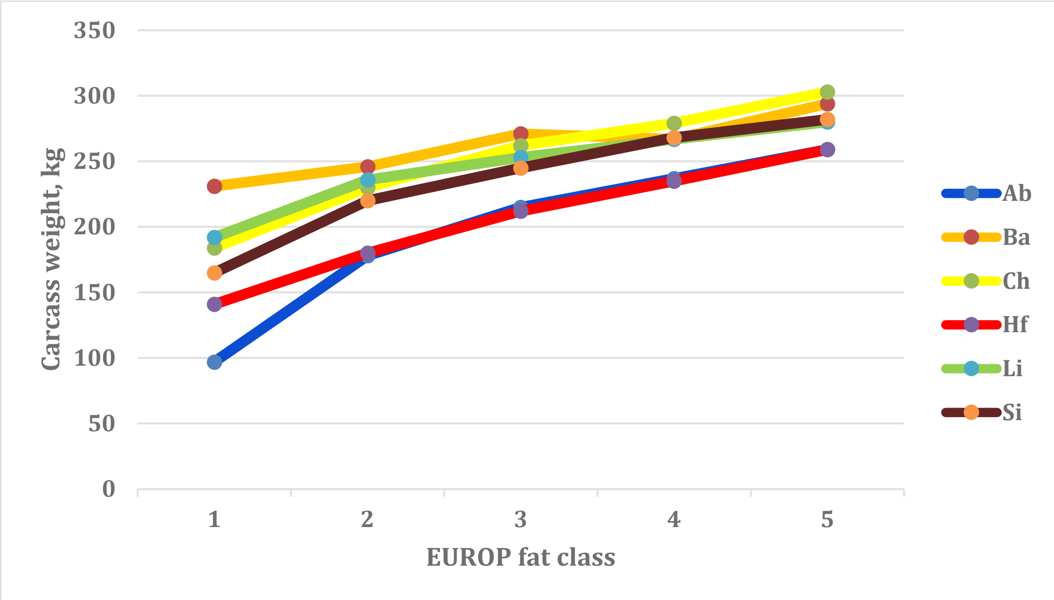


**Figure 12.** EUROP fat class and carcass weight of heifers in experiment IV. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental.

### 3.1.6. Valuable cuttings

The proportions of muscle, fat and bone in the carcass determines the amount of trimmed meat available for sale (Price 2017). Carcass composition largely determines carcass value. A high proportion of muscle with a low proportion of bone and an optimum level of fat represents a superior carcass (Oprzadek et al. 2001). The distribution of muscle, bone and fat is largely a function of maturity (Robelin 1986). Most phenotypic conformation differences between beef cattle types are due to differences in maturity, as well as muscle, bone and fat share and distribution. In general, Continental breeds have a higher meat proportion compared to British breeds (e.g. Koch et al. 1976) and bulls are more muscular than heifers (Berg & Butterfield 1976, Purchas et al. 2002) which were also observed in experiments I–V.

In I the yields of tenderloin, loin and entrecote were 13, 4 and 5% higher, respectively, for Ch than in for Hf bulls. The hind quarter cuttings of the Ch bulls were also greater compared to the Hf bulls. The yields for the outside round, inside round, corner round and roast beef were 9–14% higher for Ch compared to the Hf bulls. The differences between Hf and Ch bulls in valuable cuttings, subcutaneous fat and bone proportions were consistent in I and II. The bone proportion of the Hf bulls was higher than that of the Ch bulls. Previously, Manninen et al. (2011) reported similar yields of valuable cuts in Hf bulls compared to I and II. Generally, the proportions of valuable cuttings are not affected by the carcass weight (Lawrence et al. 2012).

In III the yields of tenderloin and entrecote were 43 and 25% higher for Li than in Ab bulls, respectively. The loin yield of the Li bulls was 13% higher than that of the Ab bulls. The valuable hind quarter cuttings were on average 26% higher for Li bulls compared to the Ab bulls. Furthermore, the yield of bones was 10% higher for the Ab bulls compared to the Li bulls. Previously, Chambaz et al. (2003) reported that Ab steers produced significantly fewer valuable cuts with the same IMF content compared to Li steers. Bartoň et al. (2006) evaluated the amount of valuable cuttings of Ab, Ch, Hf and Si breed bulls. In their study Ch and Si breeds produced a significantly higher proportion of valuable cuttings than Ab and Hf breed bulls and Hf bulls produced the most subcutaneous fat. Oprzadek et al. (2001) reported the lowest separable fat and the highest valuable cut yields for Li breed bulls when compared to Red Ab, Hf and Ch bulls. Red Ab and Hf bulls had the highest separable fat yield and Ch bulls had the highest amount of bone (Oprzadek et al. 2001). Generally, breed differences are consistent, and according to the literature, Continental breeds tend to produce more valuable cuts and less subcutaneous fat compared to British breeds (Oprzadek et al. 2001, Chambaz et al. 2003, Bartoň et al. 2006). In contrast to I, II and III, the bone proportion of British breeds have been found to be less than that of Continental breeds in some previous studies (Oprzadek et al. 2001, Bartoň et al. 2006, Alberti et al. 2008). However, there have been also conflicting results when comparing the bone yield between different beef breeds. For example, Jones et al. (1984) and Laborde et al. (2001) observed that bone yields tended to be greater in early maturing breeds compared to late maturing breeds at a common back fat end point. In contrast, Gregory et al. (1994) reported greater bone yields in Si compared to Ab bulls.

The amounts of valuable cuttings were similar across the experimental and commercial data sets. These estimates were also consistent with values reported in the literature, which vary from 17–40% (Shackelford et al. 1995, Strydom & Smith 2005, Schutt et al. 2009, Manninen et al. 2011, Bureš & Bartoň 2012). In IV and V the valuable cuttings were measured automatically in the slaughter line. The breed effects were clear and were according to previous literature (e.g. Koch et al. 1976, Bartoň et al. 2006, Holló et al. 2012). In general, Continental breeds produced higher yields of valuable cuttings and less subcutaneous fat compared to British breeds. Comparing Ab and Hf breeds, the yields of loin, inside round, outside round and corner round were higher for Hf bulls compared to Ab bulls (IV). These results are contrary to Bartoň et al. (2006) who reported that valuable cuttings of Hf bulls were significantly lower than that of other studied breeds.

When comparing Continental breeds, Ba and Li bulls seemed to achieve the highest percentage of many valuable cuttings (IV). For example, the yields of inside and outside round were significantly higher for the Ba and Li bulls compared to the Ch and Si bulls (IV). This is in accordance with Listrat et al. (2001) who reported that Ba steers produced 13% more muscle than Ch steers. Chambaz et al. (2001) concluded that the tender loin amount was the highest for Ba steers, but overall Li steers showed the greatest proportion of premium cuts.

The yield of subcutaneous fat was 49 and 78% higher for the Hf bulls compared to the Ch bulls in I and II, respectively (Figure 13). In III the yield of subcutaneous fat was 132% higher in Ab bulls than that of Li bulls. In IV and V subcutaneous fat thickness was significantly lower for Hf bulls than for Ab bulls. The previous literature is unanimous that British breeds produce more subcutaneous fat than the Continental breeds regardless the end point (e.g. Oprzadek et al. 2001, Chambaz et al. 2003, Schenkel et al. 2004, Bartoň et al. 2006, Williams et al. 2010). Consistent with III, the least amount of fat produced by Li breed was also found earlier by Chambaz et al. (2001) and Cuvelier et al (2006a). Bartoň et al. (2006) concluded that, in general, the animals of earlier maturing breeds produced relatively more fat than later maturing breeds despite the fact they are slaughtered at a significantly lower LW. Chambaz et al. (2003) observed that Ab steers produced significantly more subcutaneous fat with the same IMF content than Li steers. Schenkel et al. (2004) reported that Ba bulls showed the least back fat thickness, followed by Li, Ch and Si bulls. In that experiment Hf bulls had the highest back fat thickness, and the second highest back fat thickness was for Ab bulls (Schekel et al. 2004).

In II, Hf × Ch crossbreeding produced on average 21% higher amounts of valuable cuts compared to purebred Hf bulls. The yield of subcutaneous fat was 12.9% lower for Hf × Ch bulls than for purebred Hf bulls (II). In III Ab × Li crossbreeding produced 10.4% more in terms of valuable cuts comparing to the purebred Ab bulls and the yield of subcutaneous fat was 22.6% lower in crossbreds than in pure Ab bulls. In V the total amount of valuable cuttings was 5.6 kg higher for Hf than Ab bulls. Crossbreeding increased the total amount of valuable cuttings by 5–6% for Ab × Ch, Ab × Hf, Ab × Li and Ab × Si crossbreds compared to pure Ab bulls. The effect of Hf crossbreeding compared to pure Hf bulls was similar but slightly lower than for the Ab breed. Hf × Ch, Hf ×Li and Hf × Si crossbreeding increased valuable cuttings by 3% compared to pure Hf bulls (V). The subcutaneous fat yield was reduced in all crossbreeding alternatives except in British crossbreds compared to pure Ab or Hf bulls (V) (Figure 13).

