Innovations in the dairy chain: Bio-economic analysis of novel breeding opportunities

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This research was conducted under the auspices of the Graduate School of Wageningen School of Social Sciences (WASS) and the Graduate School of Wageningen Institute of Animal Sciences (WIAS).

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Thesis
submitted in fulfillment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. dr. M.J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Tuesday December 20, 2011
at 1.30 p.m. in the Aula.

Demeter, R.M.
Innovations in the dairy chain: Bio-economic analysis of novel breeding opportunities.

PhD thesis, Wageningen University, the Netherlands (2011)
With references, with summaries in English and Dutch

ISBN 978-94-6173-208-8

Abstract

Demeter, R.M. (2011). Innovations in the dairy chain: Bio-economic analysis of novel breeding opportunities. PhD thesis, Wageningen University, the Netherlands.

In recent years, there has been a growing interest in the dairy sector to move from producing bulk dairy commodities towards producing specialized dairy products aimed at niche markets. Dairy farmers consider shifting from commodity milk to raw milk with specialized composition to meet consumer or industrial demands. In this context, the objectives of the thesis were 1) to assess qualitatively future scenarios to create value added in the dairy chain and 2) to *ex-ante* assess quantitatively the technical and economic implications at farm level of producing differentiated raw milk by using genetic selection. A two-step approach was applied, where the first step assessed qualitatively the strategic opportunities offered by a wide range of novel methods emerging at various stages in the production chain, whereas the second step assessed quantitatively the implications of specific strategies on farm level. The main findings indicate that creating value added is vital for the sustainable growth of the dairy industry, and producing raw milk with specialized characteristics by using novel breeding concepts can play an important role in this process. The *ex-ante* quantitative assessments have found no evidence that implementing novel genetic selection strategies to change fat or protein composition in milk would have large effects on herd production and profitability. The stakeholders of the dairy industry should initiate joint action plans to capitalize on the opportunities offered by recent milk genomics research.

Preface

On starting my doctorate studies more than four years ago, I had three main goals in my mind to accomplish: exploring and learning new things, achieving something significant that others could benefit from, and improving myself as independent thinker. Now as my studies are completed, it is time to conclude whether the once set out goals have been achieved. First, I have learnt lots about various scientific disciplines and their interactions in multidisciplinary research. Also, I have improved my abilities towards understanding and solving problems, becoming a better communicator, and I have gained valuable skills for my future career. However, let me leave it to the reader to decide whether the research in this thesis can fulfil expectations and thus be beneficial to greater public. On the whole, I am happy with the process and outcomes of my studies, and I am very much indebted to a number of people.

I would gratefully acknowledge my thesis supervisiors. Johan, thank you for being a real mentor to me all along. You have contributed greatly to my understanding of conducting research and have shaped my way of thinking about many issues. Alfons and Miranda, thank you for believing in me and offering me the possibility of pursuing doctoral studies. You have provided me with great flexibility in my research and with a friendly working environment at your department. Anders, although you became my supervisior halfway, your contribution was essential. Your methodological achievments in the area of modeling complex agricultural systems are truly unique, and I want to thank you for teaching me some of your techniques. I also greatly appreciate the hospitality during the time I spent at your department. Thank you all for guiding me, I feel indeed honoured to be given the chance to stand on your shoulders.

My thanks also go to the secretariats of the Animal Breeding and Genomics Centre and the Business Economics Group, especially to Ada Wiggerman and Anne Houwers, for always making sure that I could focus only on my research. I also owe many thanks to my office mates and other colleagues at the Business Economics Group for creating a pleasant every-day working environment. Furthermore, I am grateful to the team members of the Dutch Milk Genomics Initiative for having inspiring project meetings once a month.

Lastly on this list, but not in fact, I want to thank the great support of my wife Agnieszka and our daughter Hanna for their patience and never ending support. Aga, if I had not met you during our studies, probably I would not have had the courage to stay abroad for another four years. But fortunately we did meet, which marked the begininning of the most beautiful episode of my life. During the last more than four years, it was so wonderful to know and feel that you are there for me in happyness and sorrow. Thank you for your patience for all the times when my mind was somewhere else, while it should have been with my family.

Róbert Demeter
Amersfoort, November 2011

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General introduction

1.1 Background

The dairy sector worldwide faces challenges including growing consumer demands for animal products in general, increasing need for greater efficiency, and growing concerns over ecological sustainability. Therefore, the dairy sector continuously looks for innovative solutions to address the challenges and create value added. An important domain of innovation is marked by the gradual shift from producing bulk dairy commodities towards producing specialized dairy products aimed at niche markets (Boland et al., 2001; Creamer et al., 2002). Techniques to produce specialized dairy products with value added have been developed at various stages within the dairy chain. An important stage is the dairy farm, where several methods exist to improve the intrinsic value of raw milk. Raw milk with specialized characteristics, also labeled as designer milks (Boland et al., 2001), can be produced by applying novel concepts in cattle breeding, cattle nutrition, and herd management. Thus, farmers are equipped to shift from producing commodity raw milk to producing raw milk with improved characteristics to meet consumer or industrial demands.

Genetic aspects of milk have been researched extensively to understand the fundamental processes in lactation in mammals, mammary tissue physiology, and the basis of milk yield and composition. Recent developments in genomics and bioinformatics, however, create an unprecedented biological information base on the genetic basis of milk (German et al., 2006). These advances, in turn, have triggered a growing industry interest in using genetics to better utilize milk's biological potential (Dooley et al., 2005). Multidisciplinary research projects focusing on the genomics of milk have emerged in several countries with a major dairy industry. Moreover, the milk genomics research community is linked through the International Milk Genomics Consortium (German et al., 2006). Milk genomics research aims to explore the natural genetic variation in milk-quality traits that can be exploited by breeding programs. Although a wide range of traits are considered (e.g., cell count, urea, vitamins, minerals, antibodies), a dominant research field is the fat and protein composition in milk.

Milk-fat composition is important because of its effect on human health (German and Dillard, 2006; Steijns, 2008), while milk-protein composition is relevant due to its effects on manufacturing properties of raw milk (e.g., Ikonen et al., 2004; Wedholm et al., 2006). Recent research has shown opportunities to improve fat and protein composition by genetic selection. First, genetic variation has been reported in milk fatty acids (Soyeurt et al., 2007; Bobe et al., 2008; Stoop et al., 2008) and major milk proteins (Bobe et al., 1999; Graml and Pirchner, 2003; Schopen et al., 2009). This genetic variation shows the possibility of changing milk composition by traditional selection. Second, specific genetic polymorphisms of genes that influence milk-fat or milk-protein profiles have been identified. Examples include genes that are involved in milk-fat synthesis, such as *DGAT1* (Schennink et al., 2007; Schennink et al., 2008) and *SCD1* (Mele et al., 2007; Moioli et al., 2007; Schennink et al., 2008), or in milk-protein synthesis, such as *CSN3* and *LGB* (McLean et al., 1984; Bobe et al., 1999; Heck et al., 2009). Information on such specific genes can be used in gene-assisted selection to improve milk composition. Recently, genomic selection was proposed to improve milk yield and milk composition as an alternative to traditional and gene-assisted selection (e.g., De Roos, 2011).

1.2 Research Interest

First, although several methods exist to create value added in the dairy production chain, an up-to-date study considering strategic opportunities offered by the wide range of novel methods is missing. Second, although scientific evidence exists that detailed milk composition can be improved by genetic selection, information on the actual implementation is almost non-existing. The latter problem is twofold. First, genomic research on milk usually reports on correlated effects of promising selection traits on milk yield traits. However, follow-up research on correlated effects on other economically important production traits (e.g., reproduction or longevity) is often missing. Second, formal model calculations of technical and economic consequences of potential selection strategies are virtually missing. Before the dairy industry implements any selection strategy, it is imperative to know how novel strategies would impact economically important traits and production costs on farms. Bio-economic modeling, which takes account of all direct and correlated effects of selection on cow performance, enables the prediction of the expected herd performance and profit.

1.3 Research Objectives

The objectives of the thesis are 1) to assess qualitatively future scenarios to create value added in the dairy production chain and 2) to assess quantitatively the technical and economic implications of producing differentiated raw milk by applying genetic selection.

1.4 Outline of the Thesis

Chapter 2 assesses qualitatively the potential for creating value added in the dairy chain. The chapter presents three scenarios that were developed in a workshop involving stakeholders and experts in the Dutch dairy sector. Scenarios address major trends including changing consumer preferences, increasing pressure for more cost-efficient production, and rising environmental concerns. Following this chapter, the thesis focuses on quantifying the technical and economic implications at farm level of one scenario, which envisions the production of differentiated raw milk with improved health or manufacturing properties.

Chapters 3 and 4 examine phenotypic associations between selection traits for improved milk composition and cow fertility traits. Effects on fertility were studied because reproduction is an economically important trait impacting farm profit. Associations between cow fertility traits and milk-fat composition, *DGAT1*, and *SCD1* genotypes are reported in chapter 3. Associations between cow fertility traits and milk-protein composition and milk-protein variants (β-lactoglobulin, β-casein, κ-casein, β-κ-casein) are reported in chapter 4. Results from these chapters are used as biological input to quantify technical and economic implications of various selection strategies to change detailed milk composition in chapter 6.

Chapter 5 develops a herd optimization and simulation model for dairy cattle, including recent methodological contributions. The model is designed to determine economically optimal insemination and replacement strategies for individual cows and simulate whole-herd results following from the optimal policies. The optimization problem was formulated as a multi-level hierarchic Markov process, and a state space model with Bayesian updating was applied for modeling the variation in milk yield level among cows. The model is used to quantify technical and economic implications of various selection strategies in chapter 6.

Chapter 6 assesses quantitatively the technical and economic effects at farm level of various selection strategies, which were envisioned in chapter 2. Strategies are modeled for either decreasing the ratio of saturated to unsaturated fatty acids in milk or increasing the proportion of total caseins in total milk proteins. Either traditional selection or gene-assisted selection was considered in each strategy. The herd optimization and simulation model developed in chapter 5, coupled with results of analyses of chapters 3 and 4 as inputs, is used to model various hypothetical herds that could result from several years of genetic selection.

Chapter 7, the general discussion, reflects on the results of the thesis and their implications from a broader perspective. The goal is not to discuss the methods and results of the individual chapters. Rather, the general discussion reviews the scientific implications, subsequently discusses the business implications, and finally discusses the future outlook.

1.5 Framework

This thesis was written within the Dutch Milk Genomics Initiative, which is a multi-disciplinary program focusing on the genetic background of detailed milk composition. The goal of the program is to identify genes that contribute to natural genetic variation in milk-quality traits, in particular in milk-fat and milk-protein composition. The program provides tools for improved breeding programs to exploit natural genetic variation in milk-quality traits and contributes to the knowledge base needed for developing innovative dairy products.

In 2005, milk and DNA samples on about 2,000 individual cows of the Dutch Holstein-Friesian population were collected from about 400 commercial dairy farms throughout the Netherlands. This creates a unique database containing detailed information on milk composition which is made available by the industrial partners for this research program. The program combines expertise in the fields of genomics, quantitative genetics, bioinformatics, proteomics, and dairy science to increase our understanding of the genetic variation in milk composition. The program builds on the combined expertise that has been developed and successfully applied to identify genes affecting production and functional traits in dairy cattle and other farm animals. The program integrates knowledge of the genetic variation in milk composition with knowledge of the relevance of milk composition for processing and human health. A unique aspect of the program is that it brings together industries involved at each end of the milk production chain, i.e., from genetic material to (specialized) dairy products.

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2

Scenarios for a future dairy chain in the Netherlands

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NJAS-Wageningen Journal of Life Sciences (2009) 56:301-323

Abstract

The objective of this study was to assess qualitatively, through a participatory approach, the potential for increasing the value added in the Dutch dairy production chain. A workshop involving stakeholders and experts in the Dutch dairy sector developed three scenarios, envisioned according to the strategic interests of the dairy chain in the Netherlands. These scenarios address major trends including changing consumer preferences, increasing pressure for more cost-efficient production, and rising environmental concerns. The scenarios indicate different directions in which the dairy chain in the Netherlands might develop in the next 5 to 20 years. The first scenario envisions the prevalence of producing differentiated raw milk with enhanced health or improved manufacturing properties. The second scenario envisions a dairy chain that is reduced to produce fresher and more individually customized dairy products with improved shelf life. The third scenario envisions ecologically sustainable dairy farming with improved animal welfare. These scenarios show that when improving the dairy sector it is important to consider the entire chain, and hence concerted and co-ordinated actions by the various stakeholders are necessary. Further studies quantifying the consequences of different scenario settings are necessary.

Key words: dairy chain, value-added, scenario, stakeholder consultation

2.1 Introduction

The dairy sector worldwide faces changing consumer demands, a need for greater efficiency and growing concerns of sustainability. First, global demand for dairy products is increasing rapidly, mostly generated by increasing population and purchasing power in developing countries (Delgado, 2003; Dong, 2006). In developed countries, demand for fresh and nutritious foods with improved shelf life is growing (Devlieghere et al., 2004), and the effect of foods on human health is an important factor in consumer purchase decisions (Kaabia et al., 2001; Rickertsen et al., 2003). Second, the dairy sector continuously strives for higher efficiency because of pressure from price- and volume-driven competition in many countries (Creamer et al., 2002). In addition, global dairy trade is likely to become less restricted because of the easing of protectionist policies of some developed countries (Dillon et al., 2008). Third, environmental sustainability concerns become increasingly important, especially those related to greenhouse-gas (**GHG**) emissions, because cattle farming is a major contributor to methane emission (Creamer et al., 2002). As a result of these trends, the dairy sector continuously looks for innovative solutions to address the trends and increase the value added.

Several methods to increase the value added have been proposed recently. Novel concepts have been investigated at each stage within the dairy production chain. However, less is known about strategies for implementing those value-adding methods and the related implications. Creamer et al. (2002) reviewed several developments in the dairy sector and envisioned future directions in which the global dairy sector might develop in the next decades. However, there is no up-to-date study considering strategic opportunities offered by the wide range of novel methods. The objective of this study is to assess qualitatively the potential for increasing the value added in the Dutch dairy production chain by developing future scenarios. Scenario development as a systematic way of thinking about the future has been used extensively in various sectors and disciplines in the past decades (Schoemaker, 1995; Swart et al., 2004). In this study, the method is used to explore future perspectives of the dairy production chain in the Netherlands. The scenarios describe different dairy production chains to help stakeholders to better adapt to the future. It is our intention to inform broadly and promote discussion, rather than to provide in-depth coverage. In line with Rotmans et al. (2000), the scenarios are presented as descriptions of different future images.

2.2 The Dutch Dairy Chain

The Netherlands is one of the largest dairy producers and exporters within the European Union. In the last decade, its yearly milk production amounted to about 11 billion kg, having the bulk of it processed into cheese, butter, milk powder, fresh dairy products, and specialties. Some 300 wholesalers and 6,800 sales outlets are involved in the trade in and sales of dairy products. The dairy sector as a whole provides around 61,000 jobs, thereby playing an important role within the Dutch economy. Similar to many European countries, dairy farming in the Netherlands is characterized by a falling number of cows, a declining number of farmers, and an increasing level of farm technology and milk yield. Nowadays, the Dutch dairy sector comprises nearly 20,000 dairy farms with about 1.4 million dairy cows. In 2007, the average production per farm reached 520 tons of milk, the average number of cows per farm about 70, and the percentage of farms with 70 cows or more nearly 40 (Anon., 2007). In 2007, the average milk yield was about 7,900 kg per cow per year, but milk yield of registered cows scored slightly higher. Holstein-Friesian is the dominant breed in the Netherlands, accounting for more than 95% of Dutch dairy cattle. The average Dutch dairy diet nowadays contains about 30% fresh grass, the remainder being a mix of grass silage, maize silage, and concentrates.

The Dutch dairy sector is dominated by a co-operative structure and is one of the most consolidated in the world. Dairy co-operatives owned by dairy farmers have been in place since the early days of the dairy industry, and the farmers have been part of the process of consolidation over the past decades. Because of a recent merger, nowadays one major internationally oriented co-operative processes almost 80% of the milk delivered to factories. The Dutch dairy sector has a strong competitive international position and is among the world's major dairy exporters with an export value of around €4.3 billion in 2007. Export revenues represent a large share of total annual sales by the sector. About 60% of Dutch dairy production is exported, the remaining being consumed on the domestic market. The EU is the most important export market, accounting for two third of total dairy export value in 2007. Within the EU, most of the Dutch export goes to nearby markets in Germany, France, and Belgium, representing about 40% of total export value in 2007 (Anon., 2007). Besides export, the Netherlands is also a major importer of dairy products, re-exporting much of this import to EU countries and beyond. In 2007, total Dutch dairy imports valued more than €2.3 billion (Anon., 2007).

In this study, the Dutch dairy production chain was considered as a case. Following the definition of Valeeva et al. (2005), who studied food safety improvement in the dairy production chain in the Netherlands, we considered the following stages: a feed production stage, a dairy farm stage, a processing-factory stage, and a retailer stage. Transportation between the stages was also considered, i.e., transport of compound feed to the dairy farm and transport of raw milk to the processing factory. Stages of catering and the actual consumption of milk and dairy products were not included. In addition to the chain description of Valeeva et al. (2005), an animal breeding stage was also considered in the present study.

2.3 Major Trends and Developments

2.3.1 Trends in the Netherlands

The contemporary trends affecting the Dutch dairy sector are in line with the aforementioned prevailing global trends. First, consumer preferences have changed in the Netherlands. In the last decade, the per capita consumption of milk and dairy products has dropped by 7% (Anon., 2007). Furthermore, the interest in the effects of diet on human health has increased recently because the composition of the Dutch diet has been found unfavorable (Van Kreijl et al., 2006). The proportion of obese people has doubled to 10% in the last 25 years, and it is predicted to increase to 15% in the next two decades (Van Kreijl et al., 2006). These authors also argue that 10% of all deaths in the Netherlands are attributable to poor diet and 5% to being overweight. They claim that loss of health resulting from unfavorable diet could be largely avoided by means of dietary interventions. Such interventions reveal great opportunities for the Dutch dairy sector. Improving the nutritional quality of milk and dairy products could contribute to a more favorable human diet, given that milk and derived products are important sources of nutrients in human diets (Lock and Bauman, 2004; Haug et al., 2007).

Second, the continuous pressure on the Dutch dairy sector for a more efficient production has increased recently too. The price of dairy commodities has been volatile over the last decade, forcing the sector towards a higher cost-efficiency and consolidation. As a result of this price pressure, the number of dairy farms has declined by nearly 30% between 2000 and 2007 (Anon., 2007), and the number of dairy processors decreased by more than half between 1985 and 2000 (Ramirez et al., 2006). In addition to volatile prices, there are other factors that can force the Dutch dairy sector towards a more cost-efficient production and further consolidation. In particular, the production of raw milk, which has been limited since 1984 by production quotas in the EU, is likely to become free of restrictions in the coming years; while the dairy trade is also likely to become less protected by European and national trade policies (Dillon et al., 2008). These policy changes are likely to continue to push milk prices downwards and necessitate increased efficiency and scale at farm and processing level to maintain profitability (Dillon et al., 2008).

Third, the Dutch dairy sector is strongly influenced by environmental concerns such as reducing energy use, decreasing nutrient losses, and lowering GHG emissions. Although the dairy sector in the Netherlands has achieved a remarkable improvement in energy efficiency since the mid-1980s (Ramirez et al., 2006), there is still a need for further progress according to a voluntary agreement between the dairy sector and the Dutch government. The Dutch dairy sector and the Dutch Ministry of Economic Affairs signed an agreement in 1994 to increase energy efficiency by 20% by the year 2000 (from 1989 values). The current requirement is an annual 2% reduction in energy use until 2020. Moreover, dairy farming in the Netherlands is highly nutrient-intensive, requiring environmental policies to restrict undesirable leaching of nutrients (Van

Bruchem et al., 1999) and high emissions of GHG (Freibauer, 2003). European and national policies have been implemented to tackle these environmental problems (Henkens and Van Keulen, 2001), forcing farmers to improve nutrient use (Berentsen and Tiessink, 2003; Groot et al., 2006; Schils et al., 2006). Nevertheless, further changes in individual farm management towards more effective and less polluting strategies are necessary (Ondersteijn et al., 2002).

In the following section, some of the major technological developments in the dairy production chain are described. Actual developments and future directions in technologies are discussed, with special attention to those that relate to the above presented trends. Covered domains include the fields of animal breeding and genetics, animal nutrition, milk segregation, milk storage, livestock waste management, food preservation, and food packaging. We touch on many areas, each of which is worthy of a full review in itself, and hence it is necessary to treat each area rather superficially.

2.3.2 Developments in animal breeding and genetics

Research has suggested selective breeding as a tool for farmers to meet specific consumer or industrial demands by exploiting the genetic variation underlying the differences among cows. First, technological properties of raw milk can be improved by selecting for variants of milk proteins that are preferable for dairy manufacturing (Dalgleish, 1993; Ng-Kwai-Hang and Grosclaude, 2003). Second, nutritional quality of raw milk can be improved, because the milk fatty acid (**FA**) composition can be improved by selective breeding, having two main directions. One way is select cows for an individual milk FA or for a group of milk FA, because several milk FA have been shown to have genetic variation (moderate to high heritabilities that tend to be lower for unsaturated FA) within various cattle breeds (Soyeurt et al., 2007; Bobe et al., 2008; Stoop et al., 2008). Another way is to select cows for particular genotypes of two recently suggested candidate genes: the *DGAT1* gene (Schennink et al., 2007) and the *SCD1* gene (Moioli et al., 2007; Macciotta et al., 2008; Schennink et al., 2008). The *DGAT1* gene plays a key role in triacylglycerol synthesis, whereas the *SCD1* gene codes for a key enzyme in the cellular biosynthesis of mono-unsaturated FA. Polymorphism of these genes have been shown to affect milk FA composition in various cattle breeds, thereby implying that selection for the favorable gene variants can be used in changing the fat composition of the cow's milk.

2.3.3 Developments in animal nutrition

By using novel cow diets, composition of raw milk can be changed to meet consumer or industrial demand. Feeding supplements can change milk-fat composition (Chilliard et al., 2000; Jenkins and McGuire, 2006) or elevate the level of valuable micronutrients (Knowles et al., 1999; Givens et al., 2004; Knowles et al., 2006) to enhance human health benefits. Also, feeding regimes based on fresh herbage and outdoor grazing have been suggested to favorably change the FA profile of raw milk (Elgersma et al., 2006). In addition to changing milk-fat composition, specifically designed cow diets can be used to increase the concentration of favorable protein fractions (Guinee et al., 1998; Murphy, 1999; Auldist et al., 2007) to improve the nutritional quality or the manufacturing properties of raw milk. Changing milk composition by feeding supplements, however, is complex because the transfer of the favorable FA to milk is significantly limited by several factors. These factors include destruction by ruminal micro-organisms, poor rates of intestinal absorption, and deposition in adipose tissue rather than in mammary fat (Jenkins and McGuire, 2006). So, the efficiency of transfer of desired nutrients from feeds to milk needs to be improved in the future. Furthermore, because animal nutrition has an impact on environmental sustainability, recent research in animal nutrition has been geared towards opportunities to mitigate the environment polluting effects of cattle diets (Frank et al., 2002; Dijkstra et al., 2007; Arriaga et al., 2009). Likely domains of future research include improving digestibility of dietary components, optimizing ruminal fermentation, improving use of N and P for the animal's benefit and reducing environmental pollution, and a further understanding the nutritional requirements of animals (Eastridge, 2006).

2.3.4 Developments in milk segregation

On-farm milk segregation presents another opportunity for the farmers to produce value-added products. First, segregation of cows within a herd can be an option to produce different milk types, and this method may be further improved by using genetic selection (Dooley et al., 2005a). Second, by using milking parlors or automated milking systems (**AMS**) equipped with new biosensor technologies, the natural variation amongst cows can be exploited. To date, biosensors in milking systems can measure several milk components indicating the cow's fertility (Mottram et al., 2002), metabolic and nutritional status (Jenkins et al., 1999; Mottram et al., 2002), and health (Reinemann and Helgren, 2004). Developments point towards milking systems designed to measure milk composition (Reinemann and Helgren, 2004). Short-wave near-infrared spectroscopy (Tsenkova et al., 1999) and mid-infrared spectrometry (Soyeurt et al., 2006) could be good alternatives for measuring milk composition online. In short, the availability of milking systems equipped with novel new biosensors would allow the segregation of different types of milk at the farm level on a daily basis.

2.3.5 Developments in milk storage

Milk storage is relevant because the storing conditions of raw milk can affect the yield, quality, shelf life, and sensory values of the derived dairy products (Ma et al., 2000; Barbano et al., 2006). Therefore, the improvement of raw milk storage on the farm and during milk collection could allow shelf life extension and better safety, because in these stages of the dairy production chain significant changes may occur in raw milk because of microbial growth (Hotchkiss et al., 2006). A recently investigated way to improve the storage of raw milk is the addition of carbon dioxide (**CO_2**), a method that inhibits micro-organisms by displacing oxygen, lowering the pH, and directly affecting their metabolism (Hotchkiss et al., 2006). The method significantly inhibits bacterial growth by adding CO_2 directly to raw milk (Ma et al., 2003; Martin et al., 2003), enriching the storage atmosphere with CO_2 (Dechemi et al., 2005), or applying low CO_2 pressure (Rajagopal et al., 2005; Hotchkiss et al., 2006).

2.3.6 Developments in livestock waste management

Over the last decades, there has been a growing concern about environmental, nuisance, and health issues of satisfactory livestock waste treatment in countries with concentrated livestock production (Burton and Turner, 2003). Developments in manure and waste management can help improving farming attributes that are important in ecological sustainability. These sustainability attributes include waste disposal, air and groundwater pollution, eutrophication, and energy usage (Van Calker et al., 2005a). In recent years, amongst other treatments the method of anaerobic digestion (**AD**) with utilization of biogas is increasingly recognized as a promising technology to produce renewable energy and to reduce environmental emissions (Abraham et al., 2007). In dairy farming, AD (also known as fermentation) has successfully been applied in many countries to recycle farm animal manure and organic wastes (Harikishan and Sung, 2003; Kaparaju and Rintala, 2003; Uludag-Demirer et al., 2008). This is a biological method relying on the growth and activity of specific groups of microbes. The AD technology not only reduces the environmental impact of the treated farm manure and waste but also generates methane as a useful by-product. Overall, the advantages of the AD method include, amongst others, the production of biogas, reduction of odors, reduction of pathogens in slurries, improving the fertilizing value of slurries, and reduction of GHG emissions (Burton and Turner, 2003).

2.3.7 Developments in food preservation

Traditional thermal inactivation techniques can cause adverse changes in the nutritional (Andersson and Oste, 1995), organoleptic (Nursten, 1995), or technological properties (Singh, 1995) of milk. Consequently, the replacement of these methods has been widely researched because of growing consumer demand for minimally processed fresher foods. Several non-thermal methods of processing milk and milk products have been investigated in recent years. The methods include membrane microfiltration (Rosenberg, 1995; Saboya and Maubois, 2000; Brans et al., 2004), high-pressure treatment (Messens et al., 2003), pulsed electric field processing (Bendicho et al., 2002; Sampedro et al., 2005), ultraviolet treatment (Reinemann et al., 2006; Altic et al., 2007; Matak et al., 2007), ultrasound processing (Villamiel and De Jong, 2000; Piyasena et al., 2003; Knorr et al., 2004), and the addition of carbon dioxide (Loss and Hotchkiss, 2003;

Hotchkiss et al., 2006; Garcia-Gonzalez et al., 2007). Although the new technologies are promising, implementing them on a large scale in the dairy sector is a problem because of their high costs.

2.3.8 Developments in food packaging

Innovative food-packaging concepts have emerged because of consumer demand for fresher foods and new retail and distribution practices such as centralization, internet shopping, and globalization (Vermeiren et al., 1999). Active and intelligent packaging systems have received most attention. Active packaging (**AP**) changes the condition of packaged food to improve shelf life, food safety, or sensory values while maintaining quality (De Kruijf et al., 2002). The AP technologies change interactions between the food, the package, and the package headspace by applying some physical, chemical, or biological actions (Rooney, 1995; Brody et al., 2001). Intelligent packaging (**IP**) includes packaging concepts that can perform intelligent functions to facilitate decision-making to improve shelf life, food safety, and quality by providing information and warning about potential problems (Yam et al., 2005). Primary value of IP systems is the ability to communicate, which is achieved by using smart packaging devices. One such device is the radio frequency identification (**RFID**) tag, which has been applied successfully at product level in the dairy sector (Regattieri et al., 2007). The RFID tags offers great potential to improve security, productivity, inventory control, and traceability in food supply chains (Wang et al., 2006), and may also be integrated with various package indicators (time-temperature indicator, gas indicator, or biosensors). Several AP and IP systems have been developed and successfully applied in many countries outside Europe. In the EU, their large scale implementation requires regulatory amendments (Vermeiren et al., 1999; De Kruijf et al., 2002; Lopez-Rubio et al., 2004).

2.4 Materials and Methods

In this paper the method of scenario development is used to compose possible future situations for the dairy production chain in the Netherlands. Scenarios answer the question: “What can happen if the Dutch dairy production chain develops in a certain way?” Therefore, the scenarios aim at exploring the possible consequences of different future developments implied by the chain’s strategic interests. The developed scenarios support a strategic orientation (Westhoek et al., 2006) because they envision different futures that the stakeholders need to prepare for in order to establish a robust long-term strategy. According to Van Notten et al. (2003), the developed scenarios are: *descriptive* – exploring possible futures; *forecasting* – exploring different developments starting from the present; *institution-based* – considering the development of the dairy production chain; *short-term* – considering a time span ranging from 5 to 20 years;

national – focusing only on the Netherlands. Regarding the process design, scenarios are: *qualitative* – presented in a narrative way without formal models; and *combining participatory approach and desk research* – constructed by collecting data from experts, stakeholders, and the literature.

The involvement of stakeholders and experts, which is an increasingly vital data collection method in recent scenario studies (Van Asselt and Rijkens-Klomp, 2002; Van Notten et al., 2003), played a key role in developing the scenarios. In 2007, a workshop was organized to investigate the potential for increasing the value added in the Dutch dairy production chain. It was inspired by the demand of chain stakeholders to improve and protect its competitive position of the Dutch dairy chain. The workshop lasted two days, and to optimally exploit opportunities there was one week between the first and the second day. Because good group support and facilitation are important (Kwok et al., 2002), the workshop took place in the T-Xchange Cell <http://www.txchange.nl>, Twente University, the Netherlands. This is a specially designed 'innovation-inducing' environment that offers opportunities for accelerating and enhancing innovation and development processes. The T-Xchange Cell can be considered a group support system, equipped with computer-based technology, involving groups of participants and facilitation (Ackermann et al., 2005).

Two main groups of participants were invited: stakeholders from the dairy production chain (8) and dairy experts (6). They were selected on the basis of their expertise and experiences in the dairy sector. Participants represented dairy co-operatives (4), a major livestock improvement company (2), dairy farmers (2), the national dairy organization (1), universities (3), and an organization linking science and business (2). Except for the overall objective, no information was given to the participants beforehand, so as to avoid any bias in the results. Under the guidance of the facilitation team (8), the participants took four successive steps, where each step resulted in information for the next step. The steps included: becoming acquainted with the problem definition and objective; identifying the current trends and developments by brainstorming to let participants broaden their solution space; constructing innovative scenarios based on the objective and on the outcomes of the brainstorming; and visualizing the scenarios to enhance the development of ideas and communication among the parties. The first two steps were taken on the first day. The first step comprised an opening plenary session, and was followed by a group session (second step) where the trends and developments were discussed. The third step and fourth step took place during the second day, when the scenarios were developed in a group session (third step), followed by a plenary session in which the scenarios were visualized (fourth step). During the group sessions the participants were divided into two groups to equally represent all stakeholders in each group.

2.5 Results

The outcomes of the workshop were a summary of the scenarios, the minutes of both days' sessions, mind maps, and pictures. Using the outcomes, three scenarios were developed that are relevant for the Dutch dairy production chain to increase the value added in the coming years: 1) scenario *Designer Milks*, 2) scenario *Active Logistics*, and 3) scenario *Glasshouse-Cow*. Below, summaries of the scenarios and their implications are presented.

2.5.1 Scenario *Designer Milks*

Designer Milks envisions the prevalence of producing raw milk with specific characteristics, meaning that farmers no longer produce commodity milk. In this scenario, the Dutch dairy production chain has a keen interest in improving the intrinsic and perceived values of milk. As initial steps in this direction have already been taken in the Netherlands, *Designer Milks* can be regarded as a baseline scenario.

In *Designer Milks* there is differentiation among farms, that is, farms deliver different types (in terms of taste and quality) of milk. Farmers use novel methods to produce specialized raw milk, including selective breeding, tailor-made cow diets, and on-farm milk segregation. First, biotechnology is intensively used to improve the dairy herds; therefore cattle genome has been further explored, enabling breeders to target specific genes in order to choose milk types that consumers or industries want. Transgenic methods are not used, because they are technologically inefficient, expensive, and rejected by consumers. Second, cows' diets are based on fresh herbage and supplemented with a number of tailor-made feeding additives to specifically change the composition of raw milk. Third, AMS is widely used in the Netherlands, and milking systems are equipped with biosensors that measure milk composition. Farmers, therefore, segregate different types of milk on a daily basis.

The differentiation of raw milk has two main objectives. First, some farms produce milk with altered fat composition by lowering the fat fractions that are proven to be injurious to human health and by increasing the healthy fatty acids. Raw milk with healthier fat is used to produce milk and derived dairy products that decrease the risk of cardiovascular diseases. Second, some farms produce milk with the desired concentrations and variants of major milk proteins; this type of milk is destined for cheese production or ingredient production. Developments in this direction are desirable as cheese production plays a central role in the Netherlands' dairy production chain: about 50% of milk is used for cheese manufacturing, and cheese exports represent more than half the chain's total export value.

This scenario assumes realization in 5 to 10 years. The fastest way to produce differentiated milk is by changing the cows' diets. Feeding supplements to change fat composition are already marketed in the Netherlands, and further developments in this area are expected. Animal breeding to achieve this scenario will take longer. Although promising results in animal selection supported by genetic tools are available, it takes several years before a breeding decision affects the cows in the herd.

2.5.2 Scenario *Active Logistics*

Active Logistics envisions the Dutch dairy production chain with innovative logistics for different milk flows. A new set-up for the dairy supply chain is established with the purpose of producing fresher and more customized milk and derived products with improved shelf life.

In *Active Logistics* the length of the dairy chain is reduced to improve overall quality and freshness. First, new methods are used for storing and transporting milk. Raw milk is no longer stored for two or three days at dairy farms without any treatments prior to collection. During on-farm storage, active storage facilities are used to inactivate bacteria in raw milk, aiming for early preservation to improve shelf life and food safety. Also, collection of raw milk from farms to dairies has changed. Tankers no longer carry merely one milk type but collect different milk types from one or more farms separately yet simultaneously. Tankers are equipped with a specifically designed container-frame to carry containers accommodating different types of milk. Active containers are used on tankers for preserving the milk, thereby further improving shelf life and overall quality during collection. As a result of the early preservation on farms and during milk collection, the processing of raw milk in dairy plants no longer involves steps of food preservation. Different milk flows are delivered directly for the manufacturing of different products.

Second, novel solutions are applied in packaging and distributing dairy foods to further reduce the chain and to enhance consumer involvement. Food packages combine active and intelligent features by, for example, adding bacteria to milk to sour it according to customer preferences. Packages are compatible with a new generation of household equipments used by consumers to customize milk and dairy products in their homes by adding fragrance, taste, or health-promoting substances. Packages also have intelligent properties (RFID tags) indicating the origin of the milk used. In short, by using novel packages, processing of raw milk into end products is further reduced, and consumers purchase dairy foods that originate from their preferred region or farm. Furthermore, novel product delivery concepts are implemented. Dairy products are purchased via the internet from dairy processors who deliver directly to consumers in a ‘cooled mailbox’. This new way of dairy distribution has two major effects. First, the retail trade in the dairy chain is reduced. Second, as dairy processors merchandize their products directly, the chain obtains more information on consumer preferences, enabling the production of product portfolios that better respond to the changing market.

The scenario *Active Logistics* can be realized in a somewhat longer term than the previous scenario. Specifically, setting up an integrated logistics and decision support system in the dairy production chain is expected to become feasible within the next 10 to 15 years.

2.5.3 Scenario *Glasshouse-Cow*

Glasshouse-Cow describes the Dutch dairy production chain with ecologically sustainable dairy farming. Central concepts of this scenario are the prevention of the on-farm losses of natural resources, the production of bioenergy, and the enhancement of animal welfare.

In *Glasshouse-Cow* the dairy farms are equipped with novel housing facilities and new on-farm technologies. Cows are kept indoors in order to strengthen the principle of closed circuit by controlling the flow of materials such as gas, water, electricity, fodder, milk, manure and biological wastes. Dairy farms are equipped with anaerobic fermentation units (digesters) to convert surplus manure and organic wastes into biogas. The digested manure is used as fertilizer in crop production, which significantly reduces the use of inorganic fertilizers. Also, the methane produced by the cows' enteric fermentation is captured by the internal ventilation system and used in biogas production. The biogas produced is utilized not only for heating and cooking on-farm but also for supplying dairy factories with biogas via existing natural gas networks. In addition to biogas, the roofing materials of the housing facilities on the farms can collect and convert solar energy into a usable energy source. The production of biogas from manure and biological wastes, together with the usage of solar energy has a twofold benefit. First, they have considerable environmental benefits by reducing not only the emissions of odor, ammonia, and GHG into the air, but also nutrient leaching and surface run-off. Second, they have economic benefits by providing alternative and renewable energy sources to the limited conventional energy sources. By using such energy sources, the scenario *Glasshouse-Cow* envisions that the dairy farming is self-sufficient in energy and no longer relies on fossil fuels.

Furthermore, because the cows are kept indoors the housing conditions of the animals are significantly improved. Dairy farmers no longer keep cows in conventional dairy stables. Instead, similar to the circumstances in which zoo animals are kept, the novel dairy housing facilities are formulated to resemble the cows' natural environment. The novel stables enclose the cows and their environment into one housing complex, where animals walk and graze inside a building constructed to resemble a pasture. Also, novel floors and lighting are implemented that are tailored specifically to the needs of the cows. Furthermore, the housing complex is covered with a transparent material to make dairy farming visible to consumers, thereby stressing the importance of the people behind the initiatives attached to animal welfare. In this scenario, the most important message to society is that milk and dairy products are healthy and made in a natural and environmentally sustainable way.

