Genetic Aspects of Calving, Growth, and Carcass Traits in Beef Cattle

Susanne Eriksson

Department of Animal Breeding and genetics
Uppsala

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Abstract

The aim of this thesis was to learn more about the genetic background of calving, growth and carcass traits of beef cattle breeds in Sweden, and to assess the possibility of including calving traits and commercial carcass traits in the genetic evaluation. In addition, the genetic relationship between field-recorded growth rate and daily weight gain at station performance testing was investigated.

The breeds studied were Charolais, Hereford and Simmental. Records of birth weight, pre-weaning gain, post-weaning gain, carcass fleshiness grade, carcass fatness grade, carcass weight, calving difficulty score and stillbirth were analysed using linear animal models. The estimated direct heritabilities were moderate to high for birth and carcass weight, moderate for pre- and post-weaning gain, carcass fleshiness and fatness grades, low for calving difficulty score and very low for stillbirth. Maternal heritabilities tended to be lower than the direct ones.

Genetic relationships between direct and maternal genetic effects were generally antagonistic. Moderate to high genetic correlations were estimated between post-weaning gain in the field and at the station, showing considerable breed differences, and the added value of station testing was questioned. Genetic relationships were generally weaker between growth traits and both carcass fleshiness and fatness grade than between growth and carcass weight. Male and female birth weights were found to be the same trait genetically, and strong genetic relationships were estimated between birth weight and calving traits. Less than unity genetic correlations between calving difficulty at first and later parities indicated that partly different sets of genes control these traits. Some antagonistic relationships were found between carcass and calving traits.

It was concluded that it would be feasible to include commercial carcass records and calving difficulty score in the genetic evaluation, and that both direct and maternal effects should be considered for pre-weaning traits. Information on correlated traits should be used for selection against stillbirth as direct selection would be inefficient due to small progeny group size and very low heritability. Joint genetic evaluation of pre-weaning gain and carcass weight was recommended to reduce selection bias.

Keywords: beef characteristics, calving ease, carcass grade, dystocia, herd-year correlations, permanent environmental effects, residual correlations, sex-specific genetic parameters, weight gain

Author's address: Susanne Eriksson, Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, P.O. Box 7023, SE-750 07 Uppsala, Sweden. E-mail: Susanne.Eriksson@hgen.slu.se

Det skall du veta att allting skapat är outgrundligt.

Alla hava vi enahanda ande, men märkvärdigast är ändå korna,
inga andra levande varelser är så oppfyllda av ande och liv,
juvret som dignar av saven och fruktbarheten och buken deras som
rymmer fyra magar och ini alla fyra är det livet, och ögonen deras
som förstår och förlåter meste allt, och skinnet som dallrar av glädjen.
Korna, dem hava blivit beklädda med andekraft.

Ur Merabs skönhet, av Torgny Lindgren.

Contents

Appendix

Publications I–V

The present thesis is based on the following publications, which will be referred to by their Roman numerals:

I. Eriksson, S., Näsholm, A., Johansson, K. & Philipsson, J. 2002. Genetic analysis of post-weaning gain of Swedish beef cattle recorded under field conditions and at station performance testing. *Livestock Production Science* 76, 91-101.

II. Eriksson, S., Näsholm, A., Johansson, K. & Philipsson, J. 2003. Genetic analyses of field-recorded growth and carcass traits for Swedish beef cattle. *Livestock Production Science* 84, 53-62.

III. Eriksson, S., Näsholm, A., Johansson, K. & Philipsson, J. 2002. Sex-specific genetic parameters for field recorded birth weight of beef calves. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production.* CD-ROM communication no 02-25.

IV. Eriksson, S., Näsholm, A., Johansson, K. & Philipsson, J. 2003. Genetic parameters for calving difficulty, stillbirth and birth weight for Hereford and Charolais at first and later parities. *Journal of Animal Science.* Submitted for publication.

V. Eriksson, S., Näsholm, A., Johansson, K. & Philipsson, J. 2003. Genetic relationships between calving difficulty and carcass traits for Charolais and Hereford cattle in Sweden. *Journal of Animal Science.* Submitted for publication.

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Introduction

Swedish beef producers are facing an increasing competition from imported beef products. The Swedish production is small-scale and follows extensive animal welfare legislation, restrictions on use of antibiotics and a ban on the use of growth-promoting hormones. The producers need to become more competitive and to produce quality beef at a reasonable cost. Besides good management of the herds, beef producers would benefit from animals with a high genetic capacity for production.

There is a consumer demand for ethically acceptable animal production systems. This underlines the importance of improving calving ability and viability of the calves as well as production traits. Easy calving, healthy animals are not only beneficial for the economy of beef breeders, but also for the satisfaction the farmers take in their work.

To achieve genetic improvement of all economically important traits in beef breeds, selection decisions should be optimized. This is a challenging task and requires knowledge about genetic background and genetic relationships between the various traits. This thesis addresses genetic aspects of calving, growth and carcass traits in beef cattle.

Background - Swedish beef breeding

Population structure

More than one-fourth, or about 165,000, of all Swedish cows are kept as beef cows today (Statistics Sweden, 2002). Most of these are of beef breeds or crosses with beef breeds. About 25,000 beef cows, of which 15,000 are purebreds registered in a herd book, are in the Swedish beef recording scheme run by the Swedish Dairy Association. Annually, approximately 4,000 purebred heifers calve (Swedish Dairy Association, 2003). The purebreds in the recording scheme constitute the breeding nucleus, and provide dams and natural service sires for production herds, and semen for use in dairy and beef herds. The main beef breeds in Sweden are Charolais, Hereford, Simmental, Limousine, Angus, Highland Cattle and Blonde d'Aquitaine, with Charolais being the predominant breed and Blonde d'Aquitaine the numerically smallest.

The total number of herds in the recording scheme is currently close to 1,400 and these are predominantly located in the southern and central parts of Sweden. The average herd size in the Swedish beef recording scheme is about 18 cows (Swedish Dairy Association, 2003). The use of AI in breeding herds is low, approximately 10–30%, as most herds have natural service bulls; hence the average progeny group size is small. The average generation intervals for Charolais, Hereford and Simmental have been estimated at about 5 years for dam–offspring and 4.3 years for sire–offspring (Stål, 2003).