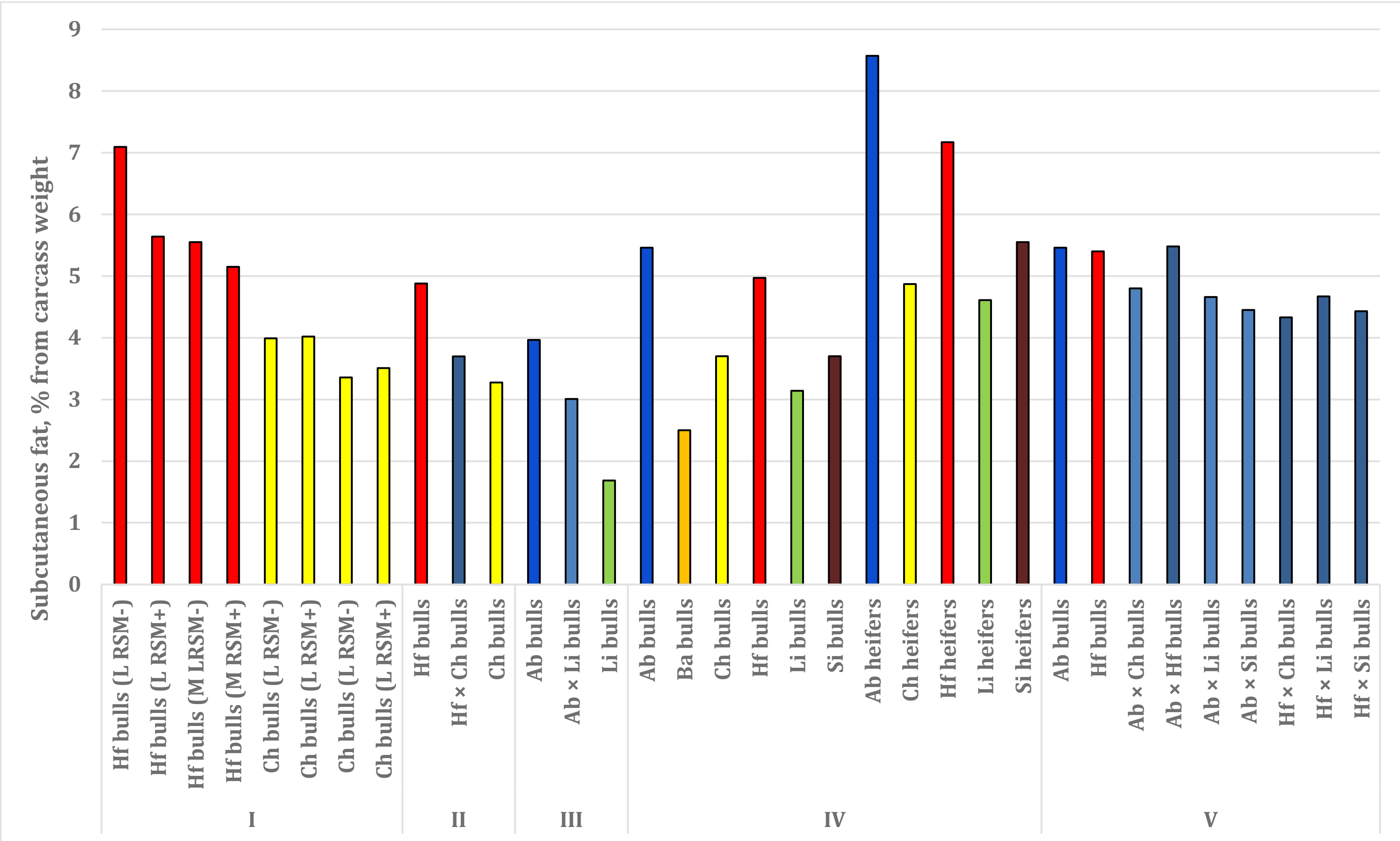


**Figure 13**. Subcutaneous fat proportion (% from carcass weight) in experiments I-V. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

Corresponding to the present results of V, Kempster et al. (1982) reported a lower saleable meat proportion from carcasses of Hf sired steers than from carcasses of Ch steers compared at 16 months of age. Additionally, Kaminiecki et al. (2009) reported the higher value of valuable cuts in Ch sired bulls than Hf sired bulls. Wheeler et al. (2005) observed that Hf sired steers had more subcutaneous fat at a constant age than Ch sired steers. Oprzadek et al. (2001) observed a higher amount of subcutaneous fat in Ab breed compared to Li breed and also concluded that Li sired animals had more lean meat in valuable cuts than other breeds. According to Oprzadek et al. (2001) Li sired bulls had the highest and Ab sired the lowest weight of tenderloin and the weight of valuable cuts was the highest for Ch and Li sired and the lowest for Ab and Hf sired progeny. Williams et al. (2010) concluded that crossbreeding Continental and British breeds seems to produce more saleable lean meat and less subcutaneous fat compared to pure British breeds which was observed also in II, III and V.

The Continental breed heifers (Ch and Li) produced the highest amount of rump meat in IV. There were differences between breeds also in yields of loin and corner round which were higher for the Hf heifers compared to Ab heifers (IV). The lower amount of valuable cuttings in Ab breed compared to Hf breed is in agreement with previous research by Oprzadek et al. (2001), in which Ch heifers produced 37, Hf 9.9, Li 46.5 and Si 26.7 kg more in the total amount of valuable cuts than Ab heifers. At the same time subcutaneous fat amount was reduced in Ch heifers by 37 kg, in Hf heifers by 14 kg, in Li heifers by 39.6 kg and in Si heifers by 30.2 kg compared to Ab heifers (Oprzadek al. 2001).

In general, heifers produce more subcutaneous fat at a similar slaughter age end point than bulls (Bureš & Bartoň 2012, Lawrence et al. 2012). The distribution of valuable cuts is also different in bulls and heifers. Bulls tend to produce more high-priced meat on the shoulder and front end, and heifers, on the other hand, have higher proportions of meat on the rump and loin (Bureš & Bartoň 2012). The higher amount of subcutaneous fat in heifers compared to bulls was observed also in IV (Figure 13). The differences in the distribution of meat between genders can be observed in the data of experiment IV.

In most countries the value of carcasses is predominantly based on carcass weight, carcass conformation, and the carcass fat score. Differences in retail value exist between different parts of the carcass (Morris et al. 1999). Many carcass payment systems are based on relatively simple estimates of carcass value. In the EUROP classification system the carcass value is formed by a 15-point classification system which attempts to describe the conformation of the animal based on the round, back and shoulder (Herring 2014). Conroy et al. (2010) reported a correlation of 0.85 between the EUROP-classification system and dissected beef carcass meat proportions. Their conclusion was that the EUROP-system explains only 73% of the variability in saleable meat yield. Beef carcass cuts are expensive traits to generate. In most cases intense labour requirements are needed to undertake the dissections. Farmers should logically be rewarded for producing a larger quantity of high value cuts. Pabiou et al. (2009) emphasized that the current EUROP grading system measuring the overall conformation and fat may not reflect differences in valuable cuttings within carcasses. Conversely, selection for increased carcass weight will, on average, increase the weight of each cut (Pabiou et al. 2009). High carcass weights are challenging for beef markets because the valuable cut size becomes inadequately large (Boykin et al. 2017). Strict criteria are often imposed by retail markets on animal and carcass credentials such as gender, age, but also the dimensions of individual primal cuts. Meat from carcasses which do not adhere to these criteria has to be either excessively trimmed, with the trimmings generally being sold at a lower value, or the carcass itself needs to enter another, often lower value, market stream (Berry et al. 2019). In this sense, the suggestion by Pabiou et al (2009) is sensible. More benefit will be gained if the selection pressure is directly on the high value cuts. Judge et al. (2019) determined significant genetic variability between carcass cuts which could be exploited for breeding purposes even when adjusted to a common carcass weight. Ultrasound scanning (e.g. of the loin muscle area, or for fat thickness) before slaughter is a viable option for assessing carcass composition (May et al. 2000, Castilhos et al. 2018).

### 3.1.7. Meat quality traits

Meat quality is a combination of appearance, eating quality and palatability. Meat eating quality may also include factors of production e.g. being welfare friendly and ecologically produced which are not directly related to the genetics of the animal (Warner et al. 2010). Overall beef eating quality is dependent upon three factors—tenderness, juiciness and flavour—as well as the interactions between these traits. Beef steaks may excel at one or even two of these traits yet may fail to meet consumer eating expectations due to the unsatisfactory level of another trait (O'Quinn et al. 2018).

The evaluation of meat quality plays a major role for consumers in determining meat purchases. Visual appearance is the prime determent of saleability, although visual appearance is known to be poorly related to palatability (Price 1995, 2014). At the moment of purchase, the visual assessment of beef meat is highly driven by the amount of internal and external fat and colour of the cut. The amount of observed fat is linked to the healthiness of the meat. The brightness and redness of the beef are linked to the freshness of the meat product. Tenderness is one of the most important factors influencing the acceptability of beef, and the most studied palatability trait of cooked meat (Beermann 2009). Marbling has been shown to have a small but positive influence on tenderness, along with other palatability traits such as juiciness and flavour (Wheeler et al. 1994). Muscle colour, fat texture, the amount IMF and its distribution are evaluated or scored in many grading and classification systems. The scores mainly indicate differences, not necessarily superiority or inferiority (Price 1995, Warriss 2010).