In the scenario *Glasshouse-Cow* dairy farming significantly reduces energy usage, nutrient losses, and GHG emissions, while it enhances the welfare of the cows. Eventually, these achievements towards an ecologically sustainable dairy farming are communicated to consumers, who are informed about the origin of the product they consume. The visions of this scenario might be the most futuristic amongst the presented scenarios. Although initial steps in the directions outlined in the scenario have been taken already in the Netherlands (including research and pilot projects), presumably the *Glasshouse-Cow* concepts could be implemented on national scale no sooner than two decades from now.

2.5.4 Major implications of the scenarios

In this section, the domains of the major implications of the developed scenarios are discussed in a qualitative manner. That is, the potential consequences are assessed without going into quantified details. The workshop participants addressed the topics economic implications, chain organization, risk factors, ethical aspects, and environmental implications.

Economic Implications. In *Designer Milks*, to preserve economically sustainable dairy farming, the health of the cows is crucial. Therefore, the new breeding and feeding strategies have to consider whether or not they have any adverse effects on the cows' fertility, susceptibility for diseases, and longevity. *Active Logistics* involves large initial investments for the different actors within the dairy production chain. The farmers need to purchase active storage facilities, while dairy processors need to invest in novel milk containers and packaging systems. The direct delivery of dairy products to consumers entails further transportation costs for dairy processors. It is important to note that the storage and collection of different milk flows are important aspects in both *Designer Milks* and *Active Logistics*. In the scenario *Glasshouse-Cow* farmers need to invest into new housing facilities and implement bioenergy-producing machinery. In turn, however, economic benefits can be realized due to energy savings from the use of generated biogas, sales of organic by-products, and reduced use of inorganic fertilizers.

Chain Organization. First, in each scenario, dairy farmers need financial incentives to be compensated for the extra on-farm costs, lost revenues, and risks. Therefore, the dairy processors have to modify their payment schemes to reward the specialized composition in *Designer Milks*, the early preservation in *Active Logistics*, and the ecological sustainability in *Glasshouse-Cow*. However, it is important that not only incentives but also government policies can force developments. For example, the introduction of new standards for milk composition or new subsidy programs for biogas production could facilitate novel management strategies. Second, *Active Logistics* has a profound impact on the organization of the dairy production chain due to the reorganized logistics, the reduced processing of raw milk into dairy products, and the new ways of distributing dairy foods. However, these changes in the dairy chain organization might be complicated given its long establishment in the Netherlands.

Changing the set-up of the Dutch dairy chain not only demands extensive consultation but also audacity and leadership.

Risk Factors. The three scenarios inherently involve uncertainties such as new production technologies and forecasted demand, expenditures, and revenues. Also, the discontinuation of a new strategy due to technology developments, decreased consumer demand, or oversupply represents uncertainty. This uncertainty is a critical point because different new methods require different initial investments and have different learning periods. Therefore, in the case of discontinuation, the break-even premiums required to cover the initial investments and lost revenues might become substantially higher. Another risk factor is the farmers' technology adoption rate, which is important in determining the introduction and volume of production. Technology adoption rate can be influenced by volatile food (milk) prices. More specifically, increasing food prices are likely to lead to higher profitability, thereby lowering the farmers' incentives to adopt innovation strategies; whereas decreasing food prices are likely to have the opposite effect. Moreover, the consumer acceptance of the novel ways of producing milk and dairy products is uncertain. It is especially important with regard to the foreign markets of the Dutch dairy chain, given that some 70% of the Dutch dairy production is exported.

Ethical Aspects. In each scenario, the implemented changes in the dairy chain have to be accepted by the Dutch consumer. In *Designer Milks*, milk with special characteristics should not be produced at the expense of the health and welfare of the dairy cows. In the case of *Active Logistics*, direct dairy distribution via internet requires regulatory changes to allow dairy processors to handle personal purchase information. For *Glasshouse-Cow*, the society needs to accept that dairy cows are kept indoors, so public discussion is necessary with Dutch consumers and community organizations that traditionally prefer to see the animals kept outside. The Dutch consumers have to be informed not only about the ecological advantages of keeping the animals indoors but also about the improved housing conditions that are specifically tailored to the needs of the animals.

Environmental Implications. Future dairy production in the Netherlands has to be ecologically sustainable, and this issue has to play a key role in developments in the Dutch dairy chain. In *Designer Milks*, therefore, the application of novel cow diets to produce differentiated raw milk should not lead to additional nutrient losses and GHG emissions. With *Active Logistics*, the reduction of the dairy supply chain by early preservation, joint transportation of different milk flows, and direct delivery to consumers can substantially change energy use in the dairy sector. With regard to the environmental considerations, the scenario *Glasshouse-Cow* is the most desirable as it aims at the creation of environmentally sustainable dairy farming.

2.6 Discussion

2.6.1 Scenario *Designer Milks*

The scenario *Designer Milks* builds on developments in farming practices such as selective breeding, animal nutrition, and farm management. In this scenario, growing consumer demand for dairy products with enhanced nutritional values is addressed by production of milk with a healthier milk-fat composition. However, scientific research is needed before deciding which fat fractions will be decreased and which increased, given that the exact impact of some fatty acids on human health are not known. German and Dillard (2006) and Steijns (2008) provide a thorough overview of the existing knowledge on how intake of dairy products may influence health, thereby offering opportunities for potential improvements. With respect to improving milk's cheese-making properties, it serves the growing aim of the processing companies for a more cost-efficient production. In the literature, a number of strategies are discussed to produce milk with specialized characteristics as improved raw materials (Boland et al., 2001).

Because the scenario *Designer Milks* considers selective breeding, a relevant aspect to consider in this scenario is the changes in breeding objectives. As discussed earlier, the new breeding strategies have to consider their effects on the cows' health and welfare. Therefore, social and ethical aspects of animal production have to be included when defining the novel breeding goals because of increased public concern (Olesen et al., 2000; Gamborg and Sandøe, 2005; Oltenacu and Algers, 2005). Another important aspect is the impact of changing raw milk composition on product quality. Regarding designer milks with improved health benefits, it has been shown that milk with a more unsaturated fatty acid profile can successfully be processed into cheese and butter with softer textures, and acceptable organoleptic and storage properties (Middaugh et al., 1988; Stegeman et al., 1992; Ryhänen et al., 2005). Regarding designer milks for more efficient dairy manufacturing, Guinee et al. (1998) found that changing protein composition to improve cheese production has no effect on the functionality (melt time, flowability, stretch and viscosity) of the end product.

2.6.2 Scenario *Active Logistics*

By reducing the length of the dairy supply chain in the scenario *Active Logistics*, the Dutch dairy chain reacts to the increasing demand for minimally processed fresher foods with improved sensory values and acceptable shelf life. The scenario builds on the advances in the following segments of the food industry: milk storage, dairy packaging systems, and food delivery practices. The visions for novel ways of distributing dairy foods are in line with the visions of Sonesson and Berlin (2003), who described scenarios for a future milk supply chain in Sweden. By studying the effects of different scenarios on the environment, Sonesson and Berlin (2003) found that the increasing demand for more and fresher products affects the environmental impact of several parts of the dairy chain.

As discussed above, the storage and collection of different milk flows are important aspects to consider in the in the scenario *Active Logistics*. There are two distinct settings. First, farmers can be fully specialized in producing one type of milk, and thus no extra storage facilities are needed on the farm. However, because the locations of the participating farmers might become more dispersed, the milk tanker collection route would have to be modified, thereby increasing transportation costs. Second, farmers could produce commodity milk as well as specialized milk. Consequently, extra storage facilities may be required to segregate different milk types on-farm and during collection, and the transportation costs are likely to grow. Dooley et al. (2005b) studied the effects of producing and segregating different types of raw milk at farm level on transportation costs for dairy farmers in New Zealand. They found that the collection of two types of milk increased the transportation costs by 4.5 to 22%.

2.6.3 Scenario *Glasshouse-Cow*

In the scenario *Glasshouse-Cow*, the Dutch dairy chain addresses the problems of nutrient losses, GHG emissions, energy consumption, and animal welfare. These issues are challenges for the nutrient-intensive Dutch dairy farming in achieving ecological sustainability (Van Calker et al., 2005a). Other possible strategies to cope with the environmental concerns of future dairy chains have been also studied in the literature. Sonesson and Berlin (2003) developed different scenarios for the Swedish dairy chain to explore the environmental impacts of future dairy chains. They found that packaging materials used, energy usage, and the transportation of the dairy products to households are important factors when improving the dairy chain from environmental point of view. Furthermore, they demonstrated that any consideration of the environmental effects of the milk supply chain must consider the entire chain. However, Sonesson and Berlin (2003) did not include agriculture in the analysis.

Scenario *Glasshouse-Cow*, therefore, offers another pathway to improve the ecological sustainability of the dairy chain by changing the conventional ways of dairy farming. Van Calker et al. (2005b) studied the sustainability of different dairy farming systems in the Netherlands. They studied the application of an already existing commercial approach in Dutch dairy farming that balances between economic growth, social progress, and environmental protection. They suggested that a holistic, bottom-up strategy, in which the partners and stakeholders of the dairy chain co-operate, is needed to develop dairy production in a more sustainable way.

In scenario *Glasshouse-Cow*, the treatment of livestock waste and the utilization of biomass have important economic considerations. Tangible economic benefits can be expected because good livestock waste treatment can become a new income source for farmers (Burton and Turner, 2003; Weiland, 2006). It is unlikely, however, that the treatment systems can fully cover their costs related to investments, labor, and land. In the European countries, therefore, in most cases net financial earnings are only possible with grants supporting the initial capital investments and with high valuation of the produced energy (Burton and Turner, 2003). Livestock-waste treatment systems are overall financial charges to the farmers, and thus they need financial compensation to remain competitive. Consequently, pressuring environmental regulations and supporting grants by local and national governments are likely to remain the major forces in promoting such environmental technologies in the EU (Burton and Turner, 2003; Abraham et al., 2007).

2.6.4 Future research

The three scenarios address different trends and build upon different technological advances. The present study discusses qualitatively the implications of the developed scenarios. In future studies, however, it will be desirable to quantify the economic consequences, in addition to a qualitative assessment. Because the field of value-added dairy methods is relatively new, so far the quantitative economic modeling has been limited to the methods described in our baseline scenario, *Designer Milks*. More specifically, the economic consequences of producing raw milk with specific characteristics have been modeled. Maynard and Franklin (2003) studied the implementation of novel cow diets to produce dairy products rich in conjugated linoleic acids (**CLA**) for small-scale US dairy farms. They showed that the farmers would break even if the retail premiums of the high-CLA products were less than 15% of their typical retail prices. Those premiums were comparable with the results of the willingness-to-pay surveys, showing great market opportunities for small-scale niche dairy product manufacturing using advances in animal nutrition. Dooley et al. (2005a) investigated the cost implications of implementing novel breeding strategies for New Zealand dairy farmers to produce two particular types of milk: milk with 'whiter milk-fat' and milk with improved cheese-making properties. In the case of the former milk type, they found that farmers would require from 38% higher milk fat prices to break even; whereas, in the case of the latter milk type the necessary premium ranged from 3 to 5% for both milk-fat and milk-protein. However, there are still aspects of producing raw milk with specialized values that have not been investigated. Certainly, important are the effects of novel production strategies on cow replacement decisions, given their high economic importance to dairy owners and managers (Dijkhuizen and Stelwagen, 1988; Lehenbauer and Oltjen, 1998). Therefore, future quantitative research is needed to investigate the effects of different strategies on cow replacement, which can be successfully done by formal model calculations (Jalvingh, 1992).

2.7 Conclusions

For the dairy chain in the Netherlands the pursuit of continuous innovation and the delivery of value-added products to consumers will be critical to ensure long-term market development in an increasingly competitive industry. The objective of this paper was to help stakeholders to better adapt to the future. Our study shows that developing scenarios using a participatory approach allows for exploring future strategies for the dairy chain. By organizing a workshop involving industry stakeholders and experts, we developed three scenarios: *Designer Milks*, *Active Logistics*, and *Glasshouse-Cow*. They address major trends affecting the Dutch dairy sector, including changing consumer preferences, increasing pressure for more cost-efficient production, and rising environmental concerns. The scenarios describe different dairy production chains in a rather extreme manner; that is, depicting the outer boundaries of what is possible to ensure that the differences between them stand out clearly. Not every vision is considered likely to occur. Rather, the scenarios indicate directions in which the dairy chain in the Netherlands might develop in the next 5 to 20 years. Although these directions are discussed separately, the scenarios are not necessarily mutually exclusive alternatives; different developments may occur simultaneously. The scenarios also show that when improving the dairy sector it is important to consider the entire chain, and hence concerted and co-ordinated actions by the various stakeholders are necessary. The study is an initial step in assessing the potential for increasing the value added in the Dutch dairy production chain. Further studies quantifying the consequences of different scenarios are necessary.

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3

Effects of milk fat composition, *DGAT1*, and *SCD1* on fertility traits in Dutch Holstein-Friesian cattle

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Journal of Dairy Science (2009) 92:5720-5729

Abstract

Recently, selective breeding was proposed as a means of changing the fatty acid composition of milk to improve its nutritional quality. Before implementing such breeding objectives, effects on other economically important traits should be investigated. The objectives of this study were to examine 1) the effect of milk-fat composition, and 2) the effect of polymorphisms of *DGAT1* and *SCD1* genes on female fertility in commercial Dutch Holstein-Friesian cattle. Data on 1,745 first-lactation cows were analyzed by fitting linear mixed models. We found that higher concentrations of *trans* fatty acids within total milk-fat negatively affected reproductive performance. Furthermore, results suggested a potential effect of the *DGAT1* polymorphism on nonreturn rates for insemination 28 and 56 d after the first service. Our results can be used to assess the correlated effects of breeding for improved milk-fat composition on reproduction, thereby allowing for better evaluation of breeding programs before implementation.

Key words: dairy cattle, milk-fat composition, *DGAT1, SCD1*

3.1 Introduction

Because of biotechnological advances and a more complete knowledge of the cattle genome, there are new opportunities for producing raw milk with specific characteristics (Boland et al., 2001; Creamer et al., 2002). By using selective breeding, different types of raw milk can be produced to meet specific consumer needs or industrial demands. Recently, the opportunities to use selective breeding to change the fatty acid (**FA**) composition of milk have been investigated extensively. Changing the milk FA profile can improve the nutritional quality of milk and thus can lead to improved dairy products for human health.

Selective breeding to change milk FA composition can take two primary directions. First, cows can be selected for an individual milk FA or for a group of milk FA, because several milk FA have recently been shown to have genetic variation within various US (Bobe et al., 2008), Belgian (Soyeurt et al., 2007; Soyeurt et al., 2008), and Dutch (Stoop et al., 2008) dairy cattle breeds. Second, cows can be selected for particular genotypes. Two genes have recently been suggested as candidates: the gene coding for acyl-CoA: diacylglycerol acyltransferase 1 (***DGAT1***) and the gene coding for stearoyl-CoA desaturase 1 (***SCD1***). The *DGAT1* gene is located on chromosome 14 in cattle (Grisart et al., 2002; Winter et al., 2002), and plays a key role in triacylglycerol synthesis. A lysine-to-alanine polymorphism in *DGAT1* (**K232A**) has been shown to affect milk FA composition (Schennink et al., 2007) and to explain some of the genetic variation in the milk-fat unsaturation indices in Dutch Holstein-Friesian cows (Schennink et al., 2008). The *SCD1* gene, which codes for a key enzyme in the cellular biosynthesis of monounsaturated FA, is located on chromosome 26 in cattle (Chung et al., 2000). An alanine-to-valine polymorphism in *SCD1* (**A293V**) has been found to influence milk FA composition in various Italian breeds (Mele et al., 2007; Moioli et al., 2007; Macciotta et al., 2008) and in Dutch Holstein-Friesian cows (Schennink et al., 2008).

Before selecting for specific milk FA or candidate genes, however, effects on other economically important traits should be investigated. A relevant trait to consider is the reproductive performance of cows, given its high economic importance to dairy owners and managers (Lehenbauer and Oltjen, 1998). Little (and contradictory) information is available on the effects of *DGAT1* variants on fertility traits (Ashwell et al., 2004; Kaupe et al., 2004; Wathes et al., 2008). Kaupe et al. (2007) found that the K allele had a negative effect on maternal nonreturn rate. Oikonomou et al. (2009), however, showed that the A allele increased the number of inseminations per conception and the presence of reproductive problems, and decreased the conception rate in the first 305 d of lactation. To our knowledge, estimates of the effects of milk FA composition and *SCD1* variants on the reproductive traits of dairy cattle are missing from the literature. The objectives of this study were to examine 1) the effect of milk-fat composition, and 2) the effect of the *DGAT1* K232A polymorphism and the *SCD1* A293V polymorphism on fertility traits in commercial Holstein-Friesian dairy cattle in the Netherlands.

3.2 Materials and Methods

3.2.1 Animals

We used data from the Dutch Milk Genomics Initiative, which focuses on the genetic background of detailed milk composition (Schennink et al., 2007; Stoop et al., 2007; Schopen et al., 2009). Data regarding 1,745 first-lactation cows distributed among 394 commercial herds throughout the Netherlands were collected. Participation invitations to the farms were based mainly on pedigree according to the database of the cooperative cattle improvement organization CRV (Arnhem, the Netherlands), which provided records on pedigree, yield, and reproduction. Each cow was over 87.5% Holstein-Friesian. The cows descended from one of either five proven bulls (807 cows), 50 test bulls (771 cows), or 15 additional proven bulls (167 cows). Offspring from the last group of bulls were added to ensure sampling of at least three cows per herd. Further details on the animals used in this study are provided by Stoop et al. (2007).

3.2.2 Phenotypes

From the records on reproductive performance, the following eight fertility traits were derived: interval (d) between the first and second calving (**CI**), interval (d) between calving and the first insemination (**DFS**), number of inseminations **(NINS)**, nonreturn rate (0/1) for insemination 28 d after the first insemination (**NR28**), nonreturn rate (0/1) for insemination 56 d after the first insemination (**NR56**), nonreturn rate (0/1) for insemination 90 d after the first insemination (**NR90**), rate (0/1) of calving after the first insemination (**CFI**), and rate (0/1) of calving after any inseminations (**CR**). Records for CI were considered missing if an animal did not have a known next calving date, or if the CI was shorter than 300 d or longer than 800 d. Records for DFS were set to missing if the DFS was smaller than 20 d or greater than 300 d. The NINS was set to missing if its value was 0 or greater than 10. These criteria were applied to exclude unrealistic, unrepresentative or erroneous records under Dutch conditions (Calus et al., 2005).

Cows were milked twice a day, and a morning milk sample from each cow was analyzed between February and March 2005. Each cow was between 66 and 282 d in lactation. Milk FA composition was measured by gas chromatography at the COKZ laboratory (Leusden, the Netherlands) as described by Schennink et al. (2007). The FA were expressed as a proportion of total fat weight. Fatty acids included in this study were grouped according to their relevance to human health (German and Dillard, 2006). Fat and protein concentrations were measured by infrared spectroscopy by using a Fourier-transform interferogram (MilkoScan FT 6000, Foss Electric, Hillerød, Denmark) at a Milk Control Station (Zutphen, the Netherlands). Furthermore, lactation yield records based on 305-d production for milk, protein, and fat were provided by CRV. In total, data regarding milk FA composition and the five production traits were missing for 19 animals.

3.2.3 Genotypes

Blood samples for DNA isolation were collected between April and June 2005. Genotyping of the *DGAT1* and the *SCD1* polymorphisms were performed as described by Schennink et al. (2007) and Schennink et al. (2008), respectively. Because either no DNA sample was available or the sample could not be genotyped unambiguously, the genotype for *DGAT1* was missing for 12 animals, and the genotype for *SCD1* was missing for 66 animals. When studying the effects of polymorphism of the candidate genes, we also accounted for production traits (see Statistical Analysis section below). To consistently study the effects of the genes, therefore, animals were excluded if no information was available about the five milk production traits.

Table 1. Descriptive statistics of individual fatty acids, fatty acid groups, and production traits of 1,726 first-lactation Dutch Holstein-Friesian cows

Trait	Mean	Minimum	Maximum	SD
Fatty acid (%, wt/wt)				
C4:0	3.51	2.44	4.57	0.28
C5 to 15[1]	1.47	0.72	3.90	0.32
C6 to 12[2]	10.73	5.10	15.50	1.24
C14:0	11.62	6.17	14.94	0.93
C16:0	32.60	22.86	42.95	2.85
C18:0	8.72	3.19	17.12	1.43
C18u[3]	22.35	15.29	41.14	2.57
CLA[4]	0.40	0.02	1.25	0.11
TFA[5]	1.64	0.75	7.74	0.41
SFA/UFA[6]	2.75	1.08	4.16	0.36
Production trait				
305-d milk yield[7] (kg)	7,622.71	3,970.00	12,404.00	1,207.57
305-d protein yield[7] (kg)	262.44	149.00	404.00	40.22
305-d fat yield[7] (kg)	326.64	170.00	509.00	48.55
Protein concentration[8] (%)	3.50	2.67	4.59	0.30
Fat concentration[8] (%)	4.36	1.46	9.08	0.70

[1] C5 to 15 includes saturated fatty acids C5:0, C7:0, C9:0, C11:0, C13:0, and C15:0.

[2] C6 to 12 includes saturated fatty acids C6:0, C8:0, C10:0, and C12:0.

[3] C18u includes the unsaturated C18 fatty acids C18:1 *trans*-6; C18:1 *trans*-9; C18:1 *trans*-10; C18: 1 *trans*-11; C18:1 *cis*-9; C18:1 *cis*-11; C18:1 *cis*-12; C18:1 *cis*-13; C18:2 *cis*-9,12; C18:3 *cis*-9,12,15; C18:2 *cis*-9, *trans*-11; and C18:2 *trans*-10, *cis*-12.

[4] Conjugated linoleic acid (CLA) includes C18:2 *cis*-9, *trans*-11.

[5] *Trans* fatty acids (TFA) include C16:1 *trans*-9, C18:1 *trans*-6, C18:1 *trans*-9, C18:1 *trans*-10, and C18:1 *trans*-11.

[6] Saturated fatty acids (SFA) include C4:0, C5:0, C6:0, C7:0, C8:0, C9:0, C10:0, C11:0, C12:0, C13:0, C14:0 *iso*, C14:0, C15:0 *anteiso*, C15:0, C16:0 *iso*, C16:0, C17:0 *iso*, C17:0, C18:0, C20:0, C21:0, and C22:0. Unsaturated fatty acids (UFA) include C10:1; C12:1; C14:1 *cis*-9; C16:1 *trans*-9; C16:1 *cis*-9; C17:1 *cis*-9; C18:1 *trans*-6; C18:1 *trans*-9; C18:1 *trans*-10; C18:1 *trans*-11; C18:1 *cis*-9; C18:1 *cis*-11; C18:1 *cis*-12; C18:1 *cis*-13; C18:2 *cis*-9,12; C18:3 *cis*-9,12,15; C18:2 *cis*-9, *trans*-11; C18:2 *trans*-10, *cis*-12; C20:1 *cis*-11; C20:2 *cis*-11,14; C20:3 *cis*-8,11,14; and C22:1 *cis*-13.

[7] Provided by CRV (Arnhem, the Netherlands).

[8] Measured on single morning test-day milk samples collected between February and March 2005.

Two data sets were formulated and used in this study. The first data set, which included 1,726 animals, was used to study the effects of milk FA composition and the *DGAT1* polymorphism on fertility traits. Descriptive statistics of FA and milk production traits of the 1,726 animals are provided in Table 1. The average 305-d milk yield was 7,623 kg, and 305-d protein and 305-d fat yields were 262 and 327 kg, respectively. Protein and fat percentages averaged 3.5 and 4.4%, respectively. The reproductive performance of the 1,726 cows in the first data set is described in Table 2. The average length of the calving interval was 411 d, and the mean interval between calving and the first insemination was approximately 90 d. Approximately 10% of the cows did not have a second calving. The second data set included 1,661 animals and was used to study the effects of the *SCD1* polymorphism; descriptive statistics for the second data set are not shown because they are similar to those of the first data set.

Table 2. Descriptive statistics of fertility traits of 1,726 first-lactation Dutch Holstein Friesian cows

Trait[1]	Cows (no.)	Mean	Minimum	Maximum	SD
CI	1,551	410.57	304	795	74.93
DFS	1,721	90.02	21	284	36.76
NINS	1,724	2.09	1	10	1.50
CR	1,726	0.90			
NR28	1,726	0.72			
NR56	1,726	0.60			
NR90	1,726	0.52			
CFI	1,726	0.44			

[1] Fertility traits were interval between the first and second calving (CI), interval between calving and the first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after the first service (NR28), nonreturn rate for insemination 56 d after the first service (NR56), nonreturn rate for insemination 90 d after the first service (NR90), and calving rate following the first insemination (CFI).

3.2.4 Statistical analysis

Initial analyses were performed by using SAS 9.1 procedures (SAS Institute Inc., Cary, NC) to determine the significance of fixed effects. By using the MIXED procedure, linear mixed models were fitted as randomized block designs (Littel et al., 2006), with 394 herds as random blocks and individual cows as units of analysis.

Three modeling steps were performed. Model [1] was used to study the effects of milk-fat composition on fertility. Model [1] included DIM (days between the date of the first calving and the date of the milk sample), age at first calving, season of calving, and sire type (three different sire groups: proven bulls, young bulls, or other proven bulls). Relations between individuals were accounted for, and the total pedigree comprised 26,300 animals and was supplied by CRV. Variance components and fixed effects solutions were calculated by using the ASReml software package (Gilmour et al., 2006). Model [1] is written as

[1]
$$y_{ijklmno}=\mu+b_1\mathrm{DIM}_i+b_2\mathrm{e}^{-0.05\mathrm{DIM}_i}+b_3\mathrm{AFC}_j+b_4\mathrm{F}_k$$
$$+\mathrm{SEA}_l+\mathrm{SCO}_m+\mathrm{HERD}_n+a_o+e_{ijklmno},$$

where y is the dependent variable (fertility trait), μ is the general mean, DIM is a fixed covariate accounting for the effect of DIM modeled with a Wilmink curve (Wilmink, 1987), AFC is a fixed covariate describing the effect of age at first calving, F is a fixed covariate that accounted for the effect of one of the individual FA or FA groups, SEA is a fixed factor accounting for the effect of the calving season (June to August 2004, September to November 2004, or December 2004 to February 2005), SCO is a fixed factor capturing the effect of the differences in genetic level between proven bull daughters and young bull daughters, HERD is a random factor accounting for the effect of groups of animals sampled in the same herd, a is a random factor accounting for the additive genetic effect of the given animal, and e is the random residual effect. Each fertility trait was analyzed separately and each individual FA or FA group was also fitted separately (80 analyses in total).

To study the effects of the candidate genes, a model similar to model [1] was used. Model [2] excluded the covariate F and the correction for DIM (because no milk production trait measured on a single-day milk sample was involved), but included a fixed factor G that captured the effect of either the *DGAT1* genotype (AA, AK, or KK), or the *SCD1* genotype (AA, AV, or VV). Each fertility trait was analyzed separately and each polymorphism was also fitted separately (16 analyses in total). Model [2] is written as

[2]
$$y_{jlmnop}=\mu+b_1\mathrm{AFC}_j+\mathrm{G}_p+\mathrm{SEA}_l+\mathrm{SCO}_m$$
$$+\mathrm{HERD}_n+a_o+e_{jlmnop}.$$

To study the effects of candidate genes adjusted for production traits, model [2] was extended with a fixed covariate P that corrected for the effect of one of the five milk production traits (model [3]). Each fertility trait was analyzed separately, each polymorphism was fitted separately, and the correction for each of the production traits was modeled separately (80 analyses in total). When correcting for protein or fat concentrations, model [3] also included DIM to correct for DIM (modeled with a Wilmink curve) because those two production traits were measured on single test-day milk samples. Model [3] is written as

$$[3] \qquad y_{jlmnopq}=\mu+b_1\mathrm{AFC}_j+b_2\mathrm{P}_q+\mathrm{G}_p+\mathrm{SEA}_l+\mathrm{SCO}_m +\mathrm{HERD}_n+a_o+e_{jlmnop}.$$

Because the models above assumed normally distributed residuals, we also fitted generalized linear mixed models by using the GLIMMIX procedure in SAS 9.1 (Littel et al., 2006) for the count and binary variables. We assumed a Poisson distribution with log link function for NINS and a binomial distribution with logit link function for CR, NR28, NR56, NR90, and CFI. By fitting generalized linear models, the same fixed effects were significant as when the above linear models were fitted; therefore, we concluded that fitting linear mixed models was robust enough to handle the nonnormally distributed fertility traits.

In the above models, each individual FA, FA group, or polymorphism was fitted separately in a series of sequential analyses. In each analysis, the null hypothesis was of no FA or a polymorphism effect on the trait of interest. Because several fertility traits were analyzed, multiple hypothesis tests were performed. However, because of the correlations between those fertility traits, not all hypothesis tests were truly independent. To account for multiple testing, we considered the analyses of 1) CI, DFS, and NINS; 2) CR and CFI; and 3) NR28, NR56, and NR90 as three independent hypothesis tests. Bonferroni correction based on the method of Šidák (1967) was applied to account for multiple testing with regard to the three groups of fertility traits.

3.3 Results and Discussion

3.3.1 Effects of milk fat composition

To study the relation between milk FA composition and reproductive performance, we used the FA profiles from 1,726 first-lactation Dutch Holstein-Friesian cows (model [1]). Estimated effects of the FA and their significance are presented in Table 3. The *trans* FA (**TFA**) were consistently found to affect reproduction, because this FA group had significant ($P < 0.05$) effects on several fertility traits. Greater TFA concentrations

Table 3. Effects of individual fatty acids or fatty acid groups[1] on fertility traits[2] of 1,726 first-lactation Dutch Holstein-Friesian cows[3]

Fatty acid	CI (n = 1,551)	DFS (n = 1,721)	NINS (n = 1,724)	CR (n = 1,726)	NR28 (n = 1,726)	NR56 (n = 1,726)	NR90 (n = 1,726)	CFI (n = 1,726)
C4:0	−8.013 ± 7.102	−0.382 ± 3.263	−0.209 ± 0.130	−0.042 ± 0.026	0.011 ± 0.040	0.037 ± 0.044	0.059 ± 0.045	0.037 ± 0.044
C5 to 15	5.804 ± 6.211	1.361 ± 2.920	0.049 ± 0.114	0.049 ± 0.023*	−0.013 ± 0.035	−0.041 ± 0.039	−0.053 ± 0.040	−0.032 ± 0.039
C6 to 12	−1.493 ± 1.611	0.042 ± 0.757	−0.009 ± 0.030	0.002 ± 0.006	−0.005 ± 0.009	−0.009 ± 0.010	−0.001 ± 0.010	−0.001 ± 0.010
C14:0	−2.211 ± 2.123	−0.218 ± 0.988	0.013 ± 0.039	0.003 ± 0.008	−0.012 ± 0.012	−0.021 ± 0.013	−0.010 ± 0.013	−0.004 ± 0.013
C16:0	0.303 ± 0.703	−0.113 ± 0.328	−0.009 ± 0.013	0.004 ± 0.003	0.000 ± 0.004	0.005 ± 0.004	0.003 ± 0.004	0.004 ± 0.004
C18:0	−1.795 ± 1.418	−1.007 ± 0.640	0.005 ± 0.025	−0.011 ± 0.005*	0.000 ± 0.008	−0.001 ± 0.009	0.006 ± 0.009	0.003 ± 0.009
C18u	0.916 ± 0.791	0.412 ± 0.372	0.014 ± 0.014	−0.003 ± 0.003	0.003 ± 0.004	0.000 ± 0.005	−0.003 ± 0.005	−0.004 ± 0.005
CLA	9.090 ± 18.18	8.531 ± 8.656	0.495 ± 0.325	−0.009 ± 0.065	−0.125 ± 0.099	−0.178 ± 0.111	−0.197 ± 0.113**	−0.149 ± 0.111
TFAs	5.037 ± 5.148	2.030 ± 2.485	0.240 ± 0.089**	−0.038 ± 0.018*	−0.055 ± 0.027*	−0.096 ± 0.030**	−0.083 ± 0.031**	−0.075 ± 0.030**
SFA/UFA	−7.706 ± 5.530	−4.150 ± 2.567	−0.072 ± 0.100	0.005 ± 0.020	−0.011 ± 0.031	0.000 ± 0.034	0.019 ± 0.035	0.022 ± 0.034

[1] Groups of fatty acids are defined in Table 1.

[2] Fertility traits were interval between the first and second calving (CI), interval between calving and the first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after the first service (NR28), nonreturn rate for insemination 56 d after the first service (NR56), nonreturn rate for insemination 90 d after the first service (NR90), and calving rate following the first insemination (CFI).

[3] Values after ± signs are corresponding SE.

*Significant ($P < 0.05$); **Significant after Bonferroni correction.

were associated with lower reproductive performance. More specifically, increased proportions of TFA within total milk-fat resulted in larger (0.24) numbers of inseminations, lower (3.8%) calving rates, lower (5.5, 9.6, and 8.3%) nonreturn rates for insemination (28, 56, and 90 d after the first service, respectively), and lower (7.5%) calving rates after the first service. Associations between TFA concentration and NINS, NR56, NR90, and CFI were significant after Bonferroni correction. Although the relations between TFA and CI and DFS were statistically nonsignificant, those results also suggest a possible negative effect of TFA for these traits.

In addition to the TFA, other significant ($P < 0.05$) relations were found. The FA group C5 to C15 had a positive effect on reproduction because a greater proportion of C5 to C15 was associated with a higher (4.9%) calving rate. Larger concentrations of the individual FA C18:0 were associated with lower (1.1%) calving rates, indicating a negative effect of C18:0. A negative effect was found for conjugated linoleic acid (**CLA**) C18:2 *cis*-9, *trans*-11 content, because a larger proportion of CLA was associated with lower (19.7%) nonreturn rates for insemination 90 d after the first service. However, because the effects for C5 to C15, C18:0, and CLA were found only on single fertility traits, and because the relations became nonsignificant after Bonferroni correction, those findings are considered inconclusive. Regarding results for the remaining FA, no statistically significant association was observed between C4:0, C6 to C12, C14:0, C16:0, C18u, and the ratio of saturated FA to unsaturated FA and any of the fertility traits.

Milk FA composition can be changed by selective breeding (Soyeurt et al., 2007; Bobe et al., 2008; Stoop et al., 2008). Our findings regarding the effects of milk FA on fertility traits can be used to predict the correlated response of selection on FA composition. Whether a breeding program should aim to increase or decrease the concentration of a given FA or FA group to meet human health considerations should be weighed against correlated effects on the health and reproduction of the cow. Because of the contradictory published effects of TFA on human health (Bauman et al., 2006; German and Dillard, 2006; Jakobsen et al., 2006; Steijns, 2008), further research is needed to support the design of breeding programs. Our results indicate that selective breeding to decrease TFA concentrations could improve the fertility of cows.

3.3.2 Effects of the *DGAT1* K232A polymorphism

To investigate the effect of the *DGAT1* polymorphism on reproductive performance, we studied a total of 1,726 animals (model [2]). The frequency of the K allele was 40%, and the distribution of the genotypes in the sample was in Hardy–Weinberg equilibrium. The estimated effects of *DGAT1* variants are presented in Table 4. Our results indicated that the *DGAT1* polymorphism had a significant ($P < 0.05$) effect on two fertility traits: NR28 and NR56. Results for the different *DGAT1* variants showed a nonadditive pattern. More specifically, the AK genotype was associated with the lowest estimates for both NR28 and NR56, followed by the AA and the KK genotypes. Relative to cows with the AA genotype, cows with the AK genotype are expected to have lower (6 and 4%) nonreturn rates at 28 and 56 d after the first service. Cows with the KK genotype, however, are expected to have higher (1 and 5%) nonreturn rates at 28 and 56 d, respectively, when compared with cows with the AA genotype. Nevertheless, the effect of *DGAT1* on NR28 and NR56 became nonsignificant after Bonferroni correction, meaning the results are suggestive rather than conclusive. Associations between *DGAT1* and the other fertility traits (CI, DFS, NINS, CR, NR90, and CFI) were statistically nonsignificant.

Table 4. Effect of *DGAT1* polymorphism on fertility traits[1] of 1,726 first-lactation Dutch Holstein-Friesian cows[2]

Trait[1]	Cows (no.)	Predicted mean of AA genotype	AA–AK	AA–KK	*P*-value
CI	1,551	398.21	4.65 ± 4.22	−0.61 ± 5.82	0.439
DFS	1,721	88.67	0.34 ± 1.93	−3.97 ± 2.69	0.212
NINS	1,724	1.79	0.06 ± 0.08	−0.05 ± 0.11	0.499
CR	1,726	0.89	0.03 ± 0.02	0.02 ± 0.02	0.140
NR28	1,726	0.79	−0.06 ± 0.02	0.01 ± 0.03	0.024*
NR56	1,726	0.68	−0.04 ± 0.03	0.05 ± 0.04	0.037*
NR90	1,726	0.60	−0.02 ± 0.03	0.04 ± 0.04	0.275
CFI	1,726	0.53	−0.02 ± 0.03	0.04 ± 0.04	0.238

[1] Fertility traits were interval between the first and second calving (CI), interval between calving and the first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after the first service (NR28), nonreturn rate for insemination 56 d after the first service (NR56), nonreturn rate for insemination 90 d after the first service (NR90), and calving rate following the first insemination (CFI).

[2] Values after ± signs are corresponding SE.

*Significant ($P < 0.05$); nonsignificant after Bonferroni correction.

Because the *DGAT1* polymorphism has a strong influence on milk-fat content and other economically important milk production traits (Grisart et al., 2002; Winter et al., 2002), the effect of *DGAT1* on fertility might be due to its correlated effect on the production traits. Further analyses, therefore, were performed by correcting for one of the five production traits (model [3]). Table 5 shows the estimated effects of the *DGAT1* variants after correcting for production traits. Similar to the results above, the *DGAT1* polymorphism had significant ($P < 0.05$) effects on NR28 and NR56, independent of which production trait was included in the model, although results remained significant post Bonferroni correction only for NR28 after adjusting for fat concentrations. Moreover, the pattern of the estimated effects of different *DGAT1* variants remained nonadditive (heterozygous disadvantage). Among the three genotypes, the AK variant was consistently associated with the lowest nonreturn rates at 28 and 56 d. In short, the results of model [3] showed that effect of *DGAT1* on milk production traits could not explain the association found between *DGAT1* and fertility traits. Furthermore, the pattern of heterozygous animals being associated with lower nonreturn rates than homozygous animals remained. In conclusion, our results from model [2] and model [3] suggest a potential effect of *DGAT1* on nonreturn rates for insemination 28 and 56 d after the first insemination.

