The development of a model for the prediction of feed intake and energy partitioning in dairy cows

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Abstract

Balancing the supply of on-farm grown forages with the production targets of the dairy herd is a crucial aspect of the management of a dairy farm. Models which provides a rapid insight of the impact of the ration, feed quality and feeding management on feed intake and performance of dairy cows are indispensable to optimize feeding strategies, allocation of feeds and purchased concentrates, in order to find the best compromise between milk performance, nutrient use efficiency, manure excretion, gaseous emissions and profitability. This thesis describes the development of the Wageningen UR Dairy Cow Model (Wageningen DCM), a model for the prediction of feed intake and performance of dairy cows. The Wageningen DCM is constructed from two modules: a feed intake model and an energy partitioning model which describes the partitioning of the ingested net energy to milk energy output and body reserves. For the development of the feed intake model a calibration dataset was compiled with 38515 weekly records of ration feed composition, diet composition, individual feed intakes, milk yield and composition, parity, days in lactation and days pregnant from 1507 cows. The feed intake model predicts dry matter intake (DMI) from feed and animal characteristics. Data of standard feed analysis were used to estimate the satiety value (SV) of numerous feeds. The SV is the measure of the extent to which a feed limits intake. The cows' ability to process the intake-limiting satiety value-units is expressed as the feed intake capacity (FIC). The FIC is estimated from parity, days in milk and days of pregnancy which are indicators of the size and physiological state of the cow. An evaluation of the feed intake model was performed using an independent dataset containing 8974 weekly means of DMI from 348 cows. On the basis of mean square prediction error (MSPE) and relative prediction error (RPE) as criteria, it was concluded that feed intake model was robust and can be applied to various diets and feeding management situations in lactating HF cows.

A second model was developed to predict the partitioning of ingested net energy (NE_L) to milk energy and body reserves. This energy partitioning model describes the baselines of daily NE_L intake and milk energy output (MEO) during successive lactation cycles of a 'reference' cow. The MEO and change in body energy of a cow is estimated from deviation of NE_L intake from the baseline. A NE_L intake above the baselines results in a higher predicted MEO and reduced mobilization of body energy reserves. Whereas, a NE_L intake below the baseline results in a lower predicted MEO and increased mobilization. The proportion of ingested NE_L partitioned to MEO depends parity number, days in lactation and pregnant, reflecting the changes in priority in energy partitioning during successive lactation cycles of a dairy cow.

The feed intake model and energy partitioning model are integrated in the Wageningen DCM. Model simulations showed that the Wageningen DCM is able to simulate the effects of diet composition, nutritional strategies and effects of cow characteristics (parity, days in milk and pregnancy) on dry matter and nutrient intake, and the partitioning of ingested NE_L into MEO and body energy. The Wageningen DCM requires easily available input data. Validation of the Wageningen DCM with external data indicated a good accuracy of the prediction of intake and milk energy output with relatively low prediction errors ≤ 0.1. The Wageningen DCM enables users to analyse and compare different feeding strategies, identify limitations of feeding strategies, formulate diets, calculate feed budgets and to develop economic and environmental sustainable feeding strategies.

Aan mijn ouders
Jan Zom (1933-2006)
Gerda Zom - van de Haterd

Voorwoord

In 1993 trad ik in dienst bij het Proefstation voor de Rundveehouderij. Al snel probeerde mijn sectiehoofd Bob Subnel mij enthousiast te maken voor het schrijven van een proefschrift. Hij voorzag namelijk dat wetenschappelijke output een belangrijk item zou kunnen worden. Bovendien was het schrijven van een proefschrift niet zo moeilijk. “Je moet gewoon vier samenhangende artikelen schrijven, een inleiding ervoor, een discussie erachter en dan een nietje er doorheen. Klaar!” Bob Subnel was samen met Robert Meijer zelf ook bezig met het schrijven van een proefschrift over de ontwikkeling van een nieuw Koemodel. Echter, in de loop van 1995 vertrok Bob Subnel naar het bedrijfsleven en raakte ik betrokken bij de ontwikkeling van het Koemodel. Toen kwam nogmaals de vraag aan de orde of ik een promotieonderzoek zou willen doen. In 1997 werd in overleg met Prof. Seerp Tamminga een “spoorboekje” opgesteld met een ambitieuze tijdsplanning. In 34 maanden tijd zou een proefschrift met 8 hoofdstukken moeten klaarliggen. Het heeft wat langer geduurd. Eind 1998 vertrok ook Robert Meijer naar bedrijfsleven. Ik kreeg daardoor als “erfenis” het hele Koemodel project in de schoot geworpen. Hiervoor ben ik grote dank verschuldigd aan Bob Subnel en Robert Meijer. Want uit de “erfenis” van het Koemodel, heb ik namelijk waardevolle elementen kunnen gebruiken voor de ontwikkeling van het Koemodel in zijn huidige vorm wat uiteindelijk heeft geresulteerd in dit proefschrift. Met name het concept van verzadigingswaarden heb ik onverkort kunnen overnemen. Het stelde mij ook in de gelegenheid om zaken naar eigen inzicht wat anders aan te pakken. Daarbij is de inzet van Geert André onmisbaar geweest. Geert heeft mij enorm geholpen om mijn ideeën te realiseren. Helaas is Geert André in 2013 overleden, maar ik zal in grote dankbaarheid aan hem terug blijven denken.

Vooral langzaam maar gestaag bleef het Koemodel zich ontwikkelen. In 2002 werd de systematiek van de schatting van de voeropname en verzadigingswaarde geaccordeerd door het Centraal Veevoeder Bureau (CVB) en gepubliceerd in de CVB tabel. Later werd het volledige Koemodel ingebouwd in het simulatieprogramma Bedrijfs Begrotings Programma Rundveehouderij (BBPR). Op basis van modelstudies BBPR zijn vele publicaties voor de veehouderijpraktijk verschenen. Wat echter nog niet zo wilde vlotten was het schrijven van wetenschappelijke publicaties. Maar vooral dankzij Ad van Vuuren die in zijn rol van co-promotor mij op het goede spoor heeft gezet is dit toch gelukt. Ad, enorm bedankt voor je waardevolle commentaar, de suggesties voor verbeteringen bij het schrijfwerk. Jou inzet en stimulerende rol zijn onmisbaar geweest. Verder wil ik Gert van Duinkerken danken voor de ondersteuning en ruimte die hij heeft gegeven om dit proefschrift te kunnen voltooien. Ook dank aan mijn promotor Wouter Hendriks, voor zijn motiverende ondersteuning. Verder wil ik al mijn collega’s van Wageningen UR Livestock Research bedanken die op wat voor wijze dan ook hebben bijgedragen aan de totstandkoming van dit proefschrift. Van mijn ouders Jan Zom en Gerda Zom - van de Haterd heb ik altijd meegekregen dat een goede scholing belangrijk is. “Kennis is macht” zei mijn vader vaak. Het is een groot geluk geweest dat ik met deze houding en instelling liefdevol ben grootgebracht. Zonder jullie had ik dit niet kunnen bereiken. Lieve Eveline dank je wel voor je wijsheid, je hulp en de ruimte die mij de afgelopen jaren hebt gegund. Je bent van onschatbare waarde.

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Chapter 1

General Introduction

1. General introduction

1.1. Aim of the thesis

A dairy farm is basically an enterprise that creates added value by converting animal feeds into animal end-products. In this context, added value can be expressed either as economic, biological or nutritional value. Desirable animal end-products include milk, culled cattle, manure while undesired products include emissions (e.g. methane and ammonia) and manure which are a potential burden to the environment. Despite, this apparent simplicity, a dairy farm is a complex system that consists of two interacting systems: the feed production system (farmland with forage crops and grassland) and the animal production system (the dairy herd). Decisions made around the forage crop and grassland management will have a cascading effect on the performance of the dairy herd and *vice versa*. At given external conditions (weather, climate, soil type), factors such as forage species, acreage of forage crops, the level of fertilization, irrigation, cutting and grazing systems and harvest methods influence both the quantity and quality of the forage produced. For example, the level of nitrogen fertilization of grassland affects dry matter (DM) yield, grass growth rate (Prins, 1983; Vellinga et al., 2004), digestibility, fibre and crude protein (CP) content (van Vuuren et al., 1991; Valk et al., 1996; Valk et al., 2000) and feed intake (Valk et al., 2000). Within a level of nitrogen fertilization, increased maturity of grass at harvest results in higher DM yields but with an increased fibre content, a reduced CP content and a reduced dry matter digestibility (Buxton and O'Kiely, 2003). The interactions between fertilization level and stage of maturity at harvest will determine the balance between DM yield and feeding value for ruminants (King et al., 2012). Other decisions around forage crop management (harvest) and cropping plan (acreage of forage crops) can also have an impact on the animal production system. For example, the stage of maturity at harvest of maize silage affects intake and performance in dairy cows (Phipps et al., 2000; Keady et al., 2008). Changes in the cropping plan (i.e. replacing grassland with silage maize or *vice versa*) affects the quantities and proportions of different feeds in the ration. For example, replacing grass silage with maize silage affects feed intake and milk production (O'Mara et al., 1998; Burke et al., 2007). Thus, the acreage of different forage crops, DM yields and quality of grazed and preserved forages will determine to a large extent diet composition and total supply of feed and nutrients to the dairy herd. Balancing the supply of feeds and nutrients from the feed production system with the production goals of the animal production system is a crucial aspect of farm management. This involves optimization of feeding strategies, allocation of available feeds and inclusion of purchased concentrate supplements, in order to find the best compromise between different targets of the animal production system such as health and milk performance, nutrient use efficiency, mineral excretion, gaseous emissions, and profitability.

The complexity and large number of variables involved makes it impossible to obtain a quick insight of the impact of managerial interventions on cow performance. Mathematical models able to predict feed intake and performance of dairy cows are useful tools that allow rapid understanding of the effects of different feeding and management strategies on cow performance and, thereby, supporting the decision making process.

In the Netherlands, Hijink and Meijer (1987) have recognized the value of mathematical models for the simulation of dairy cow performance and developed the “Cow-Model” (Koemodel). This model simulates voluntary roughage intake, fat corrected milk yield and body reserves (Hijink and Meijer, 1987). The main outputs of the Cow-Model are the predicted roughage intake and required concentrates input to meet a user-defined level of milk energy output (MEO) specified as actual or potential fat corrected milk yield. The required input variables are days in milk (DIM), daily concentrate allowance, net energy value (NE_L ;van Es (1978)) of the roughage, body weight and MEO. The Cow-Model has gained a wide spread acceptance amongst farmers, nutritionists and consultants of the feed industry as a tool to calculate concentrate supplementation and evaluation and comparison of different feeding strategies and forage options. Key factors of the success of the Cow-Model of Hijink and Meijer (1987) are the limited number of input variables and it’s ease to operate and the provide the user with clear interpretable information.

However, there are increasing doubts about flexibility and accuracy of the Cow-Model and some assumptions are disputed because they are not in line with the situations in common farm practice or not valid from a biological point of view.

The lack of flexibility of the Cow-Model is associated with rigid polynomial functions used to describe the standard curves of roughage intake capacity and milk yield. These functions allow only a fixed lactation length of 305 and a calving interval of 365 days. This calving interval is not in line with the calving intervals observed in farm practice, being on average 417 days in the Netherlands (CRV, 2012). The functions of standard curves of roughage intake capacity and milk yield prohibit the simulation of the effects of variation in lactation length and calving interval on feed intake and milk production.

The Cow-Model assumes a feeding system in which cows are fed *ad libitum* roughage with separate feeding of concentrate supplements. However, under practical farm conditions, there is greater diversity of variation in feeding systems such as use of partial and total mixed rations.

Another point of concern is the limited biological and physiological meaning of the Cow-Model. Complex relations in the Cow-Model are based on assumptions from experts or are described by simple algorithms (Hijink and Meijer, 1987). The Cow-Model assumes that all body reserves mobilized during early lactation are completely restored at the end of lactation (Hijink and Meijer, 1987). However, in reality, body reserves behave much more dynamic, depending on parity, stage of lactation, pregnancy and nutritional status (Bauman and Currie, 1980). In addition to these drawbacks and limitations, the Cow-Model of Hijink and Meijer (1987) was parameterized on the basis of a relatively small number of observations (n = 157) from cows fed *ad libitum* with grass silage supplemented with concentrates.

Since the introduction of the model in 1987, cows and feeding practices in the Netherlands have changed significantly. For example, 305-d FPCM production increased from in 7500 kg in 1990 to 9300 kg in 2011 while average lactation length has increased from 305 to 355 days, together with an increase in the use Holstein-Friesian genes (CRV, 2012). Simultaneously, the proportion of maize silage in dairy cow rations has increased (CBS, 2013). Consequently, the conditions on which the Cow-Model was parameterised do not longer apply to the current situation on farms. Predictions of empirical models are only valid within the limits of the underlying datasets, which implies that predictions made with the Cow-Model of Hijink and Meijer (1987) are possibly no longer accurate for the modern-day dairy farm.

The major disadvantage of the Cow-Model is that it is not a truly predictive model able to predict animal performance in response to feeding management. The standard roughage intake capacity curve and the amounts of body energy available for mobilisation are linearly scaled with potential or target 305-d FCM yield. In addition, the Cow-Model assumes that cows will be supplemented with concentrates up to a level equal to the NE_L requirements for the (potential) MEO, maintenance, and calculated growth. Therefore, simulations with different dairy rations would always result in equal (user defined) MEO yields but with possibly different roughage and concentrates supplementation. This implies that the Cow-Model predicts only changes in concentrate supplementation in response to changes in feeding management which is a limited scope. The lack of flexibility, the limited biological meaning and the doubts about the accuracy of the Cow-Model called for the development of an alternative model for the prediction of feed intake and performance in dairy cows. To date, there are only a few models published capable to predict simultaneously feed intake, milk production and partitioning of ingested energy in dairy cows. Recent models such as GrazeIn (Faverdin et al., 2011) and e-Cow (Baudracco et al., 2012) are less suitable for a broad application in the Netherlands. Application of GrazeIn would require that the users must adopt the French net energy and metabolizable protein evaluation system, since predicted feed intake in this model partly depends on the energy and protein balances. This is a significant barrier for those who are using other energy and protein evaluation systems or are not familiar with the French feed evaluation systems. The e-Cow model is designed to predict herbage intake and performance of dairy cows grazing pastures in temperate regions and is therefore less suitable for intensive dairy farming systems based preserved forage.

1.2. Objectives

The objectives
This alternative model should be:

1) able to provide accurate predictions of feed intake and milk production body weight and body weight change in dairy cows

2) allow a reasonable biological explanation

3) easy to operate with inputs available on commercial farms

4) flexible and easy to modify and maintain

5) able to simulate a wide range of management and feeding practices on commercial farms.

The alternative model must be suitable as a tool for the formulation of dairy cow rations and feed budgeting, evaluation of feeding management, support of strategic decision making.

1.3. Outlines of the thesis

This thesis focusses on the development of a model for the prediction of the effects of animal and feed related factors and their interactions on DM and net energy intake and partitioning of ingested net energy to milk and body reserves in dairy cows.

Chapter 2 describes the concept and parameterization of a model for the prediction of the voluntary feed intake in dairy cows on the basis of 38515 individual weekly means of the performance of 1507 cows and considering the four criteria mentioned above.

Chapter 3 is devoted to the evaluation of the feed intake model using mean square prediction error (MSPE) and relative prediction error (RPE) as statistical criteria.

Chapter 4 is dedicated to the development of a deterministic model that predicts the partitioning of ingested net energy and the nutritional and physiological driven changes of body reserves using a dataset 20467 individual cow records and considering the four criteria mentioned above. The data used to calibrate the model comprised of 20467 records with the complete weekly means of dry matter intake (DMI), NE_LI, diet formulation, nutrient composition, milk yield and composition, body weight, DIM, days pregnant and parity number from 1294 individual cows

Chapter 5 presents the integration of the feed intake model (described in Chapter 2) and the energy partitioning model (described in Chapter 4) into the Wageningen UR Dairy Cow Model (Wageningen DCM). Furthermore, Chapter 5 includes an evaluation of the accuracy of the Wageningen DCM using mean square prediction error (MSPE) and relative prediction error (RPE) as statistical criteria.

Chapter 6, the General Discussion, focusses on aspects of different modelling approaches, suggestions for further improvements of the Wageningen DCM, and on the limitations and scope of the Wageningen DCM.

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Chapter 2

Development of a model for the prediction of feed intake by dairy cows 1. Prediction of feed intake

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Abstract

A study was undertaken to develop a model for the prediction of dry matter intake by lactating Holstein Friesian dairy cows. To estimate the model parameters, a calibration dataset was compiled with the data from 32 feeding experiments conducted at 9 different sites. The database contained weekly information on 1507 lactating Holstein Friesian dairy cows regarding their diet composition and feed analysis, together with their individual voluntary feed intake, milk yield (MY), milk composition, parity, days in lactation and days pregnant.

Dry matter intake was predicted from feed and animal characteristics. The feed chemical composition and digestibility can be related to feed degradation, bulk volume, intake rate, palatability and other factors influencing feed intake. Therefore, the data of standard feed analysis were used to estimate the satiety value of numerous commonly used feeds and forages. The satiety value is the measure of the extent to which a feed limits intake. The cows' ability to process the intake-limiting satiety value-units is expressed as the feed intake capacity, which is predicted from parity, days in milk and days of pregnancy which are indicators of the size and physiological state of the cow. This study shows that feed intake can be predicted using a limited number of easy-to-measure inputs that are available on commercial farms, yet reasonably biologically sound. Because the model inputs are not related to animal output (milk yield or body weight), future extension of the intake model with models for the prediction of animal performance is possible.

Keywords: feed intake, intake capacity, dairy cattle, modeling

1. Introduction

Models able to predict voluntary feed intake by lactating dairy cows are useful tools to optimize allocation of home-grown and purchased feeds to dairy cattle and to formulate dairy rations. Feed intake has a major impact on the performance of dairy cattle and the performance of dairy farms as a whole. Therefore, feed intake models are most valuable if they can be combined with other models that predict animal responses in terms of milk yield (MY), body weight (BW) change, nutrient use efficiency and gaseous emissions to feed and nutrient intake. For example, such models can be used for development and evaluation of feeding strategies aimed at realizing milk production goals, maximizing economical benefits and minimizing environmental burden.

Dairy cows vary in feed intake and milk performance. This variation can be attributed to variation in the chemical composition, nutritive value and physical properties among and within different types of feed for dairy cattle, but also to variation in feed intake capacity (FIC) attributable to differences in animal characteristics such as genetics, and physiological state (e.g. age, stage of lactation, pregnancy, size). Models that do not include either animal or feed characteristics are only valid for very specific groups of animals or diets. Therefore, it is essential that both, effects of feed and animal characteristics are incorporated into prediction models for feed intake by dairy cows. Earlier published feed intake models have already emphasized the importance of including both diet and animal characteristics as explanatory variables for dry matter intake (DMI) by dairy cattle (Forbes, 1977; Vadiveloo and Holmes, 1979; Jarrige et al., 1986; Kristensen and Ingvartsen, 1986; Hijink and Meijer, 1987; Halachmi et al., 2004). However, what these models have in common is that they include animal outputs (i.e. MY, herd average MY, BW) as model inputs. Consequently, these models are primarily predicting a DMI required to maintain a given MY and BW and they cannot be combined with other models predicting the effects of changing feed and diet composition on DMI and nutrient intake and hence MY and BW change. Therefore, the objective of this study was to develop the conceptual outlines, structure and parameterization of a model that predicts the voluntary feed intake by dairy cows. This model should be 1) easy to operate with inputs available on commercial farms; 2) applicable for a wide range of management and feeding practices; 3) allow integration with other models predicting the responses in cow performance (MY, BW change) to feeding strategy.

2. Conceptual outlines of the model

2.1. Principles of the feed intake model

For the development of a model for the prediction of feed intake in lactating dairy cows, we have adopted the basic principles of fill-unit systems (Jarrige et al., 1986; Kristensen and Ingvartsen, 1986). In fillunit systems, cows and feeds are described in terms of FIC (fill-units/d) and a Fill (fill-units/amount of feed), respectively. The DMI is calculated as the ratio between FIC and Fill (Equation 2.1).

$$\mathrm{DMI\,(kg/day)} = \frac{\mathrm{FIC\,(Fill\,units/day)}}{\mathrm{Fill\,(Fill\,units/kg\,DM)}} \tag{2.1}$$

The advantage of fill-unit systems is that they allow separation of variation in feed intake into variation caused by animal factors and variation caused by feed factors. The FIC is determined by the ability of the animal to process intake constraining feed factors (the fill), which can be related to factors, such as size, age and stage of lactation. The fill is determined by intake restraining (or promoting) properties of the feed, which can be related to factors, such as taste, digestibility and bulk volume. It is assumed that an *ad libitum* fed cow will eat until the total amount of consumed fill-units is equal to the FIC.

An additional advantage of fill-unit models is that they are easy to modify and more flexible than linear regression models, because extension of the model with alternative feeds or inclusion of new animal factors does not necessarily require re-estimation of all model parameters.

2.2. Feed intake capacity

Many concepts have been proposed to describe feed intake by dairy cows (Ingvartsen, 1994). In these concepts, BW and MY are often used as explanatory factors for feed intake. This approach make sense if it is assumed that cows are driven to achieve a level of energy intake that matches their requirements which implies that feed intake is ‘pulled’ by animal production. Body weight is regarded as an important factor for the prediction of DMI. A review of feed intake models by Ingvartsen (1994) indicates that dry matter intake of lactating increases from 0.66 to 2.5 kg per 100 kg increase in BW in lactating cows. Body weight is correlated with the size and capacity of the digestive tract (Allison, 1985; Doreau et al., 1985). Although rumen fill has no exclusive role in controlling feed intake (Ketelaars and Tolkamp, 1992), larger digestive organs may facilitate a greater ruminal content and thereby a higher voluntary intake. Therefore, MY, BW and BW measured shortly before prediction (Halachmi et al., 2004) could be useful explanatory variables of feed intake. Especially, to formulate diets and calculate concentrate supplementation to meet the requirements for a given level of milk yield. However, the use of MY and

BW as input variables is problematic when a feed intake model is used to predict the long-term effects of alternative feeding strategies (e.g. different forage options, forage to concentrate ratios) on animal performance and economics. Firstly, MY and BW are unknown at the time of prediction (Ingvartsen, 1994). Secondly, there is no direct relationship between actual BW and feed intake at any stage of lactation. In early lactation, cows mobilize body reserves and lose BW, whereas at the same time intake increases. In late lactation and pregnancy, when BW peaks, intake can be depressed either or both due to metabolic and hormonal changes (Ingvartsen and Andersen, 2000) and occupation of abdominal space by the growing uterus and fetus at the expense of the rumen and intestinal tract. In addition, BW and BW change are interfered by the effect of variation in DMI on rumen and gut fill (Chilliard et al., 1991). It is obvious that models using MY and BW as inputs to predict intake, cannot be combined with models that use feed and nutrient intake to predict MY and BW as outputs. Therefore, we have adopted the idea of Bines (1985) to assume that the shape of feed intake curve is similar to that of a lactation curve and to analyze it by an equation that uses days in lactation as a time scale. This is justified by the fact that the typical pattern of the feed intake curve coincides with the complex metabolic, physiological and hormonal changes during the lactation cycle (Ingvartsen and Andersen, 2000). This pattern is characterized by a feed intake depression around calving. Intake increases rapidly during the first part of the lactation, followed by a gradual decline. Further, we propose to use maturity or age as an alternative measure for cow size instead of BW. Age is very easy to measure and the size of the cow is related to age, as indicated by increasing average and post calving BWs with higher parity number (Koenen et al., 1999; van den Top et al., 2000). Previous published models have also recognized age as a factor influencing feed intake, either by using scaling factors to adjust feed intake for parity (Jarrige et al., 1986) or by using different equations for primiparous and multiparous cows (Kristensen and Ingvartsen, 1986). Rumen fill may be an intake constraint which also may depend on the cows' maturity. It has been suggested that differences in intake constraints between young and old cows were due to differences in intake behavior and mouth morphology (Boudon et al., 2009).

In conclusion, age, parity, stage of lactation and gestation are closely related with the cow's size and metabolic status and thereby important factors that influence feed intake capacity. Therefore, we propose a curve model of the FIC of which the shape is determined by parity, stage of lactation and stage of gestation. First, we assume that the *'base feed intake capacity'* (bFIC) of a cow increases as a function of parity similar to an asymptotic growth curve (Equation 2.2) ; Secondly, the curve of the bFIC is adjusted for the stage of lactation (Equation 2.3) and gestation (Equation 2.4) resulting in the FIC curve (Equation 2.5). Equation (2.2) reflects the concept that older more mature cows have a larger capacity for feed intake, absorption and utilization of nutrients because they have larger and better developed visceral organs and tissues than younger cows.

$$\mathrm{bFIC(p,d)} = \alpha_0 + \left(\alpha_1 - \alpha_2 \times \mathrm{d}\right) \times \left(1 - e^{-\rho_\alpha \times \left((\mathrm{p} - 1) + \mathrm{d}/365\right)}\right) \tag{2.2}$$

In which, bFIC(p,d) is the base feed intake capacity (units/d), p is parity number, d is days in lactation, α_0 is the initial level of the bFIC at onset of first lactation, α_1 is the maximum increase of the bFIC, α_2 is the interaction parameter of interaction between d and p, ρ_α is the rate parameter of the increase of bFIC from α_0 to the asymptotic level. The age of the cow is calculated as (p-1)+ d/365. Thus, at the start of the first lactation (p = 1; d = 0), bFIC(p,d) equals to α_0 (Figure 2.1). The asymptotic level of the bFIC (p = ∞; d = ∞) is equal to $\alpha_0+\alpha_1\alpha_2$d.

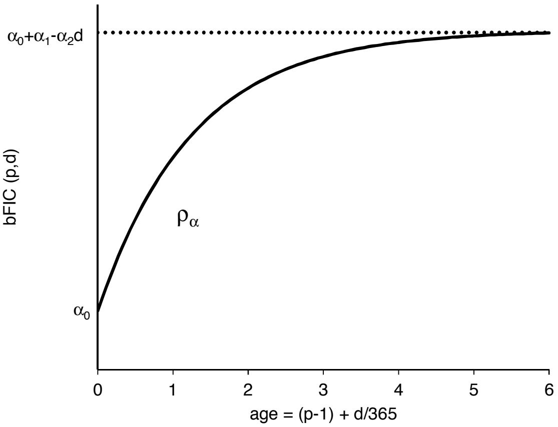

Figure 2.1 Evolution of the base feed intake capacity (bFIC) as function of age calculated from parity number (p) and days in lactation (d) (see Equation 2.1). Parameter α_0 is the initial level of the bFIC at onset of first lactation, α_1 is the maximum increase of the bFIC, α_2 is the interaction parameter of the interaction between p and d, ρ_α i s the rate parameter of the increase of bFIC from α_0 to the asymptotic level. At the start of the first lactation (p = 1; d = 0), bFIC(p,d) equals to α_0. The asymptotic level of the bFIC (p = ∞; d = ∞) is equal to $\alpha_0+\alpha_1\alpha_2$d

The changes in FIC related to stage of lactation are incorporated in the model by multiplying bFIC with adjustment factor (L(d)) for days in lactation (Equation 2.3). The adjustment factor for stage of lactation L(d) includes an asymptotic function representing the increasing (first) phase of the lactation curve (I(d); Equation 2.3a) and a logistic function which represents the declining phase of the feed intake curve (D(d); Equation 2.3b). The exponential of the product of I(d) and D(d) was used to calibrate the effect of stage of lactation to 1 (L(d) = e^0; no adjustment) at the start of the lactation.

$$\mathrm{L(d)} = e^{\left(\mathrm{I(d)} \times \mathrm{D(d)}\right)} \tag{2.3}$$

$$I(d) = \beta \times \left(1 - e^{-\rho_{\beta} \times d}\right) \tag{2.3a}$$

$$D(d) = \left(\frac{1}{1 + e^{\rho_{\gamma} \times (\ln(d) - \gamma)}}\right) \tag{2.3b}$$

The increasing (first) phase of the lactation curve, is represented by I(d) (Equation 2.3a) in which parameter β is the maximum (asymptotic) level of this function and parameter ρ_{β} the rate of increase and d days in lactation (Figure 2.2). The declining phase of the lactation curve is represented by D(d) (Equation 2.3b) in which ρ_{γ} is rate parameter of the declining phase, γ is time-point of maximum adjustment declining phase. At the start of lactation (d = 0), D(d) approaches 1. The inflection point of the logistic function occurs at time $d = e^{\gamma}$ from which the function will gradually approach zero.

The change in FIC related to stage of gestation is incorporated in the model by multiplying bFIC with a linear adjustment factor (P(g)) for the stage of gestation (Equation 2.4), in which δ_g is the rate parameter and g is days of gestation.

$$P(g) = \left(1 + \delta_g \times \left(\frac{g}{220}\right)\right) \tag{2.4}$$

In which, P(g) relative change of bFIC for days of gestation, g is days of gestation and δ_g is the rate parameter. It is assumed that cows are dried off at day 220 of gestation. Multiplication of equations (2.2), (2.3) and (2.4) describes the evolution of a cows' FIC as function of parity, days in lactation and days of gestation:

$$FIC(p,d,g) = \left(\left[\alpha_0 + (\alpha_1 - \alpha_2 \times d) \times \left(1 - e^{-\rho_{\alpha} \times ((p-1) + d/365)}\right)\right] \times e^{\frac{\beta \times \left(1 - e^{-\rho_{\beta} \times d}\right)}{1 + e^{\rho_{\gamma} \times (\ln(d) - \gamma)}}} \right) \times \left(1 + \delta_g \times \left(\frac{g}{220}\right)\right)$$

(2.5)

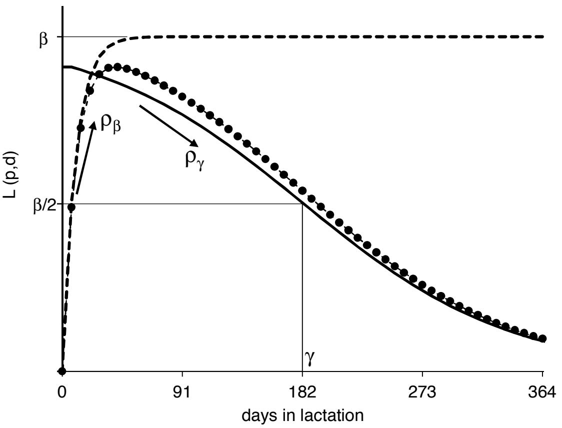

Figure 2.2 The adjustment factor L(d) for stage of lactation (Equation 2.3), The asymptotic function representing the increasing (first) phase of the lactation curve (Equation 2.3a) is indicated with the dashed line, the logistic function (Equation 2.3b) which represents the declining phase of the feed intake curve is displayed with the solid line. The product of these functions is represeted with the line with dots (•). Parameter β is the maximum (asymptotic) level of this function and parameter ρ_β the rate of increase and d days in lactation. Parameter ρ_γ is rate parameter of the declining phase of the lactation curve, γ is time-point of maximum adjustment declining phase.

2.3. Feed factors: satiety value

The term "fill-unit" suggests that intake is limited by the bulk volume of the feed. Physical limitation may be an important factor in regulating the intake of low digestible diets, but this may not be the case with high digestible diets for high yielding dairy cows. Rumen fill as the only factor regulating intake has been argued by Grovum (1995). Alternative factors, such as the osmotic effects of intra-ruminal acetate and propionate, hypertonicity of blood, hormones, volatile fatty acid absorption may also induce satiety (Grovum, 1995). For example, high digestible diets may result in an increased molar proportion of propionate, which subsequently could reduce DMI by increasing insulin secretion (Grovum, 1995). Alternatively, high digestible diets may also result in a depressed ruminal pH. Low ruminal pH levels are associated with a reduced DMI (Krause et al., 2002). Therefore, we propose a system that estimates feed specific satiety values (SV) from the chemical composition and digestibility of the feed. The SV of a feed, which indicates the extent to which a feed causes satiety and thereby constraining the intake, is described by an exponential function (Equation 2.6).

$$SV_p = e^{\left(\lambda_{p0}+\lambda_{p11}(x_{p1}-\bar{x}_{p1})+\lambda_{p12}(x_{p1}-\bar{x}_{p1})^2+\ldots+\lambda_{pn1}(x_{pn}-\bar{x}_{pn})+\lambda_{pn2}(x_{pn}-\bar{x}_{pn})^2\right)} \tag{2.6}$$

In which, SV_p is the satiety value of feed *p* (/kg DM), λ_{p0} is a feed specific parameter, λ_{pn1} is the parameter of the linear effect of feed *p* and feed characteristic *n*, λ_{pn2} is the parameter of the quadratic effect of feed *p* feed characteristic *n,* x_{pn} is the concentration of feed component *n* in feed *p*, $\bar{x}_{pn}$ is mean concentration of feed component *n* in feed *p*, n is feed component *n* (dry matter (DM), crude protein (CP), crude fiber (CF), *in vitro* digestible organic matter (dOM), ash, sugar, starch (g/kg DM), NH_3-N) and p is feed *p* (1,…,n). Grass silage is the most important forage in dairy cow in stall fed diets was used as a standard. Therefore, the feed specific parameter λ_{p0} of grass silage was defined as zero. Consequently, calculation of the SV of a "standard grass silage" (i.e. grass silage with an average composition $x_{pn} - \bar{x}_{pn} = 0$) with exponential function (Equation 2.6) results in SV = e^0 = 1.

2.3.1. Prediction of DMI

Combining equation (2.5) and (2.6) yields the following model for DMI (kg/d):

$$DMI = \frac{FIC}{\sum_P f_p \times SV_p} \tag{2.7a}$$

In which f_p is the fraction op feed *p* in the diet on a DM basis and SV_p is the satiety value of feed *p* (/kg DM) (*p* = 1,…,n). When a diet is supplemented with fixed amounts of feed, then the voluntary DMI (VDMI) is calculated according to equation (2.7b).

$$DMI = \frac{FIC - \sum_q DMIs_q \times SV_q}{\sum_p f_p \times SV_p} \tag{2.7b}$$

In which $DMIs_q$ the fixed amount (kg DM) of supplement *q* and SV_q is the satiety value of supplement q. When (a mixture of) supplemental forage or concentrate is offered, than the substitution rate (SR) of the basal ration by supplemental feeding is calculated by equation (2.8)

$$SR = \frac{\sum_q f_q \times SV_q}{\sum_p f_p \times SV_p} \tag{2.8}$$

In which f_q is proportion supplement *q* of total supplementation on a dry matter basis, and SV_q the satiety value of supplement *q*. The proportion of a feed in the whole can be calculated from the proportion in the fixed DMI amounts, and the proportion of the feed in the free accessible feed mixture.

3. Materials and methods

3.1. Calibration dataset

A calibration dataset was compiled from 32 feeding experiments conducted at different experimental sites in the Netherlands (Table 2.1). The calibration dataset consisted of 38515 individual weekly means of total DMI, the proportion each feed in the diet on a DM basis, chemical composition, digestibility and feeding value of each feed, MY, milk fat, protein and lactose concentration and BW of 1507 unique cows. It also contained records of parity number, calving date and conception date of each cow, except for experiments 11 and 12 in which the conception dates were missing. Missing conception dates were calculated as calving date minus 275. Feed composition and digestibility were available for each batch of feed, except for experiments 11 and 12 in the concentrations of ash, starch and sugars were not available. Lacking data were assigned as missing values. These experiments were excluded from parameter estimation when parameters other than CP and crude fiber were used to estimate the SV of concentrate. Only data from clinical healthy cows were used. An overview of diet composition and animal performance is presented in Table 2.2. There was no information on date of birth present in the database. Therefore, age was calculated from parity and stage of lactation (parity number-1) + days of lactation/365. Approximately, 42% of the total observations were from pregnant cows. The proportions of total observations per weeks of lactation and the proportion of observations in pregnant animals are displayed in Figure 2.3. Details on the proportions of DMI of each feed, number of feed samples and chemical compositions of the feeds included in the diets are provided in Appendix 1.

