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Towards predicting consequences of management strategies on lifetime efficiency of individual dairy cows

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Abstract (in English)

Historically, genetic selection for greater milk production in dairy cows has worked well when environmental conditions are favorable to gene expression, typically unlimited access to a high quality feed and water, neutral ambient temperature, and low pathogen load. The environment in dairy production, especially in grazing systems, is, however, increasingly variable due to climate change and societal demand for a more sustainable agriculture. Different breeding and feeding strategies might thus be chosen by farmers according to their local conditions. Selecting animals that adapt well to future herd environments is important and it requires an ability to predict how animals respond to a change in the environment in which they are placed, i.e. how they partition obtained nutrients between life functions when resources are limiting. This implies describing their capability to cope, or their robustness. In this context, the extent to which nutrients are partitioned to the vital functions (health and fertility) is clearly important. In this thesis, an existing lifetime nutrient partitioning model was further developed to simulate lifetime productive and reproductive performance and thereby allow prediction of lifetime efficiency of individual cows across feeding systems. The model is individual-based and it has incorporated the possible performance consequences of cows on their probability of reproducing. Generally, the whole model consistently simulated productive and reproductive performance of different genotypes of cow. We have also provided information on the range and distribution of genetic-scaling parameters needed for the model. It was shown that cows selected for increased milk production had an inferior fertility and shorter longevity compared to cows that produced less milk. At the animal level, despite having a shorter lifespan and a lower reproductive performance selected cows were still more efficient than non-selected cows in terms of energy captured in milk over energy intake throughout the lifespan. This conclusion might be extended to lifetime nitrogen efficiency since we found a positive correlation between energy and nitrogen efficiency. At farm level, economic indicators such as costs and returns of heifer replacement, veterinary treatment, artificial insemination, and environmental impact should be included to fully assess the lifetime profitability of cows in difference scenarios. The societal concern on animal welfare is also an essential issue. Simulations showed that cows fed low concentrate had worse productive and reproductive performance, and lifetime efficiency than high fed ones. This thesis has shown that modeling approach can be a useful tool for testing future selection and management strategies, and it has developed some key elements needed to do this.

Keywords: dairy cow, nutrient partitioning, lifetime efficiency, modelling, reproduction

Abstract (en français)

Historiquement, la sélection génétique chez la vache sur la production laitière a été efficace, car l'expression du potentiel génétique n'était pas limitée par les conditions d'élevage du fait d'un accès non limité à une alimentation de qualité, de conditions thermiques favorables, et d'une maitrise croissante des pathologies. Les conditions environnementales concernant la production laitière sont désormais plus variables du fait du changement climatique et de la demande sociétale pour un développement durable de la production agricole. Les éleveurs peuvent donc sélectionner différentes races et différentes stratégies alimentaires adaptées à leurs conditions locales. Sélectionner des animaux adaptés à leur environnement nécessite de prédire leur réponse aux changements de cet environnement, par exemple, comment la limitation des ressources alimentaires peut affecter la partition des nutriments entre les différentes fonctions vitales. Ceci implique de décrire et prédire leur capacité d'adaptation à ces situations, i.e. leur robustesse. Dans ce contexte, la caractérisation de la partition des nutriments entre les fonctions de production et les fonctions vitales (santé, fertilité…) est cruciale. Dans cette thèse, nous développons un modèle préexistant de partition des nutriments durant la carrière de la vache laitière pour modéliser ses fonctions de production et ses performances de reproduction afin de prédire leur efficacité individuelle dans différents systèmes d'alimentation. Le modèle est individu-centré, et il inclut la représentation des effets des performances de production sur la probabilité de reproduction des vaches. Globalement, le modèle simule les performances de production et de reproduction de vaches de différents génotypes de façon satisfaisante. Il permet également de renseigner des informations sur l'amplitude et la distribution de paramètres génétiques dérivés du modèle. Nos résultats montrent que les vaches sélectionnées pour la production laitière sont moins fertiles et ont une longévité plus faible que celles non sélectionnées. Néanmoins, ces vaches sélectionnées sont plus performantes durant l'ensemble de leur carrière pour leur efficacité énergétique (énergie fixée dans le lait / énergie ingérée) que les vaches faiblement productives. Cette conclusion peut être extrapolée à l'efficacité azotée du fait de la corrélation positive entre efficacité énergétique et azotée que nous avons montrée. Au niveau de l'exploitation, des indicateurs économiques comme le retour sur investissement des génisses de remplacement, les coûts vétérinaires ou d'insémination, et l'impact environnemental devront être inclus pour obtenir une évaluation complète de la rentabilité économique des vaches dans ces différents scénarios. La demande sociétale concernant le bien-être animal doit aussi être intégrée. Nos résultats montrent que les vaches restreintes en concentré ont de moins bonnes

performances de production et de reproduction, et une moindre efficacité que celles alimentées de façon plus libérale. Cette thèse montre que la modélisation peut constituer un outil pour tester différentes stratégies de sélection et différents schéma de management du troupeau, et fournit certains indicateurs pour ces objectifs.
Mots-clés: vache laitière, partition des nutriments, efficacité, carrière, modélisation, reproduction.

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List of abbreviations

ADF	Acid detergent fibre
AI	Artificial insemination
AIC	Akaike's information criterion
BCS	Body condition score
BW	Body weight
CP	Crude protein
CR	Conception rate
DCP	Digestible protein
DE	Digestible energy
DFC	Days from calving
DFC	Days to first service
DIM	Days in milk
DM	Dry matter content
DMI	Dry matter intake
DOP	Days from calving to conception
e_D	Dietary energy density
E_{eff}	Energy efficiency
E_{Intake}	Energy intake
E_{Milk}	Energy in milk
FE	Feed efficiency
FSC	Conception to first service
G	Genotype
G × E	Genotype by environment interaction
GE	Gross efficiency
GHG	Greenhouse gas
LCONC	Likelihood of conception
$LCONC_{BCS}$	Likelihood conception as function of body condition score
$LCONC_{EB}$	Likelihood conception as function of energy balance status
$LCONC_{MY}$	Likelihood conception as function of milk yield

LTE	Lifetime efficiency
MCF	Milk fat concentration
MCL	Milk lactose concentration
MCP	Milk protein concentration
ME	Metabolizable energy
MY	Milk yield
NDF	Neutral detergent fibre
N_{eff}	Nitrogen efficiency
P	Phenotype
PC	Principal component
PCO	Proportion of concentrate
r	Pearson correlation
R^2	Coefficient of determination
RFI	Residual feed intake
RPE	Relative prediction error

List of Publications

ARTICLES

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Chapter 1

General Introduction

1.1. Context of thesis

1.1.1. The challenges of an efficient dairy production

An increasing world human population, projected to reach 9.6 billion by 2050 (United Nations Development Programme, 2009), and a greater demand on agricultural land for non-agricultural activities imply that the dairy industry will face the challenges of meeting human consumption, competing for grain and feed resources with other livestock industries, and biofuel production (Berry, 2009; Gonzalez-Recio et al., 2014). At the same time, the increase of consumer and public concern on the environmental impact of milk production has established pressures on milk producers to mitigate greenhouse gas (GHG) emissions from their farms. The dairy sector, specifically, contributes around 4% CO_2-equivalent to the global anthropogenic GHG emissions (FAO, 2010), including mainly methane (CH_4), nitrous oxide (N_2O) and carbon dioxide (CO_2). In this context, improved feed efficiency (FE) of dairy cows, which is commonly defined as the ratio between milk output and feed intake, is of clear importance for the dairy industry to meet the challenges of future consumption requirements and sustainable farming objectives. Furthermore, given that feed is by far the largest expense in the total variable costs of milk production, e.g. more than 50% as estimated by Shalloo et al. (2004), any improvement of FE would have a substantial influence on the profitability of dairy farms (Britt et al., 2003). Cabrera (2009), using a milk price of 0.26$/kg and a total mixed ration (TMR) cost of 0.22$/kg of dry matter intake, indicated that income increased approximately 5$/cow/day when feed efficiency (kg milk/ kg dry matter intake) increased from 1.1 to 1.9. The recognition of the importance of FE in dairy industry has led to a global effort to improve this trait (for example: Berry, 2009; Hayes et al., 2013; Gonzalez-Recio et al., 2014; Pryce et al., 2014).

1.1.2. Increasing efficiency through selection on milk yield

So far, the improved FE in dairy cows has mainly been achieved indirectly through increased milk production (Hietala et al., 2014), by improving genetics, nutrition, and management (Wall et al., 2010; Connor et al., 2011). The strong genetic correlation between milk yield and FE (r = 0.79, Oldenbroek, 1989) indicates that the selection for increased milk yield alone should also improve feed efficiency without the requirement of measuring individual animal feed intake. With a greater yield per cow, fewer cows are needed to obtain the same level of milk output, and consequently reducing total feed requirement, land use, manure production, and GHG emissions. Modern high-producing dairy cows can produce approximately 40 to 50 kg of milk per day in early lactation, and the production of as high as 60kg/d is not uncommon (VandeHaar and St-Pierre, 2006). Such an enormous increase in milk yield has been attributed to approximately 50% of improved genetics and 50% of improved feeding and management (Pryce and Veerkamp, 2001; Pryce et al., 2004). Certainly, genetics has played an important role in the increase in milk production during the last decades, but proper nutrition and management are compulsory to enable high-producing cows to attain their genetic merits.

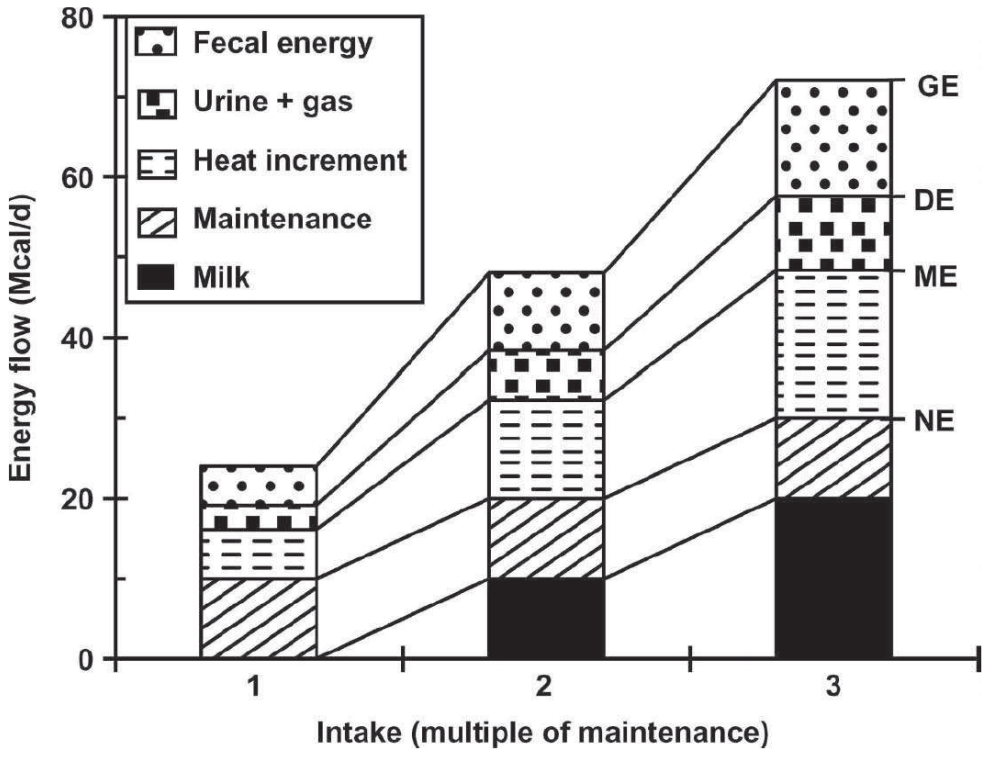

Figure 1.1. Level of production and energy flow. As a cow eats more feed and produces more milk, a smaller proportion of energy intake is used for maintenance [Source: VandeHaar and St-Pierre (2006)].

The biological process underlying this improved production efficiency is known as the "dilution of maintenance" effect (Figure 1.1) occurring with increased energy intake and milk production, i.e. when a cow eats more feed to support milk production a smaller proportion of that feed is used for maintenance, and it is thus more efficient (Bauman et al., 1985; VandeHaar and St-Pierre, 2006). An intuitive example was given by VandeHaar and St-Pierre (2006): a cow of 625 kg has a maintenance requirement of approximately 10 Mcal of net energy for lactation (NE_L) per day which is assumed to be constant; if she consumes twice as much feed intake compared to maintenance (20 Mcal of NE_L/d), then 10 Mcal or 50% is captured in milk and 50% is for maintenance; if she consumes three times the maintenance intake, then 67% of feed intake is captured in milk while only 23% is for maintenance.

1.1.3. Limitations of selection focused on milk yield and towards selection for lifetime efficiency

The benefits of increased FE in terms of milk production have, however, not been straightforward. The single-trait selection for greater milk production has been shown to be associated with the significant declines in health, fertility, and consequently productive longevity of dairy cows (Royal et al., 2000; Pryce et al., 2004; Dillon et al., 2006). The reported consequences generally include delayed resumption of postpartum estrus cycling, increased incidence of abnormal cyclicity, less expression of estrus, and poor conception rate (Butler, 2000; Kerbrat and Disenhaus, 2004; Dobson et al., 2008) (see Table 1.1 for examples); increased prevalence of metabolic diseases such as ketosis, metritis or fatty liver (Gillund et al., 2001; Giuliodori et al., 2013), and mastitis (Lassen et al., 2003). These resulting problems of selection for higher milk production do not only impair the benefits of improved feed efficiency through, for example, increases in veterinary and reproductive costs, and environmental losses, they also impact on productive longevity through increased involuntary culling for reproductive failure and health problems. The lower longevity would reduce lifetime efficiency because the shorter the productive life, the longer is the rearing (non-productive) phase as a proportion of the lifespan, and thus the lower the lifetime efficiency. Animal welfare is also affected (Oltenacu and Algers, 2005). A considerable body of research has, therefore, been conducted to elucidate the mechanisms involved, and the different factors of the genotype-production-nutrition complex that affect reproductive performance of animals [see reviews of Pryce et al. (2004), Lucy (2007) or Friggens et al. (2010)].

A general explanation for the declines in fertility and health is based on the arguments of nutrient prioritization: postpartum high-producing cows prioritize to channel their obtained nutrients towards milk production, and then body condition, and only after these immediate needs are met the reproductive processes are resumed (Leroy et al., 2008b). This prioritization creates a nutrient highway from the digestive tract and body reserves to the udder (Lucy, 2001). There is a decrease followed by a replenishment of body fatness in early and late lactation. In this context, if feed efficiency is considered over the lifespan of the animal then, the extent to which nutrients are partitioned to the vital functions such as health and fertility is clearly important. Leroy et al. (2008a), however, pointed out that the energy needed to develop, mature, and ovulate a follicle, to form a corpus luteum, and to maintain early pregnancy is negligible in comparison to energy required for milk production and maintenance. This suggests that there might be other indirect indicators or physiological mechanisms reflecting the effects of such a nutrient partitioning process on animal health and fertility. These indicators have been discussed in the literature including milk yield, body fatness, and body fat mobilization (Lopez et al., 2004; Roche et al., 2009; Yániz et al., 2008; Cutullic et al., 2012; Friggens et al., 2010).

Table 1.1. The decline in fertility of Spanish dairy cattle in the period 1991 – 2007*

Time period	1991 – 1995	1996 – 2000	2003 - 2007
Total number of cows	6306	6405	10493
Inseminated cows (%)	87.0	81.2	82.1
Pregnancy at first AI (%)	39.1	34.8	32.3
Ovarian hypofunction (%)	3.8	10.2	12.0
Annual milk yield per cow (kg)	8300	9660	11221

* Data of Yániz et al. (2008).

The physiological mechanisms of the effects of milk yield, and body fat mobilization on fertility have been investigated (Veerkamp et al., 2000; Butler, 2003; Garnsworthy et al., 2008; Senatore et al., 2010), whereas the physiological linkage between body fatness and fertility is still unclear although the evidence has been reported (Wright et al., 1992). However, the individual effects of milk yield, body fatness, and body reserve mobilization are not easy to be differentiated because of their inter-correlation; only a few authors have attempted to investigate this issue (Wright et al., 1992; Cutullic et al., 2011). The metabolic disorders in postpartum dairy cows relating to the excessive elevated non-esterified fatty acid, β-hydroxybutyrate, and urea that lead to excessive steatosis and ketogenesis have been associated with reduced animal health and

reproductive performance (De Wit et al., 2001; Gillund et al., 2001; LeBlanc, 2010). In summary, the negative consequences of focusing excessively on an increasing milk production, and thereby the consequences on long-term efficiency, emphasizes the need to be able to predict the process in which dairy cows partition their obtained nutrients in priority between physiological functions. This would allow a better optimization of the linking between animal health and fertility and the complex milk yield - body fatness - body fat mobilization. The essential biological elements needed in modelling nutrient partitioning in dairy cows have been recently discussed within the perspective of including information on animal genotypes (Friggens et al., 2013). The interaction between genotype and environment (G × E) modulates expression of the process of nutrient partitioning and animal performance, and thus it has also to be considered, especially in the context of an increasingly variable environment of the future (Bryant et al., 2005; Friggens and Newbold, 2007).

Genotype by environment interactions occur when the size of the animal response to a change in environment, for example, a decrease in feed availability is different for different genotypes (Simm, 1998). These interactions might lead to different consequences on animal health and reproduction, and thus they may affect lifetime efficiency. In dairy production, many studies have detected G × E interactions and investigated their subsequent influences on production, health, and fertility of the animals (Veerkamp et al., 1994; Pryce et al., 1999; Calus, 2006; Horan et al., 2005; Delaby et al., 2009; Cutullic et al., 2011). The experiments of Delaby et al. (2009), Cutullic et al. (2009), and Cutullic et al. (2011) have, for example, evaluated the influences of two feeding strategies on productive and reproductive performance of two breeds: Holstein selected for milk production, and Normande selected for dual-purpose of milk-meat. The results have shown that the low dietary energy feeding strategy (i.e. ~10 MJ metabolizable energy/ kg of dry matter intake) led to a low milk yield but a high loss of body condition, whereas the high dietary energy feeding system (i.e. ~10.8 MJ metabolizable energy/ kg of dry matter intake) led to a high milk yield with a low loss of body condition. The extent of decreasing milk yield from the high to the low energy feeding in Holstein cows was larger than Normande cows. High milk yield and high rate of loss of body condition have been well known to be contributors to the declined animal health and fertility (Pryce et al., 2001; Berry et al., 2003). In terms of breed, Normande cows had a significantly better re-calving rate than Holstein cows (52 versus 35%). The high energy feeding tended to have a better re-calving rate compared to the low energy feeding in both Normande and Holstein breeds (58 versus 46%, and 38 versus 32%, respectively). In the context of future climate change where environmental conditions might be altered, feed

resources might be under pressure, different breeding and feeding strategies might be chosen by the farmers, thus representing a need to predict the adaptive responses of the animals in these situations. An obviously important question might, for instance, be: Is the intensively selected production animal well suited with a free-range low input system? (Friggens et al., 2013). This is particularly important for dairy cows in grazing systems where their environment might vary more widely than that of other livestock species.

During this thesis, different aspects of FE were tackled based on the perspective of predicting nutrient partitioning and in relation to the farm selection and management strategies. Thus, the next section provides some general information on FE, nutrient partitioning regulation, interrelationship between nutrient partitioning and FE, and possible consequences of management strategy on animal productive and reproductive performance, and therefore efficiency.

1.2. Common measures of feed efficiency in dairy cattle and their implications

In dairy production system, gross efficiency (GE), and residual feed intake (RFI) are the two common measures of FE (Brody, 1945; Koch et al., 1963; Berry, 2009). The most appropriate definition is, however, still unclear (Berry and Crowley, 2013). Defining FE for lactating animals is more complicated than for growing ones because they undergo lactation cycles featuring by a rapid catabolism of body reserves (mainly adipose tissue) immediately after parturition, followed by an anabolism of these reserves in late lactation, although in thin animals body reserves can be reconstituted in early lactation (Garnsworthy and Topps, 1982). Any measurements of FE must, therefore, take into account such a contribution of body reserve mobilization. Another issue is that, FE has normally been evaluated in terms of energy (or mass), with nitrogen being accounted for via only its energy content (Zamani et al., 2008). However, as attention on environmental impact of emissions of NH_3 and N_2O has increased, not only energy efficiency but also nitrogen efficiency should be studied. Key questions would then be that whether energy and nitrogen efficiency are affected by the same factors, and what is the relationship between them. Though the environmental impact of phosphorous excretion, and maybe other minerals, has been recognized (Wu et al., 2000; Knowlton and Herbein, 2002) it is out of the scope of the current thesis. Further studies that incorporate phosphorous efficiency are, therefore, highly recommended.

1.2.1. Gross efficiency

Gross efficiency is defined as the ratio of output to input, i.e. milk produced/dry matter intake (kg/kg), energy in milk/energy intake (Mcal/Mcal) or nitrogen in milk/nitrogen intake (g/g) (Brody, 1945). This is the most common measure of milk production efficiency in literature because it is easy to measure, explain, and compare across populations. GE has a moderate heritability of 0.14 – 0.37 (Van Arendonk et al., 1991; Vallimont et al., 2011), and has been included in dairy cattle breeding programs of Ireland, Australia, and New Zealand where the breeding goal is on increased milk-solid production (Coleman et al., 2010).

There are, however, several problems limiting the usage of GE as a selection criterion that have been discussed in a numerous studies (Wang et al., 1992; Veerkamp and Emmans, 1995; Berry and Crowley, 2013). Firstly, since it is expressed as a ratio it suffers from an increase of the error variance as a proportion of total variance in the statistical analysis (Lison, 1958); and moreover selection for the trait can be unpredictable if selection pressure is disproportionate between the two components traits, for example, milk yield and feed intake (Gunsett, 1984). Secondly, gross feed efficiency has a high genetic correlation with milk yield [r = 0.79; (Oldenbroek, 1989)], implying that selection for milk production alone would also improve FE. Such a genetic selection for milk yield has been associated with an increased body reserve mobilization in early lactation (Berry et al., 2003). Thirdly, GE does not differentiate the partial efficiencies for maintenance, lactation, pregnancy, and body tissue gain or loss (Veerkamp and Emmans, 1995).

This undesirable relationship between single trait selection and other important production characteristics has resulted in a development of other indices (e.g. longevity) that balance between production and functional traits such as health and fertility (VanRaden, 2004; Shook, 2006; Norman et al., 2010). Miglior et al. (2005) reviewed a number of selection indices used in dairy cattle breeding program for 15 countries in the world and showed that in one decade most of them have reduced the emphasis on milk production to approximately 50% in order to achieve other breeding goals such as longevity, udder health, or calving ease. Nutritional and management strategies have also been explored to reduce the consequences of such an unfavorable relationship [see reviews of Lucy (2001) and Friggens et al. (2010)].

1.2.2. Residual feed intake

Residual feed intake, sometime referred to net feed efficiency, is an alternative measure of feed efficiency which was first proposed by Koch et al. (1963), and now is increasingly popular in the dairy industry and research approaches. RFI can be defined as the difference between actual feed intake and feed intake predicted from animal performance. The prediction of intake from performance can be done in two ways: nutrient requirements, commonly energy, are computed using feed table, for example, that of INRA-AFZ (Sauvant et al., 2004) or NRC (2001); or more commonly by comparison among contemporaries within the same population by regressing energy intake on energy sinks such as metabolic body weight, body weight change, and energy corrected milk yield (Coleman et al., 2010). Additional energy requirements for physical activity and pregnancy might also be included (Pryce et al., 2014). Dairy cows with negative values of RFI consume less dietary energy intake than expected from their performance relative to their contemporaries, and are therefore more efficient, whereas inefficient cows eat more feed than expected, i.e. positive RFI.

Because RFI is, by definition, phenotypically independent of the energy sinks included in the estimate of energy intake, it allows comparison between individuals differing in production level (Herd and Arthur, 2009). The difference in residual feed intake might be due to the true difference in efficiency among animals, random noise, or bias in the regression coefficients for the respective regressors (Berry, 2009). Five major physiological processes that are likely contributing to the variation in RFI have been discussed by Herd and Arthur (2009) consisting of intake of feed, digestion of feed, metabolism (anabolism and catabolism associated with and including variation in body composition and milk composition), physical activity, and thermoregulation.

The disadvantage of residual feed intake is that it is more difficult to compute and can be more difficult to explain than GE. Richardson and Herd (2004) conducted a study on Angus steers following divergent selection for RFI, estimated that only 73% variation in RFI would be explained by variations in heat production from metabolic processed, body composition, and physical activity, 27% of variation in RFI remained unexplained. It is also important to explore whether this improved net feed efficiency will exhibit the same undesirable effects on health and fertility of animals as have been discussed for high-producing cows or high gross efficiency, or eventually other undesirable consequences.

1.2.3. Biological components underlying variation in feed efficiency

An understanding of biological processes that create variation in feed efficiency is necessary for improving feed efficiency. Given the multiple definitions of feed efficiency, the biological sources of variation also depend upon how it is defined. In terms of gross efficiency, four biological processes have been drawn as the major sources for its variation including digestion and nutrient absorption, maintenance requirement, utilization of metabolizable energy for production, and nutrient partitioning (Bauman et al., 1985). Thus, the improvement in GE can be obtained as a result of changes in such processes. Especially, nutrient partitioning is attributed to the major source for the historic gain in gross efficiency and is the physiological basis for the differences in genetically superior cows (Reddy and Krishna, 2009).

Digestion and nutrient absorption

The chemical composition and physical characteristic of feedstuffs can have a major effect the digestibility (Bauman et al., 1985). It has also been well known that when the level of feed intake increases relative to the requirement of maintenance, the digestion of feed (as measured by total tract disappearance) tends to decrease (Nousiainen et al., 2009; Huhtanen et al., 2009). Conversely, most studies with lactating dairy cows suggest little variation between animals in apparent digestibility under standardized conditions and a similar level of intake (see review of Veerkamp and Emmans, 1995). Thus management of feeding can considerably influence the digestive efficiency but genetic improvement seems to be of minor importance.

Maintenance requirement

A variation in maintenance requirement might exist between cows differing in body size and ages (Mowrey and Hershberger, 1982). It might also be affected by diet, management, and environment. Fibre content of diet, grazing condition or heat stress can be considered as examples for (Agnew and Yan, 2000; Collier et al., 2005). Few studies have, however, investigated the variation in maintenance requirement of dairy cows under standardized conditions. Moreover, maintenance requirement is not influenced by genetic merit for milk production in Holstein Friesians (Holmes et al., 1983; Dong et al., 2013).

Utlization of metabolizable energy for milk production

There are differences in the partial efficiency of utilization of metabolizable energy for different physiological functions (maintenance, growth, lactation, fattening, and pregnancy), and between type of diet (Agnew and Yan, 2000). Such a variation is associated to the pathway of

absorbed nutrients and the specific products being formed. For example, when protected fat is fed to dairy cows the secretion of milk fat and the partial efficiency of utilization of metabolizable energy for milk production are increased which implies a very low cost of energy related to the conversion of absorbed fatty acids to milk fat compared to the energy cost of de novo synthesis of milk fatty acids (Smith, 1990). However, under typical conditions of nutrient supply and milk composition little variation in partial efficiency for milk synthesis can be expected (Tolkamp and Kyriazakis, 2009).

Nutrient partitioning

Nutrient partitioning has been attributed as the major source of the historic gains in feed efficiency of dairy cows (VandeHaar and St-Pierre, 2006; Reddy and Krishna, 2009). High genetic merit cows partition a greater proportion of nutrient intake to the mammary gland for milk synthesis and this is associated with an increase in the voluntary intake, whereas low genetic merit cows have a lower voluntary intake but if they do consumer more intake they would use it for excessive body reserves deposition rather than milk synthesis. Thus, genetic selection for high milk production does not only lead to cows that direct more absorbed nutrients for milk synthesis but also eat more to support the greater milk yield (Yan et al., 2006; Xue et al., 2011). The feeding management such as changing diet composition can also affect nutrient partitioning (Oba and Allen, 2000). The principle of increased feed efficiency by changing nutrient partitioning direction is based on the "dilution of maintenance" effect as described previously. The side-effect of such an increased partition of nutrient intake to synthesizing milk on lifetime efficiency has been aforementioned.

In the case of residual feed intake, its way of calculation has removed the animal difference in nutrient partitioning by adjusting feed efficiency for differences in, for example, milk yield, milk composition, body weight, or body composition. Thus variation in nutrient partitioning is not a component of RFI but it would include animal differences in digestive efficiency and nutrient absorption, maintenance requirement and partial efficiency of utilization of nutrient for milk synthesis (see review of Herd and Arthur, 2009).

1.3. Genetic improvement and animal efficiency interrelationship: from the perspective of nutrient partitioning

In this section, we describe a representation of the physiological regulations of nutrient partitioning in dairy cows, which is likely to incorporate the influence of farm management

decisions (feeding, reproduction, culling and replacement but also the choice of animal genotype) on animal performance. We argue that such representation is necessary to predict lifetime efficiency especially when external pressures on farm management increase.

Between genotypes variation in physiological regulation of nutrient partitioning plays an important role for successful lactation, and represents the physiological basis for the improvements in productive efficiency, and also for the deteriorations of health and fertility that emerge in high milk producing cows (Garnsworthy et al., 2008). Moreover, when animals are transferred to the environments that differ from where they originated they might perform differently; and this is termed as genotype by environment interaction previously. Such an interaction would result in different consequences on animal performance, health, and reproductive performance, and eventually animal efficiency.

1.3.1. Physiological regulations of nutrient partitioning

The term "nutrient partitioning", in broad sense, refers to the processes by which available nutrients are partitioned in varying proportions to different physiological functions; and in dairy nutrition it refers particularly to the partition of obtained nutrients between milk outputs and body reserves (Friggens and Newbold, 2007). Two types of physiological regulation of nutrient partitioning have now been well recognized in the literature including homeostasis and homeorhesis (Bauman and Currie, 1980).

Homeostatic control (Figure 1.2b; right-box) refers to the maintenance of physiological equilibrium or constant conditions in the internal environment (Bauman and Currie, 1980). There are many clear examples of homeostasis such as regulation to maintain body temperature or the consumption of food and partition of nutrients during absorptive and post-absorptive periods. The intake of a meal results in the changes in concentrations of blood metabolites, and an increased ratio of insulin to glucagon. These changes lead to a greater uptake of glucose by the liver (for glycogen synthesis), and by adipose tissue (for lipid synthesis). During the post-absorptive period when the uptake of nutrient has been diminished the insulin-glucagon ratio decreases sufficiently to result in mobilizations of glycogen and lipid stores. Obviously, there is an acute regulation, i.e. homeostasis, of plasma glucose concentration by the reciprocal actions of insulin and glucagon to ensure the proper balance in glucose supply and utilization by body tissues and organs during absorptive and post-absorptive periods. Homeostatic control is directed to the survival of an individual when facing with the environmental disturbances, e.g. extreme shortage of nutritional resources.

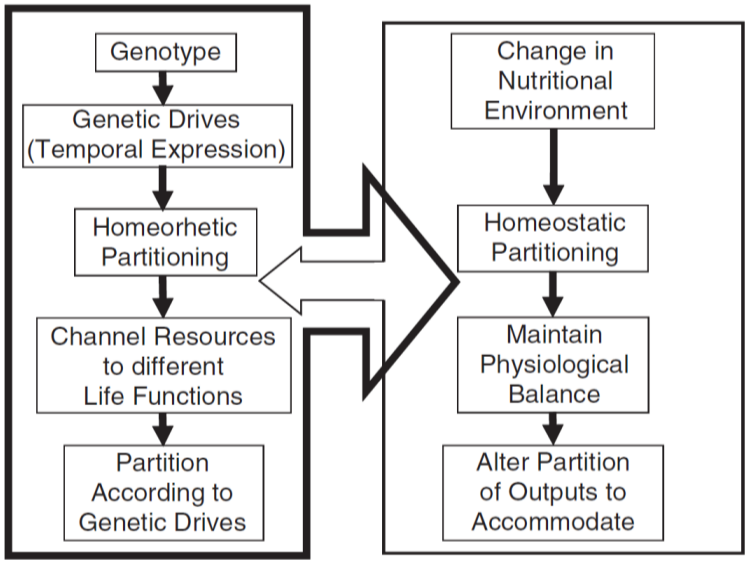

Figure 1.2. A schematic representation of the two types of nutrient partitioning: homeostasis and homeorhesis [Source: Friggens et al. (2013)].

It has, however, been well documented that nutrient partition changes with physiological stage of the animals (Kirkland and Gordon, 2001). Lipolysis and lipogenesis are, for example, up- and down-regulated in different stages of a reproductive cycle (Chilliard et al., 2000), and there are also endocrine changes (Bauman, 2000). The net result of these changes is that nutrients are allocated to different organs, life functions, and end-products (Friggens and Newbold, 2007). Clearly, this type of partition occurs not as a function of changing nutritional environment, but rather with physiological stage, which is commonly defined as homeorhesis (Bauman and Currie, 1980) or teleophoresis (Chilliard et al., 2000).