Table 5. Effect of *DGAT1* polymorphism on fertility traits[1] when correcting for production traits of 1,726 first-lactation Dutch Holstein-Friesian cows[2]

Trait[1]	Cows (no.)	Predicted mean of AA genotype	AA–AK	AA–KK	*P*-value
Correcting for 305-d milk yield					
CI	1,551	396.06	8.18 ± 4.17	8.54 ± 5.84	0.122
DFS	1,721	88.25	1.80 ± 1.92	−0.40 ± 2.73	0.523
NINS	1,724	1.79	0.11 ± 0.08	0.06 ± 0.11	0.393
CR	1,726	0.89	0.03 ± 0.02	0.03 ± 0.02	0.110
NR28	1,726	0.79	−0.06 ± 0.02	−0.01 ± 0.03	0.021*
NR56	1,726	0.68	−0.04 ± 0.03	0.03 ± 0.04	0.051*
NR90	1,726	0.60	−0.03 ± 0.03	0.01 ± 0.04	0.360
CFI	1,726	0.53	−0.03 ± 0.03	0.02 ± 0.04	0.328
Correcting for 305-d protein yield					
CI	1,551	397.37	5.36 ± 4.18	3.26 ± 5.80	0.446
DFS	1,721	88.72	0.72 ± 1.92	−2.52 ± 2.69	0.432
NINS	1,724	1.80	0.08 ± 0.08	0.01 ± 0.11	0.573
CR	1,726	0.89	0.03 ± 0.02	0.03 ± 0.02	0.114
NR28	1,726	0.79	−0.06 ± 0.02	0.00 ± 0.03	0.025*
NR56	1,726	0.68	−0.04 ± 0.03	0.04 ± 0.04	0.051*
NR90	1,726	0.60	−0.02 ± 0.03	0.02 ± 0.04	0.360
CFI	1,726	0.53	−0.02 ± 0.03	0.03 ± 0.04	0.304

Table 5. Continued

Trait[1]	Cows (no.)	Predicted mean of AA genotype	AA–AK	AA–KK	*P*-value
Correcting for 305-d fat yield					
CI	1,551	401.46	−0.62 ± 4.31	−7.32 ± 5.92	0.413
DFS	1,721	90.06	−1.31 ± 1.97	−6.17 ± 2.74	0.072
NINS	1,724	1.84	0.01 ± 0.08	−0.12 ± 0.11	0.459
CR	1,726	0.90	0.03 ± 0.02	0.02 ± 0.02	0.241
NR28	1,726	0.78	−0.05 ± 0.03	0.01 ± 0.03	0.031*
NR56	1,726	0.67	−0.03 ± 0.03	0.06 ± 0.04	0.038*
NR90	1,726	0.59	−0.01 ± 0.03	0.04 ± 0.04	0.266
CFI	1,726	0.53	−0.01 ± 0.03	0.05 ± 0.04	0.230
Correcting for protein concentration					
CI	1,551	400.32	7.59 ± 4.33	4.00 ± 6.07	0.212
DFS	1,721	90.89	1.91 ± 1.99	−1.18 ± 2.82	0.375
NINS	1,724	1.87	0.07 ± 0.08	−0.04 ± 0.12	0.497
CR	1,726	0.90	0.03 ± 0.02	0.01 ± 0.02	0.300
NR28	1,726	0.78	−0.06 ± 0.03	0.01 ± 0.04	0.026*
NR56	1,726	0.67	−0.03 ± 0.03	0.06 ± 0.04	0.039*
NR90	1,726	0.57	−0.02 ± 0.03	0.04 ± 0.04	0.261
CFI	1,726	0.53	−0.02 ± 0.03	0.04 ± 0.04	0.272
Correcting for fat concentration					
CI	1,551	397.75	12.29 ± 4.52	12.95 ± 6.58	0.023*
DFS	1,721	90.06	2.96 ± 2.08	0.95 ± 3.05	0.307
NINS	1,724	1.81	0.17 ± 0.08	0.14 ± 0.12	0.148
CR	1,726	0.90	0.03 ± 0.02	0.02 ± 0.03	0.191
NR28	1,726	0.80	−0.08 ± 0.03	−0.03 ± 0.04	0.009**
NR56	1,726	0.70	−0.07 ± 0.03	−0.01 ± 0.04	0.032*
NR90	1,726	0.60	−0.06 ± 0.03	−0.04 ± 0.04	0.135
CFI	1,726	0.56	−0.06 ± 0.03	−0.03 ± 0.04	0.128

[1] Fertility traits were interval between the first and second calving (CI), interval between calving and the first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after the first service (NR28), nonreturn rate for insemination 56 d after the first service (NR56), nonreturn rate for insemination 90 d after the first service (NR90), and calving rate following the first insemination (CFI).

[2] Values after ± signs are corresponding SE.

*Significant ($P < 0.05$); **Significant after Bonferroni correction.

Research has suggested that *DGAT1* might play a role in reproduction. First, in a recent study Schmidt et al. (2006) found that *DGAT1* was expressed in ovaries of hormone-treated rats. According to Schmidt et al. (2006), this finding suggests that *DGAT1* might be important for the cellular proliferation and differentiation needed for reorganization in the ovary, because the gene is important for mitosis in other tissues and is induced by FSH. Second, bovine chromosome 14, where *DGAT1* is located, has been studied extensively for QTL related to many economically important traits in cattle. Several studies have reported QTL, including *DGAT1*, on bovine chromosome 14 that affect various (male) fertility traits in different dairy cattle breeds (Daetwyler et al., 2008; Kolbehdari et al., 2008). In short, there is evidence that *DGAT1* could affect reproductive performance.

However, little is known about the direct association between the *DGAT1* polymorphism and reproductive traits in cattle. Kaupe et al. (2007) studied the allele-substitution effect on reproductive traits and showed a negative effect of the K allele on maternal nonreturn rate. Oikonomou et al. (2009), in contrast, found the A allele to be associated with a greater number of inseminations, lower conception rates, and a greater chance of reproductive problems. Kaupe et al. (2007) and Oikonomou et al. (2009) studied the gene substitution effect, meaning that the effects of the *DGAT1* polymorphism were captured by linear regression coefficients estimated for the covariate corresponding to the number of copies of the substitution allele. The pattern of our results, however, was different from those two studies.

Investigating the effects of the *DGAT1* polymorphism on fertility traits is important because this information can be used to evaluate selective breeding programs that exploit this polymorphism. As proposed by Schennink et al. (2007), the *DGAT1* polymorphism can be used in selective breeding to change the milk FA composition. They demonstrated that increasing the frequency of the A allele would be desirable from a public health point of view because of the association of this variant with more unsaturated FA. According to Schennink et al. (2007), an increase in the frequency of the A allele could lead to a decrease in the C16:0 fraction and an increase in the unsaturated C18 fraction by approximately 5 to 10%. Our results suggest that such a breeding goal could have consequences on reproduction. Replacing cows with the AK genotype with cows with the AA genotype could be positive, because it could lead to improved nonreturn rates for insemination (28 and 56 d) after the first service. However, increasing the frequency of the A allele by replacing cows with the KK genotype could have undesirable effect on reproductive performance. Because the allele frequencies found in our sample suggest a considerably greater proportion of AK than KK animals, selecting for cows with the AA genotype seems to be the most desirable with regard to nutritional quality concerns and the reproductive performance of the cows.

3.3.3 Effects of the *SCD1* A293V polymorphism

To study the effects of the *SCD1* polymorphism on fertility, we analyzed a sample of 1,661 first-lactation Dutch Holstein-Friesian cows (model [2]). The frequency of the A allele was approximately 73%, and the genotypes were in Hardy–Weinberg equilibrium. The estimated effects of the *SCD1* variants are presented in Table 6. As the results indicate, we found no significant effect on any of the reproductive traits. This finding was further reinforced by the results of the extended model correcting for production traits (model [3]; results not shown).

Stearoyl-CoA desaturase (**SCD**), which is also called Δ^9-desaturase, is an enzyme that introduces a *cis* double bond between carbon atoms C9 and C10 of the FA chain, thereby desaturating saturated FA to monounsaturated FA. Several SCD genes have been isolated in several species, and the isoforms are differentially distributed in different tissues.

Recent research has suggested that SCD isoforms might play a role in female fertility in mammalian species. Moreau et al. (2006) were the first to show the expression of SCD1 and SCD2 in rat ovary. They found several-fold higher expression for SCD2 than for SCD1, indicating that SCD2 is responsible for the Δ^9-desaturase activity in the ovary. Because the oocyte is rich in unsaturated FA, according to Moreau et al. (2006) monounsaturated FA formed in the cumulus cells via SCD2 activation can play a vital role in fertility. This assertion is based on the fact that removal of cumulus cells at the time of fertilization often results in lower fertilization rates in most mammalian species (Wang and Niwa, 1995; Zhang et al., 1995).

Table 6. Effect of *SCD1* polymorphism on fertility traits[1] of 1,661 first-lactation Dutch Holstein-Friesian cows[2]

Trait[1]	Cows (no.)	Predicted mean of AA genotype	AA–AV	AA–VV	*P*-value
CI	1,493	398.21	2.75 ± 4.05	5.72 ± 7.81	0.676
DFS	1,656	87.22	0.41 ± 1.88	1.96 ± 3.67	0.866
NINS	1,659	1.84	−0.03 ± 0.08	−0.04 ± 0.15	0.928
CR	1,661	0.90	0.02 ± 0.02	0.04 ± 0.03	0.318
NR28	1,661	0.76	0.01 ± 0.02	−0.01 ± 0.05	0.894
NR56	1,661	0.67	−0.01 ± 0.03	−0.01 ± 0.05	0.923
NR90	1,661	0.59	0.00 ± 0.03	−0.02 ± 0.05	0.935
CFI	1,661	0.53	−0.02 ± 0.03	−0.02 ± 0.05	0.814

[1] Fertility traits were interval between the first and second calving (CI), interval between calving and the first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after the first service (NR28), nonreturn rate for insemination 56 d after the first service (NR56), nonreturn rate for insemination 90 d after the first service (NR90), and calving rate following the first insemination (CFI).

[2] Values after ± signs are corresponding SE.

In the literature we found only one genome-wide scan that reported a QTL on bovine chromosome 26, where *SCD1* is located, affecting female reproductive performance. Thomasen et al. (2008) detected a QTL on bovine chromosome 26 that affects calving traits in Danish Holstein cattle.

To our knowledge, however, no previous study investigating a direct association between any isoforms of the SCD gene and reproductive traits in any mammalian species has been published. The present study did not detect any significant association between the Δ^9-desaturase isoform SCD1 and female reproductive performance in dairy cattle. Because of its effect on milk FA composition, *SCD1* has been considered as a candidate gene to be used in breeding programs for improving the nutritional value of milk (Mele et al., 2007; Moioli et al., 2007; Schennink et al., 2008). Our findings indicate that selection based on *SCD1* genotypes would not affect the reproductive performance of the cows.

3.4 Conclusions

The objective of this study was to examine the effect of milk-fat composition, *DGAT1*, and *SCD1* on fertility traits in commercial Dutch Holstein-Friesian dairy cattle. Data on 1,745 first-lactation cows were analyzed by fitting linear mixed models. Greater concentrations of TFA within total milk-fat negatively affected reproductive performance. Our results suggest that *DGAT1* has a potential effect on nonreturn rates for insemination 28 and 56 d after the first service. Results for *DGAT1* display a nonadditive pattern, with heterozygous genotypes associated with lower estimates for nonreturn rates than homozygous genotypes. Our findings suggest that a breeding program selecting for animals with the AA genotype would be the most desirable with regard to the nutritional quality of milk and the reproductive performance of cows. Results of this study can be used to assess the (economic) effects of changing milk-fat composition. Consequently, selective breeding programs can be better evaluated before implementation.

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4

Relationships between milk protein composition, milk protein variants and cow fertility traits in Dutch Holstein-Friesian cattle

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Journal of Dairy Science (2010) 93:5495-5502

Abstract

Selective breeding can change milk protein composition to improve the manufacturing properties of milk. However, the effects of such breeding strategies on other economically important traits should be investigated before implementation. The objectives of this study were to examine the association between cow fertility traits and 1) milk protein composition and 2) milk protein variants (β-lactoglobulin, β-casein, κ-casein, and β-κ-casein) in commercial Dutch Holstein-Friesian cattle. Data on 1,644 first-lactation cows were analyzed by fitting linear mixed models. Greater relative concentration of a_{S1}-casein within total milk protein had a positive phenotypic relationship with nonreturn rates and calving rate after first insemination. Furthermore, results showed virtually no significant relationship between cow fertility and concentration of other milk proteins or milk protein variants. Results of this study can be used to assess the correlated effects of breeding for improved milk protein composition on reproduction, thereby allowing for better evaluation of breeding programs before implementation. Our findings suggest that selecting cows based on milk protein composition or milk protein variants for improved manufacturing properties would have no negative influence on the reproductive performance.

Key words: dairy cattle, milk protein composition, milk protein variant, female fertility

4.1 Introduction

Recent research has shown opportunities to change the protein composition of bovine milk by selective breeding (Heck et al., 2009; Schopen et al., 2009). Changing protein composition is important because of its effect on the manufacturing properties of milk. For example, cheese manufacturing properties (cheese yield, milk coagulation time, and curd firmness) are influenced by protein composition (e.g., Auldist et al., 2004; Wedholm et al., 2006). In several countries, a large proportion of raw milk produced is destined for cheese production. In the Netherlands, for example, over 50% of the milk is used for cheese manufacturing, and cheese exports represent more than half of the dairy industry's total export value (Demeter et al., 2009a). Therefore, improving milk protein composition for dairy processing by selective breeding can increase the economic outcome of the dairy industry.

Recently, several studies have shown large variation in the relative concentration of the major milk proteins (Bobe et al., 1998; Bordin et al., 2001). Furthermore, research has found that a considerable part of this variation is genetic (Bobe et al., 1999; Graml and Pirchner, 2003; Heck et al., 2008). In a recent study, Schopen et al. (2009) found moderate to high intraherd heritabilities for milk protein composition in Dutch Holstein-Friesian cattle, ranging from 0.25 to 0.80. These results suggest the possibility of changing milk protein composition by using conventional selection methods. Furthermore, cows can be selected for particular genetic variants of milk proteins. When genetic variants are associated with the composition of milk protein, information on the genotype can be used for selecting animals. Milk protein genes have been studied extensively in cattle, and large genetic variation has been identified (e.g., Farrell et al., 2004; Caroli et al., 2009) that offers opportunities for animal breeding.

Before selecting for specific milk protein or genetic variant, however, effects on other economically important traits should be investigated. A relevant trait to consider is the reproductive performance of cows, given its high economic importance. The relationship between protein-related production traits (e.g., protein concentration or protein yield) and fertility have been investigated extensively (e.g., Dematawewa and Berger, 1998; Roman and Wilcox, 2000). However, the knowledge on the relationship between cow fertility and protein composition and protein variants is limited and in some cases contradictory. Regarding the β-LG genotype, Lin et al. (1987) and Tsiaras et al. (2005) found significant association with several fertility traits. Other studies (Hargrove et al., 1980; Ruottinen et al., 2004), however, did not detect any significant relationship between β-LG variants and reproductive traits. Regarding the β-CN genotype, Hargrove et al. (1980) reported a significant relationship with a single fertility trait (probability of conception), whereas, Lin et al. (1987) reported no effect. Regarding the κ-CN genotype, studies consistently found no significant association with fertility traits (Hargrove et al., 1980; Lin et al., 1987; Tsiaras et al., 2005). Ruottinen et al. (2004) examined the effects of β-κ-CN haplotypes on reproduction and reported a significant effect on a single trait (days to first service). Further analyses on the effects of β-κ-CN haplotypes are certainly warranted. To our knowledge, no studies have investigated the relationship between milk protein composition and cow fertility. The objectives of this study were to examine the association between 1) the relative concentrations of major milk proteins; 2) the genetic variants of β-LG, β-CN, and κ-CN; and 3) the β-κ-CN haplotypes and fertility traits in commercial Holstein-Friesian dairy cattle in the Netherlands.

4.2 Materials and Methods

4.2.1 Animals

This study is part of the Dutch Milk Genomics Initiative, which focuses on the genetic background of detailed milk composition (Schennink et al., 2007; Heck et al., 2009; Schopen et al., 2009). Data on 1,644 first-lactation cows distributed among 390 Dutch commercial herds were used. The farms were invited to participate based mainly on pedigree according to the database of the cooperative cattle improvement organization CRV (Arnhem, the Netherlands). Records on pedigree, yield, and reproduction were also provided by CRV. The cows descended from one of either 5 proven sires (762 cows), 50 test sires (721 cows), or 15 additional proven sires (161 cows). Offspring from the last group of bulls were added to ensure sampling of at least 3 cows per herd. Each cow was at least 87.5% Holstein-Friesian. Further information on the animals used in this study is provided by Stoop et al. (2007).

4.2.2 Fertility traits

From the records on reproductive performance provided by CRV, the following fertility traits were derived for all 1,644 cows: interval (d) between the first and second calving (**CI**), interval (d) between calving and the first insemination (**DFS**), number of inseminations (**NINS**), nonreturn rate (0/1) for insemination 28 d after the first insemination (**NR28**), nonreturn rate (0/1) for insemination 56 d after the first insemination (**NR56**), nonreturn rate (0/1) for insemination 90 d after the first insemination (**NR90**), rate (0/1) of calving after the first insemination (**CFI**), and rate (0/1) of calving after any inseminations (**CR**). Records for CI were considered missing if an animal did not have a known next calving date, or if the CI was less than 300 d or greater than 800 d. Records for DFS were set to missing if the DFS was less than 20 d or greater than 300 d. The NINS was set to missing if its value was 0 or greater than 10. These criteria were applied to exclude unrealistic, unrepresentative, or erroneous records under Dutch conditions (Calus et al., 2005). Descriptive statistics on the fertility traits are provided in Table 1. The average CI was 411 d, and the mean DFS was approximately 90 d. Cows had about 2.1 services on average, and approximately 10% of the cows did not have a second calving. Mean nonreturn rates ranged from 52 to 72% for the different time intervals.

Table 1. Descriptive statistics of fertility traits and milk protein composition of 1,644 first-lactation Dutch Holstein Friesian cows

Trait	Cows (no.)	Mean	SD	Minimum	Maximum
Fertility traits[1]					
CI	1,482	410.71	75.41	304	795
DFS	1,639	90.02	36.76	21	284
NINS	1,642	2.08	1.45	1	10
CR	1,644	0.90	0.29		
NR28	1,644	0.72	0.45		
NR56	1,644	0.60	0.49		
NR90	1,644	0.52	0.50		
CFI	1,644	0.44	0.49		
Proteins[2]					
α-LA	1,644	2.45	0.31	1.02	3.67
β-LG	1,644	8.35	1.19	4.08	12.36
α_{S1}-CN	1,644	33.69	1.59	24.75	39.84
α_{S2}-CN	1,644	10.34	1.38	4.66	14.21
β-CN	1,644	27.19	1.57	20.70	33.37
κ-CN[3]	1,644	4.01	0.58	2.29	6.12
CN-index[4]	1,644	0.87	0.01	0.83	0.94

[1] Fertility traits were interval (d) between first and second calving (CI), interval (d) between calving and first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after first service (NR28), nonreturn rate for insemination 56 d after first service (NR56), nonreturn rate for insemination 90 d after first service (NR90), and calving rate following the first insemination (CFI).

[2] Expressed as percentage of the specific protein in the total protein fraction (wt/wt), except for CN-index.

[3] Only k-CN in the nonglycosylated mono-phosphorylated form.

[4] CN-index = (α_{S1}-CN + α_{S2}-CN + β-CN + κ-CN)/(α-LA + β-LG + α_{S1}-CN + α_{S2}-CN + β-CN + κ-CN).

4.2.3 Protein concentrations

Morning milk samples, one from each cow, were collected from each cow between February and March 2005. The samples were preserved with 0.03% wt/wt sodium azide until analysis. The cows were milked twice a day, and each cow was between 66 and 282 d in lactation. The milk samples were used to estimate the relative concentrations of the six major milk proteins: α-LA, β-LG, α_{S1}-CN, α_{S2}-CN, β-CN, and κ-CN for all 1,644 cows by capillary zone electrophoresis as described by Heck et al. (2008) and Heck et al. (2009). Table 1 shows the descriptive statistics of the relative concentration of major milk proteins and milk protein composition. The largest protein fraction was α_{S1}-CN with an average relative concentration of 33.69% wt/wt, followed by β-CN and α_{S2}-CN, with average relative concentrations of 27.19 and 10.34% wt/wt. Furthermore, the mean proportion of total caseins within total milk proteins (**CN-index**) was 87%. These figures are similar to those reported by Heck et al. (2008) and Schopen et al. (2009), who analyzed slightly different subsets of the same Dutch Holstein-Friesian population.

4.2.4 Genotypes

Blood samples for DNA isolation were collected between April and June 2005. Genetic variants of β-LG were determined by using a SNaPshot single-base primer extension assay (Applied Biosystems, Foster City, CA), analogous to Visker et al. (2010). The β-LG protein variants A and B were determined, and the genotypes were missing for 44 animals from the total 1,644 animals (AA: 513 cows, AB: 838 cows, and BB: 249 cows).

Regarding genetic variants of β-CN, polymorphisms were genotyped using a SNaPshot single-base primer extension assay (Applied Biosystems, Foster City, CA) as described by Visker et al. (2010). Genotypes were used to determine β-CN protein variants A^1, A^2, A^3, B and I. Due to no available DNA sample or ambiguous genotyping, the genotypes for β-CN were missing for 65 animals from the total 1,644 animals (A^1A^2: 455 cows, A^2A^2: 389 cows, A^2I: 333 cows, A^1I: 165 cows, A^1A^1: 127 cows, II: 44 cows, A^2B: 32 cows, A^1B: 17 cows, IB: 15 cows, and A^2A^3: 2 cows). Furthermore, the two records for β-CN variant A^2A^3 were excluded from further analyses.

Regarding variants of κ-CN protein, relevant polymorphisms were genotyped using the SNaPshot single-base primer extension method (Applied Biosystems, Foster City, CA) as described by Heck et al. (2009). Protein variants A, B, and E were determined for κ-CN. Genotypes for κ-CN were missing for 32 animals from the total 1,644 animals due to no available DNA sample or unambiguous genotyping (AA: 642 cows, AB: 555 cows, AE: 179 cows, BB: 124 cows, BE: 97 cows, and EE: 15 cows).

4.2.5 Haplotypes

The β-κ-CN haplotypes were inferred with PHASE v.2.1.1 (Stephens et al., 2001) from β-CN and κ-CN protein variants as described by Visker et al. (2010). Seven β-κ-CN haplotypes were identified: A^1A, A^1B, A^1E, A^2A, A^2B, BB, and IB. Because either no DNA sample was available, or the sample could not be genotyped unambiguously for β-CN or κ-CN, or the haplotype could not be inferred unambiguously, haplotypes were missing for 104 animals. Furthermore, the records for two copies of A^1B haplotype were set as missing because they were available only for three cows. An overview of the haplotype frequencies is provided in Table 2.

Table 2. Number of cows according to the number of copies of the β-κ-CN haplotypes of 1,540 first-lactation Dutch Holstein-Friesian cows

Haplotype	Number of copies			Total
	0	1	2	
A^1A	1,114	361	65	1,540
A^1B	1,373	164	0	1,537[1]
A^1E	1,264	261	15	1,540
A^2A	418	797	325	1,540
A^2B	1,430	105	5	1,540
BB	1,478	62	0	1,540
IB	992	504	44	1,540

[1] The records for two copies of A^1B haplotype were set missing because they were available for only three cows.

4.2.6 Statistical analysis

To study the association between the relative concentrations of the six major milk proteins or the CN-index and the fertility traits, two modeling steps were performed. Because the protein compositions were measured on milk samples taken at different lactation stages, the data on milk proteins and CN-index were first preadjusted for lactation stage. With the composition traits as dependent variables, univariate linear models were fitted (models not shown) using GLM procedure in SAS 9.1 (SAS Institute Inc., Cary, NC) to model the effect of DIM (days between date of first calving and date of milk sample) modeled with a Wilmink curve (Wilmink, 1987). The composition traits adjusted for lactation stage were then used for further analyses in model [1]. Other effects in model [1] included the age at first calving, the season of calving, and the sire type (three different sire groups: proven bulls, young bulls, or other proven bulls). Relationships between individuals were accounted for, and the total pedigree comprised 26,300 animals and was supplied by CRV. Variance components and fixed effects solutions were calculated using the ASReml software package (Gilmour et al., 2006). Model [1] is written as

$$[1] \qquad y_{ijklmn}=\mu+b_1\text{AFC}_i+b_2\text{PCON}_j+\text{SEASON}_k+\text{SCODE}_l+\text{HERD}_m+a_n+e_{ijklmn},$$

where y is the dependent variable (fertility trait); μ is the general mean; b_1 is the regression coefficient associated with AFC, which is a fixed covariate describing the effect of age at first calving; b_2 is the regression coefficient associated with PCON, which is a fixed covariate accounting for the effect of the adjusted relative concentration of one of the six major milk proteins or the CN-index for lactation stage; SEASON is a fixed factor accounting for the effect of the calving season (June to August 2004, September to November 2004, or December 2004 to February 2005); SCODE is a fixed factor capturing the effect of the differences in genetic level between proven bull daughters and young bull daughters; HERD is a random factor accounting for the effect of groups of animals sampled in the same herd; a is a random factor accounting for the additive genetic effect of the given animal; and e is the random residual effect. Each fertility trait was analyzed separately and each protein concentration and CN-index was also fitted separately (56 analyses in total).

To study the relationship between the milk protein variants and the fertility traits, a model similar to model [1] was used. Model [2] excluded the covariate PCON, but included a fixed factor PVAR that captured the effect of the β-LG genotype (AA, AB, or BB), the β-CN genotype (A^1A^2, A^2A^2, A^2I, A^1I, A^1A^1, II, A^2B, A^1B, or IB), the κ-CN genotype (AA, AB, AE, BB, BE, or EE), or the number of copies (0, 1, or 2) of the seven β-κ-CN haplotypes (A^1A, A^1B, A^1E, A^2A, A^2B, BB, or IB). Each fertility trait was analyzed separately and each protein variant and haplotype was also fitted separately (80 analyses in total). Model [2] is written as

[2]
$$y_{iklmno}=\mu+b_1\mathrm{AFC}_i+\mathrm{PVAR}_o+\mathrm{SEASON}_k\\+\mathrm{SCODE}_l+\mathrm{HERD}_m+a_n+e_{iklmno}.$$

Because the models above assumed normally distributed residuals, generalized linear mixed models were also fitted by using the GLIMMIX procedure in SAS 9.1 (Littel et al., 2006) for the count and binary variables. A Poisson distribution with log link function was assumed for NINS, and a binomial distribution with logit link function was assumed for CR, NR28, NR56, NR90, and CFI. By fitting generalized linear models, the same fixed effects were significant as when fitting the above linear models; therefore, we concluded that linear mixed models were robust enough to handle the nonnormally distributed fertility traits.

In the above models, the effects of protein concentrations, genotypes, and haplotypes on each fertility trait were tested separately in a series of sequential analyses. In each analysis, the null hypothesis was of no effect on the fertility trait of interest. Because several fertility traits were analyzed, multiple hypotheses were tested. However, due to the correlations between those fertility traits, not all hypothesis tests were truly independent. To account for multiple testing, the analyses of (i) CI, DFS, and NINS; (ii) CR and CFI; and (iii) NR28, NR56, and NR90 were considered as three independent hypothesis tests. Bonferroni correction based on the Šidák method (Šidák, 1967) was applied to account for multiple testing with regard to the three groups of fertility traits, analogous to Demeter et al. (2009b).

4.3 Results and Discussion

4.3.1 Effects of milk protein composition

To investigate the association between the relative concentration of major milk proteins and reproductive performance, the milk protein profiles from 1,644 first-lactation Dutch Holstein-Friesian cows were used (model [1]). The estimated effects and their significance are presented in Table 3. The relative concentration of milk protein α_{S1}-CN was found to have a relationship with several fertility traits. The results indicate that a greater relative concentration of α_{S1}-CN is associated with better female reproductive performance. More specifically, a 1% wt/wt increase in the relative α_{S1}-CN concentration is expected to result in 1.9% greater nonreturn rate at 28 d, 2.7% greater nonreturn rate at 56, 2.9% greater nonreturn rate at 90 d, and 2.5% greater calving rates after the first service. Associations between the relative α_{S1}-CN concentration and NR28, NR56, NR90, and CFI remained significant after Bonferroni correction. The relationship of the relative α_{S1}-CN concentration with other fertility traits was statistically nonsignificant. However, the estimated effects for CI and NINS also suggest the positive relationship between greater relative α_{S1}-CN concentration and female reproductive performance. Moreover, to further investigate the relationship between the relative α_{S1}-CN concentration and cow fertility traits, model [1] with linear and quadratic effects for α_{S1}-CN was also tested. The results (not shown) indicated no significant quadratic effect, thereby confirming the linear relationship.

In addition to α_{S1}-CN, two other significant ($P < 0.05$) relationships were found. First, a greater relative concentration of α-LA was associated with a lesser (8.9%) nonreturn rate after 28 d, thereby indicating a possible antagonistic relation between α-LA concentration and cow fertility. Second, a greater relative concentration of β-CN was associated with a lesser (2.76 d) calving interval, thereby suggesting a positive effect of milk β-CN concentration on reproduction. However, these associations were found only for single fertility traits and became nonsignificant after correcting for multiple testing. Therefore, these findings were considered inconclusive. Regarding the other major milk proteins, no significant association was detected between β-LG, α_{S2}-CN, κ-CN, and CN-index and any of the fertility traits.

To our knowledge, this study is the first to report on the direct association between the relative concentrations of major milk proteins and fertility traits in cattle. Our findings indicate a positive relationship between greater relative α_{S1}-CN concentration and reproductive performance. On the one hand, the relative concentration of α_{S1}-CN has positive genetic correlations with milk (0.52) and protein (0.29) yields (Schopen et al., 2009). These production traits are known to have antagonistic relationship with fertility traits (e.g., Nebel and McGilliard, 1993; Dematawewa and Berger, 1998). Consequently, a greater relative α_{S1}-CN concentration would be expected to entail higher milk and protein yields, which in turn would be expected to negatively influence female fertility

Table 3. Association between the relative concentration of the six major milk proteins or the CN-index and the fertility traits[1] of 1,644 first-lactation Dutch Holstein-Friesian cows[2]

Proteins[3]	CI (n = 1,482)	DFS (n = 1,639)	NINS (n = 1,642)	CR (n = 1,644)	NR28 (n = 1,644)	NR56 (n = 1,644)	NR90 (n = 1,644)	CFI (n = 1,644)
α-LA	0.746 ± 6.587	1.353 ± 3.053	0.029 ± 0.121	0.028 ± 0.024	-0.089 ± 0.037*	-0.042 ± 0.041	-0.031 ± 0.042	0.009 ± 0.041
β-LG	-0.925 ± 1.687	-0.102 ± 0.784	0.012 ± 0.032	0.006 ± 0.006	-0.005 ± 0.009	-0.010 ± 0.011	-0.010 ± 0.011	-0.005 ± 0.011
α_{S1}-CN	-0.531 ± 1.264	0.361 ± 0.586	-0.045 ± 0.023	-0.002 ± 0.005	0.019 ± 0.007**	0.027 ± 0.008**	0.029 ± 0.008**	0.025 ± 0.008**
α_{S2}-CN	0.741 ± 1.446	-0.772 ± 0.678	0.006 ± 0.027	0.005 ± 0.005	-0.004 ± 0.008	-0.007 ± 0.009	-0.011 ± 0.009	-0.009 ± 0.009
β-CN	-2.755 ± 1.265*	-0.839 ± 0.587	-0.006 ± 0.023	0.000 ± 0.005	-0.011 ± 0.007	-0.009 ± 0.008	0.002 ± 0.008	0.001 ± 0.008
κ-CN[4]	0.548 ± 3.504	0.389 ± 1.632	-0.029 ± 0.065	-0.004 ± 0.013	-0.017 ± 0.020	-0.040 ± 0.022	-0.029 ± 0.022	-0.027 ± 0.022
CN-index[5]	15.98 ± 144.8	-18.28 ± 67.08	-1.973 ± 2.713	-0.552 ± 0.534	0.854 ± 0.834	1.123 ± 0.906	1.284 ± 0.927	0.657 ± 0.918

[1] Fertility traits were interval (d) between first and second calving (CI), interval (d) between calving and first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after first service (NR28), nonreturn rate for insemination 56 d after first service (NR56), nonreturn rate for insemination 90 d after first service (NR90), and calving rate following the first insemination (CFI).

[2] Values after ± signs are corresponding SE.

[3] Expressed as percentage of the specific protein in the total protein fraction (wt/wt), except for CN-index.

[4] Only κ-CN in the nonglycosylated mono-phosphorylated form.

[5] CN-index = (α_{S1}-CN + α_{S2}-CN + β-CN + κ -CN)/(α-LA + β-LG + α_{S1}-CN + α_{S2}-CN + β-CN + κ-CN).

[*] Significant ($P < 0.05$); [**] significant after Bonferroni correction.

traits. The results of the present study, however, do not support this prior expectation because a positive association was found between the relative concentration of α_{S1}-CN protein and cow fertility traits.

On the other hand, the detected positive relationship is in agreement with the effect of the polymorphism in the α_{S1}-CN (*CSN1S1*) gene (which encodes the α_{S1}-CN protein) on reproductive performance. In US Holstein cattle, Hargrove et al. (1980) found that cows with the α_{S1}-CN BC genotype had greater probability of conception relative to cows with the BB genotype. The BC genotype has also been found to be associated with greater α_{S1}-CN concentration than the BB genotype (McLean et al., 1984; Graml and Pirchner, 2003). That is, the genetic variant of α_{S1}-CN protein that is associated with greater relative α_{S1}-CN concentration is also associated with better female reproductive performance. According to the study by Heck et al. (2009), α_{S1}-CN protein variants B and C can be detected in Dutch Holstein cows; however, the frequency of the α_{S1}-CN C allele in the population is low (0.3%).

The relationship between concentration of major milk proteins and cow fertility traits is of importance, because the findings can be used to assess the correlated effects of breeding programs on economically important traits. Recent research has shown that selective breeding can be used to improve the milk protein composition of bovine milk. Studies have shown large variation in the relative concentration of the major milk proteins (Bobe et al., 1998; Bordin et al., 2001). Furthermore, a considerable part of this variation is genetic (Bobe et al., 1999; Graml and Pirchner, 2003; Heck et al., 2008). In a recent study, Schopen et al. (2009) found moderate to high intraherd heritabilities for milk protein composition in Dutch Holstein cattle. Changing milk protein composition by selection is desirable because it can result in raw milk with improved manufacturing properties. For cheesemaking, raw milk with high concentrations of α_{S1}-CN, β-CN, and κ-CN and with high proportion of κ-CN within total CN is desirable (e.g., Wedholm et al., 2006). Results of the present study indicate that selective breeding to increase α_{S1}-CN concentration could improve cow fertility, whereas selection to increase other desirable protein fractions would not affect reproductive performance.

4.3.2 Effects of milk protein variants

To study the effects of β-LG variants on fertility traits, a sample of 1,600 animals was analyzed (model [2]). As the *P*-values indicate (Table 4), no statistically significant relationship was found between β-LG genotype and cow fertility traits. Few studies have investigated the direct association between the β-LG genotypes and reproductive traits in cattle. On the one hand, Lin et al. (1987) reported a significant effect on age at first conception, age at first calving, and gestation length. On the other hand, other studies (Hargrove et al., 1980; Ruottinen et al., 2004; Tsiaras et al., 2005) found no significant relationship between β-LG genotypes and several fertility traits. Therefore, the conclusions of the available studies are contradictory. This study failed to detect any significant association between β-LG variants and cow fertility traits, thereby further supporting the hypothesis of no association.

Table 4. Significance (*P*-values) of the association between β-LG, β-CN, κ-CN, and β-κ-CN variants and fertility traits[1] on first-lactation Dutch Holstein-Friesian cows[2]

Variant	CI	DFS	NINS	CR	NR28	NR56	NR90	CFI
Genotypes								
β-LG (n = 1,600)	0.957	0.424	0.442	0.587	0.161	0.233	0.133	0.099
β-CN (n = 1,577)	0.359	0.819	0.317	0.391	0.207	0.151	0.222	0.407
κ-CN (n = 1,612)	0.306	0.804	0.212	0.263	0.071	0.392	0.475	0.523
Haplotypes								
A^1A (n = 1,540)	0.718	0.779	0.817	0.788	0.421	0.100	0.221	0.513
A^1B (n = 1,537)	0.482	0.242	0.588	0.404	0.944	0.642	0.621	0.978
A^1E (n = 1,540)	0.130	0.855	0.126	0.395	0.720	0.711	0.459	0.332
A^2A (n = 1,540)	0.070	0.506	0.990	0.090	0.730	0.828	0.973	0.829
A^2B (n = 1,540)	0.188	0.296	0.243	0.319	0.678	0.946	0.807	0.905
BB (n = 1,540)	0.058	0.546	0.457	0.423	0.828	0.389	0.548	0.286
IB (n = 1,540)	0.733	0.887	0.120	0.698	0.128	0.017*	0.059	0.221

[1] Fertility traits were interval (d) between first and second calving (CI), interval (d) between calving and first insemination (DFS), number of inseminations (NINS), calving rate (CR), nonreturn rate for insemination 28 d after first service (NR28), nonreturn rate for insemination 56 d after first service (NR56), nonreturn rate for insemination 90 d after first service (NR90), and calving rate following the first insemination (CFI).

[2] Values after ± signs are corresponding SE.

*Significant ($P < 0.05$).

To study the relationship between β-CN variants and fertility traits, a sample of 1,577 animals was analyzed (model [2]). The high *P*-values reported in Table 4 indicate no statistically significant relationship. Only two earlier studies analyzing the association between β-CN variants and cow fertility traits have been reported. Hargrove et al. (1980) found that the β-CN genotype had a significant effect on the probability of conception. However, Lin et al. (1987) did not find any significant association. To our knowledge, this is the first study to report on the effects of the β-CN protein variants B and I on cow fertility traits. The B allele, which is known to be common for β-CN protein (Farrell et al., 2004), has been shown to have a frequency of approximately 2% in the Dutch Holstein-Friesian cows (Heck et al., 2009; Visker et al., 2010). The I allele was recently detected for the first time in the Dutch Holstein-Friesian population by Visker et al. (2010), exhibiting 19.2% allele frequency. The present study did not detect any significant association between any β-CN variant and cow fertility traits.