Table 2.1 Summary of the developmental dataset including dietary treatments, milk performance, body weight and dry matter intake (DMI)

			Number[3] of		Milk yield (kg/d)		Milk fat yield (g/d)		Milk protein (g/d)		Body weight (kg)		DMI (kg/d)	
Exp[1].	Site[2]	Main ingredients of the diet	Cows	Obs.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
1	WHB2	Grass silage. maize silage. concentrates	84	1062	32.7	6.5	1508	320	1101	206	595	78.2	21.6	3.1
2	WHB2	Grass silage. maize silage. concentrates	38	399	20.8	4.1	1064	208	700	133	582	64.7	18.9	3.1
3	WHB3	Grass silage. maize silage. concentrates	28	395	34.1	6.9	1571	308	1172	209	606	72.3	22.3	3.0
4	ZV	Grass silage. concentrates	47	423	32.6	5.5	1424	255	1029	176	583	68.2	20.9	3.5
5	WHB3	Fresh grass. maize silage. concentrate	46	476	25.0	5.5	1060	193	838	161	598	66.9	20.0	2.5
6	WHB2	Fresh grass. maize silage. concentrate	34	600	28.1	5.6	1221	224	918	179	549	62.8	20.6	3.0
7	WHB2	Fresh grass. maize silage. concentrate	42	768	30.7	5.1	1389	226	1011	148	594	51.7	20.0	2.3
8	WHB3	Grass silage. GEMS. concentrate. dry by-products	54	718	24.9	4.4	1063	199	795	135	573	52.0	18.5	2.4
9	WHB3	Fresh grass. GEMS. concentrate	48	766	29.7	6.1	1290	272	977	194	605	62.5	21.0	2.8
10	WHB3	Grass silage. GEMS. fodder beet. concentrate. dry by-products	56	839	30.9	5.6	1405	284	1017	172	599	71.6	19.6	3.2
11	’t Gen	Dehydrated grass. grass silage. maize silage. concentrate	306	7216	27.5	5.2	1134	196	951	150	540	51.7	20.1	2.9
12	’t Gen	Dehydrated grass. grass silage. maize silage. concentrate	262	6551	29.6	6.7	1184	267	1012	186	570	59.1	20.1	3.0
13	MH	Grass silage. maize silage. concentrates	38	760	35.3	3.9	1405	174	1106	103	593	54.4	21.3	2.4
14	AH	Fresh grass and grass/clover. concentrate	28	252	22.4	4.2	1004	166	812	129	604	57.1	18.3	1.8
15	AH	Fresh grass and grass/clover. concentrate	37	451	26.9	6.1	1093	208	919	177	598	54.5	19.0	2.3
16	AH	Fresh grass and grass/clover. concentrate	41	565	29.2	5.4	1204	216	1016	153	619	65.3	20.5	2.3
17	AH	Fresh grass and grass/clover. concentrate	42	572	29.0	5.3	1205	193	964	160	616	63.2	19.9	1.9
18	AH	Grass silage and grass/clover silage. red clover silage. concentrate	30	314	30.4	4.9	1362	230	1048	147	643	55.3	21.9	2.0
19	AH	Grass silage and grass/clover silage. red clover silage. concentrate	30	390	31.9	6.1	1368	220	1061	155	638	56.4	21.6	2.2
20	CD	Grass silage. maize silage. cereal-WCS. concentrate. dry by-products	40	599	30.7	5.4	1473	294	1020	177	634	74.5	19.5	2.6

Table 2.1 continued on the next page

Table 2.1 Continued. Summary of the developmental dataset including dietary treatments, milk performance, body weight and dry matter intake (DMI)

Exp[1].	Site[2]	Main ingredients of the diet	Number[3] of		Milk yield (kg/d)		Milk fat yield (g/d)		Milk protein yield (g/d)		Body weight (kg)		DMI (kg/d)	
			Cows	Obs.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
21	CD	Grass silage. maize silage. cereal-WCS. concentrate. dry by-products	42	609	30.2	6.1	1396	333	1000	189	635	77.1	20.5	2.8
22	CD	Grass silage. maize silage. cereal-WCS. concentrate. dry by-products	39	581	33.0	6.7	1499	357	1059	193	637	65.8	20.6	2.6
23	AH	Lucerne silage. concentrate	24	192	32.0	4.6	1346	200	1001	136	601	62.8	24.0	2.9
24	CD	Lucerne silage. concentrate	41	400	30.8	5.7	1371	290	1004	185	615	55.8	21.1	3.0
25	CD	Lucerne silage. concentrate	45	435	29.1	6.7	1313	333	945	205	621	72.6	19.8	3.6
26	WBH4	Grass silage. maize silage. GEMS. concentrate. dry by-products	172	6780	31.6	10.5	1334	385	1112	314	644	71.3	21.5	3.5
27	BZ	Grass silage. concentrates. crushed wheat	45	529	30.4	5.4	1386	254	1002	160	580	63.1	19.9	2.8
28	BZ	Grass silage. concentrates. crushed wheat	45	537	28.5	4.7	1272	213	959	145	592	65.2	18.6	2.5
29	WBH2	Grass silage. maize silage. concentrates	79	1395	30.8	6.0	1439	300	1011	182	598	68.2	21.8	3.0
30	WBH2	Grass silage. maize silage. concentrates	84	1635	33.5	6.9	1479	321	1131	221	633	78.6	23.0	3.0
31	ZV	Grass silage. concentrates. pressed beet pulp	39	584	29.9	5.1	1311	245	974	165	587	80.7	20.7	4.0
32	ZV	Grass silage. concentrates. pressed beet pulp	39	722	29.8	5.0	1331	208	1003	152	601	63.3	20.7	2.5

1 Exp = Experiment References Exp 1-3 (Feil et al., 2000a); Exp 5-7 (van Duinkerken et al., 2000); Exp 8-10 (Zom, 1996); Exp. 11-13 Unpublished; Exp 13-19 (Remmelink, 2000); Exp 20-222; (van Duinkerken and Bleumer, 2000); Exp 23-25 (Boxem et al., 1999);Exp 26 (Meijer et al., 1998);Exp. 27, 28 (Feil et al., 2000b); Exp 29-32 (Zom et al., 2001)

2 Site – Experimental site AH = Aver Heino, Heino,;BZ = Bosma Zathe, Ureterp; CD = Cranendonck, Soerendonk; 't Gen, Lelystad; MH= Minderhoudhoeve , Swifterbant; WBH2, WBH3 = Waiboerhoeve Dairy Unit 2, 3, Lelystad; WBH4 = Waiboerhoeve High Performance Unit, Lelystad; ZV = Zegveld

3 Number of cows = number of unique cows; Number of Obs = Number of observations individual weekly per cow.

Table 2.2. Mean, minimum, maximum values and standard deviation of feed intake, milk yield, milk constituent yield, and body weight in the developmental database from 38515 individual weekly observations from 1507 unique cows

	Mean	Minimum	Maximum	s.d.
Feed intake				
Dry matter intake (kg/day)	20.7	4.5	37.8	3.1
Concentrate intake (kg DM/day)	7.8	0.0	15.0	2.5
Concentrate as proportion of DMI	0.38	0.0	0.77	0.11
Milk production				
Milk yield (kg/day)	29.9	5.5	71.4	7.3
Fat (g/day)	1275	202	3194	308
Protein (g/day)	1013	186	2278	219
Days in milk	115	1	584	82
Parity number	2.4	1	11	1.6
Days pregnant	26	0	235	48
Body weight (kg)	593	400	963	74

In all experiments, high genetic merit Holstein-Friesian cows were housed in cubicle sheds, milked twice daily, and had unrestricted access to forage and drinking water. The cows, managed according to practice typical to the Netherlands, were individually fed using transpondercontrolled concentrate feeders and feed access doors or weighing troughs.

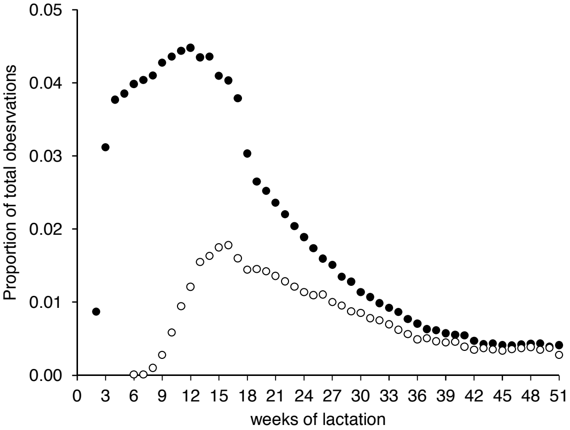

Figure 2.3 Proportion of total observations (n=38,515) per weeks of lactation (●) and proportion of total observations in pregnant animals (○).

In all experiments, fresh forage mixtures were offered once or twice daily and the refusals were weighed and removed daily. To ensure *ad libitum* intake of forage (mixtures), the quantities offered were such that the refusal weight was at least 10% of the amount offered. In most experiments concentrates were fed separately from the forage using computer controlled dispensers. However, in all experiments a part of the concentrate was mixed with the forage. The diets had a balanced nutrient composition and were formulated to meet the recommendations for net energy for lactation (NE_L) (van Es, 1978), intestinal digestible protein (DVE), rumen degradable protein balance (OEB) (Tamminga et al., 1994) and trace minerals (Commissie Onderzoek Minerale Voeding (COMV), 1996) which were in use at the time the experiment was conducted .

The grass silages were harvested from swards that predominantly consisted of perennial ryegrass (> 80%) or mixed swards with perennial ryegrass and clover (experiments 18 and 19). In experiments 31 and 32, grass silages were harvested from swards that consisted of naturally occurring grasses with a low proportion of perennial ryegrass (< 25%). Before ensiling, grass and legumes were wilted for 24 to 48 h and after that harvested with a precision chop harvester. Fresh grass and fresh grass/clover mixtures were zero-grazed by daily harvesting with a diskmower and a self-loading wagon without additional cutting. To mimic herbage quality at grazing, fresh herbage was cut when the sward surface height was between 15 and 20 cm, corresponding with DM yields that ranged between 1400 and 2000 kg DM/ha above 5 cm cutting height, corresponding with a rising plate meter height of 17 cm. The concentrations of DM, CP, CF, ash, sugars and dOM in fresh cut grass and grass/clover mixtures were determined in composite samples created from daily samples which were pooled on a weekly basis.

Maize silage, ground ears of maize silage (GEMS) and cereal whole crop silage (WCS) were harvested using precision chop harvesters with a theoretical chop size between 5 and 9 mm. Kernel processors were used to ensure that the grain kernels were sufficiently damaged. All silages were stored in clamps that were compacted with heavy equipment, sealed with plastic sheets and weighed down with a sand load or sandbags. The silages were made without the use of silage additives.

Individual feed intake and MY were recorded daily. Weekly, milk samples were collected during 2 or 4 consecutive milkings and analyzed for fat, protein and lactose. Analysis of the milk samples was performed at the laboratory of Qlip (Zutphen, Netherlands). Weighed means of the fat, protein and lactose concentration were calculated also on a weekly basis. Body weights were recorded three times a week or daily, depending on the experimental procedures, and one weekly mean BW was calculated for each cow.

All feeds were analyzed for the concentrations of dry matter (DM), crude protein (CP), crude fiber (CF) and ash. Spectrophotometric analysis was used to determine nitrogen concentration. Subsequently, CP was calculated as 6.25×N-Kjeldahl (ISO, 1979, 1997, 2005). The ash concentration was determined gravimetrically after incineration in a muffle oven at 550° C (ISO, 1978, 2002). The CF concentration was determined from the weight difference after cooking in successively 0.3 N H2SO4 and 1.5 N NaOH followed by incineration of the remains at 550° C (NEN, 1988) Sugar concentration was determined in grass(/clover) silage, fresh herbage, alfalfa silage, concentrates and by-products as described by (van

Vuuren et al., 1993). Starch concentration was determined in maize silage, GEMS cereal-WCS, concentrates and by-products. Starch concentration was determined as glucose using the amyloglucosidase method (Bergmeyer, 1970) after releasing the starch by heating in a boiling water bath in the presence of 2 N HCl. Forage, and occasionally concentrates, were analyzed for *in vitro* organic matter digestibility (OMD%) according to the method of (Tilley and Terry, 1963). The concentration of *in-vitro* digestible organic matter (dOM) was calculated as (1000-ash)×OMD%/100. The NH_3-N fraction (NH_3-nitrogen as percentage of total nitrogen) was determined in grass silage, alfalfa silage and cereal-WCS. The chemical composition of the feeds is presented in Table 2.3

Table 2.3. Number of feed batches, mean compositions with standard deviation of the feeds included in the developmental dataset

			Feed component															
			DM (%)		CP (g/kg DM)		CF (g/kg DM)		dOM (g/kg DM)		Ash (g/kg DM)		Sugar (g/kg DM)		Starch (g/kg DM)		NH3-N (%)	
	No.	No.Batches	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Grass silage	1	202	44.8	10.22	170	30.7	240	18.5	674	28.4	111	19.3	80	40.1			7	2.7
Fresh herbage	2	185	14.7	2.92	182	39.9	230	22.6	705	32.9	114	17.9	118	55.0				
Legumes silage	3	29	32.2	5.28	183	18.5	275	38.2	577	38.2	145	29.2	3	16.6			12	2.1
Maize silage	4	227	33.4	3.00	81	8.3	193	17.7	695	23.3	52	8.7			325	39.0		
GEMS	5	53	54.0	5.84	87	7.3	77	13.9	821	20.7	23	4.8			575	44.0		
Cereal-WCS	6	18	39.8	4.39	74	7.9	283	21.2	569	31.7	51	16.7			171	59.9		
Concentrates	7	218	89.7	1.12	182	111.3	140	36.9			100	17.5	115	28.9	82	60.3		
Fodder beet	8	12	16.3	0.89	64	10.2	68	10.2	850	10.9	81	9.7	560	65.2				
Crushed wheat	9	4	87.8	0.71	127	2.6	27	2.5	832	13.3	17	0.6			592	12.4		
Dehydrated grass	10	115	88.0	1.75	191	28.3	203	31.1	722	29.7	115	16.1						
Pressed beet pulp	11	8	21.9	0.91	94	6.9	205	4.9	791	13.4	64	19.0	23	22.9				

3.2. Modeling procedures

The parameters of the equations of FIC and SV combined in equation (2.7a) were estimated simultaneously using a non-linear regression analysis based on a maximum likelihood method, according to the Gauss-Newton iteration of the FITNONLINEAR of Genstat. The initial models for the SV included: fresh grass, grass silage, alfalfa silage, red clover silage, maize silage, GEMS, cereal-WCS, concentrate and dry by-products, fodder beet, crushed wheat, dehydrated grass and pressed beet pulp. Each cycle of parameter estimation started with the complete models for FIC and SV, once iteration had converged, non-significant parameters were removed from the models. In a subsequent step, the remaining parameters were estimated again. Adjustments to the models were checked on the basis of the goodness of fit and bias. Strongly-correlated model parameters were in turn removed from the model and the remaining model parameters were estimated again. The option with the model parameter with the best fit was retained in the final model. This was done to keep the model as simple as possible and minimize the number model parameters. This because inclusion of non-significant parameter does not contribute to an improved prediction error, but results in unnecessary complexity of the model. Finally, the remaining model included only significant and relevant explanatory parameters.

4. Results and discussion

The dataset consisted of data of feeding experiments with high merit Holstein Friesian cows, kept under similar housing conditions and which were offered a range of different forages and forage to concentrate ratios. Cow handling, breeding and feeding methods were performed according to management protocols which were the same at each experimental site. Because of the origin of the developmental dataset, the use of the model is limited to well managed high merit lactating Holstein Friesian cows first calving at 2 years of age with a normal BCS (range 2 to 4 on a 5 point scale).

4.1. Feed intake capacity

The final model for FIC that remained after elimination of non-significant parameters is given by equation (2.9) (See equation (2.2), (2.3), and (2.4) for description of the parameters). The estimates of the parameters are given in Table 2.4. The curves of the FIC during successive lactations are displayed in Figure 2.4:

$$\mathrm{FIC(p,d,g)}\left(\left[\alpha_0+\alpha_1\times\left(1\text{-}e^{-\rho_\alpha((\mathrm{p}\text{-}1)+\mathrm{d}/365)}\right)\right]\times e^{\beta(1-e^{-\rho_\beta \mathrm{d}})}\right)\times\left(1-\delta_{\mathrm{g}}\times\left(\frac{\mathrm{g}}{220}\right)\right) \tag{2.9}$$

Contrary to some existing models, our model predicts different intake curves for successive parities. In particular, the shape of curves during first and second parity differs from later parities as displayed in Figure 2.4. The total annual FIC of first, second and third lactation cows relative to the annual FIC of a mature cow (parity number ≥4) amounted to 0.82, 0.95 and 0.98, respectively. The increase of the predicted FIC during the first, second and third lactation corresponds with the increase in DMI in stall fed cows receiving a TMR with concentrate (500 g DM/kg DM) as observed by (Oldenbroek, 1989) and in grazing cows as observed by (Kennedy et al., 2003). Differences in both level and shape of FIC curves during successive parities are probably associated with the increase in age and size of the cow. The capacity of the digestive tract is correlated with the size of the animal (Allison, 1985; Doreau et al., 1985), and rumen fill may be an intake constraint which depends on maturity (Boudon et al., 2009). In first parity cows, the predicted maximum intake capacity is reached at the end of lactation. A similar intake pattern for dairy heifers was observed by (Oldenbroek, 1986).

Table 2.4. Estimated parameters of the model for feed intake capacity (FIC(p.d.g))

Model: $$FIC(p,d,g)\left(\left[\alpha_0+\alpha_1\times\left(1\text{-}e^{-\rho_\alpha((p-1)+d/365)}\right)\right]\times e^{\beta(1-e^{-\rho_\beta d})}\right)\times\left(1-\delta_g\times\left(\frac{g}{220}\right)\right)$$

Parameter	Estimate	Standard error
α_0	8.0838	0.0997
α_1	3.2956	0.0478
ρ_α	1.2758	0.0282
β	0.3983	0.00105
ρ_β	0.05341	0.00169
δ_{220}	0.06907	0.00932

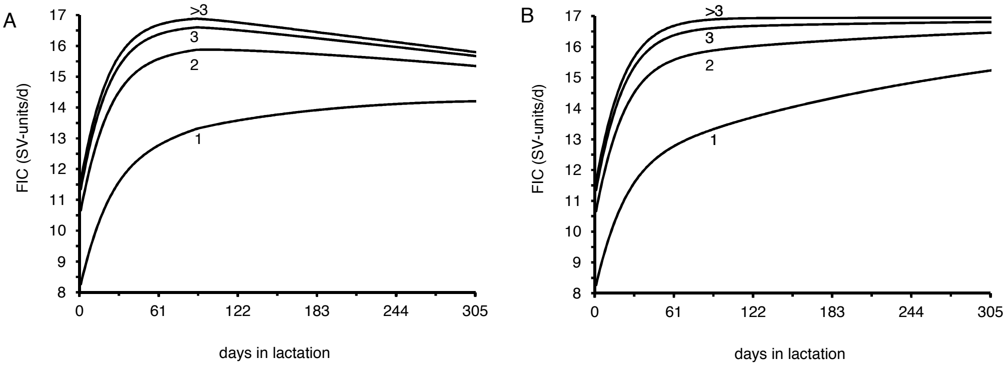

Figure 2.4 The evolution of the feed intake capacity (FIC) during the course of the lactation. Graph A: the FIC of pregnant Holstein Friesian cows, conception at 90 *post-partum*. Graph B: the FIC of non-pregnant Holstein Friesian cows.

The results indicate that age calculated from parity and day in lactation can be used as an alternative for BW to express the size of a cow. Because birth dates were not available in the developmental dataset, age was calculated from parity and stage of lactation (age = (parity -1) + days in lactation/365). The complex metabolic, physiological and hormonal changes are closely related with calving, onset of lactation and pregnancy (Ingvartsen and Andersen, 2000). Therefore, an age calculated from parity and days in lactation is probably a better indication of the physiological status and changes in FIC than real time age. Moreover, in intensive dairy production systems, first calving occurs usually around an age of 2 years with little variation.

Within lactation, the model predicts that FIC increases rapidly from calving onward during the first months after calving. This typical pattern is associated with changes in metabolism, lactation and tissue mobilization and is related to complex regulation mechanisms and signals from nutrients, metabolites, hormones and neuropeptides (Ingvartsen and Andersen, 2000). The low feed intake around calving may also be related to adaptation of the rumen microbial population during the transition period (Goff and Horst, 1997). In addition, the time required for adaptation of rumen epithelium (Mayer and Liebich, 1980; Liebich et al., 1982; Mayer et al., 1986; Liebich et al., 1987) may also be an important factor in the increase of FIC during early lactation. During early lactation, rumen papillae reach their maximum size 7 to 9 weeks after changing over from a low-energy to a high-energy diet (Mayer et al., 1986; Liebich et al., 1987; Bannink et al., 2005). The change in FIC during the course of the lactation may be also associated with changes in volume of rumen, small intestine, and in liver weight (Baldwin et al., 2004).

During the curve-fitting process the logistic function D(d) (Equation 2.3b) was eliminated from the initial model. As a result, FIC does not decline during the progress of the lactation. However, a linear adjustment factor for stage gestation is included in the model. As a result, the FIC of pregnant cows starts to decline linearly from the first day of gestation. At day 220 of gestation (time point of drying off), the FIC would be 0.93 × the FIC of a non-pregnant cow with the same parity number and stage of lactation. This reduction in feed intake compares to the observations of Ingvartsen et al. (1992) who found a relative decline of 0.015 per week of the voluntary DMI of pregnant dairy heifers from the 26th week of pregnancy onward. This implies that on day 220 of pregnancy the FIC of pregnant cows drops to 0.925 × the FIC of a non-pregnant cow in the same stage of lactation. The work of Hayirli et al. (2003) showed that DMI by pregnant cows can be accurately described with a non-linear function. However, according to this model, a depression in DMI is only noticeably beyond day 259 and day 233 of gestation in primiparous and multiparous, respectively. Whereas, the use of our model is intended for lactating cows that are dried off around day 220 of pregnancy. Thus, before the time a non-linear depression of DMI is noticeable.

Variation in feed intake capacity between animals may be caused by differences in genetic potential for milk production. It is observed that feed intake can vary between breeds (Oldenbroek, 1984; Dillon et al., 2003) and within breeds between selection strains (McCarthy et al., 2007; Sheahan et al., 2011). There is a genetic correlation between milk yield and feed intake (van Aarendonk et al., 1991). Therefore, selection for increased milk yield should result in an increased feed intake capacity. This would justify the inclusion of a factor related to potential milk production in the model. However, it is difficult to establish the milk production potential of dairy cows. Feeding, management and housing conditions are seldom non-limiting throughout the whole lactation. The developmental dataset contains data from high merit Holstein-Friesian cows which were managed according good farming practice using uniform cow handling, breeding and feeding protocols which can be considered as good farming practice. Under these conditions we assume that the cows were able to express their genetic potential and that variation in feed intake is primarily attributable to variation in animal characteristics (parity stage of lactation, gestation) and feed characteristics (diet and feed composition). When the model is applied to other breeds or selection strains than high merit Holstein Friesian cows, FIC should be adjusted for breed or genetic potential.

Variation in feed intake between animals is possibly also related to differences in BCS at calving. A literature review by (Remppis et al., 2011) indicates that well-conditioned cows exhibit a lower DMI and greater NEB in early lactation. Unfortunately, there were no data on BCS present in the developmental dataset. Therefore, BCS was not included in the model. Therefore, DMI of cows might be over-estimated in obese cows.

4.2. Satiety values (SV)

The parameter estimates of the models for the SV of each feed are presented in Table 2.5.

Table 2.5 Parameter estimates of the satiety value (SV), the standard error (s.e.) is displayed between brackets.

Model[1]: $SV_p = e^{(\lambda_{p0}+\lambda_{p11}(x_{p1}/10-\bar{x}_{p1}/10)+\lambda_{p12}(x_{p1}/10-\bar{x}_{p1}/10)^2+.\lambda_{p21}(x_{p2}-\bar{x}_{p2})+\lambda_{p22}(x_{p2}-\bar{x}_{p2})^2+\lambda_{p31}(x_{p3}-\bar{x}_{p3})+\lambda_{p32}(x_{p3}-\bar{x}_{p3})^2+\lambda_{p41}(x_{p4}-\bar{x}_{p4})}$

	Feed	p	Grass silage 1	Fresh cut grass(/clover) 2	Legumes silage 3	Maize silage 4	GEMS 5	Cereal-WCS 6	Concentrates 7	Fodder beet 8	Crushed Wheat 9
Parameters											
Constant		λ_{p0}		-83.34×10^{-3}	-58.59×10^{-3}	-216.58×10^{-3}	309.4×10^{-3}	-113.2×10^{-3}	-1148.3×10^{-3}	-367.3×10^{-3}	-281×10^{-3}
		s.e.		(4.18×10^{-3})	(7.16×10^{-3})	$(7.46\times10^{-3)}$	(12.4×10^{-3})	(13.8×10^{-3})	(20.2×10^{-3})	(35.7×10^{-3})	(35.7×10^{-3})
DM		$\bar{x}_{p1}$	450		320	330	540				
	linear	λ_{p11}	-1.613×10^{-3}		-5.54×10^{-3}	-2.737×10^{-3}	-11.79×10^{-3}				
		s.e.	(0.216×10^{-3})		(1.06×10^{-3})	(0.986×10^{-3})	(1.85×10^{-3})				
	quadratic	λ_{p12}	0.0991×10^{-3}		0.807×10^{-3}	2.962×10^{-3}					
		s.e.	(0.018×10^{-3})		(0.142×10^{-3})	(0.21×10^{-3})					
CP		$\bar{x}_{p2}$	170								
	linear	λ_{p21}	-0.3321×10^{-3}								
		s.e.	(0.0837×10^{-3})								
	quadratic	λ_{p22}									
		$\bar{x}_{p3}$	240					283	140		
CF	linear	λ_{p31}	1.551×10^{-3}	-0.206×10^{-3}	0.428×10^{-3}			5.216×10^{-3}	1.335×10^{-3}		
		s.e.	(0.125×10^{-3})	(0.0147×10^{-3})	(0.129×10^{-3})			(0.31×10^{-3})	(0.212×10^{-3})		
	quadratic	λ_{p32}		0.0142×10^{-3}							
		s.e.		(0.0030×10^{-3})							
		$\bar{x}_{p4}$		705		695					
dOM	linear	λ_{p41}		-0.7443×10^{-3}		-0.559×10^{-3}					
		s.e.		(0.0771×10^{-3})		(0.14×10^{-3})					
SV	Mean		1.00	0.93	0.96	0.83	0.74	0.89	0.35	0.69	0.76
	Minimum		0.90	0.88	0.91	0.78	0.65	0.75	0.28		
	Maximum		1.16	1.10	1.03	1.04	0.82	1.07	0.40		

[1] Model parameters: $x_{p1}, x_{p2}, x_{p3}, x_{p4}$ = the observed concentrations of DM, CP, crude fiber (CF) and digestible organic matter (dOM) in feed *p*, respectively. $\bar{x}_{p1}, \bar{x}_{p2}, \bar{x}_{p3}, \bar{x}_{p4}$ = the mean concentrations of DM, CP, crude fiber (CF) and digestible organic matter (dOM) in feed *p*, respectively, p is feed p (1,…,9),

4.2.1. Grass(/clover) silage

The SV of grass(/clover) silage was described by the concentrations of DM, CP and CF. The predicted curvilinear relationship between the SV and DM concentration of grass silage reached a minimum SV at 450 g DM/kg, and increased there above. This is in agreement with Huhtanen et al. (2007) which observed that grass silage intake increased quadratically, up to of 420 g DM/kg and declined with higher DM concentrations. A decreasing SV of grass(/clover) silage with increasing DM concentration up to 450 g/kg is also in agreement with the observations that wilting of grass up to moderate DM concentration results in higher silage DMI of cattle (Teller et al., 1993; Patterson et al., 1996; Offer et al., 1998; Wright et al., 2000). The influence of DM concentration on DMI is complex. Reduced DMI with low silage DM concentration can be due to numerous factors such as internal water, bulk volume, ruminal outflow and silage fermentation products such as ammonia and bioamines (Teller et al., 1993; Dulphy and van Os, 1996; Wright et al., 2000; Huhtanen et al., 2007). Grass/clover silage with a DM concentration above 450 g/kg is possibly more difficult to consume than moist grass silage because of its coarser texture which may explain the increasing SV above 450 g DM/kg.

The SV of grass(/clover) silage decreased linearly as the CP concentration increased. The increased SV of grass silage at a low CP concentration is probably related to the classical effects of maturity of the grass at harvest. Increased maturity is associated with a reduced OM digestibility and CP concentration as well as increased fiber concentration. In addition, low CP concentration may be also indicative for a negative rumen degradable protein balance (OEB) which has an adverse effect on fiber digestion (Tamminga et al., 1994). Low CP concentration and (a negative OEB) may cause a shortage in the supply of nitrogen to rumen microbes relative to the supply of fermentable organic matter.

In grass silage, high fiber concentration are associated with a reduced digestibility (Bosch et al., 1992; Deboever et al., 1993; Huhtanen et al., 2007). A reduced digestibility may explain the increase of the SV of grass silage as CF concentration increases. Recent work shows that the intake of grass silage is highly influenced by its digestibility (Huhtanen et al., 2007). In addition, a high CF concentration results in a longer rumination and chewing time per kg DM, whereas an increased rumination and chewing time per kg DM results in a reduction of DMI (Deboever et al., 1993). A strong negative correlation between CF concentration and voluntary DMI was also observed in dehydrated grass (Schukking, 1974).

4.2.2. Fresh grass(/clover)

The SV of fresh grass(/clover) was determined by the concentrations of CF and dOM. A curvilinear relationship was observed between the SV of fresh grass and grass/clover and CF concentration. The predicted SV decreases to a minimum level at 237 g CF/kg DM and increase above. A reduced intake resulting from an increased SV at high CF concentration can be explained by a greater resistance to particle size reduction and hence to a reduced outflow rate from the rumen. High CF concentration in fresh grass(/clover) is known to be accompanied by high concentrations of cellulose and lignin and a reduced OMD% resulting in a lower intake (DeBrabander et al., 1996). An increasing SV of fresh grass/clover with low CF concentration, may be related to a lack of physical effective fiber resulting in subclinical rumen acidosis. Low rumen pH and sub-clinical rumen acidosis may depress DMI (Krause et al., 2002). The SV of fresh grass decreased linearly as the dOM concentration increased. This effect of dOM on SV be associated with higher rates of OM disappearance from the rumen as dOM increases (van Vuuren et al., 1991). In addition, a low dOM concentration may be also accompanied with a high ash fraction as result from contamination with soil during harvest. Contamination with soil may reduce palatability and intake.

Water content is often considered as an important factor that influences herbage intake (Verite and Journet, 1970; Butris and Phillips, 1987; Phillips et al., 1991). However, water content (or DM concentration) was purposely not included in the model, because herbage DMI by dairy cows is restricted by internal, but not external water (Estrada et al., 2004). With the common methods of the analysis of DM concentration, is it not possible to distinguish external water (from rainfall) from internal water. Moreover, in the developmental dataset DM concentration was based on weekly means, whereas herbage DM concentration can vary significantly within and between days, depending on time of day and weather conditions. Therefore, most of the variation in DM concentration will be leveled out by calculation of these weekly means.

4.2.3. Legume silages

The SV of legume silage was described by the concentrations of DM and CF. Initially, we developed separate equations for the SV of lucerne and red clover silage, but during the calibration process it appeared that the model parameters and behavior of these equations were very similar. Therefore, we decided to develop one equation for legume silage to be applied for both lucerne and red clover silage. Similar to grass silage, an increased SV at a low DM concentration is possibly associated with greater bulk volume and silage fermentation. Wilting legume silage up to a high DM concentration may result in a relatively higher loss of the high digestible leave fraction (Boxem et al., 1999). Therefore, an increased SV above 337 g DM/kg is possibly also related to a reduced digestibility due to loss of leaves. The positive linear relationship between CF concentration and the SV of legume silage is likely to be due to the adverse effects of a reduced digestibility on intake when fiber concentration is increased as observed in grass silages (Bosch et al., 1992; Deboever et al., 1993; Huhtanen et al., 2007).

4.2.4. Maize silage, GEMS, cereal-WCS silage

The SV of maize silage was described by the concentrations of DM and dOM. There was curvilinear relationship between the SV of maize silage and the DM concentration which showed a minimum SV at 335 g DM/kg. The SV decreased linearly with an increasing dOM concentration. The curvilinear relationship between DM concentration and the SV of maize silage is in agreement with the relationship between DM concentration and DMI observed by (Phipps et al., 2000).

The effects of DM concentration on the SV of maize silage are attributed to changes in chemical composition, digestibility and morphology of the maize crop as the plant matures. For example, increased maturity results in lower NDF and higher ADF and ADL concentrations in the leaf and stem fraction (St Pierre et al., 1987; Russell et al., 1992; van Dijk et al., 2005). Advancing maturity is also accompanied with higher starch concentration but a reduced degradation rate of starch in the rumen (Philippeau and Michalet-Doreau, 1997; Philippeau et al., 1999; Sutton et al., 2000). Although cell wall digestibility decreases during maturation, the digestibility of total organic matter is hardly affected because a reduced cell wall digestibility is compensated by a smaller leaf to grain ratio (Russell et al., 1992; Philippeau and Michalet-Doreau, 1997; Sutton et al., 2000; van Dijk et al., 2005). An increased dOM concentration in maize silage resulted in a reduced SV, which is probably related to a larger proportion of grain and a higher rate and extent of degradation and passage from the rumen. Higher DMI of silage from maize genotypes with improved digestibility have also been reported elsewhere (Barriere et al., 1995; Emile et al., 1996).

The SV of GEMS was shown to be inversely linearly related to the DM concentration. The increase in DM concentration is accompanied with a reduction of fiber concentration and an increase of starch and dOM concentration. Most likely, GEMS becomes more ‘concentrate-like’ as the DM concentration increases.

The SV of cereal-WCS increased linearly with CF. This is likely a reflection of the classical effect of reduced digestibility with increased crop maturity. Increased maturity of triticale-WCS is accompanied with higher concentrations of CF, NDF, DM and starch, and reduced OM digestibility (Kasper and Everts, 2003).

4.2.5. Concentrates

We developed one equation for the SV of concentrates including compound concentrates and dry byproducts. The SV of concentrate increased linearly with an increasing CF concentration. Inclusion of CF in the model as the only explanatory variable provided the best fit. However, CF concentration is confounded with the concentration of CP and starch and sugars. Therefore, it may be that induction of satiety is not exclusively determined by the CF concentration, but that the CF concentration is at least an indicator of the whole complex of feed factors that may affect intake. Therefore, the effect of CF on the SV of concentrate is probably more statistical than causal. The SV of concentrate increases linearly with an increasing CF concentration independent from the proportion of concentrate in the diet. Consequently, substitution of forage by concentrate is constant. This approach is similar to the Danish Fill unit system, which assumes also a constant fill value (Kristensen and Ingvartsen, 1986). However, some studies show that increased concentrate feeding decreases voluntary DMI in a non-linear manner (Hijink and Meijer, 1987; Thomas, 1987; Faverdin et al., 1991). This is due to both the filling effect and reduction of fiber digestion under the influence of easy fermentable carbohydrates from concentrate (Stensig et al., 1998). A non-linear effect of the level of concentrate feeding (C_{DMI}; kg DM/day) was tested by addition of an exponential term to the model for the SV of concentrate.

$$SV_p = e^{(\lambda_{p0}+\lambda_{p11}(x_{p1}-\bar{x}_{p1})+\lambda_{p12}(x_{p1}-\bar{x}_{p1})^2+....+\lambda_{pn1}(x_{pn}-\bar{x}_{pn})+\lambda_{pn2}(x_{pn}-\bar{x}_{pn})^2)} \times e^{\rho_{\kappa} \times C_{DMI}} \qquad (2.10)$$

However, ρ_κ was non-significant (-0.0245; s.e. 0.0221) and did not result in an improved goodness of fit, and was therefore not included in the model for the SV of concentrate. The work of Faverdin et al. (1991) shows that substitution of forage by concentrate may depend on the energy balance of the cow. However, a system for the prediction of feed intake that includes the energy balance of the cow would require knowledge of MY and BW. This would be conflicting with our aim to develop a model for the prediction of DMI which should allow integration with other models predicting the responses in cow performance (MY, BW change) to feeding strategy. From equation (2.8) it follows that a low SV of the basal diet results in a high substitution rate of the supplement. Consequently, SR will increase with a higher DMI (and hence energy intake) from the basal diet. Thereby, is albeit indirectly, the effect of energy supply on the substitution rate of concentrates included in the model.

