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Genetic analysis of meat quality in BeefxDairy crossbred calves

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Cover photo	Taken for the FutureBeefCross

Preface

This master thesis marks the end of the master's degree in Agrobiology - Animal Health and Welfare, at Aarhus University. In this thesis is included a review on meat quality and results from a genetic analysis of new meat quality traits. The project was 60 ECTS. The project has given a big insight in the problems around introducing new traits in genetic models, and the problems which might arise for coordinating a project based on new registrations.

I would like to thank my supervisors Morten Kargo and Margrethe Therkildsen, for the support and guidance in the work with this project, as well as inclusion in the project FutureBeefCross. A big thank you should also go to PhD. Student Fie Følbæk Gravgaard, for the practical work with getting registrations on meat quality measures.

Abstract

Beef and Dairy crossbreeding have been gaining popularity in Denmark in recent years. The current breeding goals of beef sires in Denmark includes carcass yield, as no registrations on meat quality is available. Evaluation of meat quality is done in other global markets and has focus on intramuscular fat content (IMF) as an indicator trait. Data from 231 BLKxHOL crossbreds were analysed for LT muscle area, IMF, shear force, cooking loss, L*-value, a*-value, b*-value and pH 72 h post-mortem. This was done with the aim to estimate additive and phenotypic variances. Registrations of classical slaughter registrations: carcass weight, EUROP conformation, EUROP fat score and colour score were also evaluated. Two datasets of 741 and 23765 animals were included for the classical slaughter registrations, to validate the use of a small sub-population as a description for the entire population. The data on the meat quality had insufficient number of registrations to estimate significant heritabilities for most traits. L* and b* values were the only traits estimated significant different to 0. Carcass weight, net daily gain and EUROP conformation was estimated to a heritability of 0.19, 0.22, 0.32 and 0.15, respectively. The three datasets could not be evaluated to have different heritability. A tendency of different heritability between sex was seen in classical slaughter traits. Further analysis is needed to conclude the level of heritability in meat quality traits.

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1. Problem statement

It is a widespread discussion that the meat consumption among Danish consumer should be reduced, especially the consumption of beef. The Danish beef production primarily relies on the male offspring from the dairy production. This reduces the carbon footprint per kg produced meat, compared to other countries suckler-based beef production. At the same time there is still a large import of beef to the Danish market. Imported beef holds not only the carbon emission from the production of animals, but also the transport of the finished product. Since beef consumption should be reduced it is likely to think customers would value high quality in the future and prefer Danish production of beef. This demands that Danish beef production can withhold the same quality of beef as the imported beef. Currently an increasing amount of calves in the dairy production are crossbred with beef sires as a way of producing slaughter-animals with higher value. Currently the breeding is mainly focused on increasing lean meat yield, calving and health traits. To further improve these sires for the future use in crossbreeding, breeding after improved meat quality might hold a big potential. In this study there has been analysed meat quality on crossbred calves between a Holstein dam and a Belgian Blue sire. The measures are made on the *Longissimus thoracis* muscle, and includes pH, colour, cook loss, intramuscular fat content and shear force as a measure of tenderness of the meat. These measures will be the basis for a descriptive and genetic analysis of meat quality. Heritabilities, phenotypic and genetic correlations will be estimated using the DMU software. Data on classical slaughter registrations, carcass weight, net gain, conformation, and fat score will be evaluated in two larger datasets, to validate the use of a small population to describe the population. The future breeding perspectives for increased eating qualities of crossbred beef and dairy calves, will be discussed based on these results.

2. Eating quality in beef cattle

2.1 Introduction

It is a main public debate today that the total meat consumption per citizen should be reduced to limit the carbon footprint. Especially beef production and consumption are the focus of this discussion, since the climate impact is significantly larger than other meat sources. The high climate impact is related to the CH_4-emission from rumination as well as a large land area needed for production (de Vries and de Boer, 2010). Danish beef industry is primarily relying on the male offspring from dairy production, as well as culled cows from the dairy herds. In 2018 the Danish abattoirs slaughtered 219.800 young bulls and 183.300 cows (Fødevarer, 2019). The bull calves are normally raised in separate facilities, slaughter calf producers, where they are fed a high energy diet to maintain a high daily gain. These calves are ready for slaughter at 8-12 months of age, often for concepts demanding high yielding carcasses from young animals. Using calves from the dairy production reduces the carbon footprint and land usage significantly compared to the suckler-based beef production. In suckler-calf production the cow is raising the calf typically in a grazing system. The cows only product is the slaughter-calf compared to the dairy-cow, which main product is the milk. The beef from the suckler-calf is therefore contributing with methane emission, both from the cow and the calf. In dairy production the calves only carry the methane emission from themselves since the cow's main output is the milk production. Raising a dairy calf in a slaughter calf production emits 8,9 kg CO_2e/kg meat. The comparable emission from a beef suckling calf raised on pasture is 23,1 kg CO_2e/kg meat (Mogensen et al., 2015). The specialized slaughter calf production is therefore beneficial in the Danish beef productions climate impact. The comparison between imported beef and dairy based beef production is likely even more. Therefore, beef produced in Denmark should be of sufficient quality to compete with imported beef.

2.2 Beef breeding in Denmark

Denmark is mainly a dairy producing country with the three main dairy breeds Holstein, Red Dairy cattle and Jersey (Almskou, 2020). As described earlier bull calves from the dairy production make up a large fraction of the total Danish beef production. In the Nordic countries the Nordic Total Merit (NTM) includes growth as a sub-index. The growth index is based on registrations of daily carcass and carcass conformation score from bull calves (NAV, 2020). The growth index is included in NTM with the weight 0,08 in HOL and 0,10 in RDC. Jersey does not include growth in NTM, which is likely due to the small stature and muscling of this breed, which makes it unfit for the slaughter-calf production (Albertí et al., 2008). The very low weighting of growth in the other breeds, means the traits are kept relatively stable (Avlsværdivurdering, 2018). The inclusion of growth traits in dairy breeding, even with a small weight, could indicate the importance of dairy cattle on the Nordic countries beef production. This means there is still a small selection for growth traits in dairy cattle.

The beef breeds that are included in the calculation of breeding values in Denmark is presented in Table 1. These breeds only make up 9% of the total cattle population and is mainly distributed on smaller farms. The beef breeds is registered in the national herdbook and has had breeding values calculated since 1992 (SEGES, 2018).

Table 1 Number of live purebred beef cattle in Denmark per February 1st 2020 and the corresponding number of crossbred calves born by a beef sire and dairy dam in 2019 (Fogh, 2020, Almskou, 2020)

Breed	Abb.	Number	Number of crossbred calves
Limousine	LIM	33682	1042
Hereford	HER	26041	248
Simmental	SIM	16018	540
Aberdeen Angus	ANG	14841	1918
Galloway	GAL	13293	
Highland Cattle	HIG	9558	
Charolais	CHA	7818	6725
Dexter	DEX	4586	
Blonde d'Aquitane	BAQ	2080	1207
Shorthorn	SHO	805	
Belgian Blue Cattle in Denmark	BLK	566	46674
Piemontese	PIE	380	
Danish Salers	SAL	358	
Original Brown Swiss	BSW	38	

The beef cattle sires have 7 breeding values published that are collected to a total merit index. The 7 breeding values can be split in functional, production and conformation traits. The functional traits describe fertility, the maternal effect of calving ease and weight gain and the direct calving and survival traits. These are based on registrations by the farmer and fertility registrations in the Nation Cattle Database. The production traits include the direct effect for weight gain, calculated as the net weight gain based on the carcass weight, and the carcass conformation by the EUROP-score. A live conformation score is evaluated by a trained classifier on a linear scale and is voluntary on cows and heifers, but all bulls for AI have to be classified at the age of 1 year (SEGES, 2018). This is weighted together to form the S-index, which is the net merit index for beef cattle in Denmark. The weighting of the 7 traits evaluated is decided by each breeds association and therefore varies from breed to breed. No beef breeds in Denmark is including traits describing the meat quality in the breeding, since there are no registrations available to form the basis for evaluation.

2.2.1 Crossbreeding with beef and dairy breeds

Terminal crossbreeding with beef semen has in later years become common practice in Danish dairy herds. Since the number of heifers in many herds is more than enough to cover the replacement rate in the herd, a fraction of the cows can be inseminated with beef semen. These crossbred calves have better growth rate, feed

efficiency and gives a higher valued animal for slaughter compared to purebred dairy calves (Dal Zotto et al., 2009). These traits cover the biggest cost of producing slaughter animals, the feed cost, and the largest determination of the price, the meat yield. This fits well in the slaughter calf production and thereby increase the profit gained for the farmer, when the demand for dairy heifers is low (Ettema et al., 2017). BeefxDairy crossbreeding is often used along with sexed semen in the dairy herd. The cows with the highest genomic value are bred with sexed semen to increase the chance that they will get a heifer. Since the calves from the lower fraction of the herd, is not needed for selection they are bred with a beef sire to improve slaughter qualities. (Ettema et al., 2017)

2.2.2 The X-index

Supplementary to the registrations on purebred offspring, the evaluation of beef sires includes records of crossbred calves to dairy cows (BeefxDairy). The calving ease, carcass conformation and net gain of crossbred animals is registered and included in the S-index of the beef bull. The registrations are also used for a net merit index for crossbreeding, the X-index. The Nordic countries calculates the X-index to select the best sires for BeefxDairy crossbreeding across beef breeds. The index is based on offspring from the beef bulls on purebred HOL, JER or RDC cows. The X-index is based on similar registrations as the S-index, but the criteria for publication of breeding values is higher reliabilities. The X-index is used for selecting beef bulls that gives easy calvings and live calves, but with high daily gain and carcass conformation, when crossbred to dairy cows (Davies and Fogh, 2019). The X-index makes it possible to compare bulls across breeds and produces the expected economic gain of using the bull, compared to the base population. This strategy is advantageous both for dairy producers and slaughter calf producers since it is breeding for higher profit and reduced costs. The X-index is not a breeding goal per se, since it is used for producing terminal crossbreds, i.e. the crossbreds are not bred to contribute to the next generation. The current X-index is evaluated across beef breeds. Since there are large differences in how many observations are registered in each breed, the comparison of breeds, might be biased by uneven distribution of animals.

2.2.3 Current crossbreeding

The three most commonly used breeds for BeefxDairy crossbreeding in Denmark is the Danish Blue Cattle (BLK), Charolais (CHA) and Angus (ANG) (Table 1). BLK is purebred a numerically small breed originating from the Belgian Blue Cattle (BLK). In Denmark it has been bred for easier calving and is now recognized as a breed on its own. BLK is known to have “double muscling” due to a deletion in the myostatin gene. Double muscled cattle has increased muscle growth and improved feed efficiency, but is also associated with difficult calvings and an unwanted practice with preventive caesareans (McPherron and Lee, 1997). Similar traits are reported in multiple breeds, i.e. CHA, BAQ, LIM and PIE. When using beef breeds in crossbreeding, the main target is to improve feed efficiency and increase growth, compared to purebred calves. Beef sires bred on dairy

cattle can slightly increase calving difficulty (Fouz et al., 2013). In Nordic X-index, the calving ease in included with a high weight.

The French breed Charolais shares many of the same qualities as BLK, whereas the ANG is a slightly smaller breed. BeefxDairy crosses sired by ANG has a slightly lower net gain and conformation score compared to BLK and CHA (Fogh, 2019). The ANG breed is however known for easier calvings, which is important in the smaller dairy breeds and in heifers in larger breeds. The ANG breed is also known to have high marbling and high eating quality (Albertí et al., 2008). In a study on crossbred calves both ANG and CHA crossbreds scored as well shaped and greatly fattened slaughter animals. Double muscled breeds, here Piemontese (PIE), which can be compared to BLK, showed well shaped but poorly fattened carcass (Albertí et al., 2008). The effect of fatness on meat quality will be discussed in later sections. Achieving measurements of the meat quality will show whether there is a possibility to further improve these crossbred calves through higher meat quality.

2.3 International beef production

Europe is the third largest producer of beef in the world. Together with USA and Brazil, these three produces 47% of the global beef (Hocquette et al., 2018). The difference in climate, culture and environmental regulations means that the production systems are very different. This has an effect both on carcass yield, meat quality and carbon emission.

In Denmark cattle beef is coming from relatively young animals and dairy cows. This is comparable to other European countries such as Netherlands, Spain and Switzerland. Countries such as the UK and Ireland produces more meat on steers and has more suckler herds for beef production (Hocquette et al., 2018). Steers and heifers could be preferred compared to bulls due to improved meat quality and less aggression after sexual maturity. Bulls however has higher growth rate, higher lean yield and improved feed efficiency (Cafferky et al., 2019)

The highest beef production worldwide is based in USA. Here the livestock is typically slaughtered between 15-28 months, where animals are raised on pasture prior to a finishing feed lot period, where they are fed a high energy diet to reach higher fat and marbling scores. Nearly all male cattle in USA is steered, since abattoirs lowers the price significantly on bulls, due to unwanted meat quality characteristics and social behaviour unfit for the feedlot system (Drouillard, 2018). The index for pricing of the beef includes a weight for marbling, as a measure for intramuscular fat. This is included as a measure of the meat quality, something that is included to ensure high quality. Australia has also included a more developed meat grading index and is therefore rewarding higher meat quality (Greenwood et al., 2018). The MSA (Meat Standards Australia) is however only used on steers and heifers, which is the main production in this country as well. A inclusion of bulls into the grading scoring is however on the drawing board, and the MSA has been shown to be able to predict beef quality across sex and also for dairy breeds (Bonny et al., 2016a).

2.3.1 Comparison of international meat grading

In European countries the carcass is scored by the EUROP-score. This was implemented in 1981, where international trade increased, and a classification of the carcass was needed for comparison of badges without need for personal inspection (EU, 1981). The grading system evaluates the lean meat yield of carcasses as the EUROP conformation score. The conformation score is 5 levels from Excellent to Poor each with three sub-levels meaning the total scale is from 1-15. The fat cover of the carcass is scored on a level from 1-5, where low is leaner. These scores are evaluated either by a grader or objective system. Comparing to other countries this system is relatively simple and is yet to introduce measures for meat quality (Table 2). The inclusion of meat quality in pricing of meat was first introduced by Japanese Meat Grading Association (JMGA, 2008). The Japanese black cattle or Wagyu is known for very high marbling and tender meat, and therefore a system was developed to reward the breed that can have up to 30% IMF content. Compared to the EUROP classification, the JMGA is less focused on yield and more focused on meat quality.

Table 2: Overview over traits evaluated in meat grading systems in the given countries (adapted from Polkinghorne and Thompson (2010))

Trait	Australia	USA	Japan	Europe
		Pre-slaughter		
Tropical breed content	V			
Hormonal growth promotant	V			
Milk fed veal	V			
Sale yard	V			
		Slaughter line		
Carcass weight	V	V	V	V
Sex	V	V	V	V
Carcass conformation		V		V
Rib fat	V	V	V	V
Meat colour	V	V	V	
Fat colour	V		V	
Marbling	V	V	V	
Meat texture		V	V	
Ossification	V	V		
		Chiller		
Hanging method	V			
Hump height	V			
Ultimate pH	V			
Eye muscle area	V	V	V	
		Post-chiller		
Cut aging	V			
Cooking method	V			

The Japanese scoring system is including the marbling and texture of fat and meat scored by a trained grader. USA uses the conformation score of the animals together with marbling in the USDA system. The USDA

quality grades were implemented to predict the eating quality based on maturity of the carcass and marbling (USDA, 2017). The ossification of the carcasses is included as a measure of the animals age and describes the amount of cartilage in the sacral and dorsal vertebrae.

The Meat Standards Australia MSA system is the currently only used that is based on an evaluation of eating quality. The MSA is a grading method where beef is graded, based on the expected eating quality of the cuts. The system was developed after meat consumption fell, due to very variable quality of Australian beef. Australia's beef industry is a mix of temperate (*Bos Taurus*) and tropic (*Bos Indicus)* breeds, production systems and climate differences, so a common scale was developed to compare different cuts from different animals. This method includes phenotypic carcass data, but also the intended cooking method of different cuts, to account for the usefulness of different meat characteristics of different cuts. *Bos indicus* breeds are known for lower meat quality compared to *Bos Taurus* breeds. This is evaluated by measuring the hump height of the carcasses after slaughter, since accurate pedigree is not always available (Polkinghorne et al., 2008). Hormonal growth promotants are also used in some practices for increasing lean weight gain but decreases the eating quality of the meat. The Milk Fed Veal (MFV) category relates to unweaned calves under 10 months with very low ossification and improved eating qualities. Preslaughter stress is also evaluated if the animals are transported to the abattoir directly or via a sale yard for auction. Based on evaluations of the four sensory traits: tenderness, juiciness, flavour liking and over-all liking, a prediction of the meat quality is based the intention for the individual cuts. All these traits are combined and are the basis for the pricing of the carcass (Polkinghorne et al., 2008). The EUROP system is therefore, in comparison, fairly simple compared to other systems used in other countries. The EUROP score is a yield estimation evaluating the muscling and the fat cover of the carcass. This focus on high bulk production of lean product might be challenged if an increased quality is demanded.

2.3.2 Challenges in the beef classification

The European beef industry is challenged by the fact that the consumer is demanding improvements in several aspects of the production. The European citizens want to eat less meat, and values local production of food (Metzger et al., 2017). Producing a product with high consumer satisfaction is therefore important. A primary concern when consumers are evaluating whether to buy beef is the fear that the cut is not tender. Therefore Danish consumers tend to buy minced meat, due to increased versatility and ensured quality (Holm and Møhl, 2000). Due to the high cost of beef, the consumers need assurance, they will be provided with a product that matches their expectations. If beef consumption is further reduced from the 16 kg/year per European citizen, it is likely to assume that consumers will still have the same budget for buying meat. Therefore, they might be inclined to choose better quality if it is available. Since BeefxDairy crosses already are common practice in the dairy industry, it is relevant to look at the meat quality of these animals. The sires are currently selected after breeding goals related to yield and health in the animals, but improved meat quality could be a future

breeding goal. This requires registrations and genetic variation in the beef sires. If the meat quality in these BeefxDairy calves could be improved by selecting the right sires, it might further improve the potential of BeefxDairy crosses. This could both be by improving the meat from the calves as a whole, but also selecting prime quality carcasses. This would further improve the economic incitement to produce higher meat quality.

2.4 What determines good meat quality?

Meat quality can be divided into four categories: safety, healthiness, satisfaction and serviceability. Safety is related to the handling of the product to avoid contamination with pathogens. This factor is in most countries considered a matter of course for food products. Healthiness of beef has been discussed recently, due to risk of certain cancers, but has also been shown to be contributing to a healthy diet (Sødring et al., 2017, Young et al., 2013). The satisfaction is mainly linked to the texture, colour and flavour of the meat. Serviceability is how well the product fits into the customers daily routine and culture. Here the versatility of the meat can be an important factor for the customer choosing to buy it (Becker, 2000).