Homeorhetic control is normally defined as the orchestrated or coordinated changes in metabolism of body tissues necessary to support a physiological stage (Bauman and Currie, 1980). The implication behind this concept is that the animals has genetic drives of the orchestrated changes in priority for partitioning available nutrients between metabolic functions and are directed towards the perpetuation of the species. This type of drive is illustrated by the bold arrow in Figure 1.2 (left-box); in other words, this control is part of the genetic make-up of the animals. An example of homeorhetic control is the regulation of mobilizing and regaining body reserves in early and late lactation, respectively (Friggens, 2003).

Such a notion of homeorhetic regulation highlights the importance of the connection between genetic selection and nutrition, and thus capability to predict the changing partitioning priorities of an animal as it ages, through physiological stages, and in response to different

nutritional environments because they play important roles in variation of lifetime efficiency of the animals. The central role of the animal in regulating nutrient partition has been discussed (Friggens et al., 2013). An advanced step of modelling nutrient partitioning of dairy cows has been made by Martin and Sauvant (2010).

1.3.2. Environmental limits and challenges emerging in the context of genetic improvement

The societal demand for a more sustainable agriculture and the future climate change imply an possible increase in the diversity of environments in which the animals will be raised (Friggens et al., 2013). It has widely been reported that dairy cattle might perform differently when moving to another environment that differs from where they originated (Veerkamp et al., 1994; Kolmodin et al., 2002; Coffey et al., 2004; Boettcher et al., 2003). This evidence for genotype by environment interaction suggests that some genotypes have a greater ability to cope or to adapt to changes in the environments. In this context, some animals might respond to a change in environment in a much stronger way than others; these animals are environmentally sensitive and are termed "specialist" genotypes. In contrast, the less environmentally sensitive animals are called "generalist". In other words, the generalist can change their genotypes to adapt to different environments whereas the specialist can hardly do so (Ten Napel et al., 2009). If animals rank differently in different environments there is a risk of selecting environmentally sensitive individuals if the selection mainly takes place in the favorable conditions, which is the case of dairy cows. It is, therefore, important to be able to predict the adaptability of the animals when they are moving to other environments.

Further, the way in which the selected genotypes of cow partition nutrient intake between life functions has also been changed; compared to Norwegian cows, Holstein Friesian cows partition more energy to the mammary gland for milk synthesis and less to body reserves (Yan et al., 2006). The comparison between a high and low feeding systems has shown that dual-purpose breed of Normande seemed to be better in adapting to the low feeding system than high producing Holstein cows through better fertility (Cutullic et al., 2011). Thus, options have to be found to select new genotypes that can adapt well with these emerging environments while still maintaining production efficiency. Given the drastic decline in fertility and health, future emphasis should be placed on longevity and lifetime performance traits in selection decisions.

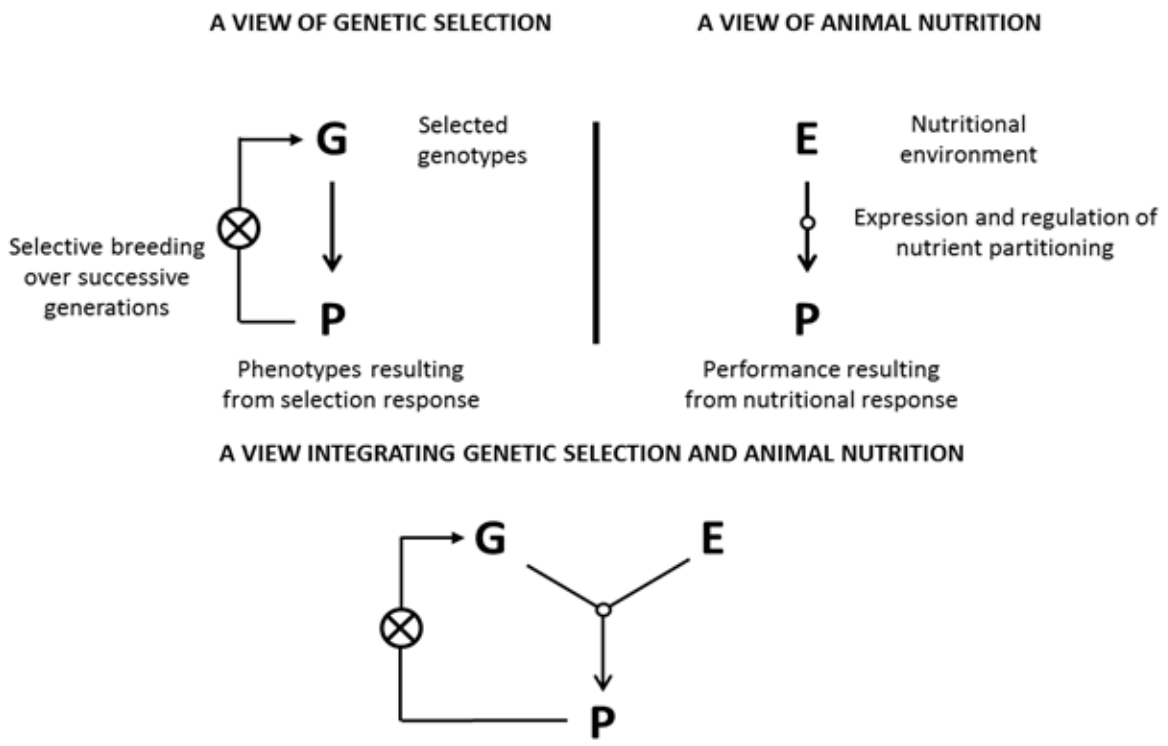

Figure 1.3. Two separates views of genetic selection as an inter-generational process of selecting elite individuals among a population of candidates, and of animal nutrition, as an intra-generational process of nutrient partitioning by individuals. The emergence of G × E interactions can be viewed as a result of combining these two processes (Re-produced from Douhard, 2013).

On the one hand, one can attempt to improve the environment so that it is less constraining to the animals, e.g. by feed supplementation. On the other hand, one can select animal that adapt well with the variations in the environment. In dairy cows, the inclusion of functional traits such as health and fertility into the selection indices has increasingly been performed (Miglior et al., 2005; Miglior and Sewalem, 2009). Though these ideas are well recognized by both animal production scientists (e.g. Blanc et al., 2007) and geneticists (e.g. Huquet et al., 2012), they are commonly considered separately (Douhard, 2013). As we have seen that the differences in the response by individuals of varying genotypes to the same nutritional treatment (environment) can be substantial it is essential that the nutritional and genetic approaches should be integrated to realistically represent the systems (Figure 1.3).

1.4. Mathematical model for integrating genetics and nutrition in dairy cattle

Generally, simulation models not only provide a tool to integrate knowledge from biological experiments but can also assist the process of decision making by predicting the outcomes of animal performance under different management strategies. In the recent review, McNamara

(2011) has indicated that the mathematical model is a powerful tool for integrating complex relationship between genetic factors, nutritional environment and time. In dairy cattle nutrition, the pioneering works of Baldwin et al. (1987a; b) and Oldham and Emmans (1989) have shown that mathematical models can be used to explore data, concepts and hypotheses related to nutrient partitioning [see review of Friggens et al. (2013) for the recent modelling advances]. Reproduction of dairy cattle has also been extensively modeled [see reviews of Blanc et al. (2001) and Vetharaniam et al. (2010)]. The simulations of production and reproduction are, however, commonly done separately. The models of Bryant et al. (2005, 2007), and Martin and Sauvant (2010), for example, have acceptably predicted the performance of dairy cows in different nutritional environments. However, these models do not integrate the possible interaction between production and reproduction. At the other extreme, the models that predict reproduction of the animals only focus on the reproductive processes (Oltenacu et al., 1980; Plaizier et al., 1998; Blanc and Agabriel, 2008). Attempts to develop a model that allow linking production and reproduction in different environments are therefore necessary. The outcomes of this type of model can be used to suggest the most suitable and profitable management strategy for a specific genotype of cow.

Chapter 2

Objective and Approach

2.1. Research objective

In this thesis, we propose that the management of the genotype by environment interaction at the animal level such as breeding and feeding strategies requires a representation of the long-term effects on both productive and reproductive performance which are the major determinants of lifetime efficiency. The overall objective of the present Ph.D. thesis was accordingly to develop a model for predicting the consequences of different management strategies on the lifetime efficiency of individual dairy cows (Figure 2.1).

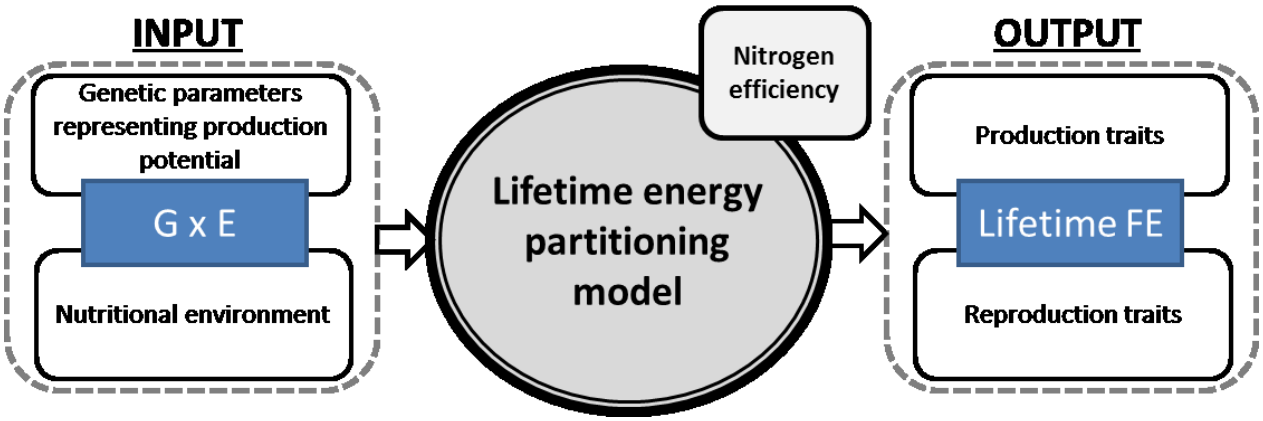

Figure 2.1. The schematic presentation of developing a model for predicting lifetime efficiency of individual cows.

Because the model in the present study was supposed to be energy-based, but nitrogen efficiency is increasingly considered in dairy industry, an important issue needed to be initially explored was what that if an improvement in energy efficiency would also lead to an improvement in nitrogen efficiency. Additionally it is well recognized that there is a significant genetic variation between individual cows of the same population in their capability to perform

in the same environment, an individual-based model should be able to take this into account. Lastly, there is an interaction between production and reproduction and it is changing when animals move to different environments, thus the realistic prediction of animal efficiency should take this into account. These three issues were identified as the key questions towards the development of a lifetime energy efficiency model of individual dairy cows.

- ***Question 1.*** *How does an improvement in energy efficiency relate to nitrogen efficiency?*

Though the efficiency of utilization of minerals such as calcium or phosphate are increasingly considered, energy and nitrogen efficiency are the most common indicators of feed efficiency in dairy production systems. Environmentally speaking, energy and nitrogen efficiency relate to the emissions of CH_4, N_2O and CO_2, which are the principle greenhouse gases. In economic terms, nitrogen efficiency used to be paid less attention because feeding more protein than required by a cow usually increases feed cost without financial return but the loss of milk due to underfeeding protein is even more expensive (VandeHaar and St-Pierre, 2006), and thus nitrogen efficiency had been evaluated simply via its energy content. However, with the increasing environmental concerns relating to nitrogen excretions, nitrogen efficiency becomes more important (Bannink et al., 2013). In the context of this thesis, a question then arises is that whether we have to develop two separate models for predicting energy and nitrogen efficiency individually, or is it possible to initially build one model that can largely account for both predicting energy efficiency and considering nitrogen efficiency as an add-on. This would only be possible if they are correlated, and if they are affected by common factors. To our best knowledge such information has not been reported in the literature. The objective of the first study was, therefore, to explore the relationship between the two major components of feed efficiency, i.e. energy and nitrogen efficiency, and possible nutritional and animal factors that affect these efficiencies, and their relationship.

- ***Question 2.*** *How to represent genetic variability in production potentials of individual cows in a lifetime nutrient partitioning model?*

It has widely been reported that there is a significant variability in performance between individual cows in the same population (e.g. Rose et al., 2004; Bastin et al., 2011). In animal breeding this variability can be quantified by recording and comparing the means of a trait for different genotypes in the same environment and represented as the estimated breeding values (Veerkamp and Emmans, 1995). Simulation models in dairy cattle, however, often assume an average population response and apply it to all animals in the same population without reference

to genetic variation between animals (see review of Bryant et al., 2005). This is even more difficult because animals differing in genetic potential might respond differently with different treatments (G × E) (Pomar et al., 2003). One approach to integrate such a genetic variation into the model for simulating different genotypes of cow is to use the estimated breeding values (Bryant et al., 2008). Another approach uses numerical parameters to scale animals differing in genetic potentials (Vetharaniam et al., 2003; Martin and Sauvant, 2010), i.e. each parameter represents a performance trait and thus allows describe genetic differences in performance. In the model of Martin and Sauvant (2010), for example, cows that differ in milk production capacity are theoretically represented by different values of parameter of ν_y, i.e. ν_y of one represents a cow that has peak milk yield of 24 kg/d in first lactation, and a high value of ν_y implies a high milk production potential and vice versa. The application of the latter approach to realistically simulate different genotypes of cow in the population, however, requires knowledge of variation of such parameters, their nature of distribution, and the possible correlations that may exist between parameters. The second study was, therefore, aimed to use an existing model of lifetime nutrient partitioning for estimate individual variability in genetic potentials for some production traits of different genotypes of cow.

- ***Question 3.*** *How to represent the effect of performance and nutritional environment on reproduction and productive lifespan?*

As indicated previously, management strategies such as breeding programs or feeding regimes might have an effect on milk yield and body reserves of dairy cows that are commonly suggested as the main determinants of the impaired health and fertility of cows (e.g. Cutullic et al., 2009, 2011). This indicates a need to be able to predict not only performance but also long-term consequences on health and reproduction of the animals under changing management scenarios. In most simulation models in dairy cattle, the reproductive process is usually represented by assuming a fixed reproductive performance such as fixed postpartum anestrus period, or fixed calving interval which are increasingly not realistic for high producing cows. Recently a few authors have incorporated the possible interaction between milk yield and body reserves and reproductive performance (Inchaisri et al., 2010; Brun-Lafleur et al., 2013), the focus of these models are within a lactation, and moreover they do not allow responses of animals in terms of production under changing nutritional environment to be simulated. Thus, the objective of this last study was to extend the model that had been used in the second study to simulate productive and reproductive performance, and lifetime efficiency of different genotypes of cow under different feeding regimes.

2.2. General approach

This section describes in general terms the research methodology that was applied during this thesis. Firstly, the meta-analysis approach was applied to explore the relationship between energy and nitrogen efficiency, and factors affecting these efficiencies. Secondly, an external data set was utilized to evaluate the suitability of a previously published model for deriving the estimates of genetic variability in genetic potentials of individual cows. Finally, the interaction between production and reproduction was incorporated in a model to explore the consequences on animal's lifetime efficiency. It was realized through incorporation of the possible influences of milk yield, and body reserves on reproductive process. Specifically, we hypothesized that high milk yield, low energy balance, and low body condition negatively affects reproductive performance of cows.

2.2.1. Study 1: meta-analysis approach to explore factors affecting energy and nitrogen efficiency, and their relationship

Building database

The initial step towards a meta-analysis was to create a database for later analyses by conducting a literature search using online search engines including ScienceDirect, Google Scholar, and Web of Science. Keywords were energy efficiency, nitrogen efficiency, dairy cows, nutrient utilization and dairy cow performance, whereas the main criterion for inclusion of a study in the meta-analysis was that it reported, or permitted calculation of, energy and nitrogen efficiency. Consequently, a data set containing in general the information on number of studies, number of observations, nutritional and animal factors possibly affecting energy and nitrogen efficiency was obtained. The next step was to define how to measure energy and nitrogen efficiency.

Energy and nitrogen efficiency derivations and their relationship

In this study, energy and nitrogen efficiency were defined as the ratios between energy in milk over energy intake (Mcal/Mcal), and nitrogen in milk over nitrogen intake (g/g), respectively. Dietary energy and nitrogen were computed at digestible level using chemical composition information obtained from feeding tables of Institut National de la Recherche Agronomique (INRA, 1988, 2010), and collaboration between INRA and Association Francaise de Zootechnie (INRA-AFZ; Sauvant et al., 2004), and equations proposed by National Research Council (NRC, 2001). The equation of Sauvant and Giger-Reverdin (2009) was applied to account

for reduced digestibility due to increased dry matter intake. Energy and nitrogen in milk were calculated using equations of NRC (2001). Details on these equations can be found in chapter III (Materials and Methods).

The correlation between energy and nitrogen efficiency was investigated in two ways: inter- and intra-study. The inter-study correlation was computed from the observed data of energy and nitrogen efficiency, whereas the intra-study correlation was the correlation after adjustment for the random effect of study.

Statistical analysis

To analyze the effects of animal and nutritional variables on energy and nitrogen efficiency, multiple linear regression was applied using the nlme and lm packages of the statistical software R. Because the data were obtained from many studies conducted over many years and in different conditions, study effect was considered as random as suggested by St-Pierre (2001).

Moreover, as energy and nitrogen efficiency were calculated as the ratios of the outputs of these respective nutrients in milk over inputs in the diet, milk yield and dry matter intake appeared in both ratios. We, therefore, would expect a strong correlation between them irrespective of any animal or diet composition factors. To overcome this problem, we decided to look at also the ratio between nitrogen and energy efficiency, which means that this "artifact" would be removed.

2.2.2. Study 2: simulating genetic variability in lifetime performance of individual cows

In this study, we evaluated a previously published model of Martin and Sauvant (2010), referred to here as GARUNS, for its capability of simulating genetic variability in nutrient partitioning and performance through the lifespan of individual cows. This model was proposed to be used later for simulating different genotypes of cow differing in genetic merit, e.g. high versus low milk production.

We used an external dataset containing records on performance, i.e. milk yield, milk composition, body weight, and dry matter intake, of individual cows of three breeds, i.e. Danish Red, Danish Holstein, and Jersey (Nielsen et al., 2003). The model was fitted to data cow by cow individually, using the Modelmaker software version 3.0 (Cherwell Scientific Ltd, 2000), to investigate the capability of the GARUNS model in capturing the individual variability in genetic production potentials of different genotypes of cow. Specifically, the cows in this data set were

kept under an environment that was assumed to be non-constraint, and thus make it appropriate to be used in our study.

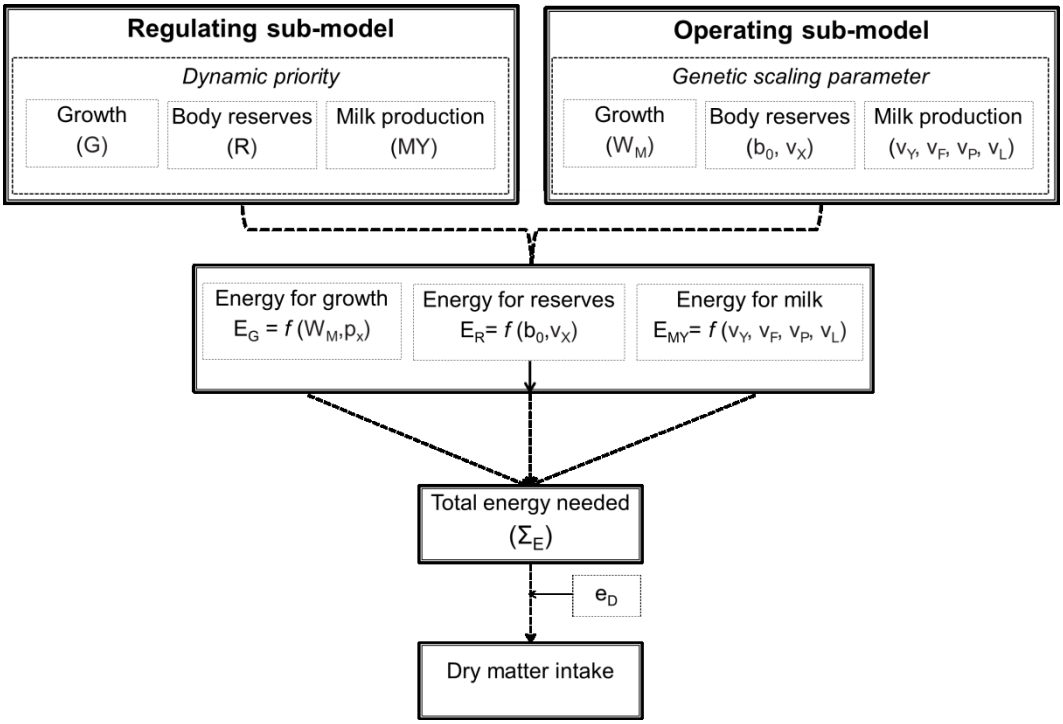

Figure 4.1. Schematic diagram of the GARUNS model [adapted with permission of Martin and Sauvant (2010)], showing how energy requirements for different life functions (growth, body reserves, and milk) are derived from genetic scaling parameters combined with lifetime profiles of relative priorities for the different life functions. The priorities for foetal growth, ageing (in regulating sub-model), and energy needed for foetal growth (in operating sub-model) are not presented as they are assumed to be common trajectories for every individual. Total energy needed is the sum of the different requirements, from which DM intake can be calculated assuming an appropriate diet energy density (e_D).

In this context, we hypothesized that if the GARUNS model fits well the individual data, the prediction accuracy should be within an acceptable range, and the residuals from individual fits should be equally distributed around zero without any specific time-trends through lactation. The prediction accuracy was evaluated using root mean square error. Since the fittings were done for three breeds through animal's life within the experiment, a statistical model that includes the effects of these two factors was used to investigate the distribution of the fitting residuals (Observed – Fitted values). If the GARUNS general trajectory of life function priority applies universally then the distribution of the residuals should be normal and one should not obtain the

significant effects of breed and day from calving variables. The general form of such a statistical model was:

$$\mathbf{Y_{ijk} = \mu + \alpha_i DFC_i + \beta_j Breed_j + \lambda_{ij} DFC \times Breed_{ij} + \delta_i DFC^2_i + \gamma_k + \varepsilon_{ijk}}$$

where Y_{ijk} is the fitting residual of BW, MY, milk fat (MCF), milk protein (MCP), milk lactose (MCL), and DMI, μ is the overall intercept across animals, α_i, β_j, and λ_{ij}, and δ_i are regression coefficients of Y on the corresponding predictors of day from calving (DFC), breed, interaction between DFC and breed, and squared DFC, respectively, γ_k is the random effect of kth animal, ε_{ijk} is the residual error which was assumed to be normally distributed with mean of 0 and variance of σ^2_e, i is the number of days from calving, j is the number of breeds, and k is number of animals.

Moreover, in order to use the model for simulating genotypes of cow it is essential to obtain knowledge on the individually derived genetic scaling parameters such as correlations between them, and (animal) factors affecting these parameters. We explored such information using the correlation matrix, and principal component analysis.

2.2.3. Study 3: predicting lifetime efficiency of different genotypes of cow under different feeding strategies

This study extended the GARUNS model to allow realistic prediction of the lifetime efficiency of various genotypes of cow, specifically high versus low milk producing, under different feeding strategies, specifically high versus low energy feeding. The general schematic representation of this extended model is shown in Figure 2.3.

By changing the genetic scaling parameters it is possible to produce different genotypes of cow differing in, for example, milk production potential, whereas the change in nutritional environment can be done through changing dietary energy density. The outputs of the GARUNS model including milk production, body weight, and energy balance were subsequently used to drive the reproduction sub-model (REPRO). Conventional reproduction models normally include different successive steps of uterine evolution, resumption of the cycle, estrus expression, conception, and embryo survival. However, the main interest of our present study was on lifetime efficiency, for which a key component is the productive lifespan of the animals. Cows that fail to establish pregnancy after a period of time are culled which leads to a shortening of the productive lifespan, this information is currently missing in the GARUNS model. Thus, the reproductive information needed is only that creates variation in the lifespan, this can be simply seen as a result of whether the cow successfully gets pregnant, and calves or not. Consequently,

instead of modelling all these reproductive steps we assumed a likelihood of conception of a viable calf (LCONC) as the final product of reproduction process, which is a result of other steps involved towards having a newborn calf, and being affected by milk yield, body condition, and energy balance. We hypothesized that a cow with high milk yield, low body condition, and low energy balance would have a low likelihood of conception. This situation might be exacerbated when cows face with environmental constraints, such as shortage of energy.

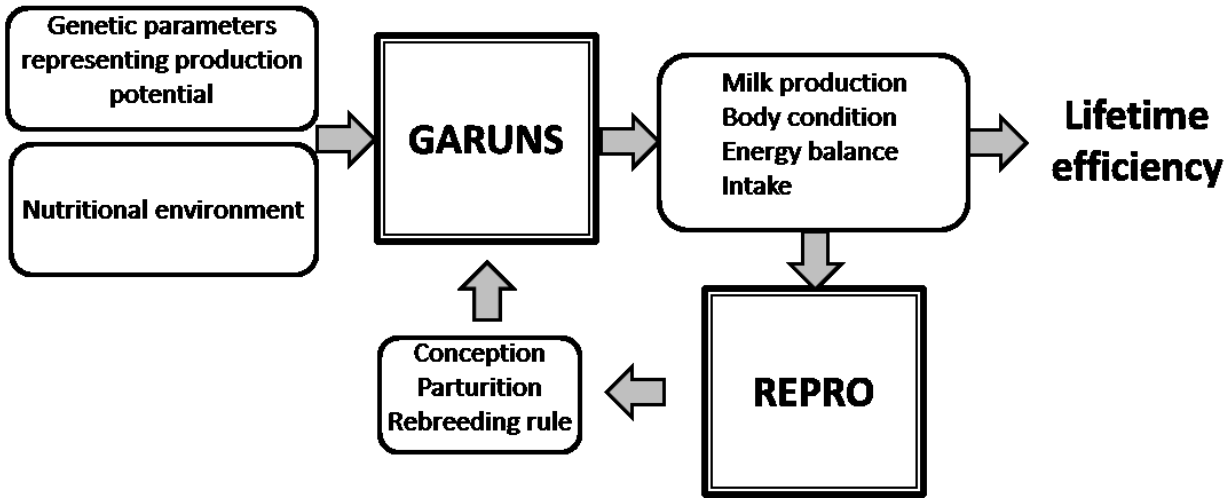

Figure 2.3. General presentation of model for predicting lifetime efficiency of individual cows

The function for the likelihood of conception is presented below:

$$\mathbf{LCONC = \mathit{f}\ (LCONC_{MY},\ LCONC_{BCS},\ LCONC_{EB})}$$

where $LCONC_{MY}$, $LCONC_{BCS}$, and $LCONC_{EB}$ are the likelihood of conceptions determined by milk yield, body condition, and energy balance. We assumed a maximal value of 0.6 ± 0.06 for LCONC which reflects the average conception rate of virgin heifers. $LCONC_{MY}$, $LCONC_{BCS}$, and $LCONC_{EB}$ were described using the logistic function as follows:

$$\mathbf{LCONC_{MY} = 2 \times (1 / 1 + \exp\ (Rat_{MY} \times MY))}$$

$$\mathbf{LCONC_{BCS} = 2 \times (1 / 1 + \exp\ (-Rat_{BCS} \times (BCS - 3))}$$

$$\mathbf{LCONC_{EB} = 2 \times (1 / 1 + \exp\ (-Rat_{EB} \times EB))}$$

where Rat_{MY}, Rat_{BCS}, and Rat_{EB} are parameters; MY is milk yield (kg/d), BCS is body condition score ranging from 0 to 5, and EB is energy balance (MJ/d).

The model's outputs such as interval from calving to conception, interval from first insemination to conception, or conception rate were compared to data from the literature to evaluate the quality of the model.

The lifetime efficiency of the animals was computed using the following equation:

$$\mathbf{LTE} = \sum_{1}^{N} \frac{\mathbf{E_{Milk}}}{\mathbf{E_{Intake}}} \times \mathbf{100}$$

where LTE is lifetime efficiency of energy utilization (%), N is day from birth to culling (day), E_{Milk} is total energy in milk (MJ), E_{Intake} is total metabolizable energy intake (MJ).

Chapter 3

Factors Affecting Energy and Nitrogen Efficiency: a Meta-analysis

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Abstract

A meta-analysis was performed to explore the correlation between energy and nitrogen efficiency of dairy cows, and to study nutritional and animal factors that influence these efficiencies, as well as their relationship. Treatment mean values were extracted from 68 peer-reviewed studies, including 306 feeding trials. The main criterion for inclusion of a study in the meta-analysis was that it reported, or permitted calculation of, energy efficiency (Eeff; energy in milk/ digestible energy intake) and nitrogen efficiency (Neff; nitrogen in milk/ digestible nitrogen intake) at the digestible level (digestible energy or digestible protein). The effect of nutritional and animal variables including neutral detergent fibre, acid detergent fibre (ADF), digestible energy, digestible protein, proportion of concentrate (PCO), dry matter intake (DMI), milk yield (MY), days in milk (DIM) and body weight (BW), on energy efficiency, nitrogen efficiency and the ratio Neff:Eeff was analyzed using mixed models. The interstudy correlation between Eeff and Neff was 0.62, whereas the intrastudy correlation was 0.30. The higher interstudy correlation was partly due to milk yield and dry matter intake being present in both Eeff and Neff. We, therefore, also explored the ratio Neff:Eeff. Energy efficiency was negatively associated with ADF and PCO, whereas Neff was negatively associated with ADF and digestible energy. The Neff:Eeff ratio was affected by ADF and PCO only. In conclusion, the results indicate a possibility to maximize feed efficiency in terms of both energy and nitrogen at the same time. In other words, an improvement in Eeff would also mean an improvement in Neff. The current study also shows that these types of transverse data are not sufficient to study the effect of animal factors, such as DIM, on feed efficiency. Longitudinal measurements per animal would probably be more appropriate.

Key words: meta-analysis, energy efficiency, nitrogen efficiency, dairy cows

Introduction

Feed efficiency (FE) in dairy production has received increasing attention because it influences not only farm profitability but also losses to the environment. Because feed costs account for more than 50% of total costs of dairy production (Shalloo et al., 2004), any improvement in FE has a direct impact on the profitability of dairy farms (Britt et al., 2003). Moreover, if nutrients consumed are not converted into milk, body reserves or a newborn calf, they are excreted into the environment, resulting in emissions of, for example, ammonia, methane or nitrous oxide (Thomassen et al., 2009). Improving FE can, therefore, be beneficial for both farm profitability and the environmental impact of milk production (Wall et al., 2010; Yan et al., 2010).

Feed efficiency is traditionally defined as the ratio of output to input [e.g., milk produced/DMI (kg/kg), energy in milk/energy intake (Mcal/Mcal) or nitrogen in milk/nitrogen intake (g/g); (Brody, 1945)]. An alternative definition of FE is residual feed intake (RFI; (kg/day or Mcal/day), which estimates the difference between actual and predicted intake (Koch et al., 1963; Prendiville et al., 2009). In genetic selection, RFI has been preferred to efficiency expressed as ratios, as selection based on ratios carries disadvantages, such as increased error variance as a proportion of total variance and a strong correlation with component traits, for example FE and milk yield (Wang et al., 1992). Residual feed intake is, by definition, phenotypically independent of component traits, but suffers from the problem of accumulation of errors in the measurements used (Herd and Arthur, 2009). Richardson et al. (2004), for example, stated that only 73% of the variation in RFI could be explained by biological mechanisms. Despite their obvious importance, in practice, neither FE nor RFI are used extensively due to the difficulties in the field of measuring their components, particularly intake, with a reasonable level of precision (McNaughton and Pryce, 2007; Moore et al., 2009). A second issue is that FE has commonly been evaluated in terms of energy (or mass), with nitrogen being accounted for only via its energy content (Zamani et al., 2008). However, attention for environmental impact of emissions of NH_3 or N_2O, which are related to N excretion, has increased. Hence, nitrogen efficiency should also be considered. In this context, a key question is whether nitrogen and energy efficiency are affected by the same factors?

FE can be measured at metabolizable, digestible or gross levels of nutrient intake (Veerkamp and Emmans, 1995; Tolkamp, 2010), which we would then call metabolic, digestible and gross efficiency, respectively. These different measures of FE may lead to different biological or

economic interpretations (Blake and Custodio, 1984). Variation in metabolic efficiency indicates primarily differences in partitioning of nutrients between milk production and other life functions. Environmentally speaking, it does not include losses in feces, gases and urine being excreted. At the other extreme, gross efficiency includes the part of feed that is not available to animals, and, as such, it is of limited value for quantifying the variability between animals in efficiency. Efficiency of use of digestible energy and nitrogen does not consider fecal losses but includes losses in gases, urine, and animal differences in partitioning of nutrients. Digestible efficiency, therefore, makes it possible to not only evaluate the environmental impact of milk production, but also to compare efficiency between animal genotypes in using feed to produce milk. Fecal losses can be estimated easily using feed chemical characteristics or in vitro degradation data (Nousiainen et al., 2009).