Breeding programme

The beef breeds in Sweden are currently genetically evaluated for direct and maternal effects for birth weight and pre-weaning gain, and for the direct effect for post-weaning gain (Swedish Dairy Association, 2003). A BLUP-animal model evaluation based on field records from the beef recording scheme was introduced in year 2000. Before that, simple indexes for comparison of individuals within herd and year were used. In these indexes, growth performance traits were weighted together, with a penalty on birth weight to reduce calving problems. Today, carcass traits and calving traits are recorded in the beef recording scheme, but these recordings are not used in the genetic evaluation.

Annually over 6,000 liveborn bull calves are recorded in the Swedish beef recording scheme. About 2,000 of these meet the requirements for growth performance and other traits set by the breed organizations, and qualify to be registered in the herd book as yearlings (Swedish Dairy Association, 2003; Svensk Avel & KRUT, 2002). The majority of these are used for natural service in nucleus breeding herds or sold to production herds.

Between 160 and 180 beef bulls are performance tested each year for post-weaning gain at a central test station. Weaned bull calves enter the station in August for an adjustment period of about 4 weeks. The actual test period is from September to March. After the test period, a simple growth index, based on birth weight, 200-day weight and daily gain at the station, is calculated for comparison of bulls within breed and test year. The bulls are also judged for conformation traits and temperament, and a health inspection is made, which includes examination of scrotal development (Svensk Avel, 1999; Svensk Avel & KRUT, 2002).

One or two of the best performing station-tested bulls per breed are selected each year as candidates for use as AI-bulls. These are evaluated for direct effects for calving difficulty and stillbirth, based on crossbred offspring results in dairy herds. Both heifers and cows are inseminated; in total 1000 doses are used. The tested beef bulls get breeding values for direct effects of calving ease and stillbirth at first and later calvings after one year. Use of beef bulls with breeding values below average for calving traits in dairy herds is restricted, but they can be used for purebreeding, depending on predicted genetic merit for other traits (Svensk Avel, 1999). Most beef semen doses collected are used for crossbreeding with dairy cows.

Expression and recording of traits

Traits of importance for beef production are expressed at various stages of the animals' lives, and some traits are only expressed by one gender. In Figure 1, the traits recorded in the Swedish beef recording scheme are placed on a time-scale to illustrate at what ages the traits are expressed.

In Sweden, calving performance is recorded by the farmer in seven classes: easy calving (unassisted), normal calving (assisted by one person), normal calving with malpresentation of the calf, difficult calving (assisted by more than one person), difficult calving with malpresentation of the calf, caesarean section or calving

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induced by hormone injection (Svensk Avel & KRUT, 2002). The calf is classified as live-born, dead at birth, dead within 24 hours, dead after 24 hours, dead due to an accident or, finally, malformed (Swedish Association for Livestock Breeding and Production, 1995).

Weighings of Swedish beef cattle are made either by technicians from the recording scheme or by the farmers themselves. Birth weight is recorded up to the age of 4 days. Weaning weight, also called 200-day weight, is recorded in the interval between 150 and 250 days of age. This interval has in some cases been extended to allow weighing between 125 and 275 days of age (Swedish Association for Livestock Breeding and Production, 1997). Yearling weight is recorded between 325 and 425 days of age. For some heifers, a 550-day weight is also recorded between 500 and 625 days of age (Svensk Avel & KRUT, 2002).

Carcass weight, fleshiness and fatness grades are measured at commercial slaughterhouses and are used in the official payment system for carcasses. The carcasses are trimmed in accordance with EU regulations and weighed warm shortly after classification. Carcass fleshiness and fatness grades are subjectively judged by trained graders in accordance with the EU system (S)EUROP (Swedish Board of Agriculture, 1998a; b).

Weights at older ages are not recorded for all animals, as some may be sold or slaughtered. Of all Charolais, Hereford and Simmental beef calves with recorded birth weight in Sweden 2002, about 85% also had a recorded weaning weight, and close to 70% had a recorded yearling weight. Only 5% of the heifers had a recorded 550-day weight (Swedish Dairy Association, 2003). Carcass data for purebred beef heifers are scarce, as the majority of the heifers are used for breeding. More data are available for young bulls and thus breeding values for selection candidates would be based on information contributed by male relatives. However, also the best bulls as regards growth rate are used for breeding and not slaughtered at a young age.
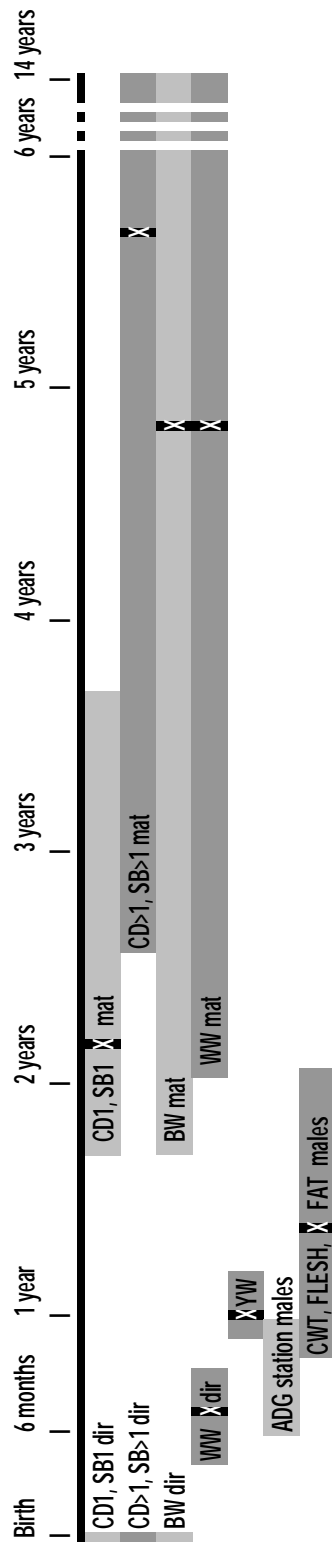
Fig. 1. Time-scale for recording of traits studied in the thesis: direct (dir) and maternal (mat) calving difficulty score (CD) and stillbirth (SB) at first (1) and later (>1) parities, birth weight (BW), male and female weaning weight (WW) and yearling weight (YW), average daily gain at station (ADG station) carcass weight (CWT), fleshiness (FLESH) and fatness (FAT) grades. Average ages at recording of weaning weight, yearling weight and carcass traits, and average age of the dam at recording of calving traits, birth weight and weaning weight are marked with X.

Genotype by environment interactions

Genetic differences between animals can only be expressed when the environment permits (Dickerson, 1962). For example, a sufficient feed supply is necessary for beef bulls to express their full growth capacity. A certain genotype may not be the best producing in all environments, and re-ranking of breeding animals may thus occur. Various types of environmental factors can interact with genotypes, *e.g.,* external physical influences, background genotype, maternal effects, social climate and economic forces (Dickerson, 1962).