Quality of beef depend on the perspective used to evaluate the beef. A customer might not evaluate quality in the same way as a farmer, and the views are also affected by cultural differences. The consumers impression of the meat is both related to visual and sensory evaluation of the meat, but also includes health, food safety and welfare (Becker, 2000). As a result of increased focus, meat quality can also be expected to have environmental impact included as a quality parameter. When beef is produced it moves through different sectors from farmer, to abattoir, to processor, to retailer, before it ends with the consumer. All these links have a different perspective of meat quality and values attributes differently when evaluating meat quality. Looking across these sectors, food safety ranks as the most important factor for a high-quality product. Eating satisfaction was however the only quality that retailers were willing to pay extra for. This was directed to tenderness and flavour. If tenderness was at a satisfactory level, the flavour of the meat becomes equally important (Igo et al., 2013).

The three main factors of meat quality are flavour, tenderness and juiciness. The ranking of these factors varies since they also show a correlation between each other. Corbin et al. (2015) showed however that flavour had a slightly higher correlation with overall liking, than tenderness and juiciness. The study was done on different cuts from the USDA-score, from animals with different levels of intramuscular fat (IMF), but all steaks were categorized as tender, with a shear force below 33.34 N. When IMF percentage in the meat cuts lowered, the panel found the beef to have a less satisfactory over-all liking, the meat was less tender and less juicy. The importance of IMF for the over-all liking of beef, even for tender cuts, has been shown in multiple studies. Minimum acceptable limit for palatability has been evaluated to an IMF-level of 3% (Savell and Cross, 1986). Meat cuts below this was evaluated as tougher and less flavourful. This is presented as the lowest acceptable limit and the review suggests that meat quality will be further improved at plateaus on 5% and 7% IMF.

Hocquette et al. (2011) found a low but significant correlation between IMF and flavour. The data showed that animals with low IMF (1.0-2.5%) had a higher correlation between IMF and flavour. With higher levels of IMF, the correlation was lower. 3% of the variability in flavour was explained by the IMF content of the meat. In comparison 16% of the variation in flavour was explained by IMF in another study with larger variability (0.3-15% IMF) (Thompson, 2004). IMF therefore seems like a good indicator trait for increased meat quality.

2.4.2 The mechanism behind beef flavour

The mechanism behind what makes good flavour is complex. The flavour of beef has been found to be determined by 18-26 flavour characteristics that can influence the taste in both a positive and negative way. The positive characteristics could be beefy/brothy, browned/grilled and buttery/beef fat, whereas the negative characteristics could be bloody/metallic, gamey, livery and fishy. These characteristics is determined by metabolites in the meat, such as fatty acids (FA), free amino acids (AA) and peptides, reducing sugars, nucleotides and vitamins (Therkildsen et al., 2018). These metabolites are affected by complex chemical reactions, during aging and cooking of the meat, where proteolysis, Maillard reactions and fatty acid degradations all are examples of the process that yields the beef flavour (Aaslyng and Meinert, 2017). The complexity of beef flavour makes it difficult to evaluate on just one factor.

IMF is, as described earlier, affecting tenderness, juiciness and flavour liking. The flavour attributes associated with consumer flavour liking is bloody/serumy, fat-like, overall sweet, salty and umami. These attributes are positively correlated with IMF content in the beef. Similarly, the attributes that lowered flavour liking, cardboard and warmed over, was negatively correlated to IMF. The IMF also showed an increased initial flavour impact and an increase in metallic and oxidized flavours (Corbin et al., 2015). When IMF increased, the moisture-percentage in the raw meat lowered. This is due to the substitution effect when increased levels of fat substitute the muscle fibres, that contain more water. Moisture content is however not the same as the juiciness of the meat. The juiciness is positively affected by the IMF, since the increased lipid content has an effect on how the initial feel is when cooked meat is eaten (Savell and Cross, 1986). IMF therefore seems to be a trait that is beneficially correlated to the mechanisms behind good flavour in beef.

2.4.3 Tenderness

Besides having a satisfactory flavour, the beef should also have a satisfactory tenderness. Tenderness can be measured by the shear force (SF). The shear force is an objective method developed to have an estimate of the tenderness of cooked meat. SF values is measured by the force, described in Newton (N), required to run a blade across a cooked sample of the meat. This method therefore excludes a possible “halo”-effect that fat can contribute with when tasted by trained or consumer panels (Corbin et al., 2015).

After slaughter, the aging period of the carcass plays an important role in the tenderisation of the meat. In the aging period the proteolytic systems of the cells will affect the tenderisation of the meat (Huff Lonergan et al.,

2010). The relationship between the tenderness of meat right after slaughter and after 14 days aging period is described in Shackelford et al. (1997) both for laboratory animals and commercially slaughtered animals. The tenderness on day 2 had a correlation on 0.68 between shear force value on day 14 of the aging period. Carcasses graded with values below 60 N on day 2 all reached an acceptable tenderness after the aging. Carcasses above 60 N showed improvements in tenderness after the aging period but failed to categorise as tender on day 14. Using a method like shear force yield a measure only on the tenderness, which might be perceived differently when the meat is consumed. Other studies have used sensory or consumer panels to evaluate beefs tenderness. The importance in tenderness has been shown as the customers are more likely to repurchase tender meat. Three levels of shear force were guaranteed in steaks, as tender (22-35 N), intermediate (40-53 N) and tough (58-71 N). The tested consumers could choose to buy the meat afterwards. Of the consumers that bought the meat 55.3% bought the tender steaks, 12.6% the intermediate and 32% the tough category. The surprisingly high proportion of tough steaks bought, might be explained by the visual appearance of the steaks. Tough steaks were leaner and had less fat trimming compared to the other steaks. However, when the consumers was asked to repurchase 94% of steaks rebought was the tender category and only 1,8% was in the tough category (Boleman et al., 1997). This was despite a price differentiation where tender meat was sold at a higher price, and shows that if tenderness is guaranteed, the customers are willing to pay extra for the meat. When consumers score tenderness there is a chance that the tenderness is influenced by the juiciness and flavour, through the so-called halo effect. The strong associations between the three makes them difficult to evaluate independently using sensory panels or consumer testing (Corbin et al., 2015).

The mechanism that makes fat contribute to increased tenderness is a topic that has been discussed for a long time (Savell and Cross, 1986). One theory is that when fat tissue increases it dilutes the protein with lipids that has a smaller density per mass. A less density demands less force to cut through the muscle. Another theory is that the connective tissue is strained due to the adipose tissue growing inside the perimysium wall. Furthermore, there is a theory saying that lipids act as a lubricator and ensures that palatability remains high in meat cooked with increased doneness. This is due to the increased water-holding capacity of lipids (Savell and Cross, 1986). The reality is likely a combination of these and by any means the IMF content is associated with tenderness in meat.

2.5 The relationship between EUROP-score and meat quality

The EUROP system is the basis for both the pricing of carcasses and the breeding of animals in both beef and dairy cattle in Denmark. The correlation between EUROP evaluation and meat quality is therefore interesting to establish if the meat quality is affected by the current practice. The meat quality is rarely recorded except for research purposes since it does not currently have a commercial use. Bonny et al. (2016b) studied the eating quality of meat cuts from animals of different EUROP conformation score. Higher EUROP-score was associated with lower sensory quality in two out of 17 muscles. Similar three muscles were associated with lower

flavour liking with higher EUROP-score. The rest of the muscles showed no correlation with sensory qualities and EUROP conformation. If there is a negative correlation, increasing the EUROP-score might have a negative impact on the meat quality. If there is no correlation between EUROP-score and meat quality in most muscles, meat quality can be increased without negatively affecting the EUROP conformation. This is however only on phenotypic correlations. Higher EUROP conformation score and lesser fat score was phenotypically correlated with less tender meat, as well as lower juiciness and tenderness in crossbred bull calves, HOLxCHA and HOLxLIM (Nogalski et al., 2019). Increasing fat score in this study showed a correlation with improved tenderness. Another phenotypic correlation was found in Spanish beef cattle between conformation score and IMF (Indurain et al., 2009). The genetic correlations between these traits is not seen in this study. There was found a moderate negative genetic correlation between EUROP-conformation and tenderness in PIE bulls, however with a very large standard error (Boukha et al., 2011). The EUROP fat score is not included in the current breeding evaluation of animals and is therefore not bred for. With breeding towards higher slaughter weight and increased conformation it is therefore likely that the fat content is lowered or kept at a stable low level. Increasing the IMF is associated with higher eating quality (Bonny et al., 2015). Most studies focusing on meat quality related to IMF-levels generally uses steers and heifers that are at least 2 years old. Older animals will have higher maturity of adipose tissue and therefore a higher accumulation of intramuscular fat. The practice in Denmark with slaughtering primarily young bull calves means that the IMF level is likely very low. Understanding the development of tissue in young animals is therefore important.

3. Tissue of the carcass and their effect on meat quality

The carcass on the slaughter line is made of three main tissues: muscle, fat and bone. A smaller fraction includes other tissues as tendons and glands. The growth of the main tissues and in the end the composition of the slaughter carcass vary at different ages, breeds and sex of the animals. The composition can be altered by feeding, production systems, which will be discussed in the following sections.

3.1 Bone tissue

The amount of bone versus muscle and fat is a measurement of the actual yield of the carcass. Breeds with high muscling, typically double muscled breeds, show a smaller fraction of bone tissue in the carcass (Albertí et al., 2008). Higher carcass conformation, which essentially is higher muscling, is negatively correlated to bone proportion of the carcass (Keane, 2011). A higher proportion of bone in the slaughter carcass is unwanted, since it shows as less yield of sellable meat. The EUROP conformation score is a measure of the carcass yield since more muscled animals will score higher (EU, 1981). A higher EUROP conformation score is therefore an indication of a higher muscle and fat-yielding carcass. Bone tissue is also used as a predictor of meat quality in the MSA and USDA as a way of estimating age in commercial cattle, where exact age is not registered (Polkinghorne et al., 2008). With age, the bones increase in ossification, as the animals mature. This is related to a decrease of tenderness with the maturation of the animal. Ossification has been shown to have a small but

negative correlation with tenderness and overall liking of beef (Park et al., 2008). Ossification is typically measured as the amount of cartilage in the vertebras and is a good indicator trait for meat quality especially for younger cattle (Bonny et al., 2016c). The mechanism behind the decrease in tenderness with age of is likely an increase in collagen crosslinks, as the animals mature. Ossification is an example of an indicator trait that without having a direct effect on meat quality, still explain some of the variation we see. This is likely through the development of other tissues relative to the development of bone cartilage.

3.2 Muscle tissue

A high muscle growth is negatively correlated with feed intake and positively correlated with daily gain and meat percentage. This affects the economy of the slaughter animal positively, and therefore muscle growth has been the primary breeding goal for beef cattle across the world. The muscle tissue is mainly consistent of water, protein, lipids and ash. The protein fraction of the muscle is relatively constant, whereas water and lipid proportions vary inversely of each other (Keane, 2011). If muscle mass is to be enhanced, it will be through either an increase in muscle fibre number in the foetal stage or muscle fibre diameter postnatally. The muscle fibres are formed in both the embryogenic and the foetal stage. In the embryogenic phase within the first 2 months of gestation, the primary myogenesis onsets. During this period mesodermal cells develop into primary muscle fibres. The number of primary muscle fibres is very limited, and the formation of more muscle fibres happen during the secondary myogenesis (Du et al., 2010). Here cells will surround the primary muscle fibres and grow into secondary muscle fibres. The secondary myogenesis is finished around the 8th month of gestation. After this period most of the muscle fibres is developed. The growth of muscle, muscle hypertrophy, after birth is by the fusing of satellite cells to the existing cells and thereby increasing muscle fibre diameter. The diameter of the muscle fibres is primarily determined by the muscle fibre type. Type Ia is the slow-twitch oxidative muscle fibres often referred to as red muscle fibres. These fibres have the smallest diameter. Type IIa is the intermediate fast-twitching oxidative muscle and Type IIb is the fast-twitch glycolytic muscle fibres with a white colour. The difference in colour is due to different content of myoglobin, a heme-protein. The number of fibres in the muscle is not increasing with age, but different between breeds (Wegner et al., 2000).

3.4 Adipose tissue

Adipose tissue is stored in three different tissues, when evaluating the slaughter animal, subcutaneous, interant intramuscular fat. Subcutaneous fat is stored in the layer below the skin and can be evaluated on live animals as body condition score. This is also what is seen on the carcass after skinning. Subcutaneous fat is currently evaluated at the Danish abattoirs using the 5 level EUROP fat score (EU, 1981). Here a moderate fatness is preferred since lean carcasses has decreased eating quality and excessive fatness can lead to increased fat trimming on the slaughter line. This is increased labour and therefore gives a price penalty. Intermuscular fat is adipose tissue located in between muscles. Intramuscular fat (IMF) is the fat located within the muscle. This is often referred to as marbling, describing white flecks or stripes occurring between muscle fibre bundles.

A visual evaluation of marbling by meat graders is an internationally used method for evaluating meat quality in JMGA, MSA and USDA. The marbling does however only account for some of the IMF. IMF also includes phospholipids and cholesterol found in the cell membranes, whereas the white flecks of IMF primarily consists of triglycerides. The IMF found within myoblasts is not an adipose tissue, but part of the structure in the muscle cell. Around 80% of the triglycerides are stored in adipocytes, and the remaining is stored within the cytoplasm of myofibers (Hocquette et al., 2010). IMF is a highlighted trait regarding meat quality due to the effect is has on tenderness, juiciness and the over-all flavour. The many positive attributions to meat quality make the development of IMF an important process to understand.

3.5 Development of IMF

The level of IMF in the muscles is determined by size and number of the intramuscular adipocytes. The development of intramuscular fat starts in the foetal stage around mid-gestation (Fève, 2005). In this stage mesenchymal stem cells are differentiating to mainly myogenic cells, and some into adipocytes. From this line fibroblasts also origins, which are collagen producing cells. The potential for cells to differentiate into adipocytes lowers with age, since the pool of stem cells depletes with increased maturity (Du et al., 2010). The key determinant to the distribution of IMF is the adipocytes originating from foetal stem cells. The development of IMF is through the growth and development of these cells, rather than generating new cells. IMF is often described as the latest maturing tissue, but onset the trait is still important in growing animals (Pethick et al., 2004).

Visually in a cross-section of a muscle, the IMF will form as small white flecks. The white flecks are developing near small blood vessels. When the adipocytes are growing the appearance of them will be less round and more branched since they are growing around muscle fibre bundles. The distribution will also be more uniform through the muscle. Therefore the shape of the IMF-fleck can be seen as a sign of the maturity of IMF (Albrecht et al., 2006). The development of IMF is likely an S-shaped curve, where deposition in early life is very limited, since this period will favour the growth of nervous system, digestive tract and muscles. Then the adipose tissue will increase in growth near a linear development and reach a plateau later in life (Hocquette et al., 2010). The linear distribution has been seen in feedlot cattle with carcass weights between 200 and 400 kg (Pethick et al., 2004). Over this carcass weight the IMF level will plateau. Slaughter animals in Danish practices are far from the plateau in IMF deposition, since the deposition of fat is less energy efficient than the deposition of muscle.

3.6 Current evaluation of IMF in beef

Traditionally marbling is used as a factor for describing the level of IMF in the tissue. Marbling has been shown to have a positive relationship with juiciness, tenderness and palatability (Wheeler et al., 1994). This has driven the evaluation for meat quality, making it a quality indicator in many countries (Table 2). The evaluated muscle is typically the *Longissimus dorsi* (LD) muscle, which is the main part of the rib eye cut.

When evaluating IMF, the LD muscle is also the main muscle reported in literature. Commercially USA is evaluating beef marbling at the 12th to 13th rib, Japan on the 6th and 7th rib and Australia at the 5th to 13th rib (USDA, 2017, AUS-MEAT, 2018, JMGA, 2008). The places of evaluation are likely determined by the cuts demanded by the buyer. In pigs there has been shown some variation in fat content along the LD muscle, and evaluation sites differed in predictive power of total IMF content in LD (Faucitano et al., 2003). The predictive power is generally high (R^2=0,79-0,95) making the evaluation site for IMF of less importance.

Subcutaneous fat has been shown to have a low phenotypic correlation on 0.17 with IMF (Reverter et al., 2003). Giaretta et al. (2018) found a moderate phenotypic correlation. An evaluation on subcutaneous fat is therefore not an accurate estimate of the IMF. The EUROP fat score was shown to affect sensory quality positively in three out of 17 muscles (Bonny et al., 2016b). The positive effect was explained by the increase in marbling. This suggests that the EUROP fat score is a poor predictor for meat quality, even though it is currently used to avoid very lean carcasses.

3.7 Breed and crossbreed differences in IMF

The degree of IMF is influenced by sex, breed, age and feeding strategies. This not only the amount of fat, but also the distribution and composition of fat (Therkildsen et al., 2018). Crossbreeding of dairy and beef cattle is primarily with BLK as the sire breed (Table 1). The choice of sire breed will influence on the meat quality of the crossbreds. The BLKxHOL crossbreds shows increased growth and conformation at slaughter compared to purebred HOL (Fogh, 2019). BeefxDairy crossbreds of other beef breeds will share many of the same characteristics, but double muscled cattle yields higher conformation scores (Hickey et al., 2007). The double muscled trait is caused by a deletion in the myostatin gene, meaning the double muscled cattle breeds are homozygotes for this deletion. Crossbreeding to dairy cattle that is not carrying this deletion make the crossbreds heterozygotes for this trait. The allele is partially recessive so the heterozygote will show some of the characteristics of the homozygote (Wiener et al., 2009). The double muscled genotype does not affect the size of the muscle fibres, but the number and distribution. BLK showed 3x the number of muscle fibres than both ANG and HOL (Wegner et al., 2000). This difference was constant from birth to 24 months of age indicating that the difference in number of fibres is established in the prenatal phase. BLK also showed a significantly larger frequencies of type IIb compared to type Ia.

Since there are changes in the structure of the muscle the meat quality might also be affected by BeefxDairy crossbreeding. The difference in frequencies of muscle fibre showed as paler meat in purebred BLK compared to HOL and ANG. The higher number of total fibres and of Type IIb was associated with less IMF, but no difference was seen in shear force (Wegner et al., 2000). Albrecht et al. (2006) found that BLK has significantly less IMF compared to HOL and ANG. It also showed that the IMF was developing according to the animals age. In HOL and ANG the IMF levels started to develop around 6 months of age. In BLK the IMF level only increased after the bulls reached 24 months. IMF was similar between HOL and ANG, which both where

significantly higher than BLK. An older Danish study done on crossbreds between SDM/RDM (Black-pied & Red Danish Dairy cattle) dams and beef sires, found that crossbreds sired by BLK had significantly less IMF content than crossbred sired by ANG (Liboriussen et al., 1982). The difference in IMF could however not be detected as differences in tenderness, both by shear force and sensory panel. The study concluded that differences meat quality between breeds where less than the hereditary differences within breeds (Liboriussen et al., 1982). Records of the shear force as means from sires of different cattle breeds ranged from 34,4-71,2 N on cooked samples aged for 14 days (Dikeman et al., 2005).