Feed efficiency for milk production depends not only on diet composition but also on animal genotype and physiological state (Blake and Custodio, 1984). Genetic potential for milk production and stage of lactation differences modify partition of absorbed nutrients into milk and other life functions. Feed efficiency should, therefore, be studied from both the nutritional and genetic points of view. A better understanding of how nutrients are partitioned has been recognized as being central to maximizing FE and minimizing environmental impact (Friggens et al., 2011). However, it has become clear later the available data did not allow the exploration of effect of animal factors on FE. In addition, insight into how Eeff and Neff are correlated and how this correlation changes in different conditions would provide a basis for maximizing or predicting FE of animals in both energy and nitrogen terms. Using a meta-analysis approach, the current study explored the correlation between Eeff and Neff, and examined common nutritional factors affecting Eeff and Neff, and their relationships.

Materials and Methods

Literature search

A literature search using the Web of Science (http://thomsonreuters.com/web-of-science/), ScienceDirect (http://www.sciencedirect.com/), and Google Scholar (http://scholar.google.com/) search engines was conducted to create a database for this study. The following keywords were used in different combinations: energy efficiency, nitrogen efficiency, dairy cows, nutrient utilization and dairy cow performance. The inclusion criteria in the database were a feed description in terms of ingredients (%), proportion of concentrate (%), dry matter intake (kg/d), milk yield (kg/d), milk fat, protein and lactose (%), body weight (kg) and days in milk (d). The

chemical composition of the diets in publications was either obtained from the reported laboratory analysis or estimated from NRC (2001), with exceptions of digestible energy and digestible protein, which will be mentioned later in this section.

Only full studies published in peer-reviewed journals were selected (abstracts, conference papers, and review articles were not considered). Eventually, 68 studies (listed in the Appendix) consisting of 306 treatment means that satisfied the above criteria were kept for further analysis.

Efficiency derivations

As indicated, FE was defined as the ratio of nutrient output in milk to nutrient input in feed, with a focus on energy and nitrogen (subsequently termed energy efficiency and nitrogen efficiency). Additionally, inputs were expressed as digestible energy or digestible protein.

Energy efficiency was calculated as the ratio between energy in milk (Mcal/d) and digestible energy intake (Mcal/d):

$$\text{Energy efficiency (\%)} = \frac{\text{MY (kg/day) x E milk (Mcal/kgMilk)}}{\text{DMI (kg/day) x DE diet (Mcal/kgDM)}} \quad [1]$$

where, MY is milk yield of an animal per day, DE diet is the digestible energy content of the diet, and E milk is the energy content of milk, which is the sum of energy of all milk components including fat, protein and lactose using the equations suggested by NRC (2001) as follows:

$$\begin{aligned}\text{E milk} = {} & \text{milk fat content (kg/kg of milk) x } 9.29 \\ & + \text{milk protein content (kg/kg of milk) x } 5.47 \\ & + \text{milk lactose content (kg/kg of milk) x } 3.95\end{aligned}$$

where 5.47, 9.29, and 3.95 are the amounts of energy released from the combustion of one kg of protein, fat and lactose, respectively (Mcal/kg; NRC, 2001).

Dry matter intake is calculated per animal per day. The DE diet was estimated using tables from Institut National de la Recherche Agronomique (INRA; 1988, 2010) and collaboration between INRA and Association Française de Zootechnie (INRA-AFZ; Sauvant et al., 2004). To account for reduced digestibility due to increased DMI, a correction was applied using the equation of Sauvant and Giger-Reverdin (2009).

$$DE_{adjusted} = DE_{standard} \times dE_{adjusted}$$

$$dE_{adjusted} = 66.8 + 20.1\ PCO - 3.37\ FI$$

where $DE_{adjusted}$ is the digestible energy after being adjusted for observed feed intake and proportion of concentrate (Mcal/kg of DM), $DE_{standard}$ is the digestible energy value obtained at maintenance level (Mcal/kg of DM), $dE_{adjusted}$ is the adjusted digestion coefficient of energy (%),

PCO is the proportion of concentrate (%), and FI (%) is the observed feed intake (kg of DM/d) expressed relative to body weight (kg).

Nitrogen efficiency was calculated as the ratio between nitrogen in milk (g/d) and digestible nitrogen intake (g/d):

$$\text{Nitrogen efficiency (\%)} = \frac{\text{MY (kg/d) x N milk (g/kgMilk)}}{\text{DMI (kg/d) x DN diet (g/kgDM)}} \quad [2]$$

where MY and DMI have already been indicated. N milk is the nitrogen content in milk, which was either obtained from data (if provided) or calculated by dividing milk crude protein content by 6.38. Likewise, DN diet is the digestible nitrogen content in the diet, which was either obtained from the study or calculated by dividing digestible protein content in the diet (g/kg of DM), obtained from INRA (1988, 2010) and INRA-AFZ (Sauvant et al., 2004), by 6.25. The effect of the proportion of concentrate and an increased feed intake on protein digestibility was assumed to be non-significant.

It can be clearly seen that milk yield and DMI appear in both Equations 1 and 2. Thus we would expect an artifactual correlation between energy efficiency and nitrogen efficiency, irrespective of any factor related to the diet or animals, with the extent of the correlation depending on how largely MY and DMI numerically contribute to the computations of energy and nitrogen efficiency. This should be taken into account when considering factors that affect energy and nitrogen efficiency, and also when studying the relationship between energy and nitrogen efficiency. Therefore, we decided to look also at the ratio of nitrogen efficiency to energy efficiency (Neff:Eeff). By analyzing this ratio, the "artifact" of milk yield and DMI is theoretically removed, and other factors that have an influence on the correlation between energy and nitrogen efficiency can be more clearly examined. This ratio is shown in Equation 3:

$$\frac{\text{Nitrogen efficiency (\%)}}{\text{Energy efficiency (\%)}} = \frac{\text{N milk (Mcal/kgMilk) x DE diet (Mcal/kgDM)}}{\text{DN diet (Mcal/kgDM) x E milk (Mcal/kgMilk)}} \quad [3]$$

In Equation 3, N milk, E milk, DE diet and DN diet are milk nitrogen content, milk energy content, digestible energy content of the diet, and digestible protein content of the diet, respectively.

Inter- and intrastudy correlations between energy and nitrogen efficiency

The correlation between energy and nitrogen efficiency was examined in two ways: inter- and intra-study. The inter-study correlation was simply computed from the observed data of energy and nitrogen efficiency, whereas the intrastudy correlation was the correlation after

adjustment for the random effect of study. The adjustment for study was made independently for energy and nitrogen efficiency, using in each case a mixed model with only the study factor included as a random effect. The residuals of these two models represent the intra-study variability in energy and nitrogen efficiency.

Statistical analysis

Because the factors that influence feed efficiency may be dependent upon each other, this probably results in confounding or bias for later estimations of regression coefficients and explanations (Silvey, 1969). The relationships among independent variables [i.e., NDF, ADF, digestible CP (DCP), DE, PCO, DMI, MY, BW and DIM] were examined by scatterplot and correlation matrix (Figure 3.1). Additionally, the residuals versus fitted plots of the models for predicting energy efficiency, nitrogen efficiency and the Neff:Eeff ratio from only one predictor were performed to check for any potential quadratic effect.

The effect of nutritional or animal variables, including NDF, ADF, DCP, DE, PCO, DMI, MY, BW and DIM, on energy efficiency, nitrogen efficiency and the Neff:Eeff ratio was analyzed using multiple linear regression. Milk yield and DMI were not included in the models for predicting energy and nitrogen efficiency, but only in the model of the Neff:Eeff ratio, to avoid artifactual correlations, as previously mentioned. Similarly, DE and DCP were not included in the model for predicting the Neff:Eeff or in the separate models for predicting energy and nitrogen efficiency if they appeared in the denominators of their efficiency calculation. Because the data used in this meta-analysis were gathered from multiple studies conducted over multiple years and in many different conditions, the study effect was considered to be random (St-Pierre, 2001). The random effects were, therefore, incorporated into the estimation procedure using a mixed effect model. The general form of the mixed model was:

$$\mathbf{Y_{ij} = B_0 + s_i + B_k X_{ijk} + e_{ij}}$$

where Y_{ij} is the dependent variable (energy efficiency, nitrogen efficiency, or the Neff:Eeff ratio), B_0 is overall intercept across studies, s_i is the random effect of ith study, $\mathbf{B}_k$ is a vector of regression coefficients of Y on the corresponding vector of predictors ($\mathbf{X}_{ijk}$), e_{ij} is the residual error, which was assumed to be normally distributed with mean 0 and variance σ^2_e, i = 1…69 studies, j = 1…306 observations, and k =1 to 9 predictors. First, the full models including all nutritional and animal variables were run. Second, the least significant variables were removed stepwise according to the degree of significance until only significant variables remained. To reduce the correlations between intercept and slope, and to make the intercept more meaningful, the

prediction variables were centred on their means. The goodness of fit of the models was evaluated internally using Akaike's information criterion(Ngwerume and Mao, 1992). For comparison across models, the coefficient of determination (R^2) was computed using the following equation from Faraway (2009):

$$R^2 = 1 - \frac{(y_i - \hat{y}_i)^2}{(y_i - \bar{y})^2}$$

where y_i is the ith observed value of efficiency, $\hat{y}_i$ is the ith predicted value of efficiency and $\bar{y}$ is the mean of efficiency, i = 1…306 observations.

To verify that the study effect was adequately accommodated by fitting it as a random effect, the final model with random effect was compared to a model where the study was included as a fixed effect. This model produced similar results to those of the model with a random study, and, therefore, will not be further discussed. Mixed and fixed effect models were performed using respectively the nlme and lm packages of the statistical software R version 2.15.1 (R Development Core Team, 2012).

Results

Data description

The main ingredients, chemical composition of the investigated diets in this meta-analysis, and their summary statistics are shown in Table 3.1. Corn silage and alfalfa silage were the predominant forages, followed by grass silage. The main source of energy from concentrate was corn, including ground corn and high moisture shelled corn. Soybean (solvent extracted, soybean expeller, extruded and heat treated) was the main source of protein supplement. Corn gluten meal, fish meal, blood and meat meal were the sources of rumen undegradable protein. Sugar cane and sugar beet molasses were used as the supplementation of sugars/energy in supporting microbial protein synthesis. Animal fat and urea were used as supplements of energy and non-protein nitrogen respectively. The data set showed a large variation in the chemical composition of the diets. Digestible protein averaged 11.08%, but ranged from 7.14 to 14.69%. Large variations were also observed in NDF and ADF content, which ranged from 17.80 to 54.50% and from 8.40 to 31.80%, respectively. The average digestible energy content was 3.16 Mcal/kg of DM.

Table 3.1. Main ingredients and chemical compositions (% of DM otherwise indicated) of the investigated diets[1].

Variable	No. of diets	Average	Minimum	Maximum	SD
Ingredient					
Corn silage	232	31.98	4.90	65.00	13.21
Alfalfa silage	150	33.18	9.80	69.80	16.89
Grass silage	49	34.11	12.40	83.00	19.24
Alfalfa hay	50	30.16	5.00	69.60	14.68
Ground corn	192	21.04	2.00	46.60	11.01
High moisture	90	30.16	5.20	45.70	9.07
Corn gluten meal	69	8.32	0.81	25.85	7.52
Soybean meal[2]	251	8.92	0.45	19.12	4.39
Cottonseed meal	52	7.86	1.70	15.00	4.08
Soybean hulls	64	5.74	1.50	17.00	2.98
Distiller's grain	46	7.73	1.20	22.00	5.18
Fish meal	47	1.73	0.30	5.00	1.17
Molasses[3]	84	3.02	0.26	10.00	2.43
Blood and meat meal	45	2.37	0.30	6.20	1.72
Fat	56	1.52	0.02	4.80	1.01
Urea	30	0.47	0.15	1.90	0.41
Chemical composition[4] (n = 306)					
CP	306	17.03	11.90	25.30	2.03
NDF	289	30.89	17.80	54.50	4.85
ADF	240	18.70	8.40	31.80	4.04
DCP	306	11.08	7.14	14.69	1.37
DE (Mcal/kg DM)[5]	306	3.16	2.47	3.80	0.22

[1]Summary statistics from 68 studies reported from the literature.

[2]Soybean meal included soybean meal 44, 48, 50% CP or solvent extracted, expelled, extruded and heat-treated soybean meal.

[3]Molasses from either sugarcane or sugar beet.

[4]DCP = digestible protein, NDF = nitrogen detergent fibre, ADF = acid detergent fibre, DE = digestible energy content of diet.

[5]INRA (1988, 2010) and Sauvant et al. (2004).

Table 3.2 illustrates the performance of animals from the studies included in the database. The average DMI was 23.18 kg of DM/d, with a range from 13.40 to 30.20 kg of DM/d. The highest milk production was 43.28 kg/d, whereas 16.33 kg/d was the lowest recorded milk production from an experiment with cows in late lactation (256 DIM). The earliest DIM recorded was 15 d and the latest DIM was 256 d. Thirty-eight studies, totaling 153 observations, had DIM <

100, whereas 30 studies, totaling 147 observations, had DIM ≥ 100. The mean value of energy efficiency was 34.09%, whereas nitrogen efficiency averaged 42.63%.

Table 3.2. Animal performance characteristics[1].

Variable	No. of diets	Average	Minimum	Maximum	SD
DMI (kg/day)	306	23.18	13.40	30.20	2.76
MY[2] (kg/day)	306	35.33	16.33	43.28	5.09
DIM (day)	302	97.00	15.00	256.00	48.00
BW (kg)	306	628.60	412.00	748.00	48.24
Energy efficiency (%)	253	34.09	23.33	44.97	4.06
Nitrogen efficiency (%)	306	42.63	29.15	64.54	6.81

[1]Summary statistics from 68 studies reported from the literature.

[2]DMI = dry matter intake, MY = milk yield, DIM = day in milk, BW = body weight.

Correlation between nutritional and animal performance variables

Figure 3.1 shows the interstudy correlations between the dietary and animal variables that were included in the subsequent analyses. It can be seen that fibre fractions (NDF and ADF) were negatively associated with the other variables, including DE, PCO, DMI, MY, and DIM. The digestible protein content of the diets was correlated with DE, PCO, MY, and DIM. Increased digestible energy content of diets depressed DMI, but had a weaker correlation with milk production. Moreover, a high energy-density diet was related to a large proportion of concentrate ($r = 0.42$). A strong positive correlation between DMI and MY ($r = 0.64$) was found in our analysis, which is consistent with the literature (Roseler et al., 1997; Martin and Sauvant, 2002; Voelker et al., 2002). Positive correlations between BW and DMI or MY imply that bigger animals tended to eat more feed and had a higher milk production.

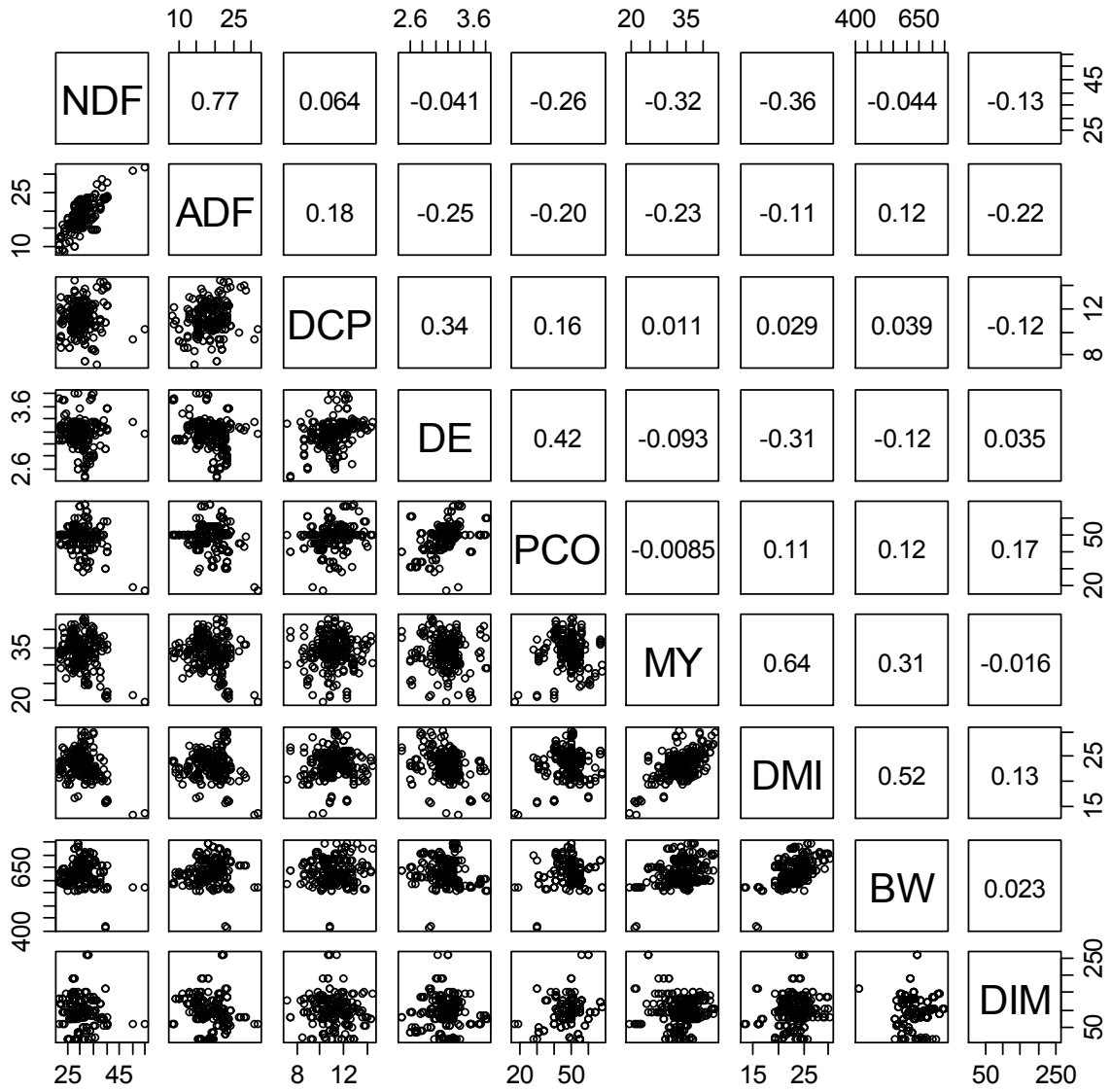

Figure 3.1. Interstudy correlation matrix between various nutritional and animals variables. NDF = neutral detergent fibre (% of DM); ADF = acid detergent fibre (% of DM); DCP = digestible protein (% of DM); DE = digestible energy content of the diet (Mcal/kg of DM); PCO = proportion of concentrate in the diet (%); DMI is in kilograms of DM per day; MY = milk yield (kg/day); BW is in kilograms per cow; DIM = days in milk (day).

Correlation between energy and nitrogen efficiency

The correlation between energy efficiency and nitrogen efficiency is shown in Figure 3.2. As expected, due to the presence of milk yield and dry matter intake in both expressions of efficiency, a positive interstudy correlation existed between energy and nitrogen efficiency in the unadjusted data (r = 0.62). However, Figure 3.2a shows that within experiments, an increase in energy efficiency was not always associated with an increase in nitrogen efficiency (e.g., top right). When the data are presented as intrastudy responses (i.e. they were corrected for the

random effect of study), the correlation was reduced (r = 0.30; Figure 3.2b). This is largely due to the greater reduction in range of the data, relative to the reduction in variation.

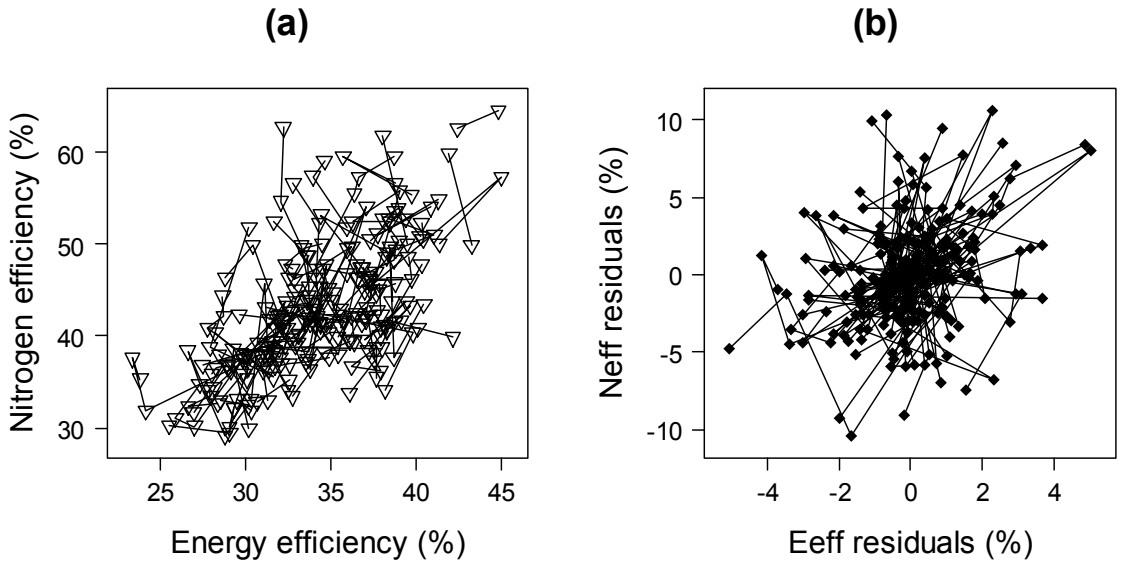

Figure 3.2. The correlation between energy efficiency (Eeff) and nitrogen efficiency (Neff) before (a) and after (b) adjustment for between study variation in both Neff and Eeff. Points joined by a line come from the same study.

Factors affecting energy efficiency, nitrogen efficiency and the Neff:Eeff ratio

The final models (i.e., including only significant variables) for predicting energy efficiency, nitrogen efficiency and the Neff:Eeff ratio are shown in Table 3.3. Figures 3.3, 3.4, and 3.5 illustrate the plots between observed and predicted values of the models predicting energy efficiency, nitrogen efficiency and the Neff:Eeff ratio, respectively. The residual analysis of the above models (plots not shown) was also performed to evaluate the model assumptions for the residuals (for example, equal variance or normality). All final models show a good prediction, with no discernible trend or pattern in the residuals.

Energy efficiency

Acid detergent fibre had a negative impact on energy efficiency ($P < 0.05$): an increase of 10% of dietary ADF content reduced energy efficiency by 1.60%. In contrast, PCO affected energy efficiency in a quadratic way (Table 3.3). The negative regression coefficient indicates that energy efficiency improved with a small increase in PCO, but decreased once PCO increased further. Digestible protein, BW, and DIM had no effect on energy efficiency ($P > 0.05$). At the mean values of ADF and PCO, energy efficiency was approximately 34%. In addition, because a strong association existed between NDF and ADF (r = 0.77), a comparison between a model using ADF

and PCO and a model using NDF and PCO for predicting energy efficiency showed that the latter produced a higher Akaike information criterion. Hence, the model including ADF and PCO best predicted energy efficiency.

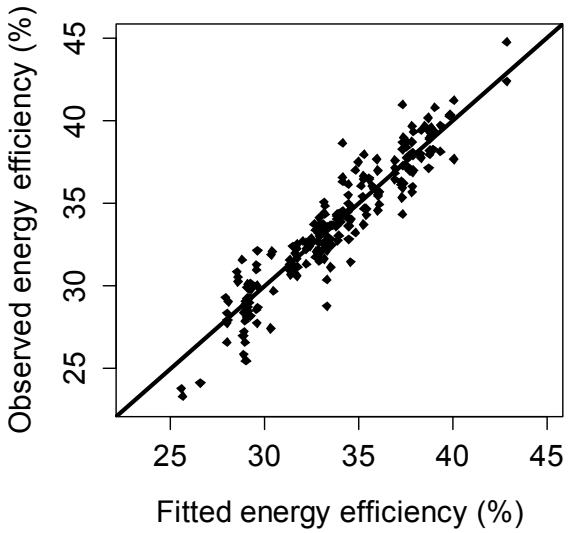

Figure 3.3. Plots of observed versus predicted values of model predicting energy efficiency.

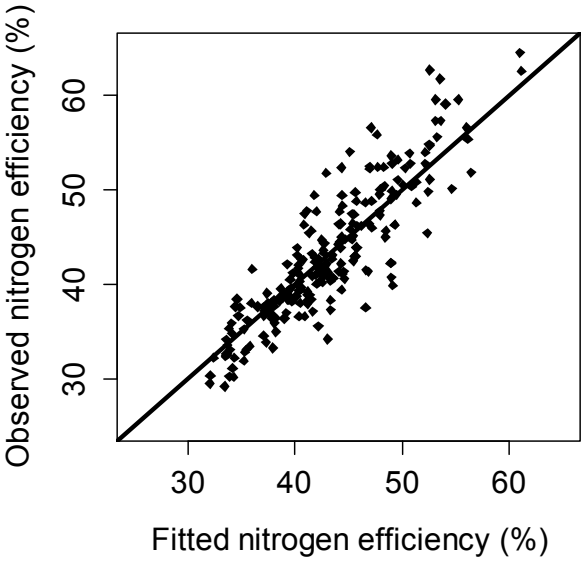

Figure 3.4. Plots of observed versus predicted values of model predicting nitrogen efficiency.

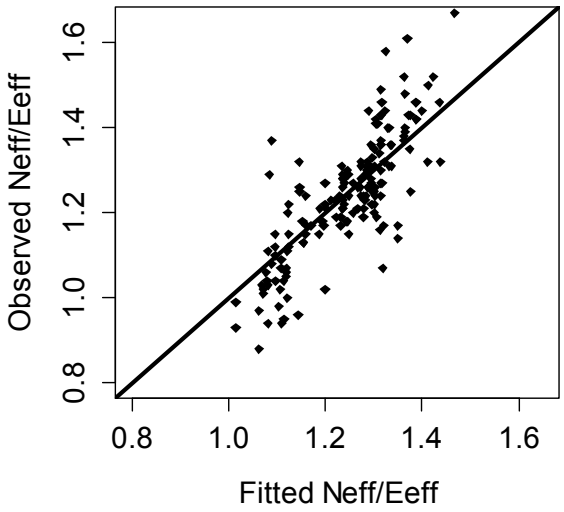

Figure 3.5. Plots of observed versus predicted values of model predicting the Neff:Eeff ratio.

Nitrogen efficiency

Table 3.3 also indicates that increasing dietary ADF and DE contents were negatively associated with nitrogen efficiency. Generally, a 10% increase in ADF or 1 Mcal increase in DE led to a 5.60 and a 6.67% reduction in nitrogen efficiency, respectively. Nitrogen efficiency was not significantly related to PCO, BW, or DIM.

Nitrogen Efficiency:Energy efficiency ratio

As can be seen from Table 3.3, the ratio between energy and nitrogen efficiency (Neff:Eeff) was significantly associated with ADF and PCO. The slope decreased with the increase in dietary ADF concentration, whereas it increased if the proportion of concentrate was increased. The Neff:Eeff ratio was not significantly influenced by DMI, BW, DIM, or MY.

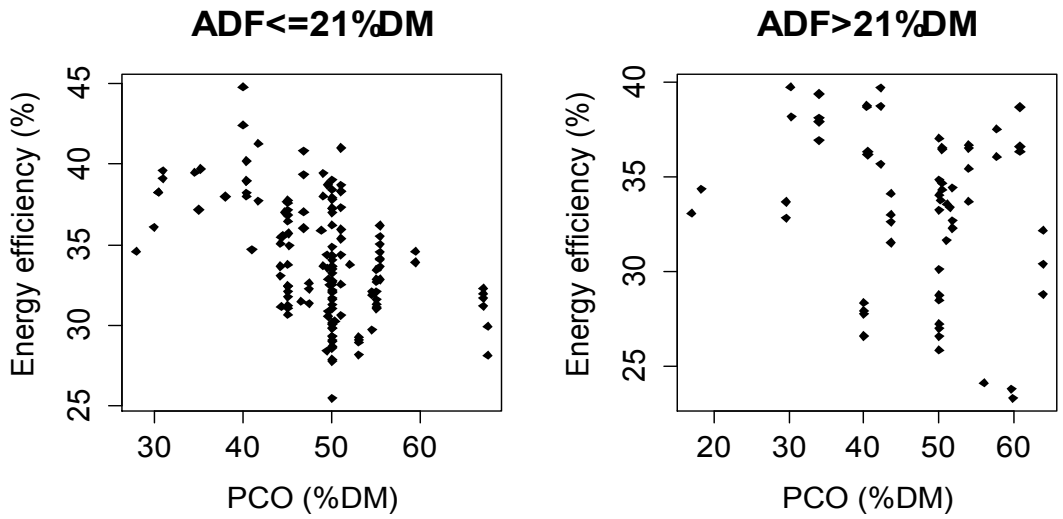

Figure 3.6. The effect of proportion of concentrate (PCO) in the diet on energy efficiency for two subsets of data: ADF ≤21% of DM and ADF ≥ 21% of DM.

Table 3.3. The full and final multiple linear regression models (after removal o**f** nonsignificant predictors) for predicting energy efficiency (Eeff; %), nitrogen efficiency (Neff; %) and the Neff:Eeff ratio[1,2].

Variables	Intercept	NDF	ADF	DE	DCP	PCO	PCO²	MY	DMI	BW	DIM	AIC	R²
Energy efficiency	34.03* (0.49)	-0.13 (0.08)	-0.02 (0.10)	-	-0.07 (0.12)	-0.19* (0.03)		-	-	0.01 (0.01)	-0.01 (0.01)	938	0.88
	34.09* (0.51)	-	-0.15* (0.08)	-	-		-0.002* (0.003)	-	-	-	-	933	0.88
Nitrogen efficiency	43.77* (1.00)	0.14 (0.20)	-0.69* (0.26)	-8.53* (2.73)	-	0.09 (0.08)		-	-	-0.01 (0.01)	-0.02 (0.01)	1284	0.79
	43.69* (0.98)		-0.56* (0.18)	-6.67* (2.24)		-		-	-	-	-	1254	0.79
Neff/Eeff	1.25* (0.02)	-2E-04 (0.005)	-0.02* (0.006)	-	-	0.004* (0.002)		-0.02* (0.004)	0.007 (0.006)	2E-04 (4E-04)	0.001* (0.001)	-188	0.70
	1.25* (0.02)		-0.02* (0.004)	-			3.98E-05* (1.96E-05)					-197	0.64

[1]For each efficiency variable, the estimates of intercept and prediction coefficients are given (with the standard errors of these estimates in parentheses). All predictions were significantly different from 0 at least at the level $P < 0.05$. Prediction variables were mean centered.

[2]NDF = neutral detergent fibre (% of DM); ADF = acid detergent fibre (% of DM); DCP = digestible protein (% of DM); DE = digestible energy content of the diet (Mcal/kg of DM); PCO = proportion of concentrate in the diet (%); PCO² = squared PCO in the diet (‰); DMI = dry matter intake (kg of DM/day); MY = milk yield (kg/day); BW = body weight (kg/cow); DIM = days in milk (day); AIC = Akaike information criterion.

* $P < 0.05$.

Discussion

The diets included in our study comprised a large variety of feeds. Major ingredients, however, were corn silage, alfalfa silage, grass silage, corn grain, and soybean meal. Corn silage and grass silage are often fed to dairy cows in European countries, in combination with barley or corn grain and soybean meal, whereas in America, grass silage is normally replaced by alfalfa silage or alfalfa hay (Huhtanen and Hristov, 2009). The main breed of dairy cows in the present database was Holstein-Friesian. Moreover, it should be noticed that approximately 70% of data in this study came from North America. The results from this meta-analysis are, therefore, most applicable to Holstein cows fed corn silage, combined with alfalfa silage/hay or grass silage, corn grain and soybean meal-based diets.

Regarding the chemical composition of the diets, the data showed a large variation in protein, energy, and fibre fractions. The average concentration of DCP was 11.08%. In the literature, most experiments report crude protein (Colmenero and Broderick, 2006; Brito and Broderick, 2007; Cabrita et al., 2007; Broderick et al., 2009) and metabolizable protein (Blouin et al., 2002; Raggio et al., 2004; Wang et al., 2007), rather than digestible protein. In terms of crude protein, the range in our study is in agreement with Huhtanen and Hristov (2009). In their meta-analysis of 425 feeding trials, dietary CP concentrations of 17.80 and 16.50% were reported for North America and Northern Europe, respectively. The average concentrations of NDF and ADF were 30.89 and 18.70%, respectively. Similar results have been found in other meta-analyses (Hristov et al., 2004; Ferraretto et al., 2013). The average value of DE was 3.16 Mcal/kg of DM, this is consistent with the report of Hristov et al. (2005), on the basis of net energy for lactation (NE_L), in which lactating cows received an average 37.9 Mcal NE_L/day.