Meat quality is a trait of an individual animal (Berry et al. 2017). Differences in eating quality between breeds are often less than between animals within breeds and are overridden by larger differences between muscles or cuts (Dransfield et al. 2003). There is a large variation in the eating quality traits of meat between individuals. Therefore identifying those individual which are able to produce prime quality meat is essential for enhancing the eating quality of the meat (Guerrero et al. 2013, Mortimer & Przybylski 2016, Berry et. al 2017). British breeds may express enhanced meat eating quality more often than other breeds. These breeds may also have more often traits which are associated with enhanced meat eating quality (Hocquette et al. 2005, Guerrero et al. 2013, Cafferky et al. 2019). Genomic tools can be used to identify and enhance the meat eating quality (Berry et al. 2017). Heterosis effects seem to improve the carcass composition. Cross-breeding could potentially benefit carcass composition through complementary blending of breed characteristics (e.g. carcass weight, cutability, and carcass quality) (Marshall 1994).

**3.1.7.1. pH**

After exsanguination, muscle is no longer able to use oxygen and to generate adenosine triphosphate (ATP). Energy metabolism is shifted to anaerobic glycolysis to generate ATP. Lactic acid produced through glycolysis accumulates inside the muscle, which leads to a decrease in the muscle pH (Shen & Du 2016). The muscle pH drops from a pH of 7.2 in living muscle to a pH near 5.6 in meat *perimortem* (England et al. 2017). The pH and rate of decline have been associated with the water holding capacity (drip loss, %), tenderness and colour of the meat (Shen & Du 2016).

The results from I–III obtained pH values in the expected range for fresh meat, showing normal *post-mortem* decreases. There were no differences in the pH between breeds in I–II. In III there was a tendency for the Ab bulls to have slightly higher pH than the Li bulls. Previously, Manninen et al. (2011) reported similar loin pH levels of Hf bulls 24 h *post-mortem* in I–II. Corresponding to the present results of I–III, Chambaz et al. (2003), Cuvelier et al. (2006a,b) and Cafferky et al. (2019) also observed that there were no differences between breed types in meat pH. However, Huuskonen et al. (2016 a,b) reported that the loin pH of Ab bulls was significantly lower compared to dairy breed Nordic Red bulls.

**3.1.7.2. Drip loss**

The water holding capacity (WHC) has severe economic considerations, based on its relation to the meat yield and eating quality. Approximately three-quarters of meat is water (Kerth 2013). Drip formation is a function of the WHC of the meat. The WHC can be defined as the ability of fresh meat to hold all or part of its own water under external forces, such as gravity, pressing, cutting, or heating (Aberle et al. 2001). The WHC is an important quality attribute as it influences the yield and quality of fresh meat and meat products (England et al. 2017). More drip occurs when the WHC is low and less when it is high (Warriss 2010). The WHC develops from release of ions from sarcolemma as the pH drops. This can detrimentally affect the ability of muscle to retain fluid via its contribution to the myofibril lattice swelling and contraction (Warriss 2010, Kerth 2013).

There were no differences found in the drip loss values between Hf and Ch breeds in I. In contrast, in II the drip loss value of the Ch bulls tended to be higher compared to the Hf bulls (Figure 14). Recently, Cafferty et al. (2019) observed that the breed type can affect the drip loss. They reported that Ab breed sired bulls and steers had the lowest drip loss

(2.2%), followed by Hf (2.5%), Si (2.5%), Li (3.0%) and Ch (3.2%) breeds. Based on this, Cafferty et al. (2019) concluded that early maturing Ab and Hf breeds have the potential for juicier meat and less reduction in the yield associated with hanging compared to later maturing Continental breeds. Additionally, Chambaz et al. (2006) and Cuvelier et al. (2006b) perceived that Ab animals had lower drip loss values compared to Li animals. However, in III the breed type or crossbreeding did not have any effects on the drip loss values of Ab, Li or Ab × Li bulls.

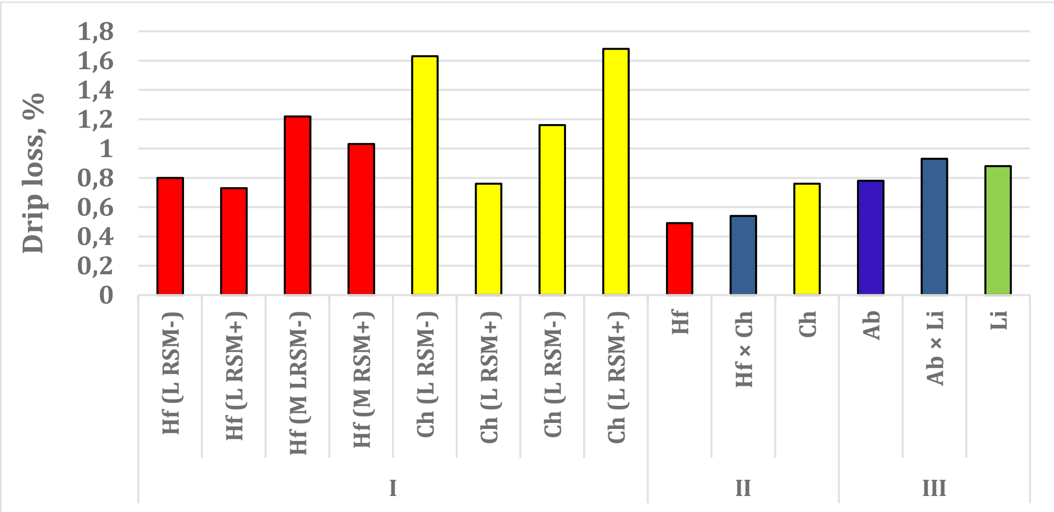


**Figure 14.** Drip loss (%) of bulls in experiments I–III. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

### 3.1.7.3. Colour

The sensory properties of food are the characteristics that consumers use to make purchase decisions. The first characteristic perceived at the time of purchase is the colour. This is often the only trait the consumer is able to consider at the time of purchase, especially in the current circuits of distribution. Consumers prefer bright red coloured meat (Ponnampalam et al. 2016). The colour of the muscle is mainly a function of myoglobin and the residual haemoglobin content (Lawrie & Ledward 2006).

Only small differences in meat colour between breeds were observed in I–III. In I the muscle lightness of the Ch bulls was higher than that of the Hf bulls while there were no differences in redness or yellowness between breeds. In II there was a tendency towards more muscle redness with Hf bulls than with Ch bulls. The Ab meat was slightly redder than that of Li bulls in III. Additionally, a small difference in yellowness in favour of Ab bulls was observed in III. There are a few breed differences in meat colour reported in literature. Some inconsistencies might be associated with management, age and fatness, especially the IMF amount, at slaughter (Koch et al. 1976, Wheeler et al. 2005, Warner et al. 2010). Generally, increasing slaughter age increases the redness of the meat (Hocquette et al. 2016). According to Lawrie & Ledward (2006), the meat colour is more affected by the animal's age and gender than by genotype. Older and more masculine animals have darker and redder muscle tissue. A higher roughage proportion in the diet also produces a darker meat colour, while muscular hypotrophy produces a substantially light meat colour (Hocquette et al. 2016).

Previously, Chambaz et al. (2006) observed no differences in redness and yellowness between Ab and Li breed steers. On the other hand, Cuvelier et al. (2006a,b) reported that Continental breeds had lower redness and higher lightness values compared to British breeds, while Ab bulls had the darkest and most red meat and Ba bulls had the lightest and less red meat colour. In that experiment the lightness value of the Li bulls was 6% higher than that of the Ab bulls, but there were no differences in redness and yellowness between Li and Ab bulls. This is in accordance with Papaleo Mazzucco et al. (2016) who observed that there were no differences between lightness, redness or yellowness between Ab and Hf steers. Ashmore & Vigneron (1988) associated increased lightness with reduced pigment content in the meat of Continental breeds. This suggests the presence of breed differences in relative muscle fibre proportions. Such physiological changes may be related to high genetic growth capacity and increased muscularity.

**3.1.7.4. Marbling score**

Marbling is an appearance factor which is commonly treated as a measure of eating quality (Wheeler et al. 1994). The term marbling refers to the appearance of white flecks or streaks of adipose tissue between the bundles of muscle fibres in bovine skeletal muscle (Harper & Pethick 2004). Marbling fat is commonly referred to as IMF, but marbling fat is structurally and compositionally distinct from true IMF or lipids which are present within the muscle cells (myocytes) (Tume 2004). Marbling is a complex phenomenon involving genetics, nutrition and the environment (Tume 2004). A common conclusion is that marbling or IMF is late developing. First abdominal fat develops, then intermuscular fat, subcutaneous fat and finally IMF (Lawrence et al. 2012). The proportional distribution of fat between carcass pools is found to be constant over a wide range of carcass fat contents indicating that the major fat depots grow in the same proportion as the animals fatten (Johnson et al. 1972, Pugh et al. 2005). Because fat is deposited at a greater rate than lean tissues later in life, the concentration of fat in muscle will increase later in an animal's life. Therefore the commercial trait, marbling, or visible IMF is a late maturing trait (Pethick et al. 2006). In general, in European feeding systems the IMF amount in bulls is 1.5–3.0% (Hocquette et al. 2011, Cafferky et al. 2019). In Finland the marbling score is considerably low, and on average it is 1.78 with Finnish grass and whole crop silage-based diets. This has been observed in purebred Ab bulls previously by Huuskonen et al. (2016a,b).

