## Breeding for Sustainable Milk Production

From Nucleus Herds to Genomic Data

Helen Hansen Axelsson

Faculty of Veterinary Medicine and Animal Science Department of Animal Breeding and Genetics Uppsala

Doctoral Thesis Swedish University of Agricultural Sciences Uppsala 2013 Acta Universitatis agriculturae Sueciae 2013:43

Cover: Helen Hansen Axelsson

ISSN 1652-6880 ISBN 978-91-576-7824-9 © 2013 Helen Hansen Axelsson, Uppsala Print: SLU Service/Repro, Uppsala 2013

# Breeding for Sustainable Milk Production – from Nucleus Herds to Genomic Data

#### Abstract

The overall aim of the research reported in this thesis was to investigate ways to mitigate deterioration in functional traits and reduce the environmental impact of milk production. The more specific objectives were to obtain new information about the selection of bull dams for functional traits in an open nucleus herd, to monitor ongoing genetic trends in functional traits, and to examine a breeding program with genomic selection and contractor herds that records specific indicator traits correlated with environmental impact.

A breeding scheme with expanded recording of functional traits in potential bull dams in a nucleus herd was simulated. The genetic trend in functional traits was found to be unfavourable in all scenarios. Improved recording of functional traits did not limit the unfavourable genetic response in fertility and udder health traits unless more economic weight was placed on functional traits in the breeding goal.

Genetic trends in fertility and udder health traits were estimated in Swedish Red dairy cattle. The estimated genetic trend for number of inseminations in lactating cows was unfavorable. The choice of model to be used for genetic evaluation influences the estimate of genetic trend, indicating that unfavorable genetic trends may not be discovered unless the traits are evaluated in a multiple-trait model including both functional and production traits.

Substantial genetic progress in breeding for environmentally friendly cows can be achieved by including environmental impact in the breeding goal, and by using phenotype records and genomic information on correlated indicator traits. The most valuable indicator traits are those with a strong genetic correlation with environmental impact that also have a high accuracy of direct genomic values. Breakeven prices for recording the indicator trait were calculated for all scenarios. They varied considerably from one scenario to another, depending on the number of phenotype records on indicator traits. Recording an indicator trait could be both genetically and economically advantageous where the genetic correlation between the trait in question and environmental impact is strong, the trait has an optimal number of phenotype records, and the reliability of direct genomic values is moderately high.

*Keywords:* Breeding program, genomic selection, functional traits, novel traits, environmental impact, breakeven price, dairy cow

*Author's address:* Helen Hansen Axelsson, SLU, Department of Animal Breeding and Genetics, Box 7023, 750 07 Uppsala, Sweden *E-mail:* Helen.Hansen@slu.se

## Contents

List o	of Publi	ications	7
Abbre	eviatio	ns	8
1	Introc	luction	9
2	Gene	ral background	11
2.1	Susta	inable milk production	11
2.2	The g	enetic relationship between milk production and functional traits	12
2.3	Increa	asing genetic gain	13
		Breeding schemes with nucleus herds	13
		Genomic selection	14
2.4	•	izing breeding programs	15
2.5		rganization of dairy cattle breeding in the Nordic countries	16
2.6	The e	nvironmental impact of milk production	18
3	Aims	of the thesis	21
4	Sumn	nary of investigations	23
4.1	Mater	ial and methods	23
	4.1.1	Experimental design and data analysis of bull dam selection	
		strategies (Paper I)	24
	4.1.2	The data analysis and the estimation of genetic trends in Swed	ish
		Red Dairy Cattle (Paper II)	25
	4.1.3	Experimental design and data analysis of breeding schemes to	
		reduce environmental impact (Paper III)	26
	4.1.4	Economic analysis of the breeding schemes to reduce the	
		environmental impact (Paper IV)	28
4.2	Main f	findings	29
	4.2.1	Genetic response in functional traits in bull dams	29
	4.2.2	Genetic trend in fertility estimated with multiple-trait model or tra	ait-
		wise	31
	4.2.3	Genetic responses in breeding schemes aiming to reduce	
		environmental impact	32
	4.2.4	Breakeven price per record in reference population	33
5	Gene	ral discussion	35

5.1	Bull dam selection in the nucleus herds	35
5.2	Genetic trend estimated with different models	36
5.3	The effect of using heifer fertility records	37
5.4	Environmental impact as a goal trait	37
5.5	Genetic gain in environmental impact	38
5.6	Indicator traits for environmental impact	39
5.7	Specialized recording herds	41
5.8	Breakeven prices	43
5.9	Choice of economic values	44
5.10	Future perspectives of sustainable breeding	45
6	Conclusions	47
7	Future research	49
7 8	Future research Avel för hållbar mjölkproduktion – från kärnbesättningar till	49
-		49 51
-	Avel för hållbar mjölkproduktion – från kärnbesättningar till	-
8	Avel för hållbar mjölkproduktion – från kärnbesättningar till genomisk information	51
<b>8</b> 8.1	Avel för hållbar mjölkproduktion – från kärnbesättningar till genomisk information Bakgrund	<b>51</b> 51
<b>8</b> 8.1 8.2	Avel för hållbar mjölkproduktion – från kärnbesättningar till genomisk information Bakgrund Sammanfattning av studierna	<b>51</b> 51 52

### List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Hansen Axelsson, H., Johansson, K., Eriksson, S., Petersson, K.-J., Rydhmer, L., Philipsson, J. (2011). Selection of bull dams for production and functional traits in an open nucleus herd. *Journal of Dairy Science* 94:2592-2600.
- II Eriksson, S., Fikse, W.F., Hansen Axelsson, H., Johansson, K. Genetic trends for fertility in Swedish Red Cattle estimated with different models. (In manuscript).
- III Hansen Axelsson, H., Fikse, F., Kargo, M., Sørensen, A.C., Johansson, K., Rydhmer, L. (2013). Genomic selection using indicator traits to reduce the environmental impact of milk production. (Accepted to *Journal of Dairy Science*).
- IV Hansen Axelsson, H., Thomasen, J.R., Sørensen, A.C., Rydhmer, L., Kargo, M., Johansson, K., Fikse, W.F. Breakeven prices for the recording of indicator traits to reduce the environmental impact of milk production. (In manuscript).

7

Papers I and III are reproduced with the permission of the publishers.

# Abbreviations

AI	Artificial insemination
BLUP	Best linear unbiased prediction
CFI	Interval between calving and first insemination
$CH_4$	Methane gas
СМ	Clinical mastitis
$CO_2$	Carbon dioxide gas
DGV	Direct genomic value
DO	Days open
EBV	Estimated breeding values
EI	Environmental impact
FT	Functional trait
FUA	Fore udder attachment
GEBV	Genomic enhanced breeding value
GHG	Greenhouse gas
LD	linkage disequilibrium
MOET	Multiple ovulation and embryo transfer
MP	Milk production
$N_2O$	Nitrous dioxide gas
NAV	Nordic Cattle Genetic Evaluation
NINS	Number of inseminations
NTM	Nordic Total Merit
PFI	Pregnant after first insemination
PY	Protein yield
RDC	Red Dairy Cattle
SCS	Somatic cell score
SNP	Single-nucleotide polymorphism
UA	Fore udder attachment
UD	Udder depth
	1

### 1 Introduction

This is an exciting time for dairy cattle breeders. The dairy industry is facing new challenges arising from the growing public interest in animal health and welfare, and the impact of milk production on the environment. At the same time production costs are increasing, while revenues from milk sales remain very low. Dairy cattle breeding is therefore changing direction and moving towards more sustainable milk production, with a focus on improved productivity and functionality. At the same time, a new approach known as genomic selection has been implemented in many breeding schemes worldwide. In genomic selection, genomic enhanced breeding values (GEBV) are estimated for selection candidates as the sum of the effects of high density markers (Pryce & Hayes, 2012). The development of genomic selection has led to a high level of expectation about increased genetic gain in dairy cattle breeding programs (Dekkers, 2010).

Breeding programs with progeny testing and intensive use of artificial insemination (AI) have for many decades been the main tools in creating a high-yielding dairy cow. Breeding values for AI bulls can be estimated very accurately with phenotypic information on large progeny groups and relatives, using methods like best linear unbiased prediction (BLUP). The weakness of this method is that the selection process from young bull calves to proven bulls takes five to six years. Animal scientists have therefore long sought to find ways to increase the accuracy of selection of young animals, and to shorten the generation interval. This would increase the genetic gain.

Breeding schemes involving the performance testing of heifers at the station – the so called nucleus herd – were expected to improve the selection of bull dams. Nucleus herds with multiple ovulation embryo transfer (MOET) have great potential to increase the genetic gain in traits with high heritability. The advantage here lies mainly in shorter generation intervals, which are due to more intensive use of young animals, and higher selection intensity on the dam

to sire path (Stranden *et al.*, 2001; Bovenhuis *et al.*, 1989; Juga & Mäki-Tanila, 1987). However, there has been concern that intensive selection among young potential bull dams will improve milk production and conformation traits, at the expense of health and fertility. These functional traits have generally low heritabilities and are unfavourably correlated with production.

Other options permitting more accurate selection of young animals became available with the implementation of genomic selection. Very young animals, or even embryos, can be genotyped, and GEBVSs can be estimated for these animals with higher accuracy than for breeding values based on parent averages (Hayes *et al.*, 2009). In this way, the best young bulls can be selected for breeding as soon as they have reached reproductive age. Generation intervals can be shortened and genetic gain can be increased not only in milk production, but also in functional traits and a variety of other traits that are complicated and expensive to record (Dekkers, 2010), including greenhouse gas emissions.

The overall aim of the research reported in this thesis was to avoid the deterioration of functional traits and reduce the environmental impact of milk production. More specific objectives were to study the selection of bull dams for functional traits in an open nucleus herd, to monitor ongoing genetic trends in functional traits, and to examine a breeding program with genomic selection and contractor herds that record specific indicator traits correlated with environmental impact.

### 2 General background

### 2.1 Sustainable milk production

The question how to ensure the sustainability of milk production is attracting more and more interest in dairy cattle breeding. Dairy cattle farmers are facing many challenges in form of constantly increasing production costs, competition on the market and public concern about animal welfare and the environment. Breeding for more sustainable milk production involves the optimization of breeding programs to ensure that there is a balance between production, animal health and welfare, and the surrounding environment. Breeding goals in dairy cattle often include many economically important traits which increase the genetic gain in production traits, and functional traits as well (Mark, 2004), and in this way the existing breeding goals increase the profitability (Groen, 2008; Steine *et al.*, 2008). Still, further development of breeding goals is necessary to achieve sustainability in milk production.

Narrow breeding goals intended to improve production levels and conformation traits were used for decades in many parts of the world. By the end of the last century, however, it became clear that the focus on selection for milk production had caused a deterioration in female fertility and had also increased the frequency of health problems as a result of unfavourable correlations between the trait groups (Rauw *et al.*, 1998). Nowadays, problems with udder health and reproduction disorders that lead to early involuntary culling are widely recognized (Ahlman *et al.*, 2011). In many countries, various functional traits are routinely recorded and included in the genetic evaluation (Mark, 2004).

Breeding organizations in the Nordic countries had started to record fertility and health traits already in the 1960s. They were pioneers in starting up national recording systems and databases for such traits (Philipsson & Lindhe,

2003). Since then, the breeding goals in Nordic countries have grown broader; they now include a variety of traits that are of economic importance.

The economic feasibility of a sustainable breeding goal is, of course, essential, but traits without an identified economic value also have to be considered. The ethical value of a trait can be much higher than its current market economic value (Nielsen *et al.*, 2005).

# 2.2 The genetic relationship between milk production and functional traits

The heritability of milk yield is moderately high ( $h^2=0.30-0.35$ ), and this has contributed to successful genetic selection for increased milk yield. Current average production in Sweden, for example, is over 9000 kg per cow and lactation (Swedish Dairy Association, 2013). That is about 30% higher than average production levels in Sweden in the 1980s. In general, the annual increase in milk yield is expected to be around 1-2% (Veerkamp *et al.*, 2008). This improved milk yield is a consequence of a need and desire to maximize the profit of milk production and lower the costs per cow. Selection for high milk yield has caused a decline in fertility (Veerkamp *et al.*, 2008); it has also increased the prevalence of a number of diseases, of which clinical mastitis is the most frequent problem (Heringstad *et al.*, 2000). These growing health and reproduction problems cause losses of income for the farmers (Steeneveld & Hogeveen, 2012; Hagnestam-Nielsen & Ostergaard, 2008).

In the Nordic breeding programs, the fertility traits most commonly measured are interval between calving and first insemination (CFI), number of inseminations (NINS), conception rate (CR), non-return rate at 56 days (NR56), days open (DO), and also reproduction disorders and different progesterone measures (Petersson, 2007; Philipsson & Lindhe, 2003; Roxström, 2001a). For udder health the incidences of clinical mastitis (CM) and somatic cell score (SCS) are used (Heringstad et al., 2000). A more novel, and still rather exclusive, way to monitor udder health is by measuring the electrical conductivity of the milk (Norberg, 2004). Unfavourable genetic correlations have been reported between milk production and fertility (Buch et al., 2011b; Philipsson & Lindhe, 2003; Roxstrom et al., 2001) and milk production and udder health traits (Buch et al., 2011b; Carlen et al., 2004; Heringstad et al., 2000). Buch et al. (2011b) estimated the genetic correlation between protein yield and the interval between calving and first insemination (CFI) at 0.30, and protein yield and number of inseminations (NINS) at 0.40. The genetic correlation between protein yield and clinical mastitis was 0.40 and between protein yield and somatic cell score was 0.22, in the same study.