4.2.6. Fodder beet and crushed wheat

Within fodder beet and crushed wheat, there were only small variations in the chemical composition and digestibility. Therefore, it was not possible to estimate the effects of the feed composition on SV of both fodder beet and crushed wheat. Therefore, the estimated SVs of fodder beet and crushed wheat were fixed and not related to feed composition (See Table 5).

4.2.7. Dehydrated grass and pressed beet pulp

We were unable to estimate a SV of dehydrated grass. Dehydrated grass was almost entirely fed to first parity cows and therefore parity and diet were confounded. In case confounded animal and feed factors, simultaneous estimation of feed and animal parameters carries the risk that, some feed or animal effects may unjustly be ascribed to other feeds or animal factors. This may explain why inclusion of dehydrated grass in the model had large effects on the estimates of animal parameters. Estimation of the SV value of dehydrated grass was possible when all animal parameters in the model were kept fixed. This resulted in a SV of 0.89 for dehydrated grass. Basically the same problem occurred with the estimation of the SV of pressed beet pulp. Pressed beet pulp was almost exclusively included in diets based on grass silage made of swards of predominantly poor quality grass species. Thus, pressed beet pulp in the diet was confounded with grass silage from swards with an extraordinary botanical composition. Therefore, during parameter estimation, a low DMI intake was ascribed to the pressed beet pulp resulting in an unrealistic high SV, which suggests the desirability of a separate model for the SV of grass silage made from swards of predominantly poor quality (natural occurring) grass species. Estimation of the SV value of pressed beet pulp was possible when all feed parameters in the model were kept fixed. This resulted in a SV of 0.73 for pressed beet pulp. The results also indicate that the current method of simultaneous parameter estimation requires complete data sets in which diet and animal factors are not confounded.

4.3. Dry matter intake

The voluntary DMI predicted with the combined models for FIC and SV (Equation 2.7a) accounted for 61.6% of the variation of DMI of individual cows with a standard deviation of 1.83 kg DM. For groups of cows standard deviation is $1.83/\sqrt{n}$, in which n is the number of animals in the group. This indicates that the model is less suitable for the prediction of feed intake by individual cows and to calculate individual concentrate allocation. However, if the model is applied to group-fed cows for strategic purposes on a farm level, individual variation will be leveled out. Due to the origin of the data, the feed intake model can be applied to farm conditions with loose housed, stall fed and high genetic merit Holstein Friesian cows (7000 to 12000 kg milk/year), first calving at an age of 2 years that have unrestricted access to feed. The model provides estimates of the SV of numerous commonly used feeds and forages in North-Western Europe. Subsequently, the model can be used for prediction of feed intake for strategic studies and planning of whole farms or groups of cows using data on herd demography including parity and stage of lactation and gestation provided by the farm management system.

However, additional research is required to create new datasets for the development of equations for the SV of some alternative feeds (e.g. pressed beetpulp, dehydrated grass, silage from natural grasslands) and for prediction of intake under grazing conditions. All available data were used to calibrate the model. Therefore, no cross validation methods were used. Splitting the dataset set into two subsets, one for calibration and one for validation, would have reduced the number of observations available for estimation of parameters. Therefore, we have chosen to use all available data for model development and to use independent data for evaluation of accuracy of DMI prediction. Model evaluation will be described in a subsequent paper (Zom et al., 2012, Chapter 3)

5. Conclusions

This study provides a model for the prediction of feed intake by lactating Holstein-Friesians dairy cows using a limited number of easy-to-measure inputs readily available at commercial farms, yet providing a reasonable explanation. Feed intake capacity is predicted from parity number, days in lactation and days pregnant. The feed intake capacity is the measure of the ability of a cow to process the intake constraining feed factors. The extent to which a feed limits the intake is expressed in term of a feed specific satiety value. For the most commonly used feeds, satiety values are estimated from the feed chemical composition and digestibility. These feed characteristics are directly or indirectly related to digestibility, bulk volume, intake rate, palatability and other factors that play a role in physical or metabolic regulation of feed intake. Because the model inputs are not related to animal output (MY or BW), future extension of the intake model with models for the prediction of animal performance is possible. The evaluation of the accuracy of DMI prediction using independent data will be discussed in Chapter 3 (Zom et al., 2012).

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Appendix

Appendix 1. Proportions of DMI, number of feed samples, and chemical compositions of the feeds included in the diets by experiment

Exp	Feed	Proportion of DMI				No.	DM[1]	sd	CP[1]	sd	CF[1]	sd	Ash	sd	Starch	sd	Sugars	sd	dOM[1]	sd	NEL[1]	sd
		Mean	Min	Max	sd	Samples	g/kg		g/kg DM												MJ/kg DM	
1	Grass silage	0.30	0.23	0.43	0.02	7	494	5.0	202	13.4	235	17.6	149	47.6			83	13.9	672	9.4	6.14	0.11
	Maize silage	0.30	0.23	0.43	0.02	8	329	1.8	83	2.4	203	11.6	47	9.2	312	15.3			703	8.4	6.41	0.10
	Concentrate	0.40	0.15	0.55	0.04	5	900	0.2	199	9.1	185	15.6	94	5.8	115	16.2	131	55.3			7.23	0.02
2	Grass silage	0.39	0.30	0.47	0.03	4	438	7.3	174	18.4	249	23.6	119	14.6			80	29.1	667	34.0	5.97	0.30
	Maize silage	0.39	0.30	0.47	0.03	5	321	1.6	81	1.6	197	13.5	52	8.6	311	19.6			706	8.0	6.45	0.09
	Concentrate	0.21	0.07	0.40	0.06	5	899	0.2	180	9.0	167	16.3	102	6.1	136	16.2	49	55.3			7.21	0.03
3	Grass silage	0.31	0.23	0.43	0.03	7	385	4.9	135	8.6	209	10.2	92	15.3			126	91.8	734	14.0	6.59	0.15
	Maize silage	0.31	0.23	0.43	0.03	7	345	2.9	69	7.1	186	14.3	49	5.3	373	48.7			724	36.0	6.65	0.40
	Concentrate	0.38	0.13	0.53	0.05	14	904	0.5	231	2.8	125	7.9	95	9.2	77	8.7	137	4.2	803	8.7	7.19	0.04
4	Grass silage	0.55	0.34	0.73	0.05	5	552	8.6	216	11.6	247	7.3	108	4.1			52	15.8	624	15.3	5.67	0.16
	Concentrate	0.45	0.27	0.66	0.05	3	895	0.6	176	7.5	151	30.1	82	11.0	172	40.1	88	25.4			7.24	0.08
5	Fresh grass	0.60	0.35	0.81	0.08	28	172	3.1	206	42.0	213	24.7	112	14.1			116	62.6	732	38.4	6.81	0.46
	Maize silage	0.22	0.06	0.36	0.06	7	345	1.2	71	4.2	188	10.7	52	3.6	373	21.3			707	19.3	6.47	0.22
	Concentrate	0.18	0.05	0.37	0.06	4	880	0.0	161	2.2	151	11.5	93	6.3	83	28.0	112	28.8	824	5.9	7.37	0.00
6	Fresh grass	0.58	0.00	0.83	0.09	17	154	1.9	199	20.7	238	10.6	113	4.2			84	27.6	682	31.8	6.26	0.29
	Maize silage	0.26	0.04	0.64	0.07	3	322	0.7	85	0.6	190	4.9	54	5.1	310	11.8			700	7.8	6.38	0.09
	Concentrate	0.16	0.04	0.56	0.08	2	902	0.3	167	0.0	162	6.4	89	1.4	26	8.5	124	8.5			7.19	0.02
7	Fresh grass	0.49	0.24	0.70	0.07	16	157	1.6	173	31.0	237	9.6	105	7.1			159	41.5	705	19.1	6.39	0.24
	Maize silage	0.27	0.11	0.67	0.06	4	330	1.2	83	0.5	195	5.2	46	1.7	344	8.6			707	4.5	6.46	0.05
	Concentrate	0.24	0.05	0.46	0.06	2	893	0.4	188	8.5	171	7.1	91	1.4	49	9.9	149				7.26	0.04
8	Grass silage	0.52	0.32	0.86	0.11	29	419	14.0	140	23.4	237	11.9	116	10.3			85	50.4	696	16.8	6.22	0.16
	GEMS	0.26	0.00	0.42	0.10	6	534	4.1	86	6.4	71	15.8	22	4.0	587	70.9	4	5.3	820	15.7	7.81	0.21
	Concentrate	0.23	0.01	0.37	0.05	12	899	1.0	266	111.2	117	38.6	120	11.5	38	35.1	124	9.7	777	11.3	6.91	0.13
9	Fresh grass	0.74	0.43	0.97	0.11	15	183	2.8	131	28.8	238	19.5	119	15.0			151	68.3	690	35.1	6.16	0.38
	GEMS	0.18	0.00	0.51	0.11	3	484	0.6	83	2.5	87	11.4	27	3.0	527	10.8	4	2.6	799	6.2	7.48	0.06
	Concentrate	0.08	0.00	0.14	0.02	3	904	0.6	194	13.2	116	3.5	109	6.6	146	2.5	186	11.0	809	5.7	6.75	0.04

[1] DM = Dry Matter, CP = Crude Protein, CF = Crude Fiber, dOM = *in vitro* digestible Organic Matter (Tilley & Terry, 1963), NEL = Net energy for lactation (van Es, 1978).

Appendix 1 continued

Proportions of DMI , number of feed samples, and chemical compositions of the feeds included in the diets by experiment

Exp	Feed	Proportion of DMI				No.	DM[1]	sd	CP[1]	sd	CF[1]	sd	Ash	sd	Starch	sd	Sugars	sd	dOM[1]	sd	NEL[1]	sd
		Mean	Min	Max	sd	Samples	g/kg		g/kg DM												MJ/kg DM	
10	Grass silage	0.61	0.00	0.94	0.09	33	502	4.1	196	18.0	231	8.0	119	6.8			111	24.2	695	23.1	6.33	0.25
	GEMS	0.04	0.00	0.49	0.07	13	473	4.3	87	4.2	91	7.9	24	6.9	526	15.9	8	3.1	797	9.2	7.46	0.10
	Fodderbeet	0.07	0.00	0.33	0.09	12	160	0.9	64	10.2	68	10.2	81	9.7			560	65.2	850	10.9	7.57	0.11
	Concentrate	0.29	0.05	0.65	0.11	25	835	2.2	232	204.6	142	52.4	108	18.0	12	6.0	108	21.7	839	56.5	7.49	0.64
11	Maize silage	0.37	0.02	0.39	0.01	71	337	3.2	85	10.8	193	18.1	52	8.7	298	9.8			688	19.9	6.25	0.22
	Dehydrated grass	0.21	0.01	0.26	0.02	74	881	1.8	193	27.0	196	33.0	119	15.1					723	31.0	6.66	0.36
	Concentrate	0.42	0.39	0.97	0.02	1	900		176		148										7.21	
12	Maize silage	0.34	0.26	0.39	0.04	41	335	2.1	80	4.7	185	18.9	49	10.5	310	11.2			692	23.5	6.29	0.26
	Dehydrated grass	0.20	0.16	0.22	0.01	41	883	1.6	188	29.6	211	23.0	111	16.9					721	26.9	6.59	0.35
	Concentrate	0.46	0.40	0.56	0.04	2	896	1.4	224		122		77								7.30	0.39
13	Grass silage	0.35	0.07	0.40	0.02	5	586	5.7	180	12.5	245	14.8	110	9.4	20	0.0	107	20.1	682	27.6	6.12	0.28
	Maize silage	0.24	0.21	0.36	0.01	3	267	0.4	94	0.0	226	3.5	56	2.1	259	7.5			653	1.5	5.92	0.00
	Concentrate	0.41	0.30	0.58	0.02	3	890	0.7	180	8.0	161	16.3	103	3.5	62	4.0					8.18	0.23
14	Fresh grass	0.81	0.69	0.90	0.05	15	131	1.5	200	21.1	222	21.5	138	11.4			74	28.7	683	14.6	6.27	0.14
	Concentrate	0.19	0.10	0.31	0.05	2	907	0.4	157	4.9	148	7.1	106	5.7	65	0.7	133	23.3			7.15	0.03
15	Fresh grass	0.78	0.60	0.96	0.06	26	132	2.0	215	36.7	210	22.5	119	18.2			82	46.3	705	26.6	6.53	0.22
	Concentrate	0.22	0.04	0.40	0.06	2	907	0.3	165	0.7	148	7.1	97	2.1	70	8.5	123	1.4			7.15	0.02
16	Fresh grass	0.59	0.39	0.73	0.06	34	132	1.3	228	20.9	215	16.5	123	13.0			36	22.8	721	25.3	6.76	0.26
	Maize silage	0.17	0.02	0.34	0.05	4	375	2.2	73	3.1	165	9.4	40	2.5	374	18.0			743	16.7	6.88	0.19
	Concentrate	0.24	0.13	0.40	0.05	3	892	0.3	157	5.2	139	15.0	92	2.3	78	6.9	134	1.2			7.27	0.02
17	Fresh grass	0.60	0.40	0.78	0.07	34	126	1.9	213	31.4	223	25.4	123	25.5			79	43.1	699	29.5	6.48	0.26
	Maize silage	0.17	0.03	0.35	0.06	4	303	0.6	74	2.2	192	10.3	48	3.1	347	27.8			711	26.8	6.50	0.30
	Concentrate	0.23	0.10	0.43	0.05	2	897	1.1	158	2.1	134	2.1	84	0.0	101	2.1	111	0.7			7.23	0.08
18	Grass silage	0.59	0.43	0.71	0.05	5	507	5.2	180	8.5	230	11.7	119	8.6					694	14.0	6.27	0.13
	Concentrate	0.41	0.29	0.57	0.05	1	901		164		127		88		88		125				7.20	
	Grass silage	0.45	0.00	0.74	0.27	6	431	10.2	198	13.8	220	18.3	127	11.4			75	20.3	695	21.2	6.36	0.24

[1] DM = Dry Matter, CP = Crude Protein, CF = Crude Fiber, dOM = *in vitro* digestible Organic Matter (Tilley & Terry, 1963), NEL = Net energy for lactation (van Es, 1978).

Appendix 1 continued

Proportions of DMI, number of feed samples, and chemical compositions of the feeds included in the diets by experiment

Exp	Feed	Proportion of DMI				No.	DM[1]	sd	CP[1]	sd	CF[1]	sd	Ash	sd	Starch	sd	Sugars	sd	dOM[1]	sd	NEL[1]	sd
		Mean	Min	Max	sd	Samples	g/kg		g/kg DM												MJ/kg DM	
19	Legumes silage	0.20	0.00	0.72	0.28	3	399	8.7	182	4.9	219	16.3	146	13.1			63	37.2	630	24.3	5.67	0.21
	Concentrate	0.40	0.26	0.66	0.05	1	898		184		137		95		53		136				7.22	
20	Grass silage	0.16	0.00	0.31	0.12	5	251	12.7	142	38.7	232	21.5	177	30.3			3	37.1	632	15.7	5.59	0.15
	Maize silage	0.08	0.00	0.29	0.12	4	291	1.5	85	3.2	213	27.4	42	5.1	300	63.7			723	28.1	6.62	0.31
	WCS	0.25	0.00	0.59	0.18	6	327	2.4	78	2.6	308	14.9	50	2.8	76	42.8			563	34.4	4.74	0.34
	Concentrate	0.52	0.39	0.77	0.05	2	899	1.4	218	210.7	132	60.8	88	15.6	73	43.8	116	2.8			7.22	0.30
21	Grass silage	0.18	0.00	0.33	0.13	7	337	2.1	127	16.6	261	9.0	117	4.5			87	15.2	667	7.6	5.87	0.09
	Maize silage	0.09	0.00	0.33	0.13	5	327	3.1	76	6.2	182	6.0	41	10.5	359	40.8			722	21.8	6.61	0.23
	WCS	0.28	0.00	0.70	0.23	7	414	0.9	64	5.2	263	11.9	60	22.7	212	21.5			586	32.8	4.99	0.32
	Concentrate	0.45	0.30	0.68	0.04	3	904	1.0	227	156.2	127	35.9	99	20.2	87	47.9	124	7.8			7.17	0.43
22	Grass silage	0.18	0.00	0.33	0.13	6	459	7.2	140	22.8	258	12.6	117	14.7			60	28.3	650	24.8	5.71	0.26
	Maize silage	0.09	0.00	0.32	0.13	4	312	1.7	74	2.4	186	3.7	40	2.6	339	9.9			712	4.5	6.51	0.05
	WCS	0.27	0.00	0.67	0.22	5	432	3.1	79	2.8	278	9.7	42	7.8	205	12.5			557	17.9	4.67	0.17
	Concentrate	0.45	0.33	0.72	0.04	2	896	1.9	221	223.4	120	41.7	84	12.7	87	48.1	108	4.2			7.21	0.48
23	Legumes silage	0.56	0.41	0.71	0.05	1	366		163		274		179				3		549		4.81	
	Concentrate	0.44	0.29	0.59	0.05	5	900	6.2	210	9.8	126	33.2	106	40.0						29.1	7.36	0.25
24	Legumes silage	0.59	0.33	0.74	0.05	12	311	4.0	195	18.5	257	37.1	141	19.7			2	1.4	575	27.2	5.14	0.30
	Concentrate	0.41	0.26	0.67	0.05	2	902	2.9	208	238.3	100	27.6	91	18.4	120	73.5	121	17.7	841	2.1	7.23	0.54
25	Legumes silage	0.57	0.25	0.83	0.06	9	290	3.8	177	14.5	293	21.7	130	14.7			3	0.7	600	34.0	5.29	0.33
	Concentrate	0.43	0.17	0.75	0.06	3	904	1.8	202	196.3	109	23.7	100	18.7	104	59.6	108	10.7	862	12.5	7.21	0.39
26	Grass silage	0.30	0.11	0.72	0.11	47	450	8.7	181	20.3	232	12.0	117	8.3			82	37.9	686	21.2	6.20	0.23
	Maize silage	0.29	0.10	0.55	0.06	43	349	2.9	81	4.5	195	15.9	55	6.5	331	38.1			677	24.0	6.31	0.25
26	GEMS	0.07	0.00	0.21	0.04	31	557	6.1	89	8.2	76	13.9	23	3.6	584	34.7			756	18.1	7.78	0.19
	Concentrate	0.34	0.00	0.71	0.12	58	895	0.8	253	84.7	127	37.5	73	5.0	135	72.4	110	25.3			7.50	0.31
27	Grass silage	0.53	0.36	0.80	0.05	6	471	5.5	208	26.3	255	21.3	111	9.5			71	22.7	658	13.8	5.98	0.20
	Crushed Wheat	0.08	0.00	0.26	0.07	2	749	0.3	137	0.7	29	0.7	17	0.0	639	13.4			875	0.0	8.39	0.07
	Concentrate	0.38	0.20	0.59	0.07	2	903	0.2	180	0.0	149	19.1	95	3.5	55	4.2	105	9.9			7.21	0.01

[1] DM = Dry Matter, CP = Crude Protein, CF = Crude Fiber, dOM = *in vitro* digestible Organic Matter (Tilley & Terry, 1963), NEL = Net energy for lactation (van Es, 1978).

Appendix 1 continued
Proportions of DMI, number of feed samples, and chemical compositions of the feeds included in the diets by experiment

Exp	Feed	Proportion of DMI				No.	DM^1	sd	CP^1	sd	CF^1	sd	Ash	sd	Starch	sd	Sugars	sd	dOM^1	sd	NEL^1	sd
		Mean	Min	Max	sd	Samples	g/kg		g/kg DM												MJ/kg DM	
28	Grass silage	0.51	0.35	0.70	0.05	6	326	3.3	173	29.0	242	24.9	121	9.9			75	24.6	669	12.4	5.99	0.18
	Crushed Wheat	0.09	0.00	0.29	0.08	2	878	0.0	133	0.0	28	4.2	18	0.0	622	4.9			898	1.4	8.62	0.19
	Concentrate	0.40	0.21	0.63	0.08	2	896	0.1	182	5.7	134	1.4			57	5.7	124	2.1			7.26	0.01
29	Grass silage	0.33	0.19	0.57	0.04	7	354	8.5	143	20.6	256	16.2	124	11.3			57	30.0	661	18.4	5.83	0.22
	Maize silage	0.24	0.17	0.44	0.03	7	324	1.2	84	2.8	194	13.8	54	7.1	325	31.2			706	16.1	6.45	0.18
	Concentrate	0.43	0.02	0.59	0.05	13	906	0.4	192	39.1	158	17.9	82	5.6	38	8.6	147	23.7			7.18	0.06
30	Grass silage	0.26	0.05	0.41	0.02	8	345	9.8	166	32.5	225	27.0	147	26.9			74	44.6	668	17.2	6.02	0.23
	Maize silage	0.37	0.08	0.58	0.03	7	311	2.4	79	4.1	190	8.5	50	4.3	325	17.7			706	9.6	6.44	0.10
	Concentrate	0.37	0.03	0.87	0.04	26	895	0.7	225	77.9	126	23.9	82	6.3	68	24.1	122	40.8	865	22.6	7.27	0.11
31	Grass silage	0.50	0.30	0.64	0.06	4	513	3.9	165	4.8	275	7.5	100	5.3			77	19.6	676	10.0	5.99	0.11
	Pressed beetpulp	0.11	0.00	0.14	0.01	4	212	0.2	102	0.5	209	2.1	79	0.0			45	5.8	804	2.5	7.24	0.04
	Concentrate	0.42	0.27	0.64	0.06	5	900	0.6	175	61.5	143	23.8			53	7.6	135	27.1			7.20	0.00
32	Grass silage	0.45	0.34	0.62	0.04	5	583	4.5	139	5.5	260	20.0	94	14.4			107	17.7	627	20.5	5.43	0.21
	Pressed beetpulp	0.12	0.00	0.17	0.02	4	225	0.9	89	2.9	201	3.0	113	12.2			5	1.0	781	10.9	6.90	0.10
	Concentrate	0.43	0.24	0.61	0.05	5	891	0.6	187	57.8	129	31.0	76	8.4	70	3.8	109	10.3			7.20	0.00

[1] DM = Dry Matter, CP = Crude Protein, CF = Crude Fiber, dOM = *in vitro* digestible Organic Matter (Tilley & Terry, 1963), NEL = Net energy for lactation (van Es, 1978).

Chapter 3

Development of a model for the prediction of feed intake by dairy cows 2. Evaluation of prediction accuracy

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Abstract

In a previous paper we have proposed a new concept of a model for the prediction of feed intake by Holstein Friesian dairy cows Chapter 2 (Zom et al., 2012). This model predicts feed intake from feed composition and digestibility and the cow's lactation number, stage of lactation and pregnancy. Contrary to many other often used models, this does not include animal performance (milk yield, bodyweight) to predict feed intake. However, BW and MY are highly correlated with DMI. Therefore, the objective of present study was to evaluate the accuracy and robustness of the novel feed intake model and to compare its accuracy and robustness with five other commonly used models for the prediction of feed intake.

An evaluation was performed using an independent dataset containing 8974 weekly means of DMI from 348 individual cows observed in 6 feeding experiments including a wide range of diets and management practices was used in this study. Sub-datasets were formed by combining the DMI data by experiment, lactation number, lactation week, and maize silage to grass silage ratios in order to compare the accuracy of the intake models for different feeding practices and groups of cows using mean square prediction error (MSPE) and relative prediction error (RPE) as criteria.

The novel model was most accurate as indicated by the MSPEs and RPEs for the whole dataset and the most of the sub-datasets. The results prove that the model of Zom et al. (2012) is able to predict DMI without the use of milk yield or body weight as inputs. It was concluded that novel model was robust and can be applied to various diets and feeding management situations in lactating HF cows.

Keywords: accuracy, model, prediction intake

1. Introduction

Prediction of dry matter intake (DMI) by dairy cattle is important to optimize allocation of forage and concentrates, compose well-balanced and cost-effective diets and evaluate the effects of feeding practices on the technical, environmental and economical performance of dairy farms. Zom et al. (2012) (Chapter 2) proposed a new model to predict DMI by dairy cattle from feed characteristics (i.e. chemical composition a and digestibility) and cow characteristics (lactation number, stage of lactation and pregnancy). An important feature of the model proposed by Zom et al. (2012) is that it does not include animal outputs as milk yield (MY) and bodyweight (BW) to predict DMI. However, BW and MY are commonly considered as important factors for explanation of DMI in dairy cows. Body weight is an indicator of the size of the cow and hence the capacity of the digestive tract. Milk yield may act as a driver for feed intake in order to meet the energy demands of the cow. Therefore, BW or metabolic weight ($BW^{0.75}$), daily (fat corrected) MY or (potential) 305 d MY are usually taken into account in models for the prediction of feed intake (e.g (Vadiveloo and Holmes, 1979; Milligan et al., 1981; Kristensen and Ingvartsen, 1986; Hijink and Meijer, 1987; NRC, 2001)). Using BW and MY as explanatory variables in feed intake models has a major disadvantage. Models that take actual observed MY and BW into account to predict feed intake cannot be used to evaluate the effects of diet and the long term effects of feeding strategy on milk production, environmental impact and economical performance because MY and BW are variables depending on DMI. In addition to that, MY and BW are unknown at the time of prediction (Ingvartsen, 1994). Because, it cannot be denied that BW and actual MY are correlated with DMI, it remains the question whether a feed model without explanatory variables related to BW and MY is capable to provide accurate predictions of DMI. Accuracy is a prerequisite for the prediction of DMI. Besides accurate, feed intake models must be robust, which means that the predictions are acceptable for a wide range of different diets and feeding strategies. Robust models are less risky than models that are highly accurate for some specific situations but that are highly inaccurate for others (Fuentes-Pila et al., 1996). Although, the model of Zom et al. (2012) provides a reasonable biological explanation, its accuracy and robustness has not been evaluated with independent data. Neither the model was compared with models that do take BW and MY into account to predict feed intake. Therefore, the objective of the present study was to evaluate the accuracy and robustness of the feed intake model developed by Zom et al. (2012) and to compare its accuracy and robustness with commonly used models for the prediction of DMI using the same independent database.

2. Materials and methods

2.1. Selection of feed intake models

Five models were selected for comparison with the model of Zom et al. (2012), the equations are presented in Table 3.1. The models were selected by the following criteria: a) model input variables must be easy measurable on commercial farms. b) model inputs should match with the data available in the validation dataset, c) applicable for a broad range of different forages. These criteria were met by the Danish Fill Unit system of Kristensen and Ingvartsen (1986), the Cornell Net Carbohydrate and Protein System (CNCPS) model of Milligan et al. (1981), Dairy Cow model of Hijink and Meijer (1987), the model of Vadiveloo and Holmes (1979) and the model proposed by the NRC (2001). A further consideration to choose the model of Kristensen and Ingvartsen (1986) was that, like the model of Zom et al. (2012), it is based on the principles of the fill unit systems in which cows and feeds are separately described in terms of feed intake capacity (FIC) and "fill", respectively. The Dairy Cow model of Hijink and Meijer (1987) was chosen because it has been commonly used in the Netherlands for the simulation feeding strategy and farm management (van Alem and van Scheppingen, 1994; Kuipers et al., 1999). In addition to that, an evaluation of the accuracy of DMI the model of Hijink and Meijer (1987) has not been published so far. The model of Vadiveloo and Holmes (1979) was chosen because the model is easy to employ, includes both cow and diet factors (MY, BW, week of lactation and concentrate intake) and has shown to provide accurate predictions of DMI (Keady et al., 2004).The models of Milligan et al. (1981) and NRC (2001) were chosen because they were developed for high yielding HF cows fed high quality diets containing a large proportion of concentrate and maize silage which corresponds with the intensive dairy production systems in North-western Europe. The model of Milligan et al. (1981), the model proposed by the NRC (2001) includes an equation developed by (Rayburn and Fox, 1993) with an adjustment for week of lactation developed by (Roseler et al., 1997a). This model has proved to give good overall predictions of DMI (NRC, 2001).

Table 3.1.
Models used to for prediction of dry matter intake (DMI) in lactating dairy cows

Model 1: Zom et al. (2012, Chapter 2))	
Dry matter intake	$\mathrm{DMI} = \mathrm{FIC}_{\mathrm{FIDC}} / \sum \mathrm{fDM}_i \mathrm{SV}_i$ Where DMI $\mathrm{FIC}_{\mathrm{FIDC}}$ = Feed intake capacity (Satiety Units/day), fDM_i = fraction of feed *i* in the diet on DM basis, SV_i is Satiety Value of feed *i* $\mathrm{FIC}_{\mathrm{FIDC}} = \{[8.0838 + 3.2956 \times (1 - e^{(-1.2758 \times (p - 1 + d/365))})] \times e^{0.3983 \times (1 - e^{-0.0534\,d})}\}(1 - 0.06907 \times (g/220))$ Where p is parity number; d is days in lactation and g is days of gestation
SV Grass(/clover) silage	$\mathrm{SV}_{\mathrm{GS}} = e^{(-1.613\times10^{-3}(\mathrm{DM}/10-45)+0.991\times10^{-3}(\mathrm{DM}/10-45)^2-0.3321\times10^{-3}(\mathrm{CP}-170)+1.551\times10^{-3}(\mathrm{CF}-240))}$
SV Maize silage	$\mathrm{SV}_{\mathrm{MS}} = e^{(-216.58\times10^{-3}-2.737\times10^{-3}(\mathrm{DM}/10-33)+2.962\times10^{-3}(\mathrm{DM}/10-33)^2-0.559\times10^{-3}(\mathrm{dOM}-695))}$
SV Cereal whole crop silage	$\mathrm{SV}_{\mathrm{CWCS}} = e^{(-113.2\times10^{-3}+5.216\times10^{-3}(\mathrm{CF}-283))}$
SV Concentrate	$\mathrm{SV}_{\mathrm{CON}} = e^{(-1.1483+1.335\times10^{-3}(\mathrm{CF}-140))}$
SV Straw	$\mathrm{SV}_{\mathrm{STRAW}} = 1.66$ Where: DM = Dry matter concentration (g DM/kg), CP = Crude protein concentration) (g/kg DM), CF = Crude fibre concentration(g/kg DM); dOM = in vitro digestible organic matter concentration (g/kg DM)
Model 2: Kristensen and Ingvartsen (1986)	
Dry matter intake	$\mathrm{DMI} = \mathrm{FIC}_{\mathrm{DFU}} / \sum \mathrm{fDM}_i \mathrm{DFU}_i$ Where DMI $\mathrm{FIC}_{\mathrm{DFU}}$ = Feed intake capacity (Fill Units/day), fDM_i = fraction of feed *i* in the diet on DM basis, DFU_i is Fill Units of feed *i*
$\mathrm{FIC}_{\mathrm{DFU}}$ Primiparous cows	$\mathrm{FIC}_{\mathrm{DFU\,primiparous}} = 5.55 - 2.22e^{-0.04\times d} + 0.006 \times (\mathrm{BW} - 500) + 0.0003 \times (\mathrm{PMYH} - 6500) + 0.15 \times \mathrm{L}$
$\mathrm{FIC}_{\mathrm{DFU}}$ Multiparous cows	$\mathrm{FIC}_{\mathrm{DFU\,multiparous}} = 7.08 - 2.95e^{-0.047\times d} - 0.0033 \times \mathrm{d} + 0.006 \times (\mathrm{BW} - 575) + 0.0003 \times (\mathrm{PMYH} - 6500) + 0.15\mathrm{L}$ Where BW = body weight, PMYH = potential milk yield in the herd (kg/year), L = correction for loose housing (loose housing L = 1; tie stall L= 0)
DFU Grass silage and hay	$\mathrm{DFUu} = 0.85 - 0.44 \times (0.0989 \times \mathrm{DE} - 0.00347 \times \mathrm{CF\%} - 0.369)$ $\Delta\mathrm{DFU}_{\mathrm{LEG}} = \mathrm{FVu}/(1 + 0.002 \times \mathrm{LEG\%}) - \mathrm{FVu}$ $\Delta\mathrm{DFU}_{\mathrm{DM}} = (4.2/(4.2/\mathrm{DFUu} + 0.1 \times \mathrm{DM\%} - 3) - \mathrm{DFUu}))$ $\mathrm{DFU}_{\mathrm{G}} = \mathrm{DFUu} + \Delta\mathrm{DFU}_{\mathrm{LEG}} + \Delta\mathrm{DFU}_{\mathrm{DM}}$
DFU Maize and cereal whole crop silage	$\mathrm{DFU}_{\mathrm{WCS}} = 0.79 - 0.44 \times (0.0989 \times \mathrm{DE} - 0.00347 \times \mathrm{CF\%} - 0.369)$

Table 3.1 (continued). Equations used to for prediction of dry matter intake (DMI) in lactating dairy cows

Model 2: Kristensen and Ingvartsen (1986)	
DFU Concentrate	$\mathrm{DFU_{CON}} = 0.22$
DFU Straw	$\mathrm{DFU_{STRAW}} = 0.90$
	Where: DFUu = uncorrected Fill Units, DE = Digestible energy (MJ/kg DM), CF% = Crude fibre content (% of DM),$\Delta\mathrm{DFU_{LEG}}$ = correction for legume content, $\Delta\mathrm{DFU_{DM}}$ = correction for DM content, LEG% = legume content (%), DM% = DM content (%),
Model 3: Miligan et al. 1981	
Dry matter intake:	$\mathrm{TDMI} = [0.0185\mathrm{BW} + 0.305\mathrm{MY}(0.4 + 0.15\mathrm{MF\%})] \times \mathrm{TF} \times \mathrm{Mud}$
	Where BW = body weight, MY = Milk yield (kg); MF% = milk fat %; TF = Temperature adjustment for DMI; Mud = Mud adjustment for DMI TF and Mud were assumed both to be assumed 1.
Model 4: Hijink and Meijer (1987)	
Dry matter intake:	$\mathrm{DMI} = \mathrm{RIC} \times \mathrm{F} \times \mathrm{NELadj} \times \mathrm{FCMadj} - \mathrm{SRCadj} + \sum \mathrm{C}_i$
	Where RIC = Roughage intake capacity, F = feed factor (F = 1 for stall fed cows), NELadj = adjustment factor for NEL content of roughage, FCMadj = adjustment for potential FCM yield; SRCadj = adjustment for substitution of roughage by concentrate; Cj = concentrate allowance concentrate *i* (kg DM/d)
	$\mathrm{RIC} = 0.7 + 7.86 \times 10^{-3}\mathrm{d} - 6.553 \times 10^{-5}\mathrm{d}^2 + 2.113 \times 10^{-7}\mathrm{d}^3 - 2.452 \times 10^{-10}\mathrm{d}^4$ if $\mathrm{RIC} \leq 1$; else $\mathrm{RIC} = 1$,where d = days in lactation
	$\mathrm{NELadj} = 4.965 + 1.3788\mathrm{NELr}$,where NELr = rNEL content of roughage (MJ/kg DM);
	$\mathrm{FCMadj} = 1 + (\mathrm{pFCM} - 6000)6.6667 \times 10^{-5}$,where pFCM = potential 305 d FCM yield (kg)
	$\mathrm{SRCadj} = (-0.744\sum \mathrm{C}_i + \mathrm{F}\sum \mathrm{C}_i + 0.023(\sum \mathrm{C}_i)^2) \times \mathrm{NELr}/6.555 \times 1/\mathrm{FCMadj}$
Model 5: Vadiveloo and Holmes (1979)	
Dry matter intake:	$\mathrm{DMI} = 0.076 + 0.404 \times \mathrm{CDMI} + 0.013 \times \mathrm{BW} - 0.129 \times \mathrm{WL} + 4.12\log \times \mathrm{WL} + 0.14 \times \mathrm{MY}$
	Where CDMI = concentrate DMI (kg/d), BW = body weight (kg), WL = week of lactation, MY = milk yield (kg/d)
Model 6: NRC, 2001	
Dry matter intake:	$\mathrm{DMI} = \left(-0.293 + 0.73 \times \mathrm{FCM} + 0.0968 \times \mathrm{BW}^{0.75}\right) \times \left(1 - e^{(-0.192 \times \mathrm{WL} + 3.67)}\right)$
	Where FCM = 4% fat corrected milk yield (kg/d), BW = body weight, WL = week of lactation

2.2. Validation dataset

An independent validation dataset was compiled from 6 different feeding experiments conducted at 3 different experimental sites in the Netherlands. An overview of the experiments and treatments is presented in Table 3.2. The evaluation dataset consisted of 8974 weekly means of DMI of individual HF cows, total DMI, the proportion each feed in the diet on a DM basis, chemical composition, digestibility and feeding value of each feed, including lactation number, calving date, conception date and predicted 305-d milk yield of the herd at the start of the experiment. Furthermore, the dataset included weekly means of individual milk yield, milk fat and protein concentration, and body weight.