Genotype by environment interactions may reduce the accuracy of selection of breeding animals, if these are selected in a different environment than their offspring will produce in. Such problems may arise if the management on a station performance testing deviates substantially from that in production herds, resulting in reduced genetic correlations between index and goal traits (Graser *et al.*, 1985). In spite of this, a station test can be motivated by more accurate data recording or recording of traits that could not be measured under field conditions.

Meyer *et al.* (1994) concluded that low milk production of dams would to greater extent restrict the growth rate of calves in breeds with high growth capacity, than in breeds with lower growth capacity. Similarly, the maternal environment may be more restrictive for males than for females. In addition, it is a common practice in beef herds to differentiate the feeding level of bull calves for slaughter and heifer calves for breeding. This suggests that male and female genotypes may be expressed in partly different environments.

Maternal effects

Maternal influence on phenotypic expressions of birth weight, calving performance and weaning weight in beef cattle is well documented (reviewed by Mohiuddin, 1993 and Koots *et al.*, 1994a). Both sire and dam influence the offspring through the genes they transmit, but the dam has an extended influence through the maternal environment she provides. Such maternal influence may be, *e.g.*, cytoplasm of the egg, uterine environment, size of the pelvic opening, strength of labour during parturition, behaviour and milk production (Baker, 1980; Meijering, 1984; Mousseau & Fox, 1998). The environmental influence of the dam on her progeny may be due to her own genotype and/or her environment (Dickerson, 1962). The maternal influence decreases with the age of the individual (Robison, 1981).

The most commonly used statistical model in animal breeding for handling direct (calf) effects and maternal effects, including the genetic relationship between these, was presented by Willham (1972; Fig. 2). According to this model, the phenotype of a calf is influenced by its own genetic value, by maternal environment provided by the dam and by other environmental effects. The maternal effect has a genetic and an environmental component. Negative genetic correlations between direct and maternal effects are commonly found in the literature (Mohiuddin, 1993; Koots *et al.*, 1994b).
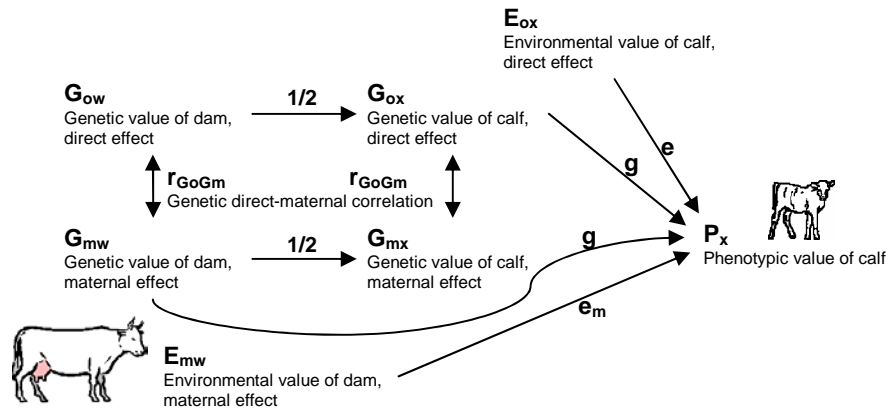
Fig. 2. A path coefficient diagram illustrating the influence of direct and maternal effects on a phenotypic value (after Willham, 1972).

Genetic antagonisms

The prediction of total genetic merit used for selection in beef breeds is complicated by the presence of genetic antagonism between some important traits. Examples of antagonistic relationships between traits are negative direct-maternal genetic correlations, and unfavourable genetic relationships between calving ability and some production traits (Hanset, 1981). An illustration of possible ways in which selection for growth rate and muscularity can influence calving ability is shown in Figure 3.

One must therefore take into account a complex system of interrelated traits when selecting the breeding stock, including traits measured for different genders and at different ages. This requires knowledge of the genetic relationships between traits. There are numerous studies on genetic parameters for various beef traits in the international literature (Mohiuddin, 1993; Koots *et al.,* 1994a), but there are generally fewer studies on genetic relationships between different groups of traits, or traits measured in different environments or for different genders or parities.
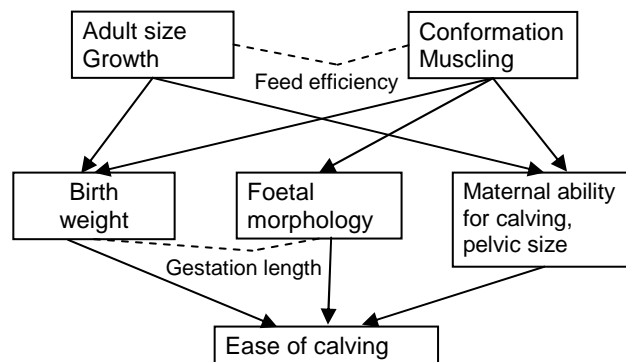

Fig. 3. Illustration of the influence of selection for growth and muscling on calving performance, through related traits (after Hanset, 1981).

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Objectives of the thesis

The main purpose of this thesis was to study genetic parameters for, and relationships between, calving, growth and carcass traits of importance for beef production. Knowledge about the genetic background for production and calving traits is needed in order to improve the genetic evaluation of beef breeds in Sweden. Increased knowledge of genetic relationships between traits is also of a more general biological interest.

The main purpose was split into specific aims in publications I–V:
- to study the relationship between central station performance test recordings and field performance test recordings of post-weaning gain (I),
- to study the genetic relationship between field-recorded growth traits and carcass traits recorded at commercial slaughterhouses, and the possibility of including these carcass traits in the genetic evaluation (II),
- to study whether male and female birth weights can be regarded as one and the same trait, genetically (III),
- to estimate genetic parameters for field-recorded calving difficulty and stillbirth and genetic correlations with birth weight, and to study the possibility of including calving traits in the genetic evaluation (IV),
- to estimate genetic correlations between carcass traits and calving difficulty or birth weight to predict possible effects of selection for beef production traits on calving traits (V).

Summary of investigations

Material and methods

Field data from the Swedish beef recording scheme were used for analyses in all publications (I–V) in this thesis. In addition, station performance testing data were used in publication I. Publications I–III included records for Charolais, Hereford and Simmental cattle, whereas the last two studies (IV–V) considered only the two major breeds: Charolais and Hereford. Only data on purebred animals were considered and the breeds were analysed separately in all publications.