The efficiencies of digestible energy and nitrogen usage of lactating dairy cows were found to be on average 34.09 and 42.63%, respectively, indicating approximately 60% losses of energy and nitrogen, as gases, urine or heat increment. VandeHaar and St-Pierre (2006) reported a value of energy efficiency varying from 17 to 20.5%, for cows from first to third lactation, when calculated on a gross energy basis. Nitrogen efficiencies, computed as protein in milk/ crude protein intake, ranging from 26 to 30% have been commonly reported (Castillo et al., 2001; Brito and Broderick, 2006; Broderick et al., 2009). Tamminga and Verstegen (1996) indicated that, generally, 70% of nitrogen intake is excreted in feces and urine. The difference between digestive and gross efficiencies of energy and nitrogen usage can be attributed to the fecal losses. The inefficiency of digestible energy and nitrogen usage is normally related to the presence of

indigestible fibre (West et al., 1997) and the imbalance in the carbohydrate:protein ratio in the rumen (Castillo et al., 2001). This imbalance impairs the rate of microbial synthesis, resulting in a low rate of fibre and protein digestion, and consequently a high rate of ammonia being excreted into the environment (Kebreab et al., 2001). A diet with an adequate energy-to-protein ratio is, therefore, of importance to maximize animal efficiency (Hoover and Stokes, 1991). In the present study, experiments with low energy and nitrogen efficiency were generally related to either high NDF (≈ 40% of DM; da Silva et al., 2007; Vander Pol et al., 2008) or high DCP (≈ 13.24% of DM; Broderick, 1992; Wattiaux et al., 1994; Groff and Wu, 2005). Additionally, the habit of feeding dairy cows high dietary protein to ensure maximal milk production could also be a cause of such a low nitrogen efficiency (VandeHaar and St-Pierre, 2006). Indeed, the economic cost in the form of milk lost due to underfeeding protein is far more than the cost of overfeeding protein as a margin of safety. In case of an excess of dietary protein, the nitrogen usage efficiency decreases sharply and a significant amount of N is lost through feces, gases, and urine (Tamminga, 1992). Therefore, research efforts should concentrate on finding ways to produce high quantity and quality of milk with as low a dietary protein as possible.

Nutritional factors affecting energy and nitrogen efficiency

Various nutritional factors have been cited in the literature that affect feed efficiency: for example, forage:concentrate ratio (Aguerre et al., 2011), carbohydrate:protein ratio (Aldrich et al., 1993), protein concentration (Cabrita et al., 2007; Broderick et al., 2009), and supplement of rumen undegradable protein (Broderick et al., 2008). Our meta-analysis shows that ADF and PCO were significantly associated with energy efficiency, whereas nitrogen efficiency was significantly associated with ADF and DE.

The negative effect of ADF on FE could be attributed to a decreasing the availability of digested nutrients for animals fed diets containing high fibre (Allen, 2000; Tjardes et al., 2002). Highly fibrous feeds tend to fill up the rumen quickly, but because they are slowly digested and passed, they limit DMI, milk production, and hence FE (Yang and Beauchemin, 2006). Moreover, highly fibrous feeds contain a limited amount of energy to support microbial growth/synthesis (Jetana et al., 2000). A diet containing an appropriate amount of fibre, however, is of importance to avoid rumen acidosis and to maximize microbial growth, rumen health, and subsequently animal efficiency. These considerations would suggest a nonlinear relationship between ADF and energy and nitrogen efficiency. However, the residual plots of the models, using ADF individually for predicting energy and nitrogen efficiency (Figures not shown), do not support

this idea, since no discernible pattern could be observed. It would be expected that, in a low-PCO diet, an increasing PCO improves energy efficiency by increasing the available energy to support microbial synthesis, but a too high-PCO diet might result in acidosis, which impairs animal performance and energy efficiency. Feeding cows with high-PCO diets may also alter nutrient partitioning (i.e., more to adipose tissues) and subsequently reduces energy efficiency, as computed in the current study. However, Table 3.3 indicates a linearly negative correlation between PCO and energy efficiency in the full model. Although ADF and PCO are to some extent correlated (r = 0.2), we suspected that they were reflecting different aspects: ADF indexing the digestible energy content of the diet, and PCO indexing the risk of acidosis. Therefore, to separate the effect of ADF and PCO on energy efficiency, we decided to split the data based on ADF. The idea was to isolate a part where the likelihood of rumen acidosis is very low (i.e., high ADF), and a part with high risk of acidosis (i.e., low ADF). Such a splitting allowed us to look at the effect of PCO on energy efficiency in these two situations, and it revealed that a significant negative effect of PCO on energy efficiency was only present in the low-ADF (≤21%) subset of data (Figure 3.6). This motivated us to incorporate a curvilinear effect of PCO on energy efficiency in the model, which was done by including a quadratic term. Statistically, such a negative regression coefficient of PCO-squared in Table 3.3 implies that energy efficiency was positively affected by low PCO, but negatively affected by high PCO. Agle et al. (2010) observed a decrease in FE, computed as NE_L, in high- versus low-PCO diets: 58.3 and 62.9%, respectively. Feeding cows with high PCO (e.g., 65-70% of DM), might result in a depression of fibre digestibility and fat yield (Moorby et al., 2006). The current study shows that a high PCO in the diet negatively affected energy efficiency, which could be the consequence of acidosis (VandeHaar and St-Pierre, 2006). However, in a diet with low concentrate (i.e., high fibre) content, energy efficiency was negatively and dominantly affected by ADF. Our study also indicates that feeding dairy cows with high PCO diets resulted in no significant improvement of nitrogen efficiency. This results is consistent with Agle et al. (2010), who reported an only marginally improved nitrogen efficiency when PCO increased from 20 to 60%.

It is important to also be aware that feeding dairy cows a high-PCO diet might alter the partition of nutrients. A high-digestible-carbohydrate diet is expected to result in an increased production of propionate in the rumen (Sutton et al., 2003; Friggens et al., 2004). Propionate is absorbed and metabolized by the liver to glucose and triggers an insulin response (Ingvartsen and Andersen, 2000), which subsequently stimulates the lipogenesis and inhibits the release of fatty acid from adipose tissue (lipolysis; Chilliard et al., 2000). Thus, feeding animals with a high-

PCO diet may result in more nutrients being partitioned to body tissue rather than milk production, and a decrease in efficiencies (calculated as milk/feed).

Relationship between energy and nitrogen efficiency

Acid detergent fibre and PCO were the only significant feed factors affecting the Neff:Eeff ratio, which is consistent with the separate regressions for each efficiency independently. This suggests that, from a nutritional point of view, a model to predict energy efficiency could be used to predict nitrogen efficiency without the need to building two separate models (i.e., nitrogen efficiency could be considered as an add-on in a model of energy-based efficiency). The routine correlation between these two efficiencies [0.62 in the present study and 0.90 in Wheadon et al. (2012)] is, in part, due to the presence of both MY and DMI in the calculation of both efficiencies. However, it is also in part attributable to the phenomenon of dilution of maintenance, as both energy and nitrogen requirements exist for maintenance. Our study further consolidates this by showing that both efficiencies are affected by the same nutritional factors.

Animal factors affecting energy and nitrogen efficiency

As stated by Blake and Custodio (1984), FE depends not only on diets but also on the genotypes, physiological states of the animals, and their possible interaction. There are clear differences in nutrient partitioning and FE between genotypes of cows (e.g., high- versus low-genetic merit), stages of lactation, and parities (Veerkamp, 1998; Dillon et al., 2003; Friggens et al., 2011). However, Table 3.3 shows that the current type of transverse database obtained from the literature is not appropriate to fully incorporate the effect of animal factors on FE. Body weight and DIM were the only factors possible to include (with the exception of MY and DMI, which were purposely excluded). Indeed, most of the studies in the literature focus on the effect of nutritional factors (e.g., dietary protein, fibre concentration, dietary energy concentration; Castillo et al., 2001; Colmenero and Broderick, 2006; Yang and Beauchemin, 2006), with little focus on the effects of breed, parity, body weight, or lactation period on energy and nitrogen efficiency (Britt et al., 2003; Prendiville et al., 2009). Other types of data (e.g., longitudinal) would be more appropriate to look at the effects of animal factors on FE.

In the present study, we found no significant effect of BW on energy or nitrogen efficiency. The significant correlations between BW, DMI, and MY (Table 3.3) indicate that larger animals ate more feed and produced more milk. However, they also had a higher maintenance requirement, which could explain the insignificant effect of BW on FE. Veerkamp (1998) pointed out that if two cows of equal BW are compared, the cow with 25% more MY will have a 10 to 15%

greater FE, whereas if two cows of equal MY are compared, the cow with 25% less BW will have a 10 to 12% higher FE. Thus, selection for smaller animals that have the same MY may represent a strategy for improving FE and reducing the environmental impact. Contrary to previous reports (Veerkamp, 1998; Britt et al., 2003), the current meta-analysis found no significant effect of DIM on FE. This probably reflects the shortage of data in early or late lactation, although it is known cows mobilize body reserves in early lactation to support milk production which affects the results of FE. Cows that mobilize more body reserves in early lactation seem to be more efficient because the usual definition of FE does not consider nutrients from such a mobilization (Connor et al., 2011). However, high rates of mobilization have been associated with reduced longevity of animals (Rauw et al., 1998) probably via increased problems of fertility (Pryce et al., 2004; Berry et al., 2008), and health (Oltenacu and Algers, 2005), which would reduce the benefit of improved FE. Thus, a better predictive capability and a biological understanding are needed of how a cow partitions her nutritional resources between life functions. Indeed, if FE is considered over lifespan of animals, then the extent to which nutrients partitioned to the vital functions such as health and fertility, is important (Friggens et al., 2011).

Conclusions

This meta-analysis shows that ADF, PCO, and DE were the common nutritional factors affecting feed efficiency. The ratio between energy and nitrogen efficiency, however, was affected by ADF and PCO content of feed only. The strong correlation between energy and nitrogen efficiency results indicates a possibility to maximize feed efficiency in terms of both energy and nitrogen at the same time. In other words, an improvement in energy efficiency would also mean an improvement in nitrogen efficiency. The current study also shows that these types of transverse data are not sufficient to study the effect of animal factors on feed efficiency. Longitudinal measurements per animal would be more appropriate.

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Chapter 4

Deriving estimates of individual variability in genetic potentials of performance traits for three dairy breeds, using a model of lifetime nutrient partitioning

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Abstract

This study explored the ability of an existing lifetime nutrient partitioning model for simulating individual variability in genetic potentials of dairy cows. Data of 102 cows including 180 lactations of three breeds: Danish Red, Danish Holstein, and Jersey were utilized. Individual cow performance records through sequential lactations were used to derive genetic scaling parameters for each animal by calibrating the model to achieve best fit, cow by cow. The model was able to fit individual curves of body weight, and milk fat, milk protein, and milk lactose concentrations with a high degree of accuracy. Daily milk yield and dry matter intake were satisfactorily predicted in early- and mid-lactation but under-predictions were found in late-lactation. Breeds and parities did not significantly affect the prediction accuracy. The means of genetic scaling parameters between Danish Red and Danish Holstein were similar but significantly different from those of Jersey. The extent of correlations between the genetic scaling parameters was consistent with that reported in the literature. In conclusion, this model is of value as a tool to derive estimates of genetic potentials of milk yield, milk composition, body reserve usage, and growth for different genotypes of cow. Moreover, it can be used to separate genetic variability in performance between individual cows from environmental noise. The model enables simulation of the effects of a genetic selection strategy on lifetime efficiency of individual cows which has a main advantage of including the rearing costs, and thus, can be used to explore the impact of future selection on animal performance and efficiency.

Key words: nutrient partitioning, dairy cow, genetic variability, dynamic model.

Introduction

Milk production efficiency is affected by the way in which dairy cows partition obtained nutrients between life functions. Generally, an efficient cow should allocate a greater proportion of nutrients towards the mammary gland, for milk synthesis (Linn et al., 2009). This traditional view of efficiency is based on the concept of dilution of maintenance, i.e. when a cow eats more feed to support milk production a smaller proportion is used for maintenance, and it is thus more efficient (Bauman et al., 1985). However, if efficiency is considered over the lifespan of an animal the extent to which nutrients are partitioned to vital functions such as health and fertility is important, since the longer the productive life the smaller is the rearing phase as a proportion, and thus greater the lifetime efficiency. These vital functions are not only related to economic (Collard et al., 2000) and environmental issues (Garnsworthy, 2004), but animal welfare (Oltenacu and Algers, 2005). Thus, being able to predict the nutrient partitioning process of cows can help improve animal efficiency and farm profitability, and reduce environmental impact.

Pioneering works of Baldwin et al. (1987a; b) and Oldham and Emmans (1989) show that mathematical models can be used to explore concepts and hypotheses, regarding nutrient partitioning in dairy cows, and have potential for predicting long-term efficiency (Dumas et al., 2008; Friggens et al., 2013). There are clear genetic differences in nutrient partitioning between cows (Yan et al., 2006) and physiological states (Kirkland and Gordon, 2001). Thus, prediction of nutrient partitioning should consider genetic variability between cows and differences in expression of their genotypes through time. By capturing these ideas, the model of Martin and Sauvant (2010a) has shown a great ability to simulate the average pattern of dynamic partitioning of energy intake and performance through lifespan of cows of different yield levels, and thus allows genetic variability to be incorporated in prediction of lifetime efficiency. This model assumes a general trajectory of dynamic partitioning of a cow's relative priority between life functions, and genetic scaling parameters are then incorporated to scale individual performance, and to simulate variability between genotypes in, for example, milk production. In other words, it assumes that performance of animals differ only in terms of scaling but not in terms of the dynamic shape.

At this moment, however, the appropriateness of the model to realistically simulate individual variability in nutrient partitioning trajectories is untested. Though the model shows a good fit to the mean values of various population data from literature (Schutz et al., 1990; Hoffman, 1997) the extent to which the assumption of one general trajectory of dynamic

partitioning of relative priority still holds when comparing different genotypes should be validated. Does the trajectory of dynamic partitioning of relative priority differ between breeds kept in the same environment? It is also important to evaluate the individual variation in genetic scaling parameters and their possible correlations and factors affecting them. Such information is necessary for setting up realistic population simulations and, in the wider context, for using the model to simulate the effects on lifetime efficiency of possible selection and management strategies.

The aim of this study was, therefore, to examine the model of Martin and Sauvant (2010a) for its capability of simulating individual variability in genetic potentials of milk yield, milk composition, growth, and body reserves usage of different genotypes of cow.

Materials and Methods

For clarity, it should be noted that this paper dealt with the situation where cows are managed in a non-constraint environment (i.e. unlimited access to a high quality feed, water or neutral ambient temperature), and thus, the performance profiles that a given cow would achieve in such an environment is referred to as genetic potential, in accordance with literature definitions of genetic potential (e.g. Oldham and Emmans, 1989).

Teleonomic model (GARUNS)

This section presents a brief introduction to the teleonomic model of Martin and Sauvant (2010a). This teleonomic model, referred to here as GARUNS, consists of a regulating sub-model providing a driving force to control the function of an operating sub-model. An adapted scheme of GARUNS is presented in Figure 4.1. The regulating sub-model describes the dynamic partitioning of a female mammal's priority between life functions: growth (G), ageing (A), regaining of body reserves (R), and energy supply of the unborn (U), newborn (N), and suckling (S) calf over a lifespan. This dynamic pattern of priorities is assumed to be general for all individual cows. The sum of these relative priorities is always equal to one. The operating sub-model uses the relative priorities to partition energy intake between foetal growth, body weight and body composition, milk yield, and milk composition over the lifespan and during repeated reproductive cycles. Genetic scaling parameters are incorporated in the operating sub-model to scale individual performance potentials of, for example, mature body size or milk production. It should be noted that these genetic scaling parameters are not simply related to the widely reported breeding values commonly used in the animal genetics literature. They act as

multipliers on the different dynamic priorities and thus provide the means to create different levels of genetic potential performance for different cows. In this context, the variation in genetic scaling parameters describes the variation in genetic potential between animals. In the model, an animal is described in terms of its genotype for growth, capacity to store and mobilize reserves, and milk production using the following genetic scaling parameters: non-labile body mass at maturity (W_M), rate of regaining body reserves per day (b_0), labile body mass mobilization index (ν_X), peak milk yield potential (ν_y), milk fat secretion (ν_F), milk protein secretion (ν_P), and milk lactose secretion (ν_L). The unit of W_M is kilogram, whereas the remaining parameters are fractions, and therefore, have no unit. Thus, to describe each genotype a specific set of these genetic scaling parameters is needed. External triggers of successful insemination (i.e. conception) drive the changes between non-reproductive and reproductive states of the animal cueing in the dynamic priority trajectories described in the regulating sub-model. As shown in Figure 4.1, the combination between dynamic priority and genetic scaling parameters makes it possible to quantify the total amount of energy required to fulfil all functions (Σ_E). The resulting dry matter intake (DMI) is quantified by multiplying Σ_E with the predetermined dietary energy density (e_D). The coefficients of energy partition to different life functions (E_G/Σ_E, E_R/Σ_E, E_{MY}/Σ_E, where E_G, E_R, E_{MY} are energy required for growth, reserves storage, and milk production, respectively) are the result of the interactions between dynamic partitioning priorities and genetic scaling parameters.

Animal data

Data used in this study were obtained from an experiment conducted at Aarhus University, Denmark from January 1996 to October 2001. The experiment has been described in detail in Nielsen et al. (2003). Briefly, three dairy cow breeds, i.e. Danish Red, Danish Holstein and Jersey, were used. In total, there were 102 cows, including 180 lactations suitable for the present study. Cows were kept in a neutral ambient temperature and were fed the same total mixed ration *ad libitum* throughout lactation with an energy density that was assumed to allow the cows to fully express their genetic potentials (i.e. non-constraining). The ingredients and chemical composition of the diet were described in Nielsen et al. (2003). The average dry matter content of the diet (DM) was 52% and the metabolizable energy density of the diet (e_D) was 11.1 MJ/kg of DM. Cows were milked twice daily, whereas milk yield and milk composition were recorded at each milking. All animals were weighed on day 2, 3, and 8 after calving and subsequently, once a week until 3 months after calving. From 3 months after calving towards the dry period they were

weighed every two weeks and once a week during the dry period. The health status of cows was also recorded (day of treatment, pre- and post-period of treatment, and healthy periods). The cows were housed throughout the year in single tie stalls.

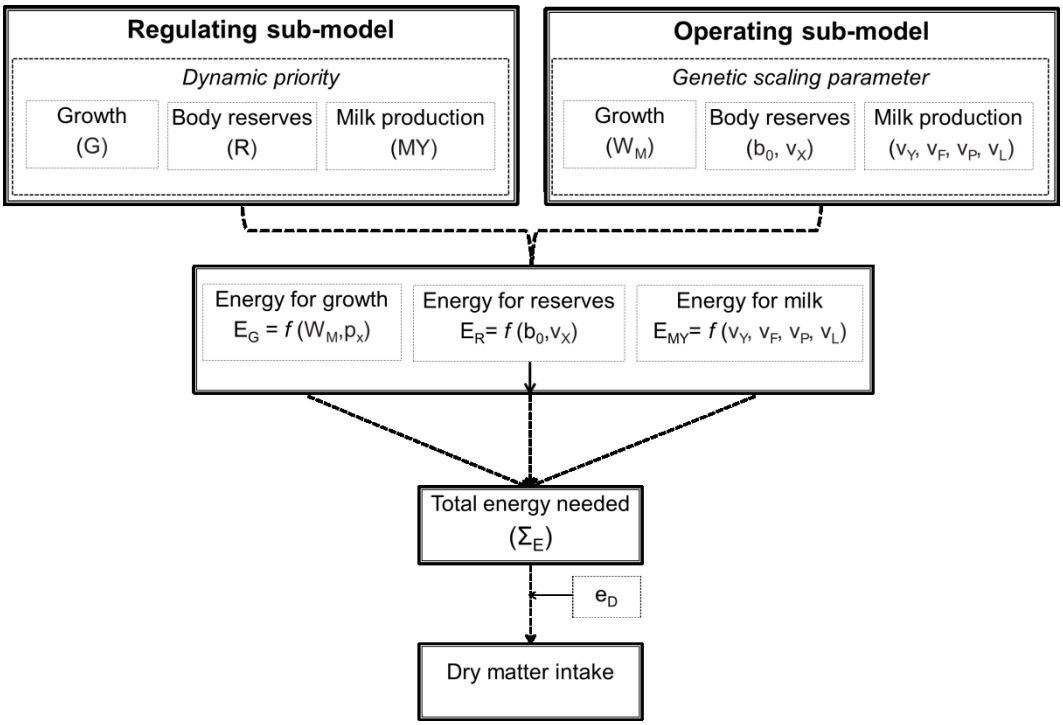

Figure 4.1. Schematic diagram of the GARUNS model [adapted with permission of Martin and Sauvant (2010)], showing how energy requirements for different life functions (growth, body reserves, and milk) are derived from genetic scaling parameters combined with lifetime profiles of relative priorities for the different life functions. The priorities for foetal growth, ageing (in regulating sub-model), and energy needed for foetal growth (in operating sub-model) are not presented as they are assumed to be common trajectories for every individual. Total energy needed is the sum of the different requirements, from which DM intake can be calculated assuming an appropriate diet energy density (e_D).

Model fitting

GARUNS uses the description of an animal in terms of its genetic scaling parameter and its relative priorities to allow calculation of the amount of energy required to meet its performance potentials. Given predetermined characteristics of diet, i.e. energy density and dry matter content, this average requirement can be converted to an estimate of DMI. The starting point of this approach is potential performance, and it can be termed as "potential output drives intake" (Emmans and Kyriazakis, 2001), which is opposite to the approach described by, for instance, Baldwin et al. (1987a; 1987b) where the starting point is a given feed intake. It is, therefore,

reasonable to fit the model with observed BW and MY, and consider DMI as the consequence. Moreover, since GARUNS assumes a general trajectory of dynamic partitioning according to the relative priority to different life functions, we hypothesized no systematic difference between predicted and observed animal performances.

The inputs of GARUNS are classified as: reproductive timing [age at first conception (PCI_0), and parturition to conception interval (PCI_c), where c is reproductive cycle number], and dietary characteristics (e_D and DM). PCI_c, e_D and DM were obtained directly from the database. No records on body weight (BW), PCI_0, and pregnancy length were available until first calving in the current database. It was, therefore, necessary to assume that all cows have the same age at first conception and a standard pregnancy length, and thus age at first calving. In other words, we adopted the shape of BW curve during the growing period of GARUNS, which has been previously calibrated using the GARUNS's database (Martin and Sauvant, 2010a). This is justified because the model is designed to accommodate differences in growth performance between individual cows only in terms of scaling and not in terms of the shape of the performance profile. In this context, the scaling difference in BW of different animals is modulated by W_M. In terms of milk production, it was hypothesized by Martin and Sauvant (2010a) that peak milk yield of a cow increases linearly by parity for all cows. However, it seemed reasonable to examine this assumption in the present dataset. To address this issue a new parameter (ν_{ypi}) was introduced to modulate the priority for milk production independently in each parity, where i is parity. ν_{ypi} is relative deviation of priority for milk production in parity i from the lifetime ν_y. It was assumed that no deviation happens in first parity, i.e. ν_{yp1} is equal to 1. In this context, the priority for milk production in parity i (ν_{yi}) is equal to ν_{ypi} multiplied by ν_y. DMI is the function of total energy requirement (Σ_E) and a predetermined e_D.

Model fitting to individual data

To derive individual genetic scaling parameters, the model was used to adjust these parameter values for each cow so as to achieve best fit with the observed performance data through sequential lactations of that cow. This calibration process was done individually, cow by cow, and once the best fit was obtained the genetic scaling parameters were recorded for that cow. It should be noted that the data used for estimating these genetic scaling parameters were different from the one used to develop and parameterize GARUNS. The model calibration was implemented and optimized with the Modelmaker software version 3.0 (Cherwell Scientific Ltd, 2000), using the Runge-Kutta 4 numerical integration procedure and a fixed integration step of 1

day. The numerical values of the genetic scaling parameters were estimated for each individual cow data series (from first to last parity) using a least square procedure performed with the simplex algorithm of Modelmaker to derive best fit parameters, with default parameter values and 100 convergence steps.

Model evaluation

The ability of the GARUNS model to fit observed data was evaluated using the root mean square error (RMSE), computed as follows:

$$\mathrm{RMSE} = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(O_i - P_i)^2}$$

where O_i and P_i are the ith observed and predicted values of BW, milk yield (MY), DMI, milk fat concentration (MCF), milk protein concentration (MCP), and milk lactose concentration (MCL), and N is the number of observations. RMSE was calculated for each day in milk (DIM) across the N cows within each parity. The relative prediction error (RPE) was then computed as 100×RMSE/(mean of the observed data). Values of RPE less than 10%, between 10 – 20%, and more than 20% indicate good, moderate, and poor prediction, respectively (Fuentes-Pila et al., 1996).

In order to examine the GARUNS assumption that the trajectory of dynamic partitioning of relative priority between life functions is general for all individuals, irrespective of breeds, mixed effect models were used. We hypothesized, if the assumption is adequate, that the slope of the regression between the residuals of prediction, (i.e., $O_i - P_i$), versus day from calving should not be significantly different from zero, nor should there be any breed effect on the slope. The general form of the mixed model was:

$$\mathbf{Y}_{ijk} = \mu + \alpha_i\mathbf{DFC}_i + \beta_j\mathbf{Breed}_j + \lambda_{ij}\mathbf{DFC}\times\mathbf{Breed}_{ij} + \delta_i\mathbf{DFC}^2_i + \gamma_k + \varepsilon_{ijk} \quad [1]$$

where Y_{ijk} are the GARUNS model fitting residuals of BW, MY, milk fat (MCF), milk protein (MCP), milk lactose (MCL), and DMI, μ is the overall intercept across animals, α_i, β_j, and λ_{ij}, and δ_i are regression coefficients of Y on the corresponding predictors of day from calving (DFC), breed, interaction between DFC and breed, and squared DFC, respectively, γ_k is the random effect of kth animal, ε_{ijk} is the residual error which was assumed to be normally distributed with mean of 0 and variance of σ^2_e, i is the number of days from calving, j is the number of breeds, and k is number of animals. Given the high numbers of observations in these regressions, and therefore, the high test power (Lin et al., 2013) at the level of the regression coefficients, significant effects of

breed were evaluated between models with and without breed included. Thus, F-values were computed as $[(RSS_2-RSS_1)/(p_1-p_2)]/[RSS_1/(n-p_1)]$ to compare model [1] and the general model having the following form:

$$\mathbf{Y}_{ijk} = \mu + \alpha_i\mathbf{DFC}_i + \delta_i\mathbf{DFC}^2_i + \gamma_k + \varepsilon_{ijk} \quad [2]$$

The differences between model [2] and model [1] were the removal of Breed and Breed×DFC interaction effects. RSS_1 is residual sum of square of model [1], RSS_2 is residual sum of square of model [2], $p_1 = 7$ is the number of parameters in model [1], $p_2 = 3$ is the number of parameters in model [2], n is the number of animals (n = 81 or 65 or 27 for first or second or third parity, respectively). Consequently, (p_1-p_2) was the numerator degree of freedom and $(n-p_1)$ was the denominator degree of freedom. F-values were computed individually for MY, BW, DMI, MCF, MCP, and MCL. Subsequently, F-values were compared to critical F-values from the F-table using corresponding nominator and denominator degree of freedom, and a significance level of 0.05. If the two models are not significantly different, it can be concluded that data for three breeds can be fitted using simple models with general intercepts and slopes (i.e. model [2]). In other words, any deviations between breeds must be small and the observed significant differences could simply be the consequence of having a large number of observations. In order to reduce the correlations between intercept and slope, data of DFC was centred on its mean.

The correlations between genetic scaling parameters and the similarities between breeds were explored using principal components (PC) analysis. Mixed effect models, and principal components analysis were performed using nlme and FactoMineR packages of the statistical software R version 2.5.2 (R Development Core Team, 2014).

Results

General quality of model fitting

An example of model simulations of BW, MY, and milk composition plotted with observed values for the first two parities is presented in Figure 4.2. Table 4.1 and Table 4.2 present the means of observed values for BW, MY, DMI, MCF, MCP, and MCL together with RPE values. The results are shown for three periods within parity and breed (week 1-15, week 16-35, and week 36-45). There were very few observations after 45 weeks of lactation, thus they were excluded from the calculations of RMSE and RPE. In general, the accuracy of predictions for BW, MY, and DMI improved slightly in parity two and three compared to parity one, which was not the case for milk composition. The accuracies for predicting performance of Danish Red, Danish

Holstein, and Jersey were similar. GARUNS accurately predicted individual BW, MCF, MCP, and MCL over three parities, which was demonstrated by the low values of relative prediction error (RPE < 13%). MY and DMI were slightly over-predicted in early- and mid-lactation (RPE < 20%), and under-predicted in the end of lactation (RPE > 20%). The late lactation period, however, contributed on average only 7% to the total lactation yield of MY and 13% to the total DMI. We also explored the change of prediction accuracy within parity by examining the relationship between daily values of RMSE across all animals versus day in milk. It turns out that the prediction accuracy tended to be lower during first four weeks and last 8 weeks. The relative magnitudes of deviations were, moreover, smaller for BW, MCF, MCP, and MCL compared to MY and DMI.

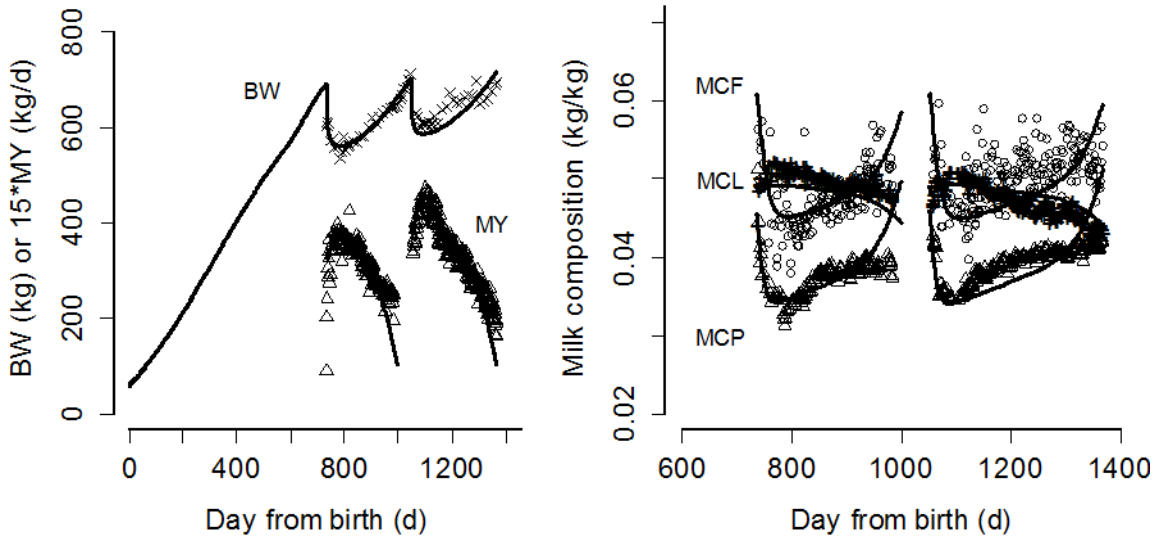

Figure 4.2. Model simulations (solid line) of body weight (BW, kg), milk yield (MY, kg/d), milk fat concentration (MCF, kg/kg), milk protein concentration (MCP, kg/kg), and milk lactose concentration (MCL, kg/kg) in first two lactations of a selected cow plotted with actual observations (symbol). For clarity of presentation, MY is shown as MYx15.

Table 4.1. GARUNS model accuracy for predicting body weight, milk yield and dry matter intake during three parities of three breeds: Danish Red, Danish Holstein and Jersey.

		Danish Red		Danish Holstein		Jersey	
	WoL	Ō	RPE	Ō	RPE	Ō	RPE
				Parity 1			
	1 - 15	543	3.6	567	3.0	369	4.6
BW	16 - 35	586	2.9	602	3.0	395	3.1
	36 - 45	640	3.3	580	2.3	446	3.6
	1 - 15	20.8	18.2	25.1	17.8	18.4	16.9
MY	16 - 35	18.9	18.0	22.9	19.3	15.9	16.7
	36 - 45	16.7	56.8	19.9	53.2	14.4	55.6
	1 - 15	16.0	19.1	18.7	20.7	13.7	26.9
DMI	16 - 35	17.9	18.3	19.7	25.2	15.8	20.7
	36 - 45	17.2	29.3	19.6	20.8	15.3	34.4
				Parity 2			
	1 - 15	608	3.9	584	2.8	408	3.6
BW	16 - 35	640	3.5	609	2.7	425	2.5
	36 - 45	672	4.1	675	3.8	470	3.7
	1 - 15	27.5	14.1	31.3	15.4	21.7	15.1
MY	16 - 35	22.1	13.4	26.1	16.9	17.6	16.8
	36 - 45	14.5	40.9	19.9	53.5	13.9	52.2
	1 - 15	18.7	21.9	20.9	18.1	16.5	22.6
DMI	16 - 35	20.1	16.4	22.1	20.0	17.6	21.3
	36 - 45	17.7	22.3	19.6	33.1	16.3	36.1
				Parity 3			
	1 - 15	715	2.9	622	3.2	447	3.8
BW	16 - 35	658	2.1	649	4.9	454	3.4
	36 - 45	576	2.3	695	4.9	477	5.6
	1 - 15	27.9	12.2	33.2	16.1	22.0	14.6
MY	16 - 35	21.7	15.7	27.3	17.2	17.7	16.9
	36 - 45	13.5	36.9	21.3	46.3	14.9	54.7
	1 - 15	18.9	18.3	22.2	19.5	16.8	23.3
DMI	16 - 35	19.6	19.5	21.7	19.3	17.5	19.5
	36 - 45	17.7	20.4	20.8	28.0	15.5	32.4

BW = body weight (kg), MY = milk yield (kg/d), DMI = dry matter intake (kg/d), Ō = mean observed value, RPE = relative prediction error (%); WoL = week of lactation.