Production systems that aims for higher meat quality, with regards to higher marbling, often slaughters older animals and primarily focus on steers rather than bulls (Drouillard, 2018, Polkinghorne et al., 2008). Steers are slower growing compared to bulls, but yield a more tender and juicy meat due to higher intramuscular fat and is comparable to heifers (Mandell et al., 1997, Cafferky et al., 2019). The fat deposition is generally lower in bulls than that of the heifers and steers, both in subcutaneous fat and IMF (Englishby et al., 2016). Bulls are also associated with higher proportion of glycolytic muscle fibres and higher collagen content, which contributes to less tender meat (Chriki et al., 2013). Bulls are generally slaughtered earlier compared to heifers and steers, since the bulls reach acceptable weight and conformation at an earlier age, but also due to difficulty in handling after the bulls reach maturity. The risk of injury both for animals and personnel makes the handling of large groups of bulls after maturity very difficult. Steers of BLKxHOL had lighter meat with less IMF compared to ANGxHOL. The low IMF content was correlated to less tender meat, evaluated by shear force and by sensory panel (Keady et al., 2017). Cafferky et al. (2019) found that BLK crossbreds had lower IMF than ANG crossbreds, but this was not associated with lower tenderness. The varying correlation between IMF and tenderness could be due to the decreased collagen content in double muscled breeds. Collagen is thought to be part of the background toughness in meat, and the accumulation and transfer from soluble to insoluble collagen with age could be an explanation to why young animals shows good eating qualities (Cross et al., 1983). However, no significant correlation between collagen and shear force on cooked samples was found studying 15 European breeds in young bulls. Lipid content and sarcomere length was associated with the shear force (Christensen et al., 2011).

Holstein cattle scored the same in flavour liking when steaks were comparable to beef breed steaks (Corbin et al., 2015)

3.9 How do you measure eating quality?

Eating quality can be evaluated either subjectively or objectively. The subjectively evaluation will be a direct measurement of the experience of eating the meat. An objectively measurement can be a correlated trait, in which the correlation to eating quality has been established. The different measurements available will be discussed in the following sections.

3.9.1 Sensory panels

Sensory panels are measuring of evaluating the eating quality of a food and is widely used in the food research. Evaluations with sensory panels can either be with trained panels and consumer panels. Trained panels are professionals hired as tasters and therefore has a lot of experience in tasting attributes. They are often selected so that they have a well-trained tasting sense and can describe the taste very detailed. These can be used to give values of the many complex taste attributes involved in beef flavour (Therkildsen et al., 2018). Consumer panels are equivalent panels, made from ordinary consumers. This panel will not be trained in tasting and therefore might have a less nuanced description of taste. The consumers, if chosen representatively for the population, can describe satisfaction with products. They can describe what qualities are wanted and evaluated by the same consumers that are choosing to buy a product. Common for these panels are the high cost of the test per sample. The high cost of the sample means that a large number of observations often is unrealistic, due to budgetary restrictions. An advantage is an increased accuracy of actual quality. When correlated traits and indicator traits are used, there will always be a loss in accuracy.

3.9.2 Objective measures

When sensory panels are not available, or not an option due to a limited budget, there are several options for measuring meat quality. Measures can be made on live animals, carcasses and in individual cuts.
The measure of pH post-slaughter is one of the most important indicators that the process from muscle to meat is developing as it should. The pH decline post-slaughter plays an important role in the tenderization post-slaughter. The fall in pH is due to the metabolic shift after slaughter. When the cells are no longer supplied with oxygen from the blood and the energy supply from creatine-phosphate is depleted, there is a shift from aerobic to anaerobic glycolytic metabolism. This means an accumulation of lactate in the cell, as the cell produces ATP from ADP. The ATP is used for releasing the actomyosin bridges in the sarcomeres. When no more ATP is present, the actomyosin bridges remains intact and the sarcomeres will remain the length they have obtained. The pH will develop from neutral to pH 5,4-5,8 and should decrease at a moderately slope (Huff Lonergan et al., 2010). The accumulation of lactate is driven by the amount of carbohydrate available in the muscle. This carbohydrate is the available glycogen in the muscle cell. If glycogen stores are depleted too fast the ATP will not be regenerated and there will be less energy for releasing the actomyosin bridges. This will lead to an increased shortening of the sarcomeres, which is associated with less tender meat (Huff Lonergan et al., 2010). The pH in the cell also influences the proteolytic systems in the cells which also influences the tenderization. Pre-slaughter factors such as stress due to transportation and grouping of animals can lead to less glycogen depots and therefore lead to an insufficient pH decline.

3.9.2.1 Meat colour

The colour of the meat is the first thing the customers sees when looking at the products in the refrigerator. When customers are selecting meat, a red colour of meat is preferred and increases the likelihood to buy

(Carpenter et al., 2001). This increased likelihood to buy was not associated with a better taste score of the meat, but only based on the visual impression of the meat. The visual appearance of the product also is strongly influenced on the choice of packaging. The main pigment in meat is myoglobin, a heme containing protein, where other pigments only plays a minor role (Belitz et al., 2005). The colour of the meat is therefore mainly determined by the myoglobin and the oxidation of this molecule. When meat is exposed to air, oxygen will saturate the myoglobin and the colour will appear brighter. This is the process called blooming, and is important before the colour of meat is measured. (Mancini and Hunt, 2005). The colour of meat is often reported by an objective measure of the L*, a* and b* values using Minolta equipment (Tapp et al., 2011). L* is the value for the samples lightness on a scale from 0 (black) to 100 (white). Some dark meat relates to decreased eating qualities in relation to pre-slaughter stress. The L* value has been shown as a good predictor to this (Mancini and Hunt, 2005). The a* value describe the redness of the sample from a scale from -60 (green) to 60 (red). The b* value describes the yellowness scales goes from -60 (blue) to +60 (yellow). The a* value is relatively easy to see in raw meat, by the occurrence of the meat. The b* value is more correlated with a brown colour, than blue or yellow nuances (Mancini and Hunt, 2005).

3.9.2.2 Shear force

Shear force has been described earlier and is an objective measure on shear force. Warner Bratzler Shear Force is the classical method used for estimation of the force required to cut through a cooked meat sample. Other measuring method has also been tested, such as slice shear force (Shackelford and Wheeler). Shear force is determined by removing a cooked sample from the meat and measuring the required power to run a blade through it. The evaluation of shear force still requires a sample cut from the carcass and needs personnel to cook and measure the shear force. An indication for the subsequent tenderness and flavour has been described earlier as IMF. As described in earlier sections IMF has a positive effect on meat quality, both with regards to tenderness, juiciness and flavour. It is therefore a very strong indication of the subsequent eating quality of the meat. Measurements of IMF can be done in different ways.

3.9.2.3 Evaluation of IMF

In commercial slaughter productions the most used evaluation of the IMF content is visual evaluation by a trained grader. This approach is used by countries such as USA, Australia and Japan (USDA, 2017, AUS-MEAT, 2018, JMGA, 2008). This method is based on the country's individual grade system based on the distribution of marbling. The scoring is typically done when the cut is compared to predefined scorecards where the level and distribution of fat streaks are an indicator of the meat quality (USDA, 2017). Even though the trainers are skilled, the evaluation of marbling will still have a level of subjectivity. Often an uneven distribution of marbling will yield a lower score than evenly distributed marbling. The limits for when a carcass is one grade or another, will be evaluated by the grader, and therefore marbling might not be a completely valid for IMF level. The visual evaluation of marbling also only encounters for the visible fraction of the IMF.

The advantage of the visual method is that it is a relatively fast method and therefore is compatible with the flow on a slaughter line. A direct sorting of the carcasses in grades can therefore mean a different pricing of the carcasses based on meat quality.

To translate a marbling score to actual level of IMF a chemical analysis is needed to chemical estimation of fat content can be done. The Chemical analysis will yield more fat content than visual fat since structural lipids and invisible depots will be included in the analysis. The chemical determination of fat is considered a very precise method, given that the sample measured is representative for the whole muscle. The distribution of marbling scores and chemical analysis follows a linear distribution (Dow et al., 2011). A rather new technology for estimation of IMF content is the use of image recognition. The fat in a cross section of the muscle can be estimated rather precise using an algorithm to recognise the content of fat. The method has shown to be highly correlated to the actual IMF, determined by chemical extraction. The image recognition showed higher correlation than the USDA marbling score did to the actual IMF content (Giaretta et al., 2018). Since there are many available methods for estimation of meat quality it should be an evaluation between expenses and precision. More expensive analysis, such as sensory panels, are often more detailed and precise in their estimate of meat quality. If indicator traits are used, a loss in precision might be compensated by the lower cost and thereby a gain in the number of observations. Which is more important should depend on the intended use of the data.

4. Breeding for increased meat quality

The interest for measuring the eating quality in crossbreds is not new. Liboriussen et al. (1982) concluded based on Danish trials with crossbreds that the difference between breeds were less than the hereditary differences within breeds. However nearly 40 years later, there is still not achieved a Danish breeding goal for meat quality. This requires that there will be available registration on traits related to meat quality. Meat quality analysis is often registered with sensory panels and advanced methods. This yields precise measurements, but for genetic purposes the number of registrations is too low, due to their cost, to be useful. Obtaining a measure on an indicator trait that has a positive effect on meat quality, and is cheaper to register is therefore an interesting possibility. In the previous sections we have discussed multiple traits influencing the meat quality of the animals. Accumulating these traits to one measure of meat quality is complex, the understanding of the individual traits is important if they are to be improved. Increasing meat quality can be done by changing management of the animals by feeding, supplements, castration and age of slaughter. Breeding the animals with the goal to improve meat quality is also possible but is currently not practiced in the Danish breeding. Since meat quality is not rewarded by the current pricing system there is no economic incitement. As described in earlier sections, both dairy and beef breeds include growth and conformation traits in their breeding goals. Inclusion of meat quality in the breeding requires breeding evaluation of the new trait, to establish whether it can be used for future breeding.

4.1 Evaluation of new traits in animal breeding

When selecting new traits for possible inclusion in the breeding, three main criteria needs to be fulfilled for the trait to be valuable for breeding. First, the trait must be important. In respective to this assignment the trait must have an influence on the meat quality and by improving the trait in a beneficial direction the meat quality should be improved. The positive effects of including this trait should outweigh the possible cost and trouble for registering the trait. Secondly, the trait must have genetic variation and the be heritable. If there is no variation in the trait and there is no additive genetic variation passed from parents to offspring, a selection response cannot be obtained. Thirdly, the measurements of the trait must be in a sufficient number to differentiate the genetically superior animals from the population. This means that the measuring of the trait should ideally be easy to obtain and at low cost to increase the power of the estimate (Berry et al., 2017). Measuring multiple traits might also contribute to the power of the estimate in the occasion that the traits are genetic correlated.

Often the precision of estimates and the price are correlated. In meat quality analysis the sensory panel estimations are very precise measures of the eating quality. The sample is evaluated in repeated measures by multiple panel members. Having multiple people evaluating a meat sample is a cost heavy observation. Indicator traits can be cheaper to obtain and therefore available in larger quantities. In genetic analysis the number of observations is important to estimate genetic parameters with sufficient power. To understand the basics of genetic parameters the standard genetic model will be presented. The phenotype we observe in the animals can be presented as the equation below

$$y_{ij} = \mu_i + g_i + e_{ij} \quad (1)$$

Here y_{ij} describes the *j*'th observation of the *i*'th animal. The environmental effect μ_i are the fixed (non-random) environmental effects affecting the *i*'th animal, that include rearing management, sex or the effect of birth year. The genetic effect g_i, is described as the sum of the additive genetic effect (g_a), the dominance effect (g_d) and the epistatic effect (g_I) of the i'th animal. The sum of residual random effects on the j'th observation of the i'th animal is described as e_{ij}. Of the genetic effects only, the additive genetic effect is passed from parents to offspring. Therefore, the additive genetic effect is the main trait of interest. The dominance and epistatic effects are often assumed to have little effect and is often included in the random residual. When looking at the observed variance we get from (1)

$$\sigma_P^2 = \sigma_a^2 + \sigma_e^2 \quad (2)$$

Where σ_p^2 is the variance of the phenotype, σ_a^2 is the additive genetic variance and σ_e^2 is the random residual variance, including the dominance variance and epistatic variance. Since dominance effects and epistatic effects are not passed to the next generation, the additive genetic effect is the main trait of interest. The proportion of phenotypic variation explained by the additive genetic variation is defined as the narrow sense heritability

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \quad (3)$$

The heritability is an estimation of the fraction of the genetic variance passed on from parents to offspring. It describes the resemblance due to genetics between the parents and the offspring. To estimate the heritability the phenotypic information is combined with pedigree information to establish the phenotypic and genetic variance. Using the heritability in a breeding perspective, is a description of the correlation between the animal's genetic value and phenotype (Mrode, 2014).

Figure 1 shows an overview of the estimated heritabilities in published literature for the traits described in the earlier sections. The heritability of the traits associated with meat quality has a relatively large range, from low to moderate heritability.

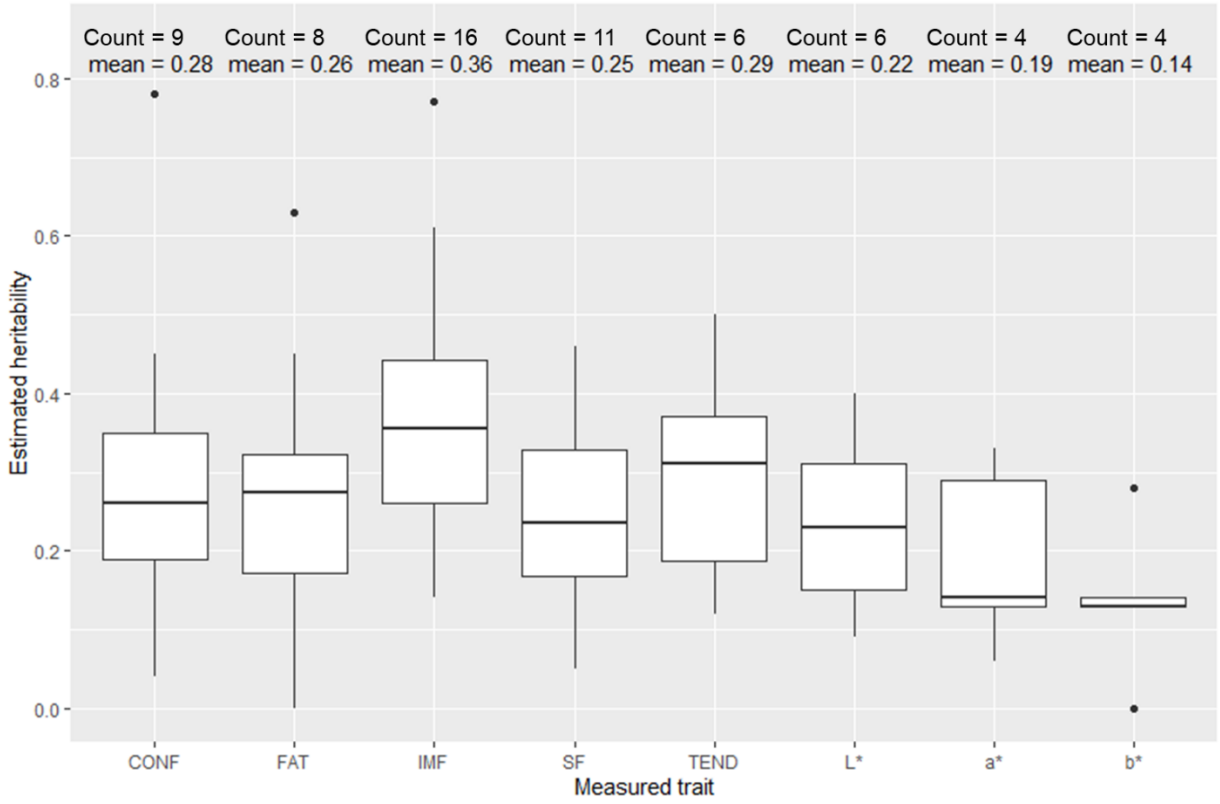

*Figure 1 Boxplot of estimates on heritabilities in literature. Means and number of studies included is given in the plot. The studies are based on multiple breeds of both crossbreds and purebred beef cattle. Dots represent values deviating from the median with more than 1.5*IQR. (IQR: Distance covered by 1st and 3rd quartile) Abbreviations: CONF: EUROP conformation score, FAT: EUROP fat cover score, IMF: Intramuscular fat content, SF: Shear force estimates, TEND: Sensory tenderness evaluated by a sensory panel, L*: lightness of the meat, a*: redness of the meat, b*: yellowness of the meat. Citation is given in appendix.*

The studies on heritability are based on different breeds and crossbreds, which can explain the difference in heritability. The heritability is defined a population specific, since different population can have different additive genetic variances (Falconer and Mackay, 1996). A low-moderate heritability should be interpreted as that in a trait as IMF, 0.2-0.6 of the variation seen in the phenotype is due to the additive genetic variation in

the genes. The heritability for meat quality related traits are in most studies estimated higher than traits such as health resistance which is included in the current breeding in Nordic countries (NAV, 2020). A higher heritability means that there is basis for a higher selection response (Falconer and Mackay, 1996). The selection response is also dependent on the intensity of selection and the variation in the trait. Improving a trait by breeding, contrary to dietary or other management changes, has the advantage that the improvement is additive. Therefore even a low heritability can improve a trait, if bred for in multiple generations (Berry et al., 2017). Since measuring meat quality is complex and consists of multiple measurable traits, the correlation between these traits are also of high importance. The correlation between two traits x and y is described by

$$r_{xy} = \frac{cov(x, y)}{\sigma_x \cdot \sigma_y} \tag{4}$$

A correlation is a measure of the proportion of variance in one trait, explained by the variance in the other trait (Mrode, 2014). Correlated traits are important since the selection of an indicator trait can be influencing the other trait. Correlated traits can be measures of traits regulated by the same genomic regions and thereby lead to a selection of both traits. It is important to know the correlated response when traits are selected for (Falconer and Mackay, 1996). The correlation an also be used to measure one trait to give information of the other.

Since measurements of the meat quality only can be measured post-mortem, studies have been made on correlated traits in live animals. The American Angus association introduced in 1997, genetic evaluation of IMF-levels measured by ultrasound on live animals, as a way of improving the marbling of the breed (MacNeil et al., 2010). Marbling is an economically important trait, in the USDA system and therefore selection for the trait is viable. Measuring of a correlated trait on live animals provide information on the animal itself and therefore improves the accuracy for the estimated breeding value (EBV) of the animal. Marbling in itself provides a visual measure of the IMF, and has been shown to be correlated to improved eating quality (Thompson, 2004). The ultrasound measurement shows a high correlation with the carcass marbling score and is therefore a useful indicator trait (Crews et al., 2003). The evaluation is done on yearling bulls and heifers, which makes the animals comparable to the levels seen in Danish slaughter animals. The measurements are done with ultrasound on live animals, which is considered a less accurate method compared to chemical measurements on meat samples. The estimation of IMF with ultrasound is however fast and relatively easy for trained personnel. It provides no direct measure of the eating quality, but the known correlation makes it an important tool for improving the trail.