The traits studied in this thesis (defined in Table 1) were post-weaning gain (I and II), pre-weaning gain (II), carcass weight, fleshiness and fatness grades (II and V), birth weight (III–V), stillbirth (IV) and calving difficulty score (IV and V). The different papers comprise estimations of genetic parameters and correlations between traits measured in different ways (I), for different genders (III) and between different traits (II, IV and V).

Fixed effects for statistical models used for analyses of genetic parameters were determined using SAS proc GLM analyses (SAS Institute Inc., 1989). Variance and covariance components were estimated using the average information

algorithm for restricted maximum likelihood (Jensen *et al.*, 1997) included in the DMU package (Jensen & Madsen, 1994).

Linear animal model analyses were used for all traits. Direct and maternal genetic effects were included in models for pre-weaning traits. Random permanent environmental effects of dam were included for pre-weaning traits where dams could have more than one calf with records, *i.e.* not for calving traits at first parity. Only direct effects were considered for post-weaning gain and carcass traits. Herd-year effects were treated as random in publications I and II, and as fixed effects in III–V, due to computational constraints and apparent confoundings with genetic effects for the categorical traits. Bivariate analyses, and for carcass traits (II) trivariate analyses, were used to estimate genetic correlations between traits.

Table 1. *Trait abbreviations and definitions used in the thesis*

Abbreviation	Trait definition
BW♂	Birth weight of male calf (kg)
BW♀	Birth weight of female calf (kg)
CD1	Calving difficulty score (1=easy, unassisted; 2=normal, assistance by one person; 3=difficult, including veterinary aid)[a] at first parity
CD>1	Calving difficulty score (1=easy, unassisted; 2=normal, assistance by one person; 3=difficult, including veterinary aid)[a] at later parities
SB1	Stillbirth at first parity (0=live born; 1=dead within 24 hours)[b]
SB>1	Stillbirth at later parities (0=live born; 1=dead within 24 hours)[b]
WG	(Pre-)weaning gain (g/d) = ((200-d weight – birth weight) / number of days between weighings)
ADGst	Average daily gain (g/d) at station performance testing of bulls after weaning = (start weight – final weight)/number of test days
PWG♂	Post-weaning gain of males (g/d) = (yearling weight – 200-d weight) / number of days between weighings
PWG♀	Post-weaning gain of females (g/d) = (yearling weight – 200-d weight) / number of days between weighings
CWT	Carcass weight (kg) as 98% of warm carcass weight
FLESH	Carcass fleshiness grade according to the (S)EUROP system (grades 1–15) where higher grades denote more swelling muscles and higher flesh content in carcass
FAT	Carcass fatness grade according to the (S)EUROP system (grades 1–15) where higher grades denote higher fat content in carcass

[a] Caesarean sections and induced calvings were rare (< 0.5%), and were thus grouped with difficult calvings. Malpresentations were included with other normal or difficult calvings.
[b] The common definition of stillbirth as stillborn or dead within 24 hours was used.

Main findings

The major results from publications I–V included in this thesis are summarised below with focus on genetic parameters and relationships between traits. Ranges of heritabilities estimated for different traits for all three breeds are presented in Table 2. Estimated genetic correlations between calving, growth and carcass traits are summarised in Table 3.

Level of heritabilities (publications I–V)

The direct heritabilities estimated for calving difficulty at first parity were low on the observable scale and low to moderate on the underlying scale (publications IV and V). These tended to be lower at later parities, even when compared on the underlying scale. Very low heritabilities were estimated for stillbirth (IV). As was mentioned earlier, the average progeny group size in Swedish beef data is small. Therefore, an inclusion of stillbirth records in the genetic evaluation would give insufficiently accurate breeding values for these to be useful for selection.

Moderate to high heritabilities were estimated for direct effects on birth weight (III–V) and carcass weight (II, V). For weight gain before and after weaning (I, II), estimated direct heritabilities were generally moderate. Moderate heritabilities were also estimated for carcass fleshiness and fatness grades (II, V), in spite of the subjective judgement of these traits. This suggests that commercially recorded carcass traits may be included in the genetic evaluation of beef breeds.

Maternal heritabilities tended to be lower than direct ones (II–V), with the largest difference between direct and maternal heritabilities estimated for birth weight. Even so, the maternal influence was significant and should not be neglected in the genetic evaluation or selection of breeding stock.

Table 2. *Ranges of direct and maternal heritabilities on the observable and underlying scales presented in publications I–V for Charolais, Hereford and Simmental, abbreviations as in Table 1*

Trait	h^2 dir. obs.	h^2 mat. obs.	h^2 dir. underl.	h^2 mat. underl.
CD1	0.10–0.18	0.07–0.15	0.16–0.30	0.12–0.24
CD>1	0.01–0.05	0.00–0.03	0.05–0.18	0.01–0.07
SB	0.00–0.01	0.00–0.01	0.01–0.03	0.00–0.03
SB>1	0.01–0.02	0.00–0.01	0.06–0.09	0.03–0.04
BW	0.28–0.57	0.06–0.15		
WG	0.31–0.41	0.12–0.21		
PWG♂	0.22–0.42			
PWG♀	0.29–0.40			
ADGst	0.11–0.42			
FLESH	0.21–0.39			
FAT	0.23–0.45			
CWT	0.22–0.70			

Relationships between birth weight and calving traits (publication IV)

Phenotypic relationships between birth weight and calving difficulty score were shown to be non-linear, with strongly increasing risk of difficulties above a certain level of birth weight. The location of this apparent threshold was dependent on the parity and breed of the dam. Less than half of the stillborn calves were born at difficult calvings; the causes of death were unknown. Genetic correlations were generally positive and moderate to high between the three traits calving difficulty, stillbirth and birth weight. Birth weight could thus be used as an indicator trait to reduce the frequency of difficult calvings and stillbirths. However, the weight of

the calves did not explain the entire variation in calving difficulty, and direct measures of calving difficulty score should be included in the genetic evaluation.

Relationships between growth traits (publication II)

Pre- and post-weaning gains were not strongly correlated. Whereas genetic correlations were positive, the environmental correlations were negative. This was most likely caused by compensatory growth effects, *i.e.*, calves with a restricted growth rate before weaning (for example with a poorly milking dam) gain weight more quickly when fed more intensively after weaning.