Table 4.2. GARUNS model accuracy for predicting milk fat concentration, milk protein concentration and milk lactose concentration during three parities of three breeds: Danish Red, Danish Holstein and Jersey.

		Danish Red		Danish Holstein		Jersey	
	WoL	Ō	RPE	Ō	RPE	Ō	RPE
				Parity 1			
	1 - 15	0.044	12.5	0.049	8.4	0.056	11.6
MCF	16 - 35	0.045	8.2	0.046	9.6	0.063	9.2
	36 - 45	0.049	9.3	0.044	7.5	0.067	7.4
	1 - 15	0.037	10.0	0.037	8.2	0.038	8.1
MCP	16 - 35	0.038	5.5	0.036	7.3	0.043	5.9
	36 - 45	0.040	15.3	0.036	6.6	0.046	13.3
	1 - 15	0.048	4.2	0.049	4.9	0.049	3.1
MCL	16 - 35	0.048	2.8	0.047	3.2	0.047	2.9
	36 - 45	0.048	7.8	0.049	3.2	0.047	6.1
				Parity 2			
	1 - 15	0.046	13.5	0.044	13.1	0.057	11.6
MCF	16 - 35	0.047	8.7	0.044	7.8	0.064	10.1
	36 - 45	0.051	10.1	0.050	10.0	0.070	7.6
	1 - 15	0.035	10.2	0.034	9.4	0.039	8.9
MCP	16 - 35	0.037	5.3	0.036	5.7	0.043	7.3
	36 - 45	0.040	10.8	0.039	14.4	0.047	11.5
	1 - 15	0.049	4.2	0.047	4.1	0.048	3.6
MCL	16 - 35	0.047	3.6	0.047	3.3	0.046	3.3
	36 - 45	0.044	3.5	0.045	5.0	0.046	5.7
				Parity 3			
	1 - 15	0.050	9.4	0.046	12.1	0.058	11.8
MCF	16 - 35	0.047	10.3	0.043	8.6	0.065	9.4
	36 - 45	0.051	9.1	0.048	11.7	0.067	10.8
	1 - 15	0.036	5.5	0.034	9.0	0.039	8.5
MCP	16 - 35	0.036	5.5	0.035	5.0	0.043	8.5
	36 - 45	0.036	6.5	0.037	13.6	0.043	16.1
	1 - 15	0.046	4.4	0.047	5.6	0.047	4.1
MCL	16 - 35	0.044	3.6	0.046	3.8	0.047	3.4
	36 - 45	0.046	1.8	0.045	4.2	0.046	5.2

MCF = milk fat concentration (kg/kg), MCP = milk protein concentration (kg/kg), MCL = milk lactose concentration (kg/kg), Ō = mean observed value, RPE = relative prediction error (%); WoL = week of lactation.

Evaluation of residuals for time-patterns

Plots of GARUNS fitting residuals (Observed – Predicted) relative to DFC are shown in Figure 4.3. The aim of the regression analysis was to evaluate if the GARUNS assumption still holds for different breeds. Thus, it was hypothesized that the slopes of regression lines between individual residual versus day from calving should not be significantly different from zero. Given the data were centred the significances of the intercepts are no longer important as they are not primary indicators of a systematic time-trend of residuals. The results of multiple regression analysis of residuals of fitting for BW, MY, DMI, and milk composition are shown in the Appendix (Table A1 and Table A2). The significant linear and curvilinear (DFC and DFC^2) effects indicate a systematic difference between the shape assumed by GARUNS and that of current data. The curvilinear effect can be seen from Figure 4.2 or the values of RPE in the last stage of lactation cycle (Table 4.1 and Table 4.2). There were linear slope differences between breeds which could suggest that the key assumption of GARUNS model does not hold for different breeds. We, however, suspected these significant differences might simply be the consequence of having a large number of observations in the test (e.g. N = 20136 for MY). Indeed, the comparison between the full model with inclusion of breed effect (model [1]) and the simple model without inclusion of breed effect (model [2]) showed no significant improvement in the capability of model fit by including breed. The F-values for fitting residuals of MY, BW, DMI, MCF, MCP, and MCL in parity one varied from 0.10 to 1.07, which are considerably smaller than the value of F-critical of 2.53 at the level of significance of 0.05. Additionally, the residual standard deviations of model [1] and model [2] were very similar, i.e. MY (2.44 vs 2.50), BW (17.22 vs 17.28), DMI (3.10 vs 3.11), MCF (0.045 vs 0.046), MCP (0.002 vs 0.002), and MCL (0.001 vs 0.001). These results generally imply that there was evidence of shape differences but the differences were very small and not important in the context of using the teleonomic model (GARUNS) for simulation studies.

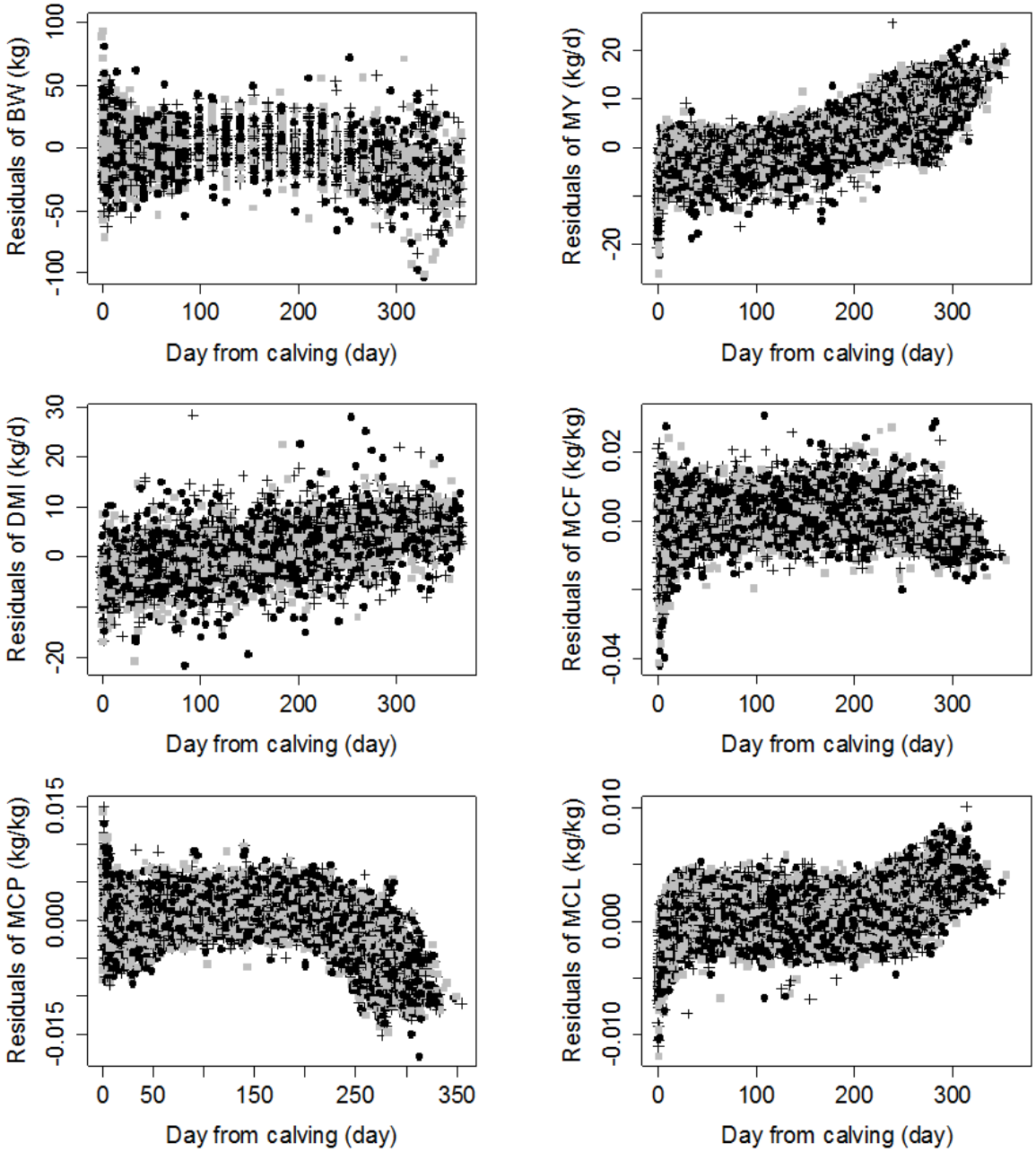

Figure 4.3. Distributions of individual residuals from GARUNS model fitting (Observed – Model fitted) for milk yield (MY), body weight (BW), dry matter intake (DMI), milk fat concentration (MCF), milk protein concentration (MCP) and milk lactose concentration (MCP) along day from calving in first parity of three cow breeds: (+) Danish Red, (■) Danish Holstein and (●) Jersey.

Table 4.3. Descriptive statistics for the genetic parameters[1] of lifetime performance derived by fitting the GARUNS model to individual cow data as described in the Method section.

	Danish Red				Danish Holstein				Jersey			
Parameter	No	Mean ± SD	Min	Max	No	Mean ± SD	Min	Max	No	Mean ± SD	Min	Max
W_M (kg)	34	531 ± 63	436	675	34	521 ± 59	405	634	34	329 ± 38	265	425
b_0 (per day)	34	1.5 ± 0.4	0.8	2.2	34	1.4 ± 0.4	0.6	2.1	34	1.4 ± 0.4	0.7	1.9
ν_x[2]	34	1.1 ± 0.3	0.7	2.8	34	1.2 ± 0.6	0.6	3.6	34	1.3 ± 0.3	0.8	2.5
ν_y or ν_{y1}	34	1.0 ± 0.2	0.6	1.6	34	1.2 ± 0.2	0.9	1.6	34	1.2 ± 0.2	0.9	1.7
ν_{y2}	27	1.0 ± 0.2	0.5	1.4	20	1.3 ± 0.3	0.9	1.8	15	1.3 ± 0.4	0.7	1.9
ν_{y3}	20	0.9 ± 0.3	0.2	1.7	NA	NA	NA	NA	NA	NA	NA	NA
ν_F	34	1.2 ± 0.1	1.0	1.5	34	1.2 ± 0.1	1.0	1.6	34	1.6 ± 0.2	1.2	1.9
ν_P	34	1.1 ± 0.1	0.9	1.2	34	1.0 ± 0.1	0.9	1.3	34	1.2 ± 0.1	1.0	1.4
ν_L	34	1.0 ± 0.03	0.9	1.1	34	1.0 ± 0.04	0.9	1.2	34	1.0 ± 0.04	0.8	1.0

[1]W_M = non-labile body mass at mature, b_0 = rate of regaining body reserves per day, ν_X = labile body mass mobilization index, ν_y = peak milk yield potential, ν_{y1} = priority for milk production in first parity, ν_{y2} = priority for milk production in second parity, ν_{y3} = priority for milk production in third parity, ν_F = milk fat secretion, ν_P = milk protein secretion, and ν_L = milk lactose secretion.

[2]The unit of the parameters is mentioned in the parentheses, otherwise unitless.

NA = result not available due to few number of observations.

Relationship between model parameters

The summary statistics for the genetic scaling parameters are shown in Table 4.3. There were large variations in genetic parameters modulating body weight of the animals, i.e. W_M, b_0 and ν_x, which represented 23, 25 and 39% of their means, respectively. The relative variations of parameters modulating milk yield and milk composition were less than 20%. There were no significant differences between three breeds in the means of b_0 and ν_L ($P > 0.05$, statistics not reported). The mean values of the remaining genetic parameters (W_M, ν_x, ν_y, ν_F, and ν_P) were similar between Danish Red and Danish Holstein ($P > 0.05$), but significantly different from those of Jersey.

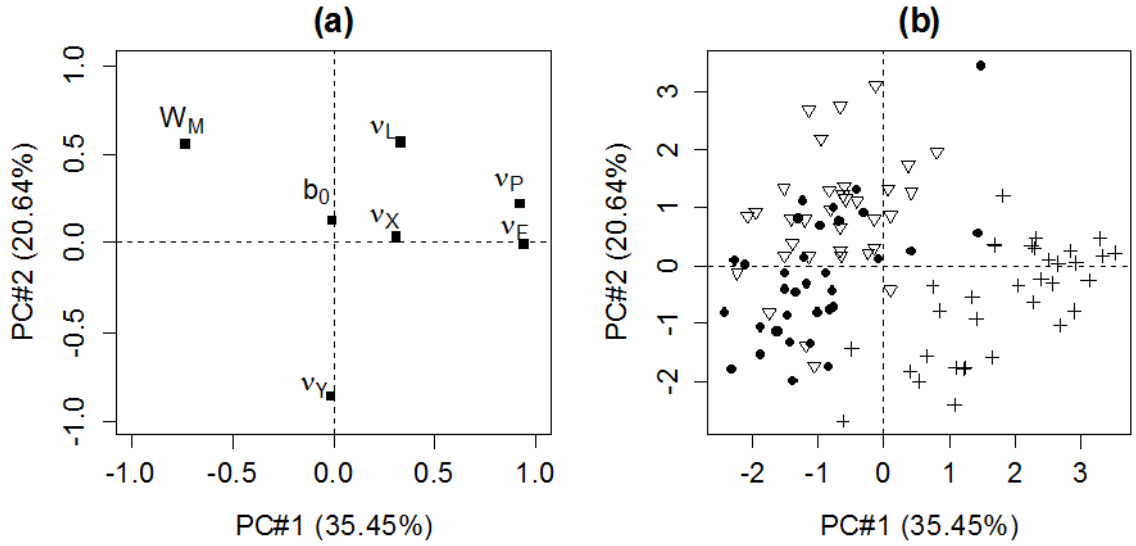

Figure 4.4. PCA loadings for principal component 1 and principal component 2 by variable (a), and scores for individual cows (b). In plot b, symbols are breeds: (▽) Danish Red, (●) Danish Holstein and (+) Jersey. The variables included are genetic parameters for mature weight (W_M), b_0 = rate of regaining body reserves per day, ν_X = labile body mass mobilization index, ν_y = peak milk yield potential, ν_F = milk fat secretion, ν_P = milk protein secretion, and ν_L = milk lactose secretion.

The correlations between genetic parameters were initially explored within each breed (data not shown). Generally, there were few significant correlations except for the followings: W_M was negatively correlated with ν_y ($r \approx -0.50$); ν_y was negatively correlated with ν_F, ν_p, and ν_L ($r = -0.20$ to -0.61); positive correlations were observed between ν_F and ν_p ($r = 0.53$ to 0.83), and between ν_p and ν_L ($r = 0.35$ to 0.57). The relationships between genetic scaling parameters were further explored with PC analysis, and are shown in Figure 4.4 and Figure 4.5. The first two principal components accounted for 56.1% of the total variation, whereas the inclusion of third and fourth

principal components increased variation accounted up to 87.1%. The variables that are close together are strongly correlated (e.g. ν_P and ν_F).

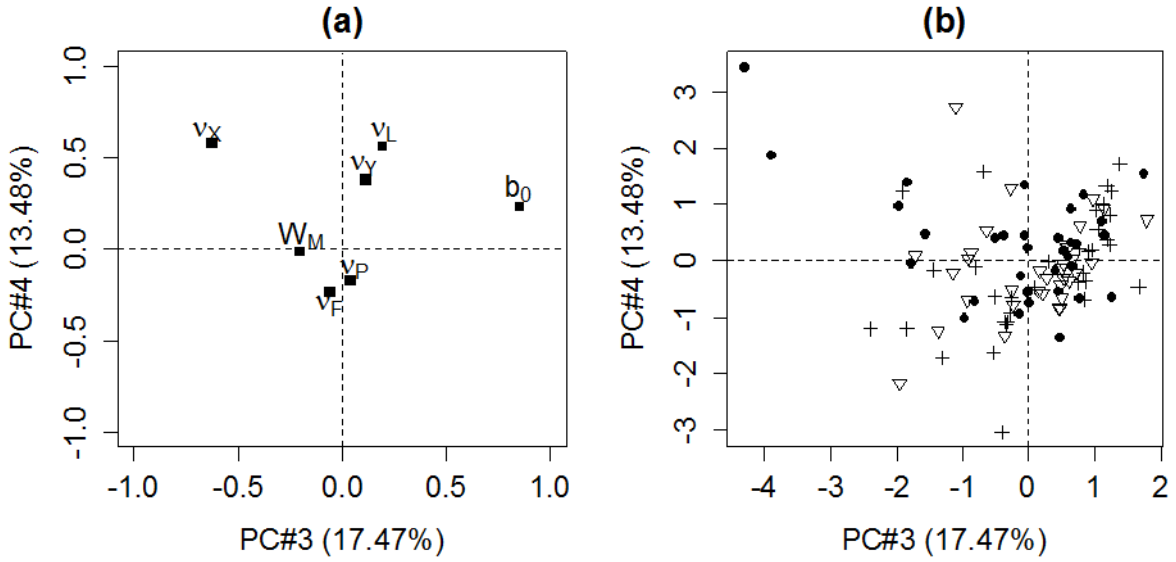

Figure 4.5. PCA loadings for principal component 3 and principal component 4 by variable (a), and scores for individual cows (b). In plot b, symbols are breeds: (▽) Danish Red, (●) Danish Holstein and (+) Jersey. The variables included are genetic parameters for mature weight (W_M), b_0 = rate of regaining body reserves per day, ν_X = labile body mass mobilization index, ν_y = peak milk yield potential, ν_F = milk fat secretion, ν_P = milk protein secretion, and ν_L = milk lactose secretion.

The loadings coefficients for each variable and each principal component are presented in Table 4.4. Loadings coefficients (**w**) describe the weight or the position of variables in each principal component. PC#1 distinguishes dairy cows with a high body weight (w = -0.74) and low concentrations of milk protein and milk fat from those with a low body weight and high concentrations of milk protein (w = 0.94) and milk fat (w = 0.92). This is mainly identifying the difference between Jersey cows and the other breeds (Danish Holstein and Danish Red; Figure 4.4a). PC#2, independently from PC#1, indicates that high values of body weight (w = 0.56) and milk lactose concentration (w = 0.57) were associated with a low value of milk yield (w = -0.86). Danish Holstein and Danish Red show some separation on PC#2 (Figure 4.4b). PC#3 separates animals with high ability of storage (w = 0.86) from animals with high ability of mobilization of body reserves (w = -0.63). PC#3 and PC#4 probably indicate differences within breed. It is difficult to distinguish between breeds from Figure 4.5b but it instead discriminates cows of high capability of mobilization from cows of high capability of storage. This may be identifying cows that have been selected for different purposes, i.e. milk production or milk-meat.

Table 4.4. Loadings and percent explained variance for principal components 1 to 7 in a Principal Component Analysis of genetic parameters for lifetime performance derived by fitting the GARUNS model to individual cow data.

Loadings	PC#1	PC#2	PC#3	PC#4	PC#5	PC#6	PC#7
W_M	-0.74	0.56	-0.20	-0.01	-0.03	0.31	0.04
b_0	-0.01	0.13	0.86	0.24	0.43	0.06	0.02
ν_x	0.31	0.03	-0.63	0.58	0.42	0.002	-0.01
ν_y	-0.02	-0.86	0.12	0.39	-0.24	0.21	-0.002
ν_F	0.94	-0.01	-0.06	-0.23	0.02	0.1	0.23
ν_P	0.92	0.22	0.04	-0.17	-0.02	0.2	-0.20
ν_L	0.33	0.57	0.19	0.56	-0.45	-0.07	0.03
% expl. variance	35.5	56.1	73.6	87.1	95.9	98.6	100

W_M = non-labile body mass at mature, b_0 = rate of regaining body reserves per day, ν_X = labile body mass mobilization index, ν_y = peak milk yield potential, ν_F = milk fat secretion, ν_P = milk protein secretion, and ν_L = milk lactose secretion.

Figure 4.6 presents the priority for milk production in parity 2 relative to that in parity 1. The slope of the regression line is significantly lower than 1 ($P < 0.05$) indicating a negative effect on milk production in parity 2 if it had been highly prioritized in the previous parity. There were insufficient data from parity 3+ to examine this relationship in higher parities.

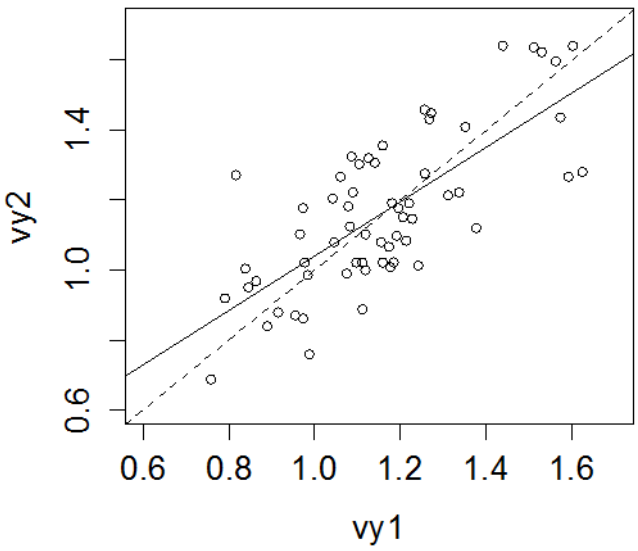

Figure 4.6. Scatter plot of the priority for milk production in parity 2 versus 1. ν_{y1} and ν_{y2} are priorities for milk production in parities 1 and 2, respectively. Dashed line: y = x, and solid line is linear regression of ν_{y1} on ν_{y2}.

Discussion

The GARUNS model was generally able to fit individual curves of body weight, and milk fat, milk protein, and milk lactose concentrations with a high degree of accuracy. Daily milk yield and dry matter intake of individual cows were satisfactorily predicted in early- and mid-lactation but significant under-predictions were found in late-lactation. Breeds and parities did not influence the prediction accuracy. Further, the inclusion of a breed effect did not significantly improve the regression models to describe time trends in the residuals of GARUNS fitting (compared to the general regression models without inclusion of breed effect). Thus, the GARUNS model can be used to simulate performance of individual cows using the assumption that the shape of relative priorities is general, and the individual variability can be simply captured using genetic scaling parameters. The general under-prediction of MY and DMI in late lactation would be explained by the difference in feeding system between the current data (i.e. Nielsen et al., 2003) and the one that Martin and Sauvant (2010) used for calibration (i.e. Schutz et al., 1990). Cows in the study of Nielsen et al. (2003) were fed with a constant energy density diet throughout lactation to allow cows to express their genetic potentials, whereas in Schutz et al. (1990) cows were fed with a step-down reduction of energy density diet from early to late lactation. This type of step feeding system is the most common one in current dairy practice (Erasmus et al., 2013; Stewart et al., 2014). The reduced dietary energy in late lactation probably results in a moderate lack of energy to allow cows to express their genetic potentials. Since the maintenance has a higher priority than other needs (Jokela and Mutikainen, 1995; Heino and Kaitala, 1999), and that in late lactation body reserves are recovered with high priority to prepare for next reproductive cycle, a shortage of energy would result in an impaired milk yield (Friggens, 2003). The high accuracy of predicting BW supports this argument. Given that GARUNS is a systemic model with separate parameters controlling the dynamic of partitioning priorities and the scaling of these according to different genetic potentials it has the flexibility to be easily recalibrated to reflect the late lactation differences highlighted with the present dataset. These results confirm the acceptability of using this teleonomic model for simulating lifetime performance of individual cows. They also suggest the dataset used is a good one for estimating genetic scaling parameters representing genetic potentials that are unaffected by any correlations between lactation stage and environment.

It has commonly been recognized that animals in the same population differ in their ability to perform, which comes as a result of variation in the nature of the animals or in the

environment (Bryant et al., 2005). The data used in this study was obtained from a long-term genetic evaluation experiment where three breeds of cow selected for different purposes were kept in the same environment; thus making it appropriate for exploring the genetic variability between individuals. In this context, given the GARUNS model fits well the observed data it can be used to separate genetic variability in performance between individual cows from environmental noise. Moreover, it can, by individually calibrating the model, derive genetic scaling parameters representing genetic potentials of each cow. Characterizing individual variation in this way is valuable as it is a prerequisite for simulation studies. In the context where (nutritional) environment is constraint, energy intake might be insufficient for animals to attain their genetic potentials thus some functions might will be given higher priority than others the rules for these adjustments are given in the companion publication of this model (Martin and Sauvant, 2010b).

To set up realistic population simulations it is important to acquire knowledge of variation and possible correlations between the model parameters (Emmans and Fisher, 1986). The summary statistics of genetic scaling parameters (Table 4.3) show no differences between Danish Red and Danish Holstein in the means of each parameter. Conversely, the means of genetic scaling parameters of Jersey were, with the exceptions of b_0 and ν_L, significantly different from that of the other two breeds. There was a significantly smaller variation in ν_L than in any of the other parameters implying a low potential for genetic change in milk lactose concentration. This result is consistent with that of other studies (Welper and Freeman, 1992; Bedö et al., 1995).

In the GARUNS model, with the exception of W_M, each genetic scaling parameter modulates a particular trait independently. Thus, the correlations between these parameters would largely be induced by the biological relationships between the traits and not by the model structure as such. Not unexpectedly, some of the genetic scaling parameters were correlated (Figure 4.4 and Figure 4.5). The results of the principal component analysis also show that the model genetic scaling parameters were affected by genotypes. The first two components accounted for up to 56.1% of the total variation of the data and mainly distinguish the genetic differences between breeds (Figure 4.4). Generally, Danish Red and Danish Holstein breeds were represented by high body weight and high milk production but low milk fat and milk protein concentrations. Jersey cows were characterized by a small weight and high milk fat and milk protein concentrations. These results were consistent with the summary statistics on the means of genetic scaling parameters between the three breeds reported in Table 4.3. Further PCs brought additional

information on genetic variation within breeds. Within breed, there were negative correlations between the genetic scaling parameters for MY and milk composition (Figure 4.5). These results agree with other studies that reported genetic correlations ranging from -0.12 to -0.34 for MY versus MCF, -0.18 to -0.36 for MY versus MCP, and -0.08 for MY versus MCL (Welper and Freeman, 1992; Pantelic´ et al., 2008; Vallas et al., 2010). The strongly positive correlation between MCF and MCP agrees with the literature ranging from 0.51 to 0.56 (de Jager and Kennedy, 1987; Welper and Freeman, 1992). The relationship between MCL and MCF and MCP varied from 0.16 to 0.53, whereas this has been reported between 0.11 and 0.29 (Welper and Freeman, 1992; Huhtanen, 2006). However, it should be noted that the relationships between the model parameters and correlations between traits reported from the literature might not be the same because they are not the direct measures of these traits but rather are representatives of those traits. The negative correlation between W_M and ν_y ($r \approx -0.50$) does not agree with literature correlation between BW and MY. Genetic correlations between BW and MY are often weak or even negative (r = -0.01 to 0.025), indicating that selection for milk yield negligibly affects BW of an animal (Morris, 1976; Brotherstone, 1994; Mason et al., 2009). However, Berry et al. (2003) reported that when BW was adjusted for body condition score the correlation became positive and ranged from 0.15 to 0.39. The negative correlation found in this study can be explained by the fact that W_M was incorporated in the equation of milk production simulation aiming to scale MY to mature body size, i.e. genetic size-scaling rule (Taylor, 2010). Interestingly, the genetic scaling parameters controlling body reserve [mobilization (ν_X) and accretion (b_0)] were not significantly correlated within breed. PC#3 differentiated cows of high ability to mobilize body reserves from those of high ability to storage (Figure 4.5) which might imply differences between cows in the temporal pattern of nutrient partitioning that underpins lactation.

Another aspect of differences in the temporal pattern was found with respect to parity. Rather than assuming a fixed ratio between parities in the genetic scaling parameter for milk production, we allowed differences between animals in the ratio. As can be seen in Figure 4.6, the priority for milk production in parity 2 tended to be impaired if it had been highly prioritized in the previous parity. However, this needs to be confirmed by longer multi-lactation study.

Conclusions

The results of this study show the value of a dynamic model of lifetime performance as a tool to derive estimates of genetic potentials of milk yield, milk composition, body reserve usage, and growth for different genotypes of cow. The model was found, across a range of dairy breeds, to

be sufficiently precise to be suitable for use in simulation studies of long-term efficiency. The correlations between model genetic parameters agreed with the related literature values, and also quantified some key components of variation in lactation performance. Thus, this model is a suitable basis for simulating the effects of genetic selection strategy on lifetime efficiency of individual cows, and thus address key questions about the impact of future selection (Friggens et al., 2010; Dillon et al., 2006; Berry and Crowley, 2013).

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Appendix

Table A1. Estimate and standard error of the regression coefficients for the mixed effect model between prediction residuals of BW, MY, and DMI of Danish Red, Danish Holstein and Jersey cows versus DFC and squared-DFC.

		Parity 1			Parity 2			Parity 3		
Variable	Breed	Intercept	DFC	DFC^2	Intercept	DFC	DFC^2	Intercept	DFC	DFC^2
BW (kg)	DR	0.568 (1.658)	-0.032^{a} (0.005)	-3.7E-04* (3.3E05)	2.500 (2.682)	-0.006^{ab} (0.007)	1.4E-04* (4E-05)	6.297 (6.734)	-0.010^{a} (0.010)	2.1E-04* (7E-05)
	DH	0.639 (1.629)	-0.064^{bc} (0.007)	-3.7E-04* (3.3E05)	-2.001 (2.742)	-0.007^{a} (0.010)	1.4E-04* (4E-05)	13.385 (6.732)	0.013^{a} (0.015)	2.1E-04* (7E-05)
	JR	-1.589 (1.657)	-0.051^{c} (0.007)	-3.7E-04* (3.3E05)	-0.126 (2.685)	-0.051^{b} (0.009)	1.4E-04* (4E-05)	7.395 (6.736)	-0.064^{b} (0.015)	2.1E-04* (7E-05)
MY (kg/d)	DR	1.320^{ab} (0.250)	0.053^{a} (3.6E-04)	1.24E-04* (2.5E-06)	0.672^{a} (0.198)	0.035^{a} (4.9E-04)	7E-05* (3E-06)	1.243 (0.473)	0.029^{a} (8.1E-04)	7E-05* (5E-06)
	DH	1.808^{a} (0.250)	0.061^{b} (4.9E-04)	1.24E-04* (2.5E-06)	2.263^{b} (0.203)	0.052^{b} (7E-04)	7E-05* (3E-06)	2.055 (0.473)	0.052^{b} (0.001)	7E-05* (5E-06)
	JR	0.954^{b} (0.250)	0.043^{c} (5E-04)	1.24E-04* (2.5E-06)	1.289^{c} (0.199)	0.038^{c} (6E-04)	7E-05* (3E-06)	1.469 (0.473)	0.039^{b} (0.001)	7E-05* (5E-06)
DMI (kg/d)	DR	1.622^{ab} (0.212)	0.022^{a} (5.8E-04)	-4.8E-06* (3.8E-06)	1.43^{a} (0.304)	0.022^{a} (7E-04)	-5E-05* (5E-06)	1.475 (0.511)	0.023^{a} (0.001)	-3.7E-05* (9E-06)
	DH	2.073^{a} (0.209)	0.028^{b} (8E-04)	-4.8E-06* (3.8E-06)	2.681^{b} (0.311)	0.029^{b} (0.001)	-5E-05* (5E-06)	2.111 (0.512)	0.029^{b} (0.002)	-3.7E-05* (9E-06)
	JR	1.176^{b} (0.213)	0.029^{b} (8E-04)	-4.8E-06* (3.8E-06)	2.196^{ab} (0.306)	0.026^{c} (0.001)	-5E-05* (5E-06)	1.373 (0.511)	0.024^{a} (0.002)	-3.7E-05* (9E-06)

Values with different superscripts within column are significantly ($P < 0.05$) different. DR = Danish Red, DH = Danish Holstein, JR = Jersey, BW = body weight, MY = milk yield, DMI = dry matter intake, DFC = day from calving.

* $P < 0.05$

Table A2. Estimate and standard error of the regression coefficients for the mixed effect model between prediction residuals of MCF, MCP, and MCL of Danish Red, Danish Holstein and Jersey cows versus DFC and squared-DFC.