Currently the breeding evaluation on cattle in Denmark include the growth and conformation traits. The national breeding evaluation includes data collected from abattoirs in the Nordic countries from 1990 and until present. The estimate on the heritability of the growth trait, therefore, has a lot of observations and power behind it. As discussed in earlier sections very few studies have evaluated the difference between eating

quality of beef and the EUROP-score of the carcass. If there is no genetic correlation, the meat quality traits could be improved without having a negative correlated response to existing breeding goals.

This study evaluates new measures of eating quality to the classical registered trait, already implemented in the breeding goal. Improvement of meat quality might be possible if there are available registrations for meat quality, either through direct measures, or by indicator traits.

5. Materials and methods

This section will describe the methods used to obtain quantitative observations for a genetic analysis. Furthermore, the editing of the data and the models used for a parameter estimation will be presented. All cattle in Denmark is registered in the national Cattle Database with an unique ID (Bundgaard and Høj, 2000). This makes it possible to follow the cattle when transferred between herds, to the slaughterhouse and to the slaughter line. The pedigree is also based on this information.

5.1 The FutureBeefCross project

Animals slaughtered for this study was part of the FutureBeefCross project, which is a collaboration between Department of Food Science and Centre for Quantitative Genetics and Genomics at Aarhus University, SEGES, Danish Crown, VikingGenetics, VikingDanmark, Frontmatec and Allflex (Miljø og Fødevarestyrelsen, 2018). The aim of this project is to produce genomic breeding values for feed efficiency, methane production and eating quality. Terminal crossbreds are produced from Holstein mothers and beef sires of either Angus (ANG), Danish Blue Cattle (BLK) or Charolais (CHA). The calves are born in Danish dairy herds and transferred to one of five slaughter calf productions, participating in the FBC project. The slaughter calf producers are chosen based on similar overall management. They are raising crossbred calves for slaughter at an age below 12 months for the "Dansk Kalv" concept. Once in the FBC herds the animals are weighed into the project at a given age, and for a period the feed intake is registered by feed stations in the pen. In the feed stations is integrated a methane detector that measures the concentration of methane in the breath. Once the animals reach an acceptable liveweight they are slaughtered ad Danish Crown in Holsted. Here the carcass of all animals will be photographed with a loin eye camera, with the aim to predict eating quality. Before slaughter 1000 calves with valid registrations on methane and feed intake, will be used to form a training dataset for a prediction of eating quality based on image analysis. On the slaughter line, when the carcass is split in anterior and posterior wing, a sample of min. 7 cm of the eye muscle area is cut and shipped for meat quality analysis at Department of Food Science at Aarhus university. This sample is analysed for *Longissimus thoracis* (LT) muscle area, IMF content, SF, cooking loss, pH, and the colour measures L* (lightness), a* (redness) and b* (yellowness). These values will be used to make a prediction of eating quality based on an image of the LT-muscle. This image is taken of all animals in the FBC project and is aiming for a total of 12000 registrations at the end of the project. The animals evaluated for eating quality in this study will be part of this training dataset. Due to available data on animals slaughtered this study will only focus on the BLK offspring.

5.2 Description of recorded traits and slaughter procedure

Three datasets will be used for data analysis (Table 3). Data A will be based on animals chosen for the FBC training data set and will therefore have observations of meat quality along with commercial slaughter

registrations. Data B is having observations on commercial slaughter registrations on all BLKxHOL animals slaughtered from the four FBC herds. Data C contains observations on slaughter registrations from all BLKxHOL slaughtered in Denmark in 2019 and 2020. Data B and Data C was included in the study to evaluate if animals chosen in a small population was representative for the entire population.

Table 3: Overview of which traits are registered in the three datasets used for genetic analysis.

Trait measured	Abbreviation	Data A	Data B	Data C
Carcass weight (kg)	CW	X	X	X
Daily net gain (kg/d)	CG	X	X	X
EUROP conformation (1-15)	CC	X	X	X
EUROP fat score (1-5)	FS	X	X	X
Colour score (1-5)	CS	X	X	X
L. Thoracis area (cm^2)	LTA	X		
IMF estimated by Soxleth method (%)	IMF	X		
Warner Bratzler Shear Force (N)	SF	X		
Cooking loss (%)	CL	X		
Lightness (1-100)	L^*	X		
Redness (-60-60)	a^*	X		
Yellowness (-60-60)	b^*	X		
72 h pH	pH	X		

The registrations on the common slaughter measurements; carcass weight, EUROP conformation and fat score, and a colour score, is registered on all slaughtered animals in Denmark. These registrations form the basis for pricing of the carcass (EU, 1981). All animals slaughtered has the EUROP-score registered in the Danish Cattle database. The EUROP-conformation and fat score are measured by a BCC-3^{TM} scanner (Beef Classification Centre). Conformation is evaluated on a 15-point scale from E+ (Excellent) to P- (Poor). The fat is evaluated on a scale from 1-5, where 1 is lean and 5 is fat (EU, 1981). The colour score is an evaluation of the fat colour on the carcass from 1-5, where 1 is very light and 5 is dark/yellow colour. The slaughter weight of the carcass, EUROP conformation, EUROP fat cover score and the colour score are recorded for the Danish Cattle Database. The net daily carcass gain was calculated as the carcass weight minus the expected carcass weight of a calf at birth, divided by the slaughter age.

$$ADG = \frac{(CW - 22)}{age}$$

The birthweight was assumed to be 44 kg in BLKxHOL crossbreds, and the net weight would be 50%.

5.2.1 Observations for meat quality traits

The calves are raised to a live weight corresponding to a carcass weight between 180 and 260 kg and age 8-12 months, and slaughtered for the concept "Dansk Kalv" (Danish Crown, 2020). The animals are slaughtered at

the facilities of the Danish abattoir, Danish Crown in Holsted. After arrival and registrations of the animals at the abattoir, the animals are stunned with a captive bolt pistol. After stunning the animals are bled and hung by the hind leg. The animals are stimulated with 100 V for 400 seconds. Before skinning of the carcass, the ear is removed for genotype sampling of the animal. The carcass is split in halves and placed in chilling room at 2℃ for 24-48 hours hung by the Achilles tendon.

After chilling the half carcass is split in pistol (posterior half) and wing (anterior half) cuts between the 5th and 6th rib. When the animals are split a worker on the line carves the carcass before the rest was cut with a carcass cutter. The carving is to ensure a clean-cut surface for the loin eye camera and thereby improve the image quality. The cut was photographed for determination of IMF by a loin eye camera produced by Frontmatec (see Figure 2). The camera is designed to rest on the cut surface of the anterior cut and photograph the *Longissimus thoracis* (LT) muscle. This is done with the aim to determine IMF later in the project.

Figure 2 Demonstration of how the picture for IMF determination is taken on the wing cut of the animal

After the picture is taken a meat sample is cut for the meat quality analysis. The sample is min. 7 cm of the eye muscle area cut from the anterior wing cut and shipped to Food Science, AU and stored at 4 ℃ until 72h postmortem. The LT-muscle is carved out for further analysis of meat quality and the rest of the cut is discarded.

The pH is measured in LT with PHM201 pH meter (Radiometer, Denmark) equipped with Metrohm probe type glass electrode WOC (Metrohm, Switzerland). The electrode is calibrated in pH 4.01 and 7.00 IUPAC buffers. The LT muscle is measured for pH at two places and the average between the two is kept. A 1 cm slice is cut to estimate the filet areal (LTA), which is the area of the cross section of the LT muscle. Lightness (L*), redness (a*) and yellowness (b*) are measured using a Minolta Chromameter CR-400 (1977). Prior to measurements the tool is calibrated using a white tile. The lightness L* is determined on a scale from 0 (black) to 100 (white). The redness is spanning from -60 (green) to +60 (red) and the yellowness scales goes from -60 (blue) to +60 (yellow). The blooming time are 30 min at room temperature before the colour is measured. The colour of the meat sample is measured at three positions on the LT muscle surface. The mean of the three values are used for further analysis.

Shear force (SF) is measured by the Warner-Bratzler Shear Force method as described by Oksbjerg et al. (2019). The sample of the LT muscle is cut into a 5 cm length. The sample is weighed, vacuum packed and

cooked for 1 hour in water bath at 62 ℃. Hereafter the sample is cooled for 30 minutes at 5 ℃ before it is weighed and cut into the texture sample. The weight loss is recorded as the cook loss (CL).

$$CL = \frac{weight_{cooked} - weight_{raw}}{weigh_{raw}} \cdot 100 \quad (5)$$

The fibre direction is determined, so four blocks is cut parallel with the fibres, 1 x 1 x 5 cm. The Shear Force is measured by running a blade through the sample and the amount of force used to cut the sample is quantified in newton (N). The average of the four samples are kept as the SF.

The estimation of the IMF is done by acidic hydrolysis and fat extraction with petroleum ether (Gerhardts HYDROTHERM and SOXTHERM®). The slices from the LT was homogenized to a uniform mass. A sample of 10 g was weighed off and inserted into the HYDROTHERM. Here the sample was hydrolysed (4 M 37% HCl) and transferred to filters for drying in a heat chamber (100 ºC in 1 hour). After drying the sample was weighed before being inserted into the SOXTHERM for lipid extraction, with petroleum ether. The weight difference before and after lipid extraction is referred to as the IMF content of the sample.

5.3 Data editing and descriptive statistics

To summarize the descriptive statistics and editing of the data, R software was used (R Core Team, 2019). For plotting the data into plots, the ggplot2 package was used (Wickham, 2016). The genetic parameter analysis was performed on all three datasets. All datasets were based on registration on terminal crossbreds of a BLK sire and a HOL mother. Data A contained the evaluations of meat quality from the FutureBeefCross animals. Results from the image recognition of IMF was not obtainable, so the trait could not be analysed in this project. Data B was made of all BLKxHOL crosses slaughtered from the 4 FBC herds. The last dataset, Data C, was made from all BLKxHOL crosses slaughtered in Denmark in 2019 and 2020. To select animals similar to the animals slaughtered for the FBC project the age was set at 12 months, since this is the limit for the concept "Dansk Kalv" (Danish Crown, 2020). Small slaughter calf producers were removed with a minimum of 10 calves slaughtered in 2019 and 2020. The pedigree was based on a sire - maternal grandsire pedigree. The pedigree was traced back 7 generations. If sire or maternal grandsire did not exist in the pedigree they were set as missing. 741 animals were registered in the pedigree.

5.4 Models for genetic parameter estimation

With the aim to estimate phenotypic correlations and genetic parameters, the DMU package is used for restricted maximum likelihood (REML) estimation (Madsen et al., 2006). The software was used for uni-variate and multivariate analysis of the traits. The parameter estimation is done by making a mixed linear model

$$y = Xb + Za + e \quad (6)$$

Where y is the vector of phenotypic observations of the trait evaluated, *b* is the vector of fixed effects, *a* is the vector of additive genetic effects and e is the vector of residual effects. *X* and *Z* is design matrices, where X assigns the fixed effects to the animals, and Z assigns the additive genetic effects to the animals. The fixed effects are systematic environmental effects that will affect the observations across animals. The additive genetic effects are assumed to be distributed by $a \sim N(0, \sigma_a^2)$. The residual effects are distributed as $N(0, \sigma_e^2)$.

The observations were used as information on the sires. We have chosen to use a sire model in this study. The sire model is using the information of the offspring to give an estimated breeding value (EBV) of the sires (Mrode, 2014). The animal model is a more used model today, since it gives information on all animals included in the evaluation. The advantage of the sire model is that the numbers of equation for the parameter estimation is lower. Since this study is don on small datasets computation cost is not an issue. The sire model has the assumption that there is no genetic relationship between dams and sire, and that dams all are mated randomly and of similar genetic merit. Since this data is based on terminal crossbreds of a beef sire and a dairy dam, and the dairy is not under selection for any meat quality traits, these assumptions makes it possible to use the sire model. Using the sire model is advantageous when evaluating different sire breeds. Between different breeds the additive genetic variation for the same trait might be different. When evaluating sires, this difference will be covered by the pedigree of the sires. The sire model is written as

$$y = Xb + Zs + e \tag{7}$$

Similar to the model in eq. (6), but the vector of additive genetic effect has been substituted by s, the vector of additive sire genetic effects. The sire effect is distributed as

$$s \sim N(0, A\sigma_s^2) \tag{8}$$

Where A is the relationship matrix of the sires and σ_s^2 is the sire genetic variance is where $\sigma_s^2 = 0{,}25\sigma_a^2$.

5.5 Single trait models

The univariate models were used to estimate the heritability of the traits. The model given below was used as the basis for the univariate analysis.

$$y_{ijklmno} = BYM_i + SLYM_j + bherd_k + sherd_l + sex_m + age_n + sire_o + e_{ijklmno} \tag{9}$$

Where:

$y_{ijklmo} = Phenotypic\ observation\ of\ trait\ of\ interest$
$BYM_i = Fixed\ effect\ for\ the\ i'th\ year * month\ of\ birth$
$SLYM_j = Fixed\ effect\ for\ the\ j'th\ year * month\ of\ slaughter$
$bherd_k = Fixed\ effect\ for\ the\ j'th\ birth\ herd$
$sherd_l = Fixed\ effect\ for\ the\ k'th\ slaughter\ herd$

$sex_m = Fixed\ effect\ for\ the\ l'th\ sex$

$age_n = The\ regression\ value\ for\ the\ slaughter\ age\ of\ the\ m'th\ animal$

$sire_o = random\ effect\ of\ the\ m'th\ sire$

$e_{ijklmo} = random\ residual\ effect$

The variables, described as y_{ijklm} above, are the traits given in Table 3. The variables are all evaluated in single trait models, with the aim to examine the fixed effects, phenotypic, genetic and residual variances. The estimation of variance was done by Average Information Restricted Maximum Likelihood Analysis (AI-REML) using the DMU package (Madsen et al., 2006). These variances will be used to estimate heritabilities for the trait. The factors included in this model was chosen based on significant effects in other genetic literature.

5.6 Multi trait models

The multivariate models were used for evaluation two or more traits simultaneously and will utilize the phenotypic and genetic variance to describe correlation structure in the data. The combination of data from multiple traits will increase the accuracy, especially for low heritability traits (Mrode, 2014). A disadvantage with the multivariate analysis is the increased computation cost, and based on a low number of observations, it might prove a challenge to achieve reliable estimation of many covariances. The multivariate model is evaluated as

$$\begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_n \end{bmatrix} = \begin{bmatrix} X_1 & 0 & \cdots & 0 \\ 0 & X_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & X_n \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_n \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & \cdots & 0 \\ 0 & Z_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & Z_n \end{bmatrix} \begin{bmatrix} s_1 \\ s_2 \\ \vdots \\ s_n \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_n \end{bmatrix}$$

Where y_i is a vector of observations on the i'th trait, b_i is the vector of fixed effects affecting the i'th trait, s_i is the vector of sire additive genetic effects of the i'th trait and e_i is the vector of residual effects on the i'th traith. X_i and Z_i is the design matrices for the i'th trait, relating fixed effects an random sire effect to the animals, respectively (Mrode, 2014). The fixed effects and traits evaluated are identical to the ones used in the single trait model. Multivariate analysis is done on all datasets, to estimate the correlations in meat quality traits and compare them to the estimate of correlations between the classically recorded traits. The models are run as pairwise bivariate models in DMU, to estimate the correlations between the traits.

5.6.1 Fixed effects

The fixed effects are included in the model to remove the effect of systematic effects that influences the observations. The fixed effect $month_i$ describes the effect of that the animal is born in the i'th month. This factor should estimate variation throughout the year. The fixed effect $bherd_j$ describes the effect of j'th birth herd. Animals born in the same herd will experience a similar environment until they are sold to the slaughter-calf

producers. This might have an effect on the performance later in life. The fixed effect $sherd_k$ describes the effect that the animal is fattened in the k'th herd. The differences in management between these producers will be caught by this effect. The sex_l describes the effect of the sex of the animal. Observations of each effect included in the genetic model is shown in Table 4, along with the range of age and the distribution of sex.

Table 4: Number of observations, number of levels for fixed effects, and range of age and distribution of sex in the different datasets.

Trait	Data A	Data B	Data C
Phenotypic obs	231	741	24255
sire_o	39	39	88
BYM	13	15	23
SLYM	9	13	18
bherd	39	63	858
sherd	4	4	220
Range of age (min, max)	(247, 363)	(211, 363)	(203, 365)
n of sex (bull, heifer)	(105, 126)	(349, 392)	(13559, 10206)

6. Reduction of the model

The effects used in the model was tested for significance using the output from the DMU package. The reduction of the model was based on the Data B (Table 3). Using this dataset for evaluating the effects, was done due to the number of animals. If Data A were used, the low number of animals, would make determination of environmental effects challenging. Data A is based on the same herds as dataset B, so the significant effects affecting the phenotypic observations are likely the same in the two datasets. Data C had much larger sample size, and therefore more power to estimate the variance components. The larger power would make it easier to detect significant effects. The comparability to the other datasets is however lower since more herds and concepts would be involved. Therefore, Data B was chosen as the dataset for detecting which fixed effects were significant in the genetic model.

6.1 Initial model

The initial model was given in eq. (9). The model was run on the traditional slaughter traits in Data B: Carcass weight, Net daily gain, carcass conformation, carcass fat score and carcass colour score. To test what effects that would affect the slaughter traits, a general linear model without a genetic component was run on all of the carcass traits similar to Eq. (9) (R Core Team, 2020). The model is given below

$$y_{ijklmn} = BYM_i + SLYM_j + bherd_k + sherd_l + sex_m + age_n \quad (10)$$

Where the description is equivalent to eq. (9). A linear model will not address the genetic relationship of the animals, but it will show if the effects are influencing the phenotypic observations. The results of the linear regression are presented in Table 5.