These are moderately strong correlations. They confirm that it is crucial to include functional traits in the genetic evaluation of cattle to avoid undesirable genetic gain in these traits. Heritability estimates of fertility measures are often lower than 6% (Buch *et al.*, 2011b; Roxström, 2001b). Also the heritability of clinical mastitis is low. The estimated heritability of clinical mastitis for Swedish Red Cattle (SRB) was 0.014 in a study by Buch (2011b), and it was found to be 0.03 in first lactation, and 0.012 in second lactation, Swedish Holstein cows (Carlen *et al.*, 2004). The heritability of SCS, which is often used as measure of udder health, is somewhat higher: a heritability of 0.14 has been reported for both SRB and Swedish Holstein first lactation cows (Buch *et al.*, 2011b; Carlen *et al.*, 2004).

In the Nordic countries, the genetic trend in udder health, based on the breeding values of progeny-tested Holstein and Red Dairy Cattle (RDC) bulls has been rather stable over the last two decades. The genetic trend in female fertility was declining in Holsteins, especially in Swedish and Danish Holsteins, until the beginning of this century, but it has been more stable since then. The same trend in RDC has been reported to be stable through years (Pedersen *et al.*, 2008).

#### 2.3 Increasing genetic gain

#### 2.3.1 Breeding schemes with nucleus herds

Nicholas and Smith (1983) were the first to show the increased genetic gain secured by using MOET and selecting animals within a nucleus herd. They proposed performance testing and the selection of young females and males without progeny testing. In their design of it, the nucleus herd was isolated from other herds. Closed nucleus herds are often used in poultry and pig breeding schemes. In dairy cattle, open nucleus herds, which allow cows from commercial herds as dams, turned out to be more convenient. Open nucleus herds increased the genetic gain almost as much as closed nucleus herds, but the variance of selection response was lower in them (Meuwissen, 1991). One of the benefits of a nucleus herd was that it allowed MOET be used more efficiently to increase the number of offspring per dam.

Open nucleus herds were also used in Sweden and Finland, mainly to performance-test potential bull dam candidates. While the breeding values of bulls are based on their daughters records, the breeding values of bull dams are estimated on the basis of their pedigree index and own performance. The accuracies of the latter's breeding values are therefore rather low. The breeding values of bull dams selected from conventional herds can also be biased by preferential treatment of the best cows (Zwald & Weigel, 2002). Selecting

young elite heifers with a high pedigree index, and performance testing them in the same environmental conditions was believed to result in more accurate selection of potential bull dams. One of the goals was also to reduce the generation interval, and therefore the bull dams were selected at the beginning of their second lactation.

The general breeding scheme for both the Viken herd in Sweden and the ASMO herd in Finland was to recruit heifers at 6 months of age from the conventional herds. They were then flushed for embryos at an age of 12-16 months and then inseminated for their own pregnancy. The first lactation was used for performance-testing of the cows. After the second calving the cows were evaluated for their conformation, and on the basis of their estimated breeding values the best cows were selected as bull dams.

Nucleus herds had the capacity to expand their recording system, and to record more traits with higher precision than was possible with conventional herds. The nucleus herd could serve as a test station for recording additional fertility traits like progesterone (Petersson, 2007), electrical conductivity as an indicator trait for udder health status (Norberg, 2004) or locomotion and claw health.

Bull dam testing in nucleus herds was of less interest following the implementation of genomic selection. Even so, it has been shown that MOET, and higher selection intensities on bull dams, may also deliver additional genetic gain in breeding programs with genomic selection (Pedersen *et al.*, 2012).

#### 2.3.2 Genomic selection

The most recent revolution in dairy cattle breeding is the so-called genomic selection first proposed by Meuwissen et al. (2001). The main principle of genomic selection is that animals with recorded phenotypes in a reference population can be genotyped for several thousand of single nucleotide polymorphisms (SNPs), and that this genotype information can then be used to calculate the SNP effects. With this information, genomic breeding values can be estimated for genotyped selection candidates (Hayes *et al.*, 2009). This means that very young animals, or even embryos, can be selected for breeding on the basis of their genomic enhanced breeding values (GEBV); this gives higher accuracies than selection for breeding value based on a pedigree index (Pryce & Daetwyler, 2012).

The reference populations currently used by breeding organizations are based on thousands of progeny-tested bulls. The implementation of genomic selection and the creation of the reference population have been particularly successful in Holstein cattle. Holstein populations in different countries are closely related; they can therefore be combined to increase the size of the reference population and the reliability of genomic breeding values (Lund *et al.*, 2011). The large number of animals in the reference population enables us to achieve high accuracies of GEBVs for both production traits and functional traits. To maintain the high level of accuracies in genomic breeding values it is essential regularly to record phenotypes with a high degree of precision. This ensures that there will be a future reference population of adequate size.

Breeding schemes that use genomic selection can be designed in a variety of ways. Buch et al. (2011a) simulated breeding schemes that they called hybrid and turbo. The hybrid scheme is used in practical breeding in Nordic countries; it combines the selection of genotyped young bulls with the conventional progeny-testing scheme. The turbo scheme is more radical. It would allow using young bulls as bull sires without progeny testing of the bulls. In it, the generation interval can be considerably reduced and higher genetic gains in breeding goal traits may be achievable (Buch *et al.*, 2011a).

Genomic selection is believed to be beneficial also when we are selecting for novel traits with limited number of phenotype records (Dekkers, 2010). Some traits are very expensive and challenging to record, and some cannot be recorded on selection candidates (Dekkers, 2010). In these cases it could be reasonable to record a novel trait in test herds, or in some other experimental setting. A reference population can then be created composed of sires of the animals with phenotype records, or the animals themselves. Some studies propose using cows in the reference population for novel traits instead of sires of the cows (Buch *et al.*, 2012). It is also important to know the relationship between the animals, as it has an effect on the accuracy of the genomic breeding values (Pszczola *et al.*, 2012). The optimal design, and in particular the size of the reference population for novel traits, is yet to be studied, but we know that the reference population needs to be large enough to give accurate breeding values in order to generate additional genetic gain.

### 2.4 Optimizing breeding programs

Successful breeding is not possible without breeders who determine the breeding goal and define the breeding objectives. Breeding is always futureorientated and tries to predict changes in marketing situations (Herold *et al.*, 2012). Several computer programs have been developed to optimize breeding programs. In the main they adopt either a deterministic or a stochastic approach. The stochastic approach uses overlapping generations and allows for great flexibility in the design of breeding programs. It is easy to model single, or multiple, stage selection and inbreeding in stochastic simulation programs (Pryce & Daetwyler, 2012). ADAM is a stochastic simulation program designed by the scientists at the Department of Genetics and Biotechnology, University of Aarhus, Denmark. ADAM allows breeding programs with various complexities to be optimized (Pedersen *et al.*, 2009). Computational time is the only limitation when using this program. ADAM permits modeling of different new reproduction technologies, such as MOET and sexed semen, and also genotype information. It uses also other computer programs to estimate random numbers and breeding values, and for optimal contribution selection (Pedersen *et al.*, 2009). ADAM calculates genetic progress, accuracies of selection per selection group, true and estimated breeding values, the age distribution of selection candidates, rates of inbreeding and inbreeding coefficient, generation interval and so on.

Deterministic approaches can be used in more simple designs of breeding program. ZPLAN (Willam et al., 2008) is a deterministic program that uses selection index and gene flow procedures. It requires different population and biological parameters of the animal population, and these have to be provided by the user. Besides genetic gains, ZPLAN calculates also economic gains of the breeding program. It also calculates discounted return, costs, and the profit of the breeding goal. The discounted return shows the monetary gain in terms of genetically improved animals in the population over the investment period (König et al., 2009). The discounted profit is calculated as the difference between the discounted return and the discounted costs. To be able to estimate the realistic discounted profit, ZPLAN requires the fixed and/or variable costs of the breeding program. When a novel trait in the breeding goal is being considered, the cost estimates might not be available. In this case, the discounted return of the breeding program and breakeven price can be calculated to evaluate the feasibility of investing in a novel trait. It can be evaluated whether the net revenue generated by the novel trait in the breeding goal is enough to cover the investment costs (Butler & Wolf, 2010). One of the main benefits of ZPLAN is its very short running time – a feature shared by and large by other deterministic simulation programs. This allows many different breeding scenarios to be analyzed in a short time. Among the weaknesses of the program are its inability to account for the Bulmer effect and the fact that it only runs one round of selection.

# 2.5 The organization of dairy cattle breeding in the Nordic countries

It was their similar breeding goals and registration schemes and the close collaboration between the Nordic breeding organizations that led to the

establishment of Nordic Cattle Genetic Evaluation (NAV), and to joint estimation of breeding values. NAV breeding values are estimated for Holstein, Jersey and RDC. RDC combines three dairy cattle breeds: Swedish Red, Danish Red and Finnish Ayrshire (Aamand, 2008). In total, there are about 364 000 RDC, 616 000 Holstein and 62 000 Jersey cows included in the evaluation Stålhammar, Viking genetic (H. Genetics. personal communication). For several years the three countries, Denmark, Sweden and Finland, have had a common total merit index (NTM) that is designed to increase the profits by weighing together various trait groups (NAV, 2008). NTM includes the following trait groups: milk production, beef production, calving traits, female fertility, mastitis, other diseases, claw health, longevity and conformation. The economic values of the traits are breed-specific and fixed for all three countries (NAV, 2008). Total economic value is divided between traits groups so that it maximizes the profit per improved animal. In Holstein the largest proportion of the relative economic weight (45%) is placed on functional traits. By contrast 33% and 22% are placed on production and conformation traits, respectively. The relative economic weights for production and functional traits in RDC are divided more equally: 37% and 39%. In RDC, more weight (24%) is placed on the conformation traits than happens with Holstein, and the main proportion of this (13%) is used for udder health traits (H. Stålhammar, Viking Genetics, personal communication). Poor udder conformation in RDC cattle has been of concern to farmers for a long time. Furthermore, since automated milking systems became common, good udder conformation has been very important for the efficiency of the milking robot.

The Nordic collaboration expanded to the breeding companies that joined in Viking Genetics. Viking Genetics was one of the first breeding companies to start implementing genomic selection. In 2008 the first genotyping of young Holstein bulls and selection of young bulls based on their genomic breeding values started. A year later genomic breeding values could be estimated for RDC bulls as well. Today, Viking Genetics genotypes about 1800 Holstein and 2000 RDC bull calves. About 275 Holstein and 300 RDC young bulls are selected on the bases of the results of the genomic evaluation. About 175 and 200 best young bulls of each breed respectively are selected for progeny testing yearly. Of those, about 15-25 bulls with highest breeding values based on pedigree index and genomic breeding values are offered for insemination as Genetics, **GENVIKPLUS** bulls (H. Stålhammar, Viking personal communication).

#### 2.6 The environmental impact of milk production

Global warming caused by the increasing concentration of greenhouse gasses (GHG) in the atmosphere is a major concern around the world. Many countries have adopted an agreement, the Kyoto protocol, to try to control and also lower the emissions of GHG internationally. The Kyoto protocol was developed by the United Nations Framework Convention on Climate Change; it came into force in 1997 (Gill *et al.*, 2010).

Agriculture accounts for a substantial proportion of the anthropogenic emissions of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O). Approximately 25% of global CO<sub>2</sub> and more than 50% of the global CH<sub>4</sub> and N<sub>2</sub>O emissions originate from crop farming (Stavi & Lal, 2013). The direct contribution of livestock has been estimated at around 9% of global anthropogenic emissions; when indirect emissions, like those associated with fertilizers, transportation of feed and products, and land use are taken into account, the emissions account for more than 18% (Gill *et al.*, 2010). The meat and dairy sector accounts for most GHG, especially CH<sub>4</sub> emissions, as often different species of ruminants are used for these purposes.

Ruminants emit a considerable amount of  $CH_4$  as a natural part of their microbial rumen fermentation (Beauchemin *et al.*, 2009). Using a laser methane detector to measure the emissions from Holstein cows, Chagunda et al. (2009) estimated average daily emissions to be about 350 grams per cow. During the fermentation volatile fatty acids, acetate, propionate and butyrate, are liberated. Acetate and butyrate, mainly produced during roughage digestion, liberate hydrogen which, in large concentrations, inhibits microbial fermentation (Beauchemin *et al.*, 2009). Methanogenic microorganisms prevent hydrogen from accumulating in the rumen by formatting it to  $CH_4$ (Beauchemin *et al.*, 2009). Propionate, mainly liberated from feed rich in starch, acts as a net hydrogen sink, and the methane production reduces. Therefore, diets rich in grain are believed to lower, while diets rich in roughage are believed to increase methane emissions (Cottle *et al.*, 2011).

Methane production depends on many different factors, including carbohydrate intake and chemical composition and rumen fermentation time (Beauchemin *et al.*, 2009). It is connected with feed intake, so reducing feed intake or the fermentability of organic matter in the rumen methane emissions can be reduced (Cottle *et al.*, 2011). However, this will have negative consequences on animal production, and it is a challenge to find nutritional options that would reduce the  $CH_4$  emission without reducing the productivity of the animals (Beauchemin *et al.*, 2009).

Various nutritional options may have quick, but short-term, effect on  $CH_4$  emissions (Beauchemin *et al.*, 2009). To reduce the emissions over the longer

term animal breeding is the best option, as the genetic changes it involves are cumulative. However, direct methane emissions are expensive and complicated to measure, and therefore the registrations cannot be performed to the extent needed to provide enough phenotype records to include this trait in the genetic evaluation of selection candidates (Wall *et al.*, 2010). This is especially true in conventional breeding programs in which bulls are progeny-tested. In the presence of genomic information, fewer phenotype records are required. The investigation of how a breeding program with genomic selection should be designed to reduce the environmental impact of dairy cattle was one of the aims of the present thesis.