Relationships between carcass traits (publication II)

Generally, genetic correlations were negative between carcass weight and fatness grade, weak or negative between carcass fatness and fleshiness grade, and weak or positive between carcass weight and fleshiness grade. The estimated genetic correlations between carcass traits differed somewhat between breeds. Preliminary analyses showed close to unity genetic correlations between age-adjusted carcass weight and net gain. Thus, expected correlated response to selection for higher carcass weight or net gain would be rather lower fatness grades, and for Charolais, higher fleshiness grades. Environmental correlations were positive between all carcass traits.

Relationships between growth and carcass traits (publication II)

Estimated genetic correlations with pre- and post-weaning gain were generally weak to moderate for carcass fatness and fleshiness grade, but moderate to strong and positive for carcass weight. The weak relationship between growth traits and both carcass fleshiness and fatness grades suggests that the latter traits need to be included in the genetic evaluation and selected for in order to achieve a higher genetic gain. The genetic variance for carcass weight was higher when pre-weaning gain was included as a correlated trait in the analyses, but the same effect was not seen for the other carcass traits. A multiple trait evaluation with pre-weaning gain would thus be expected to reduce the selection bias in breeding values for carcass weight.

Relationships between calving and carcass traits (publication V)

Carcass weight was positively genetically correlated with both direct and maternal effects on birth weight and with direct effect on calving difficulty score, but weakly or even negatively correlated with maternal effect on calving difficulty score. The interpretation of this was that selection for higher carcass weight would increase dam size at calving, and thus to some extent compensate for higher birth weights of calves. Higher carcass fatness grade was genetically correlated with lower birth weights and in most cases also with lower calving difficulty scores. Highly variable genetic correlations with carcass fleshiness grade were found. A moderately unfavourable genetic correlation was estimated between carcass fleshiness grade and maternal effect for calving difficulty score at first calving.

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Station vs. field recording of post-weaning gain (publication I)

Estimated heritabilities were about equal for average daily gain at a central station performance testing, and under field conditions. Genetic correlations between growth rate recorded in the field and at the station were moderate to high. Differences were found between breeds, with highest genetic correlations for Charolais (0.80–0.90) and lowest for Hereford (0.51–0.65). This was explained by genotype by environment interactions, as differences in management at station and under field conditions were greater for Hereford than for the other breeds. Comparisons of breeding values for post-weaning gain indicated that some of the very best animals with regard to this trait remained in their original herds, and had not been selected for station testing.

Gender differences (publications I, III and IV)

The estimated genetic correlations between post-weaning gain at station and under field conditions were higher when only males were considered, than when field records for females and station records for males were used (publication I). In the study on birth weight (III), however, correlations between the male and female traits were close to unity. This suggested that male and female growth rates would mainly appear as different traits later in the calves' lives.

Phenotypic differences between males and females were present already at birth, with higher average birth weights for males than for females (III, IV). The frequency of difficult calvings and stillbirths (IV) were considerably higher for bull calves than for heifer calves, probably mainly a consequence of the higher birth weights of bull calves. Average post-weaning gain was also higher for males than for females (I). For both birth weight (III) and post-weaning gain (I), phenotypic variances were higher for males than for females. For post-weaning gain, both genetic and residual variances were higher for males than for females. For birth weight, however, direct genetic variances were higher for females, whereas maternal genetic variances tended to be higher for males.

Direct-maternal genetic correlations (publications II–V)

Genetic correlations between direct and maternal effects in publications II–V were generally negative. This was found both for birth weight and calving traits (III–V) and for pre-weaning gain (II). The unfavourable direct-maternal correlations indicate that selection only for the direct (calf) effect on calving performance, calf viability, or pre-weaning growth capacity, would in the long run be detrimental to maternal ability.

Table 3. Summary of genetic correlations[1] between field-recorded traits estimated for Charolais (above diagonal) and Hereford (below diagonal). For standard errors, see Appendixes II–V; trait abbreviations as in Table 1

		Direct additive genetic effects								Maternal additive genetic effects			
		BW	CD1	SB1	WG	PWG♂	FLESH	FAT	CWT	BW	CD1	SB1	WG
Direct	BW	-------	0.62	0.74			0.04	-0.05	0.53	-0.41	0.03	0.36	
	CD1	0.72	-------	0.96			-0.12	0.42	0.28	-0.17	-0.13	-0.38	
	SB1	0.92	0.95	-------						0.12	-0.41	-0.42	
	WG				-------	0.28	-0.03	-0.01	0.49				-0.51
	PWG♂				0.17	-------	0.20	-0.03	0.56				-0.02
	FLESH	-0.24	0.54		0.14	0.52	-------	-0.18	0.38	0.03	0.42		-0.02
	FAT	-0.17	0.04		0.30	-0.18	-0.79	-------	-0.08	-0.21	-0.20		0.21
	CWT	0.11	0.29		0.59	0.76	0.03	-0.40	-------	0.20	-0.09		0.39
Maternal	BW	-0.27	0.34	-0.17			0.31	-0.38	0.30	-------	0.46	0.54	
	CD1	-0.13	-0.50	-0.77			0.54	-0.17	0.02	-0.28	-------	0.98	
	SB1	0.43	-0.29	-0.46			0.17	0.10	0.35	-0.95	0.96	-------	
	WG				-0.32	0.24							-------

[1] Direct-maternal genetic correlations shown are arithmetic means of estimates from the different analyses.

General discussion

This thesis considers traits expressed at various stages of an animal's life - from birth to slaughter. All traits studied showed genetic variation, and were more or less influenced by environmental factors. This indicates that genetic progress can be made for these traits, though selection is complicated by complex genetic relationships among them.

Data and analyses

Differences in heritability estimates

For some of the traits, the range of heritability estimates (presented in Table 2) was wide, due partly to differences in heritabilities estimated for the different breeds, as the range within each breed was smaller. For example, the range of estimates for daily gain at station was 0.11–0.16 for Simmental and 0.35–0.38 for Charolais (publication I). Generally, the lowest heritabilities were estimated for Simmental and the highest for Hereford (I–III).

For birth weight, not only breed differences were responsible for the wide range of estimates, but also differences between genders, with higher heritabilities for females than for males (III). The lowest value (0.28) was estimated for male Simmental calves and the highest (0.57) for female Hereford calves. For post-weaning gain, however, the heritabilities estimated for males and females were similar (I).

Breed and gender differences could not alone explain the very wide range of heritabilities (0.22–0.70) that were estimated for carcass weight. Higher heritabilities for this trait were estimated in publication II when carcass weight was analysed together with pre-weaning gain. Due to computational constraints, the inclusion of pre-weaning gain in the analyses could not be accomplished in publication V.