Table 5: Significance of the effects in linear regression on the respective slaughter traits. The level of significance is shown by p-value from Fishers

Trait	Fixed effect					
	BYM_i	$SLYM_j$	$bherd_k$	$sherd_k$	sex_m	age_n
CW	$4.24 \cdot 10^{-4}$	$7.23 \cdot 10^{-9}$	0.13	0.9	$< 2 \cdot 10^{-16}$	$< 2 \cdot 10^{-16}$
CG	$2.57 \cdot 10^{-8}$	$3.49 \cdot 10^{-4}$	0.15	0.89	$< 2 \cdot 10^{-16}$	$< 2 \cdot 10^{-16}$
CC	0.02	0.81	0.24	0.58	$1.38 \cdot 10^{-6}$	0.01
FS	0.35	$6.79 \cdot 10^{-7}$	0.16	0.25	$< 2 \cdot 10^{-16}$	$2.0 \cdot 10^{-4}$
CS	$1.28 \cdot 10^{-6}$	$7.56 \cdot 10^{-5}$	0.66	0.47	0.83	$1.69 \cdot 10^{-12}$

The effects for birth herd and slaughter herd shows no significance with the observed slaughter traits in Data B, which consists of data from 741 BLKxHOL crossbreds in the four FBC herds. 63 dairy herds are delivering 11.76 calves on average to the four slaughter calf productions. The distribution of these calves is however not even, since the range of delivered calves is from 1 to 144. An effect for birth herd would capture differences in calves from different herds. Since the calves unequally distributed from many herds, the effect was not suitable to use as a fixed effect. Inclusion of the birth herd as a random effect was tested in the genetic model. A genetic model with random environmental effects is extended from Eq (7).

$$y = Xb + Wc + Zs + e \tag{11}$$

Were c describes the common environmental effects, and W is the design-matrix assigning the environmental effect to the observation (Mrode, 2014). The model from Eq. (9) was run in DMU on the slaughter traits in data B with birth herd as a random effect. The estimated parameter of the random effect variance had a very large standard error, and only in carcass conformation was the effect different from 0. Since the model we would like to use, should be common for all traits, the effect of birth herd was removed. Even though the first period in the dairy herds are important for the calves, it was not detectible on the slaughter traits with this data. The model was therefore modified to

$$y_{ijklmn} = BYM_i + SLYM_j + sherd_l + sex_m + age_n \tag{12}$$

6.2 Slaughter herd effect

The calves are raised in the slaughter-calf production, making the slaughter calf herd a likely environmental effect to affect the phenotypic observations. The linear regression (Table 5) did however find no significant effect of this variable. Since the linear regression is insignificant, the effect $sherd$ likely contributes with very

little information to the slaughter trait. The model from Eq. (12) was run in DMU where $sherd$ is included as a fixed effect. This was run as a Mixed linear model, where information on the animal's pedigree is included. The estimate of the fixed effect and the standard error of the effect is presented in Figure 3. The figure presents the estimated effect of the fixed effect along with the standard error of the estimate. These are presented in the output of DMU. The estimates show that while there is a numerical difference between the estimates, it is not significantly different between the herds. This means the estimate of the mean between the herds cannot be estimated accurately enough to determine whether there is a true mean difference between the herds.

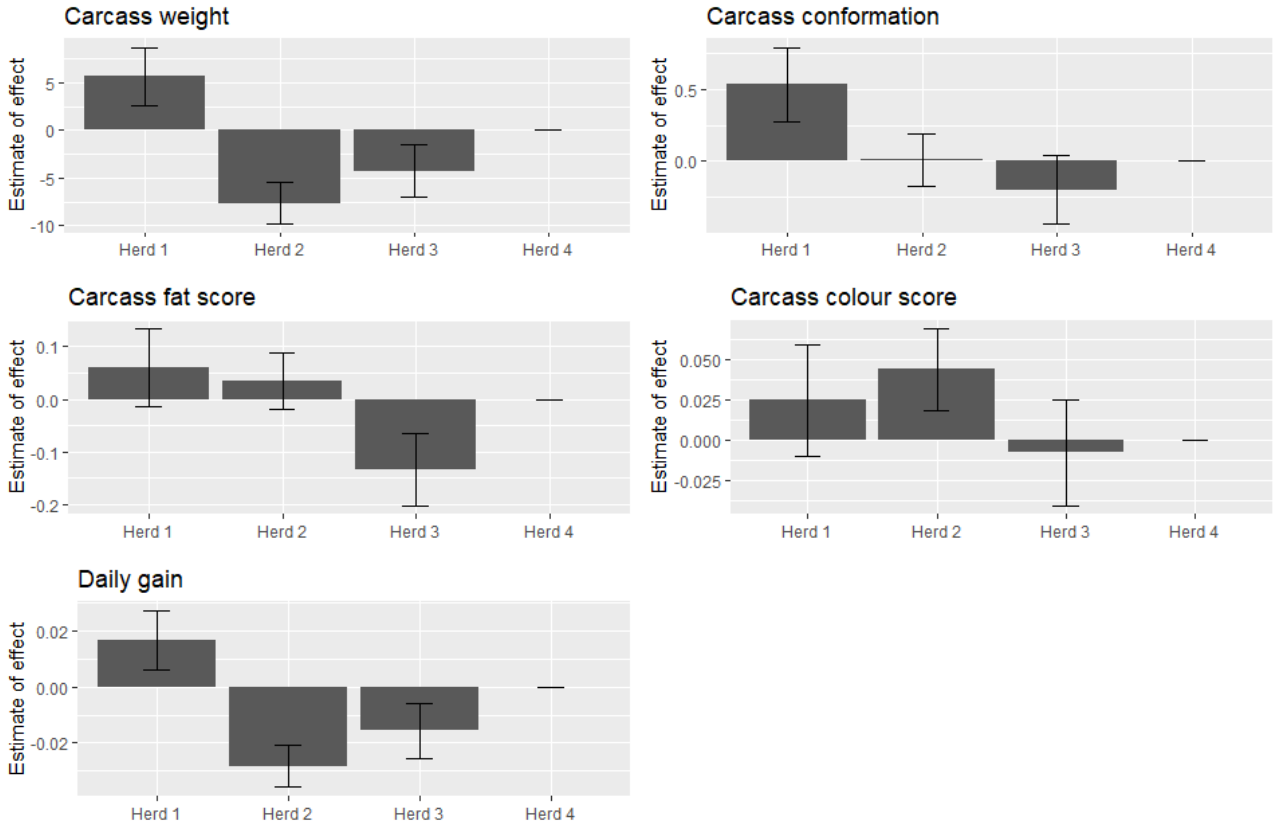

Figure 3: Plot of the estimated fixed effects of the slaughter herd from DMU after running the model in Eq. (12). Error bars are included as a depiction of the standard error of the estimate.

The four herds contributing with different number of calves to the dataset (Figure 4). Ideally the number of animals would be evenly distributed, but in both Data A and Data B, Herd 2 had much more observations than the other herds. It might be problematic that the largest proportion of the animals come from the same herd, since it can influence the estimation of parameters. The herds were chosen from similar management practices, which might explain no significant differences are found in the linear regression and the estimates of fixed effects from DMU. The effect of slaughter herd was however kept since there were numerical differences in the estimate of the fixed effect. Even though the difference was not significant, it is the best correcting the difference between herds. Biologically it is reasonable to think that the herd will influence the animals.

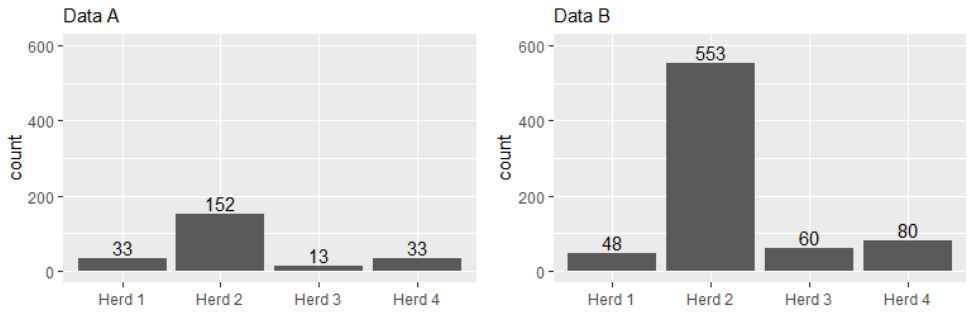

Figure 4: Number of observations in each herd in Data A (left) and Data B (right).

6.3 Correction for age

The model includes BYM, SLYM and age of the animals. They were all significant in most of the linear regression. Since they all describe the age of the animals, they will be confounded and describe the same effect. The first effect evaluated was SLYM since this effect is likely covered by including birth (BYM) and slaughter age in the model. The model from Eq. (9) included all three effects. The estimate of the SLYM is shown in Figure 5. Comparing the estimate with standards errors, only few estimates that are significantly different. In carcass weight and daily gain, animals born in July 2019 is different compared to animals born later than October 2019.

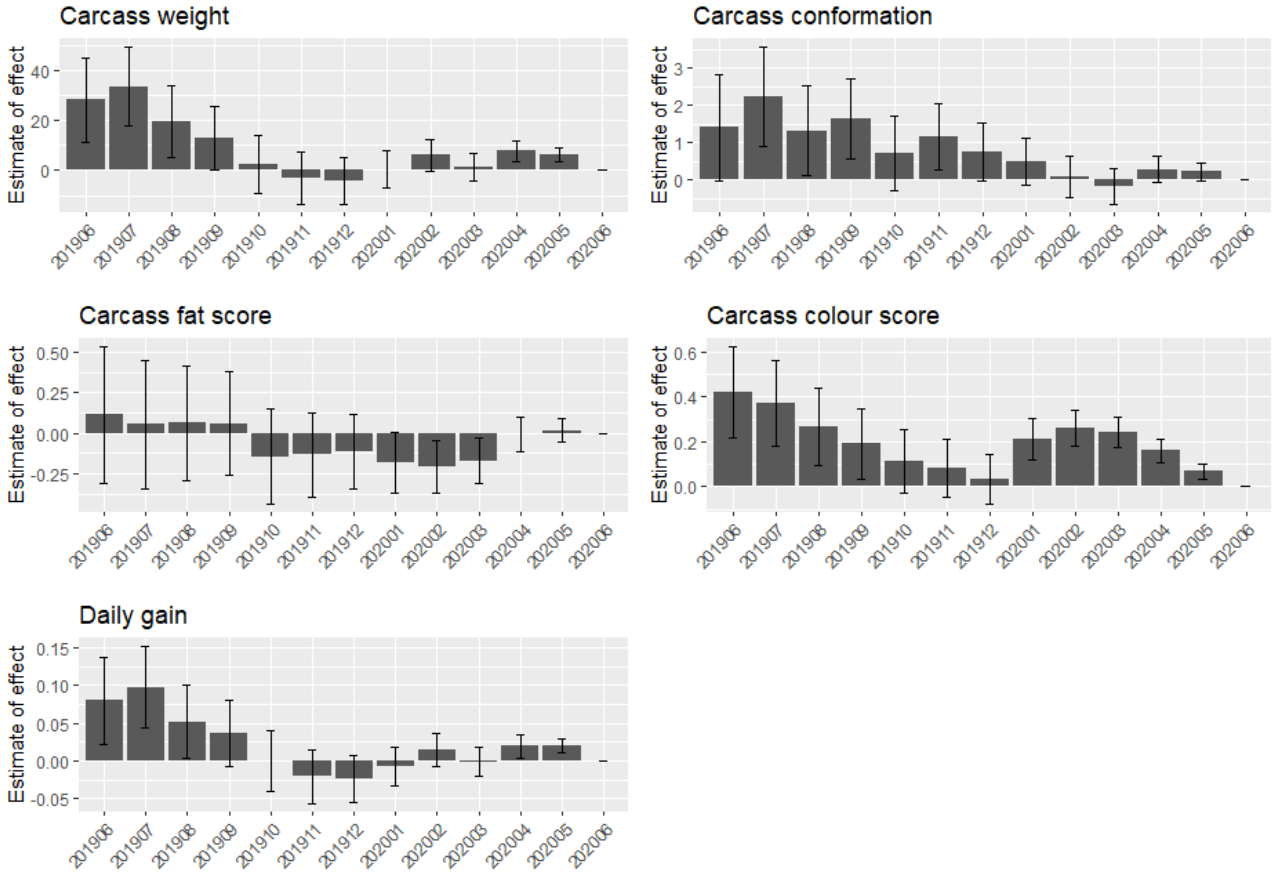

Figure 5: Plot of the estimated fixed effects of SLYM on the respective slaughter traits

Since the effect is likely covered by BYM and age in the model, and it explains very little difference in the groups, the effect was removed. When aiming to evaluate genetic parameters on small datasets limiting the number of levels for environmental effects, will make more degrees of freedom available for parameter estimation. The BYM was pooled into a season effect, based on three months interval. This gives us the current model:

$$y_{ilmn} = BYS_i + sherd_l + sex_m + age_n \quad (13)$$

Where BYM is renamed to BYS after pooling the months into quarters.

6.4 Age and sex

The age variable is currently included as a linear regression in the model. This means the animals phenotypes are adjusted based on a linear regression according to their age. This assumes that traits evaluated are behaving as linear distribution with age. Growth curves in animals are rarely linear and from the introduction (p. 16) we know that the growth traits are not developing as linear traits. The calves are however slaughtered in a relatively short period, so the curve of this trait might be close to linear in this dataset. If the age is not linear, this can be solved with using the age as a fixed effect, on the slaughter age in months. A fixed effect will compare the mean values of the traits in each group, here slaughter age in months. This will therefore account for non-linearity in the data. The animals are evaluated in a dataset containing both sexes. This can be a challenge for the correction of age as a fixed effect. Figure 6 shows the distribution of age in each of the datasets in bulls (red) and heifers (blue) as overlapping histograms.

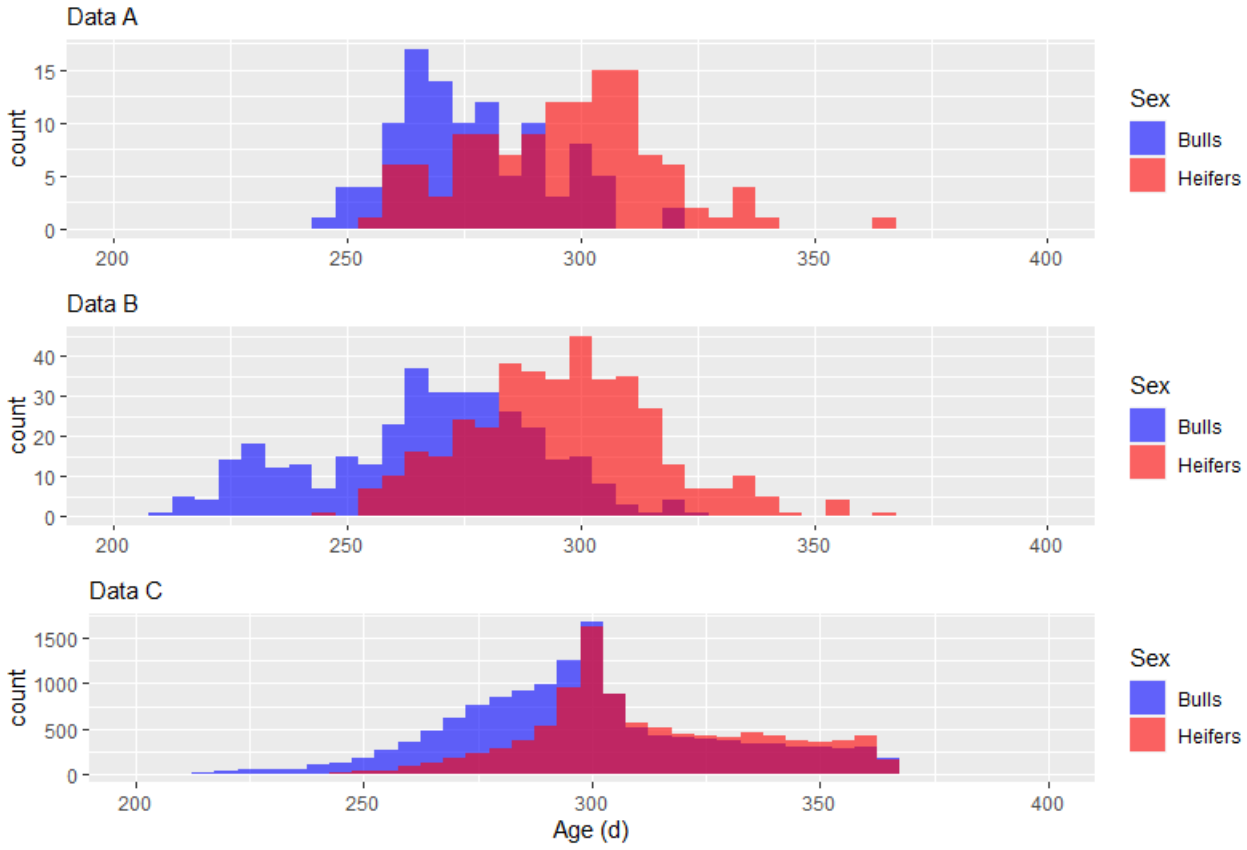

Figure 6: Histogram over the distribution of age across the datasets. In each plot the bulls (blue) are plotted with the heifers (red) as overlapping histograms. Area in dark red are the overlapping areas of the histograms.

The heifers are generally slaughtered later than the bulls, likely due to their lower daily gain, meaning the producers are keeping them for longer to maximize the price for the carcass. If the heifers are selected differently for slaughter than the bulls, the age correction will be confounded between the sexes. A fixed effect will only be able to correct between two groups with different means. If the two groups are selected differently the effect will not be common for the sexes. To take this into account the data can either be divided into two datasets based on sex, or the fixed effect for age can be joined with sex so we have an age*sex effect. To avoid small groups of age in bulls was edited to 7, 8 and 9+ months and the heifers to 8, 9 and 10+ months in Data A and Data B. Data C has sufficient animals in all months to keep the original groups. The models tested in the joint dataset was

$$y_{iln} = BYS_i + sherd_l + agemonth \cdot sex_n \quad (14)$$

Where the agemonth*sex effect will cover the interaction between age and sex. This means the agemonth variable will be evaluated within each sex. This will account for difference in growth curves between sexes. A fixed effect can adjust the phenotype by the mean of the groups compared, but only if the groups has the same variance. If the bulls and heifer are different only in the value of the evaluated trait and not in the variance, a

fixed effect will be sufficient. The estimate of the fixed effect and the SE from DMU is presented in Figure 8Figure 7.

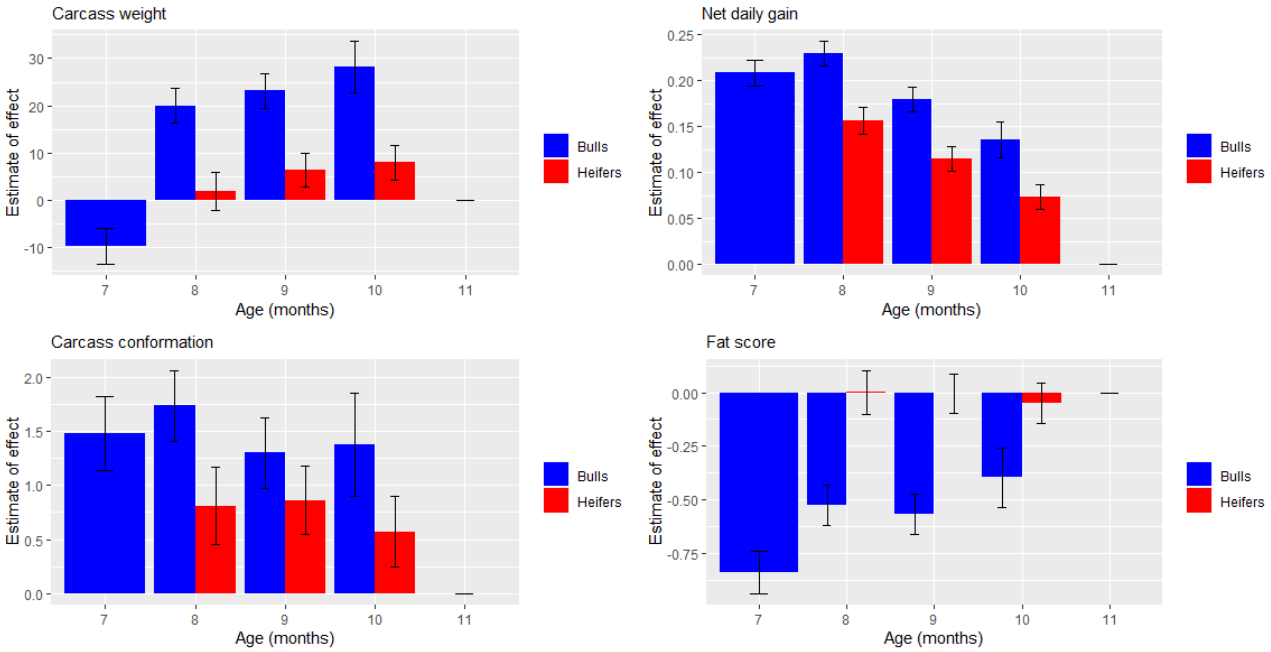

*Figure 7: Estimate of the fixed effect for agemonth*sex in Data B. Error bars are the SE on the estimates.*

The estimates on the fixed effects of carcass weight shows that the difference between the bulls and heifers. The relative difference between age within the two sexes seem to follow the same trend from 8 till 10 months. The heifers at 11 months (SE not given in DMU output) is however not following the distribution. These animals have a lower carcass weight compared to the other age groups. The same group is also lower in carcass conformation and net daily gain. This could suggest that heifers slaughtered at 11 months of age is animals that are growing less and is kept for longer to compensate for the slower growth. If this is the case a linear regression effect of age would not be accounting for this selection. This would likely flatten out an age regression in slaughter weight and therefore not provide an accurate adjustment according to age.