Another option is to use indirect selection and correlated indicator traits.  $CH_4$  emissions depend on many different characteristics of a dairy cow: for example, size and body weight, production level, feed conversion ability, dry matter intake, longevity, and health and fertility. (Bell *et al.*, 2011; Wall *et al.*, 2010; Hegarty *et al.*, 2007). All these traits affect the quantity  $CH_4$  emitted by a cow per kg of milk she produces. It can be assessed what her total environmental impact will be, that is how much  $CH_4$  she emits per her lifetime milk production. Selection on correlated indicator traits can be as successful as selection on the goal trait itself, especially when the correlation is fairly strong and a large number of phenotype records on the indicator trait are available (de Haas *et al.*, 2011).

Moreover, to be able to set up a breeding program that will reduce the environmental impact it is essential to get accurate genetic parameters for  $CH_4$  emissions and other GHG emissions from cows. Therefore, different techniques that can measure the emissions precisely and provide sufficient phenotype records to permit estimation of the heritabilities and correlations with other breeding goal traits are being investigated and developed by researchers in several countries (Storm *et al.*, 2012).

### 3 Aims of the thesis

The general aim of this thesis was to investigate breeding strategies in dairy cattle designed to improve selection for functional traits and to reduce the environmental impact of milk production. More specific objectives were to study the selection of bull dams for functional traits in an open nucleus herd, to analyze the choice of method on the estimated trend in functional traits, and to study breeding schemes with genomic selection that use contractor herds to record specific indicator traits correlated with environmental impact. The following hypotheses were tested:

- Deterioration of functional traits due to bull dam selection in an open nucleus herd can be avoided by implementing an expanded and improved system for recording of female fertility and udder health traits (Paper I);
- The estimated genetic trend in fertility observed in the full multiple-trait model is more unfavourable than the genetic trend estimated with the model where traits are analyzed group-wise (Paper II);
- Phenotype information collected by recording specific indicator traits of environmental importance in contractor herds can be implemented in breeding schemes with genomic selection in order to reduce the environmental impact of milk production (Paper III);
- The indicator traits with highest genetic gain in environmental impact are the most beneficial in economic terms to record (Paper IV);

### 4 Summary of investigations

### 4.1 Material and methods

Papers I, III and IV were simulation studies using either a deterministic or a stochastic approach. In Paper II, milk recording data provided by the Swedish Dairy Association were analyzed. Figure 1 illustrates the connections between the papers. A condensed version of materials and methods of each paper is presented here.



*Figure 1.* Breeding for sustainable milk production; a schematic illustration of connections between studies included in this thesis.

# 4.1.1 Experimental design and data analysis of bull dam selection strategies (Paper I)

In this study a bull dam selection scheme used in a Nordic open nucleus herd was imitated. All heifers recruited to the nucleus herd were presumed to be sired by proven bulls that had been progeny-tested with 100 effective daughters for production and functional traits. The selection index included the following information sources: phenotypic records for protein yield, cow fertility and udder health from the milk recording system, and additional fertility and udder health traits recorded in the nucleus herd. Three information sources (sire, maternal grandsire and own performance) were simulated for each trait group. The contrasting scenarios were designed by varying bull dam information. Heifer records, and 1<sup>st</sup> and 2<sup>nd</sup> lactation records, were included in own performance.

In total, 8 scenarios with varying amounts of phenotypic information for the bull dams were simulated using a deterministic approach (Table 1).

*Table 1.* Scenarios included in the first simulation study (Paper I), abbreviations and available information on bull dams

Scenario	Information known on bull dam
Ped	Only pedigree index, based on traits recorded in the field
Р	Protein yield
PF	Protein and fertility
PU	Protein and udder health
PFU	Protein, fertility and udder health
PFUAd	Protein, fertility, udder health and additional records on fertility and udder health
PFURes	Restricted index, based on the same information as in scenario PFU
PFUAdRes	Restricted index, based on same information as in scenario PFUAd

The breeding goal consisted of protein yield, female fertility and udder health, and it was fixed for all scenarios. The breeding goal traits were ascribed economic weight from NAV, with some adaptations.

The recorded traits were divided into field-recorded traits (traits in the milk recording system) and additional nucleus-recorded traits. The field-recorded fertility traits were: pregnant at first insemination (PFI), interval between calving and first insemination (CFI), reproductive disorders (RD); and udder health traits were clinical mastitis (CM), lactation somatic cell score (LSCS), and the two udder conformation traits fore udder attachment (FUA) and udder depth (UD). The additional traits recorded on the bull dam candidates in the nucleus herd were: heat intensity, progesterone, CFI with doubled heritability and CM and LSCS with higher heritability than recorded in the field.

The genetic and phenotypic correlations, the heritabilities and the phenotypic standard deviations for all traits were either average values – based on literature review or (when the realistic values were not available) assumptions. The genetic correlation matrix was converted into a positive definite matrix by applying a bending procedure.

The phenotypic information on protein yield, fertility and udder health in each scenario was combined into an index using b-values, the phenotypic measures, and additive genetic covariances between the index traits and the breeding goal traits.

Total genetic gain in monetary units, the genetic gain in single traits in genetic standard deviation units, and the accuracy of the selection index, were all calculated using the general equations for one round of selection considering only bull dams.

Furthermore, bull dam total weights were derived using restricted index theory (Brascamp, 1984) to set the genetic response in specific functional traits to zero. The restriction index was applied for 4 fertility traits and 2 udder health traits in two scenarios with or without the additional records from the nucleus herd.

4.1.2 The data analysis and the estimation of genetic trends in Swedish Red Dairy Cattle (Paper II)

The dataset, including phenotypic records on female fertility (NINS; CFI), udder health (CM; SCS) and conformation (UD; UA) and protein yield (PY), as well as the pedigree data, was provided by the Swedish Dairy Association. In general, phenotypic records were available from 1990 to 2007, with a few exceptions; heifer NINS data were available from 1989, and udder conformation data covered 1992-2007. The pedigree data were created using a sire-dam structure which was traced back as many generations as possible.

Variance components were estimated before genetic trends. The dataset covering the first ten years of the given time period and three lactations for each trait was used in the analysis. Only progeny information on AI-bulls was included in the dataset, and therefore all bulls with progeny in less than ten herds were excluded. Animal models were used to estimate the variance components, and (co)variance for the genetic trend estimations were calculated with the AI-algorithm in the DMU-package (Madsen & Jensen, 2000).

Breeding values were estimated with the DMU5 software (Madsen & Jensen, 2000). The full datasets for cows and heifers were used in these estimations. Genetic trends were estimated for AI-bulls and cows using both a full multi trait model and the model where the traits were sorted into three

groups (protein, fertility and udder health). The trends were estimated with and without heifer data.

Spearman rank correlations were estimated between indices from the evaluation with a full multiple-trait model and from trait-wise multiple-trait models. Bulls and cows were ranked on the basis of their breeding values for each goal trait from evaluations from these two models.

# 4.1.3 Experimental design and data analysis of breeding schemes to reduce environmental impact (Paper III)

The breeding goal consisted of 3 traits: milk production (MP), functional trait (FT) and environmental impact (EI). EI was a new trait defined as total enteric GHG emissions from the cow including the heifer period per lifetime of milk production. EI was given the same economic value as MP ( $\in$ 83). Negative economic value was used because the aim was to reduce EI. It was assumed that phenotype records and genomic information were available for MP and FT, but not for EI. Instead, phenotype and genotype records of various indicator traits (IT) correlated with EI were used.

The indicator traits for EI were divided into three categories: large-scale, medium-scale and small-scale indicator traits. The large-scale traits were stayability (STAY) and stature (STAT) of the cow. The medium-scale traits were liveweight (LW) and GHG measured in the breath of the cow (BRH). The small-scale traits were residual feed intake (RFI) and methane measured in the respiration chambers (METH).

Six main scenarios were considered for simulation. In these scenarios, three traits were included in the breeding goal (MP, FT and EI) and three traits were recorded (MP, FT and IT). An additional scenario without an indicator trait was also simulated. Owing to uncertainty about the genetic parameters for the traits BRH and METH, additional scenarios including these traits were tested. These scenarios included unfavorable, neutral or favorable correlations between the indicator trait and MP and FT, and two levels of assumed accuracies (0.1 and 0.4) in the direct genomic values (DGV) for METH (Table 2).

The genetic parameters used for the breeding goal traits MP and FT were the same as those used in NAV. The genetic parameters for EI were assumptions based on a literature review in this field. It was assumed that EI was favorably correlated with MP, and FT, and has moderately high heritability. Also the genetic parameters of indicator traits either were based on real values obtained from the literature or were assumptions. The genetic correlations between EI and indicator traits were set to values that determined by how strongly IT was connected with enteric emissions of  $CH_4$ . DGVs were generated for all genotyped animals by modeling them as separate genomic traits. The heritability of each genomic trait was equal to 0.99 and a genetic correlation with the observed trait equal to the assumed accuracy of DGV. The accuracies of DGVs ( $r_{IA}$ ) were calculated using the method described by Goddard (2009). These calculations were used to achieve the  $r_{AI}$  for MP, FT, STAY, STAT, LW and BRH. The  $r_{AI}$  for RFI and METH were set to given values.

Table 2. Description of the scenarios in Paper II. Indicator traits, scale of recording, genetic correlations  $(r_g)$  between breeding goal traits and the indicator traits, heritabilities  $(h^2)$ , and accuracies of direct genomic values  $(r_{IA})$  used in scenarios<sup>1</sup>

Scenario	Indicator trait	$h^2$	r <sub>g</sub> EI	$r_g  \mathbf{MP}$	r <sub>g</sub> FT	$r_{IA}$
No IT	No indicator trait	-	-	-	-	-
Large-scale -	- milk recording herds					
STAY	Stayability	0.02	-0.30	0.20	0.20	0.67
STAT	Stature	0.40	0.10	0.35	0.10	0.72
Medium-scal	e – AMS herds					
LW	Liveweight	0.30	0.20	0.20	0.10	0.70
BRH <sub>F</sub>	Breath of the cow	0.20	0.50	-0.10	-0.10	0.69
BRH <sub>U</sub>	Breath of the cow	0.20	0.50	0.10	0.10	0.69
Small-scale – contractor herds						
RFI	Residual feed intake	0.35	0.60	-0.45	0.20	0.46
METH <sub>N4</sub>	Methane gas	0.25	0.80	-0.05	0.00	0.40
$METH_{F4}$	Methane gas	0.25	0.80	-0.20	-0.20	0.40
METH <sub>N1</sub>	Methane gas	0.25	0.80	-0.05	0.00	0.10
METH <sub>F1</sub>	Methane gas	0.25	0.80	-0.20	-0.20	0.10

<sup>1</sup> EI – environmental impact, MP – milk production, FT – functional traits.

The breeding scheme used in the simulations was selected as the best of four designs tested by Buch et al. (2011a). The main difference between this breeding scheme and a conventional one is that genotyped young bulls are intensively used in the breeding here. This results in a generation interval that is approximately half the length of that in a conventional breeding scheme.

The stochastic simulation program ADAM (Pedersen *et al.*, 2009) was used to test the scenarios for annual monetary gain, genetic gain per single trait, and rate of inbreeding. The period used in each scenario was 25 years. All scenarios were replicated 100 times. The results were averaged over years 11–25. Years 1–10 were excluded from the calculations to avoid noise caused by the establishment of the equilibrium of age structure and the Bulmer effect.

Fisher's Least Significant Difference (LSD) was used to assess whether the differences between scenarios were significant at 5% level.

# 4.1.4 Economic analysis of the breeding schemes to reduce the environmental impact (Paper IV)

In Paper IV, the same scenarios as those in Paper III were analyzed for discounted return (DR) and the breakeven price per record in the reference population with the deterministic simulation program ZPLAN (Willam *et al.*, 2008). A breeding scheme similar to the one in the previous study was used, with the difference that both breeding nucleus and commercial cow population were simulated. All bull dams and genotyped young bulls were selected within the genotyped females in the breeding nucleus. The young bulls were divided according to their GEBVs into young bulls and superior young bulls. The superior young bulls sired the next generation young bulls, bull dams and 75% of the commercial cows. The gene flow and the selection groups used are shown in Table 3.

 Table 3. Gene flow matrix used for the breeding scheme simulated in Paper IV.

 Selection groups

	Selection groups			
	Young bulls (YB)	Superior young bulls (S-YB)	Bull dams (BD)	Cows (HC)
YB		1. S-YB $\rightarrow$ YB	2. BD→YB	
S-YB		3. S-YB→S-YB	4. BD→S-YB	
BD		5. S-YB→BD	6. BD→BD	
HC	7. ҮВ→НС	8. S-YB→HC		9. HC→HC

Instead of accuracy of DGVs, half of the reliability of DGVs (used in Paper III) was used as the LD information and the parent average were handled separately in ZPLAN. The LD information was used to calculate progeny equivalents (additional daughter records) traits included in the selection index (Thomasen et al., 2013). The same prediction formula (Goddard, 2009) as that in the previous study was used to estimate the reliabilities of DGVs. However, a correction was made which changed the original numbers of animals and/or offspring per animal in the reference populations; this resulted in larger reference populations in Paper IV than those in Paper III.

The economic analysis was performed by calculating the difference between DR in scenarios with an indicator trait and scenario No IT, where no records on indicator trait were included. This difference was the additional gain in discounted return (AGDR). AGDR was then multiplied by the population size (250 000 cows) to get the maximum cost for recording a new trait (MCNT). To be more precise, MCNT is the amount that the recording of a new

28

trait may cost at a maximum if the same level of discounted profit is achieved as that in scenario No IT. MCNT was divided by the number of phenotype records for the indicator trait in the reference population to get the breakeven price per record in the reference population.