Remaining differences in heritability estimates between publications could be due to the use of partly differing data sets or differences in statistical models, (*e.g.,* fixed or random herd-year effects). Records of carcass traits have only been available from 1995 onward. For computational reasons, when several correlations were to be estimated, the number of years with observations on growth traits was reduced in publication II, compared with publication I. For the same reasons the number of years with observations of calving traits was restricted in publication IV, compared with publication V.

Herd-year effects were treated as random in publications I and II. For computational reasons, fixed herd-year effects were used in the analyses of birth weight in publication III, where larger data sets and maternal effects were analysed. Initial attempts to use random herd-years for analyses of the categorical calving traits gave unrealistically high heritabilities, possibly due to confounding between random effects. Hence fixed herd-year effects were chosen for analyses in publications IV and V.

Linear models for categorical traits

In this thesis, linear animal models were used to estimate genetic parameters for all traits, including categorical traits. For the carcass fleshiness and fatness grades, a large number of classes were used. For calving difficulty score, only three and for stillbirth only two classes could be used for analyses, however. The use of threshold methodology for such traits would be theoretically more suitable. Initial attempts to use threshold models for analyses of the calving traits gave unrealistic heritabilities, even with highly simplified statistical models. This was probably due to extreme category problems and, as linear models seemed to be more robust and gave estimations closer to literature values, these were chosen for the analyses. Minor differences between threshold and linear methodology in predictive ability and estimation of heritabilities were found in studies on sheep and beef field data (Gates *et al.*, 1995; Ramirez-Valverde *et al.*, 2001).

The use of linear methodology also made possible the use of animal models, which take into account all genetic connections between contemporary groups. The use of animal model instead of sire model has been shown to be more efficient, and less sensitive to the presence of selection or confounding between sires and contemporary groups (Gates *et al.*, 1999). In a study of beef data, Ramirez-Valverde *et al.* (2001) concluded that, especially for animals with few offspring, the animal model including maternal effects was superior to the sire-maternal grandsire model.

Age effects for growth rate

The effect of age at weighing was not included in the statistical models for pre- and post-weaning gain in publications I and II. For practical reasons, Swedish beef farmers tend to weigh animals born at different dates all at the same time, as long as they are within the rather wide age-limits allowed in the recording scheme. Therefore, animals born early in the year are likely to be older at weighing than those born somewhat later. If the growth curve between weighing deviates substantially from linearity, this may affect the comparison of animals. However, in additional analyses (not shown), inclusion of age at weighing in the model for pre-weaning gain did not alter the results significantly. The effect of birth season presumably took into account a large part of the difference in age at weighing.

Environmental covariances between maternal effects

Negative genetic correlations between direct and maternal effects on birth weight, calving traits and pre-weaning gain were estimated in publications II–V. Some authors have suggested that direct-maternal correlations may be biased downwards due to negative environmental covariances between maternal effects in adjacent generations (Baker, 1980; Robinson, 1996). An example of a negative environmental relationship is that excessive feeding of a heifer calf, due to a rich milk supply by her dam, impairs the development of secretory tissue in her own udder. Environmental dam–daughter covariances are for practical reasons commonly ignored in genetic analyses and were not considered in this thesis. Such covariances may have had some influence, especially on the relatively high

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negative estimates for weaning gain. However, Meyer (1992) reported that an environmental dam–offspring covariance has to be quite large to significantly influence the estimation of genetic parameters.

Birth weight - an optimum trait?

The birth weight of a calf is a result of its pre-natal growth in the uterus and there is a positive relationship between birth weight and gestation length (Meijering, 1984). For most species, a high birth weight is associated with greater physiological maturity, more energy reserves and better isolation, and thus with better chances of survival of the newborn (Lawrence & Fowler 2002; Grandinson, 2003). For cattle, a high birth weight is genetically associated with high growth rate later in life (Mrode, 1988). Positive genetic correlations between carcass weight and both direct and maternal effects on birth weight were found in publication V.

However, in some species, for instance in cattle, a high birth weight can cause difficulties at birth. For cattle, too large a calf in relation to the dam's inlet pelvic dimensions is the most common cause of calving difficulty, which increases the risk of stillbirth (Meijering, 1984). It is thus not surprising that phenotypic relationships between birth weight and calving traits may be non-linear, as was found for frequency of difficult calvings and birth weight in publication IV and in earlier studies on cattle (Philipsson, 1977; Berger *et al.*, 1992).

As was indicated in publications IV and V, the size of the calf vis-à-vis that of its dam may be of greater importance for the calving process than the birth weight *per see* (Meijering, 1984). Breed differences in relative birth weight may explain some of the variation in calving performance between breeds (Berglund, 1987). Hanset (1981) suggested that artificial selection for beef traits, *e.g.*, rapid growth or heavy muscling, can move a breed away from equilibrium between traits of the dam and foetus influencing the calving process. Examples of such traits are size and conformation of dam and foetus, length of gestation and maturity at birth, *etc.* To find a new equilibrium point may be difficult due to the complexity of interactions between dam and foetus (Hanset, 1981).

The calf's own genes for prenatal growth control its birth weight to a larger extent than does the maternal genetic influence (publications III-V; Koots *et al.*, 1994a). However, as the direct and maternal genetic effects are negatively correlated, both have to be considered when selecting breeding animals. Negative direct-maternal genetic correlations are also present for calving ability and stillbirth (publications IV-V; Koots *et al.*, 1994a). A simple explanation for such a relationship may be that small heifer calves, with a good chance of an easy birth, tend to be smaller on reaching maturity and consequently run a greater risk of difficult calvings when they become dams.

The complexity of growth

Growth defined as an increase in weight over time is a rather crude measure of an animal's development, as the main interest lies in the growth of specific parts, such as muscle, fat or bone. To what extent animals lay down muscle or fat is dependent on management and feeding strategies, but has also a genetic background. There are considerable differences in body composition between breeds (Marshall, 1994), and between males and females within breed (Crews & Kemp, 2001).

Changes in body weight, shape and composition during growth and fattening of cattle are regulated by a complex system of growth factors like growth hormone (GH), insulin-like growth factor I (IGF-I), insulin, thyroid hormones and sex steroids. Sex steroids are important causes of difference in growth of entire males, castrates and females, as testosterone is a potent muscle growth stimulant that counteracts fat deposition (Bruckmaier *et al.*, 1998; Lawrence & Fowler, 2002).