From the six experiments in the dataset three experiments (Exp.1, 2 and 3) were conducted under an organic farm management system. The grass silages in these experiments were harvested from swards that consisted of predominantly perennial ryegrass and white clover. Experiments 4, 5, 6 were conducted under a conventional farm management system with grass silages harvested from swards that consisted of perennial ryegrass mono-cultures.

Experiment 6 was designed to study the effects of diet composition on the emission of ammonia from a dairy barn (van Duinkerken et al., 2005). This experiment had a 3×3 factorial design with 3 levels (0, 500, 1000) of rumen-degradable protein balance (OEB) (Tamminga et al., 1994) and 3 different maize silage to grass silage ratios (100/0, 50/50, 0/100) in the basal diet. There were three experimental periods (replicates) of 27 weeks with 9 consecutive treatment periods. The dataset of Experiment 6 include full lactation intake and milk production records.

Forages and feeding practices. Before ensiling grass/clover and grass were wilted for 24 to 48 h and after that harvested with precision chop harvesters. Maize silage and cereal-WCS were harvested with precision chop harvesters with grain crackers. The theoretical length of cut of maize silage and cereal-WCS was between 5 and 8 mm, and the clearance of the grain crackers was adjusted to ensure grain kernels were sufficiently damaged. The silages were stored in clamps or bunker silo's and were compacted with heavy equipment, sealed with plastic sheets and weighed down with a sand load or sand bags. No silage inoculates were used.

In all experiments, fresh forage mixtures were offered once or twice daily and refusals were removed and weighed daily. To ensure *ad libitum* intake of the forage mixtures, the quantities offered were such that the refusal weight was at least 10% of the amount offered. In all experiments compound concentrates were fed separately from the forage mixtures using computer controlled dispensers. In Experiments 4, 5, and 6, small quantities of dry by-products were mixed with the forage. Within experiments the level of concentrate was fixed for treatment groups. There were no differences in concentrate feeding between cows within treatment groups. However, the formulation of the diets was such that, based on recommendations for NEL (van Es, 1978) and protein intestinal digestible protein (DVE) (Tamminga et al., 1994), excessive over-feeding was avoided. The levels of OEB aimed to be at least 0 and the concentrations of minerals were according to the recommendations of (Commissie Onderzoek Minerale Voeding (COMV), 1996).

Animals and measurements. In all experiments, high genetic merit Holstein-Friesian cows (predicted herd average 305 d milk yield ranged from 7500 to 9400 kg) were used (Tabel 3.3) Cows were housed in cubicle sheds, milked twice daily, and were given unrestricted access to drinking water. The cows were individually fed using transpondercontrolled concentrate feeders and feed access doors with weighing troughs (Insentec, Markenesse, Netherlands). Individual feed intake and milk yield were recorded daily. Weekly, milk fat and protein concentration were analyzed in milk samples collected during 2 (Expt. 6) or 4 Expt. 1-5) consecutive milkings. Milk analysis was performed by Qlip (Zutphen, Netherlands) using an automatic infrared analyzer. Weighed means of the fat and protein concentrations were calculated on a weekly basis. Body weights were recorded daily.

The forages and concentrates were analyzed for dry matter (DM), crude protein (CP), crude fibre (CF) and ash, ammonia-N (grass silage only), sugar and starch (concentrates and maize silage only). In addition, forages were analyzed for *in-vitro* organic matter digestibility (OMD%). The procedures of the analysis of feed composition, OMD% and calculation of feeding values were identical to those described by Zom et al. (2012)

Table 3.2. Summary of experiments included in the evaluation dataset

Experiment 1 (Feil, 2000)	
Site	Aver Heino
Cows	48
Treatment period	week 1-27 of lactation
Farming system	Organic
Major diet ingredients	Grass-white clover silage and maize silage (70/30 on a DM basis) individual supplemented with compound concentrates
Dietary treatments	Three methods of concentrate allocation: flat rate, decreasing and intermediate method
Experimental design	Continue block design
Experiment 2 (Feil and van Schooten, 2001)	
Site	Aver Heino
Cows	48
Treatment period	week 1-28 of lactation
Farming system	Organic
Major diet ingredients	Two basal diets: Grass-white clover silage and maize silage (70/30 on a DM basis) or grass-white clover silage and cereal WCS (70/30 on a DM basis) individual supplemented with compound concentrates
Treatments	Two basal diets with three methods of individual concentrate allocation: flat rate, decreasing and intermediate method
Experimental design	Continue block design
Experiment 3 (Zom et al., 2002)	
Site	Aver Heino
Cows	30
Treatment period	8 consecutive weeks mid lactation
Farming system	Organic
Major diet ingredients	Grass–white clover silage and maize silage, (65/35 on a DM basis) individual supplemented with compound concentrates
Treatments	No treatment (control group)
Experimental design	Continue block design
Experiment 4 (Wageningen UR Livestock Research unpublished data)	
Site	Lelystad, Dairy Unit 2
Cows	68
Treatment period	week 1 - 15 of lactation
Farming system	Conventional
Major diet ingredients	Grass silage, maize silage, soy bean meal (47/47/6 on a DM basis) individually supplemented with compound concentrate
Treatments	No treatment (control group)
Experimental design	Continue block design

Table 3.2 continued. Summary of experiments included in the evaluation dataset

Experiment 5 (van Duinkerken et al., 2003)	
Site	Lelystad, Dairy Unit 2
Cows	68
Treatment period	week 1 - 16 of lactation
Farming system	Conventional
Major diet ingredients	High energy diet: grass silage, maize silage, soy bean meal (33/61/6 on a DM basis) Low energy diet:: grass silage, maize silage, wheat straw (38/33/29 on a DM basis) Individually supplemented with compound concentrate
Treatments	Prototyping of a novel system for the allocation of concentrates utilizing individual real time data of milk response (Andre et al., 2007).
Experimental design	Continue block design
Experiment 6 van Duinkerken et al. (2005)	
Site	Lelystad, Dairy Unit 4
Cows	86
Treatment period	whole lactations
Farming system	Conventional
Major diet ingredients	Silage from perenial rye grass swards, maize silage, compound concentrate, soy bean meal
Dietary treatments	Three maize to grass silage ratios (100/0, 50/50, 0/100)×Three levels of OEB (0, 500, 1000), Individually supplemented with compound concentrate
Experimental design	Change-over

Table 3.3. The means and standard deviation (s.d.) of feed intake, milk production, lactation characteristics and body weight of the individual cow data by experiment

Experiment1)	1		2		3		4		5		6	
	mean	s.d.	mean	s.d.	Mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Feed intake												
DMI (kg/d)	19.5	3.3	19.0	2.7	21.6	2.2	22.5	3.6	22.6	4.0	21.3	3.3
Concentrate (kg DM/d)	5.8	2.4	6.2	2.1	6.5	1.5	8.6	1.7	10.4	3.6	7.5	2.0
Milk production												
Milk yield (kg/d)	28.0	6.9	25.7	5.2	27.6	4.5	36.0	7.5	35.5	8.3	30.4	8.2
Fat yield (kg/d)	1.24	0.3	1.21	0.3	1.27	0.2	1.58	0.3	1.61	0.3	1.39	0.3
Protein yield (kg/d)	0.93	0.2	0.84	0.2	0.95	0.1	1.22	0.2	1.25	0.3	1.05	0.2
305 d FCM yield												
predicted (kg/cow)2)	7598	1411	7454	1272	7657	1165	8980	1690	9384	1839	8857	1839
herd average (kg/cow)3)	8166	-	8147		7602	-	8425	-	8236	-	7942	-
Lactation data												
Lactation number	3.2	1.9	3.1	2.0	4.0	2.2	2.5	1.5	2.6	1.6	2.4	1.7
Days in lactation	103	58	103	54	108	52	55	30	64	34	160	98
Days pregnant	24	38	30	41	18	56	8	10	5	11	50	68
Body weight (kg)	632	73	615	68	656	55	603	73	591	59	625	68

1) Expt. 1 = Feil (2000), Expt. 2 = Feil and van Schooten (2001), Expt. 3= Zom et al. (2002), Expt. 4 = Unpublished data Wageningen-UR Livestock Research, Expt. 5 = van Duinkerken et al. (2003), Expt. 6 = van Duinkerken et al. (2005). 2) Means of predicted 305 day milk yield from the milk recording program at the start of the experiment; 3) Current herd average at the start of the experiment

2.3. Sub-datasets of experiments, parity and stage of lactation

The predicted DMI of each cow in the whole dataset were used to evaluate the overall accuracy of the feed intake models. A model can be considered as robust when it provides accurate predictions of DMI for wide range of different diets and management practices. Therefore, to evaluate robustness, the predicted DMI of each cow was combined by experiment (i.e. dietary treatment), by lactation number (1, 2, 3, and > 3) and by lactation week (1 to 45). Subsequently, data of Experiment 6 (van Duinkerken et al., 2005) were used to evaluate the effects of large changes in diet composition on the accuracy of the prediction of DMI. Models that provide good predictions for most of the datasets can be considered as robust (Fuentes-Pila et al., 1996). However, a high accuracy for some datasets and a low accuracy for others, may indicate a lack of robustness and that the prediction accuracy is related to specific conditions (e.g. diets, type of cow). Such a model is probably more suitable for specific situations than for general use.

2.4. Statistical criteria for testing of accuracy

The accuracy of feed intake models (i.e. goodness of fit) is usually evaluated by statistical criteria (e.g. (Rook et al., 1990; Rook et al., 1991; Fuentes-Pila et al., 1996; Roseler et al., 1997b) The mean square prediction error (MSPE), mean prediction error (MPE) and relative prediction error (RPE) were used as criteria for the accuracy of prediction of DMI and robustness. The MSPE is calculated as follows:

$$\mathrm{MSPE} = \sum(\mathrm{A}-\mathrm{P})^2/n \qquad (3.1)$$

where A is the actual DMI, P the predicted DMI and *n* the number of pairs of A and P being compared. According to (Bibby and Toutenberg, 1977) the MSPE can be considered as the sum of three components: mean bias $(\bar{\mathrm{A}}-\bar{\mathrm{P}})$, indicates the differences between the actual and predicted means of DMI, line bias $(\mathrm{S}_\mathrm{P}^2(1-b)^2)$ and random variation around the regression line of A on P $(\mathrm{S}_\mathrm{A}^2(1-\mathrm{r}^2))$. Accordingly, MSPE is calculated as follows:

$$\mathrm{MSPE} = (\bar{\mathrm{A}}-\bar{\mathrm{P}})^2 + \mathrm{S}_\mathrm{P}^2(1-b)^2 + \mathrm{S}_\mathrm{A}^2(1-\mathrm{r}^2) \qquad (3.2)$$

where $\bar{\mathrm{A}}$ is the means of actual DMI, $\bar{\mathrm{P}}$ is the means of predicted DMI, S_A^2 is the variance of actual DMI, S_P^2 is the variance of predicted DMI, *b* is the slope of the regression of A on P with intercept zero, and r is the correlation coefficient of A and P. Large deviations of *b* from 1 are indicative of underlying inadequacies in the structure of the model. When *b* is < 1, the model tends to underestimate at low actual DMI and to overestimate at high actual DMI, or in reverse when *b* is >1.The mean prediction error (MPE) is calculated as the square root of the MSPE $(\mathrm{MPE} = \sqrt{\mathrm{MSPE}})$. The relative prediction error (RPE) is calculated as MPE as proportion of the actual DMI (Rook et al., 1991). The values of the mean bias, MSPE, MPE and RPE were calculated for the whole dataset and for each sub-dataset The size of the RPE is used as a criterion for accuracy and robustness (Fuentes-Pila et al., 1996). According to Fuentes-Pila et al. (1996) we assumed that RPEs ≤ 0.1 indicates good predictions; RPEs > 0.1 and ≤ 0.2 indicates acceptable predictions; and RPEs > 0.2 indicates poor predictions. A model is considered as robust if the as the RPEs for most of the datasets is ≤ 0.1. (Fuentes-Pila et al., 1996).

3. Results

3.1. Overall accuracy of the prediction of DMI

The results of the evaluation of the overall model accuracy are presented in Table 3.4. In the present study, the model of Zom et al. (2012) provided the most accurate predictions of DMI as indicated by a mean bias close to zero, lowest MSPE and RPE, explaining 0.69 of the variation in DMI. The RPE was 0.10, indicating a good prediction accuracy (Fuentes-Pila et al., 1996). The contributions of mean bias and random error to MSPE were both close to zero. Consequently, MSPE was almost completely due to random error.

The MSPE values of the models of Milligan et al. (1981), Kristensen and Ingvartsen (1986) and NRC (2001) were slightly different (Table 3.4.) indicating a similar prediction accuracy. The model of Milligan et al. (1981), and NRC (2001) over-predicted mean DMI proportionally by 0.03 and 0.05, respectively. The model of Kristensen and Ingvartsen (1986) under-predicted mean DMI proportionally by 0.06 and tended to overestimate DMI at low actual DMIs and underestimate at high actual DMIs as indicated by the *b* value. The model of Hijink and Meijer (1987) was ranked as second least accurate to predict DMI as indicated by MSPE, mean bias, and line bias (Table 3.4). This model under-predicted mean DMI proportionally by 0.08. The contribution of bias and random error to MSPE were proportionally 0.24 and 0.75. The model of Hijink and Meijer (1987) tended to overestimate DMI at low actual DMI and underestimate at high actual DMI as indicated by the *b* value. The model of Vadiveloo and Holmes (1979) was tested as the least accurate equation to predict DMI as indicate by the highest MSPE, mean bias and line bias. This model under-predicted mean DMI proportionally by 0.16. The contribution of bias and random error to MSPE were 0.68 and 0.30, respectively.

Table 3.4. Comparison of accuracy of the prediction of DMI and components of the mean square prediction error MSPE by six different models using a dataset including 8974 observations of individual DMI by 348 cows

Observations	DMI kg/d					Variance					
	Actual	Predicted	bias	*b*[1]	r^2	S_A^2[3]	S_P^2[4]	MSPE[5]	MPE[6]	RPE[7]	Rank[8]
Zom et al. (2002)	21.0	21.0	0.0	1.00	0.69	12.67	8.99	3.99	2.00	0.10	1
Kristensen and Ingvartsen (1986)	21.0	19.6	1.4	1.07	0.64	12.67	6.30	6.47	2.54	0.12	3
Milligan et al. (1981)	21.0	21.5	-0.5	0.97	0.52	12.67	8.71	6.38	2.53	0.12	2
Hijink and Meijer (1987)	21.0	19.3	1.7	1.08	0.27	12.67	7.28	12.25	3.50	0.17	5
Vadiveloo and Holmes (1979)	21.0	17.8	3.2	1.18	0.65	12.67	7.20	14.86	3.85	0.18	6
NRC (2001)	21.0	22.1	-1.1	0.95	0.55	12.67	11.07	7.01	2.65	0.13	4

[1] *b* = the slope of the regression of actual (A) on predicted (P) intake with intercept zero, [2] r = correlation coefficient of A and P, [3] S_A^2 = the variance of actual DMI, [4] S_P^2 = the variance of predicted DMI, [5] $\text{MSPE} = (\overline{A} - \overline{P})^2 + S_P^2(1 - b)^2 + S_A^2(1 - r^2)$, [6] MPE= mean prediction error = √MSPE, [7] RPE is relative prediction error = MPE/A

3.2. *Accuracy and effects of experiment*

The accuracy of predicted values of individual DMI combined by experiment are presented in Table 3.5. Based on the MSPE criterion, the model of Zom et al. (2012) was the most accurate for 4 out of 6 sub-datasets of experiments (Expt. 1, 2, 4, 5 and 6) and second best for 2 sub sub-datasets. For all sub-datasets the RPEs were ≤ 0.1, indicating a good robustness.

The model of Kristensen and Ingvartsen (1986) was most accurate for the sub-dataset of Expt. 2 (*ex aequo* with the model of Zom et al. (2012)), the model of Milligan et al. (1981) was most accurate for sub-dataset of Expt. 3 and NRC (2001) was most accurate for the sub-dataset of Expt 4. The models of Hijink and Meijer (1987) and Vadiveloo and Holmes (1979) were the second least and least accurate for each sub-datasets of experiments, respectively. The inaccuracy of these models was invariably due to severe underestimation of DMI.

Table 3. 5. Comparison of accuracy of the prediction of DMI and components of the means square prediction error (MSPE) by six different models investigated in six sub datasets of different experiments

		DMI (k/d)					Variance					
Expt.	No.Obs.	Actual	Predicted	bias	b^1	r^2	$S^{2\ 3}_A$	$S^{2\ 4}_P$	MSPE[5]	MPE[6]	RPE[7]	Rank[8]
Model 1: Zom et al. (2012)												
1	1307	19.5	19.7	-0.2	0.99	0.77	10.68	6.69	2.53	1.59	0.08	1
2	1145	19.0	19.6	-0.6	1.00	0.72	7.56	7.37	2.42	1.55	0.08	1
3	140	21.6	21.9	-0.3	0.99	0.35	4.94	2.60	3.32	1.82	0.08	2
4	941	22.5	21.2	1.3	1.06	0.71	13.27	9.21	5.52	2.35	0.10	2
5	1114	22.6	22.2	0.4	1.01	0.70	15.84	15.09	4.98	2.23	0.10	1
6	4327	21.2	21.4	-0.1	0.99	0.61	11.06	6.44	4.31	2.08	0.10	1
Model 2: Kristensen and Ingvartsen (1986)												
1	1307	19.5	19.7	-0.2	0.99	0.73	10.68	5.79	2.87	1.69	0.09	2
2	1145	19.0	19.4	-0.4	0.98	0.70	7.56	4.98	2.42	1.55	0.08	1
3	140	21.6	20.3	1.3	1.07	0.49	4.94	1.81	4.31	2.08	0.10	4
4	941	22.5	20.2	2.3	1.12	0.76	13.27	7.73	8.72	2.95	0.13	4
5	1114	22.6	20.1	2.5	1.12	0.71	15.84	10.78	10.75	3.28	0.15	3
6	4327	21.2	19.4	1.8	1.10	0.65	11.06	4.16	7.21	2.68	0.13	4
Model 3: Milligan et al. (1981)												
1	1307	19.5	20.8	-1.2	0.94	0.70	10.68	7.37	4.71	2.17	0.11	3
2	1145	19.0	20.0	-1.0	0.95	0.55	7.56	5.83	4.47	2.11	0.11	3
3	140	21.6	21.3	0.2	1.01	0.53	4.94	2.75	2.37	1.54	0.07	1
4	941	22.5	22.8	-0.3	0.98	0.57	13.27	11.30	5.81	2.41	0.11	3
5	1114	22.6	22.6	-0.1	0.99	0.44	15.84	9.94	8.83	2.97	0.13	2
6	4327	21.2	21.6	-0.4	0.98	0.57	11.06	7.73	4.94	2.22	0.10	2
Model 4: Hijink and Meijer (1987)												
1	1307	19.5	18.5	1.0	1.05	0.40	10.68	4.03	7.47	2.73	0.14	5
2	1145	19.0	18.3	0.7	1.04	0.24	7.56	3.50	6.29	2.51	0.13	5
3	140	21.6	19.1	2.5	1.13	0.06	4.94	2.21	10.85	3.29	0.15	5
4	941	22.5	20.3	2.2	1.10	0.34	13.27	6.58	13.67	3.70	0.16	5
5	1114	22.6	21.2	1.3	1.06	0.35	15.84	9.95	12.17	3.49	0.15	5
6	4327	21.2	19.8	1.4	1.02	0.07	11.06	5.99	12.30	3.51	0.17	5
Model 5: Vadiveloo and Holmes (1979)												
1	1307	19.5	17.1	2.5	1.15	0.80	10.68	5.01	8.37	2.89	0.15	6
2	1145	19.0	16.8	2.2	1.14	0.73	7.56	3.64	7.20	2.68	0.14	6
3	140	21.6	17.8	3.7	1.21	0.45	4.94	1.86	16.80	4.10	0.19	6
4	941	22.5	18.8	3.7	1.20	0.78	13.27	6.46	16.69	4.08	0.18	6
5	1114	22.6	19.4	3.2	1.16	0.79	15.84	7.95	13.46	3.67	0.16	6
6	4327	21.2	17.6	3.6	1.20	0.50	11.06	5.72	18.94	4.35	0.20	6
Model 6: NRC (2001)												
1	1307	19.5	21.1	-1.6	0.92	0.56	10.68	8.57	7.37	2.71	0.14	4
2	1145	19.0	20.5	-1.5	0.92	0.56	7.56	6.39	5.66	2.38	0.13	4
3	140	21.6	22.5	-0.9	0.96	0.42	4.94	3.59	3.70	1.92	0.09	3
4	941	22.5	22.1	0.4	1.01	0.62	13.27	17.43	5.18	2.28	0.10	1
5	1114	22.6	22.6	0.0	0.99	0.27	15.84	17.28	11.55	3.40	0.15	4
6	4327	21.2	22.7	-1.5	0.93	0.61	11.06	9.03	6.58	2.56	0.12	3

Expt. 1 = Feil (2000), Expt. 2 = Feil and van Schooten (2001), Expt. 3= Zom et al. (2002), Expt. 4 = Unpublished data Wageningen-UR Livestock Research, Expt. 5 = van Duinkerken et al. (2003), Expt. 6 = van Duinkerken et al. (2005).

[1] b = the slope of the regression of actual (A) on predicted (P) intake with intercept zero, [2] r = correlation coefficient of A and P, [3] S^2_A = the variance of actual DMI, [4] S^2_P = the variance of predicted DMI, [5] $\text{MSPE} = (\bar{A} - \bar{P})^2 + S^2_P(1 - b)^2 + S^2_A(1 - r^2)$, [6] MPE= mean prediction error = √MSPE, [7] RPE is relative prediction error = MPE/A

3.3. Accuracy and lactation number

The predicted values of DMI for each cow were combined by lactation number (1, 2, 3 and >3) (Table 3.6). Based on the MSPE criterion, the model of Zom et al. (2012) was the most accurate for all lactation number sub-datasets. The RPEs were ≤ 0.1 for each lactation number sub-dataset. The model of Kristensen and Ingvartsen (1986) under-predicted DMI for all lactation numbers. The *b* values >1 indicate that the model Kristensen and Ingvartsen (1986) tended to under-estimate at high actual DMIs. The model of Milligan et al. (1981) over-predicted DMI of cows with lactation number 1, 3 and > 3. The model of NRC (2001) consistently over-predicted intake for all lactation numbers. The models of Hijink and Meijer (1987) and Vadiveloo and Holmes (1979) gave the least accurate prediction for the lactation number sub-datasets, with RPEs substantially higher than 0.1.

3.4. Accuracy and effects of lactation week

Mean bias and RPE of the model predictions by week of lactation are presented in Figure 3.1 and 3.2, respectively. The mean bias of the model of Zom et al. (2012) was always less than 1 kg DM/day, with RPEs close to 0.1, indicating a good to acceptable prediction accuracy. During all weeks of lactation, the model of Kristensen and Ingvartsen (1986) consistently underestimated DMI (Figure 3.1). The RPEs by week of lactation were between 0.12 and 0.19 indicating acceptable prediction accuracy (Figure 3.2). The model of Milligan et al. (1981) failed to provide accurate predictions of DMI during the first weeks of lactation, as indicated by large mean bias due to over estimation of DMI (Figure 3.1) and RPEs > 0.20 (Figure 3.2). The model of NRC (2001) under-predicted DMI during the first months of lactation, but over-estimated DMI thereafter. The accuracy of intake prediction by week of lactation indicated that the model of Hijink and Meijer (1987) gave poor predictions, as indicated by a large mean bias due to underestimation of intake (Figure 3.1). The accuracy of intake prediction by week of lactation by the model of Vadiveloo and Holmes (1979) was also poor, as indicated by a large mean bias and RPEs. The inaccuracy was invariably due to severe underestimation of DMI (Figure 3.1).

Table 3.6 Comparison of accuracy of the prediction of DMI and components of the mean square prediction error (MSPE) by six different models investigated in sub datasets of cows with different lactation number

Lactation Number	No. Obs.	DMI kg/d		bias	b[1]	r^2	S_A^2 [3]	S_P^2 [4]	MSPE[5]	MPE[6]	RPE[7]	Rank[8]
		Actual	Predicted									
Model 1: Zom et al. (2012)												
1	2674	18.2	18.4	-0.2	0.99	0.59	7.78	4.73	3.22	1.80	0.10	1
2	2596	22.1	21.9	0.2	1.01	0.57	10.06	5.97	4.39	2.09	0.09	1
3	1497	22.3	22.2	0.1	1.01	0.56	10.35	5.51	4.60	2.15	0.10	1
>3	2207	22.2	22.3	0.0	1.00	0.58	10.35	5.63	4.38	2.09	0.09	1
Model 2: Kristensen and Ingvartsen (1986)												
1	2674	18.2	17.4	0.8	1.05	0.54	7.78	2.80	4.19	2.05	0.11	2
2	2596	22.1	20.2	1.8	1.09	0.57	10.06	4.05	7.78	2.79	0.13	4
3	1497	22.3	20.6	1.8	1.09	0.49	10.35	3.73	8.52	2.92	0.13	4
>3	2207	22.2	21.0	1.2	0.11	0.48	10.35	3.74	9.84	3.14	0.14	5
Model 3: Milligan et al. (1981)												
1	2674	18.2	19.0	-0.8	0.96	0.36	7.78	3.20	5.56	2.36	0.13	3
2	2596	22.1	21.9	0.2	1.01	0.42	10.06	5.55	5.84	2.42	0.11	2
3	1497	22.3	23.1	-0.8	0.96	0.34	10.35	9.35	7.47	2.73	0.12	2
>3	2207	22.2	23.2	-1.0	0.95	0.36	10.35	7.32	7.72	2.78	0.13	2
Model 4: Hijink and Meijer (1987)												
1	2674	18.2	18.7	-0.5	0.98	0.08	7.78	6.07	7.46	2.73	0.15	5
2	2596	22.1	19.9	2.2	1.13	0.15	10.06	6.69	13.49	3.67	0.17	5
3	1497	22.3	19.9	2.4	1.14	0.19	10.35	5.95	14.24	3.77	0.17	5
>3	2207	22.2	20.4	1.8	1.10	0.45	10.35	6.62	8.96	2.99	0.13	4
Model 5: Vadiveloo and Holmes (1979)												
1	2674	18.2	15.9	2.3	1.14	0.49	7.78	3.12	9.22	3.04	0.17	6
2	2596	22.1	18.1	4.0	1.22	0.59	10.06	5.53	20.03	4.48	0.20	6
3	1497	22.3	18.7	3.7	1.19	0.56	10.35	4.96	18.07	4.25	0.19	6
>3	2207	22.2	19.0	3.2	1.17	0.64	10.35	5.64	14.29	3.78	0.17	6
Model 6: NRC (2001)												
1	2674	18.2	19.8	-1.6	0.92	0.43	7.78	7.36	7.07	2.66	0.15	4
2	2596	22.1	22.6	-0.5	0.98	0.43	10.06	8.82	5.95	2.44	0.11	3
3	1497	22.3	23.5	-1.2	0.94	0.40	10.35	9.35	7.67	2.77	0.12	3
>3	2207	22.2	23.5	-1.3	0.94	0.39	10.35	9.34	8.02	2.83	0.13	3

[1] *b* = the slope of the regression of actual (A) on predicted (P) intake with intercept zero, [2] r = correlation coefficient of A and P, [3] S_A^2 = the variance of actual DMI, [4] S_P^2 = the variance of predicted DMI, [5] $\text{MSPE} = (\bar{A} - \bar{P})^2 + S_P^2(1 - b)^2 + S_A^2(1 - r^2)$, [6] MPE= mean prediction error = √MSPE, [7] RPE is relative prediction error = MPE/A

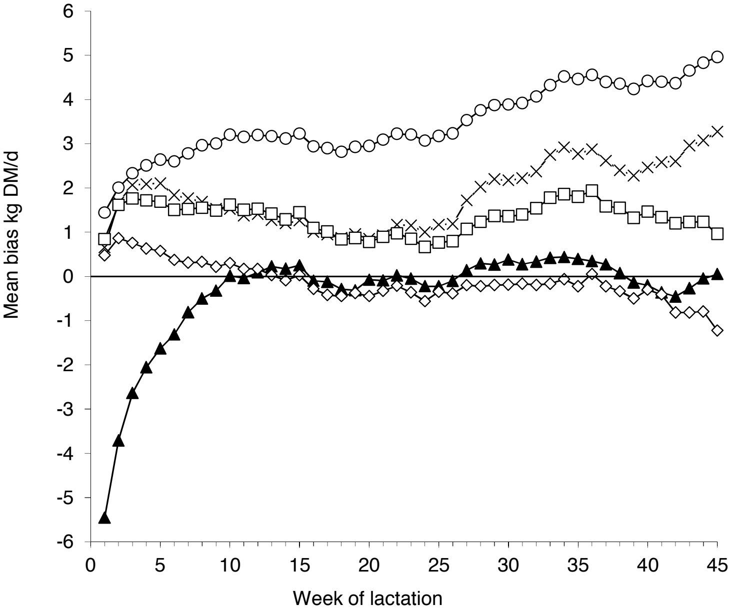

Figure 3.1 Mean bias (predicted minus observed kg DM/day) by week of lactation. The model predictions indicated by lines with ◇ refer to Zom et al. (2012), □ to (Kristensen and Ingvartsen, 1986), ▲ to (Milligan et al., 1981), × to (Hijink and Meijer, 1987) ○ to (Vadiveloo and Holmes, 1979) and + to NRC (2001).

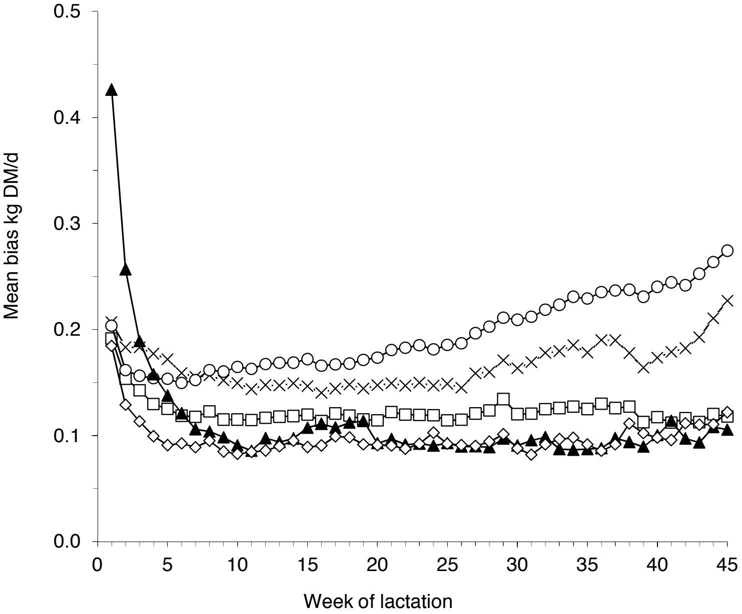

Figure 3.2 Relative prediction error (RPE) calculated as the square root of MSPE as proportion of actual intake by week of lactation. The model predictions indicated by lines with ◇ refer to Zom et al. (2012), □ to (Kristensen and Ingvartsen, 1986), ▲ to (Milligan et al., 1981), × to (Hijink and Meijer, 1987) ○ to (Vadiveloo and Holmes, 1979) and + to NRC (2001).

3.5. *Accuracy and the effects diet change*

Data of Experiment 6 (van Duinkerken et al., 2005) were used to assess the accuracy of prediction of DMI and to examine the prediction accuracy with different feeding regimes and diet compositions. During the successive treatment periods all cows were fed either one of three different basal diets with different maize silage to grass silage ratios. The changes in milk production, energy intake and diet composition during the course of the experiment are displayed in Figure 3.3. Figure 3.4 shows the actual and predicted DMI for each of the tested models. For each maize silage to grass silage ratio (100/0, 0/100, 50/50), the model of Zom et al. (2012) provided the most accurate predictions of DMI as indicated by the lowest mean bias, MSPEs and RPEs (Table 3.7). The levels RPEs indicate that the predictions were good to acceptable for maize silage to grass silage ratios. The DMI predicted by the model of Zom et al. (2012) consistently followed the changes in actual DMI (Fig. 4).

The DMI predicted by the model of (Kristensen and Ingvartsen, 1986) followed to some extent the variation in actual DMI (Figure 3.4), but not as close as the model of Zom et al. (2012) (Figure 3.4). This model under-predicted mean DMI of the 100/0, 50/50 and 0/100 diets proportionally by 0.05, 0.05 and 0.09, respectively.

The model of Milligan et al. (1981) under-predicted mean DMI of the 100/0 diet proportionally by 0.02, whereas DMI of the 50/50 and 0/100 diets were over-predicted by proportionally 0.02 and 0.08, respectively. This implies that this model is more accurate for diet with large proportion maize silage, but less accurate for grass silage based diets. The NRC (2001) provided reasonable predictions for diets containing maize silage

The DMI predicted by the model of Hijink and Meijer (1987) model followed only vaguely the variation in actual DMI (Figure 3.4). This model over under-predicted mean DMI of the 100/0 and /100 diet and 50/50 diet proportionally by 0.18 and 0.10, respectively. Whereas, the model over-predicted mean DMI of the 0/100 diet proportionally by 0.01. This suggests that the model is only accurate for grass silage based diets and should not be used for diets with maize silage. The Vadiveloo and Holmes (1979) under-predicted mean DMI of the 100/0, 50/50 and 0/100 diets proportionally by 0.22, 0.18 and 0.12, respectively.

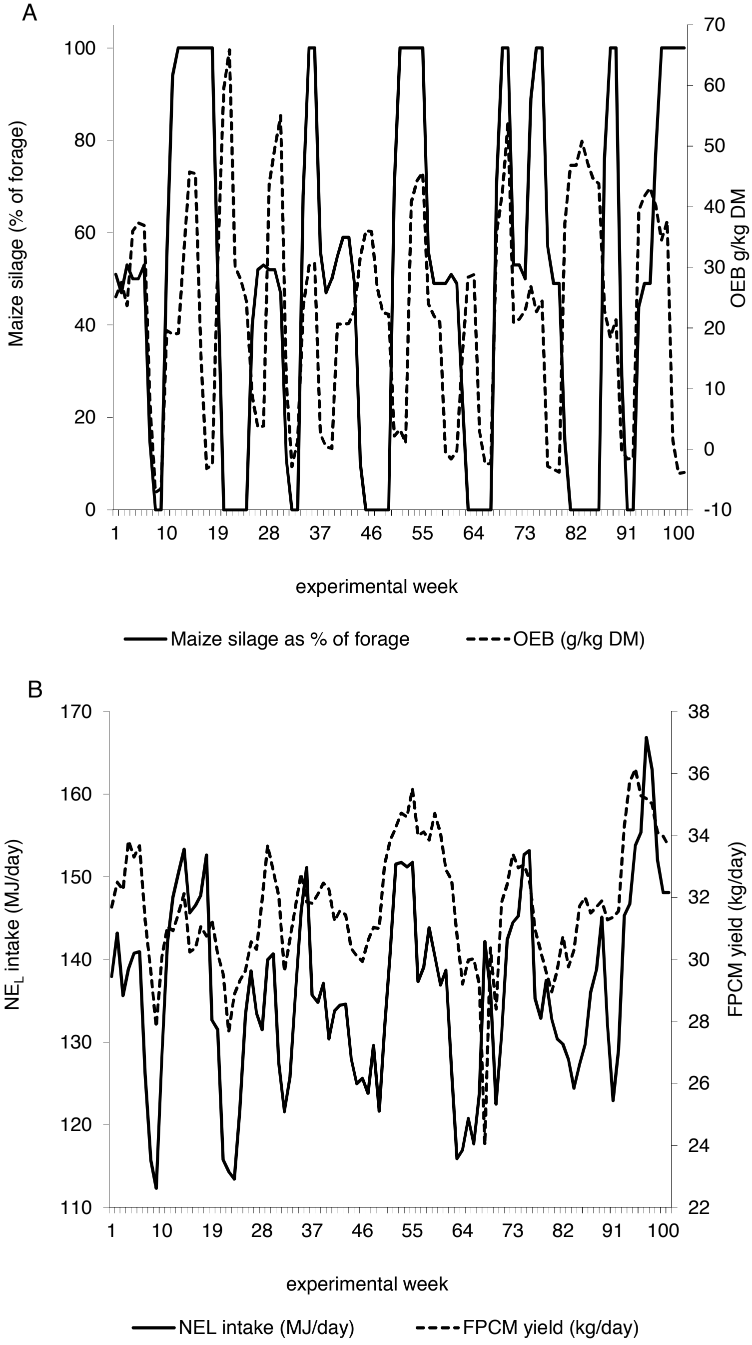

Figure 3.3 Upper graph (A) displays the dietary treatments in Experiment 6 (van Duinkerken et al., 2005). Solid line: maize silage as proportion of total forage and level of rumen degradable protein (OEB) (Tamminga et al., 1994). The lower graph (B): the solid line shows the net energy intake for lactation (NEL) and dashed line fat and protein corrected milk yield (FPCM; 1 kg FPCM = 3.05 MJ NEL; CVB, 2006).