### 4.2 Main findings

#### 4.2.1 Genetic response in functional traits in bull dams

In Paper I, the genetic gains in functional traits and in protein yield were estimated using bull dam records from the nucleus herd. The genetic responses in fertility and udder health traits were unfavorable throughout the scenarios (Table 4). The additional records, or expanded recording of correlated indicator traits, resulted in additional gain in PY, but not in functional traits. The genetic response in CFI, for example, became more unfavorable when the nucleus-recorded CFI with doubled heritability was added to the index (scenario PFUAd). Restricting genetic change in functional traits (zero genetic change) decreased the genetic gain in protein yield from 0.7 to 0.5 genetic standard deviation units.

Scenario <sup>1</sup>							$Traits^2$							
	PFI 0	PFI 1	PFI 2	CFI 1	CFI 2	RD 0	RD 1	RD 2	CM 1	CM 2	PΥ 1	PY 2	ľHI	$\mathbf{S}_{\mathrm{H}}$
Ped	-0.09	-0.17	-0.17	0.17	0.16	-0.01	0.05	0.04	0.11	0.10	0.52	0.50	0.53	60.34
	-0.12	-0.24	-0.24	0.24	0.24	-0.01	0.08	0.08	0.16	0.16	0.70	0.69	0.72	81.94
Ц	-0.13	-0.25	-0.25	0.24	0.23	-0.01	0.08	0.07	0.16	0.16	0.71	0.70	0.72	82.21
U	-0.12	-0.24	-0.24	0.24	0.24	-0.01	0.08	0.08	0.22	0.21	0.72	0.71	0.73	82.90
PFU	-0.13	-0.25	-0.25	0.24	0.24	-0.01	0.08	0.07	0.18	0.18	0.72	0.70	0.73	82.81
PFUAd	-0.12	-0.24	-0.24	0.26	0.26	-0.01	0.08	0.08	0.22	0.22	0.73	0.72	0.74	83.73
PFURes <sup>3</sup>	0.08	0.00	0.00	0.00	0.00	-0.03	-0.01	-0.01	0.00	0.00	0.48	0.47	0.52	60.30
PFUAdRes <sup>3</sup>	0.07	0.00	0.00	0.00	0.00	-0.03	-0.01	-0.01	0.00	0.00	0.48	0.48	0.54	60.77

$\overset{(2)}{\sim}$ Table 4. Genetic response per generation (genetic standard deviation units) in field recorded traits, accuracy of the index ( $r_{H1}$ ) and total response ( $S_{H}$ ) in Euros depending on the amount of information used for bull dams (Paper I)
--

<sup>3</sup> Genetic change was restricted to zero for PFI1, PFI2, CFI1, CFI2, CM1 and CM2

4.2.2 Genetic trend in fertility estimated with multiple-trait model or trait-wise Estimated genetic trend for NINS in lactating cows was unfavorable (Figure 2). The same trend in heifers was neutral. Favorable genetic trend was discovered in CFI and in udder conformation traits. Also the estimated genetic trend in PY was favorable, as expected. Estimated genetic trend for CM and SCS differed for AI bulls and cows, being favorable in AI bulls and slightly unfavorable, or neutral, in cows (Figure 3). Estimated genetic trends differed between two used models. The genetic trend for NINS estimated with a full multiple-trait model was clearly more unfavorable than it was when a model including only fertility traits was used.



*Figure 2.* Genetic trends (mean EBVs in genetic SD units) for Swedish Red maiden heifers and cows with own records, estimated with full multiple-trait model (full) including all traits in the study and with trait-wise multiple-trait model (tw) including fertility traits only. NINS0, NINS1 and NINS2 are number of inseminations per service period in heifers, first lactation cows and second lactation cows, respectively.



*Figure 3.* Genetic trends (mean EBVs in genetic SD units) for first lactation traits in Swedish Red cows with own observations, estimated with full multiple-trait model including all traits in the study. PY = protein yield, CFI = calving to first insemination, CM = clinical mastitis, NINS = number of inseminations, SCS = somatic cell score, UA = fore udder attachment, UD = udder depth.

# 4.2.3 Genetic responses in breeding schemes aiming to reduce environmental impact

Annual monetary gain and genetic gain in MP, FT and EI were estimated. The highest annual monetary gain was achieved in scenario STAY. The annual monetary gain in scenarios with medium- or small-scale indicator traits varied from  $\notin$ 50.5 to  $\notin$ 47.5. The genetic gain in EI was favorable in all scenarios. However, the highest genetic gain in EI was observed in scenario BRH<sub>F</sub> where it was 34% higher than in scenario No IT (Table 5). The rate of inbreeding per generation varied from 0.66-0.73%, and was lowest in scenarios using METH as indicator trait and highest in scenario LW.

marked with a circle and the scenario with the lowest gain is marked with a square							
Scenario <sup>1</sup>	$\Delta G$	$\Delta G_{MP}$	$\Delta G_{FT}$	$\Delta G_{EI}$			
No IT	46.6	0.251	0.161	-0.152			
Large scale			_				
STAY	51.4	0.259	0.184	-0.180			
STAT	49.4	0.260	0.180	-0.160			
Medium scale							
LW	48.1	0.246	0.171	-0.166			
BRH <sub>F</sub>	50.5	0.238	0.171	-0.203			
$BRH_{\rm U}$	48.9	0.235	0.159	-0.198			
Small scale							
RFI	49.6	0.252	0.164	-0.183			
$\mathrm{METH}_{\mathrm{N4}}$	49.5	0.241	0.166	-0.192			
METH <sub>F4</sub>	49.8	0.242	0.171	-0.191			
${\rm METH}_{{ m N1}}$	47.5	0.246	0.174	-0.156			
$METH_{F1}$	47.7	0.247	0.173	-0.158			

Table 5. The annual genetic gain ( $\Delta G$ ) in  $\mathcal{E}$  and the genetic response in milk production ( $\Delta G_{MP}$ ), functional traits ( $\Delta G_{FT}$ ) and environmental impact ( $\Delta G_{EI}$ ) in genetic standard deviation units in the scenarios simulated in Paper III. The scenario with the highest gain is marked with a circle and the scenario with the lowest gain is marked with a square

<sup>1</sup>For abbreviations see Table 2.

### 4.2.4 Breakeven price per record in reference population

Breakeven prices per record in the reference population were estimated for scenarios with different indicator traits for EI. There were large differences in breakeven prices between the different scenarios. The largest amount of money could be spent on recording METH with low accuracy of DGVs. Breakeven price for investment in scenario BRH<sub>F</sub>, which was superior among all scenarios in genetic gain in EI, was €29.

Table 6. The discounted return (DR;  $\epsilon$ ) in all scenarios and the additional gain in discounted return (AGDR;  $\epsilon$ ) compared to scenario No IT, the maximum cost of recording new traits (MCNT;  $\epsilon$ ), and the breakeven price per phenotype record ( $\epsilon$ ) in the reference population and the number of phenotype records (NPR). The scenarios are sorted by the breakeven price

	~ 1	, ,		•	1
Scenario <sup>1</sup>	DR	AGDR	MCNT <sup>2</sup>	NPR	Breakeven price
No IT	283.0				
STAY	302.4	19.4	4,842,500	1,400,000	3
STAT	293.6	10.6	2,642,500	600,000	4
LW	295.7	12.7	3,167,500	195,000	16
$BRH_{\rm U}$	300.2	17.2	4,292,500	195,000	22
$BRH_F$	305.3	22.3	5,567,500	195,000	29
RFI	298.7	15.7	3,917,500	6,300	622
$\mathrm{METH}_{\mathrm{N4}}$	300.2	17.2	4,292,500	5,700	753
METH <sub>F4</sub>	302.5	19.5	4,867,500	5,700	854
$\mathrm{METH}_{\mathrm{F1}}$	294.2	11.2	2,792,500	250	11,170
METH <sub>N1</sub>	294.2	11.2	2,792,500	250	11,170

<sup>1</sup> For abbreviations see Table 2.

 $^2$  MCNT is calculated as following: AGDR x Population size (250 000 cows) and the breakeven price is a product of MCNT divided by the number of phenotype records (NPR) for the indicator trait.

### 5 General discussion

The research project reported in this thesis revolves around five hypotheses. In the following subsections, conclusions reached about these hypotheses as well as the connections between them are discussed.

### 5.1 Bull dam selection in the nucleus herds

Gathering the best females of the population into a nucleus herd for individual performance testing in the same environmental conditions and selecting the most superior cows as dams of sires was seen by the breeders as a good way to improve the selection of bull dams. There was, however, a realistic concern that the relatively short performance testing period would favor the selection of highly heritable traits. Therefore we tested the hypothesis that deterioration of functional traits due to bull dam selection in an open nucleus herd can be avoided by an expanded and improved system of recording fertility and udder health traits. By an improved and expanded recording system we mean that the nucleus environment can be used to perform phenotype registrations more precisely than in conventional herds (Mocquot, 1988). For example, trait CFI could be affected by different management decisions in the conventional herds. In the nucleus herd, the main goal is to uncover the genetic potential of the bull dam candidates, and therefore all cows are managed in the same way. Also the individual milk tests can be taken more frequently in the nucleus herds than is common followed in the routines of the national milk recoding system. Even introducing the recording of new indicator traits like progesterone could be done more easily in a nucleus herd. In our simulation study, we tested various scenarios with different amounts of information on the individual cow. On the basis of the results obtained from these simulations it was concluded that improved recording of functional traits on individual cows did not help to avoid the unfavorable genetic response in fertility and udder health traits.

Instead, the additional information on functional traits, helped to increase the genetic gain in protein yield.

In Paper I, the focus was on the individual cow and the way the selection of bull dams contributes to the total genetic response of the population. The genetic gains in functional traits found in bull dams might not be the same in the sire-son selection path. AI-bulls have much larger influence on the next generation cow population than bull dams (Van Tassell & Van Vleck, 1991). Thus, the unfavorable trends found in the simulation study may not occur in conventional herds in the current breeding scheme. In Paper II, genetic trends in functional traits in AI-bulls and cows were estimated.

### 5.2 Genetic trend estimated with different models

A multiple-trait model was used to estimate the total genetic progress of the current Nordic breeding goal and the gain per goal traits. The use of the multiple-trait model, and thus the inclusion of production traits with high heritability in the analysis, might have been the reason why unfavorable genetic gains in functional traits were achieved in Paper I. According to Teepker and Smith (1990) in such multiple-trait settings, a trait with high heritability will dominate, in the index, over less heritable traits such as the functional traits. However, multiple-trait model analysis is theoretically more accurate (Meuwissen & Woolliams, 1993). In Paper II, a multiple-trait and multiple-trait models with separate traits groups, were compared. The results confirmed that these models give somewhat different estimated genetic trends in functional traits. The model where traits are separated group-wise underestimated the genetic trend in functional traits. This is supported by Sun et al. (Sun et al., 2010), who also found that a multiple-trait model including both production and fertility traits was more precise in predicting the genetic trend in fertility traits. According to Buch et al. (2011b) the multiple-trait models are most valuable in the genetic evaluation of cows, because here the accuracy of genetic evaluations is higher due to the cow's own performance records. Moreover, the choice of sire or animal model determines the added value of a multiple-trait model. In sire-models the cow phenotype records are not included in the evaluation and therefore the multiple-trait analysis is of less value in combination with a sire model than it is with an animal model (Buch et al., 2011b).
### 5.3 The effect of using heifer fertility records

Accurate breeding values can be obtained only if many phenotype records on lowly heritable traits are available. Some of the fertility traits can be recorded on heifers, and these phenotype records could be applicable in genetic evaluation (Pryce et al., 2007). In both Paper I and Paper II, the phenotype records on heifers were included. In Paper I, heifer information on conception rate, heat intensity and reproductive disorders was included in the simulation. Favorable genetic gain was observed in reproductive disorders in heifers, and the genetic gain in conception rate was less unfavorable in heifers than it was in cows. However, the addition of heifer information to the index had no observable effect on genetic gain in fertility traits in cows was observed. Thus, the heifer information did not deliver additional indicator traits for fertility traits expressed and measured later in life. It was also found in Paper II, that the effect of adding information on fertility in heifers was small. This could be explained by moderate correlations between a trait recorded in heifers and the same trait recorded in first lactation cows. In Paper II, the genetic correlation between NINS in heifers and NINS in first lactation cows was 0.47. Roxtröm et al. (2001) found a higher genetic correlation between these traits (0.67). Still, when compared to the genetic correlations found between NINS in first and second lactation and second and third lactation, these correlations are much lower. The genetic correlation between the first and the second lactation was 0.88 in Paper II. Roxström et al. (2001) estimated correlations that were close to unity (0.94 and 0.93, between first and second and second, and third lactation, respectively). These correlations indicate that NINS in heifers is not the same trait as NINS in lactating cows. Similar patterns in genetic correlations in fertility traits between heifers and lactating cows were observed by Tiezzi et al. (2012). They concluded that heifer fertility and cow fertility are different traits, and that the former is not a good indicator of the latter. Physiological requirements in heifers and cows are different. A heifer does not need to spend energy on production, and she is not in negative energy balance as lactating cows often are in the beginning of their lactation (Leroy et al., 2008). Cows' increased expenditure of body reserves has negative effect on fertility and may delay their ability to conceive (Pryce et al., 2004).