		Parity 1			Parity 2			Parity 3		
Variable	Breed	Intercept	DFC	DFC^2	Intercept	DFC	DFC^2	Intercept	DFC	DFC^2
MCF (kg/kg)	DR	0.002[a] (2.3E-04)	-1.7E-05[a] (7.8E-07)	-2.5E-07[*] (5.5E-09)	0.002[a] (3.1E-04)	-2.7E-05[a] (9.7E-07)	-2.1E-07[*] (7.0E-09)	0.002 (5.3E-04)	-3.5E-05[a] (1.6E-06)	-2.3E-07[*] (1.1E-08)
	DH	0.002[a] (2.3E-04)	2.2E-05[b] (1.1E-06)	-2.5E-07[*] (5.5E-09)	0.002[a] (3.2E-04)	-2.7E-05[a] (1.4E-06)	-2.1E-07[*] (7.0E-09)	0.001 (5.3E-04)	-4.3E-05[b] (2.2E-06)	-2.3E-07[*] (1.1E-08)
	JR	0.003[b] (2.3E-04)	5.0E-05[c] (1.1E-06)	-2.5E-07[*] (5.5E-09)	0.003[b] (3E-04)	7E-06[b] (1.3E-06)	-2.1E-07[*] (7.0E-09)	0.002 (5.3E-04)	5.0E-06[c] (2.2E-06)	-2.3E-07[*] (1.1E-08)
MCP (kg/kg)	DR	0.001 (1.9E-04)	-3.1E-05[a] (4.3E-07)	-2E-07[*] (3.1E-09)	0.0013 (2.1E-04)	-2.3E-05[a] (5.6E-07)	-1.6E-07[*] (3.9E-09)	0.001 (4.3E-04)	-2.4E-05[a] (7.3E-07)	-2.2E-07[*] (4.7E-09)
	DH	0.001 (1.9E-04)	-2.8E-05[b] (6.1E-07)	-2E-07[*] (3.1E-09)	0.0012 (2.2E-04)	2.3E-05[a] (8.1E-07)	-1.6E-07[*] (3.9E-09)	0.001 (4.3E-04)	-3.2E-05[b] (9.8E-07)	-2.2E-07[*] (4.7E-09)
	JR	0.001 (1.9E-04)	2.0E-05[c] (5.9E-07)	-2E-07[*] (3.1E-09)	0.0017 (2.1E-04)	-2.1E-05[b] (7.7E-07)	-1.6E-07[*] (3.9E-09)	0.002 (4.3E-04)	-2.8E-05[c] (1.0E-06)	-2.2E-07[*] (4.7E-09)
MCL (kg/kg)	DR	4.9E-04[*] (2.04E-04)	1.3E-05[a] (2.3E-07)	6.1E-08[*] (1.6E-09)	-6.1E-04 (2.3E-04)	-1.4E-06[a] (2.7E-07)	4.6E-08[*] (1.9E-09)	-0.001[a] (3.1E-04)	-5.0E-06[a] (5.2E-07)	3.3E-08[*] (3.3E-09)
	DH	5.5E-04 (2.05E-04)	1.2E-05[b] (3.16E-07)	6.1E-08[*] (1.6E-09)	-1.6E-04 (2.4E-04)	8.4E-06[bc] (3.9E-07)	4.6E-08[*] (1.9E-09)	-8.3E-04[ab] (3.1E-04)	1.5E-06[b] (6.9E-07)	3.3E-08[*] (3.3E-09)
	JR	3.6E-04 (2.04E-04)	1.0E-05[c] (3.1E-07)	6.1E-08[*] (1.6E-09)	-8.1E-05 (2.3E-04)	8.1E-06[c] (3.7E-07)	4.6E-08[*] (1.9E-09)	-3.3E-05[b] (3.1E-04)	2.2E-05[c] (7.1E-07)	3.3E-08[*] (3.3E-09)

Values with different superscripts within column are significantly ($P < 0.05$) different.

DR = Danish Red, DH = Danish Holstein, JR = Jersey, MCL = milk fat concentration, MCP = milk protein concentration, MCL = milk lactose concentration, DFC = day from calving, DFC^2 = squared DFC.

[*] $P < 0.05$

Chapter 5

Extending a lifetime nutrient partitioning model to include performance consequences on probability of reproducing and thereby allow prediction of lifetime efficiency of dairy cows

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Animal (In preparation)

Abstract

Reproductive success is a key component of lifetime efficiency, i.e. ratio of energy in milk (MJ) to energy intake (MJ) over the lifespan, of cows. At the animal level breeding and feeding managements might substantially impact on milk yield, body condition, and energy balance of cows which are known as major contributors to reproductive failure in dairy cattle. This study extended an existing lifetime performance model to incorporate the performance consequences as a result of changing breeding and feeding strategies on probability of reproducing and thereby allow prediction of cow lifetime efficiency**.** The model is dynamic and stochastic with an individual cow being the unit of modelling and one day being the unit of time. To evaluate the model, a French data including Holstein and Normande cows fed with high concentrate diet and a Scottish data including Holstein cows selected for high (selected line) and average (control line) genetic merit for fat plus protein, fed with high versus low concentrate diets were used. Generally, the model consistently simulated productive and reproductive performance, lifespan, and lifetime efficiency of various genotypes of cow across feeding systems. On the French data, the model adequately simulated reproductive performance of Holstein cows but slight under-predictions were found for Normande cows. On the Scottish data, concenption to first service was comparably simulated while interval traits were under predicted which is mainly due to the discrepancy in management issue. Genetic selection for greater milk production impaired reproductive performance but not lifetime efficiency. Effect of high versus low concentrate feedings on reproductive performance was well accommodated. Further works should include economic indicators to allow more accurately simulate lifetime profitability in different scenarios.

Keywords: dairy cow, lifetime efficiency, reproduction, nutrient partitioning

Introduction

It is now widely accepted that the single-trait selection for greater milk production in dairy cattle has been associated with significant declines in animal health (Berry et al.., 2011) and reproductive performance (Albarrán-Portillo and Pollott, 2013). These problems not only impair lifetime production efficiency of dairy cows via reduced longevity by increasing involuntary culling (Seegers et al.., 1998), they also increase veterinary and reproductive costs (Hogeveen et al.., 2011), environmental losses (Garnsworthy, 2004), and affect the animal welfare (Oltenacu and Algers, 2005). An increased milk yield, a negative energy balance, and a low body condition have commonly been considered as the major biological contributors to the loss in longevity of dairy cows [see reviews of Lucy (2001) and Friggens et al.. (2010)]. However, the individual effects of milk yield, energy balance, and body condition on reproduction have been difficult to quantify because they are often correlated. Experiments specifically designed to break these correlations are unfortunately rare (Wright et al.., 1992), and a modeling approach to integrate all available data seems necessary (Blanc et al.., 2001). Management strategies such as breeding (e.g. selecting for high versus low genetic merit cows) and feeding (e.g. high versus low energetic diets) programs can alter milk yield and body reserves, and consequently reproductive performance (Cutullic et al.., 2009, 2011). In this context, if we wish to predict lifetime efficiency there is a need of being able to predict responses of dairy cows in terms of both productive and reproductive performance under different management strategies. Such a predictive capability is especially important in the case of dairy production environments where a wide variation might be present between genotypes of the animal and between the environments in which they are managed.

Individual-based herd models that describe each single animal can be used to simulate animal responses to management practices (Brun-Lafleur et al.., 2013). Unfortunately, in most of these models, the reproductive process is represented by assuming a fixed efficiency such as fixed calving to ovulation or fixed parturition to conception intervals (Allore et al.., 1998; Blanc and Agabriel, 2008; Martin and Sauvant, 2010). Though recent works of Inchaisri et al.. (2010) and Brun-Lafleur et al.. (2013) have recognized the possible influences of milk yield and body reserves on reproductive performance, the simulations of these traits are only based on genetic potential and physiological stages, without a possibility of including an interaction with feeding regimes. Additionally, these models are only developed for a single lactation and thus cannot be used to predict the lifetime performance and lifetime efficiency of the animals.

The objective of our study is therefore to extend a previously published lifetime nutrient partitioning model of Martin and Sauvant (2010) for predicting lifetime efficiency of individual dairy cows under various selected management strategies by incorporating the possible influences of animal performance on reproductive performance. We hypothesize that a high milk yield, a low energy balance, and a low body condition negatively affect reproductive performance, and thereby productive lifespan which is expected to have consequences on lifetime efficiency of dairy cows.

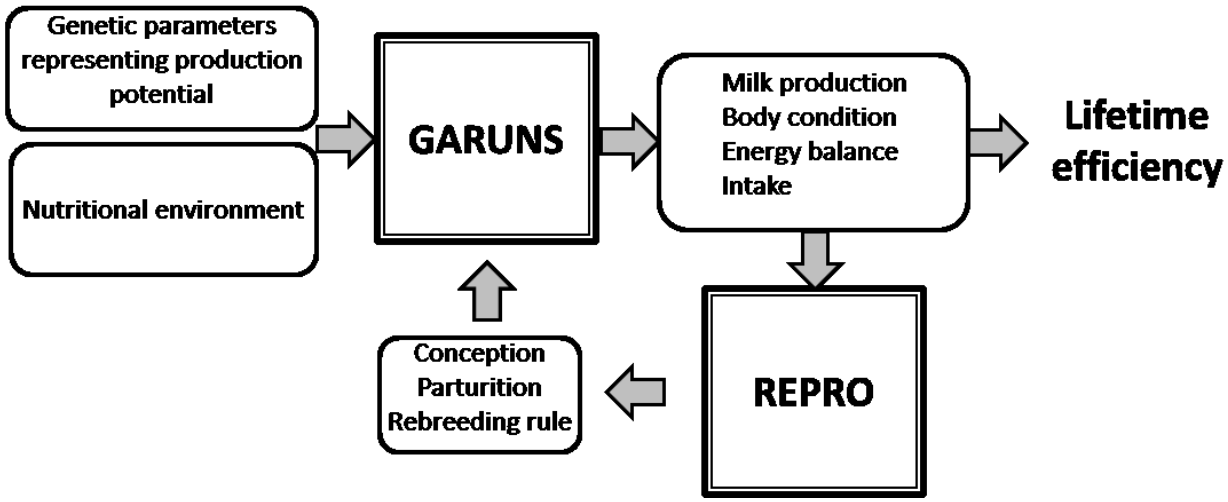

Figure 5.1. Schematic presentation of the model for predicting lifetime efficiency of individual cows.

Materials and Methods

The model used in this study is dynamic and stochastic with the individual cow being the unit of modelling and one day being the unit of time. The lifetime of a cow is considered from birth till culling. The schematic presentation of this model is presented in Figure 5.1. The core of this extended model relies on the lifetime nutrient partitioning model of Martin and Sauvant (2010), referred to here as GARUNS, which simulates lifetime performance of individual cows. The inputs of GARUNS include genetic scaling parameters (to be specified in next section), feeding information (i.e. dietary energy density), reproductive (i.e. conception and parturition), and management (i.e. culling) events. The outputs of GARUNS are daily feed intake, milk yield and composition, fetal growth, calf birth weight, body weight and composition, body condition score, and energy balance throughout the lifespan of a cow. The reproduction sub-model developed in the present study uses information of milk yield, body condition score, and energy balance from GARUNS as its inputs to simulate reproductive responses of conception and parturition, and culling decision which are in turn transferred to GARUNS. In the present study, the lifespan of individual cows is mainly affected by reproductive performance and culling

policy. The effect of diseases, for example, mastitis, ketosis or fatty liver on survivability of cows is not currently incorporated.

Description of lifetime nutrient partitioning model (GARUNS)

The GARUNS model consists of a regulating sub-model providing a driving force to control the function of an operating sub-model. An adapted scheme of GARUNS is presented in Figure 5.2. The regulating sub-model describes the dynamic partitioning of a female mammal's priority between life functions: growth (G), ageing (A), regaining of body reserves (R), and energy supply of the unborn (U), newborn (N), and suckling (S) calf over a lifespan. This dynamic pattern of priorities is assumed to be general for all individual cows. The sum of these relative priorities is always equal to one. The operating sub-model uses the relative priorities to partition energy intake between foetal growth, body weight and body composition, milk yield, and milk composition over the lifespan and during repeated reproductive cycles. Genetic scaling parameters are incorporated in the operating sub-model to scale individual performance potentials of, for example, mature body size or milk production. It should be noted that these genetic scaling parameters are not simply related to the widely reported breeding values commonly used in the animal genetics literature. They act as multipliers on the different dynamic priorities and thus provide the means to create different levels of genetic potential performance for different cows.

In this context, the variation in genetic scaling parameters describes the variation in genetic potential between animals. In the model, an animal is described in terms of its genotype for growth, capacity to store and mobilize reserves, and milk production using the following genetic scaling parameters: non-labile body mass at maturity (W_M), rate of regaining body reserves per day (b_0), labile body mass mobilization index (ν_X), peak milk yield potential (ν_y), milk fat secretion (ν_F), milk protein secretion (ν_P), and milk lactose secretion (ν_L). The unit of W_M is kilogram, whereas the remaining parameters are fractions, and therefore, have no unit. Thus, to describe each genotype a specific set of these genetic scaling parameters is needed. External triggers of successful insemination (i.e. conception) drive the changes between non-reproductive and reproductive states of the animal cueing in the dynamic priority trajectories described in the regulating sub-model.

As shown in Figure 5.2, the combination between dynamic priority and genetic scaling parameters makes it possible to quantify the total amount of energy required to fulfill all functions (Σ_E). The resulting dry matter intake (DMI) is quantified by multiplying Σ_E with the

predetermined dietary energy density (e_D). The coefficients of energy partition to different life functions (E_G/Σ_E, E_R/Σ_E, E_{MY}/Σ_E, where E_G, E_R, E_{MY} are energy required for growth, reserves storage, and milk production, respectively) are the result of the interactions between dynamic partitioning priorities and genetic scaling parameters.

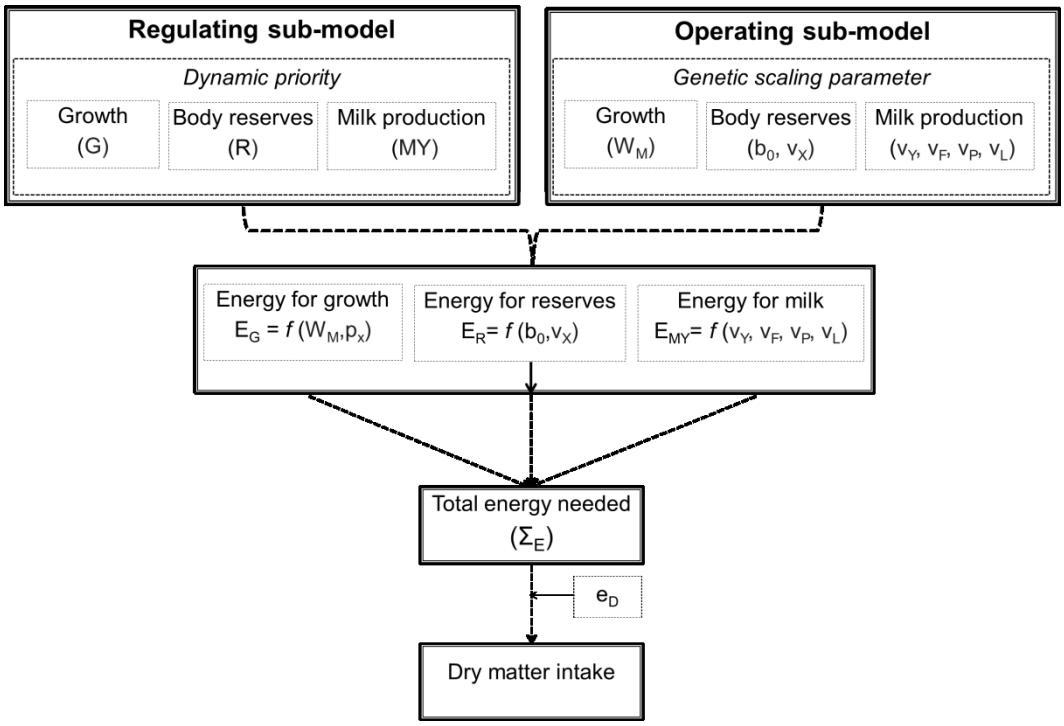

Figure 5.2. Schematic diagram of the GARUNS model [adapted with permission of Martin and Sauvant (2010)], showing how energy requirements for different life functions (growth, body reserves, and milk) are derived from genetic scaling parameters combined with lifetime profiles of relative priorities for the different life functions. The priorities for foetal growth, ageing (in regulating sub-model), and energy needed for foetal growth (in operating sub-model) are not presented as they are assumed to be common trajectories for every individual. Total energy needed is the sum of the different requirements, from which DM intake can be calculated assuming an appropriate diet energy density (e_D).

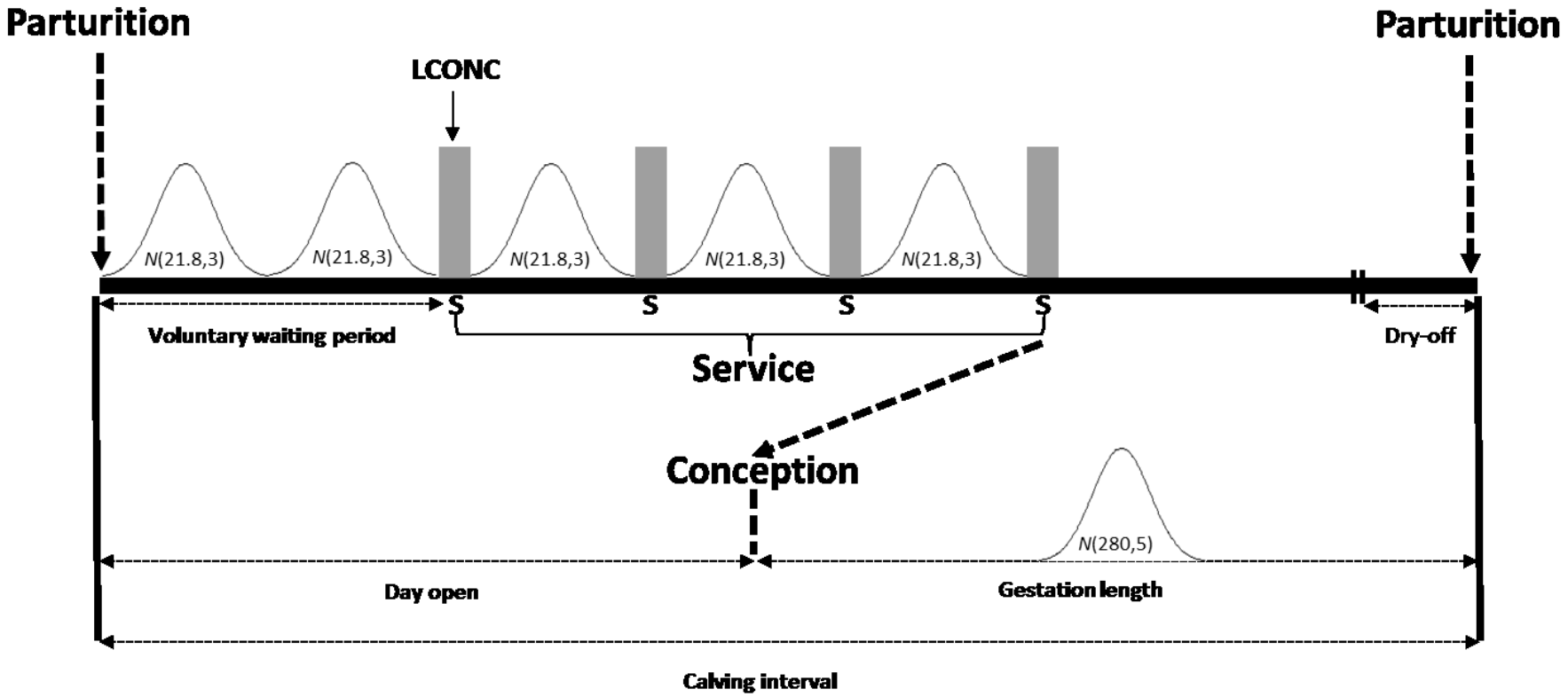

Figure 5.3. Representation of the reproduction sub-model. This is simply a visualization of the model and thus the time scale is not necessarily correct.

Description of the reproduction sub-model

Because the main interest of this study is on lifetime efficiency of individual cows, for which a key component is the lifespan of the animals, the reproductive information needed is only that which creates variation in the lifespan. This can simply be seen as a result of whether or not, and when, the cow successfully gets pregnant, and calves. Instead of modelling all the individual steps of the reproductive process such as uterine evolution, resumption of estrus cycle, estrus expression, conception, and embryonic survival, we assume a likelihood of conception of a viable calf (LCONC) as the final product of the reproductive process, which is the accumulative result of other steps involved towards having a newborn calf. In accordance with literature LCONC is assumed to be affected by milk yield, energy balance, and body condition of the cow (Lucy, 2001; Friggens et al., 2010). The influences of parity (primiparous versus multiparous), estrus number, and disease on LCONC are not explicitly incorporated. The key reproductive events in our reproduction sub-model consist of conception and parturition. Figure 5.3 shows that after parturition, cows are assumed to have a period of postpartum anestrus of around 21.8 ± 3 days (Darwash et al., 1997). Thereafter the cow is assumed to have an estrus of 3 days duration which takes place every 21.8 ± 3 days from the previous estrus period (Darwash et al., 1997). The breeding period is commenced after a voluntary waiting period, here set to 50 days (Löf et al., 2012). Prior to the end of the voluntary waiting period and out of the 3-day estrus windows, LCONC is zero. During the breeding period, artificial insemination is assumed to take place at every estrus with a LCONC greater than a threshold value (0.4) to reflect the idea that weak estruses will be poorly expressed and then not detected by the inseminators. Insemination is simulated using a random draw from a uniform distribution, U (0, 1). A cow is assumed pregnant if the insemination value is smaller than the LCONC value. LCONC is calculated using LCONC components determined by milk yield, energy balance, and body condition of the cows, i.e. $LCONC_{MY}$, $LCONC_{EB}$, and $LCONC_{BCS}$, respectively (Equation 1). We assume a maximal value of LCONC of 0.6 ± 0.06 which is supported by a reported variation between 57 – 63% of the conception rate of Holstein virgin heifers (Kuhn et al., 2006). This assumption is made in light of our initial hypothesis that fertility is mainly affected by a high milk production, a negative energy balance, and a low body condition, which do not exist in virgin heifers. Consequently, LCONC is computed as follow:

$$LCONC = 0.60 \times (LCONC_{MY} \times LCONC_{EB} \times LCONC_{BCS}) \quad [1]$$

The gestation length is assumed to follow a normal distribution, N (280, 5) days, as reported by Hansen et al. (2004). Factors that influence gestation length such as breed, age, or birth weight of the calf were not taken into account.

Effect of milk production on likelihood of conception

The underlying mechanism for the negative effect of milk yield (MY) on fertility of dairy cows was investigated by Wiltbank et al. (2006). As high milk yield is supported by high dry matter intake and consequently high blood flow in the liver, it increases the speed of clearance of both estradiol and progesterone. The low concentration of plasma estradiol reduces the stimulation of the centers that control estrus behavior, and thus the behavioral expression of estrus, whereas a reduced circulating concentration of progesterone is associated with a low pregnancy rate (McNeill et al., 2006). In this study, it is assumed that as soon as the cows are producing milk it has a negative effect on LCONC, which increases in a sigmoid manner with increasing milk yield. The likelihood of conception resulted from the effect of milk yield ($LCONC_{MY}$) is quantified in equation 2.

$$LCONC_{MY} = 2 \times (1 / 1 + \exp (Rat_{MY} \times MY)) \quad [2]$$

where MY is daily milk yield (kg/d), and Rat_{MY} is a constant parameter implying the extent of the effect of milk yield on the likelihood of conception. The value of Rat_{MY} (0.012) was estimated from the study of Cutullic et al. (2011) in which the experiment was designed to separate the effect of MY on reproductive performance from the effects of energy balance and body condition.

Effect of energy balance on likelihood of conception

The effect of negative energy balance (NEB) is commonly attributed to the suppression of the pulsatility of luteinizing hormone (LH) and reduces the ovarian responsiveness to LH stimulation (Butler, 2000). During the period of negative energy balance, plasma glucose, insulin and insulin-like growth factor-I (IGF-I) are reduced. Insulin is known to stimulate bovine follicular cell (Spicer et al., 1993) whereas IGF-I is critical to ovarian follicular development (Butler et al., 2006). Consequently, NEB shifts the course of postpartum ovarian activity and strongly influences the resumption of ovarian cycles (Senatore et al., 2010). Other authors have also reported an inferior oocyte quality in negative energy balance cows (Snijders et al., 2000; Walters et al., 2002; Leroy et al., 2008). The effect of NEB on the likelihood of conception ($LCONC_{EB}$) is formalized in equation 3.

$$LCONC_{EB} = 2 \times (1 / 1 + \exp (-Rat_{EB} \times EB)) \quad [3]$$

where EB is daily energy balance (MJ/d) and Rat_{EB} is a constant parameter. The value of Rat_{EB} (0.027) was derived from the study of Wright (1992). This experiment on beef cattle was designed to break the correlation between body fatness and body mobilization by applying two feeding levels during lactation to cows that had previously been made thin or fat. Thus, it is possible to separate the effect of body condition and negative energy balance on reproductive performance, if we assume that there was no effect of MY. Energy balance is computed as follow:

$$EB = E_{Intake} - (E_{Growth} + E_{Maintenance} + E_{MY} + E_{Pregnancy}) \quad [4]$$

where EB is energy balance (MJ/d), E_{Intake} is energy intake (MJ/d), E_{Growth}, $E_{Maintenance}$, E_{MY}, and $E_{Pregnancy}$ are energy requirements for growth, maintenance, milk production, and pregnancy (MJ/d). Energy is measured as metabolizable energy.

Effect of body condition on likelihood of conception

In literature, some authors have observed the depressed reproductive performance in thin compared to fat cows (Wright et al., 1992; Pryce et al., 2001; Veerkamp et al., 2001). Low body condition is related to low level of leptin which is also linked to reproductive function (Spicer, 2001). The effect of body condition on the likelihood of conception ($LCONC_{BCS}$) is formalized in equation 5. To measure body fatness of cows, we use body condition score (BCS) on scale of 0 to 5 (0 = emaciated and 5 = extremely fat). It is assumed that a level of BCS ≥ 3 has no effect on $LCONC_{BCS}$.

$$LCONC_{BCS} = 2 \times (1 / 1+\exp(-Rat_{BCS} \times (BCS - 3)) \quad [5]$$

where Rat_{BCS} is a constant parameter. The value Rat_{BCS} (0.425) was obtained from the study of Wright and co-workers (1992).

Culling policy

The reproductive culling rules assumed for the present study are as follows. Cows are culled if they fail to get pregnant after 4 inseminations and the level of milk on that day is < 25 kg/d. If the insemination number is > 4 but cows are still producing ≥ 25 kg/d of milk, a fifth insemination is allowed, if this does not result in pregnancy they are culled. To take into account the fact that some cows might not express estrus for a long time, we include another culling rule in which cows are culled anyway if they are not pregnant after 160 days postpartum. For simplicity, at this stage, the effects of other management factors such as age, or population structure on culling decision were not taken into account.

Model implementation and evaluation

The model was implemented with C++ programing language on the RECORD platform (Bergez et al., 2013). To evaluate the model, two data sets were selected. In the first data set, of Cutullic et al. (2011) and Delaby (personal communication, 2014), two breeds of cow (Holstein Friesian selected for milk yield and dual-purpose Normande cows) fed with high concentrate were used to evaluate the effect of genetic selection on reproductive performance and lifetime efficiency. The second data set comes from the long-term experiment carried out at the Langhill Dairy Cattle Research Center (Pryce et al., 1999; Coffey et al., 2004). In the Langhill data, the high and low feeding systems were applied to two lines of Holstein Friesian cows: control line and the line that had been selected for kilograms of fat plus protein yield. This allows testing the effect of genotype and feeding interaction.

The GARUNS model was first adjusted to simulate populations of cows that match their performance in the selected data sets. This was done using the genetic scaling parameters that represent milk production level (ν_y), mature size, (W_M), rate of regaining body reserves per day (b_0), and labile body mass mobilization index (ν_X). The higher the values of ν_y and W_M, for example, the higher the capability of producing milk and the larger the cows. We assume that all cows share the same capability of secreting milk fat (ν_F), milk protein (ν_P), and milk lactose (ν_L), and thus milk composition. The within population variability in ν_y, W_M, b_0, and ν_X was simulated using the standard deviations and correlations reported by Phuong et al. (2015).

Low feeding was regulated using a parameter of dietary energy density (e_D) to reduce the total energy intake of cows, and thus the performance (i.e. milk yield and body weight) to the level reported in the real data, whereas high feeding implies no limitation of energy intake and thus allows animals to achieve their genetic potential. Simulated results on conception to first service (FSC), days from parturition to first service (DFS), days from parturition to conception or day open (DOP), and calving interval (CI) were then compared with that of data sets. In order to test the repeatability of the model, each scenario was run 20 times, with 200 cows each.

Calculation of lifetime efficiency

The lifetime efficiency of individual cows in each scenario was calculated using the following equation:

$$LTE = \sum_{1}^{N} \frac{E_{Milk}}{E_{Intake}} \times 100 \qquad [6]$$

where LTE is lifetime efficiency (%), E_{Milk} is total energy in milk (MJ), E_{Intake} is total energy intake (MJ), and N is time from birth to culling (day).

Results

An example of the model simulation of two genotypes of cow differing in milk production level and body condition score is given in Figure 5.4, using the genetic scaling parameters of ν_y, W_M, b_0, and ν_x. In this example, the high MY and low BCS curves represent the average Holstein cow fed high concentrate diet in the experiment of Cutullic et al. (2011), whereas the low MY and high BCS curves represent the average Normande cow. Figure 5.4 shows that the GARUNS model adequately simulated lactation and BCS curves of the average Holstein and Normande cows. No comparison in body weight curves could be made due to insufficient reported data, but the simulated live weights one week postpartum of 678 and 700 for Holstein and Normande cows, respectively, were comparable with the reported data. More generally, different populations of cow that differ in their genetic production potential, for instance, high versus low milk producing cow, could be simulated by scaling the above genetic scaling parameters up and down. Performance of control and selected cows of the Langhill data were also simulated in the same way (data not shown).

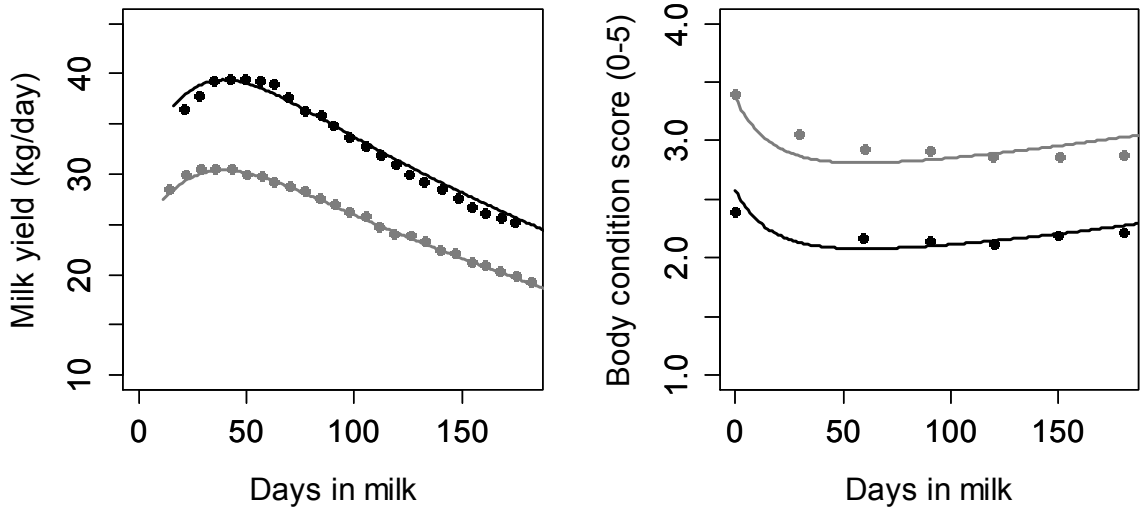

Figure 5.4. Model simulation of milk yield and body condition score of Holstein and Normande cows in the Le Pin data. Circles are observed data and lines are simulated outputs. Blacks represent Holstein whereas greys represent Normande cows.

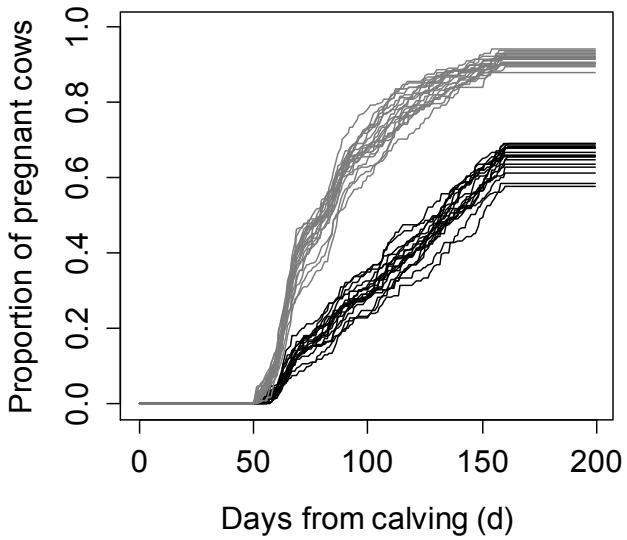

Figure 5.5. Simulated proportion of pregnant cows by days in milk of Holstein (black lines) versus Normande (grey line) cows of Le Pin data. Each line is one repetition of a simulation with 200 cows in the simulated population.

Effect of genotypes on reproductive performance and lifetime efficiency

The simulated reproductive performance, lifespan, and lifetime efficiency of the two genotypes of cow in the example of Figure 5.4 are presented in Table 1. The model satisfactorily predicted conception rate to first service of the Holstein cows (41 versus 38%), but considerably under-predicted that of the Normande cows (48 versus 58%). In both genotypes, days to first service, days open, and calving interval were comparably simulated.

High genetic merit for milk production cows (Holstein) have an inferior reproductive performance than low genetic merit ones (Normande), i.e. lower conception rate, higher days to first service, days open, calving interval, and shorter lifespan. Despite having worsen reproductive efficiency and shorter productive longevity high milk producing cows still have higher lifetime efficiency than the low milk producing cows. The proportion of cows that get pregnant by days in milk is lower for simulated Holstein compared to Normande cows (Figure 5.5). Table 5.1 also shows a high consistency between the simulations with low values of standard deviation.