As a growing animal approaches maturity, its increase in body weight levels off and the ratio of fat to protein deposition increases. As fat deposition is costly, the energetic efficiency of growth decreases with advancing maturity. Maturation rate and mature size differ between breeds (Webster, 1980). Some studies have suggested that selection of beef cattle for increased growth rate results in later maturing lean types (Koch *et al.*, 1982; Perry & Arthur, 2000).

Similar to the findings in publication II in this thesis, several authors have presented negative correlations between fat measurements and muscularity or between fat and lean content of carcass (Gregory *et al.*, 1995; Hirooka *et al.*, 1998; Morris *et al.*, 1999). The correlations between carcass weight and different measures of carcass fatness vary between studies, probably due to differences in management systems, including age at slaughter, and breeds studied.

Carcass traits can be adjusted for different end-points: age, weight or finish. Traits adjusted for these different factors may be biologically different (Koots *et al.*, 1994a). In this thesis (II), where age-adjustments of carcass traits were used, estimated genetic correlations between carcass weight and fatness were generally weak and negative, whereas those between carcass weight and carcass fleshiness grade were weak or positive.

Consequences of selection for growth rate on maternal ability

Selection for lean growth and heavy muscularity does not seem to be beneficial for the maternal ability of dams. Low carcass fatness grade and high carcass fleshiness grade seemed to be genetically associated with greater calving difficulty of heifer dams (publication V; MacNeil *et al.*, 1984; Splan *et al.*, 1998). Selection for increased carcass weight, however, did not seem to be detrimental to calving ability as a dam trait (publication V; Splan *et al.*, 1998). This was probably due to a correlated response in dam size which is related to an increased pelvic area (Naazie *et al.*, 1991).

The results in publication II in this thesis indicated that selection for direct effects on pre-weaning gain or leanness of carcass would impair the maternal effect on

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pre-weaning growth of calves, while selection for higher post-weaning gain or carcass weight would not. The maternal effect on pre-weaning gain is to a large extent determined by the dam's milk production (Meyer *et al.*, 1994). In selection experiments with beef cattle, small differences in milk production and milk quality have been found between cows in lines selected for high vs. low growth, favouring the high growth lines (Mrode, 1988; Herd, 1990).

Using cross-fostering experiments, Herd (1990) concluded that a calf's growth capacity and appetite influenced the expression of its dam's milk production, which may complicate the relationship between growth and milk production in beef cattle. Moreover, even if dams from lines selected for high growth rate show a slightly increased milk production, the energy requirements of their calves may increase even more, and thus milk supply may be more restrictive for growth of calves in high-growth lines than in low-growth lines (Herd, 1990). This could partly explain the negative correlation between direct and maternal effects on pre-weaning gain.

Selection criteria

The role of station performance testing

The results reported in publication I in this thesis did not support the need for a relatively expensive station performance testing of post-weaning gain. This was especially so for the Hereford breed, for which daily gain on the station was not the same trait genetically as daily gain under field conditions. This indicated presence of genotype by environment interactions. Feeding intensity differed for the breeds under field conditions, but not at station testing. With a different feeding regime at the station for Hereford, a closer relationship between the goal and index trait might be achievable.

The added value of station performance testing would be greater if traits were recorded at the station that could not easily be recorded under field conditions. Such traits could be feed intake and feed efficiency measures. However, this would require investment in technical equipment, and the benefit of including such data in the genetic evaluation would have to be quantified prior to implementation. Feed efficiency is favourably genetically correlated with growth rate (Koots *et al.*, 1994b), and a correlated response to the current selection for increased daily gain may be expected.

Station performance testing may, however, have beneficial effects other than increased genetic gain. The station may act as an incentive for breeders to improve their results, and it may add marketing values. Breeding bulls tested at the station can be claimed to have an added value as individuals, as their ease of handling, conformation and veterinary status are documented.

Gender differences

Stålhammar and Philipsson (1997) suggested that pre- and post-weaning gain of males and females should be treated as different traits in the genetic evaluation of Swedish beef breeds. For post-weaning gain, this was supported by the findings in publication I. Birth weight, however, was found to be the same trait for males and

females (III). The evolvement of gender differences during the growth period may have different explanations. Differences in feeding levels of males and females can be expected to be increased by the farmers as the animals get older, which may make genotype by environment interactions more obvious. Furthermore, the influence of sex steroids increases as the animals approach sexual maturity.

Calving traits

Gestation length and body measurements of the dam have been suggested as indicator traits for calving ability. Gestation length is rarely recorded for beef cattle, as natural service is common in beef herds. Also, gestation length is a less effective selection criterion than birth weight or calving difficulty score (Bennett & Gregory, 2001), and selection for shorter gestation length may affect calf viability (Hanset, 1981). Selection for body measurement traits such as hip height or pelvic area are expected to have opposite effects on direct and maternal effects for calving difficulty, and would be less efficient than direct selection for birth weight or calving difficulty (Cook *et al.*, 1993; Bennett & Gregory, 2001).

Whereas the estimated genetic parameters indicated that records of calving difficulty score could be used in the genetic evaluation, this was not the case for stillbirth. Stillbirth is an economically important trait, but its direct inclusion in the Swedish beef breeding evaluation was found to be not feasible, due to low accuracy in selection (IV). Correlated response in stillbirth could be achieved by selection on calving difficulty score and birth weight, given the strong correlations reported in publication IV, but these were high in comparison with literature values. Assuming literature values, the genetic variation in SB explained by CD and BW would amount to 30–70%. A recommendation for improvement of the recording scheme is to assign unique identification numbers to all stillborn calves and to record their birth weight. There are few other traits suitable for indirect selection on stillbirth. Increased knowledge of causes of stillbirth of calves despite easy calving would aid in the search for correlated traits.

Parity differences

The incidences of calving difficulty and stillbirth were considerably higher at first calving than at later calvings, as is commonly reported in the literature (Philipsson, 1996). High, but not unity, genetic correlations were generally found between calving traits at first and later parities. Biologically, partly differing causes are important for calving difficulty at first and later calvings. Too large a calf in relation to the dam's inlet pelvic dimensions seems to be a more important cause of dystocia in heifers, whereas a posterior or abnormal presentation of the calf, weak labour, uterine torsion and insufficient dilatation of the cervix are of importance especially in older cows (Meijering, 1984). Heifers have not yet reached their full mature size. Differences in size and deposition of fat and muscle between heifers and older cows may influence the relationships between carcass traits and calving traits at first and later parities, as was indicated in publication V. Calving difficulty at first and later parities should thus be regarded as different traits.