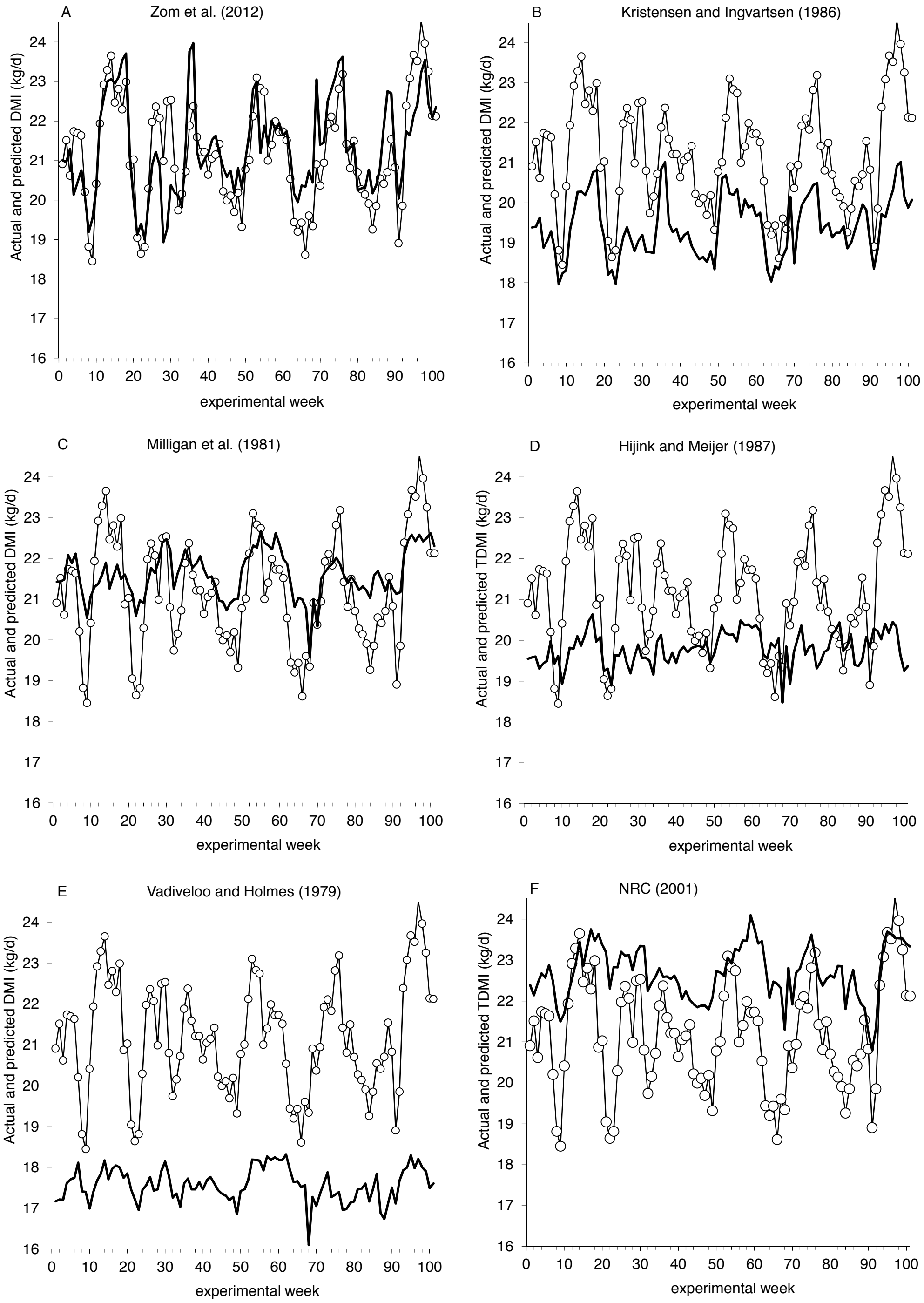

Figure 3.4 Actual DMI (solid lines with ○) and predicted DMI (bold solid lines) by the models of Zom et al. (2012) (graph A), Kristensen and Ingvartsen (1986) (graph B), Milligan et al. (1981) (graph C), Hijink and Meijer (1987) (graph D), Vadiveloo and Holmes (1979) (graph E) and NRC (2001) (graph F).

4. Discussion

The model of Zom et al. (2012)provided the most robust and accurate predictions of DMI as indicted by MSPE, MPE and RPEs. The results prove that the model of Zom et al. (2012) accurately predicts DMI without the use of MY and BW as inputs. Exclusion of MY and BW in models for the prediction of DMI is beneficial, because this approach allows combination with models for the prediction of animal performance in response to changes in feed and nutrient intake. Moreover, parity, stage of lactation and pregnancy are easy to measure on commercial farms. The RPEs of the predictions by the model of Zom et al. (2012) were for most of the sub-datasets below 0.1 or slightly above 0.1 indicating that the model is robust (Fuentes-Pila et al., 1996). These result suggest that the model of Zom et al. (2012) provides good to satisfactory predictions for various feed management situation and animals. The RPEs of all other models tested in this study were for most of the sub-datasets above 0.10. Good robustness is also demonstrated the small variation effect on mean bias and RPEs of the DMI predictions after extreme changes of the maize silage to grass silage ratio (Expt. 6). Such, extreme dietary changes may require some adaptation time of the microbial population in the rumen (Goff and Horst, 1997). Although, the model of Zom et al. (2012) is not able to account for ruminal adaptation on variation in DMI, the predicted DMI followed consistently the changes in actual DMI. Random variation, the unexplained variation between individual cows, was the major component of MSPE for the model of Zom et al. (2012). The MSPEs in the present study are for individual cows and on a weekly base. Because the model is developed for strategic purpose, DMI will be predicted for groups of cows or whole dairy herds. In that situation, individual variation may be cancelled out, and therefore prediction error will be less than for individual cows.

The evaluation dataset was independent from the developmental dataset, in a way that the evaluation data originated from cows, feeds, diets, experiments and personnel which were all different from those included in the developmental dataset. However, the data used for model evaluation were collected under feeding, environmental, housing and other management conditions which are typical for the Netherlands. This similarity between the developmental and evaluation dataset might have contributed to a better accuracy of model of Zom et al. (2012) compared to the other models. This problem is inherent the comparison of empirical models. However, the study demonstrates that an accurate prediction of DMI is possible without using factors related to MY and BW.

The model of Kristensen and Ingvartsen (1986) provided acceptable predictions of DMI. However, the model under-predicted DMI for most of the sub-datasets. Under-prediction of DMI may be related to changes in breeding and genetic potential since the 1980s when this model was developed. An upward correction of the predicted DMI may possibly reduce mean bias and MSPE. The model of Kristensen and Ingvartsen (1986) use potential milk yield in the herd as an input for the prediction of DMI. However, this potential milk yield is indistinctly defined. In this study, we have assumed average actual 305 day milk yield in the herd as the potential milk yield. This assumption influences the accuracy of the prediction. Assuming a potential milk yield higher than the actual 305-d milk yield in the herd would result in an increased DMI and thereby have reduced the mean bias.

The models of Milligan et al. (1981) and NRC (2001) provided in general acceptable predictions of mean DMI. However, the models of Milligan et al. (1981) and NRC (2001) seems less suitable for cows in early lactation and for cows fed diets largely based on grass silage. The observed over-prediction of DMI in early lactation by the model of Milligan et al. (1981) is in agreement with similar observations of (Roseler et al., 1997b). The inaccuracy of prediction for early lactation cows can be attributed to the fact that the model of Milligan et al. (1981) use MY and BW to predict DMI. However, the increase of DMI in early lactation lags behind the increase in MY (Bines, 1979, 1985). Other factors such as stage of lactation and cow size have a greater influence on DMI than MY (Bines, 1979, 1985). The higher accuracy of the model of Milligan et al. (1981) as observed for the data set of Experiment 3 can be explained by the absence of early-lactation cows in this specific experiment. This may have reduced the mean bias and subsequently MSPE. Contrary to the model of Milligan et al. (1981), the model of NRC (2001) includes an adjustment for reduced DMI during early lactation (Roseler et al., 1997a). However, DMI this adjustment seems to be an over-correction as indicated by an underestimation of DMI during early lactation.

The poor prediction of DMI in grass silage fed cows by the models Milligan et al. (1981) and NRC (2001) can be attributed to the fact that, these does not include feed or diet variables and that these models were developed in USA using data from HF dairy cows consuming diets containing a large proportion of maize silage. Although, the models of Milligan et al. (1981) and NRC (2001) does not include feed or diet variables, the predicted DMI followed the actual DMI after changes in the ratio of maize silage to grass silage in dairy cow rations. However, it is demonstrated that alteration of diet composition changed energy intake and hence MY (Figure 3.3). Because the models of Milligan et al. (1981) and NRC (2001) use MY as a prediction variable, the changes in predicted DMI were results of changes in MY. However, it is obvious that the observed changes in DMI were not driven by sudden changes in MY, but the changes in MY were driven by changes in DMI. This underlines that MY is not an appropriate explanatory variable to predict mean DMI and stresses the importance of inclusion of feed variables in the model for the prediction of DMI in dairy cattle. It demonstrates also that models which use MY or other animal outputs to predict DMI cannot be used when the ultimate objective is to predict the effects of changing feeding strategies on animal performance.

The model of Hijink and Meijer (1987) severely underestimated DMI for cows with lactation numbers 2, 3 and >3, but not for first lactation cows. This is probably due to the absence of any age or lactation number variable in the model of Hijink and Meijer (1987). The poor accuracy of the model of Hijink and Meijer (1987) can also be explained by the small number (n = 154) of observations from individual cows that were used to develop the model Hijink and Meijer (1987). Empirical models are only reliable within the limits of the underlying data sets. Therefore, a model based on a small number of data is likely to be less accurate.

In the present study the model of Vadiveloo and Holmes (1979) was the most inaccurate equation to predict DMI. However, a study of Keady et al. (2004), showed that the model of Vadiveloo and Holmes (1979) provided the most accurate predictions of DMI compared to five other commonly used models including the model of Milligan et al. (1981). The poor accuracy of the model of Vadiveloo and Holmes (1979) in our study can be attributed to various factors such as differences in genetics and diet composition. The model of Vadiveloo and Holmes (1979) was developed in the late 1970s using data from Ayrhire and British Friesian cows fed diets based on grass silage and hay, producing approximately 20 kg milk/day and consuming 15 kg DM/d. These conditions are probably more similar to the evaluation dataset used by Keady et al. (2004) than the evaluation dataset used in the present study. The dataset of Keady et al. (2004) included data from cows fed grass silage based diets and consuming 17 kg DM /d. Whereas, in the present study, the evaluation dataset contained data from high producing HF dairy cows fed diets containing various forages and consuming approximately 21 kg DM/d. Another, explanation for the poor accuracy of the model of Vadiveloo and Holmes (1979) is that, other than concentrate level, feed characteristics are not included in the model. In a previous paper we have pointed out that DMI is influenced by feed composition and digestibility (Zom et al., 2012). Therefore, the Vadiveloo and Holmes (1979) is not suited to account for changes DMI caused by changes in diet composition.

5. Conclusions

Five models for the prediction of feed intake were evaluated. Compared to five other models, the model of Zom et al. (2012) was most accurate as indicated by a low mean bias, MSPEs and RPEs across all evaluation data subsets, indicating that the model is robust and can be applied to various dairy rations and cows of lactation number, stage of lactation and pregnancy. The results show that accurate predictions of DMI are possible without the use of animal performance (e.g. milk yield, body weight) as inputs. Random error as proportion of MSPE for individual cows was large across all models. This may indicate that these models are likely better suited for prediction of the DMI of groups of cows than for individual cows.

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Chapter 4

Modeling ingested net energy partitioning in dairy cows

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Abstract

A model was developed to predict the partitioning of ingested net energy (NE_L) to milk energy and body reserves. This energy partitioning model describes the baselines of daily NE_L intake and milk energy output during successive lactation cycles of the average cow with the average NE_L intake. This average cow is defined as the 'reference cow'. Deviation of NE_L intake from the baseline is the estimator for changes in milk energy output. A NE_L intake above the baselines results in an increased milk energy output and reduced mobilization or increased deposition of body energy reserves. Whereas, a NE_L intake below the baseline results in a reduced milk energy output and increased mobilization or reduced deposition of body reserves. In the model, the proportion ingested NE_L partitioned to milk increased with parity number, but declined with increasing DIM and energy intake, reflecting the changes in priority in energy partitioning during the life and successive lactation cycles of a dairy cow. This results in different lactation curves and responses in milk energy output and body energy to variation in NE_L intake for cows different in lactation number, stage of lactation and pregnancy.

The predicted changes in body reserves and milk responses to changes in energy intake were compared with data from literature. This comparison indicated that the model provides realistic predictions of milk response and change of body reserves. It was concluded that proposed model provides a basis to predict of milk response of dairy cattle to changes in feeding strategy and diet composition.

Key words: partitioning of NEL, milk production, mobilization, dairy cows, modeling

1. Introduction

To formulate dairy cow rations with the aim to minimize feeding costs, optimize feed allocation and maximize revenues from milk, it is necessary to quantify the impact of the composition of the dairy cow ration on (net) energy intake and subsequently milk production. Current energy systems are designed to estimate (net) energy requirements of a cow with a certain milk yield, but cannot predict the response in milk yield to changes in energy intake. This inability is demonstrated by the practical observation that the response in milk yield to changes in the intake of net energy for lactation (NE_LI) is usually far below the theoretical maximum of 1 kg 4%-fat and 3.3%-protein corrected milk (FPCM) per 3.1 MJ NE_LI (Coulon and Remond, 1991; Schei et al., 2005). The explanation for this is that feeding below requirements is (partly) buffered by mobilization of body reserves, whereas feeding above requirements results in increased deposition or reduced mobilization of body reserves.

The prediction of milk responses to changes in NE_LI is complex because partitioning of ingested energy depends on stage of lactation, parity, genotype and energy balance (Coulon and Remond, 1991; Kirkland and Gordon, 2001a, b; Hansen et al., 2006). In addition, the milk response to changes in NE_LI is also influenced by the supply with other possibly limiting nutrients such as protein (Coulon and Remond, 1991; Brun-Lafleur et al., 2010). This complexity raises difficulties to predict the effects of feeding strategy on milk production. Simple models that simulate the complex dynamics of milk production response and changes of body reserves to energy intake would allow to evaluate the long-term impact of different feeding strategies (e.g. different forage to concentrate ratio’s, diet and forage composition) on dairy cow performance and the subsequent effects on farm economics and environmental burden. So far, no simple models are available that can simulate the effect of NE_LI on milk energy output (MEO), and change of body reserves while taking into account both the nutritional and physiological driven changes in the partitioning of ingested net energy. The aim of this study is to develop a framework for a simple deterministic model that predicts effects of NE_LI on MEO and nutritional and physiological driven change of body reserves in HF dairy cows using easy onfarm measurable input parameters.

2. Model description

2.1. *Principle Outlines*

The model is designed to predict on a daily basis and during successive lactation cycles, the partitioning of NE_L (van Es, 1978) in lactating HF dairy cows. The requirements for maintenance, pregnancy, milk production, growth and changes in body reserves and feed value are expressed in NE_L. In our approach, we have defined a 'reference cow' which is the average HF cow in the population (*i.e.* the developmental dataset). The daily NE_LI (NE_LI_R) and milk energy output (MEO_R), during the successive lactation cycles of the reference cow are used as baselines representing the average HF cow in the population. The deviation in NE_LI of an individual cow from NE_LI_R is used as an estimator for the milk energy output (MEO) and mobilization and deposition of body reserves of that individual cow.

It is assumed that NE_LI_R is equal to the sum of NE_L demand for maintenance (NE_LM), MEO, pregnancy (NE_LP), developmental growth (NE_LG), and NE_L deposition or mobilization (NE_LR) in body reserves (Equation 4.1).

$$NE_LI_R = NE_LM + MEO_R + NE_LP + NE_LG + NE_LR \tag{4.1}$$

The baseline of MEO_R is calculated from FPCM derived from the baselines of MY_R, MF_R and MP_R using an energy value of 3.05 MJ NE_L/kg FPCM (CVB, 2012) (Equation 4.2).

$$MEO_R = 3.05 \times MY_R(0.337 + 0.06 \times MP_R + 0.0116 \times MF_R) \tag{4.2}$$

For simplicity, we assume that NE_LM, NE_LG and, once the animal is pregnant, NE_LP are unavoidable and fulfilled with the highest priority, and that these NE_L sinks are not influenced by the plane of NE_LI. It has been recognized that mobilization of body reserves has both a genetically and a nutritional driven component (Friggens et al., 2004). This means that, during early lactation, even in cows fed high quality diets, milk production is supported by genetically driven mobilization of body reserves. Therefore, it is assumed that NE_LR is partly genetically driven (or pre-determined), which implies that mobilization of body reserves is partly unavoidable. Although, mobilization may be partly unavoidable, the extent of mobilization can be influenced by the plane of nutrition. An increased energy intake, for example by inclusion of a larger proportion of concentrate in the diet, results in both a reduced mobilization of body energy and an improved MEO (Reist et al., 2002; Coffey et al., 2004; Schei et al., 2005). Thus, alteration of NE_LI results in simultaneous changes MEO and energy retention. In our approach, we use the deviation of NE_LI from the baseline NE_LI (ΔNE_LI) to estimate the deviation of milk energy output (ΔMEO). It is assumed that the remainder of ΔNE_LI that is not partitioned to ΔMEO, (ΔNE_LI minus ΔMEO) is partitioned to body energy. In a situation where $\Delta NE_LI < 0$, an additional amount of

NE_L above NE_LR baseline (ΔNE_LR) is mobilized, whereas in a situation where $\Delta NE_LI > 0$ an additional amount NE_L above the NE_LR baseline is retained. The apparent net mobilization of NE_L ($netNE_LR$) is $netNE_LR = NE_LR + \Delta NE_LR$. Consequently, ΔNE_LI is partitioned between ΔMEO and energy in body reserves ΔNE_LR according to:

$$NE_LI_R + \Delta NE_LI = NE_LM + NE_LG + NE_LP + MEO + \Delta MEO + NE_LR + \Delta NE_LR \tag{4.3}$$

Because NE_LM, NE_LG and the genetically driven part of NE_LR are connected to each other, and for reasons of simplicity we have combined these items into NE_LU_R (Equation 4.4), which is explained later on in the following section.

$$NE_LU_R = NE_LM + NE_LG + NE_LR \tag{4.4}$$

To describe the baselines curves of NE_LU, MY_R, MF_R, MP_R and body weight (BW_R) we adopted the curve model developed by Zom et al. (2012) as a general model. This model describes the feed intake capacity of dairy cows as function of the cows' physiological status parameterized by parity number, DIM and days pregnant. The general model was modified for the curves NE_LU, MY_R, MF_R, MP_R and body weight (BW_R) as explained later on in this paper.

2.2. *Modeling Unavoidable Energy Demand of the Reference Cow*

The NE_L demands for NE_LM, NE_LG and the genetically driven part of NE_LR are assumed to be unavoidable. These demands are, although in a different direction, closely related to the age of the cow, body size and stage of lactation. Because, NE_LM, NE_LG and NE_LR are connected to each other, it is difficult to separate the amounts of NE_LI portioned among these items.

The NE_LM depends on the size or (metabolic) body weight ($BW^{0.75}$) of the cow. Body weight increase with parity number (Oldenbroek, 1989; Koenen et al., 1999; Nielsen et al., 2003), which implies that NE_LM increase with parity number. However, the increase in (metabolic) BW is asymptotic, with a decreasing growth and growth rate with advancing maturity. Consequently, NE_LG will decrease with parity number.

As the size of the cow increase the amount of body reserves potential available for mobilization will also increase as indicated by the observations that the amounts of body reserves mobilized in early lactation increase with parity number (Oldham and Friggens, 1989; Gallo et al., 1996; Dechow et al., 2002; Nielsen et al., 2003; Friggens and Badsberg, 2007). This implies that the amount of NE_LR mobilized increase with parity number associated with an increase in size.

The amounts of NE$_L$I partitioned to NE$_L$M, NE$_L$G and NE$_L$R are not only influenced by age or parity number, but are is also influenced by the stage of lactation. Within a lactation cycle, NE$_L$M, NE$_L$G and NE$_L$R all vary due to changes in the priorities of energy partitioning. In general, body reserves are mobilized in early lactation to support milk production, whereas in later stages of lactation, mobilized body reserves are restored which causes variation in NE$_L$G and NE$_L$R during the course of the lactation cycle. Changes in mobilization and deposition of body reserves causes variation in BW and successively variation in NE$_L$M. Because their interdependence and for reasons of simplicity we have combined NE$_L$M, NE$_L$G and the genetically driven part of NE$_L$R in our model assembled into NE$_L$U$_R$. The baseline of NE$_L$U$_R$ is described by Equation (4.5) which incorporates both the effects of age and stage of lactation on NE$_L$U$_{R:}$

$$\mathrm{NE_LU_R}(\mathrm{p},\mathrm{d}) = \left(\alpha_0 + (\alpha_1 - \alpha_2\mathrm{d}) \times \left(1 - e^{-\rho_\alpha((\mathrm{p}-1)+\mathrm{d}/365)}\right)\right) \times \left(1 - (\alpha_3 + \alpha_4 \times (\mathrm{p} - 1 + \mathrm{d}/365)) \times e^{-\rho_\beta \times \mathrm{d}}\right) \quad (4.5)$$

The first term of the equation, before the multiplication sign, represents the curvilinear increase of the energy demands as function of an age derived from parity number (p) and DIM (d) (age = p-1+d/365). The start level of NE$_L$U$_R$ at p = 1 and d = 0 is represented by α_0, α_1 is maximum increase of NE$_L$U$_R$, α_2 is the interaction parameter for stage of lactation and parity and ρ_α is the rate parameter increase of NE$_L$U$_R$. The second term, after the multiplication sign, is an adjustment of the energy demands for stage of lactation during successive parities in which α_3 is a constant, α_4 is the parameter for the interaction between age and stage of lactation and ρ_β is a rate parameter of adjustment for stage of lactation.

Equation (4.5) results in an asymptotic curvilinear increase of the baseline of NE$_L$U$_R$ which reflects the asymptotic growth of the cow as function of age and subsequent increasing demands of energy for maintenance and amounts of body reserves that are potential available for mobilization. This implies also diminishing energy demands for growth as result of a lower growth rate with increasing maturity. In addition to that, it includes an adjustment for the changing energy requirements for maintenance, growth and mobilization that occurs during the course the lactation.

2.3. Modeling Baselines of Milk Yield, Milk Constituents and Body Weight

Milk yield and milk constituents yield increase with parity number (Ray et al., 1992; Coulon et al., 1995; Arbel et al., 2001; Coffey et al., 2004; Mellado et al., 2011). The increased milk production with higher parity numbers is correlated with BW and mammary gland weight (Linzell, 1972), greater udder secretory tissue volume (Knight and Wilde, 1993), increased feed intake capacity (Zom et al., 2012), and differences in hormonal status influencing partitioning of nutrients into milk (Wathes et al., 2007). Within a lactation cycle, changes in milk production are associated with an exponential increase of udder secretory tissue volume during gestation and early lactation and an involution of secretory cells during mid and late lactation (Knight and Wilde, 1993; Sørensen et al., 2006). Similar to milk production, BW varies as a function of age and within a lactation cycle BW varies due to the nutritional and genetically driven mobilization of body reserves and to pregnancy. Milk production and BW are a function of age and stage of lactation. Therefore, MY_R, MF_R, MP_R and BW_R were predicted with modifications of the general lactation curve model (Zom et al., 2012). This model has the following structure:

$$Y(p,d,g)_i = B(p,d)_i \times L(d)_i \times P(g)_i \qquad (4.6)$$

in which, $Y(p,d,g)_i$ is the performance of the reference cow (*i*= MY, MF, MP, or BW) during successive lactations as function of parity number (p), and DIM and stage of gestation (g). The term $B(p,d)_i$ is the basal performance level of the reference cow as a function of parity number; $L(d)_i$ is a multiplicative adjustment factor of performance for DIM; $P(g)_i$ is a multiplicative adjustment factor of performance for days of gestation The basal performance level $B(p,d)_i$ is described by Equation 4.7

$$B(p,d)_i = \left(\alpha_0 + (\alpha_1 - \alpha_2 d)\right) \times \left(1 - e^{-\rho_\alpha \times \left((p-1) + d/365\right)}\right) \qquad (4.7)$$

Equation (4.7) is an asymptotic function, in which, p is parity number, d is DIM, α_0 is the initial level of the $B(p,d)_i$ at p = 1 and d = 0, α_1 is the maximum increase of $B(p,d)_i$, α_2 is the parameter of interaction between d and p and ρ_α is the rate parameter of the increase of B(p,d) from α_0 to the asymptotic level.

The curves of MY, MF, MP, or BW are typically characterized by a first phase in which a rapid increase (MY) or a rapid decline (MF, MP, BW) until peak or nadir occurs. After the peak or nadir, MY gradually declines while MF, MP and BW increase. In order to incorporate these effects, the curve of $B(p,d)_i$ is adjusted for the stage of lactation by multiplication with adjustment factor L(d)*i* (Equation 4.8).

$$\mathrm{L(d)}_i = e^{\left(\mathrm{I(d)}\times\mathrm{D(d)}\right)} \tag{4.8}$$

$$\mathrm{I(d)}_i = \beta\times\left(1-e^{-\rho_\beta\times\mathrm{d}}\right) \tag{4.8a}$$

$$\mathrm{D(d)}_i = \frac{1}{1+e^{\rho_\gamma\times\left(\ln(\mathrm{d})\text{ - }\gamma\right)}} \tag{4.8b}$$

Equation 4.8 describes $L(d)_i$ the changes in the performance of the reference cow (*i*= MY, MF, MP, or BW) during the course of the lactation which is the exponential of function I(d) (Equation 4.8a) and D(d)*i* (Equation 4.8b). Asymptotic function I(d) is the adjustment factor for the first phase of the lactation (before peak or nadir), in which β is the asymptotic level, and ρ_β the rate parameter and d is DIM. Logistic function $D(d)_i$ the change in performance during the second phase of the lactation curve (after peak of nadir), ρ_γ is a rate parameter, γ is time-point of maximum adjustment declining phase. At the start of lactation (d = 0), D(d) approaches 1. The inflection point of the logistic function occurs at time $d = e^\gamma$.

The exponential of the product of $I(d)_i$ and $D(d)_i$ was used to calibrate the effect of stage of lactation to 1 ($L(d) = e^0$; no adjustment) at the start of the lactation.

The change in performance related to stage of gestation is incorporated in the model by multiplying $B(p,d)_i$ with adjustment factor $(P(g))_i$ (Equation 4.9).

$$\mathrm{P(g)}_i = \left(1+\delta_\mathrm{g}\times\left(\frac{\mathrm{g}}{220}\right)^{\rho_\delta}\right) \tag{4.9}$$

In which, g is days of gestation and δ_g is the rate parameter and ρ_δ is shape parameter of adjustment for pregnancy. It is assumed that cows are dried off at day 220 of gestation. Multiplication of equations (4.7) with (4.8) and (4.9) yields the complete curve model of MY_R, MF_R, MP_R or BW_R:

$$\mathrm{Y(p,d,g)}_i = \left(\left[\alpha_0 + (\alpha_1 - \alpha_2 \times \mathrm{d}) \times \left(1 - e^{-\rho\alpha \times ((\mathrm{p}-1)+\mathrm{d}/365)}\right)\right] \times e^{\frac{\beta \times \left(1 - e^{-\rho\beta \times \mathrm{d}}\right)}{1+e^{\rho\gamma \times (\ln(\mathrm{d}) - \gamma)}}} \right) \times \left(1 + \delta_{\mathrm{g}} \times \left(\frac{\mathrm{g}}{220}\right)^{\rho_\delta}\right) \tag{4.10}$$

2.4. *Modeling milk ΔMEO in response to ΔNE_L intake*

The response of a cow in terms of changes in MEO to an increased or decreased NE_LI is estimated from ΔNE_LI, which is the deviation the actual NE_LI from the $NE_LI_{R,}$ ($\Delta NE_LI = NE_LI - NE_LI_R$). The proportion of ΔNE_LI partitioned to milk energy (ΔMEO) and body reserves (ΔNE_LR) is described by equations (4.11) and (4.12).

$$\Delta \mathrm{MEO} = \mathrm{MEO_R} \times \left(e^{\mu} \times \left(\frac{\mathrm{NE_LI_R} + \Delta \mathrm{NE_LI}}{\mathrm{NE_LI_R}} \right)^{\beta_1} - 1 \right) \tag{4.11}$$

In which, μ is the constant and β_1 is the parameter for effect of the relative difference in NE_LI. The part of ΔNE_LI that is not partitioned towards MEO is assumed to be retained energy. Therefore, the nutritional driven part of the change of body reserves (ΔNE_LR) can be calculated as follows:

$$\Delta \mathrm{NE_LR} = \Delta \mathrm{NE_LI} - \Delta \mathrm{MEO} \tag{4.12}$$

Thus, NE_LI above the baseline ($\Delta NE_LI > 0$) results in an increased MEO together with a reduced mobilization or increased deposition of body energy reserves compared to the reference cow; a NE_LI below the baseline ($\Delta NE_LI < 0$) results in a reduced MEO together with an increased mobilization or reduced deposition of body energy reserves compared to the reference cow.

Table 4.1 Summary of the developmental dataset including diet ingredients, milk performance, body weight and dry matter intake (DMI)

			Number[3] of		Milk yield (kg/d)		Milk fat yield (kg/d)		Milk protein (kg/d)		Body weight (kg)		DMI (kg/d)	
Exp[1].	Site[2]	Main ingredients of the diet	Cows	Obs.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
1	W2	Grass silage, maize silage, concentrates	84	1062	32.7	6.5	1.51	0.32	1.10	0.21	595	78.2	21.6	3.1
2	W2	Grass silage, maize silage, concentrates	38	399	20.8	4.1	1.06	0.21	0.70	0.13	582	64.7	18.9	3.1
3	W3	Grass silage, maize silage, concentrates	28	395	34.1	6.9	1.57	0.31	1.17	0.21	606	72.3	22.3	3.0
4	W3	Fresh grass, maize silage, concentrate	46	476	25.0	5.5	1.06	0.19	0.84	0.16	598	66.9	20.0	2.5
5	W2	Fresh grass, maize silage, concentrate	34	600	28.1	5.6	1.22	0.22	0.92	0.18	549	62.8	20.6	3.0
6	W2	Fresh grass, maize silage, concentrate	42	768	30.7	5.1	1.39	0.23	1.01	0.15	594	51.7	20.0	2.3
7	W3	Grass silage, corn ears silage, concentrate,, dry by-products	54	718	24.9	4.4	1.06	0.20	0.80	0.14	573	52.0	18.5	2.4
8	W3	Fresh grass, corn ears silage, concentrate	48	766	29.7	6.1	1.29	0.27	0.98	0.19	605	62.5	21.0	2.8
9	W3	Grass silage, corn ears silage, fodder beet, concentrates	56	839	30.9	5.6	1.41	0.28	1.02	0.17	599	71.6	19.6	3.2
10	AH	Fresh grass and grass/clover, concentrate	28	252	22.4	4.2	1.00	0.17	0.81	0.13	604	57.1	18.3	1.8
11	AH	Fresh grass and grass/clover, concentrate	37	451	26.9	6.1	1.09	0.21	0.92	0.18	598	54.5	19.0	2.3
12	AH	Fresh grass and grass/clover, concentrate	41	565	29.2	5.4	1.20	0.22	1.02	0.15	619	65.3	20.5	2.3
13	AH	Fresh grass and grass/clover, concentrate	42	572	29.0	5.3	1.21	0.19	0.96	0.16	616	63.2	19.9	1.9
14	AH	Grass silage and grass/clover silage, red clover silage, concentrate	30	314	30.4	4.9	1.36	0.23	1.05	0.15	643	55.3	21.9	2.0
15	AH	Grass silage and grass/clover silage, red clover silage, concentrate	30	390	31.9	6.1	1.37	0.22	1.06	0.16	638	56.4	21.6	2.2
16	CD	Grass silage, maize silage, cereal-WCS[4], concentrate, dry by-products	40	599	30.7	5.4	1.47	0.29	1.02	0.18	634	74.5	19.5	2.6
17	CD	Grass silage, maize silage, cereal-WCS[4], concentrate, dry by-products	42	609	30.2	6.1	1.40	0.33	1.00	0.19	635	77.1	20.5	2.8
18	CD	Grass silage, maize silage, cereal-WCS[4], concentrate, dry by-products	39	581	33.0	6.7	1.50	0.36	1.06	0.19	637	65.8	20.6	2.6
19	AH	Lucerne silage, concentrate	24	192	32.0	4.6	1.35	0.20	1.00	0.14	601	62.8	24.0	2.9
20	CD	Lucerne silage, concentrate	41	400	30.8	5.7	1.37	0.29	1.00	0.19	615	55.8	21.1	3.0
21	CD	Lucerne silage, concentrate	45	435	29.1	6.7	1.31	0.33	0.95	0.21	621	72.6	19.8	3.6

Table 4.1 Continued Summary of the developmental dataset including diet ingredients, milk performance, body weight and dry matter intake (DMI)

Exp[1].	Site[2]	Main ingredients of the diet	Number[3] of Cows	Number[3] of Obs.	Milk yield (kg/d) Mean	Milk yield (kg/d) s.d.	Milk fat yield (kg/d) Mean	Milk fat yield (kg/d) s.d.	Milk protein (kg/d) Mean	Milk protein (kg/d) s.d.	Body weight (kg) Mean	Body weight (kg) s.d.	DMI (kg/d) Mean	DMI (kg/d) s.d.
22	W4	Grass silage, maize silage, corn ears silage, concentrates	172	6780	31.6	10.5	1.33	0.39	1.11	0.31	644	71.3	21.5	3.5
23	BZ	Grass silage, concentrates, crushed wheat	45	529	30.4	5.4	1.39	0.25	1.00	160	580	63.1	19.9	2.8
24	BZ	Grass silage, concentrates, crushed wheat	45	537	28.5	4.7	1.27	0.21	0.96	145	592	65.2	18.6	2.5
25	W2	Grass silage, maize silage, concentrates	79	1395	30.8	6.0	1.45	0.30	1.01	182	598	68.2	21.8	3.0
26	W2	Grass silage, maize silage, concentrates	84	1635	33.5	6.9	1.49	0.32	1.13	221	633	78.6	23.0	3.0

1 Exp = Experiment References Exp 1-3 (Feil et al., 2000a); Exp 4-6 (van Duinkerken et al., 2000); Exp 7-9 (Zom, 1996); Exp 10-15 (Remmelink, 2000); Exp 16-18; (van Duinkerken and Bleumer, 2000); Exp 19-21 (Boxem et al., 1999);Exp 22 (Meijer et al., 1998);Exp. 23, 24 (Feil et al., 2000b); Exp 25, 26 (Zom et al., 2001) 2 Site – Experimental site AH = Aver Heino, Heino; BZ = Bosma Zathe, Ureterp; CD = Cranendonck, Soerendonk; W2= Waiboerhoeve Dairy Unit 2; W3 = Waiboerhoeve Dairy Unit 3, Lelystad; W4 = Waiboerhoeve High Performance Unit, Lelystad

3 Number of cows = number of unique cows; Number of Obs = Number of observations individual weekly per cow

4 Cereal-WCS = whole crop silage from small cereals

3. Materials and methods

3.1. *Calibration dataset*

The dataset used to calibrate the model comprised 20467 records with the complete weekly means of dry matter intake (DMI), NE_LI, diet formulation, nutrient composition, milk yield and composition, body weight, DIM, days pregnant and parity number from 1294 individual cows. The data were obtained from 26 feeding experiments using high merit HF dairy cows fed various diets ranging from more or less lipogenic (grass and grass silage based diets) to glucogenic (maize silage based diets) conducted at 6 different experimental sites in the Netherlands (Table 4.1). Data on cow performance are presented in Table 4.2.