## 5.4 Environmental impact as a goal trait

In Paper III, EI was expressed as total enteric GHG emissions from the cow including the heifer period per lifetime milk production. Enteric emissions from cows are often given in kg per kg of milk – a measure sometimes referred to as emission intensity (Cottle *et al.*, 2011). According to Garnsworthy (2011)

lifetime production efficiency is the main driver for environmental impact of cattle. It is important to consider both the heifer period and maintenance requirements when calculating the emissions per output (Garnsworthy, 2011). Methane emissions can also be expressed as total emissions from the dairy sector, farm or animal, or methane yield, which is g methane per kg of feed (Hegarty & McEwan, 2010).

Selection for reduced EI by using a correlated indicator trait was successful in terms of genetic gain. Even a scenario without EI in the breeding goal (thus reflecting the current breeding goal) resulted in favorable genetic gain in EI. This is mainly due to favorable, and moderate, correlations between EI and MP, and between EI and FT. The true correlations between EI and the other breeding goal traits are as yet unknown. However, it is reasonable to assume that these correlations are indeed favorable. There are studies that emphasize the favorable connections between lower CH<sub>4</sub> emissions and increased level of productivity as well as improved fertility and health (Bell *et al.*, 2011; Wall *et al.*, 2010; Garnsworthy, 2004). Garnsworthy (2011) presented results showing that the good fertility and increased lifetime decreases considerably the amount of CH<sub>4</sub> produced per kg of milk. He also emphasized that in order to reduce the environmental impact of milk production systems it is important to reduce the wastage in form of early culling of cows with poor fertility and disease.

In Paper III, EI was defined as a trait that included the enteric  $CH_4$  emissions and other GHG emissions from a dairy cow, such as  $CO_2$ ,  $N_2O$  and ammonia ( $NH_3$ ). Environmental impact as such is not only about GHG emissions. It may also include the excretion of nitrogen and phosphorus, and the use of fossil energy or cultivated land (Garnsworthy, 2011; Janzen, 2011).

## 5.5 Genetic gain in environmental impact

The hypothesis that specific indicator traits recorded in a small number of contractor herds can be implemented in breeding schemes with genomic selection with a favorable outcome was tested in Paper III. The simulation showed, however, that annual monetary genetic gain was highest in the scenario which included an indicator trait recorded on a large scale (STAY), and this was despite the low heritability of this indicator trait and the modest correlation between EI and the indicator trait. Nevertheless, the genetic gain in environmental impact was highest in scenarios including an indicator trait with a high correlation with the breeding goal trait EI and high accuracy of direct genomic breeding values. The annual monetary gains were somewhat lower in these scenarios than they were in the best large-scale scenario, but they were still significantly higher than in the scenario that did not include any indicator

trait for the environment. So genetic progress in EI is possible when specific indicator traits are used; however, it requires a reference population of adequate size so that the accuracies of direct genomic breeding values are reasonably high. In this study the indicator traits were related to environmental impact, but the simulated results are valid for any trait that has a moderate heritability but is complicated to record: for example, coagulation properties of milk, or energy balance in cows.

#### 5.6 Indicator traits for environmental impact

It was assumed that EI was not recorded in any herd, i.e. that no phenotype records were available for EI. Instead, correlated indicator traits were used. As EI mainly represented enteric CH<sub>4</sub> emissions from dairy cows, it was natural that the highest genetic correlation (0.80) was simulated between EI and CH<sub>4</sub> measured in the respiration chambers. The respiration chambers are the most favored and precise technology for measuring any gas emission from animals. The chambers are also used for individual recording of feed intake. The air flow to and from the chamber is monitored, and the composition of air entering in and leaving from the chamber is measured in gas sensors (Storm *et al.*, 2012). The weaknesses of the respiration chambers are that they have very limited testing capacity (being applied to one animal at a time) and the fact that their construction demands substantial investments (Storm *et al.*, 2012). The cost and complexity of recording, and the relatively small number of phenotype records are the main reasons why no real estimates of heritabilities for enteric CH<sub>4</sub>, or correlations between this trait and production (or other traits), are available. De Haas et al. (2011) used feed intake and information on energy requirements to predict methane emissions. They estimated a heritability of 0.35 for predicted methane emissions, and its phenotypic correlation to dry matter intake was close to unity (0.99).

There are, however, alternative technologies to measure  $CH_4$  emissions from individual animals. One of them is the Fourier transform infrared method. This measures gases in the breath of the cow during milking (Lassen *et al.*, 2012). It is used mainly in the automated milking systems (AMS), as here only one or two devices are needed to measure the emissions from all of the lactating cows in the herd. Lassen et al. (2012) measured  $CH_4$  and  $CO_2$ emissions from two Danish cattle breeds. They calculated the repeatability of  $CH_4 - CO_2$  ratio to be 0.39 in Holsteins and 0.34 in Jerseys, which indicates that breath data could be feasible for use in genetic evaluation. They also found favorable correlations between feed intake and  $CH_4$ , but no correlation was found with milk production. In Paper III, both unfavorable and favorable

correlations were used between breath measurements and milk production and functional traits, and a correlation of 0.50 between EI and  $CH_4$  in recorded in breath. As more data on GHG emissions from breath become available, accurate correlations can be estimated. Whatever the direction of the correlations turns out to be, this technique has a potential to provide an adequate number of accurate phenotype records of the sort needed to breed for reduced environmental impact, especially if the heritability of  $CH_4$  measured in breath is moderately high, as first estimated by Lassen (2011).

Environmental impact also has high genetic correlation with feed intake and feed conversion ability, since a major part of cultivated land is used for feed production (Janzen, 2011). Furthermore, enteric  $CH_4$  is affected by feed intake (Hegarty et al., 2010; Hegarty & McEwan, 2010). Residual feed intake (RFI) was used as representative of feed efficiency in Paper III. RFI is reported to be a trait with moderately high heritability (de Haas et al., 2011; Waghorn & Hegarty, 2011; Herd, 2008). The genetic correlation used between EI and RFI in Paper III was 0.60. De Haas estimated genetic correlations between RFI and predicted methane emissions measured at different lactation stages that varied from 0.18 to 0.84 and were highest at the beginning of lactation. A negative favorable genetic correlation between RFI and MP and a positive unfavorable correlation between RFI and FT were used in our simulation study. Very few studies have reported genetic relationships between RFI and milk production, and RFI and functional traits. De Haas et al. (2011) presented a negative genetic correlation between RFI and fat and protein corrected milk. Herd and Arthur (2009) studied the physiological aspects of RFI in beef cattle and found that animals with low RFI had less body fat. This might have negative effects on female fertility (Waghorn & Hegarty, 2011). It is reasonable to suppose that these results can be extrapolated to dairy cattle. A moderately strong genetic relationship between female fertility and body condition score has been reported in several studies (de Haas et al., 2007b; Pryce & Harris, 2006; Veerkamp et al., 2001).

In a contrast with beef cattle, increasing body size (liveweight and stature) in dairy cattle is considered negative for the environment. Maintenance requirements depend of the body weight of the animal. In pursuit of the aim of reducing the CH<sub>4</sub> emissions, therefore increased efficiency due to lower energy requirements for maintenance has been proposed (Yan *et al.*, 2010). However, physiological aspects of production level, body size and energy efficiency are complicated. Stature tends to have moderate to high heritabilities and a favorable correlation with production, meaning that larger cows have higher milk yields (de Haas *et al.*, 2007a). The challenge is to keep the optimal size and body weight of the dairy cow as well as a high level of production.

<sup>40</sup> 

In the simulation study (Paper III), stature and live weight were recorded in different ways. Stature was assumed to be recorded on first lactation cows in herds participating in national milk recording. Live weight was assumed to be recorded in the AMS herds with the weighing scales used to weigh the cows. With information about stature and heart girth, it is possible to calculate the body weight rather accurately. However, by weighing cows regularly, changes in live weight can be monitored precisely. This would be a good management tool for feeding decisions. Moreover, avoiding overfeeding of, especially, the dry cows and pregnant heifers is beneficial for both farm efficiency and the environment.

The large-scale indicator trait, stayability, represented the longevity of the cows. Longevity in cows has been reported to be beneficial for the environment (Bell *et al.*, 2011; Garnsworthy, 2011). This is mainly due to the fact that cows continue to have an impact on the environment when they are not producing milk, i.e. during heifer period and in dry periods between lactations. The total amount of methane emitted per lifetime milk production decreases significantly if the cow produces milk for multiple lactations (Garnsworthy, 2011). Another way in which longevity can reduce the environmental impact is through fertility and health. Poor fertility and udder health problems are the most common causes of involuntary culling in cows (Ahlman *et al.*, 2011). Good fertility in dairy cows reduces the need for replacement heifers and thereby also the total GHG emissions at the farm level (Garnsworthy, 2004). Longevity is included in the Nordic breeding goal with an economic weight that is about 3% of the total economic weight of the breeding goal (Hans Stålhammar, Viking Genetics, personal communication).

## 5.7 Specialized recording herds

The hypothesis was that specific indicator traits of environmental impact recorded in contractor herds can be implemented in breeding schemes with genomic selection in order to reduce the environmental impact of milk production. Contractor herds are specialized herds where very specific indicator traits are recorded, that cannot be recorded in connection to monthly milk-testing in the large-scale milk recording scheme. Recording these traits requires equipment that is often very expensive; also using them presumes advanced knowledge in this field. In Paper III, we divided the indicator traits into three groups, of which two would require contractor herds to be established. The medium-scale and small-scale indicator traits had different equipment requirements. To record liveweight, for example, the investment in a weighing scale required is not very large. However, planning of cow traffic

and a certain amount of extra labor is still needed, so it cannot be expected that all farmers would be willing to weigh their animals. In AMS herds the cow traffic is already controlled, and here the installation of a digital weighing scale would be rather simple. The equipment to measure the second medium-scale trait, GHG in the breath of the cow, is designed to be used in AMS herds. Currently, it is in the research phase, and high costs are connected with it. Still, the breath-recording technique has the potential to be implemented in practice for monitoring GHG emissions and feed efficiency (J. Lassen, Department of Molecular Biology and Genetics, Aarhus University, Denmark, personal communication).

The recording of the small-scale indicator traits RFI and METH, on the other hand, requires equipment such as individual feeding stations or respiration chambers (Hellwing *et al.*, 2012). Modern developments in respiration chambers have lowered their construction costs (Hellwing *et al.*, 2012), and they can also be used for measuring other aspects of nutrition and feeding (Storm *et al.*, 2012). Even so, they will most probably remain confined to research herds or nucleus herds. Very probably, there will be more collaboration between countries to unite the datasets and make the most use of data collected in respirations chambers.

Schaeffer (2006) was the first to propose using cooperator herds in breeding programs with genomic selection. There this approach was mainly orientated towards genotyping all cows and recording already known and also novel traits, as well as ensuring the reference population where haplotype interval effects could be re-estimated (Schaeffer, 2006). Such a web of contractor herds could also become a breeding nucleus from which dams of young bulls are selected (Schaeffer, 2006). The current situation of nucleus herds is, however, different. Their role changed with the implementation of genomic selection. Individual performance testing of bull dams was no longer of interest. One of the benefits of nucleus herds was the effective use of MOET. It has been shown that use of MOET in bull dams increases the genetic gain even in breeding programs with genomic selection (Pedersen et al., 2012). The breeding scheme suggested by Schaeffer (2006) could still become a reality. One driver for this may be the need to have a contractor herds for recoding new traits, but it is more likely that such a network of herds could be established to genotype cows and create a cow reference population (H. Stålhammar, Viking Genetics, personal communication).

### 5.8 Breakeven prices

The objective was to evaluate the breeding scheme with genomic selection, and with a specific indicator trait for environmental impact, in terms of annual monetary genetic gain and the maximum recording cost per record in the reference population. The recording of a new trait will generate an additional cost that has to be added to the total cost of a national breeding program. We have only investigated the room for investment for the new indicator traits and not the total cost of a breeding program. We calculated the breakeven price that can, at a maximum, be invested per record of a new indicator trait to avoid falling below the profit in scenario No IT. If the recording cost per record is in practice lower than this breakeven price, additional profit will be the result. One should remember, however, that this breakeven price per record depends on the level of economic value for EI, and on the population size. In this study EI had the same economic value as MP in the main scenarios. The variation of economic values for EI showed how the breakeven price changes as economic value changes. This is obviously caused by changes in DR against a background of fixed size in the reference population. Population size is another important parameter in calculations of the breakeven price. We used a population size of 250 000 cows. When population size is increased the maximum cost for recording a new trait increases as well, which results in a higher breakeven price (i.e. a greater room for investment).

Since accurate estimates of the cost of recording new traits are not available, the evaluation of discounted returns of the breeding goal is the most efficient way to measure the feasibility of investing in a recording system for a new trait. The discounted return shows the economic revenue from the breeding scheme; it presents a comparison with the original situation (No IT). Similar analyze of returns have been performed to evaluate breeding programs which invest in new, advanced breeding technologies like genomic selection or cloning (Butler & Wolf, 2010; König *et al.*, 2009).

From one scenario to another, the breakeven price per record in the reference population varied considerably. Scenarios with high annual monetary gain and high genetic gain in EI resulted in lower breakeven prices than scenarios with small genetic response, since more phenotype records were needed in the former. Given this, it would be valuable to know what the marginal benefit of the additional genetic gain in EI is, i.e. how much dairy cattle breeders are willing to invest to achieve the high level of genetic gain. Sometimes it is worth settling for less genetic progress at lower cost; sometimes the best course is to find alternative ways contain the investment requirements.