To study the relationship between κ-CN genotypes and fertility traits, we analyzed a sample of 1,612 animals was analyzed (model [2]) and found no statistically significant relationship (Table 4). This result is in line with that of other studies found in the literature. Earlier studies (Hargrove et al., 1980; Lin et al., 1987; Tsiaras et al., 2005) consistently reported no significant effect of the κ-CN locus on cow fertility. Therefore, the present results confirm those earlier conclusions. Furthermore, to our knowledge the present study is the first to report on the effects of κ-CN variant E on reproductive traits. The E allele has been recently detected in the Dutch Holstein-Friesian population with an allele frequency of 9.2% (Heck et al., 2009). In the present analyses, no relationship between the E allele and fertility traits was detected.

To estimate the effects of β-κ-CN haplotypes on fertility traits, a sample of 1,540 animals was analyzed (model [2]). The observed haplotype frequencies are presented in Table 2. Our analyses did not detect a significant relationship between the β-κ-CN haplotypes and the fertility traits (Table 4), except for the association between IB haplotype and NR56 ($P = 0.017$). However, this latter association occurred for a single trait only and became nonsignificant after Bonferroni correction. Therefore, the results suggest that cow fertility is virtually unaffected by the β-κ-CN haplotype in Dutch Holstein-Friesian cattle. We found only a single study reporting on the association between β-κ-CN haplotypes and cow reproductive traits. Ruottinen et al. (2004) detected a significant effect on the number of days from calving to first service in Finnish Ayrshire cows; however, they concluded that the β-κ-CN haplotypes have virtually no effect on female reproduction. Our results agree with this conclusion.

Investigating the effects of genetic variants of milk proteins on economically important traits is important because this information can be used to evaluate gene-assisted selection strategies. The influence of protein genes on milk protein composition and cheesemaking properties has been thoroughly investigated, and the protein genes have been generally considered as candidates for improving milk protein composition (e.g., Caroli et al., 2009). The present study indicates that selection based on β-LG, β-CN, and κ-CN genotypes and β-κ-CN haplotypes would not affect the female reproductive performance in Dutch Holstein-Friesian cattle.

4.4 Conclusions

The objective of this study was to examine the relationship between cow fertility traits and milk protein composition and milk protein variants in commercial Dutch Holstein-Friesian dairy cattle. A greater relative concentration of α_{S1}-casein within total milk protein had a positive phenotypic relationship with nonreturn rates for insemination 28, 56, and 90 d after first service and with calving rate after first insemination. Furthermore, results did not show any significant association between β-LG, β-CN, and κ-CN genotypes and β-κ-CN haplotypes and cow fertility traits. The findings of the present study suggest that a breeding program aiming to improve the manufacturing properties of milk by selecting animals based on milk protein composition or milk protein variants would have no negative influence on the reproductive performance of cows. Results of this study can be used to assess the (economic) effects of changing milk protein composition, which consequently allows for better evaluation of selective breeding programs before implementation.

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5

A multi-level hierarchic Markov process with Bayesian updating for herd optimization and simulation in dairy cattle

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Journal of Dairy Science (2011) 94:5938-5962

Abstract

Herd optimization models, which determine economically optimal insemination and replacement decisions, are valuable research tools to study various aspects of farming systems. The aim of this study was to develop a herd optimization and simulation model for dairy cattle. The model determines economically optimal insemination and replacement decisions for individual cows and simulates whole-herd results that follow from optimal decisions. The optimization problem was formulated as a multi-level hierarchic Markov process, and a state space model with Bayesian updating was applied to model variation in milk yield. Methodological developments were incorporated in two main aspects. First, we introduced an additional level to the model hierarchy to obtain a more tractable and efficient structure. Second, we included a recently developed cattle feed intake model. In addition to methodological developments, new parameters were used in the state space model and other biological functions. Results were generated for Dutch farming conditions, and outcomes were in line with actual herd performance in the Netherlands. Optimal culling decisions were sensitive to variation in milk yield but insensitive to energy requirement for maintenance and feed intake capacity. We anticipate that the model will be applied in research and extension.

Key words: economics, optimization, dairy cattle, Markov decision process

5.1 Introduction

The economic optimization of dairy herd performance is vital for dairy producers. In the past decades, models with optimization and simulation purposes have been used to support decision making in dairy herds regarding insemination and culling decisions. Optimizing insemination decisions is important because sub-optimal calving intervals lead to financial losses (e.g., Van Arendonk and Dijkhuizen, 1985; Dekkers, 1991). Optimizing cow replacement is important because the farmer's culling policy influences farm profitability as the direct costs related to replacement heifers represent a significant part of total costs (Lehenbauer and Oltjen, 1998; Fetrow et al., 2006). A large number of models have been developed to address the problem of economically optimal insemination and replacement strategies (see e.g., Van Arendonk, 1984; Kristensen, 1994; Lehenbauer and Oltjen, 1998).

To model the optimization problem for inseminations and replacements, two main techniques have been traditionally applied: the marginal net revenue (**MNR**) approach and the Markov decision process (**MDP**) approach. The main differences between the two approaches is that the MDP approach can account for seasonal variation, continuous genetic improvement, and variation within traits, whereas the MNR approach cannot (Van Arendonk, 1984). The MDP approach, therefore, has been more frequently applied and was also used in this study.

When using the MDP approach, optimal decisions depend on the criterion of optimality. Possible criteria of optimality include the maximization of total expected rewards, total expected discounted rewards, expected average rewards per unit of time, or expected average rewards per unit of expected physical input or output (Kristensen, 1994). The MDP can be optimized by value iteration, policy iteration, or linear programming (Kristensen, 1994). Each optimization method has been applied in dairy cattle. Value iteration has been often used since the 1960s (e.g., Giaever, 1966; Stewart et al., 1977; Van Arendonk, 1985b). Policy iteration has been applied since the 1980s (e.g., Kristensen, 1987, 1989; Houben et al., 1994; Mourits et al., 1999), after Kristensen (1988, 1991) introduced the notion of hierarchic Markov process (**HMP**). Linear programming has been the least used, and only two studies (Yates and Rehman, 1998; Cabrera, 2010) have used linear programming to our knowledge.

Two important methodological developments have been realized recently in the area of herd optimization. First, Kristensen and Jørgensen (2000) extended the concept of HMP by introducing the notion of multi-level hierarchic Markov process (**MLHMP**). MLHMP decreases the problem of the "curse of dimensionality", which refers to exponentially growing state space in real-world applications (Kristensen and Jørgensen, 2000). To date, few studies have applied the MLHMP technique in dairy cattle. Bar et al. (2008, 2009) estimated costs of generic clinical mastitis, whereas Cha et al. (2010) calculated cost of different types of lameness. Nielsen et al. (2010a) determined optimal culling decisions based on daily milk yield measurements. The above models were formulated as 3-level MLHMP and demonstrated that real-world applications with large state space can be modeled efficiently.

Second, Nielsen et al. (2010b) introduced a formal description of embedding a Bayesian updating technique into a MDP. Specifically, they provided a general framework for applying a state space model (**SSM**) in a MDP. State space models provide statistical method for modeling variation in biological traits (between animals and over time). SSM applies Bayesian updating to predict future development in the trait modeled, while taking all past information into account. The method contributes to the solution of the problem of "uniformity", which refers to the problem of defining and measuring highly variable biological traits (Ben-Ari et al., 1983; Kristensen, 1994). In dairy cattle, Nielsen et al. (2010a) have applied SSM to model daily milk yield in the context of automated milking systems. They also estimated herd specific SSM variance parameters from daily milk yield records.

The objective of this study was to develop a dairy herd optimization and simulation model. The model determined economically optimal insemination and replacement decisions for individual cows (as described by a set of state variables) and simulated whole-herd results. The optimization problem was formulated as a MLHMP, and SSM was applied to model actual milk yield level. Optimal decisions were found by maximizing total expected discounted net revenues. Methodological contributions were presented in two main aspects. First, this study was the first to formulate a 4-level MLHMP for the dairy herd optimization problem to obtain more tractable and efficient model structure. Second, we incorporated a recently developed cattle feed intake model to obtain more precise predictions on feed intake and feed costs. In addition to methodological contributions, new biological parameters were used in the SSM and other biological functions. Results were presented for farming conditions in the Netherlands. In the future, the model will be used to assess herd level implications of genetic selection strategies. This paper, therefore, reported whole-herd results to validate model behavior and evaluate methodological contributions and new biological parameters.

5.2 Materials and Methods

The model consists of two parts: a bioeconomic module and a mathematical module. The bioeconomic module calculated technical and economic performance of individual cows during their productive life. The mathematical module optimized insemination and replacement decisions based on predictions from the bioeconomic module. Optimal decisions were found by maximizing total expected discounted net revenues. Optimal decisions were calculated for all individual cow states. A cow state was the combination

Table 1. Summary of key price, biological, and management inputs used for the base scenario[1].

Inputs	Base values
Management inputs	
Age at first calving (mo)	24
Proportion of outdoor grazing on annual basis (%)	25
Proportion of concentrate in diet (%)	28
Length of keeping newborn calf (d)	7
Minimum open period in lactation (mo)	2
Maximum lactation length (mo)	18
Annual discount rate (%)	5
Biological inputs	
Mature mean 305-d milk yield (kg)[2]	9,000
Mature mean 305-d fat content (%)[2]	4.25
Mature mean 305-d protein content (%)[2]	3.45
Variation coefficient of 305-d milk yield (%)	12
Heritability of milk yield	0.40
Repeatability of consecutive 305-d milk yields	0.55
Correlation between true and estimated BV for milk yield	0.60
Cow mature live weight (kg)	650
Calf birth weight (kg)	40
Calf survival rate in first week (%)	92
Length of oestrus cycle (d)	21
Heat detection rate (first oestrus)	0.30
Heat detection rate (later oestruses)	0.60
Price inputs (€)	
Milk carrier (100 kg)[3]	−3.20
Milk fat (kg) [3]	2.85
Milk protein (kg) [3]	7.50
Roughage (100 kg DM) [3]	10.12
Concentrate (100 kg DM) [3]	16.25
Bull calf (kg) [3]	2.50
Carcass (kg) [3]	1.75
Regular veterinary cost (per cow per 305-d)[4]	120
Cost of fixed production assets[3]	115
Monthly insemination cost (per cow)[4]	25
Replacement heifer[5]	1,500

[1] Base scenario represents average Dutch dairy farm in 2008-2009.

[2] Provided by the cooperative cattle improvement organization CRV (Arnhem, the Netherlands).

[3] KWIN (2009).

[4] Personal communication (Henk Hogeveen, Utrecht University, Utrecht, the Netherlands).

[5] Personal communication (Monique Mourits, Wageningen University, Wageningen, the Netherlands).

of main properties characterizing a cow. A cow could be in a state described by one of 12 parities, 8 present-open periods, 8 previous-open periods, 18 lactation stages, 13 classes of estimated milk yield potential when entering the herd as heifer, 13 classes of updated milk yield potential when starting a new lactation, and 169 classes for actual milk yield level. The mathematical module, furthermore, simulated whole-herd results following optimal decisions for individual cows.

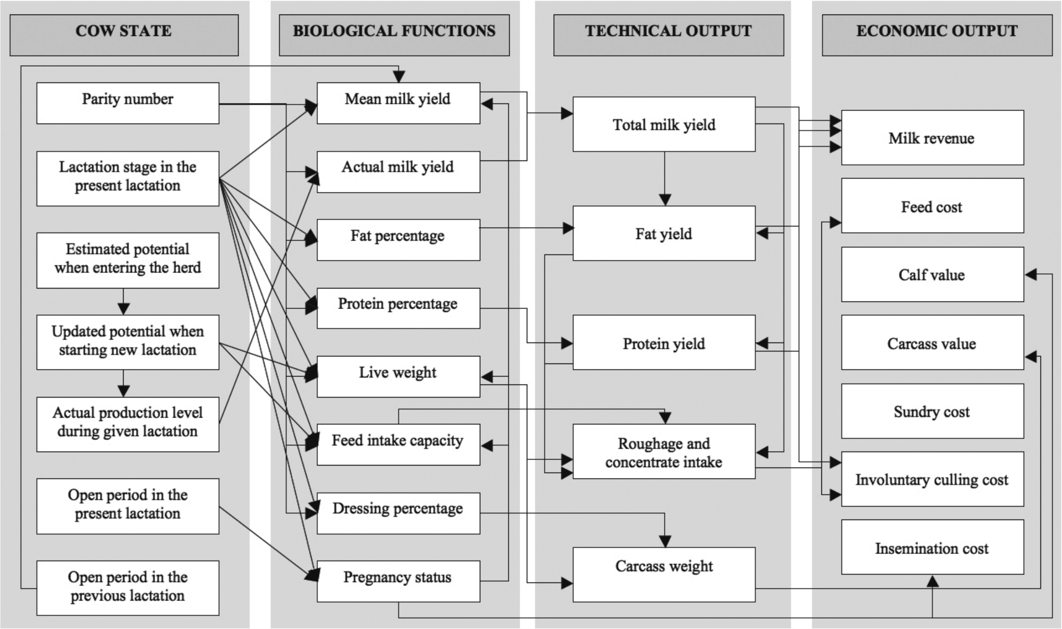
We considered only milk production and assumed that rearing young stock and producing feed crops were isolated from milk production. Replacement heifers and feedstuffs, therefore, were purchased from other separated business units or from the market. Farmer's labor was not included in calculation of costs, so net revenues represented financial compensation to the farmer for labor and management. Input values and model parameters were selected to simulate performance of Holstein-Friesian cows in the Netherlands (Table 1). The model worked with monthly (30.5 d) time intervals. The prices represented Dutch farming conditions during 2008-2009. Seasonality in performance and prices was not included.

The model included two key assumptions concerning herd constraints. First, fixed herd size was assumed, i.e., a cow was immediately replaced after culling. The replacement problem, therefore, was treated as single-component system, assuming unlimited supply of heifers (Kristensen, 1992). This is not always valid in practice, because heifer supply is not exogenous to the farming process. Ben-Ari and Gal (1986) and Kristensen (1992) suggested to treat the replacement problem as multi-component system. The drawback of their approach was that finding an exact solution was computationally prohibitive. To date, no application has been reported, and finding exact solution to the multi-component approach remains unsolved. Second, milk production quotas were not considered. Under production quota, the herd constraint is a fixed amount of milk to produce. Maximization of expected average rewards per unit of expected output, therefore, is a more relevant criterion of optimality (Kristensen, 1991). Applying the latter criterion would solve the problem of selecting which cows to keep in the long run. The problem of determining how many cows to keep at a given time, however, would not be solved. The latter problem, in principle, could be solved by using the multiple-component approach with maximizing expected average rewards per unit of expected output (Kristensen, 1992). To date, however, such method has not been developed.

5.2.1 Bioeconomic module

The bioeconomic module was formulated by using the framework of Van Arendonk (1985a). Relative to the original model of Van Arendonk (1985a), the present model had three contributions: SSM was used to model milk yield and capture variation in milk yield potential among individual cows; novel insights on deriving feed intake capacity and actual feed intake were incorporated; several new biological input values and parameters were included to reflect current population characteristics. We considered three revenues (milk, calves, and carcass) and five costs (feed, insemination, replacement heifer, loss due to involuntary culling, and sundries). Revenues and costs were calculated monthly, and their difference resulted in net revenues. The bioeconomic module, furthermore, was used to compute physical inputs and outputs, and transition probabilities for all possible cow states. An overview of the bioeconomic module (excluding prices and transition probabilities) is shown in Figure 1.

Figure 1. Schematic representation of the structure of the bioeconomic module (excluding transition probabilities and prices).



Milk Yield. We assumed the following model for a cow's monthly total milk yield

[1] $$M_{i,j}=\mu_{i,j}+\Sigma_t Y_{i,j,t},$$

where $M_{i,j}$ was the total milk yield (kg) in month j in parity i, $\mu_{i,j}$ was the mean milk yield (kg) in month j in parity i, and $Y_{i,j,t}$ was the daily deviation from the mean milk yield (kg) on day t in month j in parity i. The term $Y_{i,j,t}$ captured the variation in milk yield among individual cows. For simplicity, we shall refer to the term $Y_{i,j,t}$ as actual milk yield, whereas the term $\mu_{i,j}$ shall be referred to as mean milk yield. In the following, we present the calculation of the actual yield, whereas deriving the mean yield is discussed in the appendix.

We assumed the following model for the actual milk yield (as deviation from the mean)

$$[2a] \qquad Y_{i,j,t}=age_i^{milk}\times(BV+PE+X_{i,j,t}),$$

where $Y_{i,j,t}$ was the actual daily milk yield (kg) on day t in month j in parity i; age_i^{milk} was the multiplicative effect of parity i on milk yield; random variable BV denoted the cow's permanent genetic capacity for milk yield (i.e., the breeding value for milk yield) (kg); random variable PE denoted the effect of permanent environment on milk yield (kg); and random variable $X_{i,j,t}$ denoted the within-lactation short term fluctuation in milk yield (kg) on day t in month j within parity i. Because both BV and PE are permanent properties of the cow over her entire lifetime, the model in equation [2a] was redefined by merging those effects as

$$[2b] \qquad Y_{i,j,t}=age_i^{milk}\times(A+X_{i,j,t}),$$

where random variable A denoted the permanent production potential of the cow for milk yield (kg) ($A=BV+PE$), assuming that $A\sim\mathrm{N}(0,\sigma_A^2)$. Variable $X_{i,j,t}$ was assumed to follow a first order autoregressive process with $X_{i,j,t}\sim\mathrm{N}(0,\sigma_X^2)$, where σ_X^2 was the variance of $X_{i,j,t}$, and autocorrelation $\rho(t)=\rho^t$, where $|\rho|<1$ (i.e., $X_{i,j,t}=\rho\times X_{i,j,t-1}+\varepsilon_{i,j,t}$). Variable $X_{i,j,t}$ can be interpreted as the cow's short term deviation from her milk production potential due to temporary environmental effects, including feeding, management, and health problems.

We formulated a SSM to model actual milk yield over time, by adapting the framework Nielsen et al. (2010a). A dynamic linear model (**DLM**) was formulated with Kalman filtering (**KF**), as described by West and Harrison (1997). The term DLM refers to a specific SSM, where the model contains normally distributed variables with linear relationship. The DLM for actual milk yield was described by the following observation and system equations

$$[3a] \qquad Y_{i,j,t}=F_i\otimes\begin{bmatrix}A\\X_{i,j,t}\end{bmatrix},\ F_i=age_i^{milk},$$

$$[3b] \qquad \begin{bmatrix}A\\X_{i,j,t}\end{bmatrix},=\mathbf{G}\times\begin{bmatrix}A\\X_{i,j,t-1}\end{bmatrix}+\mathbf{w}_{i,j,t},\ \mathbf{G}=\begin{bmatrix}1&0\\0&\rho\end{bmatrix},\text{ and }\mathbf{w}_{i,j,t}=\begin{bmatrix}0\\\varepsilon_{i,j,t}\end{bmatrix},$$

where $\mathbf{w}_{i,j,t}\sim N(0,\mathbf{W})$, with

$$[3c] \qquad \begin{bmatrix}0&0\\0&(1-\rho^2)\times\sigma_X^2\end{bmatrix}.$$

First, the observation equation (equation [3a]) specified the relationship between the observed variable $Y_{i,j,t}$ and the latent variables $(A,X_{i,j,t})$. Second, the system equation (equation [3b]) specified the relationship between the latent variables $(A,X_{i,j,t})$ from time $t-1$ to time t. Furthermore, $\mathbf{W}$ denoted the covariance matrix of random variable $\mathbf{w}_{i,j,t}$ in parity i.

We assumed that the conditional prior distribution of the latent variables given all available information (denoted by $\mathbf{D}$) available up to the beginning of any parity i was $(A,X_{i,0,0})' \mid \mathbf{D}_{i,0,0} \sim \mathrm{N}(\mathbf{m}_{i,0,0},\mathbf{C}_{i,0,0})$, where mean and covariance matrices were specified as

$$[4] \qquad \mathbf{m}_{i,0,0} = \begin{bmatrix} \hat{A}_{i,0,0} \\ 0 \end{bmatrix} \text{ and } \mathbf{C}_{i,0,0} = \begin{bmatrix} \sigma^2_{e_{i,0,0}} & 0 \\ 0 & \sigma^2_X \end{bmatrix},$$

where $\hat{A}_{i,0,0}$ denoted the prior expectation of the cow's permanent production potential before she would start producing in given parity i, and $\sigma^2_{e_{i,0,0}}$ denoted the variation around $\hat{A}_{i,0,0}$.

For $i=1$, $\hat{A}_{i,0,0}$ in equation [4] can be interpreted as the prior estimate of the cow's permanent potential for milk yield. We allowed $\hat{A}_{i,0,0}$ to have different values, i.e., replacement heifers differed in permanent potential for milk yield when entering the herd. This was different from the DLM of Nielsen et al. (2010a), because they assumed cows to be average heifers when entering the herd, i.e., $\hat{A}_{1,0,0}=0$. For $i>1$, $\hat{A}_{i,0,0}$ in equation [4] can be interpreted as the updated estimate of the cow's permanent potential for milk yield. For $i>1$, $\hat{A}_{i,0,0}$ was always set equal to $\hat{A}_{i-1,J,1}$ where J denotes the last month within parity $i-1$ when the cow was still producing. That is, the expectation for the cow's permanent milk yield potential at the beginning of parity i was always set equal to its estimated value on the first day of the last producing month in parity $i-1$. For example, if $\hat{A}_{i,0,0}$ equaled 5 in any parity i, it meant that the cow was estimated to have 5 kg additional daily yield relative to the mean in parity $i-1$ and was expected to have 5 kg additional daily yield in the following parities.

The variance $\sigma^2_{e_{i,0,0}}$ in equation [4] can be interpreted as estimation uncertainty for the cow's permanent production potential. This estimation uncertainty was updated and reduced through the learning process from having monthly observations on the cow's actual milk yield. Each time a new observation was made, the estimate of the cow's permanent production potential A became more accurate. For $i=1$, $\sigma^2_{e_{i,0,0}}$ can be interpreted as the prior uncertainty that was specified to initialize the DLM. In fact, the value of $\sigma^2_{e_{i,0,0}}$ was the conditional variance of the cow's latent A value given her estimated breeding value for milk yield. For $i>1$, $\sigma^2_{e_{i,0,0}}$ can be interpreted as the updated uncertainty. For $i>1$, the value of $\sigma^2_{e_{i,0,0}}$ was always set equal to $\sigma^2_{e_{i-1,J,1}}$ where J denotes the last month within parity $i-1$ when the cow was still producing. That is, estimation uncertainty at the beginning of parity i was always set equal to its value on the first day of the last producing month in parity $i-1$.

We used KF to make predictions for actual milk yield and update posterior distributions of the latent variables. Predictions were made daily, whereas updates were made monthly. First, regarding daily predictions by KF, let $\mathbf{D}_{i,j,1} = (Y_{i,1,1}, Y_{i,2,1}, Y_{i,3,1}, \ldots, Y_{i,j,1}, \mathbf{m}_{i,j,0}, \mathbf{C}_{i,0,0})$ denote a cow's actual daily milk yields on the first day in each month up to month j in parity i, including prior information about the latent variables. Then, by letting $\mathbf{m}_{i,j,1}$ denote the conditional mean of the latent variables on the first day in month j in parity i, it follows that

$$[5] \qquad \mathbf{m}_{i,j,1} = \begin{bmatrix} \hat{A}_{i,j,1} \\ \hat{X}_{i,j,1} \end{bmatrix} = \mathbb{E}\left[\begin{bmatrix} A \\ X_{i,j,t} \end{bmatrix} \middle| \mathbf{D}_{i,j,1}\right].$$

Given the posterior distribution of the latent variables on the first day in month j in parity i, i.e., $(A, X_{i,j,1})' \,|\mathbf{D}_{i,j,1} \sim \mathrm{N}(\mathbf{m}_{i,j,1}, \mathbf{C}_{i,j,1})$, KF was used to predict actual daily milk yield for each day t in month j in parity i (Theorem 4.1 in West and Harrison, 1997) as

$$[6] \qquad \mathbb{E}(Y_{i,j,t}|\mathbf{D}_{i,j,1}) = age_i^{milk} \times (\hat{A}_{i,j,1} + \rho^{t-1} \times \hat{X}_{i,j,1}).$$

The expected total monthly milk yield for any month j in parity i was then obtained by summing expected actual daily milk yields and adding monthly mean milk yield as

$$[7] \qquad \mathbb{E}(M_{i,j}|\mathbf{D}_{i,j,1}) = \mu_{i,j} + \Sigma_t \mathbb{E}(Y_{i,j,t}|\mathbf{D}_{i,j,1}).$$

Second, regarding monthly updates by KF, given all information available up to the first day in month j in parity i, the conditional distribution of $(\mathbf{m}_{i,j+1,1}|\mathbf{m}_{i,j,1})$ was the multivariate normal distribution (adapted from Nielsen et al., 2010a)

$$[8] \qquad \begin{aligned} &[(\hat{A}_{i,j+1,1}, \hat{X}_{i,j+1,1})|(\hat{A}_{i,j,1}, \hat{X}_{i,j,1})] \\ &\sim \mathrm{N}[(\hat{A}_{i,j,1}, \rho^{30.5}\hat{X}_{i,j,1}), (Q_{i,j+1,1}\mathbf{B}_{i,j+1,1}\mathbf{B}'_{i,j+1,1})], \end{aligned}$$

with $\mathbf{B}_{i,j+1,1} = \mathbf{R}_{i,j+1,1} F_i Q^{-1}_{i,j+1,1}$, $\mathbf{R}_{i,j+1,1} = \mathbf{G}\mathbf{C}_{i,j,1}\mathbf{G}' + \mathbf{W}$, and $Q_{i,j+1,1} = F_i \mathbf{R}_{i,j+1,1} F_i$. The scalar F_i and the matrices $\mathbf{G}$ and $\mathbf{W}$ were defined in equations [3a], [3b], and [3c], respectively. By having monthly updates, we assumed that a single record on actual milk yield was available monthly. We chose this approach to mimic the test-day milk recording system used in the Netherlands. Because it was reasonable to assume that actual milk yield was known with certainty once a month, no measurement error was included in the model for actual milk yield in equation [2b]. We assumed that monthly updates occurred on the first day of the month. That is why $\hat{A}_{i,0,0}$ and $\sigma^2_{e_{i,0,0}}$ were set equal to $\hat{A}_{i-1,J,1}$ and $\sigma^2_{e_{i-1,J,1}}$ for $i>1$. Because of monthly updating, monthly transitions between actual milk yield classes were allowed. Monthly updating was different from Nielsen et al. (2010a), who used KF to update daily.

The variance structure of the SSM can be described by the parameters σ_A^2, σ_X^2, $\sigma_{e\ 1,0,0}^2$, and ρ. In Nielsen et al. (2010a), these parameters (together with mean milk yield) were estimated by analyzing herd data from daily milk recordings. In this study, however, we used a more general approach. We derived parameters that were not dependent on a specific herd or method of milk collection. Variance parameters were based on available literature information (details described in the appendix). The advantage of using literature based parameters is that this approach does not require extensive data analyses and adjustments to other production conditions are less complicated. Note, however, when the intention is to use the model on a farm, using herd specific parameters is advantageous. The purpose of the model, therefore, determines which parameters should be used. Because this model was built primarily for research purposes, we used variance parameters that were based on literature information.

Milk Revenues. Monthly milk revenues were calculated from monthly yields of milk, fat, and protein. Calculations for fat and protein yields are discussed in the appendix. According to the current payment scheme in the Netherlands, the amount of milk was penalized, whereas the amount of fat and protein were rewarded. The base milk payment prices are in Table 1.

Feed Intake. The feed intake was derived from total energy requirement, which equaled the energy required for maintenance, production, weight gain, and pregnancy, minus the energy available from fat mobilization. Energy requirement depended on age, lactation stage, and pregnancy stage. Energy from feed ration had to meet total energy requirement. We assumed that feed ration contained sufficient amount of protein and other nutrients. Feed intake, therefore, was determined by only total energy requirement. Energy was expressed in VEM (Dutch feed units of net energy), and 1,000 VEM was equivalent to 6.9 MJ net energy (**NE**). Feed intake, NE, satiety values, and prices were expressed on dry matter (**DM**) basis.

First, total monthly NE requirement was computed, that included NE requirement for maintenance, milk production, live weight change (positive or negative), and pregnancy. Energy requirement of maintenance and milk production was calculated from (CVB, 2007)

[9] $$ader_{i,j}=(42.4\times alw_{i,j}^{0.75}\times 1.05+442\times adfpcm_{i,j})\times[1+(adfpcm_{i,j}-15)\times 0.00165],$$

where $ader_{i,j}$ was the average daily NE required (VEM per day) for maintenance and milk production in month j in parity i; $alw_{i,j}$ was the average live weight (kg) in month j in parity i; and $adfpcm_{i,j}$ was the average daily fat and protein corrected milk (kg per day) in month j in parity i. The calculations of $alw_{i,j}$ and $adfpcm_{i,j}$ are in the appendix. We assumed that energy requirement for maintenance was influenced by time spent on outdoor grazing. Cows that are managed in a full time (24 hrs daily) outdoor grazing farming system have 20% higher NE requirement for maintenance than cows housed in free-stall barns (CVB, 2007). Because cows in the Netherlands are usually kept outside for 6 months of the year for 12 hrs per day, the basic energy requirement for maintenance in equation [9] was increased by 5%.

Energy requirement of weight gain was calculated based on the average daily gain in the given month. The average daily gain, which accounted for age related growth and reserve tissue deposition, was calculated using the live weight function described in the appendix, excluding the effect of pregnancy. In the lactating months, energy requirement of weight gain was 3,000 VEM per kg live weight (CVB, 2007). In the dry months, 10% higher energy requirement was used because weight gain is less efficient in this period (Van Arendonk, 1985a). In the months when the cow mobilized reserve tissue, total NE requirement was decreased by energy from fat mobilization. We assumed that reserve tissue was utilized with 80% efficiency (CVB, 2007), so NE from 1 kg mobilized reserve tissue equaled 2,400 VEM.

Energy requirement of pregnancy was set to 450, 850, 1,500 and 2,700 VEM per day, within the 6th, 7th, 8th, and 9th months of pregnancy, respectively. We assumed, furthermore, that the energy requirement of pregnancy in earlier months was negligible (CVB, 2007).

Second, monthly feed intake capacity was computed. The cow's feed intake capacity depended on her parity, lactation stage, and pregnancy stage. Feed intake capacity was computed using a recently developed cattle feed intake model in the Netherlands (CVB, 2007). The daily feed intake capacity was expressed in satiety values (SV) and was calculated as

[10] $$dfic=\begin{pmatrix}\{\alpha_0+\alpha_1\times[1-\exp(-\rho_\alpha\times\alpha)]\}\\ \times\{\beta\times[1-\exp(-\rho_\beta\times d)]\}\end{pmatrix}\times[1-\delta\times(g/220)],$$

where $dfic$ was the daily feed intake capacity expressed in SV; α was an input value expressing the age of the cow (α = parity – 1 + number of days in lactation/365); d was an input value expressing the number of days in lactation; g was an input value expressing the number of days pregnant; α_0 was a parameter describing the initial feed intake capacity in the first parity (SV/day); α_1 was a parameter describing the asymptotic level of maximum increase of daily feed intake capacity (SV/day); ρ_α was a parameter for the rate of increase in feed intake capacity (per day); β was a parameter describing the maximum level of adjustment for stage of lactation relative to the basic curve; ρ_β was a parameter for the rate of increase in feed intake capacity at the beginning of the lactation (per day); and δ was a pregnancy parameter. The values of α_0, α_1, ρ_α, β, ρ_β, and δ were set to 8.743, 3.563, 1.140, 0.3156, 0.05889, and 0.05529, respectively (CVB, 2007). Because cows with higher milk yield potential generally have higher feed intake capacity, we adjusted $dfic$ in such way that every 1% increase in milk yield potential resulted in 0.32% increase in $dfic$. Daily feed intake capacities were summed monthly to derive the cow's monthly feed intake capacity.

Third, the monthly total NE requirement and the monthly feed intake capacity were combined to obtain monthly feed rations. Average ration was assumed to contain 72% roughage and 28% concentrate (Van Bruggen, 2008). Roughage composition was assumed to be 26.4% fresh grass, 40.3% grass silage, 33.3% maize silage (Van Bruggen, 2008). The NE content and SV of the roughage components were assumed to be: 955 VEM/ kg DM and 0.91 SV/ kg DM for fresh grass; 889 VEM/ kg DM and 1.03 SV/ kg DM for grass silage; and 958 VEM/ kg DM and 0.81 SV/ kg DM for maize silage. The weighted NE content and SV of roughage were 929 VEM/ kg DM and 0.93 SV/ kg DM. Concentrate was assumed to be standard concentrate with an NE content of 1044 VEM/ kg DM and SV of 0.32 SV/ kg DM. The NE contents and SV were obtained from near-infrared reflectance spectroscopy carried out by Blgg (Oosterbeek, the Netherlands). Monthly ration was computed by maximizing roughage intake. Restrictions were imposed to ensure that the NE content of the ration met the monthly total NE requirement; the actual feed intake (SV/mo) was not higher than the monthly feed intake capacity; and minimum 2 kg concentrate was given to the cows daily.

Feed Costs. Roughage price per kg DM was €0.072 for fresh grass, €0.104 for grass silage, and €0.122 for maize silage (KWIN, 2009). The prices of roughages were weighted with their proportion in total roughage. Weighted roughage price and concentrate price are in Table 1.

Calf Revenues. We assumed that newborn calves were sold one week after their birth. Calf value was based on birth weight, survival rate, and price. Average birth weight was 40 kg in each parity (KWIN, 2009). Survival rate, including the first week after birth, was 92% in each parity (KWIN, 2009). The price for bull calf was €2.5 per kg (Table 1), and the value of heifer calf was €40 lower than that of a bull calf (KWIN, 2009). We assumed equal probabilities for having bull or heifer calf. To account for costs during the first week after birth, €4.5 was subtracted from calf value. This cost equaled the price of 3 kg skimmed milk powder that is normally given to newborn calves in the Netherlands during the first week after birth (KWIN, 2009). Weighting the values of bull and heifer calves with the chances of having them, the average calf value equaled €69, which was already corrected for the costs during the first week after birth. Calf revenues were assigned to the first month of lactation.

Carcass Revenues. The carcass value of a cow was determined by her live weight, her dressing percentage (proportion of carcass weight in live weight), and the carcass price. Live weight was calculated using the function described in the appendix, excluding the effect of pregnancy. Dressing percentage depended on parity and lactation stage. Specifically, dressing percentage was computed from the average dressing percentage for a given parity and the additive adjustment factor for the month within lactation. The input values were taken from Van Arendonk (1985a). The carcass price, which was already adjusted for costs associated with the sale of the animal, is in Table 1. The calculation of carcass revenue described thus far referred to cows that were culled because of low production or poor fertility (i.e., voluntarily culling). The calculation of carcass revenue from cows that were culled because of other reasons (i.e., involuntarily culling) is discussed in the subsection on involuntary culling.

Sundry Costs. This category included three cost items. Firstly, we imposed an interest rate (5% annually) on the cow's carcass value at the beginning of each month. Should the farmer decide to keep the cow for another month, the interest that could have been realized in that month on the carcass revenue represents an opportunity cost. Secondly, sundries included veterinary costs. In the Netherlands, the average veterinary cost for a mature cow is about €135 per year (KWIN, 2009), which is an average for healthy and diseased cows. The veterinary costs of healthy cows, therefore, are somewhat lower. Within lactation, veterinary costs were: €40 in month 1; €10 in months 2, 3, and 4; €15 in the first dry month, and €5 in all other months (Henk Hogeveen, Utrecht University, the Netherlands; personal communication). Veterinary costs were the same for each parity. Thirdly, we included the cost of fixed production assets (Table 1), that accounted for the aggregate expenses of stable, milking parlor, milk tank, manure and feed storage, grazing land, machinery, water, and electricity.

Reproduction and Related Costs. The monthly marginal probabilities of conception following insemination were calculated by using the approach of Mourits et al. (1999).

Table 2. Monthly marginal probabilities of conception for various parities and lactation stages.

Parity	Month after calving							
	2	3	4	5	6	7	8	9
1	0.23	0.41	0.50	0.47	0.48	0.47	0.45	0.45
2	0.25	0.44	0.54	0.51	0.52	0.51	0.47	0.46
3	0.26	0.46	0.56	0.52	0.54	0.52	0.48	0.46
4	0.26	0.46	0.56	0.52	0.54	0.52	0.48	0.46
5	0.25	0.44	0.54	0.51	0.52	0.51	0.47	0.46
6	0.24	0.43	0.53	0.49	0.51	0.49	0.46	0.46
7	0.24	0.42	0.51	0.48	0.49	0.48	0.45	0.45
8	0.23	0.40	0.50	0.46	0.48	0.47	0.44	0.44
9	0.22	0.38	0.47	0.44	0.45	0.45	0.42	0.43
10	0.21	0.37	0.46	0.42	0.44	0.43	0.41	0.42
11	0.20	0.35	0.43	0.40	0.42	0.41	0.39	0.40
12	0.19	0.34	0.42	0.38	0.40	0.39	0.38	0.39

The monthly marginal conception probabilities were calculated from heat detection rates (Table 1) and conception rates. The conception rates were corrected for parity and lactation stage. Average conception rate for each parity was taken from Jalvingh et al. (1993). Parity specific average conception rates were then corrected for lactation stage by multiplicative adjustment factors from Inchaisri et al. (2010). Heat detection rates and conception rates were independent of milk yield potential and length of previous calving interval. Heat detection rates, furthermore, were independent of parity. The monthly marginal probabilities of conception are presented in Table 2. The prices of first and later inseminations are around €27 and €15 in the Netherlands (Henk Hogeveen, Utrecht University, the Netherlands; personal communication). For simplicity, however, we assigned a fixed cost of €25 to the month of insemination, and this cost also accounted for re-inseminations during the given month.

Involuntary Culling and Related Costs. Replacements for other reasons than low production or failure to conceive were referred to as involuntary culling. Involuntarily culled cows included dead cows or cows sold for slaughter because of health problems. The monthly marginal probabilities of involuntary culling were calculated by using the approach of Van Arendonk (1985a). The probabilities were corrected for parity and lactation stage, but they were independent of milk yield potential and length of previous calving interval. Calculations used two input values: the probability of involuntary culling during each parity and the monthly proportion of involuntary culling within each parity. To illustrate, monthly marginal probabilities of involuntary culling with a fixed calving interval of 12 mo are in Table 3.