Table 5.1. Effect of high versus low genetic merit for milk production on reproductive performance and lifetime efficiency of dairy cows

	Model simulation		Le Pin data	
Trait	Holstein	Normande	Holstein	Normande
FSC	41 ± 2	48 ± 1	38	58
DFS	84 ± 2	67 ± 1	80	75
DOP	98 ± 2	85 ± 1	97	92
CI	379 ± 2	367 ± 1	377	376
LSP	1762 ± 55	2875 ± 146	NA	NA
LTE	45	41	NA	NA

FSC = first service conception (%); DFS = days from calving to first service (d); DOP = days from calving to conception or days open (d); CI = calving interval (d); LSP = lifespan (d); LTE = lifetime efficiency (%);NA = not available.

Effect of genotypes and feeding levels on reproductive and lifetime efficiency

Table 5.2 presents the simulated reproductive traits in comparison to their corresponding records in the Langhill data. The simulated conception rates at first service are comparable to that of data. Days to first service are on average 10 days longer in simulated results compared to the data records whereas the simulated days open and calving interval are shorter than that of database. The patterns of reproductive performance, lifespan, and lifetime efficiency for control and selected cows are similar to what observed in Table 5.1. Generally, cows selected for maximal milk production have a lower reproductive performance, and thus a shorter lifespan. However, lifetime efficiency of individual cows is mainly driven by milk production level rather than reproductive performance and lifespan, which might explain why simulated LTE of the selected cows is higher than that of the control animals. No clear effect of levels of concentrate feeding on reproductive performance could be observed in the simulation. These results are confirmed by the plots of the simulated proportion of cows getting pregnant of control and selected populations in high versus low concentrate feedings presented in Figure 5.6.

Table 5.2. Simulated reproductive performance, lifespan, and lifetime efficiency versus data records of Langhill cows

	Model simulation				Langhill data			
Trait	Control	Select	HC	LC	Control	Select	HC	LC
FSC	46 ± 2	42 ± 2	44 ± 2	44 ± 3	45 ± 3	39 ± 2	42 ± 2	41 ± 3
DFS	68 ± 1	78 ± 1	74 ± 5	73 ± 5	72 ± 1	77 ± 1	77 ± 1	72 ± 1
DOP	86 ± 1	94 ± 1	89 ± 4	89 ± 3	106 ± 3	124 ± 3	117 ± 3	113 ± 3
CI	367 ± 1	374 ± 1	370 ± 4	370 ± 4	383 ± 3	395 ± 3	389 ± 3	389 ± 3
LSP	2961 ± 122	2137 ± 65	2523 ± 415	2574 ± 439	NA	NA	NA	NA
LTE	44	47	47	46	NA	NA	NA	NA

FSC = first service conception (%); DFS = days from calving to first service (d); DOP = days from calving to conception or days open (d); CI = calving interval (d); LSP = lifespan (d); LTE = lifetime efficiency (%);HC = high concentrate; LC = low concentrate; NA = not available.

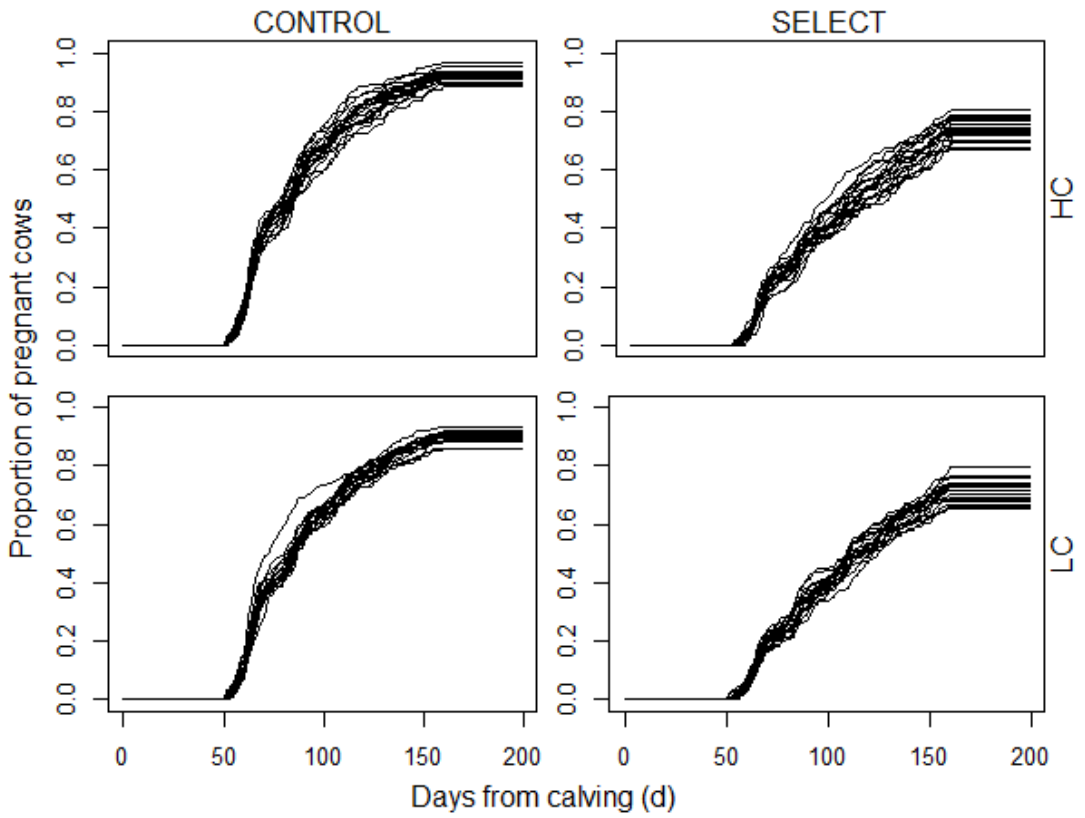

Figure 5.6. Simulated proportion of pregnant cows for the Langhill data: HC = high concentrate and LC = low concentrate. Each line is one repetition of a simulation with 200 cows in the simulated population

Discussion

The main purpose of this study is to incorporate the consequences of performance levels on reproductive success of individual cows into an existing lifetime performance model, and thereby allow prediction of their lifetime efficiency. Because the major focus of this model is on lifetime efficiency, for which a key component is productive lifespan, the key reproductive outcome needed in the model is probability of pregnancy. Thus, instead of modelling all the individual steps of the reproductive process as do many conventional reproduction models, we focused on the final product of the reproductive process by assuming a likelihood of conception of a viable calf, and making this likelihood sensitive to the performance levels, i.e. milk yield, body condition, and energy balance. This allowed the model to evaluate at each time-step within the relevant phases of lactation whether, and when the cow gets pregnant, or not. Based on these reproductive outcomes the model was able to include variation in productive lifespan in the simulation of lifetime performance and lifetime efficiency. This model development was evaluated using two datasets with varying performance levels. To simulate different genotypes of cow genetic scaling parameters are used to create differences in production levels such as milk

yield, growth capacity, mature size, etc. (see Figure 1 and the description of the GARUNS model section).

Comparison of simulation outputs on reproductive performance with selected data and literature

Generally, the whole model showed a good capability of consistently simulating reproductive performance, lifespan, lifetime performance, and lifetime efficiency of various genotypes of cow across nutritional environments. Apart from the under-simulation of conception rate to first service of the Normande cows the simulated outputs for other traits were comparable with the records of Cutullic et al. (2011). The under-prediction of conception rate of the Normande cows was probably due to the facts that the constant parametersin the present reproduction sub-model, i.e. Rat_{MY}, Rat_{EB}, and Rat_{BCS}, were derived from the studies where Holstein cows were used. Indeed, there have been reports of significant innate variation between breeds for reproductive performance though fed with the same diet (Snijders et al., 2001; Dillon et al., 2003; Cutullic et al., 2011).

In comparison to the Langhill data (Pryce et al., 1999), the model adequately predicted conception rate to first service and days to first service but under-predicted days open and calving interval. The under-predictions of DOP and CI might be caused by the difference in management of the voluntary waiting period: in this model we set up a voluntary waiting period of 50 days whereas it is on average 60 days in the Langhill data for both selected and control cows (Smith; personal communication, 2014). In the United Kingdom, Wills (2012) stated that the voluntary waiting period of dairy cows is between 60 – 65 days. In particular, the model was able to reproduce the reproductive performance of cows fed high versus low concentrate, i.e. Pryce et al. (1999) showed no considerable difference in the reproductive performance between cows fed high versus low concentrate. Working on the same data at Langhill, but with a division of records into heifers and cows over two lactations, McGowan et al. (1996), however, reported that low concentrate feeding heifers had a better reproductive performance but an opposite pattern was observed on cows. In the data of Pryce et al. (1999) 34% of records were from heifers. Further, the effect of high versus low concentrate feeding (or dietary energy density) is not consistent in the literature: there are studies reported a better reproduction of low concentrate compared to high concentrate feeding cows such as Horan et al. (2005) and Walsh et al. (2008), there are also studies in opposite side such as Jonsson et al. (1999), Pedernera et al. (2008), and Wall (2008). Cutullic et al. (2011) showed a lower proportion of cows being inseminated over breeding time when fed

with low energy density diet compared to cow fed control diet. This indicates a necessity of considering carefully the difference between heifers and cows in their capability to reproduce, especially in the way they respond to a change in (nutritional) environment.

In the literature, at the similar levels of milk production (≈ 38 kg at peak) and body weight (≈ 600 kg post calving), data from Ireland also show that Holstein Friesian cows fed high concentrate diet had a first service conception rate that varied from 40 to 45%, an overall conception rate of around 77%, a calving to first service interval of 73 to 78 days, a calving to conception interval of 91 to 99 days, and number of services per calf of 2.1 to 2.7 (Snijders et al., 2001; Horan et al., 2005). These values are comparable to the present simulated values. The simulated lifespans of the Holstein cows in either control or selected lines fed high concentrate are comparable with reports from the literature, i.e. the simulated lifespan varies from 2137 to 2961 days whereas it is approximately 2200 days for British Holsteins (Pritchard et al., 2013), and 2128 days for Dutch Holsteins (CRV, 2014). In this model we assume that all cows start breeding at 450 days and because the gestation length is on average 280 days, the productive life (time from first calving to culling) can therefore be expected to be around 1819 days or 4.4 lactations (i.e. lifespan/calving interval). This is higher than the reported mean productive lives of Austrian Holstein cows of 3.3 lactations (Knaus, 2009), British Holstein cows of 1500 days (Pritchard et al., 2013), and that of American Holstein of 3 lactations on average (Hare et al., 2006). Such a longer lifespan might be explained by the fact that in the present study the lifespan of individual cows is mainly driven by reproductive performance and a simple culling policy. The effect of diseases, for example, mastitis, ketosis or fatty liver on survivability of cows is not currently incorporated.

Effect of genotype and feeding system on reproductive performance and lifetime efficiency of individual cows

The simulation outputs have showed that the genetic selection for greater milk production decreases reproductive performance. High yielding cows took longer to be inseminated or to get pregnant and thus have a longer calving interval than the low milk producing individuals. Though the conception rate to first service was not different between the two genotypes, the overall conception rate, or the proportion of cows getting pregnant (Figure 5.6), and the lifespan (Table 5.2) were reduced in the high genetic merit, i.e. selected, compared to the low genetic merit, i.e. control, cows. These results are consistent with literature comparisons of differences in genetic merit for milk production (Snijders et al., 2001; Horan et al., 2005; Veerkamp et al., 2003; Lopez et al., 2004; Yániz et al., 2008). Interestingly, in terms of efficiency, the present version of

the model suggests that such decreases in reproductive performance and lifespan are probably compensated by the high milk production level which explains the slightly higher lifetime efficiency of the selected compared to the control cows (47 versus 41%, Table 5.2). In the present study, we define LTE simply as the ratio of total energy captured in milk over total energy intake and thus the improvement of LTE relies on the principle of diluting the maintenance requirement by improving the level of milk production (VandeHaar and St-Pierre, 2006) or the reduction in the number of unproductive days (Lormore and Galligan, 2001). At the animal level, the milk production level has a more influence on LTE than the effect of productive life. Blank et al. (2012) found a strongly positive correlation between lifetime efficiency (kg of milk/cow/day) and milk yield (R^2 = 0.8) for cows of the same lifespan, but no significant correlation between productive lifespan and lifetime efficiency could be found (R^2 not reported). Our result is also in agreement with the spreadsheet model of Jones (2005) in which he computed the financial impacts of reducing annual milk production to extend the productive life of dairy cows. The annual returns were estimated using some specific assumptions on annual milk production, feed consumption, milk prices, and feed prices. The simulated results showed that the net financial effect of sacrificing milk production for a longer productive life for dairy cows was generally a loss. However, neither the study of Jones (2005) nor the present study take into account the other economic benefits of having a longer productive life such as more female calves available for replacement or decreased costs of veterinary treatments and artificial insemination, and the societal concerns on the animal welfare issues, which are especially important if we consider production efficiency at the farm level. VandeHaar (2014), for example, indicated that the feed consumed by heifers can account for 15 to 30% of the amount of feed of a cow during her lifetime. The published estimates of the economic losses of clinical mastitis, for example, range from €61 to €97 per cow on a farm (Hogeveen et al., 2011). At the farm level, the increased productive life and consequently longevity will lead to fewer replacement heifers being required to achieve the same level of output thus reducing the replacement costs; more offspring are produced, and more intensive selection is possible (Bell et al., 2011). Garnsworthy (2004), using a modelling approach, reported that improved longevity lowered environmental impact, for example, 27% of methane produced on farms is expected to be produced by herd replacements and thus by lowering the number of heifer replacements methane emission would also be mitigated. These points of discussion indicate the need of further analyzing LTE not only at the individual but also at the herd levels if we wish to fully evaluate the consequences of future management strategies.

In terms of the effect of feeding system, the simulated outputs show that there were no clear differences in the reproductive performance, lifespan, and lifetime efficiency between the low and the high concentrate feeding groups. The plots (not shown) of simulated individual effect of milk production, body condition score, and energy balance on likelihood of conception, i.e. $LCONC_{MY}$, $LCONC_{BCS}$, and $LCONC_{EB}$, respectively, of cows in high versus low concentrate feeding groups indicate that the likelihood of conception in the low feeding group is reduced through the low body condition score and negative energy balance but this is compensated by the low milk production, whereas the major negative effect of high feeding on likelihood of conception is relied on the high production of milk. These results are in agreement with the conclusion of Cutullic et al. (2011), they concluded that low fed cows, on the one hand, may suffer from a greater body condition loss and poorer body condition but on the other hand, they may benefits from a lower milk yield level.

Conclusions

The whole model consistently simulated productive and reproductive performance, lifespan, and lifetime efficiency of various genotypes of cow across feeding systems. The differences between simulated and observed data for several traits were mainly due to the discrepancies in assumed reproductive management. The simulated effect of genotypes on reproductive performance was in agreement with the selected database. Genetic selection for greater milk production impaired reproductive performance. Lifetime efficiency, defined simply in terms of energy ratio, was slightly higher for high genetic merit cows compared to the lower genetic merit individuals due to the compensation of milk quantity over the longer productive life. The effect of a poorer nutritional environment on simulated reproductive performance was well modelled with respect to the selected database. Further works need to be done for carefully simulating/investigating the effect of a reduced feeding on reproductive performance of heifers and cows. Economic indicators and other management factors should also be incorporated to fully and more accurately simulate lifetime profitability in different scenarios.

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Chapter 6

General Discussion

6.1. Introduction

An increasing demand for sustainability of livestock farming systems is driving the need to investigate novel selection and management strategies to reduce feed costs and to mitigate the environmental impact of milk production, which can only be met through improved feed efficiency (Berry and Crowley, 2013). The milk production efficiency of a dairy herd is the sum of the individual female's lifetime efficiency which depends upon the length of their productive lives and the quantity of milk produced and feed intake during that period (Britt et al., 2003; Sawa et al., 2013). A striking characteristic of the individual cow efficiency is its variability which is in large part due to the animal differences in production potential and nutrient partitioning as the consequence of selection and management (Bauman et al., 1985; Friggens and Newbold, 2007). In this context, understanding the biological basis for individual variability is central to exploring the ability of the whole system to adapt to a changing environment. Because the on-farm assessment of lifetime efficiency remains difficult as it requires a lot of information to be recorded in a long period (Manafiazar et al., 2012), a modelling approach might offer an alternative for investigating influences on lifetime efficiency of possible selection and management strategies. Compared to other species, this is of special importance to the case of dairy cows where wide variations can exist and where we have to meet the future challenges of profitability and sustainability. This Ph.D. thesis was part of a Marie Curie Initial Training Network, GreenhouseMilk, with the overall ambitions to better understand the role of dairy genetics for nutrient partitioning and energy efficiency in the overall greenhouse gas output of dairy systems, to provide tools to assist farmers select "efficient and environmentally friendly" cows that suit their systems, and to particularly consider the role of genetics in the whole farming system including feeding strategy and management policies such as housing period, fertilization

and manure management. As a contribution to such ambitions of the GreenhouseMilk project, to reiterate, the work of the present thesis was aimed to ultimately develop a model for simulating the consequences of different breeding and feeding strategies on the lifetime efficiency of individual cows. To reach this general objective, three key research questions were identified and were successively explored in Chapter 3, Chapter 4, and Chapter 5:

- Q1. *What does an improvement in energy efficiency relate to nitrogen efficiency?*
- Q2. *How to represent genetic variability in production potentials of individual cows in a lifetime nutrient partitioning model?*
- Q3. *How to represent the effect of performance and nutritional environment on reproduction and productive lifespan?*

In Chapter 3 it was shown that energy and nitrogen efficiency, which are the two common indicators of feed efficiency in the literature, were significantly and positively correlated. Energy efficiency, nitrogen efficiency, and their relationship were affected by the common feed factors of acid detergent fibre (ADF), digestible energy (DE), and proportion of concentrate (PCO). These results indicated that, at the animal level fed the same diet, an improvement of lifetime energy efficiency would also lead to an improvement of lifetime nitrogen efficiency. Consequently, they supported our decision that we can initially build one model that can largely account for both predicting energy efficiency, and considering nitrogen efficiency as an add-on. Thus, in Chapter 4 an existing lifetime nutrient partitioning model was investigated for its capability of simulating variability in genetic production potential of individual cows, using an external dataset. The results showed that the model could satisfactorily simulate genetic variability in production potential across a range of dairy breeds, and thus could be used for studying the effect of selection and management strategies on the long-term efficiency. The starting distributions of the model genetic scaling parameters which are prerequisites for a simulation study were also explored. Chapter 5, with inclusions of findings from Chapter 4, successfully incorporated the possible consequences of varying performance levels such as milk yield, body condition, and energy balance on reproductive efficiency, and thus allowed simulating lifetime efficiency of individual dairy cows under various selected scenarios. The whole model consistently simulated productive and reproductive performance, lifespan, and lifetime efficiency of various genotypes of cow across feeding systems. On a control feeding, the effect of genotypes on reproductive performance is logical with the selected database. Genetic selection for a greater milk production impairs reproductive performance. Genetic selection for a greater milk production impaired

reproductive performance. Lifetime efficiency, defined simply in terms of energy ratio, was slightly, but not significantly, higher for selected cows compared to control cows due to the compensation of milk quantity over the longer productive life. The effect of a poorer nutritional environment on simulated reproductive performance was well accommodated with respect to the selected database.

The intention of this chapter is to provide a general synthesis of the main points from the previous chapters in the context of future dairy industry to meet the challenges of changing environments while keeping profitability and sustainability. In addition to the achievements, the possible shortcomings will also be addressed. In the first part the importance of considering both energy and nitrogen efficiency in the context of modelling lifetime efficiency is discussed. The second part addresses the challenges of being able to incorporating individual genetic variability in production potential into a nutritional model as this is one of the common limitations of many dairy production models. We then discuss about the possible trade-offs between short-term and long-term efficiency under different breeding and feeding strategies, taking into account the interaction between genotype by environment. The chapter is ended with general conclusions from this thesis.

6.2. State-of-the-art of feed efficiency and possibility to integrate nitrogen efficiency into energy efficiency based model

The significances of improving feeding efficiency in dairy industry to meeting the future challenges of profitability and sustainability have been extensively discussed in the previous chapters. It has also been indicated that both energy and nitrogen efficiency are important to a consideration of the feed efficiency, particularly in terms environmental impact, because they are associated with the major greenhouse gas emissions such as methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O) (Weiske et al., 2006; Steinfeld et al., 2006).

In Chapter 3, the meta-analysis approach was selected to investigate explore factors affecting feed efficiency of lactating dairy cows in terms of both energy and nitrogen, the relationship between energy and nitrogen efficiency, and possible animal and nutritional factors that might affect these efficiencies and their correlation. A meta-analysis can be defined as a systematic review that utilizes a statistical method to integrate research findings from multiple independent studies (St-Pierre, 2001). Compared to a single classical experiment in which the observations are usually made under a narrow condition that is specific to such a study in question, and thus

normally has a low statistical power (Jennions, 2003), a meta-analysis aggregates research findings from many studies, and it increases sample size and the statistical power (lower type I error) (Sauvant et al., 2008). Consequently, the results from a meta-analysis are often generic and can be applied to a wide variety of conditions with a greater confidence (Phillips, 2005). In such a type of systematic review, an experimental average or a treatment average is often the experimental unit rather than an animal which is normally the replicate in a randomized or controlled experiment.

The summary of results of 306 treatment means extracted from 68 peer-reviewed studies collected in the literature showed that the efficiencies of digestible energy and nitrogen usage of lactating dairy cows were found to be on average 34.09 and 42.63%. These results indicate that approximately 60% of energy and nitrogen intake are lost, as gases, urine or heat increment which do not only reduce the profitability of dairy farms but also contributes to the increasing global greenhouse gas emissions. The contribution of dairy production systems to the environmental load has now been well recognized and summarized in the reviews of, for example, Bannink et al. (2013) or Hristov et al. (2013). It should be noted that, in the present study, the calculations of energy and nitrogen efficiency were performed at the digestible level, i.e. digestible energy and digestible protein. In the literature, studies on energy efficiency are most often expressed as energy in milk over net energy intake, and studies on nitrogen efficiency are often expressed as nitrogen captured in milk over crude nitrogen intake (Castillo et al., 2001; Reynal and Broderick, 2005; Olson et al., 2011; Cabrera and Kalantari, 2014). The argument for choosing to focus on digestible energy and protein was that digestible efficiency includes the losses in gases, urine, as well as animal differences in partitioning of nutrients. Thus, it allowed us to not only evaluate the environmental impact of milk production, but also to compare metabolic efficiency between animal genotypes in using feed to produce milk (Chapter 3). Gross efficiency includes the part of feed that is not available to animals, and, as such, it is of limited value for quantifying the variability between animals in efficiency. The variation in metabolic efficiency, i.e. when energy intake is computed as net energy, mainly reflects the difference between animals in the way in which animals partition nutrient intake between metabolic functions.

In nutritional terms, the inefficient utilizations of energy and nitrogen to producing milk are usually attributed to the presence of indigestible fibre (West et al., 1997; Lund et al., 2007; Holtshausen et al., 2011; Zebeli et al., 2012), and the imbalance in the carbohydrate:protein ratio

in the rumen (Castillo et al., 2001; Fanchone et al., 2013). A significant body of research has been focused on the methods to improve digestibility of feed or to optimize the balance between nutrients in the ration (see, for example, meta-analyses of Nousiainen et al., 2009; and Huhtanen et al., 2009). In addition, genetic selection for increased milk production and management techniques such as increased milking frequency or photo period have also been found to improved feed efficiency (Connor et al., 2011; Wall et al., 2010; Bannink et al., 2013). It is clearly shown that genetic selection for milk yield has played an important role for the improving feed efficiency during the last decades (Pryce and Veerkamp, 2001; Pryce et al., 2004). The biological basis for the higher energy and nitrogen efficiency in the modern dairy cows relies mainly on the phenomenon of dilution of maintenance costs, that has been discussed previously, in addition to the improvement digestive efficiency (Bauman et al., 1985; Vérité and Delaby, 2000; VandeHaar and St-Pierre, 2006). However, it has been shown that such a genetic selection for a single milk yield trait is associated with reductions in health and reproductive performance of the animals, so that it needs to be carefully considered.

Chapter 3 showed that there was a positive correlation between energy and nitrogen efficiency. The routine correlation between these two efficiencies [r = 0.62 in the present study and 0.90 in Wheadon et al. (2012)] which is, in part, due to the presence of both milk yield and dry matter intake in the calculation of both efficiencies (Equation 1 and 2 of Chapter 3), and also to the dilution of maintenance phenomenon, as both energy and nitrogen requirements exist for maintenance. This result suggested that, from a nutritional point of view, a model to predict energy efficiency could be used to predict nitrogen efficiency without the need to building two separate models (i.e., nitrogen efficiency could be considered as an add-on in a model of energy-based efficiency). Our further results consolidate this by showing that both efficiencies are affected by the same nutritional factors. It should, however, be aware that this study did not consider the effect of protein quality, for example, degradability on the relationship. Table 3.3 shows that 30% of variation in the relationship between energy and nitrogen efficiency remained un-explained. Moreover, the interaction between energy and protein is also an important issue, Brun-Lafleur et al. (2010), for example, reported that milk yield increases more rapidly with an increase in energy supply when the level of protein supply is high compared to the maintenance requirement, than when the low protein diet.

In this meta-analysis it was, however, not possible to fully explore the effects of animal factors on energy and nitrogen efficiency using this type of transverse database obtained from the

literature. Days in milk and body weight were the only factors possible to include. Most of the studies in the literature focus on the effect of nutritional factors (e.g., dietary protein, fibre concentration, dietary energy concentration; Castillo et al., 2001; Colmenero and Broderick, 2006; Yang and Beauchemin, 2006), with little focus on the effects of breed, parity, body weight, or lactation period on energy and nitrogen efficiency (Britt et al., 2003; Prendiville et al., 2009). Taking days in milk as an example, most studies were performed with cows in mid-lactation, whereas very few studies were performed on early lactation cows. Researchers have often avoided early lactation period for conducting nutritional and management studies because the measurements during this period are fraught with a high degree of variability as the consequences of quickly changing physiological status from pregnant and non-lactating to non-pregnant and lactating, and the high incidence of health problem (Drackley and James K, 1999). We, therefore, recommended that longitudinal measurements such as those in long-term genetic evaluation projects at the Langhill Dairy Research Centre (Coffey et al., 2004), Aarhus University (Nielsen et al., 2003), Institute National de la Recherche Agronomique (Delaby et al., 2009), or at the Agriculture and Food Development Authority (Horan et al., 2005) would be more appropriate to look at the effects of animal factors on feed efficiency.

6.2. Challenges of incorporating individual variability into a nutritional model

The success of breeding programs is dependent on our ability to identify animals that have a greater capability to perform compared to their herd-mates across the prevailing range of environments. Results from the literature have widely shown that there is a significant variability in performance between individual cows in the same population (e.g. Rose et al., 2004; Bastin et al., 2011). Genetic variation between animals is an intrinsic characteristic of a population due to the different combination of alleles or genes inherited from their parents (Lacy, 1997), and it offers a possibility to select for animals that are superior in a particular environment. Studies intend to separate genetic from environmental variation are usually performed by recording and comparing the means of different genotypes (breeds or selected versus control animals) in the same environment. Further, animals that differ in genetic potentials might respond differently to a change in the (nutritional) environment (Kennedy et al., 2002), that is commonly termed as genotype by environment (G × E) interaction (Falconer, 1989). The key underlying process of the G × E interaction is call plasticity; genotypes that exhibit a wide range of variation in phenotypes across environments are plastic, while those that are more stable across environments are robust (Bryant et al., 2005). In this context, on the one hand it seems like a good idea to select for cows

that are robust for milk production because they can maintain milk production level across environment, but on the other hand low plasticity also implies that the genetic gains in milk production with improvements in environment would be less than with cows that are plastic. The key issue is that when nutrient availability is decreased some functions are prioritized over others, supplying resources for one function implies that the resources for one or more other functions will be reduced, and thus, robust cows maintain milk production as an expense of other functions. In this context, the consequences of such a trade-off will depend on the target functions being negatively influenced by the maintenance of milk production. There is evidence to suggest that the functions of health and fertility are impacted in the case of intensive dairy production (Lucy, 2001; Pryce et al., 2004; Friggens et al., 2010).

Mathematical modelling has long been recognized as a tool to integrate knowledge from biological experiments and assist the process of decision making by predicting the outcomes of animal performance under different management strategies. The two aspects of individual variability and interaction between genotype and environment, however, make it difficult to translate the average population responses into individual animal responses in the context of model simulation (Pomar et al., 2003). This partly explains why most of simulation models in dairy cattle often simulate the average cow of the herd without reference to genetic variation between individuals and the differences in their response to changing environment (Bryant et al., 2005). In other words, these models generally assume a unit genetic correlation between traits across environments. A possible solution for these problems is to develop individual-based model which seeks to describe individual variability and subsequently extend to the herd level (Congleton et al., 1997; Puillet et al., 2010). In order to integrate individual variability into the model one can use the estimated breeding values (Bryant et al., 2008). Estimated breeding values provide measures of genetic potential for a particular trait of an animal (Falconer, 1989); however, they do not include information of differences in performance of genotypes in different environment (Calus, 2006). To describe phenotypic variation across environment (G × E), reaction norm that describes the phenotype expressed by that genotype over a range of environment is then used (Kolmodin et al., 2003). Breeding values for reaction norm parameters can be estimated, if phenotypic values of a large number of animals in a reasonably wide range of environments are available, thus, making this approach to probably be costly (Kolmodin et al., 2002).

Recently, the idea of using mechanistic approach for dealing with these issues has been proposed in pigs (Doeschl-Wilson et al., 2007). Generally, such a model starts with the description of performance free from the environmental influence. Under non-limiting conditions, these genetic profiles of performance represent genetic potential. The model parameters represent underlying biological traits. The varying environmental inputs are hence incorporated to simulate the phenotypic response of genotypes using some repartitioning rules (for example, those described in Martin and Sauvant, 2010a).

In dairy cattle, Vetharaniam et al. (2001) and Martin and Sauvant (2010b) have attempted to applied the same approach as described above to simulate genetic variability in milk production, milk composition, body weight or body reserve accretion. In the study of Martin and Sauvant (2010b), for example, these parameters are termed genetic scaling parameters and noticeably each parameter regulates a particular trait independently. However, there are questions need to be addressed before the genetic scaling parameters can be used to realistically simulate different genotypes of cow in the population: Do these genetic scaling parameters provide sufficient flexibility to enable simulations of a wide range of variability of animals within breed as well as of animals of different breeds? Which profile among the possible combination of genetic parameters are realistic pattern of performance? Answering these questions requires knowledge of variation of such parameters, their nature of distribution, and the possible correlations that may exist between parameters. Such a knowledge on genetic scaling parameters for the model of Vetharaniam et al. (2001) has been explored by Bryant et al. (2007).

In Chapter 4, we explored the above questions for the model of Martin and Sauvant (2010b). We showed that the lifetime nutrient partitioning model of Martin and Sauvant (2010b) can be used for further investigation of consequences of future selection and management strategies on the long-term efficiency of individual dairy cows. Because it was general enough to accommodate three different breeds, there was some under-prediction of daily milk yield and dry matter intake observed in late lactation. This was mainly due to the difference in feeding system between the data used for calibrating the original GARUNS model, in which cows were fed with step-down dietary energy, and the data used for validating the model in Chapter 4 in which a constant energy density diet was offered to cows throughout their lactations cycles. Given that the ultimate purpose of GARUNS is to realistically simulate lifetime performance of commercial herds differing in production level under different feeding systems, the original calibration in GARUNS developed using data that reflect the practical situation would seem to be appropriate.

In addition, these under-predictions in late lactation only accounted for 7 and 13% compared to the total milk yield and total dry matter intake, and thus they are not expected to have a significant effect in the context of simulation studies.

It was also shown that the correlations between the model genetic scaling parameters agreed with the related literature values, and also quantified some key components of variation in lactation performance. Thus, it can be concluded that this model is a suitable basis for including genetic variability in performance parameters for major life functions such as milk production, body reserve usage and size and simulating the impact of future selection and management strategies on lifetime efficiency of individual cows.

6.2. Trade-off between short-term and long-term efficiency

Milk production and reproductive performance of individual cows are the major determinants of profitability of dairy farms (Sawa et al., 2013). Ideally dairy cows should produce milk and calves over a period of many years. The last decades witnessed an enormous increase in milk production as the result of improvements in genetics, feeding, and management. According to Pryce and Veerkamp (2001) and Pryce et al. (2004) the increase in milk yield can be attributed to approximately 50% of improved genetics and 50% of improved feeding and management. Consequently, milk production efficiency computed as milk output over feed intake has been significantly raised via the dilution of maintenance effect (Vérité and Delaby, 2000; VandeHaar and St-Pierre, 2006). Recently, there is increasingly debate among dairy producers and researchers about the antagonistic relationship between increased milk production and reproductive performance and health of the cows. High producing cows often show a poor fertility and health (Butler, 2000; Kerbrat and Disenhaus, 2004; Dobson et al., 2008; Giuliodori et al., 2013). Increased milk yield, negative energy balance, and low body condition, besides the enlarging herd size, have commonly been considered as the major contributors to the loss in longevity of dairy cows [see reviews of Lucy (2001) and Friggens et al. (2010)]. Given the drastic declines in reproductive performance and vitality, emphasis should be placed on longevity and lifetime performance (Knaus, 2009).