According to literature, the breed type or breed crossing affects the marbling score. In general, the British breeds increase and the Continental breeds reduce IMF content (Gregory et al. 1994, Williams et al. 2010). This is in agreement with I–III in which the marbling score of British breeds was 62% higher, on average (including both loin and entrecote), compared to Continental breeds. Additionally, Johnson et al. (1988) found that higher marbling scores were associated with British breeds than Continental breeds.

However, in constant back fat IMF tended to be similar between early and late maturing breeds when the animals are fed with high grain finishing diets (Crouse et al. 1985, Mandell et al. 1998, Laborde et al. 2001).

In I and II Hf bulls produced the most marbled beef. The marbling score of the Hf bulls was on average 1.59 and for Ch bulls it was 1.07, so the marbling score was 48% higher for the Hf bulls compared to the Ch bulls. Previously, Williams et al. (2010) concluded that Hf breed reduced marbling score 42% less than Ch when compared to Ab. In III the marbling score of the Ab bulls was on average (including both loin and entrecote) 1.45 and for Li bulls it was 0.46, hence the marbling score of the Ab bulls was on average 219% higher than that of the Li bulls. This is in accordance with many previous studies in which the marbling score of Ab animals has been the highest and Li animals have had the lowest marbling score compared to other observed breeds, while the marbling scores of Hf and Ch breeds have been intermediate (Koch et al. 1979, Gregory et al. 1994, Wheeler et al. 1996, Rios-Utrera et al. 2006, Williams et. al 2010). For example, Williams et al. (2010) observed that the marbling score of Ab animals was 71% higher than that of Li animals. Additionally, Papaleo Mazzucco et al. (2016) concluded that the least marbling was found in Li crossbred steers in grazing conditions compared to British breeds. Gogaoua et al. (2016) observed that Ab crossbred bulls had twice the amount of IMF compared to Continental crossbred bulls. Aass & Vangen (1998) concluded that the superiority of Ab animals in terms of the IMF content of their meat has been demonstrated in many studies, and Hf animals have been generally ranked similar or somewhat lower than Ab animals for this trait, while Ch animals showed the lowest degree of marbling in the meat.

The Ab breed increased the marbling score the most when used in crossbreeding (Koch et al. 1979, Gregory et al. 1994, Wheeler et al. 1996, Rios-Utrera et al. 2006, Williams et. al 2010). Johnson et al. (1988) also found that in crossbreeding greater marbling scores were associated with British than Continental breeds, while Rios-Utrera et al. (2006) found the least effects for marbling score with Li breed. Experiment II showed a similar trend as Hf crossbreeding tended to increase marbling compared to the purebred Ch bulls. In III Ab crossbreeding increased the marbling score compared to the pure Li bulls.

In I–III *longissimus lumborum* muscle samples were on average 30, 49 and 86% more marbled compared to *longissimus thoracis* muscle samples, respectively. Generally, the IMF content strongly depends on the size and number of intramuscular adipocytes (Cianzio et al. 1985). The studied muscle affects the marbling score. Muscles vary in the chronology of IMF development. Adipocytes appear earlier in the *longissimus dorsi* muscle than the *pectoralis* (Cianzio et al. 1985). There are many comparative studies of bovine muscles published (e.g. Johnston et al. 1975, Dryer et al. 1977, Young & Bass 1984, Picard et al. 1995, Chriki et al. 2012). These studies show significant compositional differences in fibre type and fibre size according to the muscle studied. There are also differences in fast and slow switch (I, IIA, IIX) muscle fibres. The oxidative, slow switch fibre types (IIX) could be associated with more IMF deposition compared to fast glycolytic muscle fibre types (Jurie et al. 2007, Chriki et al. 2012) which could lead to a more fully developed flavour from these muscle type (Jurie et al. 2007). Compositional variations in fibre type can also appear within the same muscle. Hunt & Hedrick (1977) showed more glycolytic fibres in the outer part of *M. semitendinosus*. The inner part was richer in oxidative fibres. The total lipid count difference between different muscles (*Longissimus thoracis* vs. *Triceps brachii*) in young bulls was observed to be 25% (Schreurs et al. 2008).

Marbling can account for over 5–10% of the variation in WBSF (Parrish et al. 1973, Wheeler et al. 1994, Magolski et al. 2013). Alternatively, Devitt et al. (2002) reported that marbling plays an important role in the juiciness and flavour of beef but, however, a limited role in tenderness. A minimum amount of IMF is needed for the flavour to be expressed. The relationship between the IMF level and a favourable flavour liking is curvilinear (Dransfield et al. 2003, Thompson 2004, Hocquette et al. 2011, O'Quinn et al. 2018). The curvilinear relationship between flavour liking and IMF plateaus in different studies at different points. Hocquette et al. (2011) observed with Continental bulls that the plateau was reached for 2–5% IMF while Thompson (2004) reported with mainly British breed steers that the plateau was reached at 14% IMF.

The lipid content plays an important role also in the juiciness of beef. O'Quinn et al (2018) reported that the marbling score explained 14–16% of variation in consumer palatability scores for each trait (tenderness, juiciness, flavour). Furthermore, IMF explained 17–21% of the variation in each trait. Meat with more fat is always less dry than lean meat when chewing in the mouth (Hocquette et al. 2016). In I and II the superiority of Hf bulls in tenderness and shear force compared to Ch bulls could be related to a higher marbling level. Previously, several authors (e.g. Gregory et al. 1994, Wheeler et al. 1996) have reported a favourable relationship between IMF content and shear force/tenderness scores. Aass & Vangen (1988) concluded that the superiority of Ab and Ab crossbreds in the IMF content of the meat has been demonstrated in many studies and Hf animals are generally ranked similarly or somewhat lower than Ab animals. This is in agreement with experiments I–III, and the Ab and Hf bulls had higher marbling scores compared to Ch and Li bulls.

### 3.1.7.5. Chemical composition

Meat is composed of water, protein and amino acids, fat and fatty acids, minerals, vitamins and other bioactive components and small quantities of carbohydrates (Lawrie & Ledward 2006). The proportions of these constituents vary with breed, gender, age at slaughter, marbling and cuts of muscles (Schönfeldt et al. 2010, Sexten et al. 2012). In general, beef constitutes 700–750 g/kg of water, 200–240 g/kg of protein and approximately 30 g/kg of fat (Sante-Lhoutellier & Pospiech 2016). Water in beef exists in three forms; free water, immobilized water and bound water (Li 2017). The water content is inversely proportional to the fat content (Li 2017). Meat from young bulls contains more water than that that of older cows (Zaujec et al. 2012). More marbled meat contains less water than meat that has less marbling (Li 2017). Meat is a good source of high biological value protein. The biological value of meat protein depends to a certain extent on its composition and process conditions. The amount of collagen is a deceive factor. Collagen is composed of hydroxyproline and other amino acids and crosslinks. These are resistant to digestive enzymes (Li 2017). Meat is generally considered to be a source of saturated, monounsaturated and polyunsaturated fatty acids (Li 2017).

In I the loin samples of Ch bulls had higher moisture and protein and lower fat contents than that of Hf bulls. In II the breed did not have an effect on the moisture composition of meat. However, the loin sample of the Ch bulls had higher protein and lower fat content compared to the Hf bulls. In III the loin of the Li bulls contained higher moisture and protein contents, but lower fat contents compared to the Ab bulls. This is in accordance with Cuvelier et al. (2006a) who concluded that the meat of Ab bulls had higher lipid and lower protein contents compared to Li bulls. Corresponding to I and II, Bureš et al. (2006) reported that the meat samples from British breed (Ab, Hf) bulls had lower moisture and protein contents but higher lipid contents compared to Continental breeds (Ch, Si). These results indicate that an increase in lipid concentration was associated with increased DM contents and reduced protein contents which is in accordance with the findings by Van Koevering et al. (1995). Similar results of greater IMF deposition and lower moisture in British breed sired steers compared to Continental breed sired steers have been reported earlier Gregory et al. (1994).

#### 3.1.7.6. Shear force

The most common and widely accepted objective measure of tenderness is shear force. This is a measure of the amount of force required to cut through, or shear, a piece of cooked or raw meat (Kerth 2013). Breed rankings for shear force agree very closely with inverse rankings for sensory tenderness (Marshall 1994). Tatum et al. (2007) and Devitt et al. (2002) listed numerous factors that affect tenderness including genetics, the time on feed, nutrition, stress, age, chilling rate, state of muscle contraction, proteolytic degradation by calpain system, amount of connective tissue, *post-mortem* aging and the cooking method. Tenderness or its opposite toughness is consistently shown to be the most important factor in consumer satisfaction with beef (Warner et al. 2010). Toughness comes from two sources. Myofibrillar toughness is the state of the contractile tissue of the muscle and background toughness is the result of the connective tissue framework supporting the muscle fibres (Price 2017). Myofibrillar toughness is strongly influenced by *post-mortem* treatment of the muscle (Koohmaraie 1994, Warriss 2010). Background toughness varies greatly between muscles. The background toughness increases with the age of the animal. As the animal matures the number and stability of the cross-links within and between collagen fibres increases (Lawrie & Ledward 2006).