All cows were ad libitum fed with a partial mixed ration (PMR) or a total mixed ration (TMR). The diets were formulated such that the metabolizable protein (DVE, (Tamminga et al., 1994)) to energy ratios were balanced (average DVE to NE_L ratio 11.2:1, s.d. 1.2; average CP to NE_L ratio 25.5:1, s.d. 3.6) and that protein supply was not limiting.

Table 4.2. Mean, minimum, maximum values and standard deviation of feed intake, milk production and body weight in the developmental database from 20467 weekly observations from 1294 individual cows

	Mean	Minimum	Maximum	s.d.
Feed intake				
DMI (kg DM/d)	21.0	7.2	33.8	3.2
NE_L intake (MJ/d)	140.0	46.7	236.2	22.5
Milk production				
Milk (kg/day)	30.7	5.5	71.4	8.0
Fat (kg/day)	1.35	0.20	3.19	0.34
Protein (kg/day)	1.04	0.19	2.28	0.25
DIM	115	1	584	87
Parity number	2.6	1	11	1.7
Days pregnant	28	0	235	50.1
Body weight (kg)	620	420	963	73

3.2. *Modeling procedures*

Procedures of parameter estimation were similar as described by Zom et al. (2012). The parameters of the equations (given by Equation 4.10) for each NE_LU_R, MY_R, MF_R, MP_R and BW_R were estimated simultaneously using a non-linear regression analysis based on a maximum likelihood method, according to the Gauss-Newton iteration of the FITNONLINEAR procedure of Genstat (VSN International Ltd, Hemel Hempstead UK). Each cycle of parameter estimation started with the complete models for NE_LU_R, MY_R, MF_R, MP_R and BW_R. Once iteration has converged, non-significant parameters were removed from the models. Excluding non-significant parameter did not increase prediction error, but reduced unnecessary complexity of the model. In a subsequent step, the remaining parameters were estimated again. Adjustments to the models were checked on the basis of the goodness of fit and bias. Strongly-correlated model parameters were removed from the model and the remaining model parameters were estimated again. The model parameter with the best fit was retained in the final model in order to keep the model as simple as possible and minimize the number of model parameters. Consequently, the remaining model included only significant and relevant explanatory parameters. Subsequently, the parameters of the model for prediction of ΔMOE (Equation 4.12) were estimated after log-transformation using the REML procedure of Genstat (VSN, International Ltd, Hemel Hempstead, UK) using the following general model:

$Y_i = \mu + \beta_1 X_i + \varepsilon_i$. In which, Y is the log-transformed relative milk response $(MEO_{LR}+\Delta MEO_{LR})/MEO_{LR)}$; μ is the constant; ß is the fixed effect of the relative difference in NE_LI given by term X, in which is $X = \ln((NE_LI_R+\Delta NE_LI)/NE_LI_R)$. Experiment and cow were included as random effects.

3.3. Model verification

Model behavior was verified in order to assess whether the model worked properly and yielded reasonable results. As described in detail below, this was done in two ways. First, by simulating the response in MEO_R, NE_LI_R, NE_LU_R, BW_R and EB to pregnancy, parity and DIM. Subsequently, it was investigated whether the calculated energy balances and changes in BW_R could be explained by changes in body composition. The second method of verification was by simulating the response in MEO to different levels of NE_LI in comparison to reported in vivo observations.

3.4. Verification of modelled response to pregnancy, parity and stage of lactation

On a daily basis, NE_LI_R, NE_LU, MEO_R and BW_R were generated for the 1st, 2nd, 3rd and 6th 305-d lactations of a pregnant and a non-pregnant reference cow. For the pregnant cow, it was assumed that conception occurs at day 90 of lactation. Subsequently, for each lactation, the net energy balance (NE_Lb_R) of the reference cow were calculated according to van Es (1978) with an additional allowance for day of gestation (g) (van den Top et al., 2000).

$$\begin{aligned} NE_Lb_R = {} & NE_LI_R - \left(0.29 \times BW_R^{0.75} + MEO_R\right) \times \left(1 - 0.00165 \times (MEO_R / 3.05 - 15)\right) \\ & - 4.4 \times (0.021 \times e^{-0.0000576 \times g}) \times (10^{(151.6665 - 151.64 \times e^{(-0.0000576 \times g)})}) \end{aligned} \tag{4.13}$$

Empty body weight of the reference cow (EBW_R) was calculated on a daily basis from predicted BW_R and DMI using the formula $EBW_R = BW_R - 4 \times DMI$ (Jarrige, 1989). The DMI was estimated using the feed intake model of Zom et al. (2012), assuming a diet, typical for the Netherlands, that consisted of ad libitum forage consisting of corn and grass silage (1:1 on a DM basis), supplemented with concentrate (Table 4.3). The proportion of concentrate in the simulated diet (i.e. the forage to concentrate ratio) was adjusted on a daily basis, such that the simulated NE_LI from the diet was equal to NE_LI_R and that minimum requirements for physical structure (DeBrabander et al., 1996) were met.

The daily change of EBW_R (ΔEBW_R) was calculated from the difference in EBW_R between two consecutive days. Daily changes in body fat (ΔBF_R), protein and water (ΔBPW_R) in body tissues were calculated from NE_Lb_R and ΔEBW by solving equations (4.14) and (4.15).

$$NE_Lb_R = NE_L/\text{kg fat} + NE_L/\text{kg protein} \tag{4.14}$$

$$\Delta EBW_R = \Delta BF_R + \Delta BPW_R \tag{4.15}$$

The assumed energy values of fat and protein were 39.7 MJ/kg and 23.8 MJ/kg, respectively (Armsby, 1917). The assumed protein to water ratio was 1:3.4 (AFRC, 1993). The efficiencies of conversion of energy from body reserves into milk energy and from ingested energy into body reserves were assumed to be 0.8 and 0.59, respectively (van Es, 1978).

Table 4.3 Assumed feed characteristics used for model simulations

Item	Grass silage	Maize silage	Concentrate	Reference
NE_L (MJ/kg DM)	5.86	6.47	7.18	(CVB, 2012)
Satiety value (SV/kg DM)	1.00	0.82	0.35	(Zom et al., 2012)
Physical structure (/kg DM)	2.80	1.52	0.31	(DeBrabander et al., 1996)

3.5. Verification of modelled response to ΔNE_LI

The prediction of MEO in response to different levels of ΔNE_LI was performed for 1st, 2nd, 3rd and 6th parity cows at 40, 80, 160 and 305 day in lactation. The simulated diets consisted of *ad libitum* grass silage and maize silage in a ratio of 1:1 on a DM basis supplemented with various amounts of concentrate (Table 4.3). In order to simulate realistic diets applying to practical situations, the proportion of concentrate in the simulated diets were such that simulated NE_LI varied between 75 to 125% of the NE_L requirements (CVB, 2012). The minimum and maximum forage to concentrate ratios in the simulated diets were defined by either the minimum requirements of physical structure in the diet (DeBrabander et al., 1996) or by the range of NE_LI being 75 to 125% of the NE_L requirements (CVB, 2012).

4. Results

4.1. *Unavoidable energy demand*

The parameters of the model that describe the unavoidable net energy demand of the reference cow are presented in Table 4.4, displayed in Figure 4.1. The unavoidable net energy demand of the reference cow NE_LU, the sum of NE_LM, NE_LG, NE_LR increases curvilinear with DIM (Figure 4.1). At the start of the lactation NE_LU is low because of mobilization of energy from body reserves ($NE_LR < 0$). The shape of the curves are different for different lactation numbers, reflecting differences in energy partitioning between cows of different age (i.e. increased maintenance and mobilization and retention of energy in body reserves and reduced growth as parity number increase).

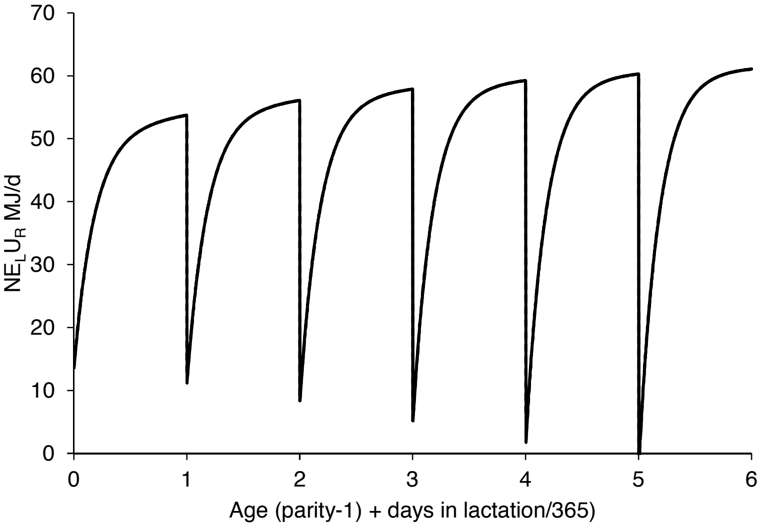

Figure 4.1 The unavoidable net energy demand of the reference cow (NE_LU_R), the sum of net energy demands for maintenance (NE_LM) growth (NE_LG) and the genetically driven mobilization of body reserves (NE_LR)

4.2. *Modifications to the initial models*

Milk yield. During parameter estimation of the MY_R, the equation of the logistic function (Equation 4.8b) needed to be modified because rate parameter ρ_γ was not significantly different from 1 (estimate 0.978, standard error 0.64). Therefore, equation (4.8b) in the model describing milk yield was modified as:

$$D(d) = \left(\frac{1}{1 + e^{\gamma}(d)} \right) \tag{4.16a}$$

For reasons of simplicity, rewritten as:

$$D(d) = \left(\frac{1}{1 + \kappa \times d} \right) \tag{4.16b}$$

Milk fat and protein concentration. Visual assessment of the plotted curves of milk fat and protein concentration indicated that in the first phase of lactation, the shape of the curves was different for cows of different parities, suggesting an interaction between parity and stage of lactation. In order to describe different shaped curves of milk fat and protein concentration for successive parities, equation (4.8a) was modified to:

$$I(d) = \beta + \tau \times \left(1 - e^{-(\rho_\alpha + \rho_\tau) \times (p - 1 + d/365)} \right) \times \left(1 - e^{-\rho_\beta \times d} \right) \tag{4.17}$$

In which, β is the constant, τ maximum decline of fat and protein concentration, ρ_α is the rate parameter, ρ_τ is rate parameter for adjustment for parity and stage of lactation. This modification allows different levels of minimum milk fat and protein with increasing parity number. The final models of the baselines for milk yield, milk fat, milk protein and BW are presented in Table 4.4. and displayed in Figure 4.2.

4.3. Marginal MEO in response to changes in NE_L intake

Energy dynamics of the reference cow were described by combining the models for NE_LU, Y_{MY}, Y_{MF}, Y_{MP}, and FPCM. Marginal milk energy response, defined as the amount of extra ΔMEO for each unit of ΔNE_LI, was calculated using the following equation:

$$\Delta MEO = MEO_R \times \left(e^{-0.04743(s.e.0.010393)} \left(\frac{NE_LI_R + \Delta NE_LI}{NE_LI_R} \right)^{0.5179(s.e.0.00807)} - 1 \right) \tag{4.18}$$

The combined models accounted for 57.3 per cent of the variation of MEO with a standard deviation of 14.7 MJ /d. The equation that described body weight over successive lactations accounted for 45.3 per cent of the variation of the body weight with a standard deviation of 54.3 kg.

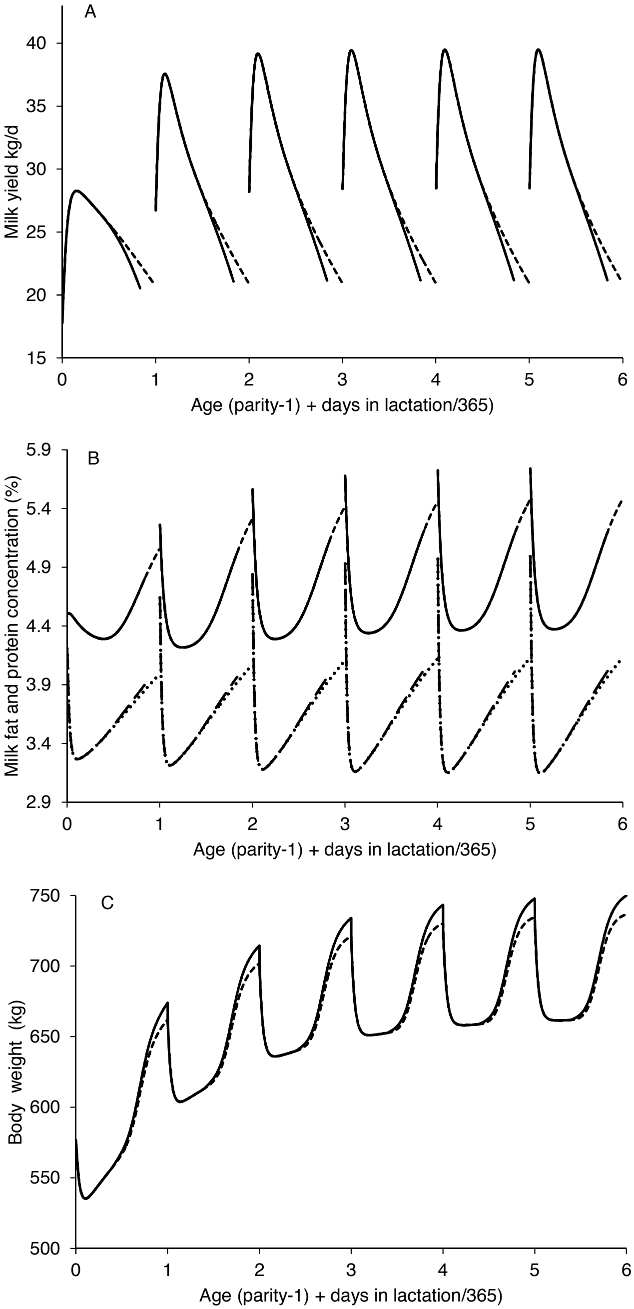

Figure 4.2 Panel A: Simulated baseline of milk production (kg/d) during 6 successive lactations of pregnant cows (solid line) and non-pregnant cows (dashed line); Panel B: Simulated baseline of milk fat and milk protein concentration (%) of pregnant cows (milk fat indicated with solid a line, milk protein indicated with a dashed line with dots) and non-pregnant cows production (milk fat indicated with a dashed line, milk protein indicated with a dotted line); Panel A: Simulated baseline of body weight (kg) during 6 successive lactations of pregnant cows (solid line) and non-pregnant cows (dashed line).

4.4. Simulation and verification of predicted milk MEO, EB, body tissue change

The results of the simulations of NE_LI_R, and MEO and FPCM yield over a 305-d lactation period are presented in Table 4.5. The higher 305-d MEO yield in non-pregnant-cows compared to pregnant cows resulted from a more persistent lactation as illustrated in Figure 4.2. The predicted total FPCM yield of the reference cow during the period of a negative EB (NEB) was 1957, 3367, 3720 and 3858 kg for parity 1, 2, 3 and 6, respectively. The calculated amounts of body fat and protein mobilized and deposited in pregnant and non-pregnant reference cows are presented in Table 4.6.

Our simulations indicate that NE_Lb_R changed from negative to positive at day 71, 91, 96, 98 for parity 1, 2, 3 and 6, respectively, and that nadir of the NE_Lb_R occurred in the first week of lactation (Figure 4.3). The simulations showed that the largest part of mobilization of body reserves takes place during the first week of lactation. During the first week of lactation, the cumulative mobilization amounted to approximately 40% of total mobilization of EBW, 52% of total mobilization of protein and 11% of the total mobilization of fat

Simulated rates of mobilization and deposition of body fat (kg/d) and protein (kg/d) are displayed in Figure 4.4. The simulations showed also that fat and protein are mobilized at different rates, and that protein retention occurs while cows were still in a NEB. In our simulations, the peak of fat mobilization occurred in week 3 of lactation with fat mobilization rates of 0.33, 0.63, 0.77 and 1.07 kg/d for parity 1, 2, 3 and 6 respectively (Figure 4.4). Maximum cumulative mobilization of fat was reached when the NE_Lb_R turn from negative to positive at 71, 91, 96 and 98 days after parturition for parity 1, 2, 3 and 6, respectively (Table 4.6).

The peak of protein mobilization occurred in week 1 of lactation with protein mobilizations rates of 0.88, 0.96, 0.98 and 0.98 kg/day for parity 1, 2, 3 and 6, respectively. Maximum cumulative mobilization of protein was reached at 38, 32, 31 and 30 days after parturition for parity 1, 2, 3 and 6, respectively. The amounts of maximum cumulative protein mobilization were 12.6, 11.5, 11.5 and 10.6 kg for parity number 1, 2, 3 and 6 respectively

Table 4.4 Parameter estimates of the baselines of $NE_LU(a,d)$ unavoidable NE_L requirements, milk yield, milk fat and protein concentration and body weight

Parameter	Estimate	s.e.	Model
	Baseline $NE_LU(a,d)$ unavoidable NE_L requirements of the reference cow[1]		
α_0	50.79435	0.42021	$NE_LU(a,d)=\left(\alpha_0+\alpha_1\times\left(1-e^{-\rho_\alpha((p-1)+d/365)}\right)\right)\times\left(1-(\alpha_3+\alpha_4\times(p-1+d/365))\times e^{-\rho_\beta\times d}\right)$
α_1	13.0824	0.001973	
ρ_α	0.2703	0.0522	
α_3	0.7444	0.0102	
α_4	0.06025	0.00334	
	Baseline $Y(p,d,g)_{MY,}$ evolution of milk yield of the reference cow during the course successive lactations		
Parameter	Estimate	s.e.	
α_0	17.153	0.412	$Y(p,d,g)_{MY}=\left((\alpha_0+\alpha_1)\times(1-e^{-\rho_\alpha\times(p-1+d/365)}\right)\times e^{\left(\frac{\beta\times\left(1-e^{(-\rho_\beta\times d)}\right)}{1+\kappa\times d}\right)}\times\left(1+\delta_g\times\left(\frac{g}{220}\right)^{\rho_\delta}\right)$
α_1	10.459	0.286	
α_2	0.0254	0.00141	
ρ_α	1.8099	0.0718	
β	0.6350	0.0594	
ρ_β	0.05245	0.00916	
κ	0.01044	0.00303	
δ_p	-0.1869	0.0179	
ρ_δ	2.493	0.308	
	Baseline $Y(p,d,g)_{MF}$ evolution of milk fat concentration of the reference cow during the course of successive lactations		
Parameter	Estimate	s.e.	
α_0	4.4966	0.0199	$Y(p,d,g)_{MF}=\left((\alpha_0+\alpha_1)\times(1-e^{-\rho_\alpha\times(p-1+d/365)}\right)\times e^{\left(\frac{\beta\times\left(1-e^{-(\rho_\alpha+\rho_\tau)\times(p-1+d/365)}\right)\times\left(1-e^{(-\rho_\beta\times d)}\right)}{1+e^{\rho_\gamma}\times(\ln(d)-\gamma)}\right)}$
α_1	1.3466	0.0865	
ρ_α	0.9635	0.0636	
β	0.2917	0.0134	
ρ_α	0.9635	0.0636	
ρ_τ	0.7475	0.0886	
ρ_β	0.0556	0.0321	
ρ_γ	4.824	0.293	
γ	5.6342	0.02374	

Table 4.4 Continued Parameter estimates of the baselines of NELU(a,d) unavoidable NEL requirements, milk yield, milk fat and protein concentration and body weight

Parameter	Estimate	s.e.	Model
	Baseline $Y(p,d,g)_{MP}$ evolution of milk protein concentration of the reference cow during the course of successive lactations		
α_0	4.321	0.0694	$Y(p,d,g)_{MP} = \left((\alpha_0+\alpha_1)\times(1-e^{-\rho_\alpha\times(p-1+d/365)}\right)\times e\left(\frac{\beta\times\left(1-e^{-(\rho_\alpha+\rho_\tau)\times(p-1+d/365)}\right)\times\left(1-e^{\left(-\rho_\beta\times d\right)}\right)}{1+e^{\rho_\gamma\times(\ln(d)-\gamma)}}\right)\times\left(1+\delta_g\times\frac{g}{220}\right)$
α_1	0.9691	0.0931	
ρ_α	0.763	0.122	
β	0.2945	0.0172	
τ	0.2517	0.0201	
ρ_α	0.763	0.122	
ρ_β	0.11357	0.00423	
δ_g	0.01657	0.00401	
	Baseline BW(p,d,g) evolution of body weight of the reference cow during the course of successive lactations		
Parameter	Estimate	s.e.	
α_0	580.64	3.5	$BW(p,d,g) = \left((\alpha_0+\alpha_1)\times(1-e^{-\rho_\alpha\times(p-1+d/365)}\right)\times e\left(\frac{\beta\times\left(1-e^{\left(-\rho_\beta\times d\right)}\right)}{1+e^{\rho_\gamma\times(\ln(d)-\gamma)}}\right)\times\left(1+\delta_g\times\frac{g}{220}\right)$
α_1	159.88	1.79	
ρ_α	0.7333	0.0199	
β	0.10852	0.0054	
ρ_β	0.07174	0.00538	
ρ_γ	10.48	1.22	
γ	5.5458	0.016	
δ_p	0.02382	0.00566	

[1] Unavoidable net energy requirements: the sum NE_L requirements of maintenance, pregnancy, developmental growth and deposition or mobilization

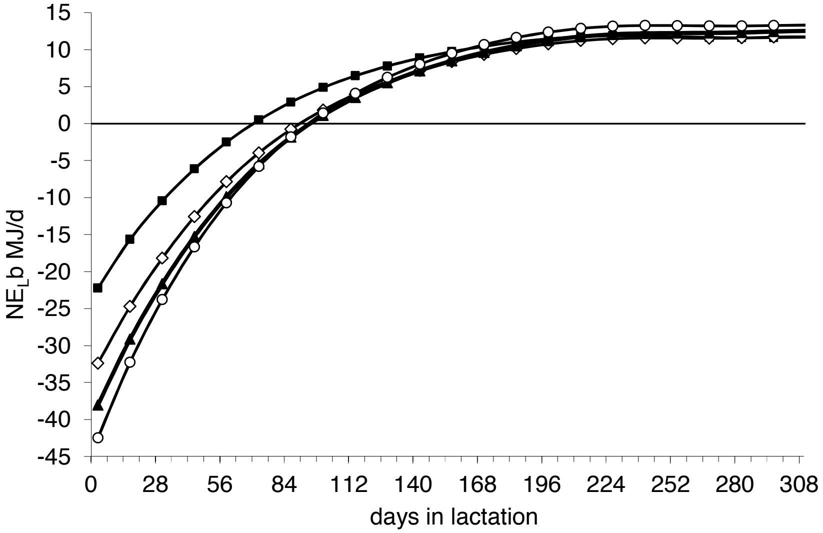

Figure 4.3 Simulated net energy balance of the reference cow in parity 1 (line marker ■), parity 2 (line marker ◇), parity 3 (line marker ▲) and parity 6 (line marker ○)

Table 4.5 Simulated total NE_L intake (NE_LI_R) and MEO and FPCM production during a 305-d lactation period in the pregnant and non-pregnant reference cow, using equations presented in table 4.

Pregnant cow (conception at 90 day in lactation)

Parity	NE_LI_R [1](GJ)	MEO_R[2](GJ)	FPCM[3] (kg)
1	37.9	24.4	8004
2	42.7	28.7	9411
3	44.0	29.7	9732
6	44.6	30.1	9863

Non-pregnant cow

Parity	NE_LI_R [1](GJ)	MEO_R[2](GJ)	FPCM[3] (kg)
1	38.7	25.3	8279
2	43.6	29.6	9705
3	44.9	30.6	10032
6	45.5	31.0	10166

[1] Total predicted intake of net energy for lactation intake by the reference cow per 305-d lactation period

[2] Total net energy output in milk by the reference cow per 305-d lactation period

[3] Total FPCM per 305-d lactation period, 1 kg FPCM contains3.05 MJ NE_L

4.5. Simulation and verification of MEO response to NE_L intake.

Simulation of the effects of different levels of NE_LI on MEO within a range 75 to 125 % of the requirements, at 40, 80, 160 and 305 DIM are presented in Figure 4.5. At each stage of lactation, MEO increased linearly with the increasing NE_LI intake. Marginal MEO response, defined as the amount of extra MEO from each extra unit of NE_LI, decreased with increasing NE_LI. As result, the apparent efficiency declined with increasing NE_LI. In early lactation (40 day in lactation), the predicted marginal milk NE_L response of a primiparous cow, was lower than in multiparous cows. The, differences in ΔMEO to ΔNE_LI between cows of different parities diminished gradually during lactation.

Table 4.6 Calculated mobilization during the period of a negative energy balance (NE_Lb_R[1] < 0) and calculated deposition during the period of a positive energy balance (NE_Lb_R >0) of the pregnant and non-pregnant reference cow in lactation 1, 2, 3 and 6

Simulated mobilization of body tissues, during the period of a negative energy balance: NE_Lb_R[1] < 0

Parity	Period[2]	ΔBW (kg)		ΔFat (kg)		ΔProtein (kg)		ΔNE_L (MJ)		
	days p.p.	total	/d	total	/d	total	/d	total	/d	/kg BW
1	0-71	36.0	0.51	15.3	0.22	12.0	0.17	714	10.1	19.8
2	0-91	51.6	0.57	34.9	0.38	9.3	0.10	1285	14.1	24.9
3	0-96	60.9	0.63	43.4	0.45	9.2	0.10	1552	16.2	25.5
6	0-98	69.0	0.70	58.8	0.60	8.5	0.09	2031	20.7	29.4

Simulated deposition of body tissues in pregnant cows (conception at 90 days p.p.), during the period of a positive energy balance: NE_Lb_R >0

Parity	Period[2]	ΔBW (kg)		ΔFat (kg)		ΔProtein (kg)		ΔNE_L (MJ)		
	days p.p.	total	/d	total	/d	total	/d	total	/d	/kg BW
1	72-305	115.9	0.50	44.9	0.19	17.3	0.07	2191	9.4	18.9
2	91-305	94.3	0.44	39.3	0.18	15.7	0.07	1936	9.0	20.5
3	96-305	85.6	0.41	42.4	0.20	13.3	0.06	2002	9.6	23.4
6	99-305	79.1	0.39	53.8	0.26	9.1	0.04	2351	11.4	29.7

Simulated deposition of body tissues in non-pregnant cows during the period of a positive energy balance: NE_Lb_R>0

Parity	Period[2]	ΔBW (kg)		ΔFat (kg)		ΔProtein (kg)		ΔNE_L (MJ)		
	days p.p.	total	/d	total	/d	total	/d	total	/d	/kg BW
1	72-305	104.0	0.44	47.1	0.20	12.3	0.05	2161	9.2	20.8
2	91-305	81.7	0.38	41.5	0.19	10.5	0.05	1898	8.9	23.2
3	96-305	73.0	0.35	44.6	0.21	8.0	0.04	1961	9.4	26.9
6	99-305	66.2	0.32	55.9	0.27	3.7	0.02	2309	11.2	34.9

[1] NE_Lb_R = Net Energy balance reference cow, average cow in the population

[2] Period = days lactation

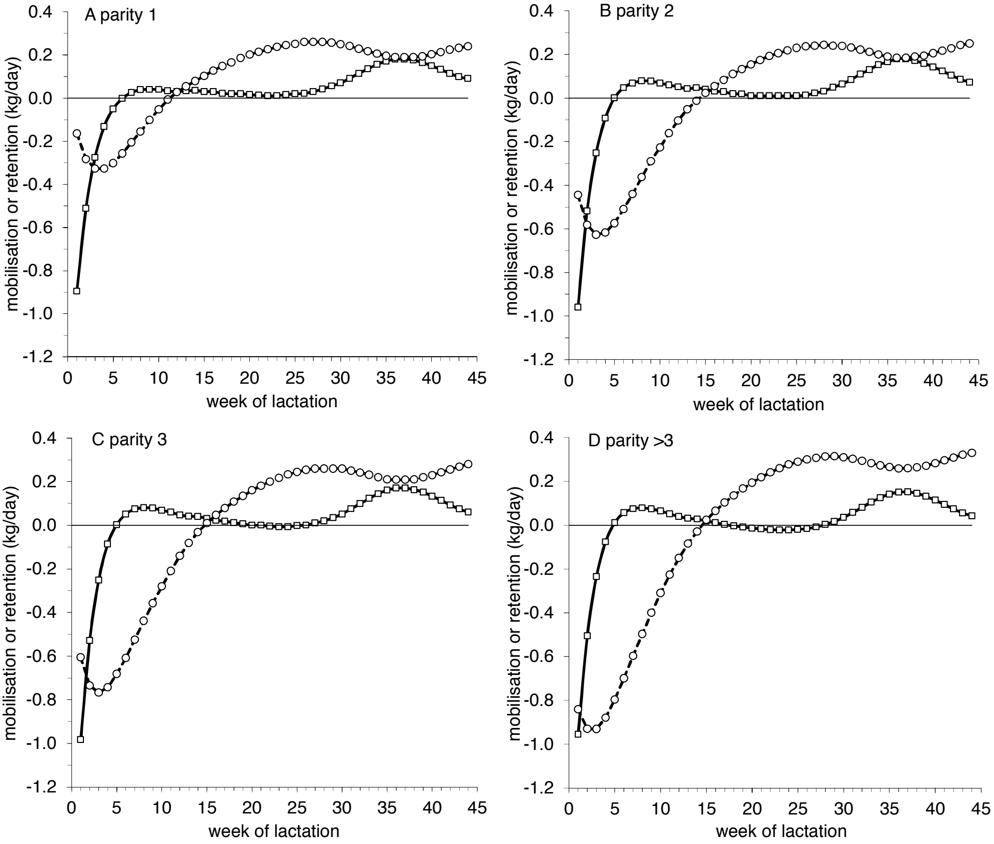

Figure 4.4 Simulated daily changes in body tissue in pregnant dairy cows in their 1st (A), 2nd (B) 3rd (C) and 6th (D) parity. Changes in body fat indicated with dashed line lines with open markers (○), changes in body protein are indicated with a solid line with square markers (□).

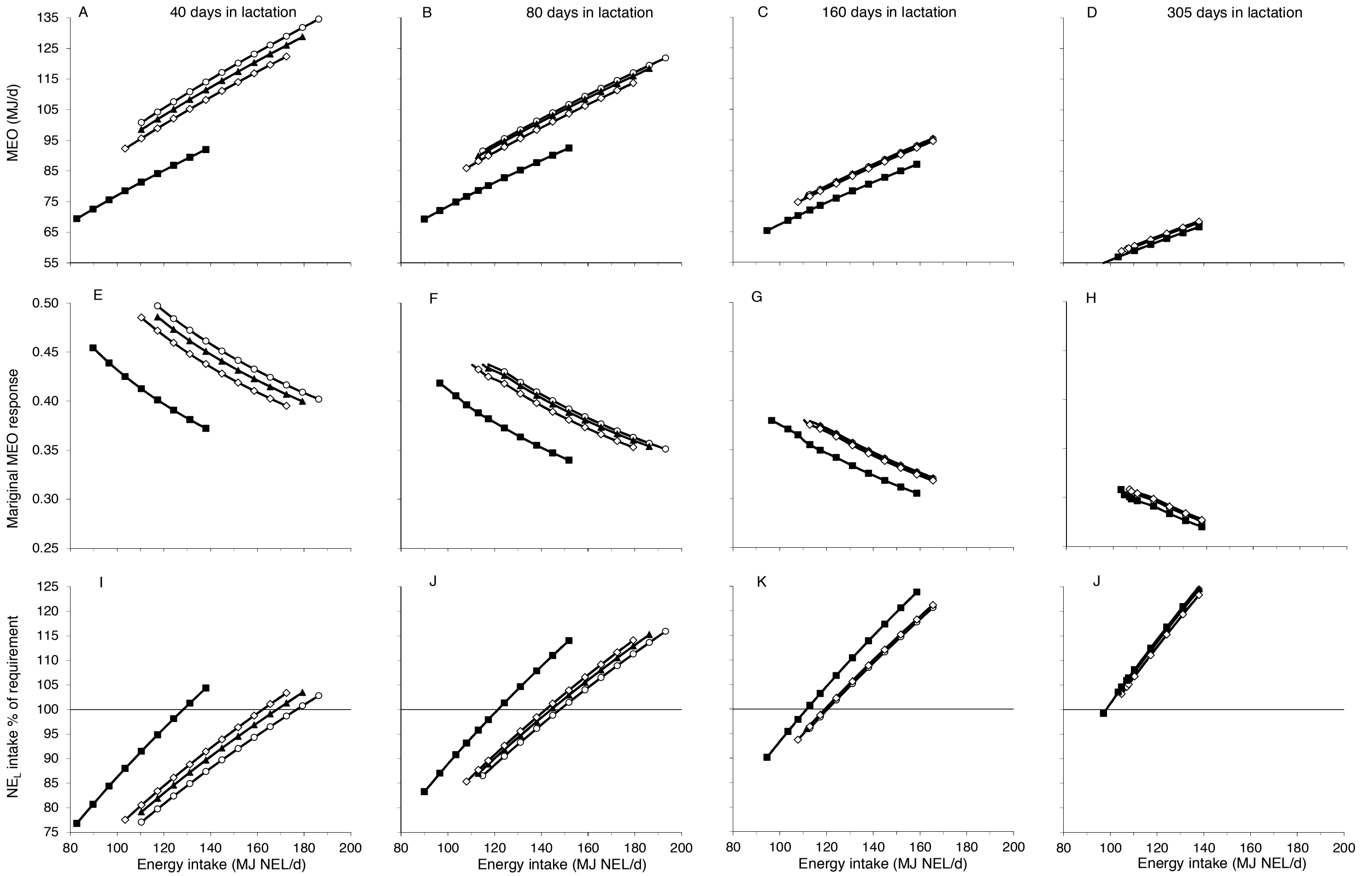

Figure 4.5 Simulated milk energy output (MEO, MJ/d) (panel A,B,C.D), marginal milk response (MEO per unit NE$_L$ intake) (panel E,F,G,H). NE$_L$ intake as % of the NE$_L$ requirement (panel I,J,K,L) at d40 (column 1), d80 (column 2), d160 (column 3) and d305 (column 4) of lactation. of 1st (■) , 2nd (◇), 3rd (▲) and 6th (○) parity cows

5. Discussion

5.1. *Developmental data and assumptions*

The underlying dataset of the model comprised data from high merit HF dairy cows producing between 7000 and 12000 kg FPCM/yr receiving ad libitum PMRs and TMRs composed from good quality forage supplemented with concentrate. The cows were calving in a good condition. The model has not been developed to describe the physiological mechanisms of energy partitioning and mobilization and deposition of reserves. The main objective of the model is to predict the effect diet composition and hence NE_LI on MEO, assuming that protein supply is not limiting. The part of NE_LI that is not partitioned to milk is assumed to be mobilized or retained as energy. The models for MEO of accounted for 57.3% of the variation of MEO of individual cows with a standard deviation of 14.7 MJ /d. This indicates that the model is not suitable for the prediction of MEO by individual cows, because of the large individual variation. However, if the model is applied to groups of cows for strategic purposes on a farm level, individual cow variation will be leveled out. For groups of cows standard deviation would be 14.7 MJ/$\sqrt{n}$, in which n is the number of animals in the group.

5.2. *Concept of baselines*

The model predicts the milk response and partitioning of NE_LI using baselines of NE_LI and MEO and actual NE_LI. The baselines represent the NE_LI intake and the milk performance of the average cow throughout successive lactations, the so called reference cow. These baselines can be interpreted as the potential intake and milk production of well managed average Dutch HF cows, calving in an appropriate body condition (BCS of 3 ± 0.5 points on a 5 point scale (Boxem et al., 1998)) and fed diets composed from good quality forage supplemented with concentrate. This approach is different from other concepts that use potential milk production and the nutritional status of the cow to predict actual milk production. In those concepts the potential milk production is based on arbitrary assumptions (Bruce et al., 1984; Hijink and Meijer, 1987) or on a theoretical lactation model (Faverdin et al., 2011). We preferred a concept with baselines, because the potential milk production of a cow is only reached under immeasurable non-limiting conditions. Even in situations when a cow has unrestricted access to forage and water and no heat stress, forage quality and forage to concentrate ratios might be limiting to show a cow's theoretical production potential.