Anyway, it is important to optimize the number of phenotype records and the size of the reference population. The number of phenotyped animals had a major effect on breakeven prices. To achieve large genetic response, the reliabilities of DGVs had to be high. Thus, more records in the reference population were required. In terms of annual monetary gain or genetic gain per single trait it makes no difference how many animals are included in the reference population in order to achieve the relevant level of reliability; from an economic perspective, however, this does make a significant difference. How a reference population for new traits should be designed has been discussed by Buch et al. (2012), Pszczola et al. (2012) and Calus et al. (2013). The reference population could be composed either of proven bulls with daughter information or genotyped cows with own records or a combination. For a new trait that is complicated and expensive to record the number of phenotype records should be as low as possible; this should keep the cost low but still be sufficient to gain the desired level of DGV reliability. Using genotyped cows with own phenotypes in the reference population reduced the total number of phenotype records needed to gain a certain level of reliability and increased the room for investment. However, with this approach, more animals have to be genotyped. We did not account for the costs of genotyping, and we used the same number of markers for both bulls and cows. Hence genotyping costs should be deducted from the breakeven price when the result is being evaluated.

#### 5.9 Choice of economic values

Economic values for breeding goal traits have an important role in this thesis. Current economic values used in NAV were adopted for all relevant traits used in the various analyses. In Paper III and Paper IV, a new trait was added in the breeding goal; this was given the same economic value as the milk production trait.

Genetic gains in functional traits were seen to be unfavorable in Paper I, meaning that the economic weights used in the selection index were too low to prevent the functional traits from deteriorating. Only the bull dam selection path was simulated, and it was not investigated if the economic values for functional traits were too low also in other selection paths. In Paper II, it was confirmed, however, that the economic value of trait NINS is too low to avoid the deterioration of this trait in the current breeding program. In Paper I, new bull dam total weights were derived in order to ensure the genetic gain in fertility and udder health was equal with zero. The derived weights were much higher than the economic weights initially used. These results suggest that

<sup>44</sup> 

when we are selecting bull dams in a nucleus herd, more weight should be put on functional traits. The economic values used in breeding goals are mostly derived to maximize the profit of dairy production in a rather short-term perspective (Groen *et al.*, 1997). In discussions about how to increase the sustainability of milk production it has been proposed that additional weight should be added to traits that are important for animal health and welfare (Olesen *et al.*, 2000). Using both market and non-market values for traits in breeding goals is an option for sustainable animal breeding (Nielsen *et al.*, 2005).

Improved fertility and udder health generate direct income through lower veterinary and insemination costs and are therefore important to farmers. Environmental impact, on the other hand, has no money attached to it, at least not in a short-term perspective. The economic value used for EI in the simulations was an assumption. As things are currently, there is no benefit for the farmer in reducing environmental impact. However, global warming and other environmental issues are already a reality. Political decisions, internationally and nationally, together with society's engagement in this matter, might in the future generate an economic (market or nonmarket) value for environmental impact.

#### 5.10 Future perspectives of sustainable breeding

It is often observed that agriculture has a major impact on the environment. Beef and dairy industries are often criticized for their emissions of enteric  $CH_4$ . At the same time the world human population is growing rapidly, and along with that demand for food is also rising (FAO, 2011b). There is a huge imbalance in food accessibility around the world. Poverty and hunger are increasing in many parts of the world, while millions of tons of food are wasted annually worldwide (FAO, 2011a). These are serious concerns globally.

According to FAO (2011b) the growth-rate of agricultural production in general is slowing down, in spite the growing demand for food. Moreover, agricultural production will have to increase by 70% by 2050 to cope with expected increase in food consumption levels (FAO, 2011b). Consumption of meat and dairy products will continue to increase; and meat consumption, especially, may double by 2050, particularly in the developing countries (FAO, 2011b). The increasing need for food, on the one hand, and the impact on the environment including, global warming, water pollution, and the use of pesticides and antibiotics, on the other, renders the role of the beef and dairy industries in sustainable food production very contradictory.

It is not news that the natural resources like arable land and fresh water are very limited (Janzen, 2011). The world cattle population is nearly 1.4 billion and it is expected to increase (FAO, 2009). A large proportion of the world's cattle population is made up of low-producing or unproductive animals (FAO, 2009). Of course, cattle production has different prerequisites in different parts of world, and it cannot be expected that high production will be possible in all environmental conditions. However, there is also a lot of waste and inefficient use of available resources. The keywords for sustainable future livestock production are improved productivity and efficiency.

Breeding has an important role in improving both productivity and efficiency; the challenge is to do it in a sustainable way. Future breeding goals will probably include more traits in an effort to cover the many aspects of cattle production. There will be more emphasis on functional traits, animal welfare and environmental impact. It is most likely that the proportion of the total economic weight placed on functional traits will increase.

# 6 Conclusions

The main conclusions of this thesis are as follows:

- Bull dams can be selected for functional traits in a nucleus herd, but such selection will require very high total (economic and non-market) weights for functional traits if undesirable genetic gain in these traits in the bull dam selection path is to be avoided.
- The introduction of new indicator traits, and of more advanced recording methods for functional traits, does not halt the deterioration of functional traits in multiple-trait settings when the main constituent of economic weight is still placed on protein yield and the functional traits are also recorded in the field and used in the progeny testing of AI bulls.
- The estimated genetic trends for number of inseminations in lactating cows are unfavorable in Swedish Red dairy cattle. In heifers the genetic trend was flat. The estimated genetic trends for interval from calving to first insemination and for clinical mastitis are neutral to favorable.
- The choice of model for genetic evaluation influences the estimate of genetic trend in some functional traits. Unfavorable genetic trends may not be discovered unless the traits are evaluated in a multiple-trait model including functional and production traits.
- Breeding goals including production and functional traits are beneficial for the environment. However, by including environmental impact in the breeding goal, and by using phenotype records and genomic information of correlated indicator traits, genetic gain in environmental impact can be enhanced significantly.
- ➤ The most valuable indicator traits for reducing environmental impact are those with a high genetic correlation (lrg≥0.3) with environmental impact that also have high accuracy of direct genomic values. Therefore, it is

important to establish a reference population that is large enough to permit adequate accuracies of direct genomic breeding values to be estimated.

- The low accuracy of direct genomic values of an indicator trait recorded on a small scale resulted in no additional genetic gain in environmental impact when a comparison was made with a scenario with no indicator trait, and this was despite a high correlation between the breeding goal trait and the indicator trait.
- The use of stayability as an indicator trait for environmental impact is beneficial genetically and economically, because it resulted in moderately high genetic gain in environmental impact, and because the recording of stayability does not generate any extra costs.
- Ideally the recording a specific indicator trait for EI will take place when: 1) the genetic correlation between IT and EI is high; 2) the reliability of direct genomic values is moderately high; and 3) the number of phenotype records for an indicator trait is optimal thus generates the desired reliability of direct genomic values.
- The design of the reference population has a substantial effect on breakeven price. In this study, a reference population consisting of genotyped cows with own phenotype records increased the breakeven price considerably. In other words, there is more room for investment in recording equipment when a cow reference population is used instead of a reference population of progeny-tested bulls.

# 7 Future research

Breeding goals for dairy cattle include more and more traits. There is still a long way to go towards sustainable milk production. Today, there is no consideration of environmental impact in the breeding goals. However, research into the best solutions in this respect has started. Novel developments such as the implementation of genomic selection can provide solutions that make the milk production more sustainable. The focus will be on the following objectives.

- Recording methane emissions and estimating accurate genetic parameters between this trait and the other traits in the breeding goal. Here it would be especially interesting to discover what the correlations between enteric methane emissions and functional traits such as female fertility are.
- Recording feed efficiency and estimating accurate genetic parameters between this trait and the other traits in the breeding goal.
- Derivation of economic values for novel traits.
- Composition of the reference population for current breeding goal traits and novel traits in particularly in medium- and small-sized breeds such as Nordic Red Cattle. An optimal design of the reference population is essential to find the balance between accuracy of genomic enhanced breeding values and cost of the breeding program.

# 8 Avel för hållbar mjölkproduktion – från kärnbesättningar till genomisk information

#### 8.1 Bakgrund

Avelsarbete för mer hållbar mjölkproduktion har blivit ett aktuellt ämne inom branschen. Det beror dels på samhällets ökande intresse för djurvälfärd och miljöfrågor och dels på allt högre produktionskostnader och låga avräkningspriser på mjölk.

De senaste åren har avelsföretagen börjat tillämpa genomisk avelsvärdering som ska ge större framsteg i avelsarbetet. Vid genomisk avelsvärdering används både egenskapsregistreringar och information om djurens DNA för att skatta avelsvärden. Genomisk avelsvärdering kan leda till snabbare genetiskt förändring eftersom även unga djurs avelsvärde kan skattas med stor säkerhet vilket minskar generationsintervallet. Genomisk avelsvärdering har visat sig mycket användbart för de egenskaper som redan är med i avelsprogrammet, och det kan även vara ett effektivt verktyg för att förbättra nya egenskaper som är svåra att registrera, så som fodereffektivitet och metangasutsläpp.

Det övergripande syftet med detta doktorandprojekt var att studera hur avelsprogram för mjölkkor bör utformas för att undvika försämring av de egenskaperna (reproduktion funktionella och hälsa) samt minska mjölkproduktionens miljöpåverkan. De specifika målen var att ta fram ny kunskap om: 1) hur urvalet av tjurmödrar i en kärnbesättning bör utföras för att ge ett genetiskt framsteg i såväl mjölkproduktion som funktionella egenskaper med låg arvbarhet, 2) hur de genetiska trenderna för funktionella egenskaper ser ut i dagens avelsprogram, 3) hur genomisk avelsvärdering och specialiserade mätbesättningar kan användas för att förbättra egenskaper som är dyra att registrera, som till exempel metangasutsläpp, och 4) det ekonomiska

utrymmet för att registrera sådana nya egenskaper i avelsprogram där genomisk avelsvärdering används.

### 8.2 Sammanfattning av studierna

Denna avhandling baseras på fyra studier varav tre är simuleringsstudier och i en studie har data från Svensk Mjölk använts. I den första artikeln studerades ett avelsprogram där tjurmödrar selekteras i en speciell besättning som kallas kärnbesättning. Tjurmödrarna väljs ut bland de kor som har kalvat två gånger. För att förstärka urvalet för de funktionella egenskaperna fruktsamhet och juverhälsa användes utvidgade registreringar av dessa egenskaper. Ett exempel på en sådan extra registrering är progesteronvärdet i mjölken som beskriver kons ägglossning. Sex scenarion med varierande mängd information om kons egen prestation i mjölkproduktion, fruktsamhetsegenskaper och juverhälsa studerades i en statistisk analys. Resultaten visade att trots utvidgade registreringar av fruktsamhet och juverhälsa så tog mjölkproduktionen över, vilket resulterade i en genetisk försämring av fruktsamhet och juverhälsa. För att balansera selektionstrycket mellan olika egenskaper används ekonomiska vikter. De ekonomiska vikter som används för fruktsamhet och juverhälsa i dagens avelsprogram tycks vara för låga. De ekonomiska vikterna för tjurmödrar som skulle behövas för att förhindra en försämring av fruktsamhet och juverhälsa var betydligt högre än de som används idag. Den viktigaste slutsatsen var att urval av tjurmödrar i en kärnbesättning bara fungerar bra om högre ekonomisk vikt läggs på de funktionella egenskaperna. En genetisk försämring kan inte undvikas enbart med hjälp av utvidgade registreringar av funktionella egenskaper.

I den andra studien var huvudsyftet att studera de genetiska trenderna i funktionella egenskaper hos svenska SRB-kor i kokontrollen, för att se om de ogynnsamma genetiska förändringarna som skattades i första studien också är påtagliga i praktiken. Data från kokontrollen innehöll kvigdata och information från kornas tre första laktationer. Två olika modeller för att skatta de genetiska trenderna jämfördes. I den första modellen analyserades alla egenskaper som är med i avelsvärderingen (mjölkproduktion, fruktsamhetsegenskaper, juverhälsa och juverexteriör) samtidigt. I den andra modellen analyserades varje egenskapsgrupp för sig. Hypotesen var att modellen som har med alla egenskaper samtidigt ger en mer sann skattning av genetiska trender, eftersom den tar hänsyn till sambanden mellan egenskaperna. När olika egenskaper analyseras var för sig kommer inte de ogynnsamma sambanden mellan mjölkproduktion och funktionella egenskaper fram. Den genetiska trenden för egenskapen antal inseminationer per dräktighet var ogynnsam för kor och

neutral för kvigor. Modellen med alla egenskaper visade på en större försämring än vad modellen med egenskapsgrupper gjorde. De genetiska trenderna för juverhälsa (klinisk mastit och celltal) samt antalet dagar mellan kalvning och första insemination var svagt ogynnsamma eller neutrala för kor och gynnsamma för avkommeprövade tjurar.