The bull calves slaughtered at 7 months are another group not following a linear distribution. Their slaughter weight is lower, and they have a slightly lower net daily gain. These calves would also be affecting a linear regression of age. This is a further argument for using the age in levels based on months might be describing the data in the best way.

The model of Eq (14) will be basis for the genetic analysis of the traits in the joint datasets. To test if genetic parameters are equal between sexes the following model is used on datasets divided into bulls and heifers

$$y_{iln} = BYS_i + sherd_l + agemonth_n \quad (15)$$

These datasets will have a lower number of observations and is therefore expected a higher standard error. Splitting an already small dataset, means the estimation of parameters will likely be challenging to describe the general population. The evaluation on genetic parameters in sex divided datasets, will therefore only be used to evaluate in genetic variances are the same in bulls and heifers. The datasets containing both sexes will be used to compare heritabilities with other studies.

7 Results

This section will present the summary statistics of the three datasets used for the genetic analysis and the results from the genetic analysis. The result will be split for the joint evaluation and the comparison of the data split into sex.

7.1 Descriptive statistics for joint datasets

Data A is based on 231 animals in total, born after 31 sires. The mean number of offspring are 7.5 per sire, but with large variation between the sires. The animals are born from October 2018 to October 2019 and slaughtered in the period August 2019 to July 2020. The distribution of sex is 105 bulls (45.5%) and 126 heifers (54.5%). The age of the animals was from 247 to 363 days with mean age at slaughter was 287 days. Data B is based on all animals slaughtered from the 4 FBC herds in the period from June 2019 to July 2020. The animals are born from August 2018 to October 2019. The distribution of sex is 349 bulls (47%) and 392 heifers (53%). The age of the animals was from 211 to 363 days at the time of slaughter, with the mean at 282 days. Data C is based on the commercially registered slaughter registrations from all BLKxHOL slaughtered in Denmark from January 2019 till June 2020. The dataset is based on 23765 animals born after 88 sires. The animals are born from October 2017 to March 2019. The distribution of sex is 13919 bulls (57.4%) and 10336 heifers (42.6%). The age of the animals at slaughter was from 203 till 365 days. The average age was 304 days. Summary statistics of the observed traits are given in Table 6.

Table 6 Summary statistics of Data A, Data B and Data C. Number of observations, mean and standard deviation is given in on each trait in the respective dataset.

	Data A			Data B			Data C		
Trait	**n**	**Mean**	**sd**	**n**	**Mean**	**sd**	**n**	**Mean**	**sd**
CW (kg)	231	215.42	17.64	741	212.93	18.56	23765	225.35	25.68
CG (kg/d)	231	0.676	0.078	741	0.680	0.076	23765	0.672	0.088
CC	231	7.56	1.20	741	7.55	1.33	23765	7.29	1.55
FS	231	2.67	0.47	741	2.68	0.47	23765	2.55	0.52
CL	217	2.99	0.10	741	2.96	0.20	23765	2.99	0.08
LTA (cm^2)	226	69.32	13.36						
IMF (%)	223	2.23	1.13						
SF (N)	223	48.68	10.38						
CL (%)	222	10.95	2.69						
L^*	230	49.29	4.23						
a^*	230	22.06	2.37						
b^*	230	11.72	1.85						
pH	230	5.63	0.06						

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score, LTA: LT muscle area, IMF: Intramuscular fat content, SF: Shear force, CL: Cooking loss, L: lightness, a*: redness, b*: yellowness, pH: pH at 72h post-mortem*

The three datasets are very comparable in the shared traits, both in mean and standard deviation. Data C has a slightly higher standard deviation in the carcass weight which is likely connected to the higher average age. The number of observations on the meat quality traits in Data A varies slightly, since some samples was not large enough to supply substrate for all analysis.

7.1.1 Results from the genetic analysis

The data presented in the previous section were basis for the genetic analysis. All three datasets were run in DMU and the results are presented in Table 7. The carcass colour score was also evaluated for genetic parameter, but due to very little variation in all three datasets, the results were not printed. The significance of the estimates was evaluated with 95%-level confidence interval $CI_{95\%}$[min, max] = [θ - 1.96*SE, θ + 1.96*SE], where the θ in the estimated parameter on h^2. Intervals covered by one standard error is $CI_{70\%}$[θ -SE, θ +SE].

Heritabilities in Data A was determined with a very large standard error, with the two measures for colour L* and b* having heritabilities significantly different from 0. The heritabilities estimated on Data B still has a high standard error. For EUROP conformation the heritability was estimated significantly different from zero,

whereas the other traits are not. In Data C there was estimated moderate heritabilities for slaughter weight, daily gain and conformation score. The EUROP fat score had a low heritability.

Table 7: Heritability estimates and the corresponding standard error in the three datasets

Trait	Datasets		
	Data A	**Data B**	**Data C**
CW	0.06 ± 0.13	0.31 ± 0.16	0.19 ± 0.04
CG	0.09 ± 0.14	0.29 ± 0.15	0.22 ± 0.05
CC	0.38 ± 0.26	0.35 ± 0.17	0.32 ± 0.06
FS	0.13 ± 0.21	0.17 ± 0.13	0.15 ± 0.04
LTA	0.12 ± 0.19		
IMF	0.46 ± 0.35		
SF	0.16 ± 0.22		
CL	0.17 ± 0.21		
L^*	0.70 ± 0.35		
a^*	0.22 ± 0.26		
b^*	0.70 ± 0.34		
pH	0.28 ± 0.24		

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score, LTA: LT muscle area, IMF: Intramuscular fat content, SF: Shear force, CL: Cooking loss, L: lightness, a*: redness, b*: yellowness, pH: pH at 72h post-mortem*

The phenotypic and genetic correlations in Data A is presented in Table 8. Due to the low number of observations not all bivariate models were able to converge and therefore there is no results. Slaughter weight has a high positive phenotypic correlation with ADG, a moderate correlation to EUROP conformation, and a lower phenotypic correlation with EUROP fat score and LTA. LTA also shows a low positive phenotypic correlation with ADG and EUROP conformation. IMF shows a moderate to low correlation with EUROP fat score. The L* value has a moderate phenotypic correlation to the b* value. The b* value has a high phenotypic correlation to the a* value. As with the heritabilities the estimate of the genetic correlation is with very large standard errors. EUROP carcass conformation does show genetic correlation EUROP fat score. The EUROP fat score also shows significant genetic correlation with IMF. The b* value has a significant genetic correlation to both the L* and the a* value.

The genetic and phenotypic correlations in Data B is shown in Table 9. The phenotypic correlations between slaughter weight and ADG is high, and a moderate phenotypic correlation to EUROP conformation. The standard error on the genetic correlations is numerically smaller than the standard error in Data A. The ADG and the slaughter weight is genetically identical with a complete genetic correlation. EUROP conformation has moderate positive correlation to the slaughter weight and ADG.

The results from the bivariate models on Data C are presented in Table 10. Phenotypic correlations are equivalent to the results from Data B. Genetic correlation between EUROP conformation and slaughter weight are high. EUROP conformation and fat score has a negative correlation. Fat score also has a low negative, but non-significant, genetic correlation with slaughter weight and ADG.

Table 8: Phenotypic (above diagonal) and genetic (below diagonal) for the traits evaluated in Data A. The Standard Error of the correlation is given in the lowered number

	CW	CG	CC	CF	LTA	IMF	SF	CL	L*	a*	b*	pH
CW		0.92	0.49	0.20	0.25	0.08	0.09	NA	0.13	-0.02	0.06	0.04
CG	-NC-		0.48	0.15	0.25	-0.01	0.07	-0.04	0.14	-0.04	0.06	0.03
CC	-0.29 ±0.69	-0.18 ±0.65		-0.03	0.23	-0.07	0.01	-0.20	0.17	0.14	0.22	0.07
CF	-NC-	1.00 ±1.72	-0.75 ±0.26		0.01	0.21	-0.07	0.09	0.06	0.11	0.12	0.01
LTA	-0.69 ±0.57	-0.42 ±0.72	-0.36 ±0.89	-0.38 ±0.86		-0.06	-0.04	-0.07	0.17	0.06	0.15	0.05
IMF	0.12 ±1.00	0.06 ±0.85	-NC-	0.76 ±0.35	-NC-		-0.02	0.07	-0.01	0.11	0.07	-0.02
SF	-NC-	-NC-	-0.11 ±0.63	-NC-	-NC-	-NC-		-0.13	-0.22	-0.25	NA	0.14
CL	-NC-	-NC-	0.06 ±0.67	-NC-	-0.36 ±1.29	0.68 ±0.44	-0.58 ±1.03		-0.23	0.15	0.02	-0.20
L*	0.48 ±1.17	0.38 ±0.79	0.06 ±0.47	0.77 ±0.77	0.74 ±0.81	-NC-	-NC-	-0.49 ±0.45		-0.05	0.56	0.03
a*	-0.08 ±1.20	0.07 ±1.01	-0.34 ±0.65	-NC-	-0.43 ±0.96	0.73 ±0.45	-0.25 ±0.91	-0.09 ±0.93	0.06 ±0.58		0.74	-0.14
b*	0.27 ±1.14	0.30 ±0.86	0.01 ±0.45	-NC-	0.54 ±0.85	-0.23 ±0.56	-NC-	-0.15 ±0.61	0.72 ±0.24	0.71 ±0.27		-0.11
pH	-NC-	-0.99 ±1.41	-0.18 ±0.58	-0.99 ±2.82	-NC-	0.47 ±0.54	0.29 ±0.86	-NC-	-0.44 ±0.47	-0.43 ±0.62	-0.57 ±0.43	

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score, LTA: LT muscle area, IMF: Intramuscular fat content, SF: Shear force, CL: Cooking loss, L: lightness, a*: redness, b*: yellowness, pH: pH at 72h post-mortem*

Table 9: Phenotypic (above diagonal) and genetic (below diagonal) for the traits evaluated in Data B. The Standard Error of the correlation is given in the lowered number

	CW	CG	CC	CF
CW		0.93	0.45	0.14
CG	1.00 ±0.01		0.47	0.14
CC	0.27 ±0.34	0.36 ±0.32		-0.04
CF	-0.16 ±0.43	-0.21 ±0.43	NC	

Table 10: Phenotypic (above diagonal) and genetic (below diagonal) for the traits evaluated in Data C. The Standard Error of the correlation is given in the lowered number

	CW	CG	CC	CF
CW		0.95	0.52	0.26
CG	1.00 ±0.01		0.52	0.25
CC	0.68 ±0.09	0.65 ±0.09		0.04
CF	-0.17 ±0.16	-0.13 ±0.16	-0.39 ±0.17	

7.2 Comparison between sex

The model from Eq (14) were basis for an evaluation on the data split into sex. The descriptive statistics of Data A is given in Table 11. Bulls were slaughtered on an avg. age of 277 days, and heifer were slaughtered at 296 days. The bulls were heavier at slaughter and had a higher ADG. Bulls had more variation in EUROP fat score compared to the heifers. Heifers had a higher IMF content.

Table 11: Descriptive statistics of the Data A split into bulls and heifers. Number of observations, mean and standard deviation is given on each trait

	Bulls			Heifers		
Trait	**n**	**Mean**	**sd**	**n**	**Mean**	**sd**
CW (kg)	105	222.63	15.74	126	209.41	16.93
CG (kg/d)	105	0.7270	0.0671	126	0.6339	0.0578
CC	105	7.96	1.30	126	7.23	1.01
FS	105	2.35	0.48	126	2.93	0.26
CL	104	2.98	0.14	113	3.00	0.00
LTA (cm^2)	100	70.40	13.35	126	68.47	13.37
IMF (%)	104	1.58	0.69	119	2.80	1.13
SF (N)	101	52.05	11.49	122	45.90	8.44
CL (%)	101	11.73	3.03	121	10.30	2.18
L^*	105	49.34	4.29	125	49.24	4.19
a^*	105	21.14	2.45	125	22.83	2.01
b^*	105	11.18	1.90	125	12.17	1.69
pH	105	5.64	0.06	125	5.63	0.05

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score, LTA: LT muscle area, IMF: Intramuscular fat content, SF: Shear force, CL: Cooking loss, L: lightness, a*: redness, b*: yellowness, pH: pH at 72h post-mortem*

Summary statistics from the other datasets, Data B and Data C divided into sex are presented in Table 12. A similar difference on ADG and slaughter weight is seen in these datasets. The bulls score slightly higher on conformation and slightly lower on EUROP fat score.

Table 12: Summary statistics for observations in Data B and Data C divided in sex

	Data B bulls		Data B heifers		Data C bulls		Data C heifers	
Trait	**Mean**	**Sd**	**Mean**	**Sd**	**Mean**	**Sd**	**Mean**	**Sd**
CW (kg)	216.18	21.13	210.03	15.37	233.27	24.65	213.33	19.98
CG (kg/d)	0.728	0.064	0.637	0.059	0.713	0.079	0.616	0.064
CC	7.93	1.46	7.21	1.09	7.63	1.67	6.85	1.23
FS	2.38	0.49	2.94	0.24	2.31	0.49	2.86	0.36

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score.

7.2.1 Genetic parameters from sex divided datasets

The heritability and standard error from the genetic analysis of sex divided datasets are given in Table 13. The heritability on Data A is estimated with a very large standard error and no heritabilities were estimated significantly different from zero. The same is true for the estimates on Data B.

Table 13: Heritability and standard errors estimate on the three datasets divided into sex.

Trait	Data A		Data B		Data C	
	Bulls	**Heifers**	**Bulls**	**Heifers**	**Bulls**	**Heifers**
CW	0.17 ± 0.38	0.06 ± 0.24	0.33 ± 0.25	0.22 ± 0.20	0.15 ± 0.04	0.33 ± 0.08
CG	0.14 ± 0.32	0.51 ± 0.41	0.17 ± 0.19	0.36 ± 0.23	0.18 ± 0.04	0.37 ± 0.08
CC	0.61 ± 0.53	0.00 ± 0.31	0.30 ± 0.22	0.15 ± 0.17	0.30 ± 0.07	0.51 ± 0.10
FS	0.00 ± 0.34	0.09 ± 0.24	0.12 ± 0.17	0.18 ± 0.16	0.16 ± 0.04	0.16 ± 0.05
LTA	0.09 ± 0.31	0.00 ± 0.26				
IMF	0.00 ± 0.49	1.55 ± 0.60				
SF	0.00 ± 0.50	0.74 ± 0.57				
CL	0.10 ± 0.29	0.58 ± 0.50				
L^*	0.42 ± 0.49	0.88 ± 0.48				
a^*	0.00 ± 0.44	0.00 ± 0.25				
b^*	0.05 ± 0.30	0.71 ± 0.48				
pH	0.20 ± 0.32	0.70 ± 0.50				

Abb:, CW: Carcass weight, CG: Net daily gain, CC: Carcass conformation, FS: Fat score, LTA: LT muscle area, IMF: Intramuscular fat content, SF: Shear force, CL: Cooking loss, L: lightness, a*: redness, b*: yellowness, pH: pH at 72h post-mortem.*

The heritability estimates on slaughter weight in Data C was estimated to low heritability in Bulls and a moderate heritability in Heifers. The estimates were not significantly different. The same pattern shows in ADG and EUROP conformation were the heifers has a numerically larger heritability than the bulls. The estimates are however still with a relatively large standard error.

8 Discussion

In the discussion, the results will be evaluated and compared to the available literature on the subject. The aim with this study was to estimate genetic parameters on meat quality traits in BeefxDairy crossbred calves. The heritabilities, phenotypic and genetic correlations was estimated both for meat quality traits and classical recorded slaughter registrations. The classical registrations were also used for an analysis whether the small dataset was representative for a larger population. A discussion of the design of the project will also be included.

8.1 Classical slaughter registrations

The classical slaughter registrations, for carcass weight, daily net gain, conformation score and fat score was included in this study to validate the genetic model, and to provide information on the correlation from existing practices, to the new traits on meat quality. These traits are currently included in the breeding goal both in Danish dairy and beef cattle, so the range of the genetic parameters is well known.

The average mean of the classical slaughter registrations was equal in all three datasets. Data C had a slightly higher average and standard deviation of slaughter weight. This can be expected since the average age of slaughter was higher and there was included more herds in the dataset. The animals across datasets had a numerically higher daily gain compared to the average of BLKxHOL slaughtered in Denmark from 2011 to 2019, both in bulls and heifers (Fogh, 2019). The conformation score is however slightly lower. The higher daily gain can be explained by a genetic progress in the period from 2011, however this could also be due to chance. Other studies of HOL and BLK crossbreds have studied heavier carcasses on older animals (Keady et al., 2017). The younger age of the animals in this study is likely contributing to very lean carcasses. The fat cover score had very little variation and was scored as medium. As seen in the comparison between sex (Table 11 & Table 12) the heifers on average scored higher compared to the bulls, but not with a significant difference. Higher fat deposition has been reported in heifers and is reported in other studies of BLKxHOL studies (Vestergaard et al., 2019, Bittante et al., 2018).

The heritability in classical registrations on Data A could not be estimated as significant different to 0 due to a too high standard error on the estimate. A high standard error was also seen in Data B. The high standard error on the estimates in these datasets is likely caused by the low number of registrations. The heritability on the classical registrations in Data C was estimated with the lowest standard error and was estimated to be low-moderate. The genetic effects of slaughter weight, net daily gain, conformation score and fat score has been studied in many populations, and the level of heritability is therefore well known. The heritability for growth traits in the Nordic HOL population was estimated to 0.28 for carcass gain, 0.29 for carcass conformation and 0.18 for carcass fat score (NAV, 2020). The heritability estimates in this study lies within range of these estimates. Heritabilities of these estimates has been shown to vary between breeds. Hickey et al. (2007) found that in Irish BeefxDairy crossbreds, sired by 8 different beef breeds, the heritability for carcass weight 0,06-0,65,

for carcass conformation 0,04-0,36 and fat score 0,00-0,40. The heritability for BLKxHOL was estimated to 0.17 (0.06), 0.33 (0.08) for carcass conformation, and 0.15 (0.06) for fat score, with standard error in parenthesis. This is very close to the estimates found in this study. A similar result in this study was a large SE in parameter estimates, when number of observations with breeds were low. In older animals the fat score has been estimated to be moderate 0.3-0.4 (Kause et al., 2015, Eriksson et al., 2004, Moore et al., 2017). The higher heritability might be explained that fat deposition in older animals are regulated by other genetic areas, than the fat deposition at younger age.