In I–III the bulls were slaughtered at high carcass weights (≥ 400 kg) and the average shear force values were above 5 $kg/cm^2$, which have been estimated to be a borderline for tough meat (Destefanis et al. 2008). In general, WBSF values have been reported to increase with increasing carcass weights and maturity (Van Koevering et al. 1995). Increasing the slaughter age is associated with tougher meat due to strengthening of the collagen structure (Lawrie & Ledward 2006). The carcass weight can be the second most influential carcass trait accounting for approximately 4% of the variation in WBSF (Magolski et al.

2013). Tough meat can also be associated with the gender of the animals. Cooked loin steaks from young bulls had 8–12% higher shear force values and generally lower sensory panel tenderness ratings compared to steers (Johnson et al. 1988). Cafferky et al. (2019) observed that the WBSF values of steers were approximately 15% lower than that of bulls.

The shear force values in I–III (Figure 15) were higher than reported in some previous studies on similar breed types (Shackelford et al. 1999, King et al. 2003). On the other hand, the shear force values reported by Papaleo Mazzucco et al. (2016) corresponded well compared to I–III. In I the shear force value of Ch bulls was 13% higher compared to Hf bulls but in II there were no significant differences between breeds or breed crosses. Previously, Wheeler et al. (2005) observed that British breed cattle produced more tender beef than Continental breed cattle in carefully controlled conditions. Johnson et al. (1988) also observed a slightly lower shear force value for British breed type animals compared to Continental type animals. Likewise some other studies have confirmed lower shear force values for Ab than other observed breeds (Gregory et al. 1994, Wheeler et al. 1996). However, this was not the case in III where no significant differences were observed in WBSF between Ab, Li and Ab x Li bulls. In agreement with III, Rødbotten et al. (2002), Chambaz et al. (2006), Cuvelier et al. (2006b) and Cafferky et al. (2019) observed no significant differences in the shear force values between Ab and Li breeds.

Two calcium activated enzymes are associated with the meat tenderness process. Calpain enzyme is the main enzyme in myofibrillar degradation during ageing. Calpastatin inhibits the degradation process (Koohmaraie 1994). Fast twitching glycolytic muscle fibres have been shown to have a higher relative proportion of calpastatin (Astruc 2014). The number of glycolytic muscle fibres increases when favouring more muscular cattle type (Plastow & Bruce 2014) which may explain some differences observed in the tenderness between the British and Continental breeds.

Several authors (Koch et al. 1979, Gregory et al. 1994, Wheeler et al. 1996, Cafferky et al. 2019) have reported a favourable relationship between marbling scores, shear force values and tenderness scores among different breeds. In I the loin (*Longissimus lumborum*) and entrecote (*Longissimus thoracis*) of Hf bulls had 39% and 44% higher marbling scores than those of the Ch bulls and the shear force value of the Ch bulls was 13% higher than that of the Hf bulls. This might be seen as a favourable relationship between marbling and shear force values. However, in II–III this effect was not observed, which is in agreement with Coleman et al. (2016) who did not observe associations between these traits. Breed crosses and breed composites tend to have less differences in meat eating quality and this is considered a result of the pure breed effect being diluted (Muir et al. 2000, Papaleo Mazzucco et al. 2016).

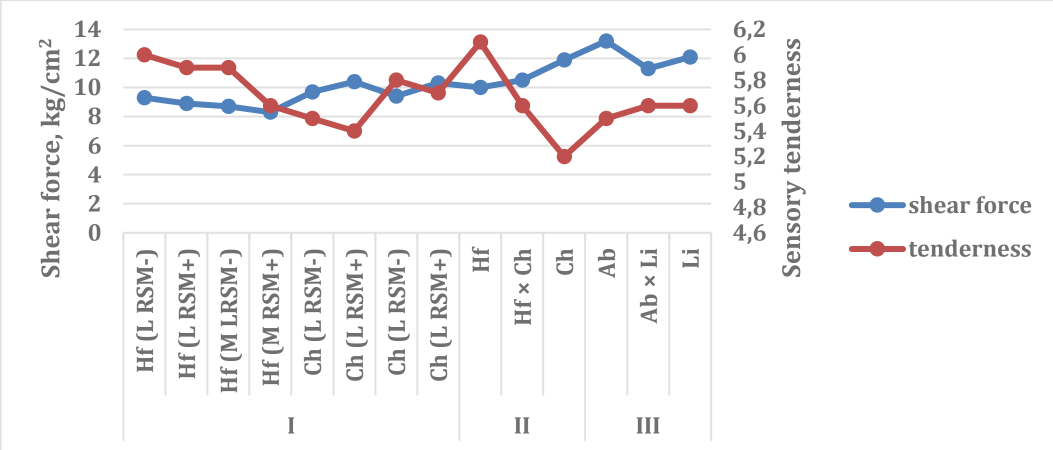


**Figure 15.** Shear force and tenderness in experiments in I–III. Ab = Aberdeen angus; Ba = Blonde d'Aquitaine; Ch = Charolais; Hf = Hereford; Li = Limousin; Si = Simmental; L = low concentrate proportion (200 g/kg dry matter); M = medium concentrate proportion (500 g/kg dry matter); RSM- = without rapeseed meal supplementation; RSM+ = with RSM supplementation.

### 3.1.7.7. Sensory analysis

Meat eating quality can be broken into tenderness, juiciness and flavour. Sometimes also other factors such as mouthfeel and overall liking are included (Warner et al 2010). Meat palatability or taste is the ultimate measure of meat quality. Even at the same fatness and IMF content, there is little difference between the sensory properties of meat from different breeds (Dransfield et al. 2003). Comparisons of the sensory quality of the meat between breeds show that, in all cases, the discriminatory factor is tenderness. In most cases tenderness is generally positively associated with the IMF content of beef (Renand 1988, Dransfield et al. 2003). The association between the IMF content and a sensory analysis of tenderness was observed by Gregory et al. (1994) in a multibreed analysis. In general, as the fat content increases the palatability increases (Kerry et al. 2002).

In I there were no differences in the juiciness and beef flavour between breeds, but there was a tendency for a 6% higher tenderness for Hf bulls compared to Ch bulls. A similar trend was observed in II where the breed had no significant effects on the beef flavour, but the tenderness was 17% higher and the juiciness was 8% higher in Hf bulls compared to the Ch bulls. Earlier, Sinclair et al. (2001) observed decreased tenderness in late maturing Ch steers compared to earlier maturing Ab steers. The higher tenderness can be related to the higher marbling score of the Hf bulls compared to the Ch bulls in I and II which would be in agreement with Gregory et al. (1994), Wheeler et al. (1996) and O'Quinn et al. (2018).

In III the breed or breed cross did not have any significant effects on the sensory quality, tenderness, juiciness or beef flavour. Correspondingly, Chambaz et al. (2006) did not observe any differences between breeds concerning the tenderness of beef. However, there was a difference in the juiciness in the meat. Limousin steers had the juiciest meat, Ch and Si steers had an intermediate level of juiciness and Ab steers had the least juicy meat (Chambaz et al. 2006). In contrast, Koch et al. (1976) observed Ab and Ch crossbred steers to have same tenderness and noted that Li and Si crossbred steers had more tough meat when comparing animals of the same age. Sevane et al. (2014) reported that Ab bulls had the highest flavour marks in 15-breed evaluation. Even though there has been consistent agreement in the literature on the favourable relationship between the marbling score and overall liking of the meat (tenderness, juiciness, beef flavour) of beef (e.g. O'Quinn et al. 2018) no relationship was found in I–III (Figure 16).

Although some reports have shown breed effects on individual flavour notes detected by instrument analysis (Sato et al. 1995, Insausti et al. 2005), individual tasters show varying abilities to detect individual flavours (Lawrie & Ledward 2006). The overall sensation is a combination of all tastes and flavours. It is very difficult to show any consistent difference which can be attributed to the breed (Price 2017). O'Quinn et al. (2018) concluded that all of the palatability traits influence consumer acceptance. The failure of even a single palatability trait dramatically increases the likelihood of overall palatability failure. This indicates that no single palatability trait is the most important.