Costs associated with involuntary culling included three items. First, a fixed cost of €100 per cow was assigned to the month of involuntary culling, accounting for additional veterinary treatments prior to removal (Henk Hogeveen, Utrecht University, the Netherlands; personal communication). Second, milk yield was decreased for involuntarily culled cows in the month of removal. The loss in milk yield depended on parity and lactation stage, and was calculated by using the approach of Van Arendonk (1985a). Because of lower milk yield, feed intake was decreased accordingly for involuntarily culled cows in the month of removal. The new feed ration was formulated by accounting for the decrease in total energy requirement for maintenance and milk production. Third, a fixed 10% loss in carcass value was assumed for involuntarily culled cows (Henk Hogeveen, Utrecht University, the Netherlands; personal communication). This fixed reduction accounted for the facts that dead cows have no carcass value, cows with feet and leg problems have reduced carcass value, and cows with other health problems have virtually unchanged carcass value (Van Arendonk et al., 1984).

Table 3. Monthly marginal probabilities of involuntary culling for various parities and lactation stages with a fixed calving interval of 12 months.

Parity	Month after calving											
	1	2	3	4	5	6	7	8	9	10	11	12
1	0.024	0.010	0.009	0.009	0.010	0.011	0.012	0.012	0.011	0.009	0.005	0.005
2	0.026	0.011	0.009	0.010	0.011	0.013	0.013	0.013	0.012	0.010	0.006	0.006
3	0.028	0.012	0.010	0.010	0.012	0.014	0.014	0.014	0.013	0.011	0.006	0.006
4	0.030	0.012	0.011	0.011	0.013	0.015	0.015	0.015	0.014	0.012	0.007	0.007
5	0.034	0.014	0.012	0.013	0.015	0.017	0.017	0.017	0.016	0.014	0.008	0.008
6	0.034	0.014	0.012	0.013	0.015	0.017	0.017	0.017	0.016	0.014	0.008	0.008
7	0.036	0.015	0.013	0.013	0.016	0.018	0.018	0.018	0.017	0.015	0.009	0.009
8	0.038	0.016	0.014	0.014	0.017	0.019	0.019	0.020	0.018	0.016	0.009	0.009
9	0.042	0.018	0.016	0.016	0.018	0.021	0.022	0.022	0.020	0.018	0.010	0.011
10	0.046	0.019	0.017	0.018	0.020	0.023	0.024	0.025	0.022	0.020	0.012	0.012
11	0.050	0.021	0.019	0.019	0.022	0.026	0.026	0.027	0.025	0.022	0.013	0.013
12	0.056	0.024	0.021	0.022	0.025	0.029	0.030	0.031	0.029	0.026	0.015	0.015

Replacement Costs. We assumed fixed herd size, i.e., a culled cow was immediately replaced. Replacement heifers were assumed to be 24 mo old and starting their first lactation. The replacement heifer price (Table 1) was independent of the heifer's milk yield potential.

5.2.2 Mathematical module

In the mathematical module, the optimization problem for inseminations and replacements was modeled as a MLHMP (Kristensen and Jørgensen, 2000). This technique combines the properties of policy iteration and value iteration in a multi-level hierarchic manner. With MLHMP detailed real-world applications with large state space can be solved with fast convergence and exact solution. The model was programmed in Java and used as a plug-in to the MLHMP software system developed by Kristensen (2003). The MLHMP software was used to compute the optimal insemination and replacement policy, and then Markov chain simulations were performed to obtain whole-herd statistics following the optimal policy.

Model Structure. The model was constructed with 4 levels, and the graphical overview of the structure is in Figure 2. At level 0, a single process (founder) existed with infinite time-horizon, where each stage represented the entire lifetime of a cow. Each stage of the founder process was expanded into a child process (child 1) at level 1. For each cow, therefore, the length of lifetime and the gained reward during her lifetime were determined by the corresponding child 1 process. The child 1 process was of finite time-horizon with a maximum of 12 stages, where each stage represented an entire lactation. Each stage of the child 1 process was then expanded into a child process (child 2) at level 2. Therefore, the length of the given lactation and the generated reward during that lactation were determined by the corresponding child 2 process. The child 2 process was of finite time-horizon with a maximum of 18 stages. The meaning of a stage at level 2 is twofold, depending on pregnancy status during the lactation. As long as a cow was open, a stage represented a month in lactation. When a cow became pregnant, however, the consecutive stage represented the entire gestation period, which was then expanded into a child process (child 3) at level 3. Therefore, the length of the pregnancy and the reward during the pregnancy period were computed by the corresponding child 3 process. The child 3 process was of finite time-horizon with a maximum of 9 stages, where each stage represented a month (30.5 d) during pregnancy.

At each level, the state space could be described by two subsets of states. The first subset was the Cartesian product of one or more state variables. The second subset included additional states, which directly represented a cow. For the additional states, properties of an individual cow (e.g., yield class) were no longer relevant because she was replaced or diseased.

Discretizing the SSM. To embed the SSM into the MLHMP framework, the two-dimensional space of the pair $(\hat{A}_{i,j,1},\hat{X}_{i,j,1})$ was discretized by using uniform discretization (Nielsen et al., 2010b). The pair $(\hat{A}_{i,j,1}, \hat{X}_{i,j,1})$ provided the necessary information to compute actual milk yield as described in equation [6]. Both variables were discretized separately into 13 intervals, with intervals having equal probabilities. We had 13 intervals because this definition of the state space led to robust results with acceptable

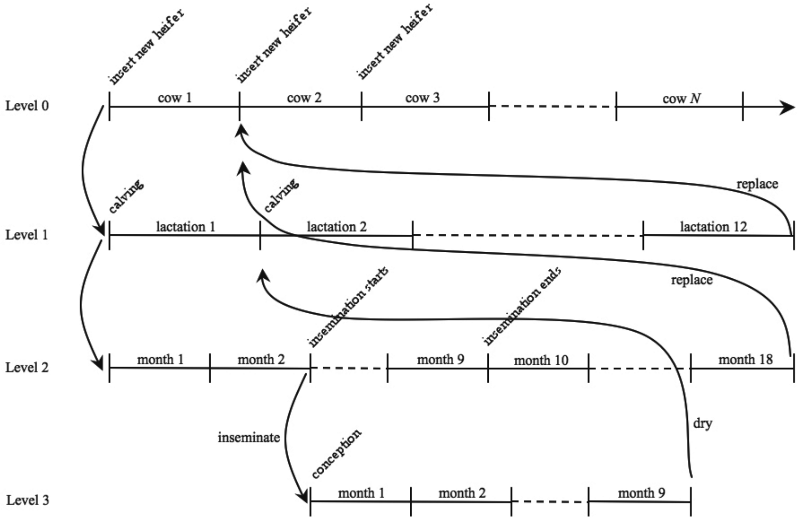


Figure 2. Schematic representation of the structure of the multi-level hierarchic Markov process model.

computing time. In fact, however, the choice of 13 intervals was arbitrary. The model was constructed in a generic way, so that any number of intervals could be used. The partition was obtained by taking the cross product of the intervals obtained for each variable. It resulted in a total of 169 rectangles of equal probabilities, and each rectangle was represented by its corresponding mean.

States and Decisions at Level 0. In the founder process, a single state variable was defined that reflected a permanent trait throughout the cow's lifetime. The state variable at level 0 represented the cow's estimated permanent milk yield potential when entering the herd as heifer. Specifically, the state variable stored the value of $\hat{A}_{i,0,0}$ from equation [4] for i=1. Because $\hat{A}_{1,0,0}$ was the expected value for $A \sim N(0,\sigma^2_A)$, the distribution was discretized to be stored in the MLHMP. The distribution was partitioned into 13 classes with equal probabilities. The state variable, therefore, had 13 levels. Only a dummy decision was defined at level 0, representing that a new heifer was inserted into the herd. The estimated permanent milk yield potential of a new heifer was independent of that of the preceding cow. Because the founder process was of infinite time-horizon, each stage had identical state and action spaces. In each stage, therefore, a cow could take any of the 13 levels of the state variable.

States and Decisions at Level 1. In the child 1 process, state variables represented traits that were permanent during an entire lactation (including dry period). We defined two state variables at level 1. The first variable represented the updated knowledge about the cow's permanent milk yield potential at the beginning of the lactation. That is, the first state variable stored the value of $\hat{A}_{i,0,0}$ from equation [4] for i>1, where for i=1 the value was equal to the state at level 0. Because $\hat{A}_{i,0,0}$ was the expected value for $A \sim N(0,\sigma^2_A)$, the distribution was partitioned into 13 levels with equal probabilities. The second state variable represented the number of open months in the previous lactation. The second variable was defined with 8 levels, allowing the open period to be minimum 2 mo and maximum 9 mo. Only a dummy decision was defined at level 1, representing that the cow started a new lactation. The state space at level 1 depended on the lactation. In the first lactation, a cow could have any of the 13 levels of the first state variable, but could not have a value for the second state variable (because there was no previous lactation yet). In later lactations, however, a cow could take any combination of the state variables, resulting in total possible states of 13×8=104.

States and Decisions at Level 2. In the child 2 process, state variables represented traits that were permanent during a month in lactation. We defined two state variables and one additional state. The first state variable represented the cow's actual milk yield in the given month. The variable stored the value of the pair $(\hat{A}_{i,j,1}, \hat{X}_{i,j,1})$ which was equivalent to $\mathbf{m}_{i,j,1}$ from equation [5]. Because $\mathbf{m}_{i,j,1}$ was the mean of a multivariate normal distribution, its value was discretized. We used a uniform discretization with 13 levels for the pair $(\hat{A}_{i,j,1}, \hat{X}_{i,j,1})$ as described earlier, resulting in 13×13=169 levels. The second state variable was a binary variable representing pregnancy state (pregnant or non-pregnant). In addition to the two state variables, a single state was included to represent that the cow was involuntarily culled.

At level 2, three decisions were defined: replace the cow immediately with a calving heifer, keep the cow for another month without insemination, or inseminate the cow and keep her for another month. However, not each decision was allowed in every month in lactation. In the first month, only a dummy action was defined representing that the cow started a new month in lactation. In the second month, two decisions were defined: keep the cow without insemination or inseminate and keep her for another month. From the third through the ninth months, all three decisions were allowed. When a decision to inseminate was made and the service was successful, the process at level 2 proceeded to the next stage, which was modeled as a child process at level 3. From the eleventh through the eighteenth months, again two decisions were allowed: replace the cow immediately or keep the cow without insemination.

The possible state space for a cow at level 2 was dependent on the lactation stage. In the first and the second months, a cow could have any values for the actual milk production level as well as could be involuntarily culled 169+1=170. From the third through the tenth month, a cow could be open or pregnant. Therefore, the second state variable was added to the state space 169×2+1=339. When a cow became pregnant, the process continued at level 3 as discussed above. From the eleventh month, a cow could no longer be pregnant because no insemination was allowed in the previous month, thus the state space was defined by the first state variable and the additional state for involuntary culling 169+1=170.

States and Decisions at Level 3. In the child 3 process, the state variables represented traits that were permanent during the entire period of pregnancy. We defined one state variable and an additional state at level 3. The state variable was equivalent to the first state variable at level 2. Therefore, it represented the cow's actual milk yield in the given month. The variable stored the value of the pair $(\hat{A}_{i,j,1},\hat{X}_{i,j,1})$, with 13×13=169 levels, as described earlier. The additional state represented that the cow was involuntarily culled. The decisions were uniform across the months of pregnancy. In each month, two decisions were defined: either replace the cow immediately with a calving heifer or keep the cow for another month. Because the same states and decisions were defined for each stage, the state space at level 3 was always defined by the state variable and the additional state 169+1=170.

Transition Probabilities. The transition from one state in the current month to another state in the next month had a transition probability. When a cow was inseminated and kept for another month, the transition probability was defined by the transition between actual milk yield levels ($\boldsymbol{p_{prod}}$), the transition into the state of being pregnant ($\boldsymbol{p_{preg}}$), and the transition into the state of being involuntarily culled ($\boldsymbol{p_{inv}}$). When a cow was kept for another month without insemination, the transition probability was defined by p_{prod} and p_{prod}. The probability p_{prod} was derived from the multivariate normal distribution in equation [8], as the integral of the density function in the intervals after discretizing the pair ($\hat{A}_{i,j,1}$, $\hat{X}_{i,j,1}$). The probability p_{preg} (Table 2) equaled the monthly marginal probability of conception, which was calculated by the bioeconomic module. The probability p_{inv} equaled the monthly marginal probability of involuntary culling, which was calculated by the bioeconomic module.

When a cow remained open after the insemination period, she was considered infertile and no longer inseminated. Such cow may be kept in the herd for a maximum of 18 mo, at which time she was replaced. In this case the process at level 2 was terminated and returned to level 0 with probability 1. Furthermore, when a decision to replace the cow immediately was made at level 2 or 3, the process at the given level was immediately terminated and returned to level 0 with probability 1. Similarly, when a cow entered the state of being involuntarily culled at level 2 or 3, the process was immediately terminated and returned to level 0 with probability 1. When a cow completed the pregnancy period at level 3 the process was immediately terminated and returned to the next stage at level 1 with probability 1, representing that the cow started the next lactation. When a cow completed the pregnancy period in the last parity, the process at level 3 was immediately terminated and returned to level 0 with probability 1.

Rewards. The rewards of the model were equal to the expected discounted economic net revenue of a cow during a stage at a level in question, given all information available (i.e., level, stage, state, decision). At level 0, the reward represented the expected net revenue of a cow during her lifetime minus the initial cost of purchasing the heifer, where the expected net revenue was calculated based on the child processes at lower levels. At level 1, the reward represented the expected net revenue of a cow during lactation plus the calf revenues, where the expected net revenue was calculated based on the child process(es) at lower level(s).

At level 2, the reward was dependent on the pregnancy status. First, for an open cow, the reward represented the expected net revenue during a month in lactation. Under decision to replace immediately, the reward equaled the carcass revenue. Under decision to keep without insemination, the reward was calculated as (milk revenue − feed cost − sundry cost) × ($1-p_{inv}$) + (milk revenue − feed cost − sundry cost + carcass revenue − cost of involuntary culling) × p_{inv}. Under decision to inseminate and keep, the reward was calculated as (milk revenue − feed cost − sundry cost − insemination cost) × ($1-p_{inv}$) + (milk revenue − feed cost − sundry cost − insemination cost + carcass revenue − cost of involuntary culling) × p_{inv}. Second, for a cow that has finished pregnancy and has calved, the reward represented the expected net revenue during the pregnancy, which was calculated in the child 3 process.

At level 3, the reward per stage represented the expected net revenue during a month in pregnancy. For a pregnant cow under decision to replace immediately, the reward equaled the carcass revenue. For a pregnant cow under decision to keep, the reward was calculated as at level 2 under the decision to keep the cow without insemination. In our model, furthermore, it was assumed that the cow was set dry in the last two months during pregnancy. In those dry months, the calculation of the reward under decision to keep excluded the milk revenues.

Optimization. An insemination and replacement policy provided a plan of which decision to take given the stage and the state of the cow. The optimal policy was found by maximizing the total expected discounted net revenues. A yearly discount rate of 5% was used. Markov chain simulations were performed to obtain whole-herd statistics following the optimal policy. The optimization and simulation algorithms are described in details in Kristensen and Jørgensen (2000). The total number of possible states was 1,480,651. This was remarkably lower than the state variables on the different levels would imply. The reduction was achieved by having only a single child process at a given level for all those states at the level above that are in fact equal processes differing only in their initial transition probabilities. This technique was applied at level 0, 1, and 2, which resulted in considerable reduction of computational complexity. For example, if each state at level 0 had been modeled with a separate child process, the total number of possible states would have been approximately 13 times higher.

5.2.3 Sensitivity analyses

The presented results focus on herd performance, resulting from optimal insemination and replacement decisions for individual cows. After running the base scenario (as described in Table 1), three groups of sensitivity analyses were performed in which a set of input and parameter values were increased and decreased proportionally by 20%. Our objective was not to test alternatives that reflect reality, but to study model behavior under extreme settings.

The first group of sensitivity analyses validated model behavior under changes in key biological and price inputs that have been previously reported to have substantial effect (e.g., Van Arendonk, 1985b; Van Arendonk and Dijkhuizen; 1985, Rogers et al., 1988a, 1988b). The following inputs were changes: monthly marginal probabilities of conception (Table 2), monthly marginal probabilities of involuntary culling (e.g., Table 3), mean mature 305-d milk yield (Table 1), and replacement heifer price (Table 1). The second group of sensitivity analyses assessed the effects of methodological contributions and new biological parameters. We evaluated the effects of changes in key input values that were used in the feed intake calculations and in the SSM, and have not been tested before. Tested input values for feed intake calculations included: energy requirement for maintenance (equation [9]), feed intake capacity (equation [10]), and adjustment factor of feed intake capacity for permanent milk yield potential (equation [10]). Tested SSM input included the phenotypic variation coefficient of 305-d milk yield (Table 1). The effect of an additional level in the MLHMP structure (relative to earlier models) was discussed qualitatively. The third group of sensitivity analyses studied the effects of variation in milk yield among individual cows. Results were compared for various

Parameters	Base scenario	Probability of conception	
		80%	120%
Results describing a herd with optimal insemination and culling policies			
Productive herd life (mo/cow)	42.2	40.5	43.1
Calving interval[1] (d/cow)	396.5	405.3	391.9
Cows with calving interval ≥14 mo[1] (%)	24.7	33.5	19.1
Annual total culling rate (%)	28.4	29.6	27.9
Proportion of voluntary cullings[2] (%)	42.5	46.0	40.7
Average technical results for a cow in a herd with optimal insemination and culling			
Milk yield (kg/mo)	734.6	726.6	738.1
Fat yield (kg/mo)	31.4	31.2	31.6
Protein yield (kg/mo)	25.6	25.3	25.7
Feed intake capacity (SV/mo)	479.3	477.9	479.8
Energy requirement (kVEM/mo)	536.3	532.3	538.0
Energy requirement (kVEM/100 kg FPCM[3])	70.0	70.2	70.0
Roughage intake (kg DM/mo)	401.1	399.2	402.2
Concentrate intake (kg DM/mo)	156.6	154.5	157.3
Average economic results for a cow in a herd with optimal insemination and culling			
Milk revenue (€/mo)	257.6	255.3	258.6
Feed cost (€/mo)	66.0	65.5	66.3
Feed cost (€/100 kg FPCM[3])	8.6	8.6	8.6
Average slaughter value (€)	528.2	528.9	527.9
Insemination cost (€/year)	48.2	57.4	41.1
Total net revenue (€/mo)	39.9	36.6	41.6
Total net revenue (€/lifetime)	1,684.1	1,481.9	1,793.2
Total net revenue (€/100 kg FPCM[3])	5.2	4.8	5.4

Table 4. Technical and economic parameters describing optimal insemination and replacement policy for base scenario and sensitivity analyses 1 (i.e., changes in monthly marginal probability of conception, monthly marginal probability of involuntary culling, mean mature 305-d milk yield, and price of replacement heifer).

[1] Based on completed lactations.

[2] Includes cows that did not get pregnant during the insemination period.

[3] Fat and protein corrected milk.

Probability of involuntary culling		Mean mature 305-d milk yield		Price of replacement heifer	
80%	120%	80%	120%	80%	120%
45.5	39.5	45.9	39.3	35.1	48.1
396.6	396.3	396.7	396.2	396.4	396.4
25.0	24.6	25.0	24.6	24.7	24.7
26.4	30.4	26.2	30.6	34.2	25.0
49.3	36.8	37.4	46.6	52.4	34.3
742.0	727.4	580.9	889.6	750.4	721.5
31.7	31.2	24.9	38.1	32.1	30.9
25.8	25.3	20.2	31.0	26.1	25.1
482.6	476.1	478.5	479.9	480.1	478.2
540.0	532.7	459.5	615.3	543.5	530.2
69.8	70.2	75.9	66.3	69.5	70.5
403.7	398.7	401.1	380.1	403.4	398.8
157.9	155.3	83.0	251.0	161.5	152.8
260.1	255.2	203.7	312.0	263.1	253.0
66.5	65.6	54.1	79.3	67.1	65.2
8.6	8.6	8.9	8.5	8.6	8.7
529.3	527.1	528.8	527.6	528.2	528.5
47.8	48.6	48.1	48.3	47.4	48.6
44.2	35.7	0.1	79.0	48.2	32.7
2,010.1	1,409.9	4.0	3,102.1	1,692.7	1,571.2
5.7	4.7	0.0	8.5	6.2	4.3

degrees of variation among cows (i.e., various number of classes specified for actual milk yield level). Our goal with the latter analyses was to illustrate the importance of variation among individual animals and its direct impact on model outcome.

5.3 Results and Discussion

5.3.1 Base scenario

The simulated annual culling rate was 28.4%, resulting in an average productive herd life of 42.2 mo per cow (Table 4), which was 2 mo shorter than actual productive herd life in Dutch herds (CRV, 2009). Because we assumed heifers to be 24 mo old when starting their first lactation, the simulated average total herd life was 66.2 mo. In practice, however, the average age at first calving is 26 mo and the average total herd life is 70 mo (CRV, 2009). The simulated average calving interval was 396.5 d, which was 18 d less than the average in the Netherlands (CRV, 2009). The difference might be because we did not model calving intervals longer than 18, or because farmers make sub-optimal insemination decisions. We found that 42.5% of all replacements were voluntary, i.e., because of low production or failure to conceive. Our results suggest that farmers might operate with sub-optimal calving intervals, whereas their culling rates are close to economic optimum under the modeled specifications.

Regarding technical and economic results (Table 4), the average monthly milk yield per cow was 734.6 kg with an average fat content of 4.28% and protein content of 3.48%. This monthly milk yield resulted in average monthly milk revenue of €257.6 per cow. Average monthly total NE requirement per cow was 70 kVEM per 100 kg fat- and protein-corrected milk (**FPCM**), and on average a cow was fed a monthly ration of 401.1 kg DM roughage and 156.6 kg DM concentrate. Mean feed cost per cow was €8.6 per 100 kg FPCM, whereas average annual insemination cost was €48.2 per cow. The average monthly net revenue per cow was €40. A herd with 75 cows, which is the average herd size in the Netherlands (LEI, 2008), would therefore generate a total net revenue of around €36,000 annually, which represents the farmer's financial compensation for labor and management. This annual total net revenue was close to current average dairy farm income in the Netherlands (LEI, 2008).

In this study, we assumed that when a cow was culled, she was sold exclusively for slaughter and was immediately replaced. These assumptions could have an effect on culling rate and net income. Regarding culling, Cardoso et al. (1999) found that when cows were also allowed to be sold for production to other farms at a higher price, annual culling rate increased from about 22 to 27%. They also found that the average monthly net revenue per cow increased from US$66.9 to US$67.4 by introducing selling for production. Regarding replacement, De Vries (2004) examined the effect of allowing temporarily delayed replacement. He found that under typical farming conditions the delayed replacement was not economically advantageous. However, in situations when fixed costs and net returns were low, and seasonality was high, delayed replacement was more advantageous than immediate replacement. In those cases, De Vries (2004) found that the annual replacement rate decreased, and the net return per cow increased. Because in our model fixed costs were already high and seasonality in performance and prices was excluded, it is reasonable to assume that delayed replacement would not be advantageous. Van Arendonk (1986), however, found large effects of seasonality on optimal replacement in the Netherlands. An extension of our model with seasonality, thus, might find financial incentives for delayed versus immediate replacement.

5.3.2 Sensitivity analyses 1: Model validation

Regarding changes in conception probabilities (Table 4), an increase of 20% resulted in lower annual culling rate (27.9%), whereas a decrease of 20% resulted in higher annual culling rate (29.6%). Lower conception probabilities resulted in more intense voluntary cullings (46%) and longer average calving interval (405.3 d). Higher conception probabilities resulted in less intense voluntary cullings (40.7%) and shorter average calving interval (391.9 d). The probability of conception, therefore, affected optimal insemination decisions and voluntary culling intensity. Voluntary culling, in turn, influenced herd composition and herd performance. Regarding technical performance (i.e., yields, energy requirement, feed intake capacity, feed intake), lower conception probabilities led to decreased inputs and outputs, whereas higher conception probabilities led to increased inputs and outputs. Regarding economic performance (i.e., costs and revenues), results changed accordingly. Average monthly net revenue per cow, for example, decreased by €3.3 when conception probabilities were decreased and increased by €1.7 when conception probabilities were increased.

Regarding changes in involuntary culling probabilities (Table 4), an increase of 20% resulted in higher annual culling rate (30.4%) and less intense voluntary cullings (36.8%), whereas a decrease of 20% resulted in lower annual culling rate (26.4%) and more intense voluntary cullings (49.3%). Optimal insemination decisions were virtually unaffected by changes in involuntary culling, because the average calving interval and the proportion of long (≥14 mo) calving intervals hardly changed. Because voluntary culling was affected, herd composition and herd performance were also affected by changes in involuntary culling probabilities. Technical and economic indicators increased for lower involuntary culling probabilities and decreased for higher involuntary culling probabilities. For example, less intense involuntary culling led to €4.3 higher average monthly net revenue per cow, whereas more intense involuntary culling led to €4.2 lower average monthly net revenue per cow.

Regarding changes in mean mature 305-d milk yield (Table 4), an increase of 20% resulted in higher annual culling rate (30.6%) and more intense voluntary replacement (46.6%), whereas a decrease of 20% resulted in lower annual culling rate (26.2%) and less intense voluntary replacement (37.4%). Optimal insemination decisions, however, were virtually not affected by the changes in mean mature 305-d milk yield. Because of the effects on voluntary culling intensity, changes had an effect on technical and economic indicators of herd performance. Higher mean mature 305-d milk yield, on the one hand, resulted in elevated average monthly milk yield (889.6 kg per cow), NE requirement (615.3 kVEM per cow), and concentrate intake (251 kg DM per cow). Lower mean mature 305-d milk yield, on the other hand, resulted in declined average monthly milk yield (580.9 kg per cow), NE requirement (459.5 kVEM per cow), and concentrate intake (83 kg DM per cow). Accordingly, the average monthly net revenue per cow increased to €79 following a 20% increase and decreased to €0.1 following a

Parameters	Base scenario	Variation coefficient	
		80%	120%
Results describing a herd with optimal insemination and culling policies			
Productive herd life (mo/cow)	42.2	46.5	39.1
Calving interval[1] (d/cow)	396.5	396.0	397.1
Cows with calving interval ≥14 mo[1] (%)	24.7	24.3	25.3
Annual total culling rate (%)	28.4	25.8	30.7
Proportion of voluntary cullings[2] (%)	42.5	36.7	46.8
Average technical results for a cow in a herd with optimal insemination and culling			
Milk yield (kg/mo)	734.6	717.2	752.5
Fat yield (kg/mo)	31.4	30.7	32.2
Protein yield (kg/mo)	25.6	25.0	26.2
Feed intake capacity (SV/mo)	479.3	476.6	482.3
Energy requirement (kVEM/mo)	536.3	527.8	545.1
Energy requirement (kVEM/100 kg FPCM[3])	70.0	70.6	69.5
Roughage intake (kg DM/mo)	401.1	399.1	402.9
Concentrate intake (kg DM/mo)	156.6	150.2	163.5
Average economic results for a cow in a herd with optimal insemination and culling			
Milk revenue (€/mo)	257.6	251.4	264.0
Feed cost (€/mo)	66.0	64.8	67.3
Feed cost (€/100 kg FPCM[3])	8.6	8.7	8.6
Average slaughter value (€)	528.2	528.8	527.6
Insemination cost (€/year)	48.2	48.4	48.1
Total net revenue (€/mo)	39.9	37.1	43.0
Total net revenue (€/lifetime)	1,684.1	1,726.8	1,681.0
Total net revenue (€/100 kg FPCM[3])	5.2	5.0	5.5

Table 5. Technical and economic parameters describing optimal insemination and replacement policy for base scenario and sensitivity analyses 2 (i.e., changes in phenotypic variation coefficient of milk yield, energy requirement for maintenance, feed intake capacity, and adjustment factor of feed intake capacity for permanent milk yield potential).

[1] Based on completed lactations.

[2] Includes cows that did not get pregnant during the insemination period.

[3] Fat and protein corrected milk.

Maintenance requirement		Intake capacity		Intake capacity adjustment factor	
80%	120%	80%	120%	80%	120%
42.1	42.4	42.8	41.6	42.3	42.1
396.4	396.5	396.7	396.4	396.5	396.5
24.7	24.8	25.0	24.6	24.8	24.7
28.5	28.3	28.0	28.8	28.3	28.5
42.7	42.3	41.7	43.3	42.4	42.6
735.0	734.2	733.2	736.1	734.3	734.8
31.5	31.4	31.4	31.5	31.4	31.5
25.6	25.6	25.5	25.6	25.6	25.6
479.3	479.3	383.5	575.3	477.3	481.3
502.4	570.2	535.7	537.0	536.2	536.4
65.6	74.5	70.1	70.0	70.0	70.0
394.4	404.0	296.6	475.2	399.1	403.1
130.1	186.5	249.1	91.3	158.3	154.9
257.7	257.5	257.1	258.1	257.5	257.7
61.1	71.2	70.5	62.9	66.1	66.0
8.0	9.3	9.2	8.2	8.6	8.6
528.2	528.2	528.3	528.2	528.2	528.2
48.2	48.2	48.2	48.3	48.2	48.2
44.8	34.8	35.3	43.1	39.8	40.0
1,886.6	1,473.0	1,511.7	1,794.0	1,684.5	1,684.4
5.9	4.5	4.6	5.6	5.2	5.2

20% decrease in mean mature 305-d milk yield.

Regarding changes in prices, model outcomes were sensitive to prices of milk and carcass, whereas they were insensitive to prices of feed, calf, and insemination (results not shown). Changes in replacement heifer price had large effects (Table 4). Lower heifer price resulted in more intense voluntary culling policy (52.4%), whereas higher heifer price resulted in less intense voluntary culling (34.3%). Annual total culling rate was more affected by decreased heifer price than by increased heifer price, reflecting the relatively high price of replacement heifers in the Netherlands. Specifically, results indicate that farmers tend to keep their cows as long as possible, and so further increase in heifer price had limited impact. Optimal insemination decisions were virtually not sensitive to changes in heifer price. Technical and economic results increased when heifer price was lower and decreased when heifer price was higher. Average monthly net revenue per cow, for example, increased by €8.3 for lower heifer price and decreased by €7.2 for higher heifer price. Our results for the sensitivity analyses on key biological and price inputs were in agreement with the results of earlier studies (e.g., Van Arendonk and Dijkhuizen, 1985; Rogers et al., 1988a, 1988b; Kalantari et al., 2010).

5.3.3 Sensitivity analyses 2: Effects of methodological contributions and new biological parameters

Methodological contributions were incorporated in two main aspects. First, an additional level to the model hierarchy was introduced to obtain a more tractable structure. Second, we included a recently developed cattle feed intake model to obtain more precise predictions on feed costs. Furthermore, we applied novel (literature based) parameters in the SSM, which modeled milk yield and captured variation in milk yield potential among individual cows.

SSM Parameterization. The sensitivity of model outcomes to the phenotypic variation coefficient of milk yield was investigated (Table 5). This parameter directly influenced the variability of latent variables A and X. Increased variation coefficient, on the one hand, resulted in more intense voluntary culling (46.8%) and thus higher average monthly net revenue per cow (€43). Decreased variation coefficient, on the other hand, resulted in less intense voluntary culling (36.7%) and thus lower average monthly net revenue per cow (€37.1). When phenotypic variation was greater, therefore, differences in milk yield among individual cows became greater, creating more opportunities for voluntary replacement that led to improved herd performance. When phenotypic variation was lower, however, differences in milk yield among individual cows became smaller, creating less opportunities for voluntary replacement that led to declined herd performance. Results for changes in phenotypic variation coefficient of milk yield were analogous to earlier results for changes in mean mature 305-d milk yield, although the effects on model outcomes were less extreme.

Feed Intake Calculations. First, sensitivity to energy requirement for maintenance was tested (Table 5). When maintenance requirement was changed, optimal insemination and culling policies were virtually unaffected. Feed intake, however, was sensitive to changes in maintenance requirement. With increased maintenance requirement, average monthly roughage and concentrate intakes per cow increased by 2.9 kg DM and 29.9 kg DM. With decreased maintenance requirement, however, average monthly roughage and concentrate intakes per cow decreased by 6.7 kg DM and 26.5 kg DM. Second, sensitivity to feed intake capacity was tested (Table 5). Changes in feed intake capacity hardly affected optimal insemination and replacement decisions, but they affected feed ration composition. When feed intake capacity was lowered, for example, average monthly intake per cow decreased by 104.5 kg DM for roughage and increased by 92.5 kg DM for concentrate. Third, sensitivity to the adjustment factor of feed intake capacity for permanent milk yield potential was examined (Table 5). The results showed that model outcomes were virtually insensitive to changes in the adjustment factor. In conclusion, changes in maintenance requirement and feed intake capacity affected feed intake and therefore net revenues. Optimal insemination and replacement decisions, however, were insensitive to changes in feed intake calculations.

MLHMP Formulation. In this study, we introduced an additional level to the MLHMP structure to model the entire pregnancy process of a successfully inseminated cow. Because the pregnancy state of a pregnant cow was constant during the gestation period, it was represented by an additional child level. Introducing an additional level to the MLHMP structure was advantageous because it made the model structure more tractable for the end-user. The additional level, furthermore, lessens computational complexity by dividing transition matrices into smaller matrices that are handled one by one (Kristensen and Jørgensen, 2000). In our model, the transition matrices at level 2 were decreased. With the present 4-level structure, the size of the transition matrix was 339×339 from stage 3 through stage 10 and 170×170 in all other stages at level 2. If the pregnancy state was not modeled as a separate child process, then the state space at level 2 would need to be extended to properly account for the information about gestation stage. Such state extension would increase the size of the transition matrices to 1,700×1,700 throughout all stages at level 2. Note, however, that other algorithms may also result in the same computational time, regardless of the additional level in the MLHMP structure (see Nielsen and Kristensen, 2006).

5.3.4 Sensitivity analyses 3: Effects of the number of production classes

Although the variation in milk yield among individual cows is an important aspect of optimization models, the degree of variation has been rather neglected in the literature. To study the impact of the degree of variation, we run the model with various number of classes for each state variable representing actual milk yield (Table 6). The tested number of classes ranged from 1 to 21, with 13 being the default value for results presented in Table 4 and 5.

Specifying more classes resulted in a convergence in several model outcomes. The proportion of voluntary replacements increased from 14 to 41% when number of classes was increased from 1 to 5, whereas it hardly changed beyond 13 classes. Optimal insemination decisions were virtually not affected, because the average calving interval and the share of long (≥14 mo) calving intervals hardly changed. Technical indicators improved when more classes were defined for milk yield. Average monthly milk yield per cow increased from 685.6 kg with 1 class to 735.9 kg with 21 classes. More classes also increased net revenue by providing more decisions to optimize. Average monthly net revenue per cow increased from €33.3 with 1 class to €40.2 with

Parameters	1 class
Total state count	19,615
Results describing a herd with optimal insemination and culling policies	
Productive herd life (mo/cow)	62.2
Calving interval[1] (d/cow)	396.4
Cows with calving interval ≥14 mo[1] (%)	25.0
Annual total culling rate (%)	19.3
Proportion of voluntary cullings[2] (%)	14.0
Average technical results for a cow in a herd with optimal insemination and culling	
Milk yield (kg/mo)	685.6
Fat yield (kg/mo)	29.3
Protein yield (kg/mo)	23.8
Feed intake capacity (SV/mo)	473.7
Energy requirement (kVEM/mo)	512.6
Energy requirement (kVEM/100 kg FPCM[3])	71.8
Roughage intake (kg DM/mo)	395.7
Concentrate intake (kg DM/mo)	138.7
Average economic results for a cow in a herd with optimal insemination and culling	
Milk revenue (€/mo)	240.1
Feed cost (€/mo)	62.6
Feed cost (€/100 kg FPCM[3])	8.8
Average slaughter value (€)	530.2
Insemination cost (€/year)	49.7
Total net revenue (€/mo)	33.3
Total net revenue (€/lifetime)	2,070.3
Total net revenue (€/100 kg FPCM[3])	4.7

Table 6. Technical and economic parameters describing optimal insemination and replacement policy for sensitivity analyses 3 (i.e., different number of milk yield classes).

[1] Based on completed lactations.

[2] Includes cows that did not get pregnant during the insemination period.

[3] Fat and protein corrected milk.

[4] Results with 13 classes refer to the base scenario.

5 classes	9 classes	13 classes[4]	17 classes	21 classes
230,371	717,383	1,480,651	2,520,175	3,835,955
43.3	42.1	42.2	42.3	42.2
396.5	396.6	396.5	396.4	396.5
25.0	25.0	24.7	24.7	24.8
27.7	28.5	28.4	28.4	28.4
41.0	42.6	42.5	42.5	42.6
726.7	733.3	734.6	735.3	735.9
31.1	31.4	31.4	31.5	31.5
25.3	25.5	25.6	25.6	25.6
477.9	479.0	479.3	479.4	479.6
532.3	535.6	536.3	536.7	537.0
70.3	70.1	70.0	70.0	70.0
400.1	401.0	401.1	401.2	401.2
153.7	156.0	156.6	156.9	157.1
254.8	257.1	257.6	257.9	258.1
65.5	65.9	66.0	66.1	66.1
8.6	8.6	8.6	8.6	8.6
528.4	528.3	528.2	528.2	528.2
47.4	47.9	48.2	48.4	48.3
38.3	39.5	39.9	40.1	40.2
1,656.5	1,660.5	1,684.1	1,695.4	1,697.5
5.1	5.2	5.2	5.2	5.2

21 classes. Benefits of more refined state space for milk yield, however, were substantial at first but gradually declined with higher number of classes.

Specifying more classes, furthermore, greatly impacted the total number of states, which ranged from 19,615 with 1 class to 3,835,955 with 21 classes (Table 6). Increasing the number of milk yield classes increased computational complexity due to the "curse of dimensionality". Refining state space, therefore, soon becomes computationally prohibitive even on modern computers. Consequently, there is a tradeoff between the number of milk yield classes and the overall state space in the MLHMP. Nielsen et al. (2010b) suggested an iterative approach of stepwise refining the number of classes by a multivariate discretization technique and each time solving the MLHMP until an acceptable difference was achieved.

In the literature, several models have defined 15 classes for milk yield (e.g., Van Arendonk, 1985b; Kristensen, 1987). Other examples, however, also exist, including 3 classes (Heikkila et al., 2008), 5 classes (Kennedy and Stott, 1993; Bar et al., 2008), and 9 classes (Boichard, 1990). Until now, only McCullough and DeLorenzo (1996) assessed the effect of different number of milk yield classes. They tested the effects of various number of classes ranging from 3 to 15. On the one hand, they found that less variation resulted in lower average milk yield. This result agrees with our findings. On the other hand, they found that net revenue decreased with higher number of classes. This finding disagrees with our results. Their findings, therefore, were inconsistent. Moreover, they reported effects only on a limited number of outputs and tested only lower number of classes than used in their base scenario.