The carcass fat colour score was omitted from the results due to very little variation. In Data A 99% of the animals scored the value 3. In Data B and Data C the number of observation on colour score 3 was 96% and 99% respectively. The very uniform score is likely because the animals in this project was raised on a concentrate diet and only offered straw as a supplement. Their main energy intake is therefore likely based in cereal-based diets, which gives a whiter fat colour (Therkildsen et al., 1998). Higher colour score is associated with a price reduction and scores above 3 will disqualify animals for the "Dansk Kalv" concept. Higher colour scores are seen in older animals raised on less energy dense diets (Vestergaard et al., 2019).

8.2 Phenotypic observations on meat quality

The registrations on meat quality was registered in Data A and estimation of genetic parameters was challenged due to low in number of observations. The number of observations varied from each trait, since not all samples had sufficient substrate for all meat quality analysis. The IMF content of the LT muscle was measured with a large standard deviation, meaning that there was a large phenotypic variation. Both the variance and the mean of the measure for IMF was higher in heifers, compared to the bulls (Figure 8). Most of the bulls are below 3%, which was suggested as the minimum acceptable limit of IMF to achieve acceptable eating quality by Savell and Cross (1986). Beef below this limit was tougher and less flavourful. The heifers are more evenly distributed across this limit and generally has a higher IMF content. A significant correlation between IMF and flavour liking was seen when levels of IMF was below 3% in young CHA bulls. Animals with IMF above 3% showed no correlation with flavour liking (Hocquette et al., 2011). A linear improvement in sensory tenderness, juiciness and flavour liking was seen in the range of IMF from 0.23-9% in cattle of mixed age and breed (Bonny et al., 2015).

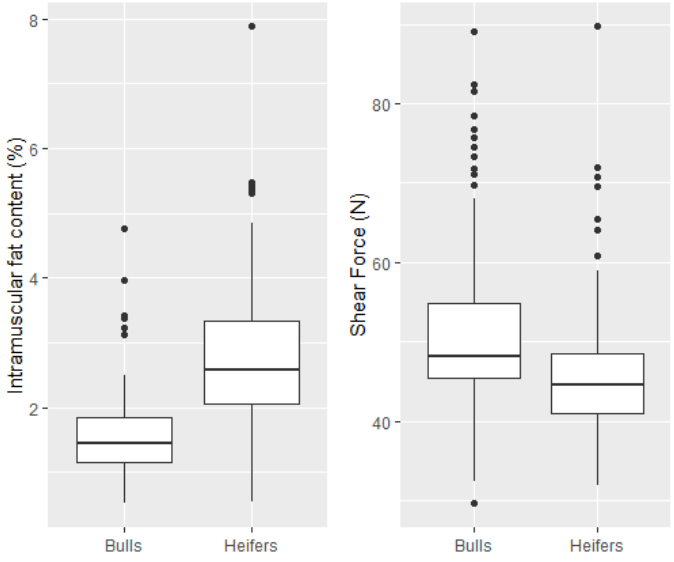

*Figure 8: The distribution of IMF and Shear Force between bulls and heifers in Data A. Dots represent values deviating from the median with more than 1.5*IQR. (IQR: Distance covered by 1st and 3rd quartile)*

Since the IMF values the mean value for IMF in both sexes in this study is below 3%, an improvement in IMF level for BeefxDairy crossbreds will give a higher meat quality. The level of IMF in this study is comparable to young purebred CHA and LIM bulls, whereas double muscled BAQ bulls had significantly lower IMF levels (Allais et al., 2014). Studies of purebred ANG has shown average IMF content between 3-4% in yearling animals (MacNeil et al., 2010, McAllister et al., 2011, Hay and Roberts, 2018). This indicates that even though the animals in this study is crossbred with a double-muscled beef breed as sire, the level of IMF is comparable to the level in other young bulls. Older animals has a higher average IMF of 10% (Torres-Vazquez et al., 2018). The IMF content in Danish SDM cattle and BBL crossbreds were estimated at 1.08 in older trials (Liboriussen et al., 1982). The low content of IMF can be expected in young cattle and shows that the deposition of IMF is at a relatively early stage.

The difference in IMF between the sexes is not seen in the distribution of Shear Force (Figure 8). This was supported by no phenotypic correlation between the two traits. No significant difference are seen between the distributions of the phenotype in bulls and heifers. The bulls has a slightly higher mean and standard deviation, as well as more observations above 70 N. SF was estimated at 72h post-mortem, meaning the meat at sale will be more tender compared to these results, due to the effects of the aging period. Shackelford et al. (1997) found that tenderness measured below 60 N at day 2 in the aging period would reach satisfactory tenderness after 14 days of aging. Carcasses measured above 60 N would be less likely to reach satisfactory levels of tenderness after aging period. As seen in Figure 8 more bulls are above this limit than heifers. Some of these animals might not reach a satisfactory tenderness.

The cooking loss was an estimation on the water holding capacity of the meat. The cooking loss in this study was lower compared to other studies that found an average cooking loss at 20% (Mandell et al., 1997, Johnston et al., 2003). This might be due to different cooking methods for estimation of cooking loss. The pH was measured to an average of 5.63, which is within the wanted range from 5.4-5.8. Only two animals were above this range with observations on 5.87 and 5.82. These animals might have been exposed to pre-slaughter stress making the drop in pH lower than the optimal.

The colour values L*, a* and b* was not different between the sexes. The colour of the meat was measured with a higher L*, a* and b* value compared to steers of beef breeds (Chambaz et al., 2001). This is likely due to the older age of the steers. A lower L* score and a* value was seen in BLK, LIM and ANG bulls slaughtered at 1 year (Cuvelier et al., 2006). Wegner et al. (2000) showed that the L* decreased with the age of the animals resulting in darker colour of the meat. Breed differences has also been seen in the colour values (Ripoll et al., 2018) This was associated with the breed having a significantly higher frequency of muscle fibres type IIb, which is the fast-twitch glycolytic fibre. This fibre type has less myoglobin than the oxidative type Ia and the intermediate IIa, which explains the lighter meat. The oxidative muscle fibres have a higher myoglobin content since the aerobic metabolism is greater in these muscles compared to the glycolytic. The muscle fibre

distribution is important for the colour of the meat. Since the type IIb has a larger cross-sectional area and is associated with high muscling breeds, high conformity of the slaughter carcass is also related to paler meat. This was seen in breeds, such as CHA and Piemontese which had a high conformation score, and also paler meat, compared to breeds such as ANG and HOL (Ripoll et al., 2018, Albertí et al., 2008). Vestergaard et al. (2000) found that an extensive rearing of young bulls on a roughage-based diet and in loose-housing was associated with darker meat compared to intensive system with concentrate-based diet. The two groups were however also of different age with the extensively raised animals being older due to less growth rate (Therkildsen et al., 1998).

8.3 Heritability estimates on meat quality traits

All heritability estimates in Data A was estimated with a large SE. If number of observations behind a heritability isn't based on very large number the standard error of the estimate gets very large (Falconer and Mackay, 1996). Until larger datasets are available the heritability cannot be closer determined. When the power of the dataset is low, only traits with a high true heritability can be estimated as significant different from 0 (Visscher et al., 2008). Originally a similar number of Angus and Charolais crossbreds should have been included in the dataset, but only very few calves were slaughtered from these breeds at the time of this project. The high standard error means that it is not possible to conclude on the range on the heritability, since it could be anywhere from 0 to 1. Therefore a overview of heritabilities in the literature will be given.

The heritability of LTA was estimated between 0.37 and 0.46, by ultrasound measurements and carcass measures (Crews et al., 2003). In Korean cattle the heritability was estimated to 0.45 (Bhuiyan et al., 2017). The IMF was not estimated to have a significant heritability based on the registrations in Data A. The heritability of IMF has mainly been studied based on ultrasound measurements in live animals, since IMF is part of the ANG breeding goal in USA (MacNeil et al., 2010). The heritability on IMF estimated by ultrasound ranges from 0.14 to 0.53 across breeds (Schenkel et al., 2003, Hay and Roberts, 2018, MacNeil et al., 2010). The study with the largest number of registrations, 73000 animals, estimated the heritability to 0.31 ± 0.01 (McAllister et al., 2011). When comparing to studies based on chemical estimation of IMF content the number of animals is significantly lower, due to the increased cost of getting the registrations. The heritability is still in the same range. Reverter et al. (2003) found a heritability on 0.38 ±0.04 in temperate breeds in Australia. Moderate heritabilities was also estimated in other studies (Mateescu et al., 2015, Mateescu et al., 2016, Allais et al., 2014). The literature available is evaluating the IMF content to be moderately heritable. A moderate heritability means that a selection response in IMF content would mean an increase in the average IMF content within relatively few generations, depending on the intensity of the selection.

The heritability on shear force was also non-significant. Shear fore was estimated to have a moderate heritability at 0.4 across breeds (Dikeman et al., 2005). The heritability of SF has been shown to be dependent on the aging period. The heritability for shear force was declining from 0.19 on day 7 to 0.05 on day 21 (Zwambag

et al., 2013). This could indicate that the effect of aging, makes the genetic effect less important. The estimate was however with large standard errors. Pratt et al. (2013) found no significant differences in heritability across the aging period from 3-21 days. Aging period does influence the shear force, but the evidence that the heritability changes over the aging period is thin.

The heritability of the colour measurements was estimated as significant for L* and b*. The very high SE does not give any indication on the value of heritability. In literature L*, a* and b* was estimated to have a low-moderate heritability across beef breeds (Pratt et al., 2013, King et al., 2010, Johnston et al., 2003, Savoia et al., 2019). The stability of the colour was also been shown to be dependent on genetic parameters in a* and b* with a low heritability estimated (King et al., 2010). Given more data on the meat quality it is likely that the heritability of the colour measurements will move towards a low-moderate heritability. When more data becomes available it can be concluded whether the estimate of heritability in the literature is within range of the BeefxDairy crossbreds in the FutureBeefCross project.

8.4 Genetic correlations

The small number of observations in Data A meant that estimation of significant genetic correlations was not always possible with the available data. A significant genetic correlation was seen between EUROP conformation and EUROP fat score in Data A. The bivariate model did not converge in Data B, but Data C also found a negative genetic correlation. The correlation was negative meaning a genetic increase in conformation will be associated with leaner carcass. Negative genetic correlation between these traits has also been reported by other studies (Eriksson et al., 2003, Englishby et al., 2016, Moore et al., 2017). Other studies found a low positive correlation between fat score and conformation (Kause et al., 2015, Hickey et al., 2007). Both the studies included older animals up till 870 days at age of slaughter. Fat deposition at older age is likely influenced by other genetic factors, than the fat score in younger animals. Johansson et al. (2009) found a low positive genetic correlation in HOL and a low negative genetic correlation in RDC (Red Dairy Cattle). Breed differences might therefore be influencing the correlations of these traits. Since EUROP conformation is included in the current breeding goal there is a selection on this trait (NAV, 2020). This means that there is likely a correlated response, meaning that the EUROP fat score is decreasing.

EUROP fat score was positively genetic correlated to IMF. There was also a low positive phenotypic correlation between the two traits. Animals with higher fat score is therefore also associated with higher levels of IMF and breeding for a higher fat score is therefore also likely to increase IMF. The fat score is however not wanted to improve, since increased subcutaneous fat might cause problems in deskinning and increased labour in trimming the carcass. Reverter et al. (2003) found a similar low positive genetic and phenotypic correlation between subcutaneous fat and IMF in beef breeds. No significant correlation was found in Angus cattle (Torres-Vazquez et al., 2018). The positive genetic correlation between the two traits, indicate that if there is selection towards more lean carcasses based on EUROP fat score, the IMF will also be lowered in these

animals. Currently the fat score is not included in the breeding goal, so no selection is done on the fat score. If future breeding is breeding for increased IMF a correlated response might be seen to increased fat scores. No studies were found that compared the IMF with subcutaneous fat at an age comparable to the animals in this study. This is probably due to the perception of IMF as a late maturing tissue.

The IMF and EUROP conformation correlation was not available, since the model did not converge. Since EUROP conformation and fat score was negatively correlated, the correlation between conformation and IMF will be interesting to see. More data on IMF will give information on whether the correlation to IMF is negative as the EUROP fat. Higher conformation classes has been shown to be negatively correlated with IMF levels in phenotypic studies (Nogalski et al., 2019). Other studies found no effect (Bonny et al., 2016b). More information is therefore needed before this correlation can be estimated.

It was expected that IMF and SF would be correlated, however the bivariate model did not converge so no information could be given on this trait. Mateescu et al. (2015) found a moderate negative genetic correlation indicating the correlation between SF and IMF. Allais et al. (2014) found a moderate negative genetic correlation between IMF and SF in CHA and BAQ, but a moderate positive genetic correlation in LIM. The phenotypic correlation between the two traits were low. In older steers with high levels of IMF the two traits was also moderate negatively correlated (Bhuiyan et al., 2017). A negative genetic correlation means, that animals with a genetic value for higher IMF are associated with higher shear force. This can either be direct, through the mechanisms of shear force and IMF content, or it can be through correlated traits.

The colour values showed a genetic correlation. There was moderate-high positive genetic correlation between L* and b* and a* and b*. No correlation was seen between L* and a*. Similar results was found in Korean steers (Bhuiyan et al., 2017).

In Data C there was more statistical power, to evaluate the genetic correlation between the classical slaughter registrations. The genetic correlation between slaughter weight and net daily gain was estimated at 1.00 ± 0.01. This means that the two traits are genetically identical. The trait for daily gain was estimated by the carcass weight divided by the age of the animal. A correlation of 0.56-0.86 between carcass weight and net gain after weaning was seen in Swedish beef cattle (Eriksson et al., 2003). In PIE bulls a genetic correlation of 0.88 was found (Savoia et al., 2019). This indicates that the genetic correlation is high. The reason for a correlation 1.00 might be the short age interval in this study from 7-12 months. Animals that has a high net gain also has the higher carcass weight. A moderate genetic correlation between carcass weight and carcass conformation was seen in Data C. The genetic correlation between carcass weight and conformation was estimated to 0.78 in young bulls (Englishby et al., 2016). Moderate correlation between carcass weight and conformation has been reported in Finnish and Swedish beef cattle (Kause et al., 2015, Eriksson et al., 2003).

Since very few estimates on genetic correlations is significant, the conclusions made on the genetic correlations are mainly based on the literature and should be interpreted with caution.

8.5 Are the data in one herd representative for the population?

The datasets, Data B and Data C, were included in this study to evaluate, if a small population, as the animals in Data A, would be representative for a larger population. Heritability estimates are population specific, by the definition. Between populations there can be difference in the segregation of the alleles affecting the trait, allele frequencies and effect sizes of genetic variants. These are all factors that are affecting the genetic variance. Different environmental variation is also likely when comparing populations (Visscher et al., 2008).

When estimating heritability on a small sub-population with the aim of using the results for further work on the population it is therefore important to know if the sub-population is representative. The estimates on meat quality are expensive measures to obtain, and therefore only a small number of observations is available. The commercially slaughter record are available for all animals slaughtered and they can therefore be used to test whether the animals in the smaller datasets has differences in heritability. The probability function of the heritability estimates in the three datasets are presented in Figure 9. The probability function is describing the probability of the dataset's true heritability, based on the estimate and the standard error of the heritability. Ideally estimated with the same mean and cover the same interval. Data A and B are estimated with larger standard error compared to Data C and therefore the probability function appears relatively flat. This can be seen as a visualisation of the power in the dataset. For carcass conformation and fat score the estimates are very close and there are no visual differences on the distributions. The carcass weight and net weight gain seem to have more difference, especially between Data A and Data B.

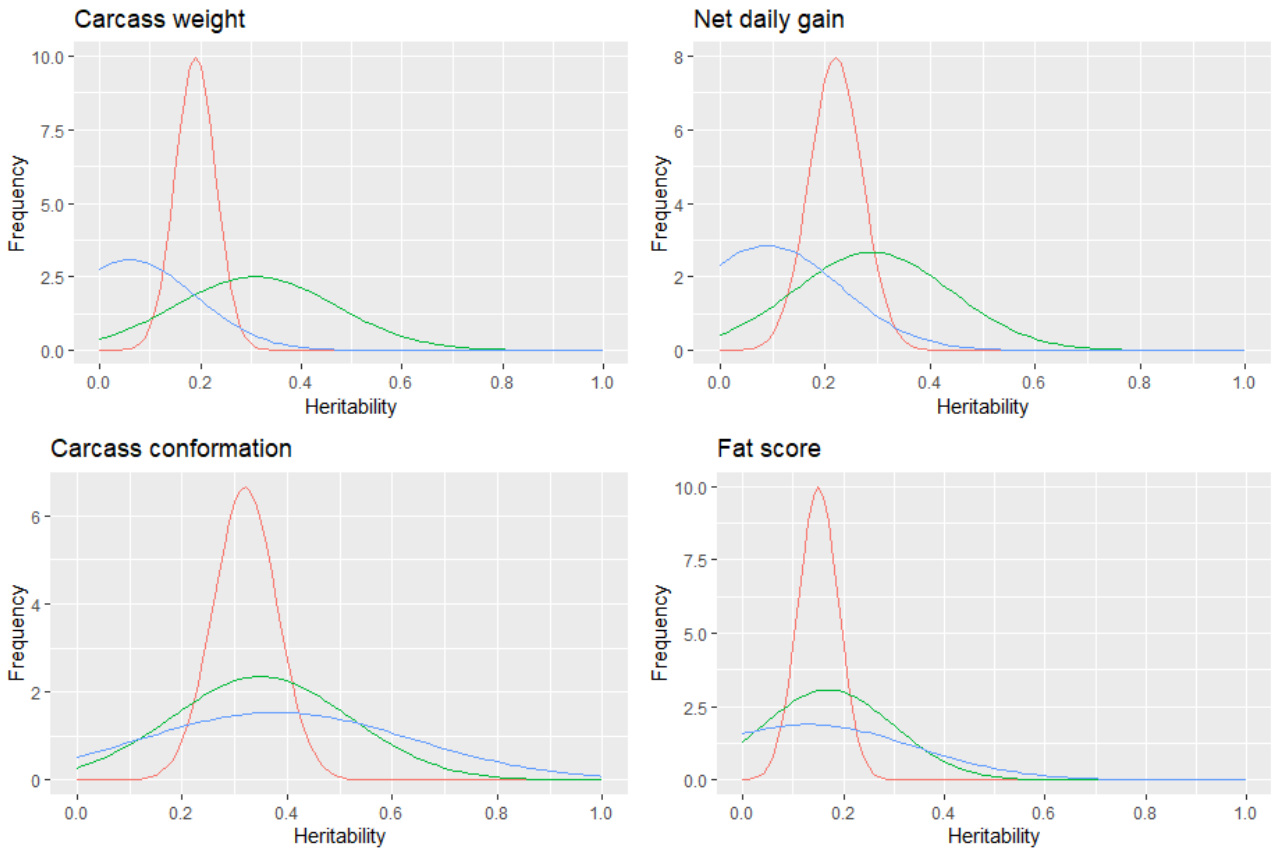

Figure 9: Probability function of the true heritability based on heritability estimates and standard error in Data A (----), Data B (----) and Data C (----)

The CI_{95} for the true heritability in Data C is presented in Table 14 along with the probability that the true heritability of Data A and Data B is contained in this interval. This is calculated via the z score (Mrode, 2014).