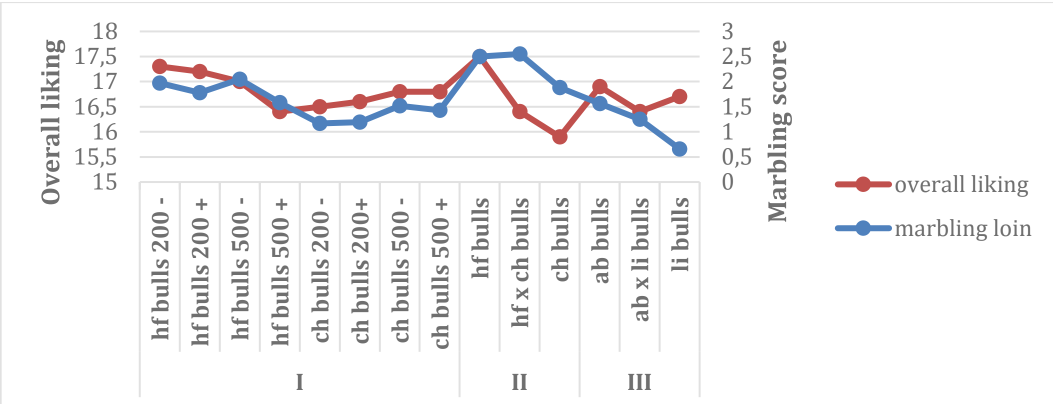


**Figure 16.** Marbling score and overall liking in experiments in I–III.

### 3.1.7.8. Fatty acid profile

The main nutritional advantage of beef is that it provides a source of high-quality protein (Herring 2014). McAfee et al. (2010) concluded that consuming moderate amounts of lean red meat valuably contributes to the intake of essential nutrients and possibly to the intake of long-chain n-3 polyunsaturated fatty acid (PUFA) and conjugated linoleic acid (CLA). The importance of the fatty acid composition of food is related to the fact that the human consumption of saturated fatty acids (SFA) raises the total cholesterol and LDL-cholesterol and increases the risk of cardiovascular heart disease. However, it has been suggested that not all SFAs have the same hypercholesterolomic effect: 18:0 has a neutral effect on plasma cholesterol level while 16:0 is less potent than 12:0 and 14:0 (Ulbricht & Southgate 1991, Daley et al. 2010). The meat's fatty acid composition may vary considerably from one animal to another due to nutrition, breed, age and gender (Yang et al. 1999). The fatty acid composition of beef is less dependent on diet than that of meat from non-ruminants and it is largely determined by key lipogenic enzymes in fatty acid synthesis pathways (Zhang et al. 2008). Intramuscular fat consists of 0.45–0.48 of SFA, 0.35–0.45 of monounsaturated fatty acids (MUFA) and up to 0.05 of PUFA. The PUFA:SFA ratio (P:S) for beef is typically low at around 0.1 (Scollan et al. 2006). A meta-analysis has shown that increasing the human dietary P:S ratio can lead to reductions in the total plasma (cholesterol) (Howell et al. 1997, Scollan et al. 2001).

The n-6:n-3 ratio for beef is beneficially low, and is typically less than 3, reflecting the considerable amounts of beneficial n-3 PUFA in beef, particularly 18:3n-3 and long chain PUFA, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). The n-6:n-3 ratio is an index which is utilized to evaluate the nutritional value of fat: a ratio below 4.0 in the diet is recommended to prevent diseases such as coronary heart disease and cancers (Simopoulos 2004). Forage is a very important component of the diet and is a cheap and abundant source of n-3 PUFA (Scollan et al. 2006). Beef also contains CLA and in particular cis-9, trans-11, trans-10, cis-12 CLA. The anticarcinogenic and antiatherogenic effects of cis-9, trans-11 and the anti-obesity effects of trans-10, and cis-12 CLA have been well documented (Belury 2003). Mateescu (2015) concluded that beef is a major dietary source of CLA.

According to Scollan et al. (2006) the predominant SFAs in beef are 14:0 (myristic acid), 16:0 (palmitic acid) and 18 (stearic acid) (Scollan et al. 2006), which is in agreement with the results of I. In I the breed had effects on the fatty acid composition of the meat, notably the amounts of 16:1 cis-9 and 18:1 cis-9 fatty acids were higher in Hf breed animals compared to Ch breed animals. Previously, Rule et al. (1997) reported that Hf crossbred steers had more 16:0, 18:0 and total SFAs than Ch crossbred steers. However, several studies have found no differences in the SFA percentage of LM lipids between early and late maturing breeds at constant times on feed (Eichhorn et al. 1986, Siebert et al. 1996).

The n-6:n-3 fatty acid ratio of the LM in the Ch bulls was 20% higher than that of the Hf bulls (I). In addition, the LM of Ch bulls contained a higher proportion of PUFA compared to the Hf bulls. In contrast to this, the LM of the Hf bulls contained a higher proportion of MUFA compared to the Ch bulls. The breed had no effect on the proportion of SFA or CLA. Breed differences and the associated effects of maturity or growth potential on the subcutaneous fat or fatty acid composition of beef are discussed in a review by de Smet et al. (2004). It is possible that the differences in carcass fat scores between breeds in I affected the differences in the fatty acid composition of the LM. De Smet et al. (2004) stated that carcass fat scores affect the meat's fatty acid profile and reported breed differences are often confounded by differences in fatness.

Lipid differences between breeds may be caused by their different history, production purpose, as well as the selection of beef characteristics in response to commercial or cultural requirements (Alberti et al. 2008, Felius et al. 2011). Laborde et al. (2001) found that the total MUFA and MUFA:SFA ratio was greater in late maturing Si animals than in early maturing Red Ab animals when feeding them high grain finishing diets. Additionally, Sevane et al. (2014) observed that large breeds had lower levels of MUFA than early maturing breeds. In some other studies on a similar finishing diet there have not been found any meaningful differences in individual and total MUFA values between early and late maturing breeds (Siebert et al. 1996, Rule et al. 1997).

Polyunsaturated fatty acids include the n-6 and n-3 fatty acid classes, which have been found to be essential for normal growth, development, reproduction, and overall human health with a recommended dietary n-6:n-3 ratio of 4:1 to 10:1 (Neuringer et al- 1988). Eichhorn et al. (1986) found greater relative amounts of 18:2n-6 and 20:4n-6 in intramuscular lipids in Continental-crosses compared to Ab cows at a constant time on feed. Laborde et al. (2001) found no breed differences in individual or total n-6 PUFA or PUFA:SFA ratios, whereas the n-6:n-3 ratio was 25% higher in Si than in Red Ab steers when fed a high grain finishing diet. Siebert et al. (1996) and Rule et al (1997) did not find any significant differences in the total amounts of PUFAs between early and late maturing breeds.

Earlier, on *ad libitum* concentrate feeding an evaluation of 15 breeds suggested that Ab bulls had a significantly lower n-6:n-3 ratio compared to Ch and Li bulls (4.58 vs. 6.75 and 6.13) (Sevane et al. 2014). Coleman et al. (2016) observed that the n-6:n-3 ratio was lower in Hf-sired steers from Ab cows compared to other crossbred cows. They concluded that meat from steers from Ab dams may be a healthier option. The higher absolute n-3 PUFA muscle content is a specific characteristic of British breeds, especially Ab, not only due to the grass-based diets generally used in the UK (Scollan et al. 2006, Sevane et al. 2014). Sevane et al. (2014) observed that Highland cattle, followed by the Ab breed, produced the most CLA in their meat. This is in agreement with Huuskonen et al. (2016a,b) who observed that Ab bulls produced slightly more CLA than Nordic Red bulls.

The results of I suggest that Hf bulls produced healthier meat with a lower n-6/n-3 fatty acid ratio and higher MUFA concentration compared to the Ch bulls. Nevertheless, many of these observed breed differences were relatively small and probably of little value from a nutritional viewpoint. Previously, Sevane et al. (2014) concluded that the focus should be more on conversion of 18:3 n-3 to 22:6 n-3 fatty acids, which would favour the lean Continental breeds for producing healthier meat. In their study which evaluated 15 breeds, Ch and Li animals produced the healthiest meat. This conversion was not that obvious in I.

## 3.2. Effects of concentrate proportion

### 3.2.1. Diet digestibility and animal performance

The apparent diet digestibility of DM and organic matter (OM) increased with an increasing proportion of barley-based concentrate in the diet (I). The substitution of grass silage with barley grain improved the digestibility, because the digestibility of barley is generally higher than that of grass silage (Luke 2020). The increased apparent digestibility of DM and OM of grass silage-based diets due to increasing concentrate feed level has been well documented previously, for example by Steen et al. (2002), Huuskonen et al. (2007) and Keady et al. (2007, 2008).

The NDF digestibility decreased by 3% with an increasing concentrate proportion in the diet (I). The reduction in fibre digestibility due to increased concentrate level has been reported previously by Huhtanen & Jaakkola 1993, Steen et al. (2002), Huuskonen et al. (2007) and Keady et al. (2007, 2008). The negative associative effect is mainly attributed to a depression of the fibre digestibility in the rumen and in the digestive tract from the inclusion of rapidly fermentable carbohydrates such as barley-based (starch) concentrates (Huhtanen & Jaakkola 1993) and sucrose (Khalili & Huhtanen 1991) in grass silage-based diets. The presence of starch and sugars reduces fibre digestion when cattle are fed diets containing cereal grains (Mould et al. 1983). In addition, barley fibre has lower digestibility compared to the fibre fraction of grass silage (Luke 2020).

Increasing the concentrate proportion led to a higher DM intake (DMI) and energy intake of the bulls (I), which is in agreement with previous studies in which increasing the supplementary concentrate level in the diet of growing cattle has reduced grass silage intake but increased the total DMI with TMR (Caplis et al. 2005, Keane et al. 2006) or with separate (Drennan and Keane 1987, Dawson et al. 2002) feeding. Mandell et al. (1998) stated that gut fill restricts DMI on high forage diets and this affects DMI especially when the LW is low. The substitution rate (SR, decrease in grass silage DMI per kg increase of concentrate DMI) was 0.81 and 0.60 for Hf and Ch bulls, respectively (I). This is in accordance with grass silage-based feeding reported by Keane (2010) (crossbred steers; SR 0.82), Manninen et al. (2010) (Hf bulls; SR 0.71 and 0.53 for farm-made concentrate mixtures and commercial compounds) and Randby et al. (2010) (dairy bulls; SR 0.75). McNamee et al. (2001) reported that the concentrate level and silage feeding value are major factors affecting the concentrate SR. Keady & Kilpatrick (2006) (beef breed bulls) and Steen et al. (2002) (beef breed steers) used high feed value grass silage and reported substitution rates of 0.91 and up to 1.00, respectively.