5.3.5 Applicability of the model

The traditional applications of herd optimization models can be grouped into three main clusters. Firstly, models have been developed to aid farmers and herd improvement organizations in insemination and culling decisions (e.g., Van Arendonk, 1988). Our model may be used to develop general management guidelines, by computing insemination value (**IV**) and retention pay-off (**RPO**) for individual cows (Houben et al., 1994). The IV represents the expected extra profit from inseminating a cow, relative to leaving her open. The RPO represents the expected extra profit from keeping a cow, relative to immediate culling. The IV and RPO can be used to rank individual cows in insemination and replacement decisions (Kristensen, 1987; Van Arendonk, 1988). Our model, moreover, can provide useful information for veterinary treatment decisions. Although the model does not have decisions about when to treat a cow, the RPO values represent the maximum amount of money that could be spent on trying to keep a cow. The RPO, therefore, gives the maximum acceptable treatment cost, above which it is more profitable to cull a cow (Van Arendonk, 1988).

Secondly, our model may be applied to study economics of animal health. Several earlier studies used herd optimization models to assess technical and economic effects of various diseases, including mastitis (Houben et al., 1994), paratuberculosis (Stott et al., 2005), lameness (Cha et al., 2010), and other cattle diseases (Gröhn et al., 2003). Our model can be useful in studying diseases, conditional that the model is extended for the examined diseases. Specifically, the state space needs to be extended to capture that a cow became diseased, and the bioeconomic module needs to be extended to account for the effect of the diseases on biological functions. The model can re-optimize insemination and culling decisions, ensuring that effects of the diseases are properly accounted for. Then post-optimization simulations can be used to compare herd performance under the base (i.e., uninfected) and the diseased scenarios. The comparison not only can unravel the effects of diseases (e.g., Stott et al., 2002; Gröhn et al., 2003; Bar et al., 2008) and but also can be used to determine the economic value of various treatment and prevention options (e.g., Yalcin and Stott, 2000; Bar et al., 2009).

Thirdly, the model presented in this study may be used to investigate the economic weight of selection traits in breeding programmes for dairy cattle. Herd optimization models provide a proper framework for such objectives (Dekkers, 1991), and several earlier applications have been reported examining the economic weight of selection traits. Studied selection traits include longevity (Rogers et al., 1988b; Stott, 1994), functional herd life (Jairath et al., 1998; Vollema et al., 2000), fertility (Boichard, 1990; Plaizier et al., 1997), and yield traits (Dekkers, 1991; Veerkamp et al., 1995). The present model can be used to derive economic weight of selection traits from the individual producer's viewpoint. Our model can optimize the production system both at the base situation and after the change in genetic merit for the studied trait. This step ensures that the possible effects of the change in the studied trait on milk production, fertility, and longevity are incorporated. Then, Markov chain simulations can be applied to calculate the economic value as the change in the discounted net revenues following a unit increase in the goal trait concerned, while keeping all other traits constant.

In addition to the three main clusters outlined above, recently novel applications have emerged that evaluated the impact of various feeding regimes. Vargas et al. (2001) assessed the effect on optimal culling patterns and herd performance of several feeding regimes, which differed in type of forage for grazing, quantity of concentrates, and allocation of concentrates during lactation. Cabrera (2010) investigated not only the technical and economic effects of various diets, but also their environmental impacts. Cabrera's herd optimization model was extended with environmental functions for manure and nutrition balance of the dairy herd, and average monthly nitrogen excretion per cow was computed. In conclusion, herd optimization and simulation models are versatile and valuable research tools for interdisciplinary studies. By applying the present model, various aspects of dairy farming systems can be investigated, including farm decision support, animal health economics, animal breeding, animal nutrition, and ecological sustainability. It is anticipated that the model presented in this paper will be used primarily in research and extension in the future.

5.4 Conclusions

Our objective was to develop a dairy herd optimization and simulation model. The model incorporated methodological developments in two main aspects. First, our model was the first to formulate the dairy optimization problem as a 4-level Hierarchic Markov Process. Relative to earlier 3-level models, we introduced an additional level to model the pregnancy period, thereby obtaining a more tractable structure. Second, we incorporated a recently developed cattle feed intake model to obtain more precise predictions on feed costs. Furthermore, we presented a novel parameterization of the SSM for milk yield, and we used several new biological parameters to reflect the current cattle population. Results were generated under Dutch farming conditions, and outcomes were in line with actual herd performance in the Netherlands. Sensitivity analyses showed that greater variation in milk yield leads to more intense culling and higher net revenue. Energy requirement for maintenance and feed intake capacity did not influence optimal herd composition, whereas they affected feed intake and economic results. Specifying more production classes increased net revenues by providing more decisions to optimize. Benefits of more classes were substantial at first but then gradually declined with higher number of classes. Future research may extend the model with environmental functions to investigate the ecological footprint of various farming settings.

Appendix

A.1 Calculation of monthly mean milk yield

The mean milk yield was calculated by the approach of Van Arendonk (1985a). The starting point was the mean 305-d milk yield at mature age (seven years) that was then corrected for the effect of parity. The mean 305-d milk yield in given parity was calculated as

$$[11] \qquad m305_i^{milk} = m305_{mature}^{milk} \times age_i^{milk},$$

where $m305_i^{milk}$ was the mean 305-d milk yield (kg) in parity i, $m305_{mature}^{milk}$ was the mean 305-d milk yield (kg) at mature age, and age_i^{milk} was the multiplicative effect of parity i on mean 305-d milk yield. In the model, the value of $m305_{mature}^{milk}$ was set to 9,000 kg based on information from cooperative cattle improvement organization CRV (Arnhem, the Netherlands). The values for age_i^{milk} were also from CRV and are presented in Table 7.

Table 7. Multiplicative adjustment factors[1] for the effect of parities on mean 305-d milk yield, 305-d fat content, and 305-d protein content.

Parity	305-d milk yield	305-d fat content	305-d protein content
1	0.73	1.01	1.01
2	0.86	1.01	1.02
3	0.94	1.01	1.01
4	0.99	1.01	1.00
5	1.00	1.00	1.00
6	1.00	1.00	1.00
7	0.98	0.99	1.00
8	0.94	0.98	0.99
9	0.94	0.98	0.99
10	0.94	0.98	0.99
11	0.94	0.98	0.99
12	0.94	0.98	0.99

[1] Provided by the cooperative cattle improvement organization CRV (Arnhem, the Netherlands).

Because in equation [11] the 305-d milk yield was calculated, the length of calving interval was implicitly assumed to be 12 months. However, in our model we assumed that the calving interval could vary due to different number of open months (see also section on the mathematical module). Therefore, a correction was included for the length of calving interval in the present lactation. This correction resulted in the calculation of the mean lactation milk yield (kg). The mean lactation milk yield was calculated from the following equation

[12] $$mlact_{i,k}^{milk}=m305_{i}^{milk}\times ci_{i,k}^{pres},$$

where $mlact_{i,k}^{milk}$ was the mean lactation milk yield (kg) in parity i with k months open in present lactation and $ci_{i,k}^{pres}$, was the multiplicative effect in parity i of k months open in present lactation. Values for $ci_{i,k}^{pres}$ were calculated as follows. The lactation curve of Van Arendonk (1985a) was adapted to include the effect of parity, lactation stage, and calving interval, and exclude the effect of seasons. The resulting lactation curve is written as

[13] $$y_{t,k}=[a-b\times t-13\exp(-c\times t)]/[1+(p/140)^2],$$

where $y_{t,k}$ was the daily milk yield (kg) at t days after calving and k months open in present lactation, a was the level parameter (kg), b was the slope during the decline in production after the peak production (kg/day), c was the initial increase of production (kg/day), and p was $t-(k\times 30.5-3.5)-122$ when $t\geq(k\times 30.5-3.5)+122$ and 0 otherwise. Different values were used for parameters a and b during the first, second, and third or higher parities. The values were 22.0, 26.5, and 31.0 for parameter a; and 0.035, 0.050, and 0.065 for parameter b. The value of parameter c was fixed at 0.125. From the definition of the parameter p it follows that pregnancy was assumed to impact milk yield 4 months (122 days) after conception. This assumption is in agreement with recent findings in various Holstein cattle breeds (see e.g., Olori et al., 1997; Brotherstone et al., 2004; Bohmanova et al., 2009).

To calculate the values for $ci_{i,k}^{pres}$, in equation [12], the lactation curve of equation [13] was fitted with different number of months open in present lactation. The value of $ci_{i,k}^{pres}$ for any k was calculated as the ratio of total lactation yield from equation [13] assuming k months open to total lactation yield from equation [13] assuming 3 months open (which corresponds to the standard 12 months long calving interval). The absolute values of lactation yields from equation [13] were not used, but only the proportional change in lactation yield at different lengths of calving interval was computed. Because cows with longer calving interval (i.e., longer open period) tend to have longer dry period (Oltenacu et al., 1980), the following formula was used to calculate the number of days in milk (**DIM**) at different open periods

[14] $$DIM_{k}=222.65+0.9\times(k\times 30.5),$$

where DIM_{k} was the realized total number of days in milk with k months open in present lactation. Practically, by using the formula in equation [14] we imposed the assumption that an extra day open resulted in 0.9 extra day in milk, which is in line with recent findings on dairy cattle (Rehn et al., 2000; Arbel et al., 2001; Österman and Bertilsson, 2003). The obtained number of days in milk from equation [14] was then incorporated in calculating $ci_{i,k}^{pres}$,. The values of $ci_{i,k}^{pres}$ for different parities and open periods are presented in Table 8.

Table 8. Multiplicative adjustment factors for the effect of calving intervals in present[1] and previous[2] parities on mean 305-d milk yield.

Calving interval (months)	Present calving interval			Previous calving interval
	Parity 1	Parity 2	Parity ≥3	
11	0.93	0.94	0.94	0.98
12	1	1	1	1
13	1.07	1.06	1.05	1.01
14	1.13	1.11	1.09	1.02
15	1.18	1.15	1.13	1.03
16	1.23	1.19	1.15	1.04
17	1.27	1.21	1.17	1.05
18	1.31	1.23	1.18	1.05

[1] Calculated by using equations [4] and [5].

[2] Based on Sadek and Freeman (1992).

A consequence of equation [14] was that different calving intervals have different lengths of dry period. Because the dry period in turn influences the milk yield in the subsequent lactation (Wood, 1985), correction for previous calving interval was necessary when computing milk production in the present lactation. Therefore, equation [12] was extended as

$$[15] \qquad mlact_{i,k,l}^{milk} = m305_{i}^{milk} \times ci_{i,k}^{pres} \times ci_{l}^{prev},$$

where $mlact_{i,k,l}^{milk}$ was the mean lactation milk yield (kg) in parity i with k months open in present lactation and l months open in previous lactation and ci_{l}^{prev} is the multiplicative effect of l months open in previous lactation. Values for ci_{l}^{prev} were derived from Sadek and Freeman (1992) and they are presented in Table 8. We used the same set of multiplicative factors for all parities, which is in line with the findings of Sadek and Freeman (1992).

Once the mean lactation milk yield was calculated, its value was distributed between monthly (30.5 d) periods to obtain the monthly mean milk yield. The lactation curve in equation [13] was used to calculate the proportions of the lactation yield at monthly intervals. To validate the obtained monthly shares of the lactation production, similar monthly percentages were calculated by using a lactation curve from Schils et al. (2007), which is a recent lactation curve applied to Dutch Holstein cattle. The computed monthly percentages from their curve were in line with the percentages from our lactation curve (results not shown). Therefore, we concluded that the lactation curve of Van Arendonk (1985a) is robust enough for computing the distribution of lactation production across months within lactation.

A.2 Calculation of SSM variance parameters

Variance parameters were obtained assuming a calving interval of 12 mo and were used regardless the actual length of calving interval. The starting point for deriving the variance parameters was the mean 305-d milk yield at mature age ($m305_{mature}^{milk}$) from equation [11]. Furthermore, we assumed a coefficient of within-herd phenotypic variation (VC_{305}) of 12% (Van Arendonk, 1991). From $m305_{mature}^{milk}$ and VC_{305}, we calculated the 305-d phenotypic variance at mature age ($\sigma^2_{P(305)}$) as

[16] $$\sigma^2_{P(305)}=(VC_{305}\times m305_{mature}^{milk})^2.$$

Then we assumed the following for decomposing the 305-d phenotypic variance

[17] $$\sigma^2_{P(305)}=\sigma^2_{A\,(305)}+\sigma^2_{X\,(305)},$$

where $\sigma^2_{A\,(305)}$ was the 305-d variance of A (kg^2) from equation [2b], and $\sigma^2_{X\,(305)}$ was the 305-d variance of $X_{i,j,t}$ (kg^2) from equation [2b]. Furthermore, we assumed the repeatability (r) of the 305-d yield to be 0.55 for consecutive lactations (Van Arendonk, 1991). Because the term A aggregates those effects on milk yield that are permanent features of the cow over lactations, the 305-d variance in permanent milk yield potential $\sigma^2_{A\,(305)}$ could be derived as

[18] $$\sigma^2_{A\,(305)}=r\times\sigma^2_{P(305)},$$

which in turn was used to calculate $\sigma^2_{X\,(305)}$ from equation [17]. Because the DLM in our model was constructed for daily yields, the 305-d variances needed to be split up into daily variances σ^2_A and σ^2_X. We assumed the following decomposition for $\sigma^2_{A\,(305)}$ and $\sigma^2_{X\,(305)}$

[19a] $$\sigma^2_{A\,(305)}=\mathbf{1}\times(\mathbf{H}_{305}\times\sigma^2_A)\times\mathbf{1}',$$
[19b] $$\sigma^2_{X\,(305)}=\mathbf{1}\times(\mathbf{H}_{305}\times\sigma^2_X)\times\mathbf{1}',$$

where $\mathbf{1}$=[305×1] vector of ones, $\mathbf{H}_{305}$=[305×305] autocorrelation matrix with $\mathrm{H}_{t,t}*=\rho_*^{|t-t*|}$ where $\rho*$ was autocorrelation coefficient, and t and $t*$ were days since the beginning of the lactation. In equation [19a] the value of $\rho*$ was equal to 1, following the system equation of DLM in equation [3b], resulting in σ_A^2 of 6.90 kg^2. In equation [19b] the value of $\rho*$ was set equal to ρ from the system equation of DLM in equation [3b]. The value of ρ was assumed to be 0.98 (Nielsen et al., 2010a), resulting in σ_X^2 value of 20.74 kg^2.

The last parameter to determine was $\sigma^2_{e_{1,0,0}}$ from equation [4], which was the distribution of $\hat{A}_{1,0,0}$ from equation [4]. The value of $\sigma^2_{e_{1,0,0}}$ represented the prior estimation uncertainty about A that can be reduced through the Bayesian learning process based on later observations. When a cow is inserted to the herd as a heifer, the prior estimate ($\hat{A}_{1,0,0}$) about her value for A is based on her estimated genetic capacity for milk production. Therefore, the value of $\sigma^2_{e_{1,0,0}}$ is the conditional variance of the cow's A value given the estimated breeding value (**EBV**) for milk yield. In other words, $\sigma^2_{e_{1,0,0}}=V(A|EBV)$, specified as

[20]
$$\begin{aligned}V(A|EBV)&=V(BV+PE|EBV)\\&=V(BV|EBV)+V(PE|EBV)\\&=V(BV|EBV)+V(PE)\\&=V(BV|EBV)+\sigma_{PE}^2,\end{aligned}$$

For the first term in equation [20], by using standard rules we have that

[21]
$$V(BV|EBV)=(1-r_{IH}^2)\times V(BV)=(1-r_{IH}^2)\times\sigma_{BV}^2,$$

where r_{IH} was the correlation between the true breeding value (**BV**) and the EBV, and σ_{BV}^2 is the daily variance of BV. The value of r_{IH} was 0.63, while the value of σ_{BV}^2 was determined as

[22]
$$\sigma_{BV}^2=h^2\times\sigma_P^2=\frac{h^2}{r}\times\sigma_A^2,$$

where h^2 was the heritability of milk yield with a value of 0.40, σ_P^2 was the daily phenotypic variance of milk yield, r was the repeatability of milk yield in consecutive lactations, and σ_A^2 was the daily variance of the permanent potential for milk yield from equation [19a]. For the second term in equation [20], because $\sigma_A^2=\sigma_{BV}^2+\sigma_{PE}^2$ we have that

[23]
$$\sigma_{PE}^2=\sigma_A^2-\sigma_{BV}^2=\sigma_A^2-\frac{h^2}{r}\times\sigma_A^2=(1-\frac{h^2}{r})\times\sigma_A^2.$$

Consequently,

[24]
$$\sigma^2_{e_{1,0,0}}=(1-r_{IH}^2)\times\frac{h^2}{r}\times\sigma_A^2+(1-\frac{h^2}{r}\times\sigma_A^2=(1-r_{IH}^2\times\frac{h^2}{r}\times\sigma_A^2).$$

A.3 Calculation of monthly fat and protein yields

The calculations for both fat and protein yield can be divided into three steps: calculating the mean 305-d fat and protein content, calculating the monthly fat and protein content for given calving interval and age, and calculating the monthly fat and protein yield. In the first step, the mean 305-d fat and protein content was calculated as

[25a] $$m305_i^{fc} = m305_{mature}^{fc} \times age_i^{fc},$$

[25b] $$m305_i^{pc} = m305_{mature}^{pc} \times age_i^{pc},$$

where $m305_i^{fc}$ and $m305_i^{pc}$ were the mean 305-d contents for fat and protein (%) in parity i, $m305_{mature}^{fc}$ and $m305_{mature}^{pc}$ were the mean 305-d contents for fat and protein (%) at mature age, and age_i^{fc} and age_i^{pc} were the multiplicative effects of parity i on mean 305-d contents for fat and protein. Values of $m305_{mature}^{fc}$ and $m305_{mature}^{pc}$ were 4.25% and 3.45%, respectively (from CRV). The age_i^{fc} and age_i^{pc} (provided by CRV) are shown in Table 7.

In the second step, the monthly fat and protein percentages were computed by satisfying two criteria. First, after weighting the monthly fat and protein percentages with the monthly relative productions (i.e., percentages derived during calculating the mean milk yield), they needed to average exactly to the mean 305-d contents from equations [25a] and [25b]. Second, because the lactation stage influences fat and protein contents, the monthly fat and protein percentages needed to have a changing pattern accordingly. In this model, the additive adjustment factors of Van Arendonk (1985a) were used to account for the lactation stage.

Once the monthly percentages were computed, the realized monthly fat and protein yields were calculated in the third step as the product of the total monthly milk yield and the monthly percentage for fat and protein. Furthermore, regarding the effect of the length of previous calving interval, Sadek and Freeman (1992) found that the correction factors for fat production and for milk production were equal. This implies that the fat concentration was not influenced by the length of the previous calving interval. Consequently, in our model we assumed that the fat and protein contents were not affected by the previous calving interval.

A.4 Calculation of fat- and protein-corrected milk yield

The average daily fat- and protein-corrected milk yield ($adfpcm_{i,j}$) in equation [9] was calculated from (CVB, 2007)

[26] $$adfpcm_{i,j} = \begin{pmatrix} 0.337 + 0.116 \times fat\%_{i,j} \\ +0.060 \times protein\%_{i,j} \end{pmatrix} \times milk_{i,j} / 30.5,$$

where $fat\%_{i,j}$ was the fat percentage (%) in month j in parity i; $protein\%_{i,j}$ was the protein percentage (%) in month j in parity i; $milk_{i,j}$ was the realized total milk yield (kg) in month j in parity i. To simplify the calculations, when the dry period started during month j, no separate calculation was made for the dry and the lactating parts for that particular month.

A.5 Calculation of live weight

The average live weight ($alw_{i,j}$) in equation [9] was determined as the average of the initial and final daily weights in month j. Those initial and final weights were calculated from the live weight function of Korver et al. (1985) as reported in Van Arendonk (1985a)

$$[27] \qquad lw_{t_a,t_l,t_p} = A\times[1-\{1-y_0\times A^{-1})^{\frac{1}{3}}\times\exp(-k\times t_a)]^3 \\ -p_1\times t_l\times p_2^{-1}\times\exp(1-t_l\times p_2^{-1})+p_3^3\times t_{pc}^3,$$

where lw_{t_a,t_l,t_p} was the live weight (kg) of a t_a days old cow at t_l days in lactation and t_p days pregnant; t_a was the number of days since the birth of the cow; t_l was the number of days since the last calving; t_p was the number of days since conception; A was the mature live weight (kg); y_0 was the birth weight (kg); k was the growth rate parameter (per day), p_1 was the maximum decrease of live weight during the lactation (kg); p_2 was the day after calving when the live weight is the lowest in the lactation; p_3 was pregnancy parameter (per day); and t_{pc} was equal to t_p-50 when $t_p-50>0$, otherwise 0. The value of t_a at the start of a new lactation was the age in that parity assuming fixed calving interval of 12 months for earlier parities. The input value for A, y_0, and p_2 were set to 650 kg, 42 kg, and 61 d, respectively. The input value for p_1 was 41 kg in first parity, 47 kg in second parity, and 50 kg in later parities. The parameter values for k and p_3 were set to 0.00315 per day and 0.0187 per day.

Relative to the live weight function in Van Arendonk (1985a), three input values were modified. First, mature weight was 650 kg, which is a more representative value nowadays (CVB, 2007). Second, the time within lactation when the live weight was the lowest was 61 d, because Van Knegsel et al. (2007) observed, using indirect calorimetry techniques, a positive energy retention in body mass in week 8 of lactation on average. Third, p_1 was dependent on the cow's permanent production potential because high yielding cows lose more weight in early lactation because of higher energy need for milk production. Following Jalvingh et al. (1993), the value of p_1 was modified according to a linear relationship specifying that every 1,000 kg additional milk production potential (on 305 d basis) resulted in 15 kg higher p_1.

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6

Economic implications of genetic selection for specialized milk composition

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Journal of Dairy Science (submitted)

Abstract

Genetic selection provides opportunities for dairy farmers to shift from producing commodity milk to raw milk with specialized composition to meet consumer or industrial demands. Our objective was to assess the economic implications at herd level of selection strategies to change milk-fat or milk-protein composition. The breeding goal for milk-fat composition was to decrease the ratio of saturated fatty acids to unsaturated fatty acids in milk. The breeding goal for milk-protein composition was to increase the ratio of total caseins to total proteins in milk. Hypothetical herds that resulted from years of selection to produce milk with altered fat or protein composition were modeled with a herd optimization and simulation model. Correlated responses on milk production, cow fertility, and functional longevity were taken into account. Each selection strategy was evaluated under the current milk-payment scheme. The economic effects, therefore, reflected the effects of the correlated responses.

Annual net revenue from an average Dutch herd was €35,900 in the base scenario (i.e., herd without selection). Regarding strategies to change milk-fat composition, annual herd net revenue increased by €100 for gene-assisted selection strategy for the AA *DGAT1* genotype. Annual herd net revenue decreased by €2,400, however, for traditional selection strategy using bulls from the current breeding scheme. Regarding strategies to change milk-protein composition, annual herd net revenue increased by €600 for traditional selection strategy using bulls from the current breeding scheme. Annual herd net revenue decreased by €700, however, for gene-assisted selection strategy for the BB *LGB* genotype. Our results can be used to identify economically optimal selection strategies and to derive the break-even premiums for farmers. The break-even premiums, in turn, can be used by dairy processors to design payment schemes to enhance the adoption of genetic selection strategies by farmers.

Key words: economics, genetic selection, milk composition, dairy cattle

6.1 Introduction

There has been an increased interest to move from producing bulk dairy commodities towards producing specialized dairy products aimed at niche markets (Boland et al., 2001; Creamer et al., 2002). Dairy producers, therefore, consider shifting from commodity milk to raw milk with specialized composition to meet consumer or industrial demands (e.g., Dooley et al., 2005; Demeter et al., 2009a). Raw milk with specialized composition can be produced by applying new knowledge in herd management, animal nutrition, and genetic selection (e.g., Boland et al., 2001). This paper focuses on producing raw milk with specialized fat or protein composition by means of genetic selection. Milk-fat composition is important because of its effect on human health (e.g., German and Dillard, 2006; Steijns, 2008). Changing milk-fat composition, therefore, can improve the nutritional quality of raw milk and hence might lead to improved dairy products for human health (Boland et al., 2001). Milk-protein composition influences cheese manufacturing properties of raw milk, including coagulation time, curd firmness, and cheese yield (e.g., Wedholm et al., 2006). Changing milk-protein composition, therefore, can improve milk as raw material for cheese manufacturing (Boland et al., 2001).

Genetic research has shown opportunities to select for milk-fat (Soyeurt et al., 2007; Bobe et al., 2008; Stoop et al., 2008) and milk-protein (Bobe et al., 1999; Graml and Pirchner, 2003; Schopen et al., 2009) composition. Little is known, however, about the economic implications of these selection strategies for dairy farmers. Consider a hypothetical dairy herd that is bred to produce milk with specialized milk-fat or milk-protein composition. How will this affect the production of this herd? How much profit will this herd generate? These are only examples of questions that need to be answered before the dairy industry (i.e., breeders, farmers, processors) implements any selection strategy. It is imperative to know how genetic selection would affect economically important traits and hence costs and revenues on farm. Model calculations can form the basis of deriving financial incentives to compensate farmers for the potential extra costs, lost revenues, and related risks (Demeter et al., 2009a). The objective of this study was to assess economic implications at herd level of genetic selection strategies to alter milk-fat or milk-protein composition. Selection based on a phenotype or a genotype was considered for both fat and protein composition. Eight selection strategies were considered, and selection for only a single trait or genotype was assumed in each strategy.

6.2 Materials and Methods

6.2.1 Model description

To study the expected performance of hypothetical herds that produce milk with valuable composition, we used the herd optimization and simulation model of Demeter et al.

Table 1. Summary of key price, biological, and management inputs used for the base scenario[1].

Inputs	Base values
Management inputs	
Age at first calving (mo)	24
Proportion of outdoor grazing on annual basis (%)	25
Proportion of concentrate in diet (%)	28
Length of keeping newborn calf (d)	7
Minimum open period in lactation (mo)	2
Maximum lactation length (mo)	18
Annual discount rate (%)	5
Biological inputs	
Mature mean 305-d milk yield (kg)[2]	9,000
Mature mean 305-d fat content (%)[2]	4.25
Mature mean 305-d protein content (%)[2]	3.45
Variation coefficient of 305-d milk yield (%)	12
Heritability of milk yield	0.40
Repeatability of consecutive 305-d milk yields	0.55
Correlation between true and estimated BV for milk yield	0.60
Cow mature live weight (kg)	650
Calf birth weight (kg)	40
Calf survival rate in first week (%)	92
Length of oestrus cycle (d)	21
Heat detection rate (first oestrus)	0.30
Heat detection rate (later oestruses)	0.60
Price inputs (€)	
Milk carrier (100 kg)[3]	−3.20
Milk fat (kg) [3]	2.85
Milk protein (kg) [3]	7.50
Roughage (100 kg DM) [3]	10.12
Concentrate (100 kg DM) [3]	16.25
Bull calf (kg) [3]	2.50
Carcass (kg) [3]	1.75
Regular veterinary cost (per cow per 305-d)[4]	120
Cost of fixed production assets[3]	115
Monthly insemination cost (per cow)[4]	25
Replacement heifer[5]	1,500

[1] Base scenario represents average Dutch dairy farm in 2008-2009.

[2] Provided by the cooperative cattle improvement organization CRV (Arnhem, the Netherlands).

[3] KWIN (2009).

[4] Personal communication (Henk Hogeveen, Utrecht University, Utrecht, the Netherlands).

[5] Personal communication (Monique Mourits, Wageningen University, Wageningen, the Netherlands).

(2011). This model had two desirable features. First, it could determine economically optimal insemination and replacement decisions for individual cows under the specified production conditions. Second, it could be used to simulate whole-herd technical and economic outputs that would follow from the optimal decisions for the individual cows. The model ensured that selection's possible correlated responses on economically important production traits were properly accounted for. The production system, therefore, could be optimized without selection (base scenario) and after selection, and technical and economic values were derived from optimized production systems (Dekkers, 1991). The overall model consists of two main parts: a bioeconomic model and a mathematical model. These model parts will be introduced briefly. Some key management, biological, and price inputs are summarized in Table 1.

Bioeconomic Model. The purpose of the bioeconomic model was to compute the revenues and costs of individual cows during their productive life. We considered only the activity of milk production: revenues (milk, calves, slaughtered cows) and costs (feed, voluntary replacement, insemination, sundries, involuntary replacement). Farmer's labor was not included in calculation of costs, so net revenues represented financial compensation to the farmer for labor and management. Revenues and costs were calculated in monthly intervals for each cow state. A cow state was the combination of the main properties characterizing a cow. A cow could be in a state described by one of 12 parities, 8 present-open periods, 8 previous-open periods, 18 lactation stages, 13 classes of estimated yield potential when entering the herd, 13 classes of updated yield potential when starting a new lactation, and 169 classes of actual yield level. Input values and parameters were selected to simulate Dutch Holstein-Friesian (**DHF**) cows. Prices represented the 2008-2009 Dutch farming conditions.

Mathematical Model. The purpose of the mathematical model was twofold. First, we optimized insemination and replacement decisions for each cow state. Second, we performed Markov chain simulations to obtain whole-herd results that followed from the optimal policies for individual cows. The optimization problem was modeled as a multi-level hierarchic Markov process (**MLHMP**), which combines the advantageous properties of two optimization methods (policy iteration and value iteration) in a multi-level hierarchic manner (Kristensen and Jørgensen, 2000). With MLHMP, detailed real-world applications with large state space can be solved with fast convergence and an exact solution. Optimal decisions were found by maximizing total expected discounted net revenues (annual discount rate of 5%). Fixed herd size was assumed, and hence a cow was immediately replaced after culling. Revenues, costs, physical quantities, and transition probabilities were computed by the bioeconomic model. The mathematical model and the bioeconomic model were programmed in Java and used as a plug-in to the MLHMP software system developed by Kristensen (2003).

6.2.2 Breeding goals and selection strategies

Selection strategies were modeled on DHF cattle, because of the large amount of recent information obtained on the genetic background of detailed milk composition in the Dutch Milk Genomics Initiative (e.g., Heck, 2009; Schennink, 2009; Stoop, 2009; Schopen, 2010). We considered selection strategies for two breeding goals: to improve milk-fat composition or to improve milk-protein composition. For each breeding goal, two traditional selection strategies based on phenotypes and two gene-assisted selection strategies based on genotypes were assessed. In total, therefore, eight selection strategies were modeled. Each phenotype was assumed to be affected by many genes and environmental factors. Each genotype was considered for a single gene, which is known to affect milk-fat or milk-protein composition. Single-trait selection was assumed for each strategy (i.e., selection for single phenotype or single genotype). The base scenario and the selection strategies are described in Table 2.

Table 2. Description of the base scenario and selection strategies.

Strategies	Description
Base scenario (herd without selection)	Mean SFA[1]/UFA[2] ratio of 2.80 Mean CN-index[3] of 87.45 Frequency of *DGAT1* A allele of 0.6[4] Frequency of *LGB* A allele of 0.6[5]
Milk-fat composition	
FTB	Mean SFA/UFA ratio of 2.58
FBS	Mean SFA/UFA ratio of 2.12
DGAT1A	Herd with AA *DGAT1* genotype cows
DGAT1K	Herd with KK *DGAT1* genotype cows
Milk-protein composition	
PTB	Mean CN-index of 89.27%
PBS	Mean CN-index of 92.88%
LGBA	Herd with AA *LGB* genotype cows
LGBB	Herd with BB *LGB* genotype cows

[1] SFA: saturated fatty acids.

[2] UFA: unsaturated fatty acids.

[3] CN-index: percentage of total caseins within total milk proteins.

[4] Source: Schennink et al. (2007).

[5] Source: Heck et al. (2009).

Breeding Goal for Milk-Fat Composition. The breeding goal for milk-fat composition was to decrease the ratio of saturated fatty acids (**SFA**) to unsaturated fatty acids (**UFA**) in milk. Decreasing the SFA/UFA ratio appears to be an important selection objective in dairy cattle, because higher level of UFA in milk seems to be positively associated with human (e.g., Maijala, 2000) and cow (e.g., Van Knegsel et al., 2007) health. Genetic variation in the ratio with moderate heritability (0.28) was found by Stoop et al. (2008). They found mean ratio of 2.80, indicating that about 74% of the milk-fat was saturated. They also reported SFA/UFA ratio of 2.17 for the lowest 5% of cows and 3.38 for the highest 5% of cows in their sample.

Traditional Selection Strategies for Milk-Fat Composition. We considered two strategies for decreasing SFA/UFA ratio in milk by traditional selection. The first strategy involved using bulls with the lowest EBV for SFA/UFA ratio from the on-going breeding scheme, which puts no selection pressure on the ratio. Consequently, there was no genetic improvement with respect to the ratio in the population average over generations. In the herds using the selected bulls, however, genetic level of the offspring with respect to the ratio reached an asymptote equal to the selection differential of the selected bulls. Of 200 annually tested sires, we considered using 25 bulls with the lowest EBV for SFA/UFA ratio. The selection intensity equaled 1.65; the accuracy of prediction equaled 0.82 (assuming 100 progeny with information and a heritability for SFA/UFA ratio of 0.28); and the additive genetic standard deviation for SFA/UFA ratio equaled 0.16 (Stoop et al., 2008). The selection differential, therefore, equaled −0.22, resulting in a lowered SFA/UFA ratio of 2.58 (**FTB**).

The second strategy involved implementation of a new breeding scheme that puts all selection pressure on decreasing SFA/UFA ratio in milk. In this strategy, cows and bulls with the lowest EBV for SFA/UFA ratio in milk were chosen as parents. This strategy led to a continuous genetic improvement with respect to the ratio in the population average over generations. We quantified the amount of genetic gain that could be achieved with this strategy by using the SelAction software (Rutten et al., 2002), following Stoop (2009). Input parameters and results of SelAction are in Appendix 1. Results showed that the single-trait genetic selection for lower SFA/UFA ratio in DHF cattle would result in an annual genetic gain of –0.027. In this study, we modeled the effects of a breeding scheme after 25 years. The duration was chosen to be in line with FTB, where maximum improvement can be achieved in about the same time. A 25-year breeding scheme (excluding start-up period) resulted in total genetic gain of –0.68 with respect to the ratio, leading to a lowered ratio of 2.12 (**FBS**).

Gene-Assisted Selection Strategies for Milk-Fat Composition. Another way to decrease SFA/UFA ratio in milk may be to select cows for *DGAT1* genotype. The *DGAT1* gene is located on chromosome 14 in cattle and was selected because Schennink et al. (2007) found that a lysine-to-alanine polymorphism (**K232A**) affects milk fatty acid (**FA**) composition in DHF cows. The *DGAT1* K232A polymorphism explained a large part of the genetic variation in milk-fat composition, e.g., 36% of the genetic variation in the SFA/UFA ratio. The same polymorphism also explains some of the genetic variation in the milk-fat unsaturation indices (Schennink et al., 2008). Studies by Schennink et al. (2007, 2008) concluded that selecting cows for the AA genotype is desirable because of its association with more UFA, less palmitic acid (C16:0), and more unsaturated C18 FA. We modeled two selection strategies: selecting for the AA genotype (**DGAT1A**) and selecting for the KK genotype (**DGAT1K**).

Breeding Goal for Milk-Protein Composition. The breeding goal for milk-protein composition was to increase the ratio of total caseins to total proteins (**CN-index**) in milk. Increasing CN-index in milk appears to be an important selection objective in dairy cattle (e.g., Schopen, 2010), because raw milk with higher CN-index has advantageous manufacturing (e.g., cheesemaking) properties (e.g., Ikonen et al., 2004; Wedholm et al., 2006). Genetic variation in CN-index with relatively high heritability (0.70) has been found by Schopen et al. (2009). They found mean CN-index of 87.45%, whereas CN-index of 85.19% for the lowest 5% of cows and 89.79% for the highest 5% of cows in their sample.

Traditional Selection Strategies for Milk-Protein Composition. We distinguished two traditional selection strategies to increase CN-index in milk. The first strategy was analogous to FTB and involved using bulls with the highest EBV for CN-index from the on-going breeding scheme, which puts no selection pressure on CN-index. Consequently, there was no genetic improvement with respect to CN-index in the population average over generations. There was, however, improvement in the genetic level of the offspring at the participating herds. Of 200 annually tested sires, we considered using 25 bulls with the highest EBV for CN-index. The selection intensity equaled 1.65; the accuracy of prediction equaled 0.97 (assuming 100 progeny with information and a heritability for CN-index of 0.70); and the additive genetic standard deviation for CN-index equaled 1.14 (Schopen et al., 2009). The selection differential, thus, equaled 1.82, resulting in an increased index of 89.27% (**PTB**).

The second strategy was analogous to FBS and involved implementation of a new breeding scheme that puts all selection pressure on increasing CN-index in milk. In this strategy, cows and bulls with the highest EBV for CN-index were chosen as parents. This strategy led to a continuous genetic improvement with respect to CN-index in the population average over generations. We quantified the amount of genetic gain that could be achieved with this strategy by using the SelAction software (Rutten et al., 2002), following Schopen (2010). Input parameters and results of SelAction are shown in Appendix 2. Results showed that the single-trait genetic selection for higher CN-index in DHF cattle would result in an annual genetic gain of 0.217. We modeled the effects of a breeding scheme after 25 years to be in line with PTB. A 25-year breeding scheme (excluding start-up period) resulted in total genetic gain of 5.43 with respect to CN-index, leading to an elevated index of 92.88% (**PBS**).

Gene-Assisted Selection Strategies for Milk-Protein Composition. Selecting cows for *LGB* genotype was assessed as an alternative to increase CN-index in milk. The *LGB* gene is located on chromosome 11 in cattle and was selected because Heck et al. (2009) and Schopen et al. (2009) found that the *LGB* genotype was associated with differences in the relative concentration of all major milk-proteins in DHF cattle. Relative to the A variant, the B variant was strongly associated with lower concentration of β-lactoglobulin, higher concentration of all other major milk proteins, and higher CN-index in milk (Heck et al., 2009). The *LGB* genotype, furthermore, explained about 90% of genetic variation in β-lactoglobulin (Heck et al., 2009) and CN-index (Schopen et al., 2009), and explained between 2% and 10% of genetic variation in other major milk proteins (Heck et al., 2009). We modeled two selection strategies: selecting for the AA genotype (**LGBA**) and selecting for the BB genotype (**LGBB**).

6.2.3 Correlated responses of selection strategies

The mathematical model optimizes the dairy production system by finding economically optimal insemination and replacement decisions. It is imperative, therefore, to know the correlated responses of the selection strategies on biological traits that influence insemination and replacement decisions. It has been shown that these traits include milk production, cow fertility, and functional longevity (e.g., Van Arendonk, 1985; Van Arendonk and Dijkhuizen, 1985; Rogers et al., 1988a, 1988b). When a selection strategy affects any of these traits, therefore, production system needs to be re-optimized to draw unbiased economic results.