Table 14: Probability that the true heritability of Data A and Data B are contained within the estimate of the CI_{95} of the heritability estimated on Data C

Trait	CI_{95}[min, max]	$P(min \leq h^2_{Data\ A} \leq max)$	$P(min \leq h^2_{Data\ B} \leq max)$
CW	[0.11, 0.27]	28.99%	29.13%
CG	[0.12, 0.32]	44.27%	35.79%
CC	[0.20, 0.44]	50.42%	34.04%
FS	[0.07, 0.23]	44.88%	28.98%

As seen in Table 16 there is none of the distributions that are significantly different. The probability that the true heritability of carcass weight in Data A and Data B is contained in the CI_{95} of Data C is 28.99% and 29.13% respectively. This relatively low probability is due to the high SE in Data A and Data B. In Data A and Data B the environmental effects should be the same. The datasets are based on the same crossbred combination in the same herds. This was the argument to use the Data B for reduction of the model, establishing which fixed effects should be included. Based on the plots of the probability functions, and the estimates on the heritability, they are slightly offset compared to each other. Data A is estimated with a lower heritability,

than both Data B and Data C. The high standard error makes the difference insignificant and the observed difference is therefore likely by chance. The low power of the dataset might cause the REML function to be very flat and therefore estimation of a maximum might be disturbed by local maxima. The differences in distribution of the heritability, we see when comparing the datasets could be explained by differences in age. In Data B younger animals are included in the observation, compared to Data A (Figure 6). The heritability for the classical slaughter trait has been shown to vary slightly between age groups in Irish beef cattle (Englishby et al., 2016). Including the younger group of animals in the data might introduce a different variance and offset the estimate. The differences we see are not significant and is likely due to chance. There is no evidence in these estimates that the traits for carcass weight, net daily gain, carcass conformation and fat score have different heritability in the three datasets. Therefore, there is no results that are implying that there should be different variance components in the three datasets, meaning that Data A is representative for the entire population of BLKxHOL. This is important since the evaluation of meat quality will be based on registrations in these herds. With the registrations of IMF by image recognition with the loin eye camera the power of the dataset will increase, and a more precise heritability can be estimated. If the animals evaluated in the herds isn't representative for animals evaluated in other herds, the breeding goal will be biased and not evaluate breeding values correctly.

8.6 Sex differences

A genetic evaluation of the dataset divided into sex was estimated to see if the heritability was different between the sexes, due to different additive genetic variance. Estimation of heritabilities on Data A with the sex divided dataset was not possible. The number of observations were too low to give a standard error low enough to draw any conclusions. Estimation on Data B also failed to yield any significant heritabilities. In Data C the number of observations was sufficient to estimate significant heritabilities. The heritabilities based on sex in Data C was not estimated as significant different between the bulls and heifers. The probability function on the two estimates on heritability in bulls and heifers are presented in Figure 10. The overlapping area of the two functions, i.e. the probability that the true heritability is found in the shared range, is 10.14% in carcass weight, 8.11 % in net daily gain, 23.30% in carcass conformation and 88.31% in carcass fat score.

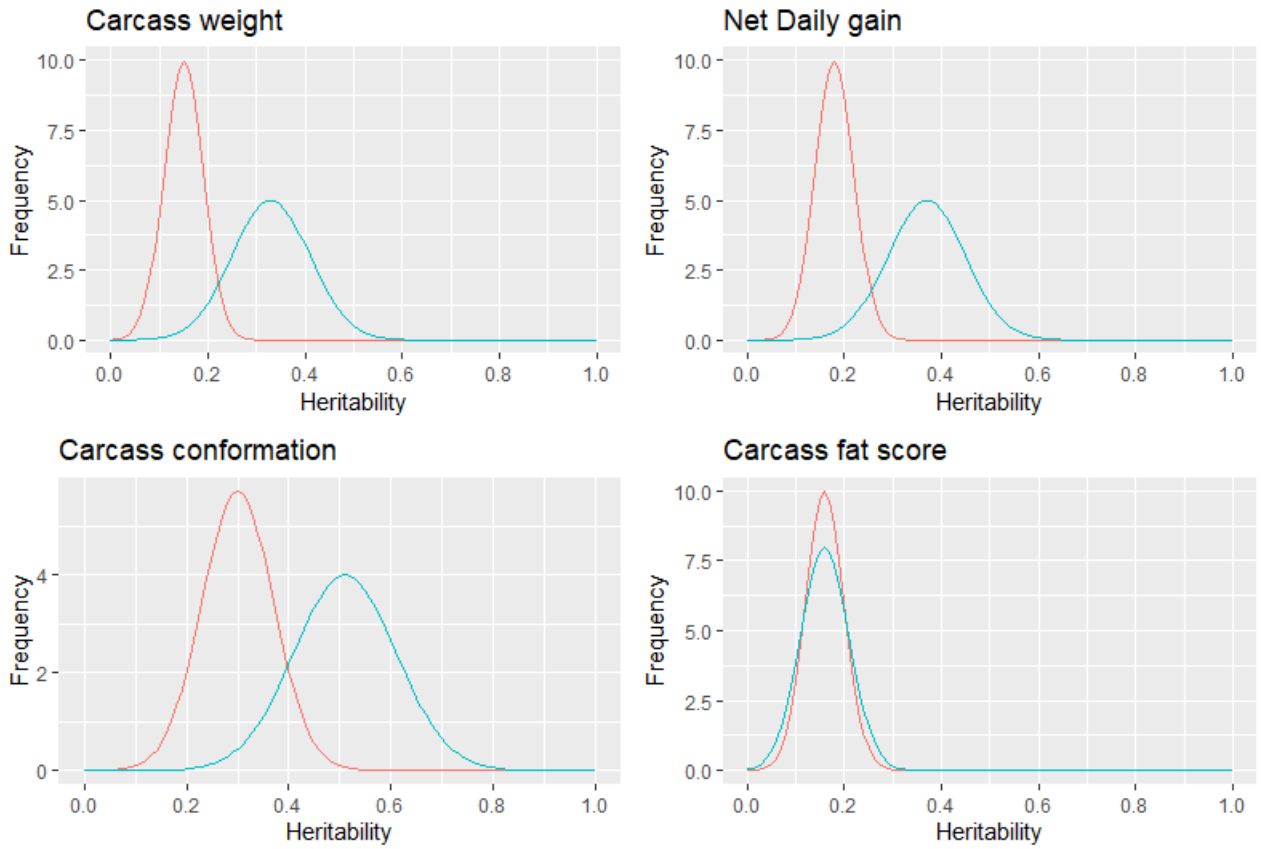

*Figure 10: Probability function of the true heritability based on heritability estimates and standard error in Data C estimated on Bulls **(----)** and Heifers **(----).***

Even though none of the differences in heritability estimates between the sexes are significant, the probability that the estimates are shared between the sexes in carcass weight, net daily gain and carcass conformation is relatively low. The probability functions are slightly offset and visually appears as two different distributions. It might be an indication that the variance components are different between the sexes. The heritability for fat score shows a heritability that is estimated equally across the sexes. This is despite the bulls had a slightly higher phenotypic variation than the heifer. The amount of variation described by genetic additive variation is therefore the same between sexes in carcass fat score.

The difference between sex in carcass weight was smaller than other studies done on BeefxDairy crossbreds. Heifers were estimated with a significantly less carcass weight and conformation, and higher fat score compared to bulls (Englishby et al., 2016). At 16 months a 21% difference was seen between BeefxDairy heifers and bulls, raised in organic systems with low-moderate energy diet and grazing (Vestergaard et al., 2019). The difference was larger compared to the 6% difference in carcass weight seen in this study. This is explained by the age interval allowed for the slaughter animals. Heifers were allowed a longer growing period to compensate for their lower daily gain. A higher difference in slaughter weight is probably obtained in older animals, were the sex difference will be more exposed.

Only few studies are found that evaluates the difference in additive genetic variances between the sexes. The heritability in carcass weight and EUROP fat score was estimated as higher in heifers compared to bulls. This was related to a higher additive genetic variance in the heifers. EUROP conformation score was not different compared between sex (Englishby et al., 2016). No significant difference in heritability on ultrasound determined IMF and LT area was seen in yearling bulls and heifers (Crews et al., 2003). An explanation for the lack of available studies on the difference in variance components between sex is likely due to the structure of the beef production. Meat quality is often related to either bulls or steers since they are the main product. A smaller proportion of heifers are slaughtered, since they should contribute to the next generation of cows. The difference in meat quality between heifers and bulls are well established and the reason that heifers often are raised along with steers for high marbling beef (Bittante et al., 2018, Venkata Reddy et al., 2015).

The current evaluation of breeding values of beef breeds in Denmark uses a fixed effect of the interaction between age and sex (SEGES, 2018). If the additive genetic variance is difference between bulls and heifers it will not be adjusted for with a fixed effect. In dairy cattle only the male offspring is evaluated for growth traits. It is assumed that the beneficial effects with increasing growth index is transferred to cows and heifers (NAV, 2020). The introduction of BeefxDairy crossbreeding does however introduce a group of heifers intended for slaughter. Phenotypically there was an indication of higher IMF in the heifers, which was established in previous sections has a high correlation to tenderness, juiciness and flavour. If more data supports that heifers of BeexDairy are higher in IMF, a separate concept for BeefxDairy heifers could be suggested, with higher guarantee for improved eating quality. This does however require more data, since the IMF difference is not significant in the current dataset.

8.7 Choices of genetic model

For the genetic analysis, a very simple genetic model was used. The traits were adjusted for the fixed effects: BYS, slaughter herd and age in months. The use of a simple model was chosen since a simple model will use less degrees of freedom to calculate fixed effects affecting the phenotype, and therefore free more degrees of freedom for estimation for the genetic parameters. Fixed effects should be included in the model if they explain systematic effects in the data. When only few fixed effects are included in the genetic model there is likely more effects that are not accounted for. These effects are likely included in the residual variation and will therefore lower the estimate of the heritability. Inclusion of unnecessary fixed effects will not include bias in the results, but will increase the prediction error on the values (Van Vleck, 1987). The effect of slaughter herd was included despite being evaluated as non-significant. It was included since the effect of the farm is a factor that is shown to affect the phenotype in many traits, and the possibility that it does not affect growth traits is unlikely. It is more plausible that the data does not have the necessary power to determine the effect.

The BYS effect was pooled from a month effect since the variation between the months were very little. Adjusting the month effect to a season effect therefore still kept the variation through the year but were evaluated

at fewer levels. This would free more degrees of freedom for the estimation of the variation. The age was adjusted for by a linear regression in the initial model. A regression is only taking up one degree of freedom in the estimation and therefore frees a lot of degrees of freedom for the parameter estimation. This is however assuming linearity. The animals in this study was slaughtered within a relatively short interval in age. Since only four levels of agemonth is included, the amount of fixed effects lost in the estimation of the mean in each level is relatively small.

The pedigree used in this model was a sire - maternal grand sire (mgs) pedigree. This is a pedigree used to lower the number of animals in the model. The most common pedigree to use is the sire-dam pedigree, where information of the dam's pedigree is included. The sire-mgs pedigree was chosen, since this is the pedigree used in the Nordic countries for current estimation of the growth index and other traits relating to BeefxDairy crossbreeding. In the case that there is a dam that has born more sires used in the pedigree, this genetic relationship is not included in the model. If genetic relationship is not accounted for the heritability will be lower than if the pedigree was estimated correct.

8.8 Design of the data

The heritability estimates were in many of the meat quality traits estimated with a very large standard error, making the estimate non-significant. The very high standard error is due to the very low power of the dataset. The number of offspring is unequal distributed among the sires, where in Data A the three most frequently used sires out of 33 are responsible for 51% of the calves. This skewness in number of offspring could possible lead to a bias of the effect, in the scenario that not all sires are distributed evenly across herds (Van Vleck, 1987). The estimation of fixed effects requires that there are genetic information shared between the levels of fixed effects to determine genetic and non-genetic effects from each other. The number of fixed effects were kept low due to the small number of observations. If sires were only represented in one level of slaughter herd, the effect of the sire could be confounded with the effect of slaughter herd. Distinguishing the sire effect and the herd effect might therefore be difficult. An interesting observation is that by including the animals in Data B the SE is not reduced. The expected SE for heritability based on half-sib families was approximated by Falconer and Mackay (1996)

$$SE(h^2) = \sqrt{\frac{32h^2}{mn}} \tag{16}$$

Where m is the number on families and n the number of offspring in each family. Data A was based on 31 sires with an average of 7.5 offspring. Theoretically this would yield an expected SE of 0,16. On Data B with 39 sires with 19 offspring on average, this would have an expected SE of 0,09. This reduction of the SE is not seen in the results and could be caused by multiple factors. The number of offspring are not distributed equally between the bulls the estimate on half sib families are based on equally distributed half-sib families. In Data B

there was included animals younger than 8 months. This group of animals were bull calves slaughtered for other concepts than “Dansk Kalv”. There is a possibility that these animals are selected based on different criteria and the slaughter weight therefore is describing a different genetic trait with a different variance. Another possibility is that the simple genetic model is not capturing all environmental effects, and that some of the fixed effects are unnecessary included in the model, so that the phenotypes are affected by this in a non-random way.

Most of the calves in the dataset was raised in one herd (Figure 4). The unequally distribution of animals was partially because on slaughter calf production, were significantly larger than the others participating in the project. The project FutureBeefCross is running over 4 year period, and the data in this study is collected within the first year the project is running (Miljø og Fødevarestyrelsen, 2018). Before animals could be selected for meat quality analysis, the feed boxes for methane and feed intake registrations had to be up and running. This meant that the herds did not start the project at the same time and will explain the difference in number of animals. This was however the data available, and by time more registrations will be available for the other herds and provide a more balanced dataset.

9. Conclusion

Meat quality is currently not included in the Danish breeding goal for beef and BeefxDairy crossbreeding. In the review an overview of meat quality strategies was presented from other markets and factors affecting meat quality was presented. Meat quality measures of BLKxHOL crossbreds was registered in four Danish slaughter calf productions. Meat quality registrations was measured for LT muscle area, intramuscular fat content, shear force, cooking loss, colour measurements L*, a* and b*, and pH at 72h postmortem. Registrations for carcass weight, daily gain, EUROP conformation and EUROP fat score was included to validate the genetic model. This was done by running the genetic model on classical slaughter registrations in datasets containing more observation on BLKxHOL crossbreds. The heritability was estimated with a large standard error due to the low number of observations in Data A. The trait describing lightness value (L*) and yellowness (b*) was estimated as having a heritability significantly different to 0. The heritability on other traits could not be estimated different from 0. Genetic correlations between EUROP fat score and IMF was observed this was in line with findings in other studies. The genetic correlations between the other classical slaughter registrations, where supported by other studies. No evidence was found to reject the hypothesis that the parameters in Data A was significantly different to the parameters estimated in Data B and Data C. Therefore, there was no reason not to reject that the estimates on the heritability in the animals selected for meat quality analysis is representative for the larger population. No significant differences were detected between heritabilites between sex, but

the results indicated that there might be difference in variance components between sex. This does however require further analysis to determine with larger accuracy.

10. Perspectives

Originally other sire breeds, CHA and ANG, should have been included in the results in equal numbers as the BLK sires. This would have increased the power behind the estimates. The number of animals aimed for in the training set is 750 crossbred slaughter calves. This is comparable to the number of observations seen in Data B, so an equivalent standard error could be expected. An increased number of observations will also make it possible to estimate which fixed effects influenced the meat quality traits. Inclusion of observations on image recognition on IMF would further increase the number of observations.

Originally this project was planned to include observation of IMF based on the image analysis. The observations on IMF would be based on image recognition of the LD and taken on the slaughter-line. However development of the algorithm for image recognition was developed on Australian animals and not compatible with the FBC animals. This is likely due to the difference in carcass fatness. If the image analysis was available there would have been significantly more observations on IMF. The accuracy of the measure might have been lower, given that image recognition only will be an indicator trait for the true IMF in the muscle. The lower accuracy will however be outweighed by the much larger number available. As seen in the comparison of the three datasets, a large number of observations are required to obtain a precise estimate on genetic parameters. Picture analysis for IMF shows promising accuracy of actual IMF content (Giaretta et al., 2018). The aim for total data size of image recognition in FutureBeefCross is 12 000 animals. This would make it able to estimate the heritability with far more accuracy and to estimate possible difference between additive genetic variances between sex.

Using a sire model with more observations will make the estimation of breeding values (EBV) possible. A breeding value for meat quality would more information available on the individual sires, and sires with superior genetic values can be chosen. Offspring from sires of a higher genetic value will on average perform better that the population mean. This is however only on average, so EBV cannot be seen at a guarantee for improved meat quality in the specific animals. An improvement of the population mean can however be obtained if EBV's are available on the sires. This raises the question: What possible response can be obtained by breeding for IMF content? If we assume the heritability is 0.36, which the mean from the literature presented in Figure 1. The selection response R is given by

$$R = h^2 S \tag{17}$$

Where i is the selection intensity and S is the selection differential. The selection differential is calculated as $S = i\sigma_p$, where i is the selection intensity and σ_p the phenotypic standard deviation. With unequal sex $S = \frac{1}{2}(S_m + S_f)$. Since the selection on meat quality only will be on sires the selection differential will be $S =$

$\frac{1}{2}S_m$. We assume 60 beef bulls are available for best third of the bulls with the highest EBV for meat quality where selected as sires to the crossbred. The phenotypic variance in IMF was estimated to 0.95 in Data A. The selection response will therefore be 0.717 and this would give a selection response on R = 0.258. This predicted selection response means that the crossbreds after the best third of available bulls would be expected to have an IMF content 0.26% above the average of the population. Since this selection response is calculated on terminal crossbreds the effect will not be additive since the breeding is not added to the next response. An alternative is to select the beef bulls based on meat quality and use registrations on the crossbred population as breeding measures for the purebred population. A breeding value for meat quality on the crossbreds can be evaluated by an animal model. Since the crossbreds are not intended for further breeding, the breeding value would serve a different purpose in these animals. A breeding value could be used as a prediction for the meat quality phenotype as suggested and thereby led to selection of animals raised to be higher in meat quality (Berry et al., 2017).

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Appendix A. - List of Literature for Figure 1.

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