The predicted full lactation production of FPCM compared well with the Dutch milk test records of 2011 (CRV, 2012). The model predicted 9031, 10516, 10941 and 10973 kg FPCM per 353-day lactation for 1st, 2nd 3rd and 4th parity cows, respectively, whereas the national Dutch milk test records indicate values of 9003, 10263, 10822 and 10952 kg FPCM per 353-day lactation of 1st, 2nd 3rd and 4th parity cows, respectively (CRV, 2012). This is an indication that the baseline of FPCM yield derived from our dataset can be used with confidence to simulate milk production during successive lactations.

5.3. *Diet composition*

The model predicts the MEO in response to NE_LI. Nutrient partitioning is also influenced by the source and type of nutrients in the diet. Iso-energetic diets, different in type of nutrients (glucogenic vs. lipogenic) influenced EB, energy mobilization and MEO in early-lactation cows (van Knegsel et al., 2007). Coulon and Remond (1991) showed that at a higher protein supply the response in milk yield with increased energy supplementation was larger. Brun-Lafleur et al. (2010) observed for mid-lactation dairy cows a significant energy × protein interaction on milk yield and milk protein content and yield. Milk energy output increased with increasing NE_LI, unless protein supply was below the requirements (Brun-Lafleur et al., 2010). The developmental dataset contained data of diets that were formulated to meet the protein requirements. Therefore, the scope of the model is limited to predict the response and partitioning of ingested energy to changes in NE_L supply in situations where protein supply is not limiting.

5.4. *Simulation and verification of MEO response to variation in NE_L intake*

The predicted milk responses to increased NE_LI are linear. Linear responses to increased NE_LI have also been observed by others (MacLeod et al., 1984; Friggens et al., 1995). Coulon and Remond (1991) observed a linear response only in early lactation, but a curvilinear response in mid lactation. The decrease in marginal response in MEO with increasing NE_LI is in agreement with findings elsewhere (Coulon and Remond, 1991; Schei et al., 2005). Our model predicted a marginal response in MEO of 0.45 MJ milk NE_L/MJ NE_L or 0.15 kg FPCM/MJ NE_L, for a multiparous cow, 40 DIM and an EB between -14 and 0 MJ NEL MJ/d. This value is similar to the response of 0.14 kg FCM/MJ NE_L (1 kg milk/UFL) in early-lactation cows as reported by Coulon and Remond (1991).

The marginal milk NE_L response to an increased NE_LI decreased during lactation. A decreasing milk NE_L response to energy intake as the lactation progresses is in line with others studies (Coulon and Remond, 1991; Kirkland and Gordon, 2001a; Prendiville et al., 2011). The lower marginal milk response in primiparous cows compared to multiparous cows is in agreement with Coulon and Remond (1991) and signifies the higher priority for growth in younger animals.

5.5. Simulation of EB and mobilization and deposition of body tissue

The simulated time of nadir of the NE_Lb_R and the magnitudes of the EB were in line with published data (Rastani et al., 2001; McNamara et al., 2003; Reist et al., 2003). Also the time when NE_Lb_R became positive was comparable to those observed in Danish Holstein cows (Friggens et al., 2007).

The simulated proportions of EBW, fat and protein mobilized were similar to the values reported by Tamminga et al. (1997).

The simulated values of total mobilization of body fat by the multiparous reference cow fitted within the lowest value of 25.5 kg (Chilliard et al., 1991) and the highest value of 82.5 kg (Komaragiri and Erdman, 1997) as reported in literature. The predicted maximum rates of fat mobilization of 0.33 kg/d and 0.66 kg/d of 1st and 2nd parity cows, respectively, were lower than the average value of 0.94 kg/d predicted by Friggens et al. (2004). The predicted maximum rate of fat mobilization of 0.77 kg/d and 1.07 kg/d, of a 3rd and 6th parity cows, respectively, were comparable to the average value 0.94 kg/d predicted by Friggens et al. (2004). The predicted rates of fat deposition in our study agreed with the value of 0.19 g/d as predicted by Friggens et al. (2004) and with values calculated from slaughter experiments by Andrew et al. (1994) and (Gibb et al., 1992) which suggest body fat deposition rates of 0.16 g/d and 0.24 g/d, respectively.

In literature a large range in body protein mobilization was reported varying between of 0.5 kg (Chilliard et al., 1991) and 32.5 kg (Martin and Ehle, 1986). The predicted maximum protein mobilization rates during the first 2 weeks of lactation were close to the value of 1.0 kg protein mobilization per day that is assumed to be needed to meet the requirements for amino acids and glucose of the mammary gland in high merit dairy cows (Bell et al., 2000).

Our calculations indicate that fat and protein are mobilized at different rates and that protein retention occurs while cows were still in a NEB. Different rates of fat and protein mobilization are in agreement with studies of (Komaragiri and Erdman, 1997; Komaragiri et al., 1998; van Knegsel et al., 2007). The model predicted a maximum accumulated protein mobilization in the reference cow at around week 5 of lactation. This is in agreement with observations of (Martin and Ehle, 1986; Komaragiri and Erdman, 1997; Tamminga et al., 1997; Komaragiri et al., 1998).

The calculated amounts of energy per kg BW mobilized and deposited increased with parity number (Table 4.6). This in accordance with the observation that the energy density of weight gain increases with age, because more mature cows gain relatively more fat and less protein than younger cows (Williams et al., 1989). The average energy density of BW mobilized was higher than the average energy density of BW deposition (Table 4.6) which is in agreement with Williams et al. (1989). During the period of a positive EB, the calculated deposition of protein is approximately 5 kg higher in pregnant cows than in non-pregnant cows. Pregnancy is associated with an increased retention of protein in maternal and fetal tissues in pregnant animals and an increase in tissue hydration (Robinson, 1986).

5.6. Milk production from body reserves

Assuming a NE_L value of 3.05 MJ/kg FPCM (CVB, 2012), the predicted milk production from mobilized body reserves by the reference cow was 234, 421, 509 and 666 kg FPCM for parity 1, 2, 3 and 6, respectively. These values are comparable with data from literature. According to NRC (2001) a typical one unit decrease of BCS on a 5 point scale during the first 2 months of lactation for a cow weighing 650 with BCS 4 would provide sufficient NE_L for 564 kg 4% fat corrected milk (NRC, 2001). Tamminga et al. (1997), calculated on the basis of mobilized energy, that multiparous cows produce between 122 and 547 kg milk (mean 324 kg, using a NE_L value of 3.17 MJ/kg FPCM) from body reserves during the first 8 weeks of lactation. Data from studies using the deuterium dilution technique indicate that total mobilization of body energy ranges from 1339 MJ (Chilliard et al., 1991) to 3658 MJ (Komaragiri and Erdman, 1997). These amounts would correspond with 350 to 960 kg FPCM (3.05 MJ/kg), respectively, assuming that all mobilized body energy is metabolizable energy utilized with an efficiency of 0.8 (van Es, 1978).

As pointed out in previous sections, the calculated changes in body energy, fat and protein fit within the ranges of published data from various studies. This indicates that model simulations are realistic. However, is should be noted that these ranges of changes in in body energy, fat and protein are very broad. Changes in body reserves are influenced by the diet compositions, level of milk production and genotype used in these studies. Our simulated levels of DMI and milk yield of mature cows (parity > 2) were comparable with levels of DMI and milk yield as reported by Komaragiri and Erdman (1997) and Komaragiri et al. (1998). The calculated mobilization of fat, protein and energy based on the model predictions were also within the ranges as reported by Komaragiri and Erdman (1997) and Komaragiri et al. (1998). We are aware of the fact that the calculated changes in body fat and protein during lactation are influenced by the assumptions regarding the fixed water to protein ratio in EBW and the factor of 4×DMI (Jarrige, 1989) to estimate rumen and gut fill. The water to protein ratio may vary with stage of lactation and the physiological status of the animal (Robinson, 1986; Andrew et al., 1994). Also, the composition of the ration (concentrate, forage type, forage to concentrate ratio) may affect rumen and gut fill (Martin and Ehle, 1986). Therefore, the use of a constant factor for rumen and gut fill and the assumptions regarding diet composition and feed intake may involve some inaccuracies in the estimation of EBW. However, the model appeared not highly sensitive for this factor. Using a of factor 3×DMI or 5×DMI to estimate rumen and gut fill resulted in 1 kg decrease and increase of fat mobilization, respectively, and a 2 kg increase and decrease of protein mobilization, respectively. Despite these possible inaccuracies, model simulations resulted in realistic changes in body fat and protein within the ranges as reported in literature. The model provides a basis for the development of a dairy cow model to estimate MEO and changes in body reserves in response to altered feeding strategy and diet composition. However, further validation with in dependent experimental data is desirable.

6. Conclusions

Milk energy output and changes in body reserves in response to changes in energy intake can be predicted using easily quantifiable input parameters. The predicted responses of milk energy output and change of body reserves are regulated by parity, stage of lactation and gestation, reflecting the changing in priorities in energy partitioning with increasing age and stage of lactation. The model takes into account physiological and genetically driven changes in body reserves. Therefore, the simulated lactation curves and responses in MEO and body energy to variation in in energy intake are different for cows of different lactation number, and different for pregnant and non-pregnant cows. Comparison of model simulations with literature data, indicated that the model predicts realistic changes in milk yield and body reserves throughout successive lactations of dairy cows. This energy partitioning model provides a basis for integration with feed intake models in order to develop a dairy cow model to predict response in performance to changes in net energy intake through feeding strategy and diet composition.

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Chapter 5

Wageningen UR Dairy Cow Model predicts the response of feeding management on feed intake and performance in dairy cows

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Abstract

The Wageningen UR dairy cow model, (Wageningen DCM), is designed to simulate the effects of nutritional strategies on dry matter and nutrient intake, and the partitioning of ingested net energy for lactation into milk energy and energy retention in dairy cows. The model integrates two separate models: a feed intake model and a net energy partitioning model. The feed intake model predicts dry matter and net energy intake which are used as inputs for the net energy partitioning model. This latter model predicts milk energy output and energy retention from both, net energy intake and the physiological driven change in energy retention. The Wageningen DCM requires easily available input data. The Wageningen DCM accounts for cow's physiological status, parameterized as lactation number, stage of lactation and pregnancy, to predict feed intake capacity and partition of ingested net energy to milk and body reserves. Consequently, simulated feed intake and response in milk energy output and energy retention changes over successive lactation cycles of the cow and is, within a lactation cycle, different between pregnant and non-pregnant cows. Model simulations show that the Wageningen DCM is sensitive to cow × feeding management interactions. Validation of the Wageningen DCM with external data indicated a good accuracy of the prediction of intake and milk energy output with relatively low prediction errors ≤ 0.1. The Wageningen DCM enables users to analyse and compare different feeding strategies, identify limitations of feeding strategies, formulate diets, calculate feed budgets and to develop economic and environmental sustainable feeding strategies.

Keywords: dairy cow, model, intake, energy partitioning, milk energy, body energy

1. Introduction

Dairy farmers are constantly challenged to adjust their operational, tactical and strategic management to maintain or improve the profitability of their enterprises under changing feed and milk prices and increasing environmental demands. Diet optimization is a key factor for farm profitability since costs for feed and feed production can range from 50 to 70% of total operating costs for milk production (Bozic et al., 2012; Vermeij et al., 2013). Moreover, diet composition and nutrient intake are dominant factors influencing the emissions of ammonia and greenhouse gasses from dairy farms (Tamminga et al., 2007; Beauchemin et al., 2008; Dijkstra et al., 2011). Optimization of feed management and diet composition in order to reduce feeding costs and losses of nutrients to the environment requires understanding of the effects of diet composition and feeding strategy (i.e. forage to concentrate ratios, different forage and feed options) on dry matter intake (DMI) and intake of net energy for lactation (NE_LI), milk energy output (MEO) and energy retention. Feeding strategy and diet composition may affect DMI and subsequent NE_LI, but predicting the impact of feeding management and diet composition on feed intake and cow response quantitatively is complex. Estimating NE_LI alone is not sufficient to predict MEO and energy retention, because partitioning of ingested energy to milk or body tissues, depends on the physiological status of the cow (i.e. pregnancy, lactation, age) governed by homeorhetic control mechanisms (Bauman and Currie, 1980). As a result of these homeorhetic control mechanisms, body reserves are mobilized to support milk production in early lactation, whereas in late lactation, more nutrients are directed towards foetal growth and body tissues. Consequently, the response of a dairy cow to variation in NE_LI will change relative to stage of lactation, pregnancy and age. Existing feeding systems for dairy cows are useful to formulate rations to balance NE_LI with the NE_L required for the production of a quantified amount of milk, but are unable to predict how dairy cows respond to changes in NE_LI. Therefore, these systems cannot be used to explore animal responses to alternative feeding management strategies. Optimization of feeding management and allocation of available feeds to determine the best compromise between different targets (profitability, farm gate nutrient balances, environmental burden) requires models that incorporate physiological status and genetically driven regulation of energy partition.

An energy partitioning model (EPM) developed by Zom et al. (submitted) predicts MEO and energy retention (ER) in response to NE_LI and to the physiological and genetically driven changes in the partitioning of NE_LI. These are parameterized by lactation number, days in milk (DIM) and days pregnant, reflecting the changes in priority in energy partitioning during the life and lactation cycle of a dairy cow.

Zom et al. (2012) have also developed a feed intake model (FIM) to predict DMI in dairy cows offered ad libitum forage and partial mixed rations with concentrate supplements or total mixed rations. The FIM predicts DMI independently from milk yield or body weight which creates the advantage that this model can be used to generate input (i.e. NE_LI) for the EPM. Combining the FIM and EPM generates a dairy cow model that predicts MEO and energy retention in response to NE_LI and the physiological status of dairy cows. The objectives of this study were (1) to combine FIM (Zom et al. 2012) and EPM (Zom et al. submitted Chapter 4) into one dairy cow model: "Wageningen-UR Dairy Cow Model" (Wageningen DCM) for the prediction of DMI and NE_LI, MEO and energy retention in lactating pregnant and non-pregnant dairy cows, (2) evaluate model behaviour and sensitivity under various theoretical feeding conditions, (3) to validate the accuracy of Wageningen DCM by comparing predictions of NE_LI, and MEO with experimental data using statistical criteria.

2. Materials and methods

2.1. Outlines of the Wageningen UR Dairy Cow Model

The Wageningen DCM predicts on a daily basis DMI, MEO and ER in Holstein-Friesian cows. The Wageningen DCM integrates two different models: a FIM predicting ad libitum feed intake (Zom et al., 2012) and a EPM predicting the partitioning of ingested NE_L into milk and body tissues (Zom et al., Chapter 4)**.** Energy intake, MEO and ER are expressed in net energy for lactation (NE_L) according to van Es (van Es, 1978).

Feed and energy intake. The FIM predicts DMI from the satiety values (SV) per kg DM of various commonly used feeds and the feed intake capacity (FIC) of the cow (Zom et al., 2012). The SV of a feed is the measure of the extent to which that feed limits intake and is predicted from the chemical composition and digestibility. The FIC is the cow's ability to process these intake-limiting SV-units. The FIC is predicted from lactation number, DIM and days pregnant (Zom et al., 2012). The predicted total intake of NE_L (NE_LI) is calculated by multiplying the predicted DMI, with the NE_L value of the diet

Energy partitioning. The EPM divides on a daily basis the predicted NE_LI into 3 components (Zom et al., Chapter 4). The first component is the combined sink of energy requirements for maintenance, growth and the genetically and physiological driven change of ER. This combined sink is assumed to be unavoidable and is referred to as NE_LU. The second component is MEO. The third component is a 2-directional flow of ER (mobilization or deposition of energy).

The EPM describes baselines of daily NE_LI, NE_LU and MEO of the average cow, the so called 'reference cow', during successive lactations. The net energy intake of the reference cow NE_LI_R equals the sum of NE_LU and MEO of the reference cow (MEO_R): $NE_LI_R = NE_LU + MEO_R$. These baselines of reference cow are considered as the potential NE_L intake, NE_LU and MEO under average feeding conditions. The deviation of the NE_LI from NE_LI_R (ΔNE_LI) is used as an estimator for deviation of MEO (ΔMEO) and ER (ΔER): $NE_LI_R + \Delta NE_LI = NE_LU + MEO_R + \Delta MEO + \Delta ER$ (Zom et al. Chapter 4).

Model inputs and assumptions. The required model inputs are presented in Table 5.1. It is assumed that the cows have unrestricted access to partial or total mixed rations, and that supplemental forage and concentrates are fed in fixed amounts per day and fully consumed. Further, it is assumed that metabolisable protein (MP) supply is not limiting and that the rumen degradable protein (RDP) balance is positive (Tamminga et al., 1994). Gestation length is set at 280 days, drying-off is set at day 220 of pregnancy and body condition score (BCS) at calving can vary between 3 and 4 on a 1 to 5 point scale.

Table 5.1 Input variables of the Dairy Cow Model (Wageningen DCM)

Animal characteristics	
Lactation number	
Days in milk	
Days of gestation	
Feeding and diet	
Proportion of ingredient in partial or total mixed rations on a dry matter basis	
Level supplemental of feeding (kg DM/cow/d) of each supplemental feed	
Net energy concentration of the feeds (MJ NE_L/kg DM), calculated according to CVB (CVB, 2012)	
Feed composition (concentration)	
Fresh grass	crude fibre, digestible organic matter
Grass silage	dry matter, crude protein, crude fibre concentration
Legumes silage	dry matter, crude fibre concentration
Maize silage	dry matter, digestible organic matter concentration
Ground maize ears silage	dry matter,
Cereal whole crop silage	crude fibre
Concentrates	crude fibre
Other feeds	CVB-table values (CVB, 2012)

2.2.1. Model evaluation

The behaviour and sensitivity of the Wageningen DCM was evaluated by analysing the response of NE_LI, MEO and ER in pregnant and non-pregnant cows to theoretical feeding strategies in which level of concentrate input and feed allocating strategies were modified. The accuracy of Wageningen DCM was assessed by comparison of model predictions with experimental data using statistical criteria.

2.1.2. Simulations of feeding management

Simulations of feeding management were performed for pregnant and non-pregnant HF cows and for lactation number 1 to 6. The assumed lactation length was 305 days. The simulated diets strategies comprised two levels of concentrate supplementation (CL; 1000 *versus* 2000 kg concentrates per lactation), and within each level of concentrates two different concentrates allocation strategies (CA; high-low (HL) *versus* flat rate (FR), graphically displayed in Figure 5.1), and within each CL × CA combination, two forage mix strategies (FM); one single forage mixture during the whole lactation (1FM) *versus* two forage mixtures (2FM) with the change between them occurring at 152 DIM, graphically displayed in Figure 5.2). The simulated 1FM strategy consisted of the ad libitum feeding of mixture of grass silage and maize silage in a ratio of 50:50 (on DM basis), containing 0.90 SV/kg DM and 6.2 MJ NE_L kg DM (=6.8 MJ NE_L/SV). The 2FM strategy consisted of a mixture of grass silage and maize silage in a ratio of 30:70 (on DM basis) containing 0.86 SV/kg DM and 6.3 MJ NE_L kg DM (=7.3 MJ NE_L/SV) until 152 DIM and thereafter a mixture of grass silage and maize silage in a ratio of 70:30 (on DM basis) containing 0.94 SV/kg DM and 6.0 MJ NE_L kg DM (=6.4 MJ NE_L/SV). Details on the input values and assumptions of the standard situations used to evaluate the behaviour of the Wageningen DCM are provided in Table 5.2. Outputs were DMI, NE_LI, MEO (GJ NE_L/305 d), ER, gross efficiency (MEO/NE_LI), and the marginal MEO response (ΔMEO/ΔNE_LI), being the change in MEO for each unit of change of NE_LI.

Table 5.2 Input values and simulated concentrate levels (CL), concentrate (CA) and forage (FA) allocation strategies.

Cow related inputs			
Lactation length	305 days		
Lactation number	1, 2, 3, 4, 5, 6		
Day of conception	90 days in milk		
Feed related inputs			
Feed composition (%)	Grass silage	Maize silage	Concentrate
Dry matter[1]	45.0	33.0	90.0
Crude protein[2]	17.0	7.0	
Crude fibre[3]	24.0	19.0	14.0
Crude ash[3]	10.9	46.0	
Crude fat[4]	40.0	35	
In-vitro OM digestibility[3]	73.2	74.0	
Sugar[5]	80.0	10	
Starch[6]	0.0	36.6	
NE_L (MJ/kg DM)	5.87	6.45	7.20
Satiety value (SV/kg DM)	1.00	0.80	0.32
Feeding management			
Concentrate levels (CL)	1000 or 2000 kg/305-d lactation		
Concentrate allocation (CA)	Flat rate or High-low (Figure 1)		
Forage allocation (FA)	1 Feeding group (Figure 5.2) 1-305 DIM 1:1 grass : maize silage (DM basis) 2 Feeding groups (Figure 5.2) 1-152 DIM: 3:7 grass: maize silage (DM basis) 152-305 DIM: 7:3 grass: maize silage (DM basis)		

[1] % of fresh weight, input for calculation satiety value (SV) grass silage and maize silage

[2] % of DM, input for calculation net energy for lactation (NE_L) value of grass and maize silage and SV of grass silage

[3] % of DM, input for calculation NE_L values of grass silage and maize silage and SV of grass silage

[4] % of DM, input for calculation NE_L values of grass silage and maize silage and SV of maize silage

[5] % of DM, input for calculation NE_L values of grass silage

[6] % of DM, input for calculation NE_L values of maize silage

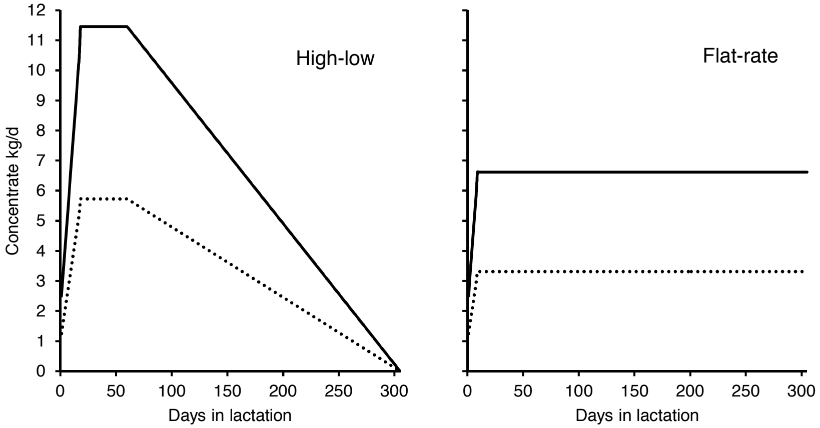

Figure 5.1 Simulated concentrate allocation strategies. Dotted line 1000 kg concentrate/305 d, solid line 2000 kg concentrate/305d allocated according to a "high-low" (left panel) or a "flat rate strategy (right panel).

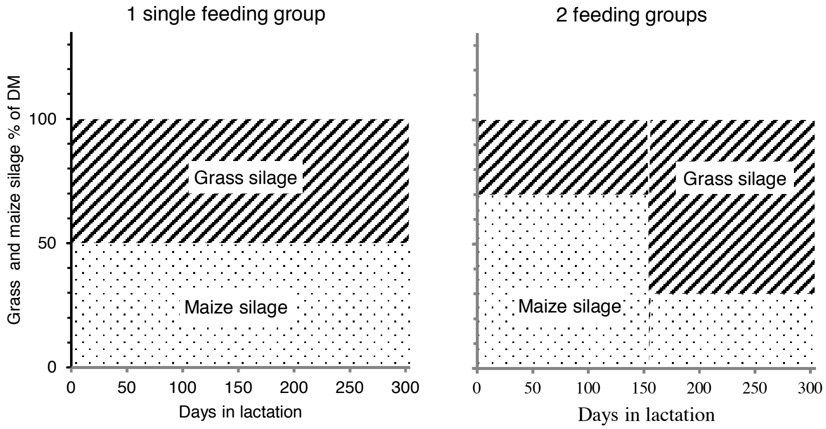

Figure 5.2 Forage allocation (FA) strategies. Left: one single feeding group, one mixture consisting of grass and maize silage 1:1 on a DM basis during the whole lactation. Right: 2 feeding groups, an early lactation mixture consisting of grass and maize silage 3:7 on a DM basis during 1-152 DIM, and a late lactation mixture consisting of grass and maize silage 7:3 on a DM basis after 152 DIM.

2.1.3. Validation with experimental data

To assess the accuracy of Wageningen DCM, the model was evaluated using three independent datasets from experiments involving different distinctive feeding strategies. Dataset 1 (Feil, 2000) and 2 (Feil and van Schooten, 2001) contained, on a weekly basis, data regarding chemical composition, digestibility, NE_L value, and proportion of the feeds included in the diet, individual DMI, MY, milk fat and protein concentration, BW, lactation number, DIM and days pregnant.

Dataset 1 included data from 48 dairy cows (12 primiparous and 36 multiparous) allocated to 3 dietary treatments in a continues block design experiment (Feil, 2000). From 1 to 210 DIM, cows in all treatment groups were individually fed ad libitum a mixture of grass/clover silage and maize silage (70:30 on DM basis). Dietary treatments were 3 strategies of concentrates distribution over the lactation period: "flat-rate", "high-low" or an "intermediate" providing approximately 1600 kg/lactation for each cow in each treatment group. Cows assigned to the "flat-rate" treatment received a fixed level of 5.2 kg of concentrates/d during 305 days. Cows on the "high-low" treatment received 12 kg of concentrates/d until 30 DIM. Thereafter, concentrate supplementation was reduced with 0.08 kg/d and terminated at 145 DIM. Cows on the "intermediate" treatment received 8.6 of concentrates/d until 30 DIM. Thereafter, concentrate supplementation was reduced with 0.04 kg/d to a level of 2.6 kg concentrates/d at 145 DIM which was maintained until 305 DIM. Concentrates were fed individually using computer controlled concentrates dispensers.

Dataset 2 included data from 48 dairy cows (12 primiparous and 36 multiparous) in a 3×2 factorial design (3 different patterns of concentrates distribution over the lactation × 2 different forage mixtures) (Feil and van Schooten, 2001). The patterns of concentrates distribution were "flat rate", "high-low" and "intermediate" and were identical as described for dataset 1. During the first 25 weeks of lactation, all cows were individually fed ad libitum with either a grass/clover silage and maize silage mixture (70:30 on DM basis) or a grass/clover silage and triticale whole crop silage mixture (70:30 on DM basis).

Dataset 3 was obtained from an experiment involving 28 cows fed a TMR with a low (100 g concentrates /kg grass silage) or high (300 g concentrate/kg grass silage) proportion of concentrates either throughout the whole lactation period or with a switch-over at mid-lactation (Friggens et al., 1998). This dataset contained the daily individual DMI, MY and BW, and on a weekly basis data on milk composition of multiparous cows during the whole lactation. The SV and NE_L of the concentrates were estimated using tabulated values for each ingredient (CVB, 2010), resulting in 0.28 SV-units and 7.81 MJ NE_L/kg DM respectively. The NE_L value and SV of the grass silage was calculated from the chemical composition as published by Friggens et al. (1998) using the CVB online feed value calculator (http://www.pdv.nl/english/Voederwaardering/cvb_products/online_feedvalue_calculator.php)). The estimated SV and NE_L value of the grass silage were 1.13 and 6.18 MJ per kg of DM, respectively.

For all 3 datasets, actual and simulated NE_LI were calculated from actual and simulated DMI, respectively and from NE_L value of the feeds. Lactation number, DIM, days pregnant and simulated NE_LI, were used as inputs to predict MEO. On a weekly basis, actual fat and protein corrected milk yield, and MEO were calculated from the weekly means of MY, the weighted means of milk fat (F%) and protein (P%) content, and assuming the energy value of milk as 3.05 MJ /kg FPCM (CVB, 2012). For each cow, weekly means of actually observed and predicted DMI, NE_LI, and MEO were calculated and compared to evaluate the accuracy of the Wageningen DCM. Mean square prediction error (MSPE), mean prediction error (MPE) and relative prediction error (RPE) were used as criteria for the accuracy of prediction of DMI and robustness according to method described by Fuentes-Pila et al. (1996). The MSPE was calculated as MSPE = $\sum(\mathrm{A}-\mathrm{P})^2/n$,\in which A and P are the actual and predicted weekly means, respectively, of each experimental group of cows, and *n* is the number of pairs of A and P being compared. The MSPE can be considered as the sum of three components: mean bias, indicating the differences between the actual and predicted means, line bias and random variation around the regression line of A on P (Bibby and Toutenberg, 1977). Accordingly, MSPE is calculated as: $\mathrm{MSPE} = (\bar{\mathrm{A}} - \bar{\mathrm{P}})^2 + \mathrm{S}_\mathrm{P}^2(1\text{-}b)^2 + \mathrm{S}_\mathrm{A}^2(1\text{-}\mathrm{r}^2)$. Where $\bar{\mathrm{A}}$ and $\bar{\mathrm{P}}$ are the means of A and P, and S_A^2 and S_P^2 are the variances of A and P, respectively, b is the slope of the regression of A on P with intercept zero, and r is the correlation coefficient of A and P. The difference between $\bar{\mathrm{A}}$ and $\bar{\mathrm{P}}$ is indicative for under ($\bar{\mathrm{A}} > \bar{\mathrm{P}}$) or overestimation ($\bar{\mathrm{A}} < \bar{\mathrm{P}}$) by the model. Large deviations of b from 1 indicate underlying inadequacies in the structure of the model. When b is < 1, the model tends to underestimate at low values of A and to overestimate at high values of A, the reverse is the case when b is >1. The mean prediction error (MPE) is calculated as the square root of the MSPE. The relative prediction error (RPE) is calculated as MPE as proportion of A (Rook et al., 1991). The values of the mean bias, MSPE, MPE and RPE were calculated for the whole dataset and for each sub-dataset. The size of the RPE is used as a criterion for accuracy (Fuentes-Pila et al., 1996). According to Fuentes-Pila et al. (1996) we assumed that RPEs ≤ 0.1 indicates good predictions; RPEs > 0.1 and ≤ 0.2 indicates acceptable predictions; and RPEs > 0.2 indicates poor predictions.

3. Results and discussion

The Wageningen DCM has been designed to predict the effects of feeding management on DMI, $\mathrm{NE_LI}$, MEO and ER on a daily basis over successive lactations of dairy cows fed ad libitum. The primary basis of the Wageningen DCM is cows' physiological status (lactation number, DIM and stage of pregnancy). The simulated lactation curves and the response in MEO and ER to variation in $\mathrm{NE_LI}$ are related to lactation number parity, DIM and pregnancy. This is a fundamental difference with most other dairy cow models that use scaling factors (Baudracco et al., 2012) or differentiate only between primiparous and multiparous cows with (Faverdin et al., 2011) or without (Rotz et al., 1999) an adjustment for chronological age. Using scale factors, implies that cows of different parity will respond in a similar manner to changes in feeding management, without considering differences in priorities in energy partitioning associated with age. Partitioning of energy is likely more influenced by homeoretic control mechanisms associated with the physiological state of the cow (the onset and stage of lactation and gestation) than a chronological age. Therefore, lactation number combined with DIM and days pregnant are better indicators of the physiological status and responses to feeding management than chronological age. Including days pregnant in the Wageningen DCM allows it to simulate different insemination strategies. Prediction of DMI with the Wageningen DCM is based on the principles of a fill unit system a, which creates flexibility to predict DMI for a broad range of feeding practices.

3.1. Simulations of lactation number, DIM, pregnancy and feeding strategies

Model simulations confirm that the Wageningen DCM is sensitive to cow × feeding management interactions with regard to DMI and partitioning of $NE_L I$ and body energy to MEO (Table 5.3, Figure 5.3).

Lactation number. Results of the model simulations within a feeding management practice, confirm that $\Delta MEO/\Delta NE_L I$ (marginal response), $MEO/NE_L I$ (gross efficiency), and nadir of energy balance increase with lactation number. The increase of $\Delta MEO/\Delta NE_L I$ with lactation number is coherent with observations of Coulon and Remond (1991) who observed a higher milk output per additional unit of ingested energy in multiparous cows than in primiparous cows. The increase in total energy mobilization and nadir of energy balance with increasing lactation number is in agreement with observations (Berglund and Danell, 1987; Coffey et al., 2004; Friggens et al., 2007).

Table 5.3 Simulation of the effects of two concentrate levels (CL) and two concentrate allocation strategies (CA) in pregnant and non-pregnant cows on predicted net energy intake, milk energy output, net energy mobilized and cumulative net energy balance**.**

	Pregnant cows				Non-pregnant cows			
CA	High-low		Flat-rate		High-low		Flat-rate	
CL (kg/305/d)	1000	2000	1000	2000	1000	2000	1000	2000
Lactation no.	Net energy intake (GJ NE_L/305 d)							
1	32.0	36.3	32.0	36.3	32.7	37.0	32.7	37.0
2	36.3	40.6	36.3	40.6	37.2	41.5	37.2	41.5
3	37.6	41.9	37.6	41.9	38.4	42.7	38.4	42.7
6	38.0	42.3	38.0	42.3	38.9	43.2	38.9	43.2
	Milk energy output (GJ/305 d)							
1	21.2	22.8	21.1	22.7	21.9	23.6	21.9	23.5
2	25.0	26.7	24.8	26.5	25.8	27.5	25.7	27.3
3	25.9	27.6	25.7	27.4	26.7	28.4	26.6	28.3
6	26.2	28.0	26.1	27.8	27.1	28.8	26.9	28.6
	Mobilized net energy balance (GJ NE_L)							
1	-0.65	-0.21	-1.04	-0.46	-0.65	-0.21	-1.03	-0.46
2	-1.34	-0.65	-1.73	-1.13	-1.34	-0.65	-1.72	-1.13
3	-1.54	-0.81	-1.92	-1.33	-1.54	-0.81	-1.92	-1.33
6	-1.84	-1.07	-2.23	-1.62	-1.84	-1.07	-2.22	-1.62
	Cumulative energy balance (GJ NE_L)							
1	0.23	2.13	0.51	2.57	0.58	2.47	0.83	2.87
2	-0.19	1.58	0.10	2.11	0.16	1.92	0.43	2.41
3	-0.34	1.42	-0.04	1.96	0.02	1.77	0.29	2.27
6	-0.62	1.13	-0.32	1.69	-0.26	1.48	0.02	2.00

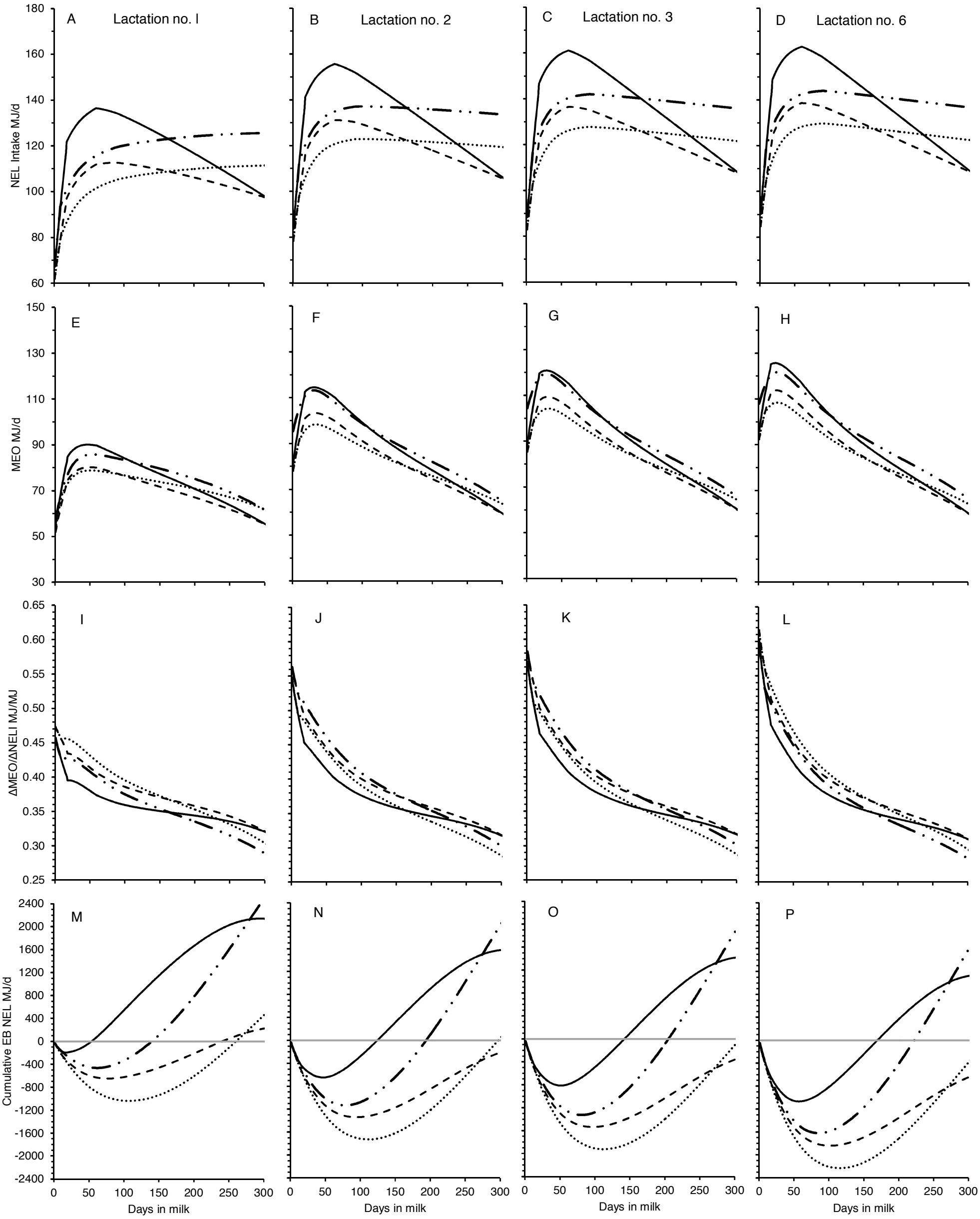

Figure 5.3 Graphic display of the model simulation of four feeding strategies comprising two levels of concentrate (CL) input (1000 and 2000 kg/305/d) allocated according to either a "flat rate" or a "high-low" strategy on the on net energy intake (NE$_L$I MJ/d, panel A to D), milk energy output (MEO MJ/d, panel E to H), marginal MEO response (ΔMEO/ΔNE$_L$I MJ/MJ, panel I to L), and cumulative net energy balance (EB) (MJ NE$_L$, panel M to P) in pregnant cows in lactation 1, 2, 3 and 6. On the x-axis days in in milk. The dotted lines (········) represents a concentrate input of 1000 kg/305-d allocated at a flat rate, the dashed lines (– – –), a concentrate input of 1000 kg/305-d allocated according to a high-low strategy, the dashed lines with dots (–··–) a concentrate input of 2000 kg/305-d allocated at a flat rate, the solid lines (—) a concentrate input of 2000 kg/305-d allocated according to a high-low strategy.