It is often thought in this case that forcing cows to milk at peak levels causes them to “wear out” sooner than they would if they were allowed to produce less milk. At the management level, this belief suggests that dairy producers might be able to extend the useful lives of their dairy cows by one or two lactations if they have cows that milk at lower levels. If the cost savings from less culling are greater than the milk returns that are lost, then a net gain is possibly achieved

from cutting back on a cow's milk production. Moreover, as indicated previously that animals that differ in genetic potentials might respond differently to a change in the (nutritional) environment (Kennedy et al., 2002). This would be common in the future dairy production where its environment might be significantly variable as the result of climate change and societal demand for a more sustainable agriculture. In this context, the design of cows that suit future environment requires an ability to predict not only performance but also long-term consequences on health and reproduction of the animals under changing management scenarios.

The model developed in Chapter 5 has successfully integrated the possible interaction between the performance traits milk yield, body condition, and energy balance and reproductive success for simulating lifetime efficiency of various genotypes of cows under high and low feeding systems. Generally, the simulated outputs were comparable with corresponding records of the selected databases. To our best knowledge, very few models of this type, i.e. ones that attempt to incorporate performance consequences on reproductive performance, have been published in the literature (Blanc and Agabriel, 2008; Inchaisri et al., 2010; Brun-Lafleur et al., 2013). In most of models of simulating performance in dairy cattle, the reproductive process is usually represented assuming a fixed efficiency such as fixed calving to ovulation or fixed parturition to conception intervals (Allore et al., 1998; Plaizier et al., 1998; Blanc and Agabriel, 2008; Martin and Sauvant, 2010b). Conversely, reproduction models are often developed without reference to production level (see reviews of Blanc et al., 2001; and Vetharaniam et al., 2010). The recent models of Inchaisri et al. (2010) or Brun-Lafleur et al. (2013) despite having recognized the possible influences of milk yield, body fatness, and energy status on reproductive performance, the simulations of these traits are only based on genetic potential and physiological stages, without a possibility of including interaction with feeding regimes, i.e. G × E interaction. Additionally, these models are only developed for a single lactation and thus cannot currently be used to predict the lifetime performance and lifetime efficiency of the animals.

In this model, simulation of genetic variability between genotypes of cow such as high versus low genetic merit for milk production could be easily done using the genetic scaling parameters described in Chapter 4. The starting distributions of these genetic scaling parameters presented in Chapter 4 were used in support the simulation process. Changes in nutritional environment can be generated by the way of limiting the maximal feed intake of the animals and thus creating constraint. The model simulated reproductive performance such as days from calving to first service, days open, calving interval, conception rate, and productive performance

such as milk production, body weight, milk composition, body composition, and feed intake. Simple culling rules were used in combination with reproductive success to decide whether the cows are allowed to stay in the herd or to be culled, and thus determines their lifespan.

The simulated outputs show that genetic selection for high milk production resulted in a reduction in reproductive performance compared to the non-selected cows. Cows kept in a nutritional constrained environment had inferior productive and reproductive performance compared to well fed cows. Specifically, the longevity of cows in this model was mainly determined by the reproductive success without reference to possible direct effects of production on survivability relative to, for example, metabolic diseases, and this probably explains why high milk producing cows still had higher lifetime efficiency than the low milk producing individuals. However, the higher number of calves produced per cow in low versus high producing groups might give some indication on the long-term effect selection for high milk yield on farm profitability. Generally, at the farm level, the increased productive life will lead to fewer replacement heifers being required to achieve the same level of output and thus reducing the replacement costs, more offspring are produced, and more intensive selection is possible (Bell et al., 2011). Garnsworthy (2004), using modelling approach, reported that improved longevity lower environmental impact, for example, 27% of methane produced on farms is expected to be produced by herd replacements and thus by lowering number of heifer replacements methane emission would also be reduced.

These points of discussion indicate the need, at the animal level, to further include the effect of production level on survivability of the animals, and at the farm level, to also take into account the benefits from calves produced which thus allows to more accurately assess the benefits of different selection and management strategies.

6.2. Conclusion

Despite having limitations that have been described in the preceding sections, the thesis has reached its initial purpose to develop a model allowing to investigate the impact of future selection and management strategies on the long-term consequences of individual dairy cows. The simulation outputs from the model were comparable with the corresponding records from selected databases. It was successful in finding a way to incorporate and simulate genetic variability in performance between individual cows as this is one of the main limitations of most of the simulation models in dairy cattle. The present model focused on lifetime energy efficiency,

the conclusion based on these results can be applied for lifetime nitrogen efficiency, as they have been shown to be positively correlated.

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Historiquement, la sélection génétique chez la vache sur la production laitière a été efficace, car l'expression du potentiel génétique n'était pas limitée par les conditions d'élevage du fait d'un accès non limité à une alimentation de qualité, de conditions thermiques favorables, et d'une maitrise croissante des pathologies. Les conditions environnementales concernant la production laitière sont désormais plus variables du fait du changement climatique et de la demande sociétale pour un développement durable de la production agricole. Les éleveurs peuvent donc sélectionner différentes races et différentes stratégies alimentaires adaptées à leurs conditions locales. Sélectionner des animaux adaptés à leur environnement nécessite de prédire leur réponse aux changements de cet environnement, par exemple, comment la limitation des ressources alimentaires peut affecter la partition des nutriments entre les différentes fonctions vitales. Ceci implique de décrire et prédire leur capacité d'adaptation à ces situations, i.e. leur robustesse. Dans ce contexte, la caractérisation de la partition des nutriments entre les fonctions de production et les fonctions vitales (santé, fertilité…) est cruciale. Dans cette thèse, nous développons un modèle préexistant de partition des nutriments durant la carrière de la vache laitière pour modéliser ses fonctions de production et ses performances de reproduction afin de prédire leur efficacité individuelle dans différents systèmes d'alimentation. Le modèle est individu-centré, et il inclut la représentation des effets des performances de production sur la probabilité de reproduction des vaches. Globalement, le modèle simule les performances de production et de reproduction de vaches de différents génotypes de façon satisfaisante. Il permet également de renseigner des informations sur l'amplitude et la distribution de paramètres génétiques dérivés du modèle. Nos résultats montrent que les vaches sélectionnées pour la production laitière sont moins fertiles et ont une longévité plus faible que celles non sélectionnées. Néanmoins, ces vaches sélectionnées sont plus performantes durant l'ensemble de leur carrière pour leur efficacité énergétique (énergie fixée dans le lait / énergie ingérée) que les vaches faiblement productives. Cette conclusion peut être extrapolée à l'efficacité azotée du fait de la corrélation positive entre efficacité énergétique et azotée que nous avons montrée. Au niveau de l'exploitation, des indicateurs économiques comme le retour sur investissement des génisses de remplacement, les coûts vétérinaires ou d'insémination, et l'impact environnemental devront être inclus pour obtenir une évaluation complète de la rentabilité économique des vaches dans ces différents scénarios. La demande sociétale concernant le bien-être animal doit aussi être intégrée. Nos résultats montrent que les vaches restreintes en concentré ont de moins bonnes performances de production et de reproduction, et une moindre efficacité que celles alimentées de façon plus libérale. Cette thèse montre que la modélisation peut constituer un outil pour tester différentes stratégies de sélection et différents schéma de management du troupeau, et fournit certains indicateurs pour ces objectifs.

Mots-clés: vache laitière, partition des nutriments, efficacité, carrière, modélisation, reproduction.

RESUME DE THESE

Comment prédire l'efficacité des vaches laitières durant leur carrière en réponse à différentes stratégies de management

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INTRODUCTION

La demande croissante de systèmes d'élevage du bétail durables amène à la nécessité de nouvelles stratégies de sélection et de management pour diminuer les coûts alimentaires et atténuer l'impact environnemental de la production laitière, ce qui ne peut être réalisé qu'en améliorant l'efficacité alimentaire. L'efficacité de la production laitière d'un troupeau est la somme des efficacités individuelles des femelles laitières durant leur carrière qui dépendent elles-mêmes de la durée de leur vie productive, de la quantité de lait produite ainsi que de la consommation alimentaire sur cette période. Une caractéristique singulière de l'efficacité propre à chaque vache est sa variabilité due en grande partie aux différences entre les potentiels de production et entre les partitions des nutriments qui découlent de la sélection génétique et du management. Dans ce contexte il est essentiel de comprendre le fondement biologique de cette variabilité individuelle pour explorer la capacité d'une filière à s'adapter à un environnement également variable. Connaitre l'efficacité des vaches par des études sur le terrain est fastidieux car cela requiert l'enregistrement de nombreuses informations sur une longue période. Ainsi, une approche par la modélisation peut offrir une alternative afin d'investiguer les effets de choix de sélection et de management sur l'efficacité d'une vache durant sa carrière. En comparaison avec les autres espèces, l'application aux vaches laitières a une importance particulière car elles présentent de larges variations et que les défis d'une demande alimentaire croissante et d'un élevage rentable et durable se présentent à nous.

Cette thèse de doctorat fait partie du projet GreenhouseMilk proposé dans le cadre de l'Initial Training Network par les Actions Marie Curie avec pour ambition générale une meilleure compréhension du rôle de la génétique dans la partition des nutriments et de l'efficacité énergétique dans les émissions de gaz à effet de serre par l'élevage laitier afin de fournir aux éleveurs des moyens de sélection efficaces et écologiques adaptés à leur système de production. L'objectif est également de considérer le rôle particulier de la génétique dans le système d'élevage en général en tenant compte des stratégies d'alimentation et de management comme la gestion du logement, de la reproduction et des effluents. En tant que participation à ces visées du projet GreenhouseMilk le travail accompli durant cette thèse devait aboutir au développement d'un modèle de simulation des effets de différentes stratégies de reproduction et d'alimentation sur l'efficacité individuelle à l'échelle de la carrière d'une vache laitière.

Nous avons émis l'hypothèse que le management du génotype via l'interaction avec l'environnement à l'échelle de l'animal comme les stratégies de reproduction et d'alimentation nécessitait une représentation des effets à long terme à la fois des performances de production et de reproduction, les déterminants majeurs de l'efficacité.

Pour atteindre cet objectif général trois questions clés ont été identifiées et explorées respectivement dans les chapitres 3, 4 et 5.

- *Question 1.* Quel est le rapport entre une amélioration de l'efficacité énergétique et l'efficacité azotée ?
- *Question 2.* Comment représenter la variabilité génétique des potentiels de production individuels des vaches dans un modèle de partition des nutriments ?
- *Question 3.* Comment représenter l'influence de la performance et de l'environnement nutritionnel sur la reproduction et la durée de la carrière ?

APPROCHE GÉNÉRALE

Étude 1: approche méta-analyse pour explorer les facteurs qui affectent l'efficacité énergétique et de l'azote, et leur relation

L'objectif spécifique de cette étude était d'explorer la relation entre les deux principales composantes de l'efficacité alimentaire, l'énergie et l'efficacité de l'azote, et d'éventuels facteurs nutritionnels et animales qui affectent ces gains d'efficacité, et leur relation, en utilisant une approche méta-analyse. Au départ, une base de données a été construite pour une analyse ultérieure en effectuant une recherche documentaire en utilisant les moteurs de recherche en ligne y compris Science Direct, Google Scholar, et Web of Science. Mots-clés sont l'efficacité énergétique, l'efficacité de l'azote, les vaches laitières, l'utilisation des nutriments et la performance de la vache laitière, alors que le principal critère d'inclusion d'une étude dans la méta-analyse était qu'il a déclaré, ou le calcul de l'énergie et de l'efficacité de l'azote autorisée. L'étape suivante a consisté à définir la façon de mesurer l'efficacité énergétique et de l'azote.

Dans cette étude, l'énergie et l'efficacité de l'azote ont été définies comme des rapports entre l'énergie dans le lait sur la consommation d'énergie (Mcal / Mcal), et de l'azote dans le lait plus de l'apport d'azote (g / g), respectivement.

L'analyse statistique

La corrélation entre l'énergie et l'efficacité de l'azote a été étudiée de deux manières: inter et intra-étude. La corrélation inter-étude a été calculée à partir des données observées de l'énergie et de l'efficacité de l'azote, tandis que la corrélation intra-étude est la corrélation après l'ajustement pour l'effet aléatoire de l'étude. Pour analyser les effets de l'animal et de variables nutritionnelles sur l'énergie et l'efficacité de l'azote, la régression linéaire multiple a été appliquée en utilisant les paquets de nlme et lm du logiciel statistique R. En outre, comme l'énergie et de l'efficacité de l'azote ont été calculées comme les rapports des sorties de ces respectif nutriments dans le lait sur les entrées dans le régime alimentaire, la production de lait et l'ingestion de matière sèche sont apparus dans les deux rapports. Par conséquent, nous nous attendons à une forte corrélation entre les indépendamment de tout facteur de composition animale ou l'alimentation. Pour surmonter ce problème, nous avons décidé de regarder aussi le rapport entre l'azote et l'efficacité énergétique, ce qui signifie que cette "artefact" serait retiré.

Etude 2 : simuler la variabilité génétique des performances individuelles des vaches laitières à l'échelle de leur vie

Dans cette étude, nous avons considéré un modèle nutritionnel de vache laitière préalablement développé dans notre équipe de recherche (GARUNS : Martin and Sauvant, 2010), et avons cherché à évaluer sa capacité à simuler la variabilité individuelle des performances à l'échelle de la vie de la vache laitière. Nous avons ensuite proposé d'utiliser ce modèle pour simuler les performances de plusieurs génotypes de vache laitière qui se distinguent en termes de valeur génétique, e.g. niveau du potentiel de production laitière.

Nous avons utilisé une base de données externe complètement indépendante des données qui avaient été utilisées pour le développement du modèle. Cette base de données contenait des informations sur les performances individuelles (rendement laitier, composition du lait, poids vif, ingestion de matière de sèche) de trois races de vache laitière (Rouge Danoise, Holstein Danoise

et Jersey). Pour chaque vache au sein de chaque race, le modèle a été ajusté aux performances à partir du logiciel Modelmaker. Cet ajustement au cas par cas devait permettre d'examiner la capacité de GARUNS à capturer la variabilité individuelle des potentiels de production pour les différents génotypes représentés.

Dans ce contexte, nous sommes partis de l'hypothèse que si le modèle GARUNS s'ajustait correctement aux données alors la précision des valeurs prédites devait être acceptable et les valeurs résiduelles devaient être distribuées autour d'une moyenne nulle sans aucune tendance à s'en écarter au cours du temps de la lactation. La précision a été évaluée à partir de l'erreur quadratique moyenne relative (RPE). Les valeurs résiduelles ont quant à elles été analysées avec un modèle statistique mixte, dont la forme était la suivante :

$$\mathbf{Y}_{ijk} = \mu + \alpha_i \mathbf{JDV}_i + \beta_j \mathbf{Race}_j + \lambda_{ij} \mathbf{JDV} \times \mathbf{Race}_{ij} + \delta_i \mathbf{JDV}^2_i + \gamma_k + \varepsilon_{ijk,}$$

où Y_{ijk} représente les valeurs résiduelles de GARUNS pour le poids vif, le rendement laitier, le taux butyreux du lait, le taux protéique du lait, et l'ingestion de matière sèche. μ est une constante, α_i, β_j, and λ_{ij}, et δ_i sont les coefficients de régression des variables Y_{ijk} pour les différentes covariables (dans l'ordre, JDV_i : jour depuis vêlage n° i, $Race_j$: race n° j, l'interaction entre JDV_i et $Race_j$, puis le carré de JDV_i). γ_k désigne l'effet aléatoire associé à l'animal n° k. Finalement ε_{ijk} est l'erreur résiduelle pour laquelle on suppose une distribution normale, une moyenne nulle et une variance σ^2_e.

En plus de l'ajustement de GARUNS aux données individuelles, nous avons aussi examiné les valeurs des paramètres de GARUNS estimées à chaque ajustement. Dans GARUNS ces paramètres contrôlent l'échelonnage génétique des performances, ils sont donc essentiels pour la simulation des performances de différents génotypes de vache laitière. Nous avons examiné les corrélations entre ces paramètres puis entre ces paramètres et les performances des animaux. Pour cela nous avons utilisé des matrices de corrélation et des analyses en composantes principales.

Etude 3 : prédiction, à l'échelle de la vie d'un animal, de sa rentabilité énergétique et de ses performances de reproduction, en fonction du génotype et de la stratégie alimentaire.

Cette étude généralise le modèle GARUNS décrit au chapitre III afin d'obtenir une prédiction réaliste des performances de divers génotypes de vaches (en particulier vaches à fort potentiel laitier v.s. vaches à faible potentiel) soumises à différentes stratégie d'alimentation (régime à forte densité énergétique v.s faible densité).

Description du modèle

Le modèle GARUNS peut être paramétré en fonction du génotype en changeant par exemple le paramètre de production laitière, et en fonction de l'alimentation en changeant le paramètre qui contrôle la densité énergétique de la ration. Parmi les sorties de GARUNS, la production laitière, le poids vif, et la balance énergétique sont utilisées pour piloter un modèle de reproduction (REPRO). Ce modèle ne permet par contre pas de décrire directement l'espérance de vie des animaux (une donnée cruciale pour évaluer les performances à l'échelle de la vie des animaux), car il ne permet pas de prédire quand sont réformées les vaches. Un modèle décrivant la stratégie de réforme a donc été ajouté, ce dernier réforme notamment les vaches qui ne sont pas gravides au bout d'un certain temps ou d'un certain nombre d'insémination. A minima, il nécessite en entrée une information indiquant si l'insémination a conduit à la mise bas d'un veau vivant. Nous avons choisi de modéliser cette dernière sous la forme d'une probabilité par insémination de conception d'un veau viable (LCONC pour ***l****ikelihood of* ***conc****eption*) sans décrire la mécanique interne et les diverses étapes de la reproduction qui amènent à la mise bas. Le LCONC agrège tous les effets qui peuvent jouer sur la conception et la viabilité du veau, il est modulé par la production laitière, l'état corporel et la balance énergétique.

Nous avons fait l'hypothèse qu'une vache avec une forte production laitière, une note d'état corporel faible, et une balance énergétique fortement négative a un LCONC faible. Cette situation peut devenir problématique lorsque les contraintes environnementales (telles que le manque d'énergie) sont fortes. Nous avons donc défini :

$$\mathbf{LCONC} = f\,(\mathbf{LCONC_{MY}}, \mathbf{LCONC_{BCS}}, \mathbf{LCONC_{EB}})$$

Avec

$$\mathbf{LCONC_{MY}} = 2 \times (1 / 1 + \exp\,(\mathbf{Rat_{MY}} \times \mathbf{MY}))$$

$$\mathbf{LCONC_{BCS} = 2 \times (1 / 1 + exp\ (-Rat_{BCS} \times (BCS - 3))}$$

$$\mathbf{LCONC_{EB} = 2 \times (1 / 1 + exp\ (-Rat_{EB} \times EB))}$$

$LCONC_{MY}$ représente l'effet de la production laitière (i.e., *milk yield*), $LCONC_{BCS}$ l'effet de la note d'état corporel (i.e., *body condition score*), et $LCONC_{EB}$ l'effet de la balance énergétique (i.e. *energy balance*). MY est la production laitière en kg/jour, BCS est la note d'état corporel (de 0 à 5, 0 correspondant à une vache très maigre), EB est la balance énergétique en MJ/jour.

Nous avons fait l'hypothèse d'une valeur maximale de LCONC de 0.06± 0.06. Elle représente le taux de conception moyen des génisses, dans lesquelles on suppose que la production laitière est nulle, et pour les quelle on suppose que la note d'état corporel et la balance énergétique n'ont aucun effet négatif sur LCONC. Après ajustement, les paramètres sont estimés à : Rat_{MY} =0.012, Rat_{BCS} =0.425, et Rat_{EB} =0.027.

Règles d'insémination et de gestation

La période d'anoestrus post-partum est modélisée par une durée de 21.8± 3 jours suivie d'un ou plusieurs cycles de 21.8± 3 jours contenants une période fertile de 3 jours. En dehors de la période fertile, LCONC est fixé à 0. Les inséminations commencent après une période d'attente volontaire de 50 jours après vêlage, et sont réalisés une fois par période fertile si LCONC est supérieur à 0.4. Ce seuil permet de modéliser le fait que les œstrus faibles sont peu exprimés par les vaches, ne sont pas détectés et ne donnent pas lieu à une insémination. Le succès d'une insémination est implémenté en tirant un nombre dans une loi uniforme comprise entre 0 et 1 : l'insémination est un succès (vache gravide) si le résultat du tirage est inférieur à LCONC. La durée de gestation est modélisée par une valeur tirée dans une loi normale de moyenne 280 jours et d'écart type 5 jours.

Règles de réforme

Les vaches gravides au bout de 4 inséminations ou moins ne sont pas réformées. Les vaches qui échouent lors des 4 premières inséminations et qui ont une production laitière inférieure à 25 kg/jour sont réformées. Une 5ème insémination est réalisée pour les vaches

produisant plus de 25kg de lait par jour, si elle est fructueuse, la vache est sauvée, sinon elle est réformée. Afin de prendre en compte le fait que certaines vaches n'expriment pas beaucoup leurs œstrus (et ne sont donc pas inséminées), toute vache non gravide au bout de 260 jours après la dernière parturition (ou le premier jour de mise à la reproduction pour les génisses) est réformée. Afin de conserver un modèle simple, les autres facteurs influents sur la stratégie de réforme (tels que l'âge des vaches ou la structure de la population) ne sont pas pris en compte.

LTE : rentabilité énergétique de l'animal pour la production de lait à l'échelle de sa vie

Le modèle (GARUNS + REPRO + réforme) permet de prédire l'intervalle vêlage-conception, l'intervalle première insémination-conception et le taux de conception. Ces sorties ont été comparées à la littérature afin d'évaluer la qualité du modèle. La rentabilité énergétique de l'animal pour la production de lait à l'échelle de sa vie est ensuite estimée par le calcul de LTE (i.e., ***l****ife****t****ime e****fficiency*) défini par l'équation suivante :

$$\mathbf{LTE} = \sum_{1}^{N} \frac{\mathbf{E_{Milk}}}{\mathbf{E_{Intake}}} \times 100$$

avec LTE le rendement énergétique de l'animal pour la production de lait (en %), E_{Milk} l'énergie utilisée pour produire du lait (MJ) et E_{Intake} l'énergie métabolisable mangée par la vache (MJ). Ces valeurs sont intégrées sur toute la vie de l'animal.

Evaluation du modèle

Le modèle de reproduction a été évalué à partir de données expérimentales décrites dans deux études : Cutullic et al. (2011) et Pryce et al. (1999). Dans le premier jeu de données, deux races de vaches sont utilisées : la Holstein-Friesian, une race sélectionnée pour son fort potentiel laitier, et la Normande, une race mixte. Dans cette étude, les vaches sont nourries avec une ration riche en concentré et une ration plus pauvre. La comparaison entre races parmi les vaches nourries avec la ration riche permet d'évaluer l'impact de la sélection génétique sur les performances de reproduction et sur LTE.

Les paramètres de GARUNS ont été ajustés afin d'obtenir des performances identiques à celles décrites dans les jeux de données précédents. Pour des raison de temps de calcul et de

disponibilité en données, seuls les paramètres génétiques représentants le potentiel laitier (ν_y), la taille à maturité (W_M), la note d'état corporel moyenne (b_0) et (ν_X) ont été ajustés. Ceci revient à faire l'hypothèse que la composition laitière est identique pour toutes les vaches. La variabilité de la population pour les paramètres ν_y, W_M, b_0 and ν_X a été simulée en utilisant les valeurs moyennes, écart types et corrélations décrites dans le chapitre 4. L'influence de l'alimentation a été simulée en modifiant le paramètre e_D qui décrit la densité énergétique de la ration. La stabilité du modèle a été évaluée en réalisant 20 simulations de 200 vaches chacune pour chaque scénario.

RÉSULTATS

1. Relation entre l'énergie et l'efficacité de l'azote, et les facteurs qui les touchent et leur relation

Corrélation entre l'efficacité énergétique et de l'azote

Comme prévu, en raison de la présence de la production laitière et la matière sèche ingérée dans les deux expressions de l'efficacité, une corrélation inter-étude positive existait entre l'énergie et l'efficacité de l'azote dans les données brutes (r = 0,62). Cependant, les résultats montrent également que, dans les expériences, une augmentation de l'efficacité énergétique n'a pas toujours été associée à une augmentation de l'efficacité de l'azote. Lorsque les données sont présentées comme des réponses intra-étude (elles ont été corrigées pour l'effet aléatoire de l'étude), la corrélation a été réduite (r = 0,30). Ceci est dû en grande partie à la plus grande réduction dans la plage des données, par rapport à la réduction de la variation. Cela suggère que, d'un point de vue nutritionnel, un modèle pour prédire l'efficacité énergétique pourrait être utilisée pour prédire l'efficacité de l'azote sans la nécessité de la construction de deux modèles distincts (c.-à-efficacité de l'azote peut être considéré comme un add-on dans un modèle d'énergie à base de l'efficacité). Notre étude renforce encore en montrant que les deux efficacités sont affectées par les mêmes facteurs nutritionnels.

Facteurs influant sur l'efficacité énergétique, l'efficacité de l'azote et le rapport de Neff: Eeff

Les résultats de la régression linéaire multiple ont montré que les fibres au détergent acide (ADF) et la proportion de concentrés (PCO) ont été significativement associés à l'efficacité énergétique et au rapport de Neff: Eeff, alors que l'efficacité de l'azote était significativement

associée à l'ADF et l'énergie digestible (ED). Plus précisément, l'ADF a eu un impact négatif sur l'efficacité énergétique (P <0,05): une augmentation de 10% des ADF dans le régime alimentaire réduite 1,60% l'efficacité énergétique. En revanche, la PCO a affecté l'efficacité énergétique de façon quadratique. Le coefficient de régression négatif indique que l'efficacité énergétique a été améliorée avec une petite augmentation de la PCO, mais a diminué une fois la PCO a encore augmenté. L'augmentation des ADF alimentaires et DE contenu a été négativement associée à l'efficacité de l'azote. En règle générale, une augmentation de 10% dans l'ADF ou une augmentation 1 Mcal de DE conduit à une réduction de 5,60 et 6,67% de l'efficacité de l'azote, respectivement. Le rapport entre l'énergie et l'efficacité de l'azote était significativement associée à l'ADF et la PCO. La pente a été diminuée avec l'augmentation de la concentration des ADF alimentaires, alors qu'elle a été augmentée si la proportion de concentrés a aussi été augmentée.

2. Examiner la capacité de GARUNS à capturer la variabilité individuelle des potentiels de production pour les différents génotypes représentés.

Qualité générale des ajustements de GARUNS aux données individuelles

Le modèle GARUNS a globalement montré un ajustement satisfaisant par rapport à plusieurs évolutions individuelles observées au cours de la lactation (poids vif, taux butyreux et protéique du lait, concentration en lactose). Pour ces variables, la faible erreur quadratique moyenne (RPE < 13%) a démontré un bon niveau de précision des prédictions. En ce qui concerne le rendement laitier et l'ingestion de matière sèche, l'ajustement était satisfaisant en début et milieu de lactation (RPE < 20%) mais inadéquat en fin de lactation (RPE > 20%). Toutefois, la fin de la lactation ne contribue en moyenne qu'à 7% de la production laitière annuelle et 13% de la consommation annuelle de matière sèche ce qui permet de relativiser l'erreur du modèle.

Par ailleurs, il est possible que la tendance du modèle à sous-estimer le rendement laitier et l'ingestion en fin de lactation soit davantage liée à des différences de conduite d'alimentation entre les animaux représentés dans la base de données et ceux utilisés pour la calibration du modèle GARUNS, qu'au modèle en lui-même. Entre races, aucune différence de qualité prédiction n'est ressortie.

Evaluation des résidus par le modèle mixte

Les résultats d'analyse des régressions effectuées à partir des valeurs résiduelles pour le poids vif, le rendement laitier et les variables de composition du lait ont révélé des effets linéaires (JDV) et curvilinéaires (JDV^2) du temps de lactation. Conformément à l'observation précédente, ceci indique une différence systématique entre la forme des évolutions des différentes variables au cours de la lactation prédites par GARUNS et celles observées dans la base de donnée. Cela pourrait aussi indiquer que GARUNS ne capture pas correctement les différences entre races. Toutefois, il est possible que les effets détectés soient seulement la conséquence du nombre important d'observations incluses dans le modèle (par exemple n = 20136 pour le rendement laitier). En effet, l'inclusion de l'effet race dans le modèle mixte ne permet pas de montrer une amélioration de la qualité de la prédiction par rapport à un modèle excluant cet effet. Ces résultats signifient que l'erreur détectée pour la forme des évolutions des différentes variables au cours de la lactation n'est pas fortement liée à la race, et donc n'est pas préjudiciable à l'utilisation de GARUNS dans des études de simulation. Ils suggèrent également que la base de données utilisée dans cette étude était adéquate pour estimer des paramètres d'échelonnage génétique indépendants de toutes corrélations entre le stade de lactation et l'environnement.

Relations entre les paramètres d'échelonnage génétique de GARUNS estimés

Le résumé des statistiques descriptives des paramètres d'échelonnage génétique de GARUNS est indiqué en Table 2. Des variations importantes ont été détectées pour les paramètres contrôlant le poids vif des animaux (W_M, b_0 and ν_x, qui représentent 23, 25 et 39% de leurs moyennes respectivement). Les variations relatives des paramètres contrôlant le rendement laitier et la composition du lait représentaient quant à elles moins de 20%. Aucune différence n'a été détectée entre races pour les paramètres contrôlant le gain de réserves corporelles (b_0) et la sécrétion de lactose (ν_L). Les autres paramètres d'échelonnage génétique étaient similaires entre la Rouge Danoise et l'Holstein Danoise mais différents de ceux estimés pour la Jersey.

Peu de corrélations entre paramètres d'échelonnage génétique ont été détectées à l'exception des paramètres contrôlant la production de lait (rendement, taux butyrique et protéique et lactose). Dans le modèle GARUNS chacun des paramètres d'échelonnage permet de

moduler un caractère zootechnique de façon indépendante des autres (mis-à-part le poids vif). Ainsi, les corrélations observées sont principalement le résultat des relations biologiques entre les caractères zootechniques et non le résultat de la structure du modèle. Ainsi, les corrélations ont pu être comparées à celles observées dans la littérature et jugées conformes. De plus, les résultats d'analyse en composantes principales ont montré que les paramètres d'échelonnage étaient fortement influencés par la race.

3. L'ajout de l'effet de performance sur la probabilité de conception permet d'estimer la rentabilité d'un animal à l'échelle de sa vie.

Le modèle intégrant GARUNS, REPRO et la stratégie de réforme permet de prédire des valeurs de poids vif, de production laitière, de note d'état corporel et de performances de reproduction cohérentes avec les données des troupeaux de Le Pin et Langhill.

Comparaison entre prédictions du modèle et données observées.

Le modèle prédit un taux de conception lors de la première insémination chez les Holstein de 41%, ce qui est cohérent avec les données de Le Pin (38%). Les résultats pour les autres facteurs dont la durée parturition-première insémination, la durée parturition-conception et l'intervalle vêlage-vêlage sont aussi prédits correctement chez les Holsteins. Par contre, les performances de reproduction des Normandes sont sous estimées par le modèle. Le modèle prédit une LTE meilleure chez les Holstein (45%) que chez les Normandes (41%) car cette dernière est surtout dépendante du niveau de production laitière. Il est important de noter que LTE ne prend pas en compte les bénéfices d'une meilleure stratégie de reproduction (tels que des frais vétérinaires ou d'insémination plus bas et un plus grand nombre de veaux). De plus l'effet négatif des troubles métaboliques sur la longévité des animaux n'a pas été pris en compte. Afin de mieux évaluer l'efficacité globale d'un système d'élevage, de telles informations doivent être intégrées.

Comparé aux données de Langhill, le modèle prédit correctement le taux de conception lors de la première insémination. Le modèle prédit des sens de variations des performances de reproductions en fonction de la sélection sur le potentiel laitier en adéquation avec les données observées.

En conclusion, le modèle GARUNS + REPRO + réforme, peut être utilisé afin de prédire les conséquences des stratégie de sélection et de gestion des troupeaux sur les performances de reproduction, la production laitière et LTE.

CONCLUSION GENERALE

Malgré les limites exposées dans la thèse nous avons atteint notre objectif initial de développer un modèle permettant d'évaluer l'impact des futures stratégies de sélection et de management sur les conséquences à long terme affectant les vaches laitières.

Les résultats issus de la simulation grâce au modèle sont comparables aux relevés des bases de données sélectionnées.

Le modèle est capable de tenir compte et de simuler une variabilité génétique des performances entre animaux, ce point étant l'un des principaux facteurs limitant de la plupart des modèles de simulation d'élevages laitiers.

Il est centré sur l'efficacité énergétique au cours d'une carrière et les conclusions basées sur ces résultats peuvent être extrapolées à l'efficacité azotée car nous avons montré qu'une corrélation positive existait entre les deux.