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Measure of body composition

Selection for growth traits did not in most cases result in correlated responses in carcass traits in selection experiments with beef cattle, reviewed by Mrode (1988). In publication II in this thesis, rather weak genetic relationships were estimated between growth traits and both carcass fleshiness and fatness grades. It would thus be recommendable to include these carcass traits in the genetic evaluation and selection of breeding stock.

The best pure-bred beef bulls are spared for breeding purposes, and bulls that are slaughtered young are thus not a random sample. Joint analyses with pre-weaning growth seem to be beneficial for the genetic evaluation of some carcass traits (Woodward *et al.*, 1992; Crews and Kemp, 1999). The results in publication II indicate that the added information from contemporaries that were not slaughtered when young may help to account for the selection bias for carcass weight.

Live measurements of body composition using ultrasound scanning of subcutaneous fat depth and eye muscle area have been shown to be useful as indicator traits for carcass composition in genetic evaluations (Hassen *et al.*, 1999; Crews *et al.*, 2003; Reverter *et al.*, 2003). Live measurements have the advantage of providing early information on breeding animals in addition to their slaughtered relatives, but are currently not recorded in Sweden. Commercial carcass data on the other hand are available and could be used for genetic evaluation without additional recording costs, and estimated genetic parameters showed potential for genetic improvement of these traits. The use of commercially recorded carcass weight, fatness and fleshiness grades would give a close connection with the breeding goal, as these traits directly determine the per kg price paid for carcasses in Sweden.

More traits of interest

The carcass traits recorded in Sweden today describe the quantity of fat and muscle in the carcass. Traits more directly related to sensory quality, such as tenderness, juiciness, shear force or marbling, may be of interest in Sweden in the future, but are currently not recorded. Carcass quality traits are generally moderately heritable, except for subjective measures such as sensory panel scores which tend to be only slightly heritable (Koots, 1994a; Marshall, 1994; Gregory *et al.*, 1995). Genetic relationships between quality and quantity carcass traits are often found to be low to moderate. The sign of correlations with marbling score for fat depth, carcass weight or growth traits seems to vary according to the age, sex and breed studied (Johnston *et al.*, 1992; Wilson *et al.*, 1993; Marshall, 1994). Literature values indicate an antagonistic genetic relationship between marbling score and cutability or muscling in some populations (Marshall, 1994).

Male and female fertility are of economic importance and traits like calving interval and scrotal circumference may be possible to record in Swedish beef herds. Scrotal circumference has been shown to be moderately heritable and weakly favourably correlated with growth rate and calving interval. Low heritabilities of calving interval have been presented in the literature (Koots *et al.*, 1994a, b).

A high incidence of hind limb disorders among beef bulls has been reported by the Swedish insurance company Agria. Initial studies on skeletal disorders in young station performance tested bulls, culled due to below average growth performance, showed joint lesions in almost all bulls in the study. The number of lesions per bull was significantly correlated with growth rate and carcass weight (Dutra, 1999). At present, information on skeletal disorders is only available for few animals. Further studies of the importance of limb disorders for animal welfare and production in the Swedish beef populations are needed. Knowledge about the possibility of counteracting such problems by selection in Swedish beef breeds would be valuable.

Conclusions

- Field recorded carcass weight, fleshiness grade and fatness grade, as well as calving difficulty score, can be included in the genetic evaluation of beef breeds in Sweden.

- The Swedish beef population structure does not allow for direct genetic evaluation of stillbirth, as the heritabilities are very low and the progeny groups are small. Stillbirth is however genetically correlated with birth weight and calving difficulty score and these traits should primarily be used for selection.

- The relationships between carcass fleshiness and fatness grade and growth traits are weak. Breeding values for these traits seem to be very little biased due to selection for growth traits. The genetic variation of carcass weight, however, seem to be more biased by sequential selection on growth rate, and multiple trait evaluation of growth and carcass traits is recommended.

- Some unfavourable genetic relationships exist between carcass and calving traits. To avoid negative effects on calving ability and viability of calves when selecting for beef production traits, calving difficulty score and birth weight need to be included in the breeding goal and considered when selecting breeding stock.

- Direct and maternal effects are unfavourably correlated and both direct and maternal effects should be included in genetic evaluations for calving performance, birth weight and pre-weaning gain.

- Calving difficulty scores at first and later parities are controlled by partly differing sets of genes and should be treated as different but correlated traits in the genetic evaluation.

- Growth traits can easily be recorded under field conditions, and with similar heritabilities as on station. The station performance testing of young beef bulls is only motivated as a selection tool if complementary traits, difficult to measure in the field, can be recorded there, and if the genetic correlation between station and field results is high.

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- Genotype by environment interactions are present for growth traits of beef cattle, causing breed differences in genetic correlations. Male and female birth weights appear to be controlled by the same sets of genes, while this is only partly so for post-weaning gain. The gender difference later in life may be due partly to genotype by environment interactions, as breeding heifers are raised less intensively than are young bulls.

Future outlook

The complex genetic relationships between traits are mentioned several times in this thesis. If the suggested inclusion of calving and carcass traits in the genetic evaluation is to be implemented, the number of breeding values available for selection by breeders will increase. For the selection of breeding stock to be successful, the traits should be weighted together in a total merit index. Economic weights adjusted for Swedish conditions need to be calculated, and it will be important to take into account the views of breeders, producers and the slaughter industry as well as the ultimate consumers in the process. Ideally, not only economic, but also ethical aspects should be considered in the selection of breeding stock.

This thesis deals with genetic analyses of the purebred nucleus. It is important to remember that the cost of genetic evaluation and selection of breeding stock should be financed by selling bulls and dams to beef production herds, which constitute about 90% of all beef herds in Sweden, and by semen sales to dairy herds. It would be interesting to be able to use results from crossbred offspring of beef bulls for selection purposes. Information from dairy herds that use beef semen would be more easily available than information from beef production herds using natural service bulls. Even today, AI-bulls of beef breeds are genetically evaluated for calving traits based on results in dairy herds. In the future, a similar evaluation for carcass traits of beef–dairy crosses may be possible. For data from beef production herds to be useful, information about the sires of calves must be recorded, which is complicated by the common practice of keeping more than one bull with the cows on the same pasture.

The rather large number of different beef breeds in Sweden, in relation to the total number of beef cows, complicates the genetic evaluation and selection. The breeding goals of different beef breeds should be clear and indicate the intended use of the breeds, for pure- and/or crossbreeding. Studies on optimum selection programmes for each of the main breeds in Sweden, and of the economic value of different crossbreeding systems, would be beneficial for beef producers.

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