Increasing the concentrate proportion led to an improvement of both LWG and carcass gain of the bulls (I). The improved growth rate was probably due to improved diet digestibility and increased DM and energy intakes with the increasing concentrate proportion. The DMI of the Ch bulls increased more compared to the Hf bulls as a consequence of increased concentrate level (I). The observed increases in LWG were 75 and 91 g/d per 1 kg increase in concentrate DMI for Hf and Ch bulls, respectively. This is consistent with grass silage feeding experiments by Martinsson (1990) with dairy bulls (84 g/d) and Manninen et al. (2010) with Hf bulls (85 and 90 g/d for farm-made concentrate mixtures and commercial compounds). Nevertheless, Huuskonen et al. (2007) reported clearly smaller response with dairy bulls (27 g/d). Prior et al. (1977) observed that the gains with energy restricted diets were better with British compared to Continental breed steers. In contrast, McGregor et al. (2012) observed that increasing the forage proportion in the diet reduced the DMI and growth more with British compared to Continental crossbred steers in the backgrounding phase. However, in the finishing phase with a high concentrate diet there were no differences in DMI between breeds (McGregor et al. 2012). Block et al. (2001) reported a lower DMI and growth for British than Continental steers during the background phase with a high forage diet.

The increasing effect of the concentrate proportion on the dressing proportion (I) agrees with earlier reports (Caplis et al. 2005, Keane et al. 2006). An increased concentrate proportion also improved the carcass conformation (I) which is consistent with Keane & Fallon (2001) and Caplis et al. (2005), but contrary to Huuskonen et al. (2007), Manninen et al. (2010) and Randby et al. (2010). A higher energy intake probably partly explains the increased conformation score with the increasing concentrate proportion. Previously, Caplis et al. (2005) reported that the carcass conformation of finishing steers increased with increasing concentrate level and energy intake. The carcass fat score increased with increasing concentrate proportion (I). According to literature, increasing the concentrate level and energy intake usually also increases the carcass fat content (Patterson et al. 2000, Keane et al. 2006, Huuskonen et al. 2007). Furthermore, higher carcass weights with increasing concentrate level probably partly explain the increased fat score, because the carcass fatness generally increases with higher carcass weights (Keane & Allen 1998).

### 3.2.2. Meat quality

Previously, Keady et al. (2007, 2008) concluded that the concentrate level has only minor effects on meat quality traits with grass silage-based diets. This was also mainly the case in I. The marbling levels were low altogether in I which might be due to the grass silage-based diet. In general, high levels of IMF deposition require excess energy consumption above the maintenance and normal production requirements (Robinson et al. 2001, Pethick et al. 2004, McKiernan et al. 2009). During finishing period, high energy grain feeding is the most effective and commonly used diet because it promotes IMF development more than forage-based feeding systems (Johnston et al. 2003, Reverter et al. 2003). Concentrate, in this case cereal grain, would generate additional glucose via gluconeogenesis from the propionate or via direct absorption of glucose in the small intestine (Rowe et al. 1999). Ørskov (1986) reported that up to 42% of dietary starch may escape ruminal fermentation and reach the small intestine. The meat IMF content can also be affected by different forage vs. concentrate interactions. Hocquette et al. (2010) suggested that the energy relative to protein in the diet and availability for utilization by the tissues is different in concentrate- and forage-based diets. An increased forage proportion changes the fatty acid metabolism in the rumen and increases the long chain fatty acid isomers of the conjugated linoleic acid that inhibits triglyceride synthesis (Kennedy et al. 2010, Bauman et al. 2011). Forage and concentrate diets have different amounts of n-6 and n-3 fatty acids which might affect the IMF proportion (Ailhaud et al. 2006).

In agreement with Caplis et al. (2005), an increasing concentrate proportion increased the muscle lightness by 3% but did not affect the redness or yellowness of LM (I). Caplis et al. (2005) reported no effects on muscle redness and yellowness between concentrate proportions of 310 and 550 g/kg DM but the muscle lightness increased with an increasing concentrate level. It is well established that muscle colour is generally darker in forage-fed than in concentrate-fed cattle (Priolo et al. 2001, Realini et al. 2004, Caplis et al. 2005, Dunne et al. 2006, Duckett et al. 2007, 2013, Berthiaume et al. 2015). Grain-fed cattle usually have more fat and glycogen, which promotes warmer *post-mortem* muscle temperatures and increases glycolysis and lactic acid formation, especially in larger muscles. The higher lactic acid formation reduces the pH and leads to less WHC and results in a paler meat colour compared to grass-fed cattle (Priolo et al. 2001, Ramanathan & Mancini 2017). The increased lactic acid formation can also result in greater oxygen consumption by myoglobin than mitochondria (Ramanathan & Mancini 2017). Competition for oxygen between myoglobin and mitochondria is the key determinant of beef colour development. Increased pH enhances mitochondria activity which reduces myoglobin oxygenation or the red colour intensity (Tang et al. 2005, Ramanathan & Mancini 2017).

The n-6:n-3 ratio of LM increased by 59% with higher concentrate levels in this study (I). The higher concentrate level also affected the proportion of MUFA which tended to be 5% higher compared to the lower concentrate level. In contrast, the low concentrate fed bulls tended to have a 4% higher proportion of SFAs compared to higher concentrate level bulls. The concentrate level had no effect on the PUFAs. In addition, the increasing concentrate level reduced the relative proportion of 15:0, 17:0, 18:1 cis-11 and 18:3 cis-9, cis-12, cis-15 fatty acids. The relative proportion of 18:1 cis-9 and 18:2 cis-9, cis-12 increased with a higher concentrate proportion. A higher concentrate proportion tended to increase the 10:0 fatty acid in the meat.

In general, pasture finishing systems produce higher quantities of n-3 PUFAs in the muscle than concentrate feeding, and forage-based diets can improve PUFA:SFA and n-6:n-3 ratios in meat (Wood & Enser 1997, Gatellier et al. 2005, Rochort et. al 2008). Forage in the ruminant diet generally accumulates n-3 PUFA in the meat (Mahecha et al. 2010). Typically, beef cattle fed concentrate diets produce meat with significantly higher n-6:n-3 ratio in comparison to forage-fed animals (Gatellier et al. 2005, Ponnampalam et al. 2006). Daley et al. (2010) reported that grain-fed beef produces lower concentrations of 18:3 cis-9, cis-12, cis-15 fatty acids and higher concentration of MUFAs (e.g. 18:1 cis-9) compared to grass-fed beef. Daley et al. (2010) also concluded that increasing the concentrate level generally increases the n-6:n-3 fatty acid ratio of the LM. A healthy diet should consist roughly of four times more omega-6 fatty acids than omega-3 fatty acids. In a review article, Daley et al. (2010) presented overall averages of 1.53 and 7.65 for grass-fed and grain-fed beef, respectively. In I the n-6:n-3 fatty acid ratio was 3.16 for lower concentrate level and 5.03 for higher concentrate level, on average.

## 3.3. Effects of protein supplementation

### 3.3.1. Diet digestibility and animal performance

In accordance with previous studies (Huuskonen et al. 2008, Huuskonen 2009b) RSM supplementation had no effect on the DM, OM or the NDF digestibility when barley grain was partly replaced by RSM (I). However, the CP digestibility was higher for RSM+ diets compared to RSM- diets (I). In general, the possible positive effect of protein supplementation on OM digestibility or fibre digestion has been most notable when the digestibility of the forage has been low (Stokes et al. 1988, Delcurto et al. 1990, Huuskonen 2009a). Some of the increased apparent digestibility of the CP in the RSM supplemented diets in this study may have reflected the better digestibility of RSM protein. Most of the increase was probably only apparent related to a decreased proportion of faecal metabolic nitrogen recovered in the faeces when the CP content increased (Minson 1982).

The average supply of CP, AAT and PBV were higher when RSM was included in the diet, but RSM supplementation did not have an effect on the DM or energy intake (I). Correspondingly, protein supplementation has been found to have no effects on DMI in grass silage-based diets in many previous experiments (Drennan et al. 1994, Huuskonen et al. 2007, Huuskonen 2009b, Manninen et al. 2011). However, in some experiments partial replacement of cereal grains by protein feeds has had a small, positive effect (3–5%) on intake (Aronen and Vanhatalo 1992, Aronen et al. 1992). Based on a meta-analysis, Huuskonen et al. (2013) concluded that the intake response of growing cattle to protein supplementation on grass silage-based diets was minimal with a maximum predicted response less than 2%, which is much smaller than the corresponding response in dairy cows.

The growth rate of the bulls tended to be slightly lower on RSM- than RSM+ diets (I). In a recent meta-analysis Huuskonen et al. (2014a) developed empirical equations predicting growth responses of growing cattle to protein intake in grass silage-based diets. They concluded that increasing the dietary CP concentration increased the LWG significantly, but the response was quantitatively small (1.4 g/d per 1 g/kg DM increase in the dietary CP concentration, on average). The response also showed diminishing responses with an increased CP concentration (negative quadratic effect) (Huuskonen et al. 2014a).