I studie III och IV studerades genetiska och ekonomiska möjligheter med ett avelsprogram som använder sig av genomisk avelsvärdering och specialiserade mätbesättningar för registrering av egenskaper som beskriver mjölkproduktionens miljöpåverkan. Olika egenskaper som skulle kunna registreras, så kallade indikatoregenskaper, användes i simuleringarna. I studien ingick sex olika indikatoregenskaper. Två egenskaper som registreras rutinmässigt i kokontrollen var kons hållbarhet (utslagen eller inte efter första laktationen) och kroppsstorlek (korshöjd). Två egenskaper som skulle kunna registreras i besättningar med mjölkrobot var kons vikt och metangasproduktion, den senare mätt i kons utandningsluft under mjölkningen. Två komplicerade egenskaper som bara skulle kunna registreras i speciella besättningar var metangas mätt i klimatkammare samt ett mått på foderutnyttjande. Varje scenario bestod av tre avelsmålsegenskaper (mjölkproduktion, funktionell egenskap och miljöpåverkan). I varje scenario mättes mjölkproduktion, en funktionell egenskap och en indikatoregenskap för miljöpåverkan. Utöver detta scenario med tre målegenskaper men utan någon indikatoregenskap för miljöpåverkan och ett scenario innehöll endast två målegenskaper, mjölkproduktion och funktionell egenskap. Det scenariot representerar det nuvarande avelsmålet som inte innehåller någon miljöegenskap. För mjölkproduktion och den funktionella egenskapen användes de ekonomiska vikter som används i den nordiska avelsvärderingen idag. Miljöpåverkan fick en negativ ekonomisk vikt (för minskad miljöpåverkan) som var lika stor som den ekonomiska vikten som användes för mjölkproduktion. De sanna genetiska sambanden mellan alla nya indikatoregenskaper och målegenskaperna är ännu inte kända. Därför simulerades både gynnsamma och ogynnsamma samband mellan olika egenskaper. Dessutom varierades säkerheten för de genomiska avelsvärdena för metangas mätt i klimatkammare, eftersom det idag är svårt att förutse hur säkra dessa avelsvärden skulle kunna bli. I studie III användes en så kallad stokastisk simulering, vilket innebär att en effekt av slumpen tas med i simuleringen och att utfallet i varje scenario simuleras många gånger. Det totala värdet av det årliga totala genetiska framsteget skattades i euro. Dessutom skattades det genetiska framsteget i var och en av målegenskaperna. Resultaten visade att det totala genetiska framsteget var högst i det scenario som använde hållbarhet som indikatoregenskap. Den genetiska förändringen i

miljöpåverkan var gynnsam i alla scenarion (minskad miljöpåverkan), även i det scenario som efterliknade det nuvarande avelsmålet. Det genetiska framsteget miljöpåverkan var dock betydligt högre när miljöpåverkan var med i avelsmålet och sådana indikatoregenskaper som metangas mätt i mjölkrobot eller metangas mätt i klimatkammare användes.

I den fjärde studien simulerades samma scenarion som i studie III, men med ett deterministiskt datorprogram. I en deterministisk simulering ingår ingen resultaten beräknas enligt de formler slump utan som finns i simuleringsprogrammet. Syftet med studie IV var att utvärdera hur stort det ekonomiska utrymmet är för registrering av specifika indikatoregenskaper för miljöpåverkan. En nollpunktsanalys genomfördes för att räkna ut hur mycket pengar registreringen av en ny egenskap får kosta utan att underskrida vinsten i ett grundscenario där ingen indikatoregenskap för miljöpåverkan registreras. I detta grundscenario har alltså dagens avelsmål utökats med en ny målegenskap för minskad miljöpåverkan, men inga nya registreringar görs. Det ekonomiska utrymmet för registrering var störst i det scenario som innehöll metangas mätt i klimatkammare där genomiska avelsvärden med låg säkerhet användes. Ju färre registreringar som görs desto lägre blir säkerheten för det genomiska avelsvärdet. Med få registreringar kan varje registrering få kosta mer och därför var det ekonomiska utrymmet störst i detta scenario. Men eftersom det genetiska framsteget i miljöpåverkan var lågt är detta scenario inte ett bra alternativ. Betydligt mindre pengar per registrering kan spenderas på registrering av hållbarhet och korshöjd samt levande vikt och metangas mätt i mjölkrobot, eftersom dessa registreringar görs på många fler kor. I praktiken kräver hållbarhet och korshöjd inga nya investeringar för att bli registrerade. Scenariot med hållbarhet resulterade dessutom i ett stort genetiskt framsteg i miljöpåverkan. Hållbarhet verkar därför mycket lovande som indikatoregenskap i ett avelsarbete för minskad miljöpåverkan. Aven metangas mätt i mjölkrobot kan vara en intressant indikatoregenskap. Det förutsätter dock att kostnaden för teknisk utrustning som mäter metangas i utandningsluft är rimliga. Ett viktigt resultat av studien är att referenspopulationens sammansättning spelar stor roll för om det är ekonomiskt lönsamt eller inte att börja registrera nya egenskaper. Det ekonomiska utrymmet för investeringar blir betydligt större när referenspopulationen består av genomiskt testade kor egna registreringar på indikatoregenskapen jämfört med med en referenspopulation som består av genomiskt testade tjurar vars döttrar har registreringar på indikatoregenskapen.

## 8.3 Framtidsperspektiv

Kärnbesättningarna miste sin betydelse för individprövning och urval av tjurmödrar när genomisk avelsvärdering började tillämpas. För att förbättra urvalet av tjurmödrar bör de potentiella tjurmoders-kandidaterna testas genomiskt. Kornas värde i referenspopulationen bör utforskas noggrannare då en referenspopulation som består av kor kan ge genomiska avelsvärden med hög säkerhet och samtidigt sänka kostnaden för registrering av indikatoregenskaper eftersom färre registreringar behövs. Ett nätverk av speciella besättningar, liknande kärnbesättningar, kan skapas för att registrera komplicerade egenskaper. Dessutom behövs det mer forskning för att fastställa nya indikatoregenskapers arvbarheter och genetiska samband mellan de nya egenskaperna och egenskaperna i avelsmålet. Det är också viktigt att skatta mellan metangasutsläpp och fruktsamhet. Den samband svåraste forskningsuppgiften är kanske att beräkna den sanna ekonomiska vikten för mjölkproduktionens miljöpåverkan.

# 9 References

- Aamand, G.P. (2008). Scandinavian co-operation in dairy evaluation. In. Nordic Cattle Genetic Evaluation.
- Ahlman, T., Berglund, B., Rydhmer, L. & Strandberg, E. (2011). Culling reasons in organic and conventional dairy herds and genotype by environment interaction for longevity. *Journal of Dairy Science* 94(3), 1568-1575.
- Beauchemin, K.A., McAllister, T.A., McGinn, S.M. & Bi, C. (2009). Dietary mitigation of enteric methane from cattle. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 4(035), 1-18.
- Bell, M.J., Wall, E., Russell, G., Simm, G. & Stott, A.W. (2011). The effect of improving cow productivity, fertility, and longevity on the global warming potential of dairy systems. *Journal of Dairy Science* 94(7), 3662-3678.
- Bovenhuis, H., Niebel, E. & Fewson, D. (1989). Implications of selection for secondary traits on MOET-nucleus cattle-breeding programs for dairy and dual-purpose breeds. *Livestock Production Science* 22(3-4), 237-254.
- Brascamp, E.W. (1984). Selection indices with constraints. *Animal Breeding Abstracts* 52(9), 645-654.
- Buch, L.H., Kargo, M., Berg, P., Lassen, J. & Sørensen, A.C. (2012). The value of cows in reference populations for genomic selection of new functional traits. *Animal* 6(6), 880-886.
- Buch, L.H., Sorensen, M.K., Berg, P., Pedersen, L.D. & Sorensen, A.C. (2011a). Genomic selection strategies in dairy cattle: Strong positive interaction between use of genotypic information and intensive use of young bulls on genetic gain. *Journal of Animal Breeding and Genetics* 129(2), 138-151.
- Buch, L.H., Sorensen, M.K., Lassen, J., Berg, P., Jakobsen, J.H., Johansson, K. & Sorensen, A.C. (2011b). Udder health and female fertility traits are favourably correlated and support each other in multi-trait evaluations. *Journal of Animal Breeding and Genetics* 128(3), 174-182.
- Butler, L.J. & Wolf, M.M. (2010). Economic analysis of the impact of cloning on improving dairy herd composition. AgBioForum 13(2), 194-207.
- Calus, M.P.L., de Haas, Y., Pszczola, M. & Veerkamp, R.F. (2013). Predicted accuracy of and response to genomic selection for new traits in dairy cattle. *Animal* 7(2), 183-191.

- Carlen, E., Strandberg, E. & Roth, A. (2004). Genetic parameters for clinical mastitis, somatic cell score, and production in the first three lactations of Swedish Holstein cows. *Journal of Dairy Science* 87(9), 3062-3070.
- Chagunda, M.G.G., Ross, D. & Roberts, D.J. (2009). On the use of a laser methane detector in dairy cows. *Computers and Electronics in Agriculture* 68(2), 157-160.
- Cottle, D.J., Nolan, J.V. & Wiedemann, S.G. (2011). Ruminant enteric methane mitigation: a review. *Animal Production Science* 51(6), 491-514.
- de Haas, Y., Janss, L.L.G. & Kadarmideen, H.N. (2007a). Genetic and phenotypic parameters for conformation and yield traits in three Swiss dairy cattle breeds. *Journal of Animal Breeding* and Genetics 124(1), 12-19.
- de Haas, Y., Janss, L.L.G. & Kadarmideen, H.N. (2007b). Genetic correlations between body condition scores and fertility in dairy cattle using bivariate random regression models. *Journal* of Animal Breeding and Genetics 124(5), 277-285.
- de Haas, Y., Windig, J.J., Calus, M.P.L., Dijkstra, J., de Haan, M., Bannink, A. & Veerkamp, R.F. (2011). Genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection. *Journal of Dairy Science* 94(12), 6122-6134.

Dekkers, J.C.M. (2010). Use of high-density marker genotyping for genetic improvement of livestock by genomic selection. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 5(037), 1-13.

FAO (2009). Livestock in balance. Accessed April 2013.

http://www.fao.org/docrep/012/i0680e/i0680e.pdf.

- FAO (2011a). Global food losses and food waste; extent, causes and prevention. Study conducted for the International Congress Save food at Interpack, Düsseldorf, Germany. Accessed April 21, 2013.http://www.fao.org/fileadmin/user\_upload/suistainability/pdf/Global\_Food\_Losses\_and\_Food\_Was te.pdf
- FAO (2011b). Mapping supply and demand for animal-source foods to 2030, by T.P. Robinson & F. Pozzi. Animal Production and Health Working Paper. No. 2. Rome. Accessed April 21, 2013. http://www.fao.org/docrep/014/i2425e/i2425e00.pdf.
- Garnsworthy, P.C. (2004). The environmental impact of fertility in dairy cows: a modelling approach to predict methane and ammonia emissions. *Animal Feed Science and Technology* 112(1-4), 211-223.
- Garnsworthy, P.C. (2011). The environmental impact of fertility in dairy cows. WCDS Advances in Dairy Technology 23, 181-190.
- Gill, M., Smith, P. & Wilkinson, J.M. (2010). Mitigating climate change: the role of domestic livestock. *Animal* 4(3), 323-333.
- Goddard, M. (2009). Genomic selection: prediction of accuracy and maximisation of long term response. *Genetica* 136(2), 245-257.
- Groen, A.F. (2008). Breeding goals to optimize production efficiency. Wallingford, UK: Cabi. Resource allocation theory applied to farm animal production. ISBN 978-1-84593-394-4.
- Groen, A.F., Steine, T., Colleau, J.J., Pedersen, J., Pribyl, J. & Reinsch, N. (1997). Economic values in dairy cattle breeding, with special reference to functional traits. Report of an EAAP working group. *Livestock Production Science* 49(1), 1-21.

- Hagnestam-Nielsen, C. & Ostergaard, S. (2008). Economic impact of clinical mastitis in a dairy herd assessed by stochastic simulation. Mastitis control: from science to practice. Proceedings of International Conference, The Hague, Netherlands, 30 September - 2 October 2008. ISBN 978-90-8686-085-2.
- Hayes, B.J., Bowman, P.J., Chamberlain, A.J. & Goddard, M.E. (2009). Invited review: Genomic selection in dairy cattle: Progress and challenges. *Journal of Dairy Science* 92(2), 433-443.
- Hegarty, R.S., Alcock, D., Robinson, D.L., Goopy, J.P. & Vercoe, P.E. (2010). Nutritional and flock management options to reduce methane output and methane per unit product from sheep enterprises. *Animal Production Science* 50(11-12), 1026-1033.
- Hegarty, R.S., Goopy, J.P., Herd, R.M. & McCorkell, B. (2007). Cattle selected for lower residual feed intake have reduced daily methane production. *Journal of Animal Science* 85(6), 1479-1486.
- Hegarty, R.S. & McEwan, J.C. (2010). Genetic opportunities to reduce enteric methane emissions from ruminant livestock. In: *Proceedings of the 9th World Congress on Genetics Applied to Animal Production, August 2010, .* Leipzig, Germany (2010).
- Hellwing, A.L.F., Lund, P., Weisbjerg, M.R., Brask, M. & Hvelplund, T. (2012). Technical note: Test of a low-cost and animal-friendly system for measuring methane emissions from dairy cows. *Journal of Dairy Science* 95(10), 6077-6085.
- Herd, R.M. (2008). *Residual feed intake*. Wallingford, UK: Cabi. Resource allocation theory applied to farm animal production. ISBN 978-1-84593-394-4.
- Herd, R.M. & Arthur, P.F. (2009). Physiological basis for residual feed intake. *Journal of Animal Science* 87(14), E64-E71.
- Heringstad, B., Klemetsdal, G. & Ruane, J. (2000). Selection for mastitis resistance in dairy cattle: a review with focus on the situation in the Nordic countries. *Livestock Production Science* 64(2-3), 95-106.
- Herold, P., Rossler, R., Momm, H. & Zarate, A.V. (2012). Development of organisation and planning in animal breeding: II. A review on breeding planning. *Archiv Fur Tierzucht-Archives of Animal Breeding* 55(5), 519-531.
- Janzen, H.H. (2011). What place for livestock on a re-greening earth? Animal Feed Science and Technology 166-67, 783-796.
- Juga, J. & Mäki-Tanila, A. (1987). Genetic change in a nucleus breeding dairy herd using embryo transfer. *Acta Agriculturae Scandinavica* 37(4), 511-519.
- König, S., Simianer, H. & Willam, A. (2009). Economic evaluation of genomic breeding programs. *Journal of Dairy Science* 92(1), 382-391.
- Lassen, J. (2011). Animal variation in methane emission from breath of Danish Red, Holstein and Danish Jersey. NordGen Workshop. In: *Effects of Climate Change on Primary Industries in the Nordic Countries*. Uppsala, Sweden. Accessed April 20, 2013.: <u>http://www.nordgen.org/ngdoc/husdyr/workshops/AnGR/AnGR-NordicNET\_JanLassen.pdf</u>.
- Lassen, J., Lovendahl, P. & Madsen, J. (2012). Accuracy of noninvasive breath methane measurements using Fourier transform infrared methods on individual cows. *Journal of Dairy Science* 95(2), 890-898.
- Leroy, J., Opsomer, G., Van Soom, A., Goovaerts, I.G.F. & Bols, P. (2008). Reduced fertility in high-yielding dairy cows: Are the oocyte and embryo in danger? Part I The importance of

negative energy balance and altered corpus luteum function to the reduction of oocyte and embryo quality in high-yielding dairy cows. *Reproduction in Domestic Animals* 43(5), 612-622.