Correlated Responses on Milk Production. Milk production has large effect on optimal culling decisions, but virtually no effect on insemination decisions. Culling becomes more intense for higher when mean milk production of the herd increases, whereas culling becomes less intense when mean milk production of the herd decreases (e.g., Van Arendonk, 1985; Rogers et al., 1988a). Milk production, therefore, influences optimal herd composition and therefore herd profit. In the model, milk production was captured by three mature mean 305-d traits: milk yield (kg), fat content (%), and protein content (%). Correlated responses of the selection strategies on these milk production traits were quantified (Appendix 3), and the proportional changes in mature mean 305-d production traits are summarized in Table 3.

Correlated Responses on Cow Fertility. The reproductive performance of cows determines optimal insemination decisions, which in turn influence optimal replacement decisions. Replacement becomes less intense when cow fertility improves, whereas replacement becomes more intense when cow fertility declines (e.g., Dekkers, 1991; Demeter et al., 2011). Reproductive performance of cows, therefore, largely influences optimal herd composition and therefore herd profit. In the model, cow fertility was captured by the monthly marginal probabilities of conception following insemination. Correlated responses of the selection strategies on cow fertility were quantified (Appendix 3), and the proportional changes in the monthly marginal probabilities of conception are summarized in Table 3.

Table 3. Proportional (%) changes in key biological inputs due to correlated responses in the strategies.

Biological Inputs	Selection Strategy							
	FTB	FBS	DG.A	DG.K	PTB	PBS	LG.A	LG.B
Mature 305-d production traits								
Mean milk yield (kg)	+3.27	+9.81	+3.82	−5.68	+1.02	+2.97	+0.58	−0.65
Mean fat content (%)	−8.46	−25.23	−6.82	+10.65	−3.40	−9.75	−0.78	+1.31
Mean protein content (%)	−1.73	−4.99	−1.88	+2.99	+0.39	+1.42	−0.14	−0.14
Monthly marginal conception probabilities (%)	NS[1]	NS	+3.42	+4.68	NS	NS	NS	NS
Monthly marginal involuntary culling probabilities (%)	+2.93	+9.27	NS	NS	NS	NS	NS	NS

[1] NS indicates that the correlated response was statistically nonsignificant ($P > 0.05$). In this case, the default biological input value was not changed when modeling the strategy.

Correlated Responses on Functional Longevity. Functional longevity can be defined as the cow's ability to delay involuntary replacement (Essl, 1998), which refers to removal that is not subject to decision making (i.e., due to low production or poor fertility). Involuntary replacement affects optimal insemination and replacement decisions (Van Arendonk, 1985; Rogers et al., 1988b). Functional longevity, therefore, has an impact on herd composition and therefore on herd profit. In the model, functional longevity was captured by the monthly marginal probabilities of involuntary replacement Correlated responses of the selection strategies on functional longevity were quantified (Appendix 3), and the proportional changes in the monthly marginal probabilities of involuntary replacement are summarized in Table 3.

6.2.4 Limitations of methodology

Three key methodological assumptions were included in the study. First, the correlated responses of the strategies were assumed to be known without error, although the parameters used for inferring correlated responses were estimated with relatively low accuracy. Sensitivity analyses, however, were performed to examine how results depended on the magnitude of correlated responses (see next section). Second, we modeled performance of hypothetical dairy herds that resulted from years of selection to produce milk with altered fat or protein composition. The actual transition period, however, was not considered. Third, the economic effects were evaluated assuming the current milk-payment scheme in the Netherlands for each strategy. Specifically, the amount of milk was penalized, whereas the amount of fat and protein were rewarded (Table 1). No premium was assumed for the altered milk-fat or milk-protein composition, however, so economic results reflected the impact of the strategies' correlated responses on milk production, cow fertility, and functional longevity.

6.2.5 Sensitivity analyses

To disentangle the contribution of the correlated responses on various traits, sensitivity analyses were performed. Because we assumed that correlated responses were known without error, it was important to understand to their proportional effects. For each strategy which had correlated responses on more than one trait, therefore, additional simulations were performed setting the correlated response on one of the traits zero. Note, however, that the correlated responses on the three mature mean 305-d milk production traits (i.e., milk yield, fat content, protein content) were treated together, and they were not set to zero individually. For FTB and FBS, which affected milk production traits and functional longevity, two additional simulations were performed: one including correlated responses on only milk production traits and one including correlated response on only functional longevity. For DGAT1A and DGAT1K, which affected milk production traits and cow fertility, two additional simulations were performed: one including correlated responses on only milk production traits and one including correlated response on only cow fertility. For the remaining strategies, no sensitivity analyses were performed because they had correlated responses on only milk production traits.

6.3 Results

6.3.1 Selection strategies

The results described technical and economic performance of a herd that follows optimal insemination and culling decisions for individual cows (Table 4). Results of the strategies were compared with results of the base scenario (i.e., herd without selection). Base results were generated by using default management, biological, and price input values (Table 1).

For FTB and FBS, which decreased mean SFA/UFA ratio to 2.58 (FTB) and 2.13 (FBS), annual total culling rate increased (28.6% for FTB and 28.8% for FBS). The proportion of voluntary culling decreased to 41.3% for FTB and 38.7% for FBS, because of the negative correlated responses on functional longevity. For FTB, monthly yields per cow increased by 22.3 for milk and 0.3 kg for protein, whereas fat decreased by 1.7 kg. For FBS, monthly yields increased by 66.3 for milk and 0.9 kg for protein, whereas fat decreased by 5.7 kg. The positive correlated responses on milk yield, therefore, could

Table 4. Technical and economic parameters describing optimal insemination and replacement policies for various selection strategies.

Parameters	Base scenario	Selection Strategy							
		FTB	FBS	DGAT1A	DGAT1K	PTB	PBS	LGBA	LGBB
	2.80[4] 87.45[5]	2.58[4] n.a.	2.13[4] n.a.	2.68[4] n.a.	2.95[4] n.a.	n.a. 89.27[5]	n.a. 92.88[5]	n.a. 86.25[5]	n.a. 89.39[5]
Productive herd life (mo/cow)	42.2	42.0	41.6	42.4	42.5	42.1	42.0	42.2	42.3
Calving interval[1] (d/cow)	396.5	396.5	396.6	395.2	394.5	396.5	396.5	396.5	396.5
Annual total culling rate (%)	28.4	28.6	28.8	28.3	28.3	28.5	28.6	28.5	28.4
Proportion of voluntary cullings[2] (%)	42.5	41.3	38.7	42.0	42.0	42.6	42.8	42.6	42.4
Milk yield (kg/cow/mo)	734.6	756.9	800.9	763.5	694.1	742.3	756.9	739.0	729.6
Fat yield (kg/cow/mo)	31.4	29.7	25.7	30.5	32.9	30.7	29.3	31.4	31.6
Protein yield (kg/cow/mo)	25.6	25.9	26.5	26.1	24.9	25.9	26.7	25.7	25.4
Roughage intake (kg DM/cow/mo)	401.1	401.8	403.2	401.5	401.3	401.6	402.5	401.0	401.1
Concentrate intake (kg DM/cow/mo)	156.6	150.8	136.6	156.9	155.8	154.4	150.2	157.4	156.3
Milk revenue (€/cow/mo)	257.6	254.3	246.0	257.6	257.7	258.0	259.3	258.2	256.7
Feed cost (€/cow/mo)	66.0	65.2	63.0	66.1	65.9	65.7	65.2	66.2	66.0
Insemination cost (€/cow/year)	48.2	48.2	48.4	47.0	46.6	48.3	48.2	48.3	48.2
Net revenue (€/cow/mo)	39.9	37.3	30.8	40.0	40.3	40.5	42.3	40.3	39.1
Net revenue (€1,000/herd[3]/year)	35.9	33.5	27.7	36.0	36.3	36.5	38.1	36.3	35.2
Net revenue (€/100 kg milk)	5.4	4.9	3.8	5.2	5.8	5.5	5.6	5.5	5.4

[1] Based on completed lactations.
[2] Includes cows that did not get pregnant during the insemination period.
[3] Assuming average Dutch farm size of 75 cows.
[4] Mean ratio of saturated to unsaturated fatty acids in milk (SFA/UFA).
[5] Mean proportion (%) of total caseins in total milk proteins (CN-index).

offset the negative correlated responses on protein content, but could not offset the negative correlated responses on fat content. Monthly milk revenues per cow dropped by €3.3 for FTB and €11.6 for FBS. Monthly concentrate intakes per cow decreased by 5.8 kg DM for FTB and 20.0 kg DM for FBS, leading to lower feed costs. Because FTB and FBS had no correlated responses on cow fertility, calving intervals and insemination costs virtually did not change. Net revenues per 100 kg milk decreased by €0.5 for FTB and €1.6 for FBS. Annual net revenues from an average Dutch herd of 75 cows, moreover, decreased by €2,400 for FTB and €8,200 for FBS.

For DGAT1A and DGAT1K, which changed mean SFA/UFA ratio to 2.68 (DGAT1A) and 2.95 (DGAT1K), annual total culling rates were virtually unaffected. Intensity of voluntary culling hardly changed, because there were no correlated responses on functional longevity. For DGAT1A, monthly yields per cow increased by 28.9 kg for milk and 0.5 kg for protein, whereas fat decreased by 0.9 kg. For DGAT1K, monthly yields per cow decreased by 40.5 kg for milk and 0.7 kg for protein, whereas fat increased by 1.5 kg. That is, the correlated responses on milk yield were offset by the correlated responses on fat and protein contents, leading to fat and protein yields similar to that in the base scenario. Milk revenues, therefore, were unchanged in both selection strategies. Similarly, roughage and concentrate intakes hardly changed, resulting in virtually unchanged feed costs. Because of the positive correlated responses on cow fertility, calving intervals decreased by 1.3 d for DGAT1A and 2 d for DGAT1K, leading to lower insemination costs. Net revenues per 100 kg milk decreased by €0.2 for DGAT1A and increased by €0.4 for DGAT1K. Annual net revenues from an average Dutch herd of 75 cows, however, increased by €100 for DGAT1A and €400 for DGAT1K.

For PTB and PBS, which increased mean CN-index to 89.27% (PTB) and 92.88% (PBS), annual total culling rates hardly changed (28.5% for PTB and 28.6% for PBS). Because there were no correlated responses on functional longevity, the proportion of voluntary culling basically did not change. For PTB, monthly yields per cow increased by 7.7 kg for milk and 0.3 kg for protein, whereas fat decreased by 0.7 kg. For PBS, monthly yields per cow increased by 22.3 kg for milk and 1.1 kg for protein, whereas fat decreased by 2.1 kg. The positive correlated responses on milk yield, therefore, could not compensate for the negative correlated responses on fat content. Monthly milk revenues per cow increased by €0.4 for PTB and €1.7 for PBS. Monthly concentrate intake per cow decreased by 2.2 kg DM for PTB and 6.4 kg DM for PBS. Monthly feed costs per cow, therefore, decreased by €0.3 for PTB and €0.8 for PBS. Because PTB and PBS had no correlated responses on cow fertility, calving intervals and insemination costs were basically the same as in the base scenario. Net revenues per 100 kg milk increased by €0.1 for PTB and €0.2 for PBS. Annual net revenues from an average Dutch herd of 75 cows, furthermore, increased by €600 for PTB and €2,200 for PBS.

For LGBA and LGBB, which changed mean CN-index to 86.25% (LGBA) and 89.39% (LGBB), annual total culling rates were virtually unchanged (28.5% for LGBA and 28.4%

Table 5a. Technical and economic parameters describing optimal insemination and replacement policies for sensitivity analyses on FTB and FBS.

Parameters	Base scenario	Correlated responses included for FTB			Correlated responses included for FBS		
		Milk production	Functional longevity	Both	Milk production	Functional longevity	Both
Productive herd life (mo/cow)	42.2	42.5	41.8	42.0	42.9	41.0	41.6
Calving interval[1] (d/cow)	396.5	396.5	396.5	396.5	396.7	396.2	396.6
Annual total culling rate (%)	28.4	28.3	28.7	28.6	28.0	29.3	28.8
Proportion of voluntary cullings[2] (%)	42.5	42.2	41.6	41.3	41.6	39.5	38.7
Milk yield (kg/cow/mo)	734.6	758.0	733.3	756.9	804.8	730.9	800.9
Fat yield (kg/cow/mo)	31.4	29.7	31.4	29.7	25.8	31.3	25.7
Protein yield (kg/cow/mo)	25.6	25.9	25.5	25.9	26.6	25.4	26.5
Roughage intake (kg DM/cow/mo)	401.1	402.1	400.7	401.8	404.4	399.9	403.2
Concentrate intake (kg DM/cow/mo)	156.6	151.0	156.4	150.8	137.1	155.9	136.6
Milk revenue (€/cow/mo)	257.6	254.6	257.2	254.3	247.2	256.4	246.0
Feed cost (€/cow/mo)	66.0	65.2	66.0	65.2	63.2	65.8	63.0
Insemination cost (€/cow/year)	48.2	48.2	48.2	48.2	48.1	48.5	48.4
Net revenue (€/cow/mo)	39.9	37.9	39.3	37.3	32.7	37.9	30.8
Net revenue (€1,000/herd[3]/year)	35.9	34.1	35.3	33.5	29.4	34.1	27.7
Net revenue (€/100 kg milk)	5.4	5.0	5.4	4.9	4.1	5.2	3.8

[1] Based on completed lactations.

[2] Includes cows that did not get pregnant during the insemination period.

[3] Assuming average Dutch farm size of 75 cows.

Table 5b. Technical and economic parameters describing optimal insemination and replacement policies for sensitivity analyses on DGAT1A and DGAT1K.

Parameters	Base scenario	Correlated responses included for DGAT1A			Correlated responses included for DGAT1K		
		Milk production	Cow fertility	Both	Milk production	Cow fertility	Both
Productive herd life (mo/cow)	42.2	42.2	42.4	42.4	42.2	42.5	42.5
Calving interval[1] (d/cow)	396.5	396.5	395.1	395.2	396.4	394.6	394.5
Annual total culling rate (%)	28.4	28.4	28.3	28.3	28.4	28.3	28.3
Proportion of voluntary cullings[2] (%)	42.5	42.5	42.1	42.0	42.5	42.0	42.0
Milk yield (kg/cow/mo)	734.6	762.6	735.6	763.5	692.9	735.9	694.1
Fat yield (kg/cow/mo)	31.4	30.4	31.5	30.5	32.8	31.5	32.9
Protein yield (kg/cow/mo)	25.6	26.0	25.6	26.1	24.8	25.6	24.9
Roughage intake (kg DM/cow/mo)	401.1	401.2	401.3	401.5	401.0	401.4	401.3
Concentrate intake (kg DM/cow/mo)	156.6	156.7	156.9	156.9	155.5	156.9	155.8
Milk revenue (€/cow/mo)	257.6	257.4	257.9	257.6	257.3	258.0	257.7
Feed cost (€/cow/mo)	66.0	66.1	66.1	66.1	65.9	66.1	65.9
Insemination cost (€/cow/year)	48.2	48.3	47.0	47.0	48.2	46.6	46.6
Net revenue (€/cow/mo)	39.9	39.7	40.3	40.0	39.8	40.4	40.3
Net revenue (€1,000/herd[3]/year)	35.9	35.7	36.2	36.0	35.8	36.3	36.3
Net revenue (€/100 kg milk)	5.4	5.2	5.5	5.2	5.7	5.5	5.8

[1] Based on completed lactations.

[2] Includes cows that did not get pregnant during the insemination period.

[3] Assuming average Dutch farm size of 75 cows.

for LGBB). Similarly, the intensity of voluntary culling basically did not change (42.6% for LGBA and 42.4% for LGBB), because the selection strategies did not have correlated responses on functional longevity. Monthly milk yields per cow increased by 4.4 kg for LGBA and decreased by 5 kg for LGBB, whereas monthly yields of fat and protein per cow were basically unchanged. Monthly milk revenues per cow increased by €0.6 for LGBA and decreased by €0.9 for LGBB. Because monthly fat and protein yields per cow changed only marginally, monthly roughage and concentrate intakes per cow virtually did not change. Because LGBA and LGBB had no correlated responses on cow fertility, calving intervals and insemination costs were basically the same as in the base scenario. Net revenues per 100 kg milk were €5.5 for LGBA and €5.4 for LGBB. Annual net revenues from an average Dutch herd of 75 cows, furthermore, increased by €400 for LGBA and decreased by €700 for LGBB.

6.3.2 Sensitivity analyses

For FTB and FBS (Table 5a), which had correlated responses on milk production traits and functional longevity, the two groups of correlated responses had an impact on annual herd net revenues in the same direction. Annual net revenue from an average Dutch herd of 75 cows decreased by €2,400 for FTB and €8,200 for FBS when both groups of correlated responses were taken into account. For only the correlated responses on milk production traits, annual net revenues from an average herd decreased by €1,800 for FTB and €6,500 for FBS. For only the correlated responses on functional longevity, annual net revenues from an average herd decreased by €600 for FTB and €1,800 for FBS. In the traditional selection strategies to decrease SFA/UFA ratio in milk, therefore, over three-quarters of total losses in annual herd net revenues resulted from the correlated responses on milk production traits.

For DGAT1A and DGAT1K (Table 5b), which had correlated responses on milk production traits and cow fertility, the two groups of correlated responses had opposite effects on annual herd net revenues. When both groups of correlated responses were taken into account, annual net revenue from an average Dutch herd of 75 cows increased by €100 for DGAT1A and €400 for DGAT1K. For only the correlated responses on milk production traits, on the one hand, annual net revenues from an average Dutch herd decreased by €200 for DGAT1A and €100 for DGAT1K. For only the correlated responses on cow fertility, on the other hand, annual net revenues from an average Dutch herd increased by €300 for DGAT1A and €400 for DGAT1K. In the gene-assisted selection strategies to change SFA/UFA ratio in milk, therefore, the correlated responses on milk production traits decreased annual herd net revenues, whereas the correlated effects on cow fertility increased annual herd net revenues. Our results indicated, furthermore, that the positive effects of the correlated responses on cow fertility outweighed the negative effects of the correlated responses on milk production traits.

6.4 Discussion

6.4.1 Correlated responses

First, the correlated responses of the strategies were inferred from different studies. Correlated responses of gene-assisted strategies on milk production traits and functional longevity, on the one hand, were inferred from a study on EBV of about 4,000 test bulls (Appendix 3). All other correlated responses, on the other hand, were inferred from studies on test-day morning milk yields of about 2,000 first-lactation cows (Appendix 3). Responses inferred from EBV of test bulls are more accurate, whereas responses inferred from test-day morning milk yields of cows are less accurate. Robustness of results to changes in the various correlated responses can be assessed from sensitivity analyses (Tables 5a, 5b). Consider the results for DGAT1A and DGAT1K, for example. When correlated responses on cow fertility were included, annual herd net revenues increased. When correlated responses on cow fertility were excluded, however, annual herd net revenues decreased. These findings indicate that model final outcomes can be sensitive to the assumptions for the correlated responses.

Second, the correlated responses of the traditional and the gene-assisted selection strategies could differ, even if they had the same breeding goal. Consider the correlated responses of PTB and PBS versus the correlated responses of LGBB, for example. Although each strategy increased CN-index in milk, their correlated responses on milk production traits were opposite (Table 3). PTB and PBS led to higher milk yield and protein content, and to lower fat content. LGBB, conversely, led to lower milk yield and protein content, and to higher fat content. This might appear contradictory, given that the *LGB* gene explains large part of genetic variation in CN-index, with the BB genotype being associated with a higher CN-index (Heck, 2009). For PTB and PBS, selection was based on a quantitative trait (i.e., CN-index). The assumption of PTB and PBS was that the infinitesimal model held and selection affected all genes influencing the quantitative trait. Among these genes, there might be some that have different correlated responses than the *LGB* gene. For LGBB, however, selection was based on a single gene that influenced CN-index. Because the *LGB* gene explains around 90% of genetic variation in CN-index (Schopen et al., 2009), it is unlikely that the infinitesimal model holds for PTB and PBS. Their predicted correlated responses, therefore, are likely to be less accurate than the predicted correlated responses of LGBB.

6.4.2 Implications for dairy farmers

Our results can be used to evaluate the economic implications at herd level of selection strategies to change milk-fat or milk-protein composition. We reflected net revenue per herd or per 100 kg milk, which is relevant depending on the production constraints of the farm. If the farm has no production quota, then herd size can be fixed, so herd net revenue is the relevant economic measure. If the farm has a production quota, however, then herd size is likely to fluctuate, so net revenue per 100 kg milk is the more relevant economic measure. In the case of a production quota, furthermore, optimal insemination and replacement policies would also need to be computed by using the criterion of optimality of maximizing expected average net revenue per unit of milk. In this study, however, the latter criterion was not applied, but results were generated by maximizing total expected discounted net revenues.

First, regarding milk-fat composition, the selection strategies changed SFA/UFA ratio in milk to a different extent. FTB decreased SFA/UFA ratio by 0.22 by using bulls from the current breeding scheme, whereas FBS decreased SFA/UFA ratio by 0.68 by using bulls from a new breeding scheme. Because FBS put all selection pressure solely on decreasing SFA/UFA ratio, it is not a realistic strategy. FBS, however, provides useful insights to the consequences of a hypothetical extreme change in SFA/UFA ratio that can be achieved by traditional selection. DGAT1A and DGAT1K selected for the AA and KK genotype of the *DGAT1* gene. DGAT1A decreased SFA/UFA ratio by 0.12, whereas DGAT1K increased SFA/UFA ratio by 0.15. Because the AA genotype is associated with lower SFA/UFA ratio in milk (Schennink et al., 2007), DGAT1A represents an alternative to traditional selection.

FTB and FBS, on the one hand, decreased annual herd net revenues by €2,400 (FTB) and €8,200 (FBS). Similarly, net revenues per 100 kg milk decreased by €0.5 for FTB and €1.6 for FBS. These findings indicate that traditional selection to decrease SFA/UFA ratio has a negative economic effect at herd level, regardless of production quota. FBS had more than three times the effect on net revenues than FTB, which is in agreement with their effects on SFA/UFA ratio. DGAT1A and DGAT1K, on the other hand, increased annual herd net revenues by €100 (DGAT1A) and €400 (DGAT1K). These findings indicate that selection for the *DGAT1* homozygotes has positive economic effects at herd level, provided that farmers have no production quota. Annual herd net revenues increased for DGAT1A and DGAT1K, which contradicts their effects on SFA/UFA ratio. Net revenues per 100 kg milk, however, decreased by €0.2 for DGAT1A, but increased by €0.4 for DGAT1K. These findings indicate that selection for the AA genotype has a negative economic effect at herd level, whereas selection for the KK genotype has a positive economic effect at herd level, provided that farmers have a production quota. Net revenues per 100 kg milk decreased for DGAT1A and increased for DGAT1K, which is in agreement with their effects on SFA/UFA ratio.

Second, regarding milk-protein composition, the selection strategies changed CN-index to a different extent. PTB increased CN-index by 1.82 by using bulls from the current breeding scheme, whereas PBS increased CN-index by 5.43 by using bulls from a new breeding scheme. Because PBS put all selection pressure solely on increasing CN-index, it is not a realistic strategy. PBS, however, provides useful insights to the consequences of a hypothetical extreme change in CN-index that can be achieved by traditional selection. Note, furthermore, that the increase in CN-index for PBS is likely to be an overestimation of what can be achieved, because it was based on the infinitesimal model. LGBA and LGBB selected for the AA and BB genotypes of the *LGB* gene. LGBA decreased CN-index by 1.20, whereas LGBB increased CN-index by 1.94. Because the BB genotype is associated with higher CN-index in milk (Heck et al., 2009), LGBB represents an alternative to traditional selection.

PTB and PBS, on the one hand, increased annual herd net revenues by €600 (PTB) and €2,200 (PBS). Similarly, net revenues per 100 kg milk increased by €0.1 for PTB and €0.2 for PBS. These findings imply that increasing CN-index by traditional selection has positive economic effects at herd level, regardless of production quota. PBS had more than three times the effect on net revenues than PTB, which is in line with their effects on CN-index. LGBA and LGBB, on the other hand, resulted in €400 higher (LGBA) and €700 lower (LGBB) annual herd net revenues. These findings indicate that selection for the AA genotype has a positive economic effect, whereas selection for the BB genotype has a negative economic effect at herd level, provided that farmers have no production quota. Annual herd net revenues increased for LGBA and decreased for LGBB, which is consistent with their effects on CN-index. Net revenues per 100 kg milk, however, increased by €0.1 for LGBA, but did not change for LGBB. These findings imply that selection for the AA genotype has a positive economic effect, whereas selection for the BB genotype has no economic effect at herd level, provided that farmers have a production quota. Net revenues per 100 kg milk increased for LGBA and did not change for LGBB, which contradicts their effects on CN-index.

Until now, little progress has been made in modeling economic implications at herd level of genetic selection strategies to change milk-fat or milk-protein composition. To our knowledge, only Dooley (2002) has performed model calculations. Dooley determined the break-even premiums required for New Zealand farmers to be economically no worse off producing specialized milk than conventional milk. Two selection strategies were considered: selecting for lower β-carotene content in milk to produce raw milk with “whiter milk fat” and selecting for BB β-lactoglobulin genotype to produce raw milk with improved cheese manufacturing properties. Dooley’s approach accounted for the correlated responses on milk production traits, whereas it did not account for the correlated responses on cow fertility or functional longevity. Dooley, furthermore, derived economic results without re-optimizing herd composition following the correlated responses. Instead, pre-defined calving spread and culling decisions were assumed, which might be appropriate under seasonal calving in New Zealand. Under different conditions, however, such assumption could lead to sub-optimal inseminations and replacements, and therefore distorted economic results (Dekkers, 1991).

6.4.3 Implications for the dairy chain

If dairy processors were to take advantage of the genetic variation in milk composition, then their payment schemes to farmers would need to be adjusted. Our results can be used to derive the break-even premiums necessary to cover direct losses incurred in the selection strategies. The break-even premiums, in turn, can be used by dairy processors to design payment schemes to enhance the adoption of genetic selection strategies by dairy farmers.

For FTB and FBS, monthly net revenues per cow decreased by €2.6 (FTB) and €9.1 (FBS), which losses would have to be recovered over monthly milk yields of 756.9 kg (FTB) and 800.9 kg (FBS). The break-even premiums, therefore, equal €0.34 (FTB) and €1.14 (FBS) per 100 kg milk when farmers have no production quota. Net revenues per 100 kg milk, however, decreased by €0.5 for FTB and €1.6 for FBS, which equal the break-even premiums per 100 kg milk when farmers have a production quota. For DGAT1A and DGAT1K, we found no direct losses in monthly net revenues per cow, i.e., no break-even premiums would be necessary when farmers have no production quota. Net revenues per 100 kg milk, however, decreased by €0.2 for DGAT1A, but increased by €0.4 for DGAT1K. When farmers have a production quota, therefore, a break-even premium of €0.2 per 100 kg milk would be necessary for DGAT1A, but no break-even premium would be necessary for DGAT1K.

For PTB and PBS, we found no direct losses in monthly net revenues per cow or in net revenues per 100 kg milk. No break-even premiums, therefore, would be necessary for PTB and PBS, regardless of whether farmers have a production quota. For LGBA and LGBB, however, monthly net revenues per cow increased by €0.4 (LGBA) and decreased by €0.8 (LGBB). For LGBA, therefore, there was no direct loss in monthly net revenues per cow. For LGBB, however, the direct loss of €0.8 in monthly net revenue per cow would have to be recovered over a monthly milk yield of 729.6 kg. When farmers have no production quota, therefore, no break-even premium would be necessary for LGBA, whereas a break-even premium of €0.11 per 100 kg milk would be necessary for LGBB. Furthermore, we found no direct losses in net revenues per 100 kg milk for LGBA and LGBB. When farmers have a production quota, thus, no break-even premiums would be necessary for LGBA and LGBB.

6.5 Conclusions

Our objective was to model the economic implications at herd level of genetic selection strategies to change milk-fat or milk-protein composition. We modeled traditional and gene-assisted selection strategies to decrease SFA/UFA ratio or to increase CN-index. For decreasing SFA/UFA ratio, we found a positive effect on annual herd net revenue by selecting for the AA *DGAT1* genotype and a negative effect on annual herd net revenue by traditional selection for lower SFA/UFA ratio. Regarding increasing CN-index, we found a negative effect on annual herd net revenue by selecting for the BB *LGB* genotype and a positive effect on annual herd net revenue by traditional selection for higher CN-index. Selection strategies were evaluated assuming the current milk-payment scheme in the Netherlands. Results, therefore, reflect the implications of the correlated responses of the various selection strategies. Our results can be used by stakeholders of the dairy industry, including breeding organizations, dairy farmers, and dairy processors, to identify economically optimal selection strategies. Results, moreover, can be used to derive the necessary break-even premiums for dairy farmers and can be applied by dairy processors to modify their milk-payment schemes.

Appendix 1

Input parameters and results of SelAction.

Description of traits based on test-day morning milk samples from Stoop et al. (2008).

Name	Var(P)	h^2
SFA/UFA[1]	0.14	0.20
Milk yield (kg)	6.92	0.29
Fat content (%)	0.51	0.47
Protein content (%)	0.09	0.53

[1] Mean ratio of saturated to unsaturated fatty acids in milk.

Simulated population: 25 sires and 200 dams

Information sources index[1].

Age class	Male Candidates	Male information source	Female candidates	Female information source
1	0	PEDIGREE	0	PEDIGREE
2	0	PEDIGREE	0	PEDIGREE
3	0	PEDIGREE	0	PEDIGREE, OP
4	0	PEDIGREE	95	PEDIGREE, OP
5	100	PEDIGREE, P	90	PEDIGREE, OP
6	99	PEDIGREE, P	85	PEDIGREE, OP
7	98	PEDIGREE, P	80	PEDIGREE, OP
8	97	PEDIGREE, P	75	PEDIGREE, OP

[1] PEDIGREE = information on related individuals using Best Linear Unbiased Prediction; OP = Own performance; P = Progeny group with 100 female progeny.

Genetic correlations based on test-day morning milk sample from Stoop et al. (2008).

Trait	Milk yield	Fat content	Protein content
SFA/UFA[1]	−0.23	0.56	0.21

[1] Mean ratio of saturated to unsaturated fatty acids in milk.

Expected annual genetic gain by selection to decrease SFA/UFA[1] and its correlated responses.

Selection	Annual	Correlated response		
trait	genetic gain	Milk yield	Fat content	Protein content
SFA/UFA[1]	−0.027	0.053	−0.044	−0.007

[1] Mean ratio of saturated to unsaturated fatty acids in milk.

Appendix 2

Input parameters and results of SelAction.

Description of traits based on test-day morning milk samples from Schopen et al. (2009).

Name	Var(P)	h^2
CN-index[1] (%)	1.88	0.70
Milk yield (kg)	5.01	0.41
Fat content (%)	0.47	0.50
Protein content (%)	0.07	0.66

[1]Mean proportion (%) of total caseins in total milk proteins.

Simulated population: 25 sires and 200 dams

Information sources index[1].

Age class	Male candidates	Male information source	Female candidates	Female information source
1	0	PEDIGREE	0	PEDIGREE
2	0	PEDIGREE	0	PEDIGREE
3	0	PEDIGREE	0	PEDIGREE, OP
4	0	PEDIGREE	95	PEDIGREE, OP
5	100	PEDIGREE, P	90	PEDIGREE, OP
6	99	PEDIGREE, P	85	PEDIGREE, OP
7	98	PEDIGREE, P	80	PEDIGREE, OP
8	97	PEDIGREE, P	75	PEDIGREE, OP

[1]PEDIGREE = information on related individuals using Best Linear Unbiased Prediction; OP = Own performance; P = Progeny group with 100 female progeny.

Genetic correlations based on test-day morning milk samples from Schopen et al. (2009).

Trait	Milk yield	Fat content	Protein content
CN-index[1] (%)	0.06	−0.19	0.04

[1]Mean proportion (%) of total caseins in total milk proteins.

Expected annual genetic gain by selection to increase CN-index[1] and its correlated responses.

Selection trait	Annual genetic gain	Correlated response		
		Milk yield	Fat content	Protein content
CN-index[1] (%)	0.217	0.016	−0.017	0.002

[1]Mean proportion (%) of total caseins in total milk proteins.

Appendix 3

A3.1 Correlated responses on milk production

For FTB and PTB, the correlated responses were inferred by using genetic parameters from Stoop et al. (2008) and Schopen et al. (2009). Genetic parameters in these studies were based on first-parity morning production traits. Correlated responses, therefore, were calculated for first-parity morning production traits and were used as proxies for the mature mean 305-d production traits of our model. To illustrate, consider the correlated response of PTB on morning milk yield. The selection intensity equaled 1.65; the accuracy of prediction equaled 0.97 (assuming 100 progeny with information and a heritability for CN-index of 0.70); the genetic correlation between the CN-index and morning milk yield equaled 0.06; and the additive genetic standard deviation of morning milk yield equaled 1.43 kg (Schopen et al., 2009). With these values, correlated response of PTB on morning milk yield equaled 0.14 kg. Schopen et al. (2009) found mean morning milk yield of 13.46 kg. The correlated response of 0.14 kg, therefore, corresponded to 1.02% increase in morning milk yield. Consequently, we increased the base mature mean 305-d milk yield by 1.02% when modeling PTB (Table 3).

For FBS and PBS, the correlated responses on milk production traits were inferred by using the SelAction software (Rutten et al., 2002). Genetic parameters used in SelAction were taken from Stoop et al. (2008) and Schopen et al. (2009) and were based on first-parity morning production traits. Correlated responses, therefore, were calculated for first-parity morning production traits and were used as proxies for the mature mean 305-d production traits of our model. The annual correlated responses from SelAction are presented in Appendices 2 (FBS) and 3 (PBS). To illustrate, consider the correlated response of FBS on morning milk yield. The annual correlated response of FBS on morning milk yield was 0.053 kg (Appendix 1). Total correlated response of FBS after 25 years, therefore, equaled 1.325 kg. In Stoop et al. (2008), mean morning milk yield was 13.50 kg. The correlated response of 1.325 kg, therefore, corresponded to 9.81% increase in morning milk yield. The base mature mean 305-d milk yield, therefore, was increased by 9.81% when modeling FBS (Table 3).

Third, for the gene-assisted selection strategies, correlated responses on milk production traits were inferred by using parameters from an unpublished study (**STUDY 1**). Associations between EBV for milk production traits and *DGAT1* genotypes or *LGB* genotypes were tested by fitting linear mixed models (Littel et al., 2006). The dataset was provided by CRV (Arnhem, the Netherlands) and included EBV of about 4,000 test bulls for three 305-d production traits: milk yield (kg), fat content (%), and protein content (%). The EBV for each milk production trait was a weighted EBV for the first three parities (CRV, 2010). Each bull was born between 1985 and 2005 and was at least 80% DHF. The statistical model included effects of breed, birth year, animal, and *DGAT1* genotype or *LGB* genotype. Family relationships between individuals were accounted for, and pedigree was supplied by CRV.

Associations between EBV for each milk production trait and both genotypes (*DGAT1* and *LGB*) were statistically significant. For the gene-assisted selection strategies, therefore, correlated responses on EBV for each weighted 305-d production traits were calculated and were used as proxies for the three mature mean 305-d production traits of our model. To illustrate, consider the correlated response of DGAT1A on EBV for weighted 305-d milk yield. Relative to the AA genotype, EBV for weighted 305-d milk yield was 356 kg lower for the AK genotype and 707 kg lower for the KK genotype. Assuming a frequency of 0.6 for the *DGAT1* A allele (Table 2), genetic mean EBV for weighted 305-d milk yield equaled 72 kg in the base scenario. Selecting for the AA genotype in DGAT1A resulted in a new genetic mean EBV for weighted 305-d milk yield of 356 kg, resulting in an increase of 284 kg. The base weighted 305-d milk yield equaled 7,448 kg, which was computed by using age correction factors from Demeter et al. (2011) and weighting factors from CRV (2010). The increase of 284 kg, thus, corresponded to 3.82% increase in weighted 305-d milk yield. When modeling DGAT1A, therefore, we increased the base mature mean 305-d milk yield by 3.82% (Table 3).

A3.2 Correlated responses on cow fertility

The correlated responses on cow fertility were inferred by using parameters from Demeter et al. (2009b, 2010). Among the fertility traits, we considered nonreturn rate (0/1) for insemination 28 d after the first insemination (**NR28**). This trait was used as proxy to measure the impact on the monthly marginal probabilities of conception following any insemination in any lactation. Because Demeter et al. (2009b, 2010) examined phenotypic associations, parameters did not reflect genetic relation between selection traits and fertility traits. We, however, assumed that parameters from Demeter et al. (2009b, 2010) were genetic effects.

There were no statistically significant relations between NR28 and SFA/UFA ratio, CN-index, or *LGB* genotypes. No correlated responses on cow fertility, therefore, were quantified for FTB, FBS, PTB, PBS, LGBA, and LGBB (Table 3). The *DGAT1* genotypes, however, had statistically significant relation with NR28. For DGAT1A and DGAT1K, therefore, correlated responses on NR28 were calculated and were used as proxies for the monthly marginal conception probabilities. Relative to the AA genotype, the AK genotype had 0.06 lower NR28 and the KK genotype had 0.01 higher NR28 (Demeter et al., 2009b). Assuming a frequency of 0.6 for the *DGAT1* A allele (Table 2), the genetic mean NR28 for *DGAT1* in the base scenario equaled –0.027. Selecting for the AA genotype in DGAT1A resulted in a new genetic mean NR28 for *DGAT1* of 0, corresponding to an increase of 0.027. Selecting for the KK genotype in DGAT1K resulted in a new genetic mean NR28 for *DGAT1* of 0.01, corresponding to an increase of 0.037. Because the sample mean of NR28 was 0.79 (Demeter et al., 2009b), increases of 0.027 in DGAT1A and 0.037 in DGAT1K corresponded to 3.42% and 4.68% increases. The monthly marginal conception probabilities, therefore, were proportionally increased by 3.42% when modeling DGAT1A and 4.68% when modeling DGAT1K (Table 3).

A3.3 Correlated responses on functional longevity

First, for traditional selection strategies, correlated responses on functional longevity were inferred by using parameters from an unpublished study (**STUDY 2**). Associations between functional longevity and SFA/UFA ratio and CN-index were tested by fitting linear mixed models (Littel et al., 2006). The dataset was provided by CRV (Arnhem, the Netherlands) and included observations on 1,917 cows. Lifetime information was available until 26 February 2010, which was used as censoring date. The tested longevity trait was length of productive life (**LPL**), i.e., the interval (d) between the date of first calving and date of culling. Mean LPL was 1308 d. Cows that were still in production, and, therefore, did not have LPL information, were assigned an LPL at censoring date. Phenotypes on SFA/UFA ratio and CN-index were pre-adjusted before the analyses for age, season, lactation stage, and herd effects. The statistical model included effects of month of culling, age at first calving, 305-d fat- and protein-corrected milk yield in first parity, and SFA/UFA ratio or CN-index.