In single feeding experiments, the effect of protein supplementation on the LWG has been rather inconsistent. The greatest responses have been observed with young animals (Jaakkola et al. 1990, Steen 1992) and often the positive effect was restricted to just the early phase of the growing period (LW below 300 kg) (Huhtanen et al. 1989, Aronen 1990). In several experiments a large proportion of the advantage of protein supplementation of young cattle was lost during the finishing period due to compensatory growth (Titgemeyer & Löest 2001, McGee 2005). In addition, results with grass silage are dependent on the quality of the silage that may vary considerably with the ensiling technique. With poorly preserved silage the response in animal performance to protein supplementation is greater than with well-preserved silage (Hussein & Jordan 1991, Huuskonen et al. 2014a). There are also observed differences between extensively and restrictively fermented silage which both may be well-preserved. For example, Jaakkola et al. (1990) observed that the growth response of growing cattle to fishmeal was greater when an enzyme solution (cellulose-glucose oxidase) was used as a silage additive instead of formic acid. Moreover, Jaakkola et al. (2006) reported that restriction of the silage fermentation by formic acid is positively related to the synthesis of microbial protein in the rumen. In I the fermentation quality of the silage was good and the silage was restrictively fermented with a high residual WSC concentration and low lactic acid concentration. Possibly the gain responses to protein supplementation would have been greater with untreated and/or poorly preserved silage.

The average LWG response to RSM supplementation was slightly higher with a lower concentrate proportion (67 vs. 45 g/d) (I). This in line with Huuskonen (2009a) who concluded that growth responses to protein supplements seem to be also related to the level of concentrate supplementation, and greater effects were observed with small amounts of concentrates. Hagemeister et al. (1980) observed a tendency towards lower rumen protein synthesis with rations containing very low (0–20%) or very high (70–100%) proportions of concentrate. According to Aronen (1992) a medium level of concentrates together with well-preserved grass silage may sustain efficient microbial protein production. Therefore, it is likely that a greater response to protein supplementation is to be expected when small rather than large amounts of concentrates are fed to growing cattle during grass silage-based feeding.

Rapeseed meal supplementation had no effect on the dressing proportion, carcass conformation or carcass fat score (I). Consistently, also Huuskonen et al. (2007, 2008, 2014a) and Manninen et al. (2011) reported that protein supplementation had no effect on the dressing proportion or carcass conformation score. Generally, RSM has not significantly affected carcass fat score in individual feeding experiments. Nevertheless, based on a meta-analysis, Huuskonen et al. (2014a) reported that increased dietary CP concentrations increased the carcass fat score. However, although significant, the effect was quantitatively minimal (Huuskonen et al. 2014a).

Recent results indicate that reducing dietary N inputs in growing cattle diet would be an effective way to reduce the urinary and manure N output, and to reduce excretions per kg LWG and carcass gain (Huuskonen et al. 2014a, Huuskonen & Huhtanen 2015). The results showed a poor utilisation of supplementary protein in growing cattle that consequently increased N emissions. A major proportion of the incremental N intake is excreted in urine (Huuskonen et al. 2014a). As urinary N is more susceptible to both leaching and evaporation compared to faecal N, the adverse effects on the environment increase proportionally more than the N output in manure. Recently published meta-analyses have indicated that the magnitude of LWG responses to increased protein supply is generally small when growing cattle are fed grass silage-based diets (Huuskonen et al. 2014a, Huuskonen & Huhtanen 2015), and that increased dietary protein has no effect on the carcass weight, dressing proportion or carcass conformation (Huuskonen et al. 2014a). Therefore, reducing dietary N input is a rational strategy to reduce the manure N output.

### 3.3.2. Meat quality

Rapeseed meal supplementation had no significant effects on the chemical composition, shear force value, drip loss, colour, marbling score or sensory analysis of LM (I). Previously, Pethick et al. (2000) used different levels of protein supplements in diets for feedlot steers. Protein supplementation did not lead to significant differences in IMF levels. Nevertheless, there was a trend for high protein diets to produce less IMF than low protein diets (Pethick et al. 2000). Their conclusion was that a simple diet based on barley and hay with no additional protein source in the form of grain legumes or urea would produce an equal result to formulated rations containing additional protein sources. The RSM supplementation had no effects on the n-6:n-3 fatty acid ratio of the LM or on the proportion of SFA, MUFA or PUFA (I). In contrast, RSM supplementation reduced the relative proportion of 10:0, 14:0, 16:0 and 16:1 cis-9 fatty acids in LM (I). To my knowledge, very little research has been done into the effects of RSM supplementation on beef fatty acid composition. However, feeds containing 18:3 n-3 (e.g. camelina meal, flaxseed, rapeseed cake) have previously improved the meat n-6:n-3 fatty acid ratio of cattle and sheep (Herdmann et al. 2010, Nassu et al. 2011, Juárez et al. 2011, Noci et al. 2011).

# 4. Conclusions

## 4.1. Concluding remarks

1. Beef breeds differ considerably in their beef producing traits. Significant breed differences were observed in the present study in growth performance, carcass traits and retail product yield. The later maturing, Continental breeds achieved higher carcass weights, produced less fat and had more valuable cuts than the earlier maturing British beef breeds. The Continental breeds exceeded British breeds in the total amount of produced meat. The later maturing beef breeds tend to have carcass traits under current Finnish feeding management practices that suit the Finnish beef production system well.
2. According to the hypothesis, the crossbred British × Continental bulls had higher growth performance and they produced better conformed carcasses and a higher proportion of valuable cuts compared to purebred British bulls. The challenge with British breeds is their early maturing breed type when aiming for high carcass weights and long feeding period. However, the growth and carcass traits can be enhanced for the current market demand by crossbreeding British breed dams with Continental breeds. This type of crossbreeding can enhance beef production under typical Finnish production conditions.
3. Continental breeds were classified with lower fat scores compared to British breeds. By using Continental breed bulls it is possible to achieve 400–500 kg carcass weights with a EUROP fat score of 2–3. When aiming for a fat score of 3 or 3+ for beef breed bulls a carcass weight range should be aimed for breed specifically. For example the following weight ranges would be optimal: Ab 366–385 kg, Ba 412–430 kg, Ch 435–455 kg, Hf 369–390 kg, Li 412–430 kg and Si 424–445. However, even up to 500 kg carcass weights with a fat score of 3 are possible for Ch bulls.
4. Continental breeds are not able to produce the same quality product on same diet as British breeds. British breeds excel Continental breeds when it comes to producing a consistent and high eating quality product on various diets. In this study, British breeds produced more intramuscular fat in the meat than the Continental breeds. British breeds produced higher sensory quality meat than the Continental breeds. British breeds also have a genetic advantage and produce a healthier fatty acid composition in the meat than the Continental breeds. British breeds had more MUFA and a lower n6:n3 fatty acid ratio in the meat.
5. In contrast to the hypothesis, crossbreeding British breeds with Continental breeds did not have significant effects on the shear force value or sensory quality (tenderness, juiciness and beef flavour) of the meat. However, Ab crossbreeding increased the marbling score compared to the pure Li bulls and Hf crossbreeding tended to increase marbling compared to the pure Ch bulls.

6. A grass silage-grain-based diet suited growing and finishing diets well for beef breeds. However, as hypothesised, the growth performance and carcass conformation improved with increasing concentrate level and Ch bulls benefited from an increased diet concentrate level more than Hf bulls. The quality and digestibility of the used grass silage is essential for good production results.
7. The concentrate level had only minor effects on meat quality traits in a grass silage-based diet. However, the concentrate level may affect the fatty acid composition in the beef. In the present study increasing the concentrate proportion increased the meat's n6:n3 fatty acid ratio.
8. Protein supplementation did not lead to any substantial advantages. In contrast, using protein supplements increases the negative environmental impacts of beef production.

Generally, producers need to consider not only growth, maternal ability, and production efficiency, but also carcass and meat quality traits to meet market demand. The overall costs of production are affected also by the feed conversion efficiency in a given farm environment, as well as the hardiness and temperament of the animals. Suckler herd producers must pay attention to the mothering characteristics, fertility, milk production, and the ease of calving and select breed combinations for crossbreeding to optimize these traits in their production. The production environment should be carefully looked at, e.g., the maintenance and feed requirement are higher for Continental breeds than for British breeds in suckler cow production. The fact is that no breed excels one single breed in every trait which is needed for successful suckler cow production. Because there are multiple traits which affect successful production, the industry should provide clear guidelines on the products which are in demand. The industry should guide producers to make the right kinds of genetic choices according to the long-term market demand. The market and consumer preferences should be evaluated on a regular basis.

## 4.2. Further research

1. Evaluating the current market and environmental demand for optimum carcass output, considering profitability and environmental aspects in different breed types including both beef and dairy breeds and their crosses.
2. Optimizing the days on feed and the energy density of the diet to achieve market demand carcass weights for different breed types.
3. Evaluating the optimized crossbreeding scheme for Finnish beef production from farm to fork.
4. Evaluating the current eating quality and fatty acid composition of wholesale beef.
5. Evaluating strategies to achieve consistent beef eating quality with grass silage-based diets for current market demand.
   Evaluating strategies to produce healthier beef quality.

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