- Lund, M.S., de Roos, A.P.W., de Vries, A.G., Druet, T., Ducrocq, V., Fritz, S., Guillaume, F., Guldbrandtsen, B., Liu, Z.T., Reents, R., Schrooten, C., Seefried, F. & Su, G.S. (2011). A common reference population from four European Holstein populations increases reliability of genomic predictions. *Genetics Selection Evolution* 43.
- Madsen, J.S. & Jensen, J. (2000). A user's guide to DMU a package for analysing multivariate mixed models. Diss.:Department of Animal Breeding and Genetics, Research Centre Foulum, Box 50, 8830 Tjele, Denmark.
- Mark, T. (2004). Applied genetic evaluations for production and functional traits in dairy cattle. *Journal of Dairy Science* 87(8), 2641-2652.
- Meuwissen, T.H.E. (1991). Expectation and variance of genetic gain in open and closed nucleus and progeny testing schemes *Animal production* 53, 133-141.
- Meuwissen, T.H.E., Hayes, B.J. & Goddard, M.E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157(4), 1819-1829.
- Meuwissen, T.H.E. & Woolliams, J.A. (1993). Responses of multi-trait selection in open nucleus schemes for dairy cattle breeding. *Animal production* 56, 293-299.
- Mocquot, J.C. (1988). Sire-son and dam-som paths research geneticists view. *Journal of Dairy Science* 71(7), 1972-1981.

NAV (2008). New Nordic Total Merit index with continued focus on profitable dairy cows.

- Nicholas, F.W. & Smith, C. (1983). Increased rates of genetic change in dairy-cattle by embryo transfer and splitting. *Animal production* 36(JUN), 341-353.
- Nielsen, H.M., Christensen, L.G. & Groen, A.F. (2005). Derivation of sustainable breeding goals for dairy cattle using selection index theory. *Journal of Dairy Science* 88(5), 1882-1890.
- Norberg, E. (2004). *Electrical conductivity of milk as a phenotypic and genetic indicator of bovine mastitis.* Diss. Foulum:Danish Institute of Agricultural Sciences.
- Olesen, I., Groen, A.F. & Gjerde, B. (2000). Definition of animal breeding goals for sustainable production systems. *Journal of Animal Science* 78(3), 570-582.
- Pedersen, J., Sørensen, M.K., Toivonen, M., Eriksson, J.-Å. & Pedersen Aamand, G. (2008). Report on economic basis for Nordic Total Merit Index. Report from Nordic Cattle Genetic Evaluation.
- Pedersen, L.D., Kargo, M., Berg, P., Voergaard, J., Buch, L.H. & Sorensen, A.C. (2012). Genomic selection strategies in dairy cattle breeding programmes: Sexed semen cannot replace multiple ovulation and embryo transfer as superior reproductive technology. *Journal* of Animal Breeding and Genetics 129(2), 152-163.
- Pedersen, L.D., Sorensen, A.C., Henryon, M., Ansari-Mahyari, S. & Berg, P. (2009). ADAM: A computer program to simulate selective breeding schemes for animals. *Livestock Science* 121(2-3), 343-344.
- Petersson, K.J. (2007). *Milk progesterone as a tool to improve fertility in dairy cows*. Diss. Uppsala:Swedish University of Agricultural Sciences.

- Philipsson, J. & Lindhe, B. (2003). Experiences of including reproduction and health traits in Scandinavian dairy cattle breeding programmes. *Livestock Production Science* 83(2-3), 99-112.
- Pryce, J. & Hayes, B. (2012). A review of how dairy farmers can use and profit from genomic technologies. *Animal Production Science* 52(2-3), 180-184.
- Pryce, J.E. & Daetwyler, H.D. (2012). Designing dairy cattle breeding schemes under genomic selection: a review of international research. *Animal Production Science* 52(2-3), 107-114.
- Pryce, J.E. & Harris, B.L. (2006). Genetics of body condition score in New Zealand dairy cows. *Journal of Dairy Science* 89(11), 4424-4432.
- Pryce, J.E., Harris, B.L. & McNaughton, L.R. (2007). The genetic relationship between heifer and cow fertility. *Proceedings of the New Zealand Society of Animal Production* 67, 388-391.
- Pryce, J.E., Royal, M.D., Garnsworthy, P.C. & Mao, I.L. (2004). Fertility in the high-producing dairy cow. *Livestock Production Science* 86(1-3), 125-135.
- Pszczola, M., Strabel, T., Mulder, H.A. & Calus, M.P.L. (2012). Reliability of direct genomic values for animals with different relationships within and to the reference population. *Journal* of Dairy Science 95(1), 389-400.
- Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N. & Grommers, F.J. (1998). Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livestock Production Science* 56(1), 15-33.
- Roxstrom, A., Strandberg, E., Berglund, B., Emanuelson, U. & Philipsson, J. (2001). Genetic and environmental correlations among female fertility traits, and between the ability to show oestrus and milk production in dairy cattle. *Acta Agriculturae Scandinavica Section a-Animal Science* 51(3), 192-199.
- Roxström, A. (2001a). *Genetic aspects of fertility and longevity in dairy cattle*. Diss. Uppsala:Swedish University of Agricultural Sciences.
- Roxström, A., Strandberg, E., Berglund, B., Emanuelsson, U., Philipsson, J. (2001b). Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish Red and White dairy cattle. *Acta Agriculturae Scandinavica Section A Animal Sciences* 51, 7-14.
- Schaeffer, L.R. (2006). Strategy for applying genome-wide selection in dairy cattle. *Journal of Animal Breeding and Genetics* 123(4), 218-223.
- Stavi, I. & Lal, R. (2013). Agriculture and greenhouse gases, a common tragedy. A review. Agronomy for Sustainable Development 33(2), 275-289.
- Steeneveld, W. & Hogeveen, H. (2012). Economic consequences of immediate or delayed insemination of a cow in oestrus. *Veterinary Record* 171(1), 17-+.
- Steine, G., Kristofersson, D. & Guttormsen, A.G. (2008). Economic evaluation of the breeding goal for Norwegian Red dairy cattle. *Journal of Dairy Science* 91(1), 418-426.
- Storm, I.M.L.D., Hellwing, A.L.F., Nielsen, N.I. & Madsen, J. (2012). Methods for measuring and estimating methane emission from ruminants. *Animals* 2(2), 160-183.
- Stranden, I., Korpiaho, P., Pakula, M. & Mantysaari, E.A. (2001). Bull selection in MOET nucleus breeding schemes with limited testing capacity. *Acta Agriculturae Scandinavica Section a-Animal Science* 51(4), 235-245.

- Sun, C., Madsen, P., Lund, M.S., Zhang, Y., Nielsen, U.S. & Su, G. (2010). Improvement in genetic evaluation of female fertility in dairy cattle using multiple-trait models including milk production traits. *Journal of Animal Science* 88(3), 871-878.
- Teepker, G. & Smith, C. (1990). Efficiency of MOET nucleus breeding schemes in selecting for traits with low heritability in dairy cattle. *Animal production* 50, 213-219.
- Tiezzi, F., Maltecca, C., Cecchinato, A., Penasa, M. & Bittante, G. (2012). Genetic parameters for fertility of dairy heifers and cows at different parities and relationships with production traits in first lactation. *Journal of Dairy Science* 95(12), 7355-7362.
- Waghorn, G.C. & Hegarty, R.S. (2011). Lowering ruminant methane emissions through improved feed conversion efficiency. *Animal Feed Science and Technology* 166-67, 291-301.
- Wall, E., Simm, G. & Moran, D. (2010). Developing breeding schemes to assist mitigation of greenhouse gas emissions. *Animal* 4(3), 366-376.
- Van Tassell, C.P. & Van Vleck, L.D. (1991). Estimates of genetic selection differentials and generation intervals for 4 paths of selection. *Journal of Dairy Science* 74(3), 1078-1086.
- Veerkamp, R.F., Koenen, E.P.C. & De Jong, G. (2001). Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *Journal of Dairy Science* 84(10), 2327-2335.
- Veerkamp, R.F., Windig, J.J., Calus, M.P.L., Ouweltjes, W., Haas, Y.d. & Beerda, B. (2008). Selection for high production in dairy cattle. Resource allocation theory applied to farm animal production. ISBN 978-1-84593-394-4.
- Willam, A., Nitter, G., Bartenschlager, H., Karras, K., Niebel, E. & Graser, H.-U. (2008). ZPLAN - Manual for a PC-Program to Optimize Livestock Selection Schemes. *Manual Version 2008* for Source Code "z10.for".
- Yan, T., Mayne, C.S., Gordon, F.G., Porter, M.G., Agnew, R.E., Patterson, D.C., Ferris, C.P. & Kilpatrick, D.J. (2010). Mitigation of enteric methane emissions through improving efficiency of energy utilization and productivity in lactating dairy cows. *Journal of Dairy Science* 93(6), 2630-2638.
- Zwald, N.R. & Weigel, K.A. (2002). Examination of methods to correct for preferential treatment among AI bull dams. *Journal of Dairy Science* 85(Suppelment 1), 32.

# Acknowledgements

The work of this thesis was performed at the Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences (SLU), Uppsala. Financial support from the Swedish Farmers' Foundation for Agricultural Research (SLF) is gratefully acknowledged. SLU fund for internationalization of postgraduate studies, (FUR), is gratefully acknowledged for providing the travel grants for participation in a conference and NOVA courses.

Throughout my PhD education I have had the honor to collaborate with many wonderful people. I would like to express my special thank to:

**Lotta Rydhmer**, my main supervisor, I am very glad that you took over the role as my main supervisor after **Jan Philipsson**'s retirement. The support and engagement I have received from you, both in good times and in difficult times, has been invaluable. I would also like to thank you for allowing me to have flexible working hours, as it helped me to combine the PhD studies with having a family and home in Jämtland, 550 km from Uppsala.

**Jan Philipsson**, my previous main supervisor, thank you for your help and support even after your retirement.

**Susanne Eriksson, Kjell Johansson** and **Karl-Johan Petersson**, my cosupervisors, thank you for always being kind and supportive, and patiently tolerating and answering all my questions.

**Freddy Fikse**, resource person whose engagement in my last two studies was equal to a contribution of a supervisor. Thank you for all your help!

Morten Kargo, Anders Christian Sørensen, Line Hjortø and Jørn Rind Thomasen, thank you so much for the great collaboration and all your help on simulation programs as well as for your friendship, and for making my stay in Foulum such a memorable experience.

Hans Stålhammar, a resource person and a senior geneticist at Viking Genetics, thank you for a good collaboration! Thank you for your warm

welcome during my visits to Viken Nucleus Herd and useful comments on my manuscripts and insight into practical breeding.

I would also like to thank the administrative staff at HGEN and especially **Harriet Staffans** for all her help from how to fill in the travel claims to scanning in documents that I forgot to bring with me<sup>©</sup>.

Sincere gratitude to all my past and present colleagues at HGEN, it has been a pleasure to be a part of this Department. My acknowledgement also goes to all the enthusiastic and happy PhD students whom I have had the honor to get to know at HGEN, at Foulum and during (NOVA) courses (just to name some: Therese Ahlman, Marie Ekerljung, Lina Carlström, Helena Eken, Anne Loberg, Sofia Nyman, Per Arvelius, Sandra Näslund, Roldan Corrales, Lina Jönsson, Helena Chalkias, Helena Lundgren, Erika Sterkenburg, Line Hjortø, Johanna Höglund, Johanna Häggman and Mirjam Vallas).

During the past five years I have travelled quite a lot especially between Alsen and Uppsala. More particularly I have spent approximately 2000 hours on a train and covered about 200 000 km during these years. Therefore, I would like to thank **my family, friends and neighbors** for all your help with babysitting, and caring for the horses and other animals.

There are three people who have had a great influence on my interest in milk production: **my grandmother Jelena Jaaniste**, professor emeritus **Olev Saveli** (Estonian University of Life Sciences) and dairy cattle farmer **Anders Nilsson** in Västerkälen. I would like to dedicate this thesis to all of you.

Last but not least, I would like to thank my dearest husband **Andréas** for his immeasurable dedication and care for our son and home. Tack för all hjälp och stöd! Det har varit en lång och tuff resa för oss båda, men nu kan det bara bli bättre <sup>(i)</sup> Jag ser verkligen framemot att ha ett riktigt liv tillsammans med dig utan ständigt packade resväskor! Och söta lilla **Ecke**, du är det bästa som hänt mig! Och tänk att innan du kom trodde jag att ta doktorsexamen var det viktigaste i livet...