There was no statistically significant association between LPL and CN-index. No correlated responses on functional longevity, therefore, were quantified for PTB and PBS (Table 3). There was, however, statistically significant association between LPL and SFA/UFA ratio. For FTB and FBS, therefore, correlated responses on LPL were calculated and were used as proxies for the monthly marginal probabilities of involuntary culling. The parameter estimate for SFA/UFA ratio was 96.55 d, indicating that increasing the ratio by one unit would result in 96.55 d longer LPL. FTB and FBS decreased the ratio by 0.22 and 0.67, which would result in 21.24 d and 64.69 d shorter LPL. Given the sample mean for LPL of 1308 d, decreases of 21.24 d and 64.69 d corresponded to 1.62% and 4.95% declines in LPL. Sensitivity analyses showed that increasing the base monthly marginal probabilities of involuntary culling by 2.93% and 9.27% resulted in about 1.62% and 4.95% decline in the simulated LPL. The base monthly marginal probabilities of involuntary culling, therefore, were proportionally increased by 2.93% when modeling FTB and by 9.27% when modeling FBS (Table 3). Similarly to the correlated responses on cow fertility, we assumed that the correlated responses on functional longevity reflected genetic effects of the selection traits.

Second, for gene-assisted selection strategies, correlated responses on functional longevity were inferred by using parameters from STUDY 1. Associations between EBV for functional longevity and DGAT1 genotypes or LGB genotypes were tested by fitting linear mixed models (Littel et al., 2006). The dataset was provided by CRV (Arnhem, the Netherlands) and included EBV of about 4,000 test bulls for functional longevity. Each bull was born between 1985 and 2005 and was at least 80% DHF. The statistical model included effects of breed, birth year, animal, and DGAT1 genotype or LGB genotype. Family relationships between individuals were accounted for, and pedigree was supplied by CRV. Associations between EBV for functional longevity and both genotypes (DGAT1 and LGB) were statistically nonsignificant. No correlated responses on functional longevity, thus, were quantified for the gene-assisted strategies DGAT1A, DGAT1K, LGBA, and LGBB (Table 3).

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7

General discussion

7.1 Introduction

The overall objective of this thesis was to study the technical and economic aspects of value-adding methods in the dairy production chain. The research was motivated by the fact that little knowledge exists on the implications of novel methods that have been proposed recently to address the prevailing trends in the dairy sector. As described in chapter 1, the overall objective was split into two sub-objectives. First, the thesis aimed at assessing qualitatively the potential for creating value added in the dairy production chain. To that end, three future scenarios were developed and evaluated in chapter 2. Second, the thesis aimed at assessing quantitatively the technical and economic implications at farm level of one scenario: producing differentiated raw milk by applying genetic selection. To that end, various genetic selection strategies to change milk-fat or milk-protein composition were modeled in chapter 6. The preceding chapters concentrated on developing a bio-economic model and on obtaining technical parameters needed for the quantitative assessment. The applied methods and results are discussed in each chapter. The present chapter will discuss the results and their implications from a broader perspective. This chapter first reviews the scientific implications, subsequently discusses the practical implications, and finally discusses the future outlook.

7.2 Scientific Implications

An important scientific implication of the thesis is that it presented an approach that can be regarded as a general framework to assess the technical and economic implications of innovative strategies in other food production chains. Specifically, the thesis presented a two-step approach, where the first step assessed qualitatively the strategic opportunities offered by a wide range of novel methods emerging at various stages in the production chain, whereas the second step assessed quantitatively the implications of specific strategies on farm level.

In the first step, the goal was to uncover a wide range of options to enable stakeholders in the production chain to identify the limits of the possible and to formulate potential joint action plans. To that end, formulation of future scenarios through a participatory method was applied. A wide range of chain stakeholders and chain experts, including scientists and non-scientists, were brought together in scenario workshops. Participation of non-scientists in the production and use of scientific knowledge is especially useful in case of complex and unstructured problems (Van Asselt and Rijkens-Klomp, 2002). Creating value added in food production chains is complex, because it concerns a large number of related problems, many disciplines, various scale levels (e.g., temporal and geographical), and many different actors (Van der

Vorst et al., 2005). Participatory methods, therefore, can be advantageous in scientific research on exploring opportunities to create value added in food production chains. Applicable methods include scenario workshops, policy exercises, focus groups, and participatory modeling (Van Asselt and Rijkens-Klomp, 2002). In this thesis, scenario workshops were organized, which are basically meetings involving various actors to develop visions and proposals for technological needs and possibilities in the future (Street, 1997).

Our results have demonstrated that developing scenarios using a participatory approach allows for exploring future strategies for food production chains. The scenarios showed that when assessing future strategic opportunities it is important to consider the entire chain, and hence concerted and co-ordinated actions by the various stakeholders are necessary. This conclusion is in agreement with the findings of Hartwich and Negro (2010), who studied the role of collaboration in research and development for innovation in New Zealand's dairy production chain. They found that New Zealand's dairy innovation system highly depends on the formal and informal collaborative partnerships amongst the various public and industry stakeholders. Participatory methods involving scientists and non-scientists are useful in developing innovation strategies for food production chains because these methods generate a shared view among stakeholders on required changes in the future. In turn, the shared view among various stakeholders can strengthen the collaboration in the food production chain.

In the second step, the goal was to *ex-ante* quantify the technical and economic implications of various selection strategies. Generally, quantitative evaluation begins at the stage within the chain where the novel methods are applied. In this thesis, genetic selection was studied that entailed novel production on dairy farms, and thus the quantitative analyses focused on the dairy farm stage of the chain. However, essential inputs were used from the preceding breeding stage. Specifically, hypothetical dairy herds that could result from years of selection were modeled by using biological parameters estimated from animal breeding models. The actual transition period was not considered in this thesis. Rather, various end-points were assessed to explore the economic potential of various promising strategies. This information can enable stakeholders of the dairy chain to identify economically optimal strategies. Then, further research can follow to assess various transition pathways for the selected strategies. A notable example of such research is the study of Dooley et al. (2005a).

The second step (i.e., quantitative analyses) was performed in three sub-steps. In the first sub-step, statistical analyses were performed that enabled calculation of correlated responses of novel selection traits on other economically important traits (i.e., traits on cow fertility and longevity). The data available for this sub-step imposed two limitations on the final outcome. First, only phenotypic consequences of selection could be studied, whereas in principle correlated genetic responses are required. The data available, however, was limited to estimate correlated genetic responses. Second, the statistical analyses applied linear mixed models, which proved to be robust enough to handle the various traits. However, other statistical methods might have been more appropriate. Longevity traits in dairy cattle, for example, are better analyzed by survival analysis (e.g., Ducrocq, 1997), which could not be applied because of limited data. The consequence of these two limitations is that the correlated effects of novel selection traits could be inferred only with relatively low accuracy.

In the second sub-step, a bio-economic model was constructed that optimized herd management decisions and simulated post-optimization results at herd level. Developing a bio-economic model was necessary because the production system in a dairy herd involves complex relationships among and between animal traits and production factors. Furthermore, it is important that the model was designed to optimize herd management decisions, namely inseminations and replacements. Optimization is relevant because the aim was to model genetic selection strategies in such way that correlated responses on economically important traits on milk yield, fertility, and longevity were taken into account. These traits are known to have considerable effects on herd profitability, and it is also known that evaluating the economic effects of changes in these traits without re-optimizing herd management decisions leads to underestimated results (Van Arendonk, 1985; Rogers et al., 1988). From a theoretical point of view, therefore, re-optimization of the production system was necessary to draw unbiased results when evaluating the various genetic selection strategies (Dekkers, 1991).

In the third sub-step, the bio-economic model, coupled with the results of statistical analyses, was applied to quantify the farm level technical and economic implications of various genetic selection strategies. To overcome the low accuracy of correlated responses, sensitivity analyses were performed to examine how final outcomes depended on the size of correlated responses. These results can be used in the future to prioritize research on accurate estimation of correlated responses of novel selection traits. Furthermore, results showed little evidence that re-optimization was warranted, because optimal decisions did not change remarkably after re-optimization. This finding, however, does not imply directly that bio-economic models without optimization, i.e., simulation models with pre-defined management decisions (e.g., Marsh et al., 1987; Sørensen et al., 1992; Shalloo et al., 2004), should be used in analogous assessments. Under different breeding goals or cattle populations, for example, correlated responses could be stronger, leading to more remarkable changes in optimal decisions. These potential changes under different conditions, however, are hard to predict beforehand, so re-optimization of the production system still appears to be an inevitable step.

The sequence of quantitative analyses above proved to be successful in quantifying the technical and economic implications at farm level of genetic selection. The approach can be directly applied for other selection opportunities in dairy cattle. Furthermore, the same sequence of analyses may be conceptually applicable to other livestock production systems. Genome research in livestock industries has progressed rapidly in the past decade (e.g., Womack, 2005), and it can be expected that an increasing number of selection opportunities will emerge that need to be assessed before implementation. Similarly to cattle, assessing genetic selection in other livestock species needs to consider the complex system of all direct and correlated effects on traits with high economic importance. An obvious example would probably be the pig industry, which actively uses genetic information to improve production (e.g., Rothschild, 2003). Analogous to cattle, optimizing herd management (i.e., insemination and replacement) decisions for individual sows are of high economic importance (e.g., Huirne, 1990; Plá, 2001; Kristensen and Sollested, 2004a, b). Therefore, evaluation of farm level implications of promising genetic selection opportunities in the pig industry should begin with correlated responses of the novel selection traits on those other traits that influence economically important herd management decisions. Then, a bio-economic model that re-optimizes the production system at the pig farm should be applied to derive unbiased results.

Besides providing a general framework, another important scientific implication of the thesis is the development of the bio-economic model itself in chapter 5. The model is a versatile research tool that allows one to examine complex problems pertaining dairy farming systems. The model has been built in a generic way, so it can be extended to investigate various aspects of dairy farming systems, including farm decision support, animal health, animal breeding, animal nutrition, ecological sustainability, and business economics (see discussion in chapter 5 on potential extensions and applications of the model). Recently, a co-operative livestock improvement organization in the Netherlands has shown interest in using the model to provide herd management guidelines to farmers and to derive economic weights of selection traits in its breeding programme. The organization has already used a conceptually similar bio-economic model, which was developed in the 1980s, to aid farmers' insemination and replacement decisions and to derive economic weights of selection traits on, for example, milk production, cow fertility, and cow longevity. Because the model in this thesis has implemented several new biological functions (e.g., on milk yield and feed intake) and new input values to reflect contemporary cattle performance and farming conditions, the livestock improvement organization is considering the replacement of its current model.

7.3 Business Implications

This thesis is one of the very few studies in the literature that have been conducted to investigate the technical and economic implications of opportunities offered by milk genomics research. If dairy processors were to take advantage of the genetic variation in milk composition, then their payment schemes to farmers would need to be adjusted.

Results in chapter 6 can be used to derive the break-even premiums necessary to cover direct losses incurred at farm level. Regarding selection to change milk-fat composition, a break-even premium of €0.34 per 100 kg milk was found for a traditional selection strategy that decreased the ratio of saturated fatty acids to unsaturated fatty acids in milk. No break-even premium appeared to be necessary, however, for a gene-assisted selection strategy selecting for the *DGAT1* AA genotype. Regarding selection to change milk-protein composition, no break-even premium appeared to be necessary for a traditional selection strategy that increase the ratio of total caseins to total proteins in milk. A break-even premium of €0.11 per 100 kg milk was found, however, for a gene-assisted selection strategy selecting for the *LGB* BB genotype. The break-even premiums found in this thesis can be used by dairy processors to design payment schemes to enhance adoption of novel selection strategies by dairy farmers.

In practice, it is likely that the actual premiums paid to farmers need to be higher than the break-even premiums calculated above. A dairy processor should not only cover direct losses, but also compensate the farmer for risks associated with the novel selection strategy. These risks might include discontinuation of a new strategy because of technology developments, decreased consumer demand, and oversupply. By applying novel selection strategies, furthermore, farmers would inherently be restricted in their choices to improve their herds. An additional risk factor is the rate at which farmers adopt new technology. This rate is important because it determines the amount and timing of supply, which is critical to meet market demand. Supply might be especially relevant for strategies aimed to produce milk with altered fat composition, because this milk could be used to produce novel consumer products, for which market demand has to be fulfilled. It is likely, therefore, that some premium to farmers is required, even for those strategies where results did not indicate direct loss in net revenue.

Premiums required by farmers, in turn, impact the economic feasibility of selection strategies, because the value added in the strategies need to outweigh the extra costs. First, raw milk with less saturated fat could be processed into niche products addressing improvement of human health. The premium a dairy processor can offer farmers depends on the price received for these niche products. Consumer demand exists for dairy products with “health-improving” fat composition (Maynard and Franklin, 2003, Peng et al., 2006). Additional scientific evidence of benefits to human health, however, is vital to develop markets for products with lower saturated fat content. Second, raw milk with more total casein could improve the cost-efficiency of manufacturing cheese. The premium a dairy processor can offer farmers depends on the efficiency gains in cheese production, which is directly related to the casein yield (which is the product of protein yield and casein-index).

The implementation assumes that the infrastructure necessary to provide phenotypes for milk quality and genotypes for the relevant genes is available. First, for traditional selection strategies, phenotypes for detailed milk composition have to be collected routinely to estimate breeding values. Phenotypes for this thesis were obtained by gas chromatography for milk-fat composition and by capillary zone electrophoresis for milk-protein composition. These methods are reliable but too costly and time consuming to be applied on large scale. Fast, inexpensive, and accurate methods, therefore, have to be developed for routine measurement. To date, the most promising method is Fourier transform infrared spectroscopy (**FTIR**), which is used routinely to measure milk-fat and milk-protein content. The FTIR has been applied successfully to measure milk-fat (Soyeurt et al., 2006; Rutten et al., 2009) and milk-protein (De Marchi et al., 2009; Rutten et al., 2011) composition with acceptable accuracy (although accuracy was higher for milk basis than for fat or protein basis). Because FTIR is fast and inexpensive, it seems to be an important alternative for routine milk recording. Second, for gene-assisted selection strategies, DNA of test bulls have to be collected and genotyped for the *DGAT1* or the *LGB* genes. Genotyping could be performed at relatively low cost by incorporating it in the SNP panel used in on-going genomic selection programmes.

Different selection strategies lead to production of different milk flows from different groups of dairy farms. Different milk flows, in turn, will affect the storage of raw milk. If farms adopting a selection strategy produce only the specialized milk type, then no extra storage facilities (e.g., vats and milk silos) are needed. If, however, farms adopting a selection strategy produce commodity milk as well as specialized milk, then extra storage facilities will be required to segregate different milks on farm and during collection. Furthermore, different milk flows will also affect the logistics of milk collection. Costs of milk transport, therefore, are likely to increase, because collection of different milks, regardless of whether the trucks carry one or more milks at a time, is expected to increase the length and number of trips required. To date, only Dooley et al. (2005b) have performed formal model calculations to quantify the effects of multiple milk streams on milk collection costs. Specifically, they modeled the effects of producing two milk types on collection costs for New Zealand dairy farmers. They found that milk collection costs increased by 4.5 to 22%, depending on rate of adoption and number of milk types collected per run. The increase in costs was higher when the rate of technology adoption was lower and when only one milk type per run was collected. Similar negative effects on milk collection costs are also likely in other dairying countries.

Creamer et al. (2002) anticipated that breeding driven by bio-technology would be one of the five key issues driving changes in global dairy farming in the coming 50 years. They envisioned, already a decade ago, that “the use of the tools of molecular biology to identify and manage natural variation in milk composition will accelerate the breeding process and give geneticists greater control over the production and composition of milk” (p. 7189). Nevertheless, in the dairy farming practice relatively little has been achieved since then, and only a small scale pilot experiment in New Zealand has been documented in the academic literature (Boland et al., 2001). Consequently, there is still plenty of work to be done. The discussion above reveals that the practical implementation will be a complex process, in which the dairy industry needs to precisely articulate what it wants in milk and then suitable testing infrastructure and payment schemes need to be developed. In the Netherlands, the bio-economic model and the final results of this thesis are used currently by a dairy processing co-operative to identify economically optimal strategies to alter detailed milk composition by genetic selection. The aim of the co-operative is to adhere the detailed composition of its raw milk supply in the long run to its strategic plan and to the anticipated consumer demands.

7.4 Future Outlook

With the development of methods to routinely measure detailed milk composition and with the rapid development of DNA technology, it is anticipated that the amount of data available for milk genomics research will increase progressively in the future. This will create more opportunities to develop tools for selection for milk quality. Furthermore, the increasing data available will allow for determining more precisely the correlated genetic responses of promising genetic selection strategies on economically important production traits. More precise information on correlated genetic responses, in turn, will enable more precise *ex-ante* quantitative assessment and hence more informed decision making by industry stakeholders.

This thesis modeled traditional and gene-assisted selection strategies to alter detailed milk composition. The future method of genetic improvement in livestock production, however, appears to be genomic selection (e.g., De Roos, 2011). Genomic selection, which is the selection of animals based on genetic merit that is estimated directly from genome-wide dense marker data, has emerged in recent years following the rapid developments in DNA technology. The main advantage of genomic selection is that young animals can be selected more accurately, thereby reducing the generation interval and substantially increasing the rate of genetic improvement. An application by De Roos et al. (2007) has demonstrated that genomic selection can accurately estimate breeding values for fat percentage in dairy cattle. In principle, genomic selection might also be applied to estimate breeding values for traits on detailed milk composition. Therefore, raw milk with specialized characteristics could be produced with significantly reduced transition period necessary for breeding. As a consequence of the reduced transition period, the dairy chain would be able to adjust the composition of its raw milk supply faster to prevailing consumer demands and market trends.

Finally, *ex-ante* economic analysis at market level should be carried out in the future to gain more complete insights into the economic implications of genetic selection strategies. Specifically, economic surplus changes, because of shifts in the supply and demand curves induced by changed primary production, could be evaluated in a partial-equilibrium framework. The literature on assessing the economic effects of genetic selection strategies at market level is limited. In the rice industry, Alpuerto et al. (2009) studied the effects of marker-assisted selection and traditional selection strategies to increase tolerance to salinity and phosphorous-deficiency, assuming a downward shift in the supply curve induced by lower rice production costs. In the beef industry, Weaber and Lusk (2010) assessed the effects of marker-assisted selection strategies to improve steak tenderness, assuming an upward shift in the demand curve induced by higher consumer willingness-to-pay for beef products.

These two examples well illustrate the various effects on market level that can be induced by applying novel genetic selection strategies in the primary production in agriculture. Similarly to the above examples, market level effects are likely to differ for selection strategies altering milk-fat or milk-protein composition. By changing milk-fat composition, on the one hand, the goal is to produce value-added dairy foods with enhanced health benefits, which is likely to have an effect on consumer willingness-to-pay and on the demand curve. By changing milk-protein composition, on the other hand, the goal is to produce commodity dairy foods at lower manufacturing costs, which is likely to have no effect on consumer willingness-to-pay and on the demand curve. The present thesis can provide useful inputs to analysis on market level effects by reporting the estimated changes in production costs of milk at farm level, thereby enabling the quantification of potential shifts of the supply curves.

7.5 Conclusions

Based on the key findings of the thesis, the following final conclusions are drawn. First, creating value added is vital for the sustainable growth of the dairy industry, and producing raw milk with specialized characteristics by applying novel concepts in genetic selection can play an important role in this process (chapter 2). Second, the thesis has shown that as long as genetic selection is used to alter fat or protein composition in milk, no remarkable negative correlated responses can be expected on the reproductive performance of cows (chapters 3 and 4). Third, *ex-ante* quantitative assessments have found no evidence that implementing novel genetic selection strategies to change fat or protein composition in milk would have large effects on herd production and profitability (chapter 6). Furthermore, it has been demonstrated that the herd optimization and simulation model developed in this thesis is able to assess complex problems pertaining dairy farming systems (chapter 6). In short, recent progress in milk genomics research offers great opportunities to the dairy industry, and because they appear to have no major adverse effects at farm level, the various stakeholders should initiate joint action plans to capitalize on these promising technological advances.

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Summary

The dairy sector worldwide is challenged by growing consumer demands for animal products in general, increasing need for greater production efficiency, and growing concerns over ecological sustainability. In recent years, there has been a growing interest in the dairy sector to move from producing bulk dairy commodities towards producing specialized dairy products aimed at niche markets. Therefore, dairy farmers consider shifting from commodity milk to raw milk with specialized composition to meet consumer or industrial demands. Little knowledge exists, however, on the implications of novel methods that have been proposed recently to address the prevailing trends in the dairy sector. The objectives of the thesis were 1) to assess qualitatively future scenarios to create value added in the dairy chain and 2) to *ex-ante* assess quantitatively the technical and economic implications of producing differentiated raw milk by applying genetic selection. Results can promote future discussions amongst stakeholders and can enable them to identify economically optimal strategies.

In chapter 2, the potential for creating value added in the dairy production chain was assessed qualitatively through a participatory approach. A workshop involving dairy industry stakeholders and experts was organized to develop scenarios, envisioned according to the strategic interests of the dairy chain in the Netherlands. Three scenarios were developed that indicated different directions in which the dairy production chain in the Netherlands might develop in the next 5 to 20 years. The first scenario envisioned the prevalence of producing differentiated raw milk with enhanced health attributes or improved manufacturing properties. The second scenario envisioned a reduced dairy production chain to produce fresher and more individually customized dairy products with improved shelf life. The third scenario envisioned ecologically sustainable dairy farming with improved animal welfare. After this chapter, the thesis focused on quantifying the technical and economic implications of the first scenario, i.e., producing differentiated raw milk by using novel concepts in genetic selection.

In chapter 3, the effects of milk-fat composition (relative concentrations of individual fatty acids and groups of fatty acids) and polymorphisms of *DGAT1* and *SCD1* genes on various cow fertility traits were examined in Dutch Holstein-Friesian cattle. Data on 1,745 first-lactation cows were analyzed by fitting linear mixed models. Results showed that a 1% wt/wt increase in the relative concentration of *trans* fatty acids was associated with greater (0.24) number of inseminations, lower (3.8%) calving rate, lower (5.5, 9.6, and 8.3%) nonreturn rates for insemination (28, 56, and 90 d after the first service), and lower (7.5%) calving rate after the first service. Furthermore, results suggested a potential effect of the *DGAT1* polymorphism on nonreturn rates for insemination 28 and 56 d after the first service, with heterozygous genotype being associated with lower rates than homozygous genotypes.

In chapter 4, the effects of milk-protein composition (relative concentration of

six major milk-proteins) and milk-protein variants (β-lactoglobulin, β-casein, κ-casein, and β-κ-casein) on various cow fertility traits were examined in Dutch Holstein-Friesian cattle. Data on 1,644 first-lactation cows were analyzed by fitting linear mixed models. Results indicated that a 1% wt/wt increase in the relative α_{S1}-CN concentration was associated with greater (1.9, 2.7, and 2.9%) nonreturn rates (28, 56, and 90 d after the first service) and greater (2.5%) calving rate after the first service. Furthermore, results showed virtually no significant relationship between cow fertility traits and the relative concentration of other major milk-proteins or milk-protein variants. This latter finding suggest that selecting for those milk-proteins or milk-protein variants would have no influence on the reproductive performance of the cows.

In chapter 5, a herd optimization and simulation model for dairy cattle was developed. The optimization problem was formulated as a multi-level hierarchic Markov process, and a state space model with Bayesian updating was applied to model variation in milk yield. Methodological developments were incorporated in two main aspects. First, an additional level to the model hierarchy was introduced to obtain a more tractable and efficient structure. Second, a recently developed cattle feed intake model was incorporated to obtain more precise predictions on feed intake and feed costs. Moreover, new parameters and input values were incorporated in the state space model and other biological functions. Results were generated for Dutch farming conditions, and outcomes were in line with actual herd performance in the Netherlands. Optimal replacement decisions were sensitive to variation in milk yield but insensitive to energy requirement for maintenance and feed intake capacity.

In chapter 6, economic implications at herd level of selection strategies to change milk-fat or milk-protein composition were assessed by using the results of statistical analyses from chapters 3 and 4 and the bio-economic model from chapter 5. The breeding goal for milk-fat composition was to decrease the ratio of saturated fatty acids to unsaturated fatty acids in milk. The breeding goal for milk-protein composition was to increase the ratio of total caseins to total proteins in milk. Hypothetical herds that could result from years of selection were modeled. Correlated responses on milk production, cow fertility, and functional longevity were accounted for. Each strategy was evaluated under the current milk-payment scheme, so economic effects reflected the impacts of the correlated responses. Annual net revenue from an average Dutch herd was €35,900 in the base scenario (i.e., herd without selection). Regarding changing milk-fat composition, annual herd net revenue increased by €100 for a gene-assisted selection strategy, whereas it decreased by €2,400 for a traditional selection strategy. Regarding changing milk-protein composition, annual herd net revenue increased by €600 for a traditional selection strategy, whereas it decreased by €700 for a gene-assisted selection strategy. Results can be used to identify economically optimal strategies and to derive the break-even premiums for farmers. The break-even premiums, in turn, can be used by dairy processors to design payment schemes to enhance strategy adoption by farmers.

In chapter 7, implications and future outlook were discussed from a broader perspective. An important scientific implication of the thesis is that it presents a general framework, which involves qualitative and quantitative analyses, for assessing novel methods in the dairy production chain. Another relevant scientific implication is the development of a bio-economic model that can be used to study complex issues pertaining dairy farming systems. The business implication of the thesis is that it quantifies the technical and economic implications at farm level of opportunities offered by recent milk genomics research. It is anticipated that increasingly larger data sets will be available in the future for milk genomics research due to developments in milk recording and DNA technology. Genomic selection might be used in the coming years to alter detailed milk composition with remarkably shorter generation interval, thereby enabling the dairy chain to adapt its raw milk supply faster. In the future, further *ex-ante* economic analyses assessing the economic effects at market level are necessary to gain more complete insights into the implications of selection strategies.

Based on the key findings of the thesis, the following final conclusions are drawn. First, creating value added is vital for the sustainable growth of the dairy industry, and producing raw milk with specialized characteristics by applying novel concepts in genetic selection can play an important role in this process (chapter 2). Second, the thesis has shown that as long as genetic selection is used to alter fat or protein composition in milk, no remarkable negative correlated responses can be expected on the reproductive performance of cows (chapters 3 and 4). Third, *ex-ante* quantitative assessments have found no evidence that implementing novel genetic selection strategies to change fat or protein composition in milk would have large effects on herd production and profitability (chapter 6). Furthermore, it has been demonstrated that the herd optimization and simulation model developed in this thesis is able to assess complex problems pertaining dairy farming systems (chapter 6). In short, recent progress in milk genomics research offers great opportunities to the dairy industry, and because they appear to have no major adverse effects at farm level, the various stakeholders should initiate joint action plans to capitalize on these promising technological advances.

Samenvatting

De zuivelsector wordt wereldwijd geconfronteerd met een toenemende vraag naar zuivelproducten, meer behoefte aan efficiency en een toenemende zorg voor duurzaamheid. Daarnaast bestaat binnen de zuivelsector de wens om over te stappen van de productie van bulkmelk naar het produceren van nicheproducten voor specifieke markten. Er is echter nog maar weinig inzicht in de gevolgen van zo'n overstap. Het doel van dit proefschrift is om 1) op een kwalitatieve manier mogelijke toekomstscenario's voor de zuivelketen in kaart te brengen, en 2) de technische en economische consequenties te berekenen van het produceren van melk met specifieke eigenschappen door toepassing van genomics technologie. Met behulp van de resultaten van het onderzoek kunnen optimale strategieën voor een overstap naar meer specifieke melkstromen bepaald worden.

In hoofdstuk 2 zijn aan de hand van een workshop met experts en vertegenwoordigers uit de zuivelindustrie een drietal scenario's uitgewerkt waar de zuivelsector in Nederland in de komende 5 tot 20 jaar op in zou kunnen zetten. Het eerste scenario betreft het produceren van melk op boederijniveau met specifieke gezondheids- of verwerkingseigenschappen. In het tweede scenario wordt een krimping van de sector voorzien waarbij uiteindelijk melk wordt geproduceerd die verser is, voldoet aan individuele consument-eisen en ook een betere houdbaarheid heeft. Het derde scenario richt zich op een ecologisch duurzame veehouderij met ook een verbeterd dierenwelzijn. Het proefschrift richt zich verder op het kwantificeren van technische en economische consequenties van het eerste scenario: het produceren van melk met specifieke eigenschappen door gebruik te maken van recente innovaties in de genomics technologie.

In hoofdstuk 3 is onderzocht wat de effecten zijn van melkvetsamenstelling en polymorfisme op de vruchtbaarheidskenmerken van Nederlands Holstein melkvee. Dit is gedaan voor twee kandidaatgenen: *DGAT1* en *SCD1*. Hiervoor zijn data van 1.745 eerste-lactatie koeien geanalyseerd. Uit de resultaten komt een negatieve associatie naar voren tussen grotere concentraties van *trans*vetzuren in het melkvet en de vruchtbaarheid van de koe. Zo neemt met een relatieve toename van transvetzuren met 1% het aantal inseminaties toe met 0,24 en het aantal keren afkalven neemt af met 3,8%. Ook lijkt er een effect te zijn van *DGAT1* polymorfisme op een aantal van de vruchtbaarheidskenmerken.

In hoofdstuk 4 zijn vergelijkbare analyses uitgevoerd voor het effect van varianten en samenstelling van melkeiwit. Hiervoor zijn data van 1.644 eerste-lactatie koeien geanalyseerd. Resultaten laten een associatie zien tussen een relatief hogere concentratie van α_{S1}-CN en een aantal van de vruchtbaarheidskenmerken. Zo neemt bij een 1% hogere concentratie van α_{S1}-CN het aantal keren afkalven toe met 2,5%. Voor de andere belangrijke melkeiwitten of -eiwitvarianten worden nauwelijks

significante relaties gevonden. Dit suggereert dat selectie van melkvee voor deze melkeiwitten en –varianten geen effect heeft op de reproductie-eigenschappen van de koe.

In hoofdstuk 5 is een optimalisatie- en simulatiemodel ontwikkeld dat tot doel heeft de technische en economische resultaten van een koe te simuleren gedurende haar hele leven. Op basis hiervan kan vervolgens het optimale vervangingsmoment worden berekend. Het model is opgezet als een multi-level hierarchic Markov proces. Variatie in melkopbrengst is gemodelleerd met behulp van een zogenaamd state space model met Bayesian updating. Er zijn twee methodologische vernieuwingen. Op de eerste plaats is de structuur van het model efficiënter gemaakt door het toevoegen van een extra level. Daarnaast is ook een recent ontwikkeld diervoedermodel opgenomen voor een preciezere inschatting van voeropname en –kosten. Gegenereerde resultaten voor Nederlandse omstandigheden komen overeen met actuele melkveeprestaties in Nederland.

In hoofdstuk 6 zijn de statistische resultaten uit de hoofdstukken 3 en 4 in het model verwerkt om de economische resultaten van selectie voor verbetering van melkvet en –eiwitsamenstelling op bedrijfsniveau te kwantificeren. Voor melkvetsamenstelling is het fokdoel om de ratio van verzadigde vetzuren ten opzichte van onverzadigde vetzuren in melk naar beneden te brengen. Voor melkeiwit is het doel om de ratio van caseïne in het totale eiwit te verhogen. Bij het modelleren is rekening gehouden met de respons op melkproductie, vruchtbaarheid en levensduur. Er is gerekend met het huidige uitbetalingssysteem voor melk; economische effecten kunnen dus worden toegeschreven aan de verschillende responsen. In de uitgangssituatie is de opbrengst voor een gemiddeld Nederlands melkveebedrijf €35.900. Bij het veranderen van de melkvetsamenstelling aan de hand van genomics technologie neemt de opbrengst met €100 per jaar toe. In geval van traditionele selectie zou dit een afname van €2.400 zijn. Met betrekking tot het veranderen van melkeiwitsamenstelling neemt de gemiddelde opbrengst per jaar €600 toe bij traditionele selectie maar is er een afname van €700 per jaar bij toepassing van genomics. Met behulp van de resultaten kunnen de meest optimale selectiestrategieën in kaart gebracht worden en kunnen de benodigde break-even premies voor melkveehouders worden berekend. Zo’n premies kunnen een stimulans zijn voor melkveehouders om over te stappen.

Hoofdstuk 7 gaat in op de bredere implicaties van het onderzoek. In het proefschrift is een conceptuele aanpak gepresenteerd om nieuwe methoden in de zuivelketen in kaart te brengen en de gevolgen ervan te analyseren. Een wetenschappelijke innovatie betreft het bio-economische model waarmee complexe vraagstukken in de melkveehouderij bestudeerd kunnen worden. Ook draagt het proefschrift bij aan inzichten voor de praktijk: wat zijn de technische en economische consequenties voor de melkveehouderij van het toepassen van recente inzichten uit het melk genomics onderzoek. Naar verwachting komen in de nabije toekomst nog meer data beschikbaar vanuit melkmonsters en DNA-onderzoek. Door gebruik te maken van de genomics technologie kunnen gewenste veranderingen in de melk in de toekomst sneller worden doorgevoerd. Hierdoor kan de zuivelindustrie sneller inspelen op bepaalde ontwikkelingen. Verder onderzoek is nodig om ook de ex-ante economische effecten voor de markt in kaart te brengen.

Uit het onderzoek volgen een aantal hoofdconclusies. Op de eerste plaats is geconcludeerd dat het creëren van toegevoegde waarde van groot belang is voor het realiseren van een duurzame groei in de zuivelsector. Het produceren van melk met specifieke eigenschappen door toepassing van de genomics technologie kan hierbij een belangrijke rol spelen (hoofdstuk 2). Op de tweede plaats kan geconcludeerd worden dat toepassing van genomics selectie voor het veranderen van de vet- en eiwitsamenstelling in melk niet samenhangt met grote negatieve gevolgen voor de reproductie-eigenschappen van melkvee (hoofdstukken 3 en 4). Ten derde, ex-ante berekeningen voor het toepassen van genomics selectie voor het veranderen van melkvet- en eiwitsamenstelling laten geen groot effect zien op productie- en winstcijfers van melkveebedrijven (hoofdstuk 6). Resultaten van het optimalisatie- en simulatiemodel illustreren dat het model in staat is consequenties van complexe vraagstukken in de melkveehouderij door te rekenen (hoofdstuk 6). Ten slotte, recent melk genomics onderzoek biedt grote kansen voor de zuivelindustrie. Doordat uit dit onderzoek geen grote negatieve gevolgen van het toepassen van genomics technologie voor de melkveehouderij naar voren zijn gekomen kan de zuivelsector hier verder op inzetten.

Curriculum vitae

Róbert Milán Demeter was born on January 25, 1983 in Jászberény, Hungary. In 2001, he entered the University of Debrecen (Hungary) to study agricultural economics. In 2005, he joined the Double Degree program between University of Debrecen and Wageningen University (the Netherlands) to study business economics at Wageningen University. In 2007, he graduated with the degree of Master of Science (with distinction) from the University of Debrecen and with the degree of Master of Science (cum laude) from Wageningen University. In 2007, he started his doctoral studies in a joint research project of the Animal Breeding and Genomics Centre and the Business Economics Group at Wageningen University. During his doctoral studies, he also spent a total of six months at the Department of Large Animal Sciences at the University of Copenhagen (Denmark). Since 2011, he works as business analyst at Royal FrieslandCampina, a dairy co-operative in the Netherlands. Róbert is married to Agnieszka, and they live in Amersfoort (the Netherlands) with their daughter Hanna.

Training and supervision plan

Description	Institution	Year	ECTS[1]
General Part			
Writing research proposal	WASS, WU[2]	2007	4.0
Competence assessment	WGS, WU[3]	2007	0.3
Writing and presenting a scientific paper	WGS, WU[3]	2008	1.2
Graduate School Part			
Introduction course	WASS, WU[2]	2007	1.5
Multidisciplinary seminar	WASS, WU[2]	2009	1.0
PhD-council membership	WASS, WU[2]	2007-09	2.5
Discipline-Specific Courses			
Animal breeding and genetics	ABGC, WU[4]	2007	6.0
Scenario development	PE&RC, WU[5]	2007	1.4
Decision science II	ORL, WU[6]	2008	6.0
Advanced herd management	LAS, UC[7]	2008	9.0
Advanced statistics	WIAS, WU[8]	2009	1.0
Survival analysis	PE&RC, WU[5]	2009	0.6
Genetics of milk quality	WIAS, WU[8]	2009	0.3
Game theory and IO methods	ED, UC[9]	2009	1.0
PhD discussion groups	BEC, WU[10]	2007-11	4.0
Teaching and Supervising			
Comp. labs: Adv. supply chain management	BEC, WU[10]	2008-09	0.5
Comp. labs: Food safety economics	BEC, WU[10]	2009	0.5
MSc thesis in Animal Breeding and Genetics	ABGC, WU[4]	2009	1.0
Conference Presentations			
Annual Congress of the ADSA, Montreal, Canada		2009	1.0
Tri-Annual Congress of the EAAE, Zurich, Switzerland		2011	1.0
TOTAL[11]			**43.8**

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[1] 1 ECTS is equivalent to 28 hours of course work.

[2] Wageningen School of Social Sciences, Wageningen University.

[3] Wageningen Graduate Schools, Wageningen University.

[4] Animal Breeding and Genomics Centre, Wageningen University.

[5] C. T. de Wit Graduate School for Production Ecology and Resource Conservation, Wageningen University.

[6] Operations Research and Logistics Group, Wageningen University.

[7] Large Animal Sciences Department, University of Copenhagen.

[8] Wageningen Institute of Animal Sciences, Wageningen University.

[9] Economics Department, University of Crete.

[10] Business Economics Group, Wageningen University.

[11] Mimimum of 30 ECTS required.

Colophon

The research described in this thesis is part of the Dutch Milk Genomics Initiative and the project "Melk op Maat," funded by Wageningen University (Wageningen, the Netherlands), the Dutch Dairy Association (NZO, Zoetermeer, the Netherlands), the cooperative cattle improvement organization CRV (Arnhem, the Netherlands), the Dutch Technology Foundation (STW, Utrecht, the Netherlands), the Dutch Ministry of Economic Affairs (the Hague, the Netherlands), and the Provinces of Gelderland (Arnhem, the Netherlands) and Overijssel (Zwolle, the Netherlands).