Days in milk. Within lactation numbers and feeding management, ΔMEO/ΔNE$_L$I declines with advancing stage of lactation (Figure 5.3). The predicted ΔMEO/ΔNE$_L$I response in early lactation, ranged between 0.38 and 0.48, which would result in 0.12 to 0.15 kg FCPM per extra MJ of NE$_L$I. This is similar to a marginal milk responses of 1 kg FPCM/UFL (1 UFL = 7.1 MJ NE$_L$) as reported by Coulon and Remond (1991). Similarly, MEO/NE$_L$I, decreases as lactation progresses. A decline in gross efficiency as lactation progresses is also reported in other studies (Coulon and Remond, 1991, Kirkland and Gordon, 2001, Prendiville et al., 2011). Across different simulated feeding management options, the average gross efficiency ranged from 0.70 to 0.90 during the first 100 DIM and from 0.52 to 0.56 during 200 to 305 DIM. These gross efficiencies were similar as those reported for HF, Jersey and crossbred cows (Prendiville et al., 2011).

Pregnancy. The model simulations indicate that both, MEO and the proportion of NE$_L$I partitioned to MEO is lower in pregnant cows than in non-pregnant cows. It seems plausible that these differences are due to homeorhetic mechanisms resulting in a higher priority of pregnancy over milk production (Bauman and Currie, 1980). As far as the authors know, no quantitative data regarding the differences in energy partitioning or efficiency during a complete lactation cycle between pregnant and non-pregnant cows have been published. However, data of field studies show a more rapid decrease of milk yield in pregnant cows than in non-pregnant cows (Bertilsson et al., 1997; van Amburgh et al., 1997). The gradual reduction can be explained by a decrease in the number of secretory cells in pregnant cows compared with non-pregnant cows due to a lower mammary cell proliferation (Nørgaard et al., 2008). The differences in lactation persistency between pregnant and non-pregnant cows as reported in literature seems to confirm the results of the model simulations.

Feeding management - concentrate level Changes in feeding management (i.e. different CL, CA and FM) may alter the SV and NE$_L$ of the ration and consequently ,NE$_L$I (Zom et al., 2012), MEO and ER (Zom, et al., Chapter 4). A simulated increase of CL reduced forage DMI and improved total DMI and NE$_L$I which subsequently increased MEO, reduced nadir of NEB and improved ER. Simulated CL had a relatively small effect on MEO. Firstly, because the effect of NE$_L$I on MEO is partly buffered by additional mobilization or retention of body energy (Zom et al., Chapter 4). Secondly, because increased CL reduces forage DMI due to substitution effects. The responses to changes in CL were similar to those observed by others (Coulon et al., 1996, Coulon and Remond, 1991, Reist et al., 2003, Schei et al., 2005). Considering the substitution of forage a response of 0.59 to 0.73 kg FPCM per kg of concentrates was predicted. This value is in the range of responses reported from in vivo studies (Aston et al., 1995, Coulon et al., 1996, Schei et al., 2005, Sutton et al., 1994).

Feeding management - concentrate allocation. Within CL, CA or FM did not affect total DMI and NE$_L$I intake over a complete lactation. Flat rate CA resulted in a marginally lower MEO per lactation, a lower peak MEO and an increased nadir of NEB and lower ER compared to cows fed according to the high-low CA. The slightly higher MEO with the high-low strategy compared to the flat rate strategy can be explained by the higher marginal MEO response in early lactation. With the simulated high-low strategy, more concentrates were allocated in early lactation when more nutrients are partitioned to milk and $\Delta MEO/\Delta NE_LI$ is higher. In addition to that, the improved NE_LI may alleviate the risk of metabolic disorders caused by a severe NEB in early lactation. Together with This simulation implies that, it is more profitable to increase NE_LI by feeding extra concentrate in early lactation than in late lactation, providing there is an adequate supply of physical effective fibre in the diet.

Feeding management - forage mixtures strategies. Figure 5.4 illustrates the analyses of different CL and CA strategies together with different FM strategies. Within CL × CA combinations, FM strategies had only negligible effects on DMI, NE_LI and MEO of a complete lactation. However, simulating the FM strategy with two feed mixtures resulted in an improved DMI and NE_LI before 153 DIM and a reduced DMI and NE_LI after 152 DIM compared to the strategy with one feed mixture for the whole lactation. This resulted in a higher peak DMI, NE_LI and reduced nadir of NEB before 152 DIM (Figure 5.4) for the FM strategy with two forage mixtures compared to the strategy with one single forage mixture. A low CL combined with flat rate CA and one FM resulted in a mobilization of body reserves of 1040, 1730, 1925 2043, 2140 and 2231 MJ NE_L for lactation number 1, 2, 3, 4, 5, and 6, respectively. Whereas, at low CA combined a with high-low CA and a FM strategy with two forage mixtures resulted in a mobilization of 526, 1110, 1288, 1396, 1487 and 1574 MJ NE_L for lactation number 1, 2, 3, 4, 5 and 6, respectively. Assuming that a decrease of 1 BCS point (on a 5 point scale) will provide 1800 MJ of NE_L (NRC, 2001), the feeding strategy with low CL, flat rate CA and one FM would result in the loss of more than 1 BCS point. A loss of more than 1 BCS point, may compromise milk production, reproduction, health, and animal welfare (Roche et al., 2009), and therefore this strategy should be rejected. The Wageningen DCM has no limits on the simulated amounts of body energy that can be mobilized and neither on the rate of mobilization. However, in reality, cows do not have indefinite body energy reserves. Therefore, the simulated amount of mobilized energy should be used as an indicator to assess whether a feeding strategy is feasible rather than for quantification of the loss of body reserves. Inclusion of ceilings for the amount and rate of mobilisation of body reserves that put a limit on the MEO should be investigated. The simulation example showed that the feeding a low CL at a flat rate GA as one FM for the whole lactation will result in severe NEB. This example also shows that a severe NEB and loss in BSC can be avoided by applying alternative feeding strategies but without the inputs of additional concentrates or high quality forage and increased feed costs. These simulations demonstrate the ability of the model to explore the effects of different strategies for allocating forages and concentrates on MEO and ER.

3.2. Validation with experimental data

The validation of the Wageningen DCM using data sets with incomplete lactations (Feil, 2000); Feil and van Schooten, 2001) of cows fed ad libitum forage with concentrates supplemented separately according to different strategies is presented in Table 5.4 and displayed in figures 5.5 and 5.6 Overall, mean bias of predicted DMI, NE_LI and MEO was low. The overall mean bias of MEO was 3.04 and 4.33 MJ/day, corresponding to a mean bias 1.0 and 1.4 kg of FPCM, for dataset and 1 and 2, respectively. The mean bias of the predictions of DMI, NE_LI and MEO were low and the obtained RPEs of predicted DMI, NE_LI and MEO for the whole dataset and within the datasets for treatment groups were lower than 0.10, indicating a good prediction accuracy and robustness (Fuentes-Pila et al., 1996). The contribution of the line bias to MSPE was close to zero indicating an adequate model structure. In all cases the contribution of line bias to the MSPE was small indicating an adequate structure of the Wageningen DCM. Overall, random error was the largest component of MSPE.

The evaluation of the Wageningen DCM (Table 5.5) using dataset 3 (Friggens et al., 1998) showed that overall, Overall, mean bias of predicted DMI was 1.39 kg DM and the overall mean bias of MEO was 3.91 MJ/day, corresponding to a mean bias 1.3 kg of FPCM.

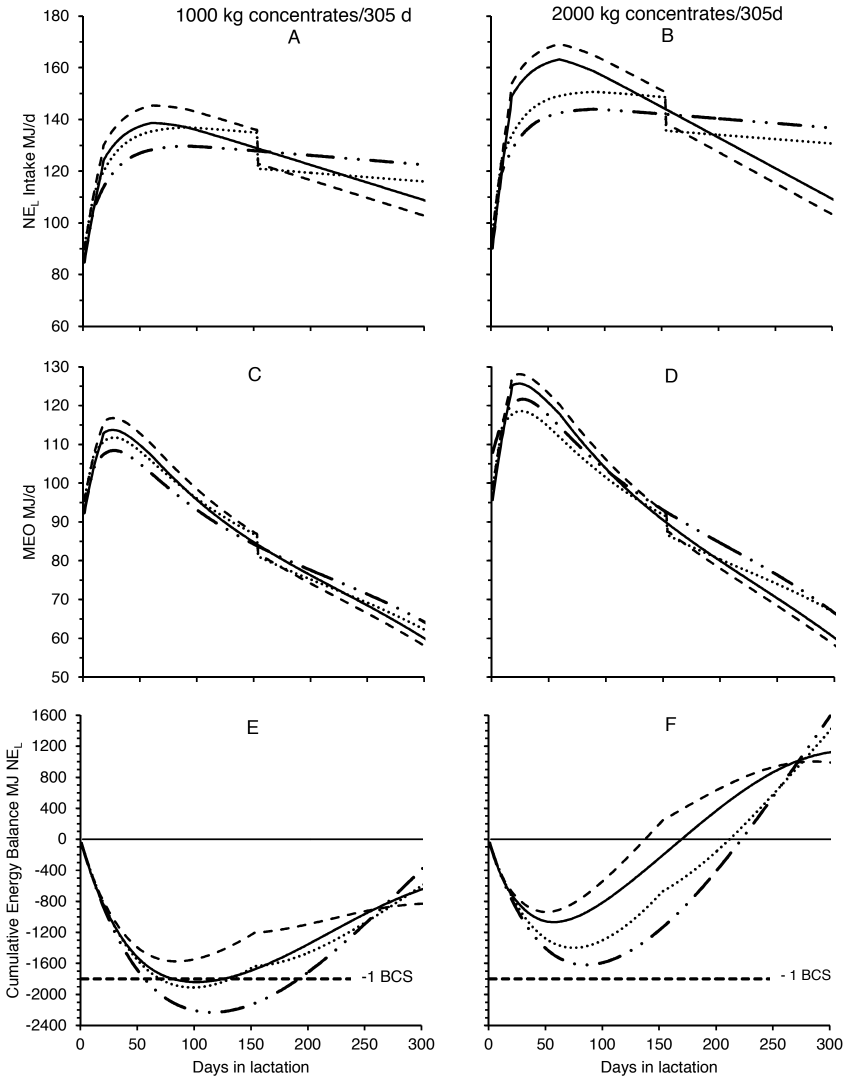

Figure 5.4 Graphic display of an example of a model simulation of 6 feeding strategies comprising two levels of concentrate (CL) input (1000 and 2000 kg/305/d) allocated according to either a "flat rate" or a "high-low" strategy, and forage allocated as one forage mixture (1:1 grass:maize silage on DM basis) for the whole lactation, two forage mixtures (3:7 grass:maize silage on DM basis before 153 DIM and 7:3 grass:maize silage on DM basis after 152 DIM) in a mature dairy cow. The left column (panel A,C,E) and right columns (panel B,D,F) represent the strategies 1000 kg and 2000 kg concentrate/305-d. respectively. Panel A and B shows the net energy intake (NE$_L$I MJ/d, column), panel C and D shows milk energy output (MEO MJ/d), and panel E and F shows the cumulative net energy balance (EB) (MJ NE$_L$). On the x-axis days in lactation. The dashed lines with dots (–··–) represents concentrate allocation at a flat rate combined with one forage mixture (1:1 grass:maize silage on DM basis) for the whole lactation. The solid lines (—) represents concentrate allocation according to a "high-low" strategy with one single forage mixture for the whole lactation. The dotted lines (········) represents concentrate allocation at a flat rate combined with two forage mixtures (3:7 grass:maize silage on DM basis before 153 DIM and 7:3 grass:maize silage on DM basis after 152 DIM). The dashed lines (– – –) represents according to a "high-low" strategy combined with two forage mixtures. The bold line indicates the loss of 1800 MJ NE$_L$ of body reserves equivalent to 1 point of BCS (NRC, 2001).

The RPEs of the prediction of DMI intake and MEO were 0.10 and 0.09 respectively, indicating an acceptable accuracy (Fuentes-Pila et al., 1996). The contribution of line bias to the MSPE was low, indicating an adequate structure of the Wageningen DCM. Negative mean biases indicate that predicted DMI and MEO are overestimated for all treatments groups. Relatively large differences in RPE of DMI and MEO existed between treatment groups, being higher for HH and LH. Dividing the whole lactation data into two subsets: one before switch-over (week 2-20 of lactation) and after switch-over (week 23-40) showed that the predictions of DMI and MEO were more accurate before than after switching over (Figure 5.7). Before the switch-over the RPEs of DMI were 0.07, 0.07, 0.05, 0.06 and 0.09 for all treatments combined, HH, HL, LH and LL, respectively. The RPEs of MEO were 0.06, 0.04, 0.07, 0.08 and 0.08 for all treatments combined, HH, HL, LH and LL, respectively. After the switch–over, the RPEs of DMI were elevated being 0.13, 0.18, 0.08, 0.15 and 0.10 for all treatments combined, HH, HL, LH and LL, respectively. Also, the RPEs of MEO were elevated after the switch-over, being 0.14, 0.13, 0.15, 0.21 and 0.05 for all treatments combined, HH, HL, LH and LL, respectively.

The observed bias and RPEs of the predicted DMI and MEO were higher for the whole lactation dataset of Friggens et al. (1998) than for the datasets of Feil (2000) and Feil and van Schooten (2001). This larger bias for the prediction of DMI and MEO for the whole lactation data can be attributed to several reasons. Firstly, inaccuracies of the estimation of the SV and NE_L value of the grass silage which may have been larger for the dataset of Friggens et al (1998) due to using table values for crude fibre, instead of analysed values for the datasets of Feil (2000) and Feil and van Schooten (2001). This would also influence the accuracy of the predictions of DMI and NE_L intake. In addition, it was assumed that the composition of the grass silage was uniform throughout the whole experiment, which was probably not the case. Secondly, the experiment of Friggens et al. (1998) was carried out as a partial switch-over design. Generating large differences in feeding level, as in the experiment of Friggens et al. (1998), can result in carry-over effects in performance of dairy cows (Huhtanen and Hetta, 2012), which can explain the larger bias for the prediction of DMI and MEO after the switch-over. The curve of predicted DMI and MEO seems to be too flat after changing-over. Both, the FIM and EPM were developed using data from continuous design experiments (Zom, et al. 2012, Zom et al. Chapter 4). Therefore the Wageningen DCM may be less suitable for situations in which a carry-over effect from previous feeding can be expected. Thirdly, the small number of cows in the experimental groups (n = 7) and large individual cow variation may have contributed to the large bias and elevated RPEs. Further validation with data from experiments over complete lactations would be desirable.

Table 5.4 Accuracy of the prediction of the Dairy Cow Model for DMI, net energy (NE_L) intake and milk energy output (MEO, MJ NE_L/d) cows fed ad libitum forage mixtures during incomplete lactations (Dataset 1 (Feil, 2000), grass and maize silage (70:30 on a DM basis); Dataset 2 (Feil and van Schooten, 2001) either grass and cereal whole crop silage or grass and maize silage (70:30 on a DM basis)). Concentrates were separately fed in equal amounts of concentrate but according to different patterns: Flat rate, Intermediate, High-Low[1].

	Actual[3]	Bias[4]					Proportion of MSPE[2]		
	(A)	(A-P)	b[5]	r^2 [6]	MPE[7]	RPE[8]	Random	Line	Bias
Dataset 1 (Feil, 2000)[9] week 1-30 of lactation									
DMI (kg/d)									
All treatments	19.44	-0.17	0.99	0.84	0.72	0.04	0.94	0.00	0.06
Flat rate	19.02	-0.03	1.00	0.60	0.55	0.03	1.00	0.00	0.00
Intermediate	19.15	-0.54	0.97	0.78	0.93	0.05	0.66	0.00	0.34
High-Low	20.14	0.03	1.00	0.91	0.67	0.03	1.00	0.00	0.00
NE_L intake (MJ/d)									
All treatments	128.00	-1.10	0.99	0.90	4.55	0.04	0.94	0.00	0.06
Flat rate	124.80	-0.20	1.00	0.64	3.51	0.03	1.00	0.00	0.00
Intermediate	126.10	-3.40	0.98	0.87	5.85	0.05	0.66	0.00	0.34
High-Low	133.10	0.95	1.00	0.95	4.30	0.03	0.95	0.00	0.05
MEO (MJ NE_L/d)									
All treatments	86.51	-3.04	0.97	0.89	6.11	0.07	0.75	0.00	0.25
Flat rate	85.84	-2.02	0.98	0.85	5.50	0.06	0.86	0.00	0.14
Intermediate	85.12	-4.20	0.96	0.87	7.45	0.09	0.68	0.00	0.32
High-Low	88.56	-2.91	0.97	0.94	5.28	0.06	0.69	0.01	0.30
Dataset 2 (Feil and van Schooten, 2001)[10] week 1-25 of lactation									
DMI (kg/d)									
All treatments	19.56	0.26	0.98	0.66	0.89	0.05	0.91	0.00	0.08
Grass/WCS									
Flat rate	19.54	0.80	0.97	0.29	0.93	0.05	0.26	0.00	0.74
Intermediate	19.54	-0.40	0.97	0.17	1.31	0.07	0.91	0.00	0.09
High-Low	19.52	0.18	1.01	0.73	0.56	0.03	0.90	0.00	0.10
Grass/Maize silage									
Flat rate	19.57	-0.24	0.99	0.23	0.69	0.04	0.88	0.00	0.12
Intermediate	20.09	-0.17	0.99	0.87	0.53	0.03	0.90	0.00	0.10
High-Low	19.10	-1.37	0.93	0.80	1.52	0.08	0.19	0.00	0.81
NE_L intake (MJ/d)									
All treatments	125.10	-2.00	0.99	0.78	5.74	0.05	0.88	0.00	0.12
Grass/WCS									
Flat rate	114.30	-3.80	0.97	0.36	4.70	0.04	0.35	0.00	0.65
Intermediate	122.10	-2.30	0.98	0.16	5.49	0.04	0.82	0.00	0.18
High-Low	123.80	1.30	1.01	0.94	3.47	0.03	0.86	0.00	0.14
Grass/Maize silage									
Flat rate	131.40	-0.90	0.99	0.66	6.94	0.05	0.98	0.00	0.02
Intermediate	130.60	-0.40	1.00	0.91	3.79	0.03	0.99	0.00	0.01
High-Low	129.00	-7.90	0.94	0.90	8.76	0.07	0.18	0.01	0.81

Table 5.4 continued Accuracy of the prediction of the Dairy Cow Model for DMI, net energy (NE_L) intake and milk energy output (MEO, MJ NE_L/d) cows fed ad libitum forage mixtures during incomplete lactations (Dataset 1 (Feil, 2000), grass and maize silage (70:30 on a DM basis); Dataset 2 (Feil and van Schooten, 2001) either grass and cereal whole crop silage or grass and maize silage (70:30 on a DM basis)). Concentrates were separately fed in equal amounts of concentrate but according to different patterns: Flat rate, Intermediate, High-Low[1].

	Actual[3]	Bias[4]					Proportion of MSPE[2]		
	(A)	(A-P)	b[5]	r^2[6]	MPE[7]	RPE[8]	Random	Line	Bias
Dataset 2 (Feil and van Schooten, 2001)[10] week 1-25 of lactation									
MEO (MJ NE_L/d)									
All treatments	87.52	-4.33	0.95	0.76	6.77	0.08	0.59	0.00	0.41
Grass/WCS									
Flat rate	81.74	-5.56	0.94	0.90	6.23	0.08	0.20	0.00	0.80
Intermediate	86.03	-5.03	0.95	0.65	7.16	0.08	0.50	0.00	0.49
High-Low	89.91	0.35	1.00	0.88	4.73	0.05	0.99	0.00	0.01
Grass/Maize silage									
Flat rate	90.41	-3.33	0.96	0.90	4.44	0.05	0.43	0.01	0.56
Intermediate	89.95	-3.59	0.96	0.64	7.67	0.09	0.78	0.00	0.22
High-Low	87.05	-8.82	0.91	0.89	9.46	0.11	0.12	0.01	0.87

[1] Flat-rate approximately 1600 kg concentrate/305 d lactation distributed according to a fixed flat-rate; High-low 1600 kg concentrate/305 d lactation

[2] Mean Square Prediction Error = $MSPE = (\bar{A} - \bar{P})^2 + S_P^2(1-b)^2 + S_A^2(1-r^2)$

[3] Actual DMI (kg/d), NEL intake (MJ/d), Milk Energy Output (MJ NEL/d)

[4] Mean bias actual (A) minus predicted (P)

[5] b = the slope of the regression of actual (A) on predicted (P) with intercept zero

[6] r = correlation coefficient of A and P

[7] MPE= mean prediction error = √MSPE

[8] RPE is relative prediction error = MPE/A

[9] n = 90 weeks × treatments

[10] n = 150 weeks × treatments

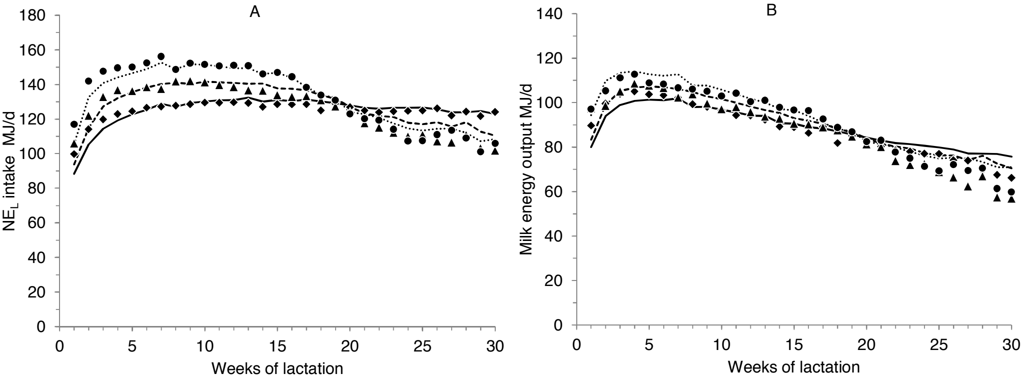

Figure 5.5 Observed (symbols) and simulated (lines) NE_L intake (left graph) and milk NE_L output (right graph) using data of Feil (2000). Treatments were different concentrate allocation regimes: flat rate, high-low and an intermediate. Flat rate feeding indicated with ♦ (observed) and solid lines (simulated), high-low is indicated with ● (observed) and a dotted line (simulated), the intermediate treatment is indicated with ▲ (observed) and a dashed line (simulated). Sixteen cows per treatment group.

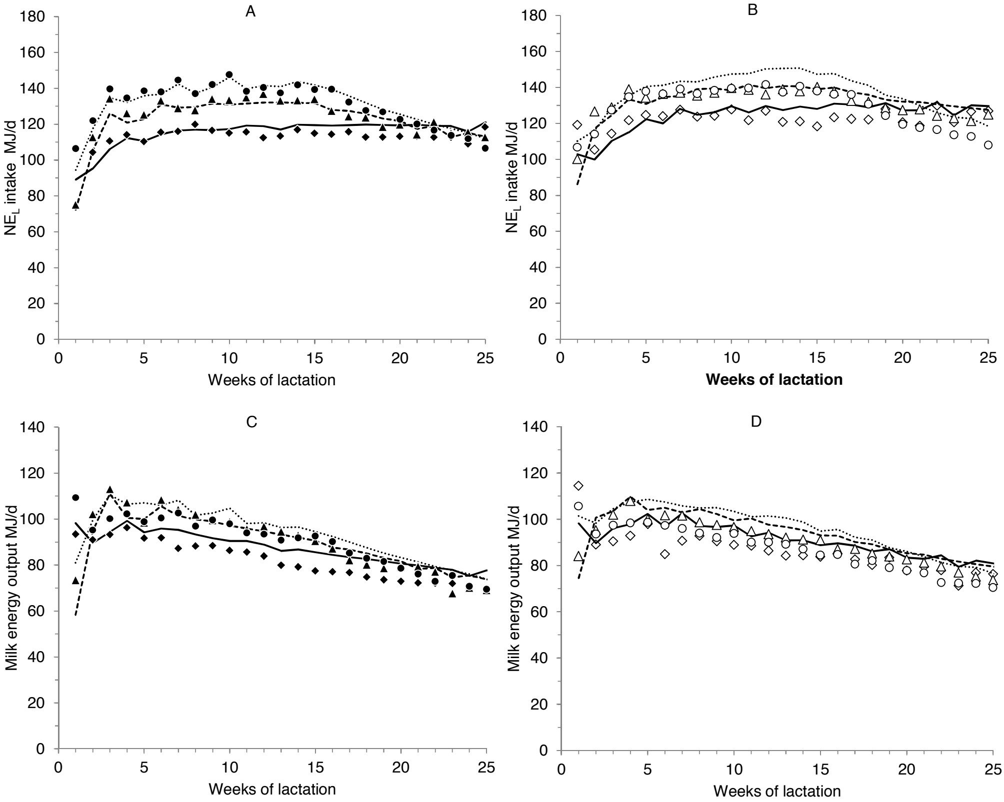

Figure 5.6 Observed (symbols) and simulated (lines) NE_L intake (graph A and B) and milk NE_L output (graph C and D) using data of Feil and van Schooten (2000). Treatments were different concentrate allocation regimes: flat rate, high-low and an intermediate with two different forage mixtures: Grass-silage plus whole crop cereal silage (black symbols, graph A and C)) or grass-silage plus maize silage (open symbols, graph B and D). Flat rate feeding indicated with ♦ and ◇ (observed) and solid lines (simulated), High-low is indicated with ● and ○ (observed) and a dotted line (simulated), the intermediate treatment is indicated with ▲ and Δ (observed) and a dashed line (simulated). Eight cows per treatment (Feil and van Schooten, 2001).

Table 5.5 Accuracy of the prediction of the Dairy Cow Model for DMI and milk energy output (MEO, MJ NE_L/d) cows fed ad libitum a TMR with a low (100 g concentrate/kg grass silage; 0.918 SV/ kg DM, 6.45 MJ NE_L/kg DM) or high (300 g concentrate/kg grass silage; 0.71 SV/kg DM, 6.90 MJ NE_L/kg DM) proportion of concentrate throughout the lactation period or with a switch-over design at mid-lactation.

	Actual[1]	Bias[2]					Proportion of MSPE[7]		
	(A)	(A-P)	b[3]	r^2 [4]	MPE[5]	RPE[6]	Random	Line	Bias
DMI (kg/d) week 2 – 40									
All treatments	18.99	-1.36	0.93	0.76	1.96	0.10	0.51	0.01	0.49
HH	20.71	-2.35	0.90	0.25	2.66	0.13	0.22	0.00	0.78
HL	20.45	0.07	1.01	0.87	1.34	0.07	1.00	0.00	0.00
LH	18.55	-1.69	0.91	0.72	1.99	0.11	0.26	0.02	0.72
LL	17.71	-1.44	0.92	0.76	1.50	0.08	0.08	0.00	0.92
MEO (MJ NE_L/d) week 2 – 40									
All treatments	85.51	-3.91	0.96	0.87	7.89	0.09	0.75	0.01	0.25
HH	94.31	-5.66	0.95	0.91	7.76	0.08	0.46	0.01	0.53
HL	90.23	-0.32	1.01	0.93	6.77	0.08	1.00	0.00	0.00
LH	79.63	-8.19	0.91	0.59	10.80	0.14	0.42	0.00	0.58
LL	77.87	-1.45	0.98	0.78	5.13	0.07	0.92	0.00	0.08

[1] Actual DMI (kg/d), Milk Energy Output (MJ NE_L/d)

[2] Mean bias actual (A) minus predicted (P

[3] b = the slope of the regression of actual (A) on predicted (P) with intercept zero

[4] r = correlation coefficient of A and P

[5] MPE= mean prediction error = √MSPE,

[6] RPE is relative prediction error = MPE/A

[7] Mean Square Prediction Error = $\text{MSPE} = (\bar{A} - \bar{P})^2 + S_P^2(1 - b)^2 + S_A^2(1 - r^2)$

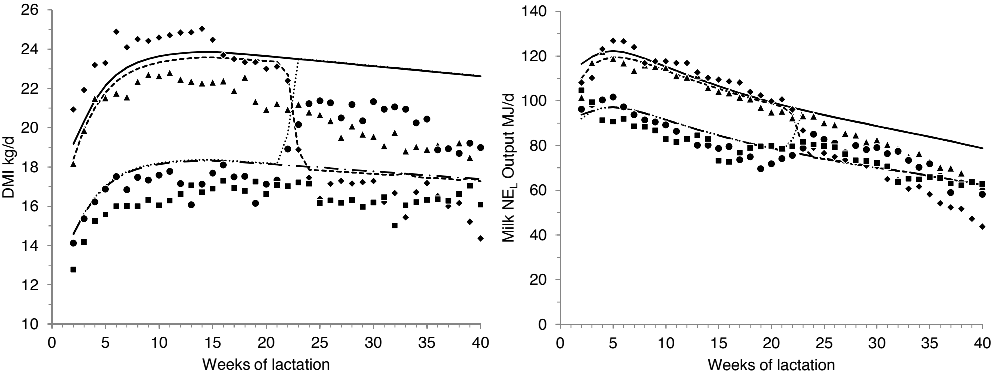

Figure 5.7 Comparison of observed values (indicated with solid symbols) and simulated values (lines) of DMI (left graph) and milk NE_L output (right graph) and predicted values (lines) of cows fed a grass silage based TMRs containing 300 g/kg fresh silage (H) (6.9 MJ NE_L/kg DM) or 100 g/kg fresh silage (L) (6.45 MJ NEL/kg) proportion of concentrates. Treatment HH (▲) and LL (■) were on the same treatment throughout the whole lactation. Cows of HL (♦) and LH (●) were switched over at week 22 of lactation from H to L and L to H, respectively.

3.3. *Scope of the Wageningen DCM*

The Wageningen DCM has been developed to simulate the direct response of feed and diet composition on DMI and the subsequent effects on $NE_L I$, MEO and ER, under the condition that other essential nutrients are not limiting. However, when common rules for the formulation of dairy rations are applied (e.g. sufficient concentrations of digestible crude protein, physical structure) milk production is usually not limited by other nutrients than energy.

The Wageningen DCM predicts milk production in terms of MEO but is not able to predict the response of diet composition or nutrient intake on milk composition or milk constituent yields.

The Wageningen DCM does not include metabolic adaptation feedback mechanisms to previous feeding and therefore does not account for possible carry-over effects. Carry over effects can be expected when there are large differences in two successive dietary treatments (Huhtanen and Hetta, 2012). However, under practical conditions radical dietary changes are unlikely.

The prediction of changes in body reserves should be used as an indicator to judge whether a feeding strategy creates a risk for excessive mobilization of deposition of body energy.

The Wageningen DCM is developed using intake and production data from individually fed dairy cows, kept indoors and offered ad libitum preserved forage or fresh cut grass. Therefore, the Wageningen DCM should be applied to cows in confinement systems. However, (Zom and Holshof, 2011) proposed an adaptation of the Wageningen DCM for grazing. Additional validation of the Wageningen DCM used is needed to test its accuracy in a grazing situation.

The Wageningen DCM is explicitly suitable to simulate the effects different feeding strategies, forage to concentrate ratios on DMI, $NE_L I$, nutrient intake, MEO and ER for groups of dairy cows in confinement systems. The outputs of the model can be further processed in additional models. For example, DMI, nutrient intake and milk production can be used as inputs for models predicting the production of greenhouse gasses and manure (Bannink et al., 2011), and diet related ammonia emissions (Velthof et al., 2012) or for calculation of variable feeding costs (Vermeij et al., 2013). The outcomes enables the user to analyse and compare different feeding strategies on a feeding group level, in order to identify situations where NE_L intake could be limiting, and to formulate diets and calculate feed budgets and for development of sustainable feeding strategies in an economical and environmental context.

4. Conclusion

The Dairy Cow Model (Wageningen DCM) is able to predict on a daily basis and for the whole lactation period, DMI, subsequent NE_LI and simultaneously the direct effects of NE_LI on MEO and changes in ER in dairy cows. The Wageningen DCM requires few inputs which are easy to obtain under practical conditions. The simulated effects of changes in NE_L intake and concentrate supplementation on milk energy output and FPCM agrees with data from literature. External validation showed a good accuracy of the prediction of DMI and milk energy output for early and mid-lactation (0-30 weeks of lactation) dairy cows. The overall accuracy of the prediction of DM intake and milk energy output during complete lactations was acceptable. The Wageningen DCM is suitable as a tool for strategic decision making, evaluation of long term feeding strategies and formulation of rations for groups of dairy cows.

A MS-Excel 2010 spreadsheet with a simplified version of the Wageningen DCM can obtained by sending a request to the corresponding author.

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Chapter 6

General discussion

6. General discussion

6.1. Introduction

This thesis focusses on the development of a model for the prediction of the effects of animal and feed related factors and their interactions on DM and net energy intake and the partitioning of ingested net energy to milk and body reserves in dairy cows. This model, named the Wageningen UR Dairy Cow Model (Wageningen DCM) is developed as an alternative for the Cow-Model ("Koemodel") developed by Hijink and Meijer (1987). This earlier Cow-Model was used as a tool for applied research, education and extension, farm planning, feed budgeting and diet formulation, evaluation of different policies and farm strategies on farm economics and farmers income (Hijink and Meijer, 1987). The main outputs of that Cow-Model were the predicted roughage intake and required concentrates input to meet a user-defined level of fat corrected milk (FCM) yield (*i.e.* the actual or target FCM yield) using the NE_L content of the roughage and concentrates and FCM yield as inputs. However, that Cow-Model had some practical limitations as outlined in the General Introduction (Chapter 1). The major disadvantage is that the Cow-Model was unable to predict the effects of diet composition and feeding management on animal performance. This was because both the standard roughage intake capacity curve and the amount of body energy available for mobilisation were linearly scaled with FCM yield which is a user-defined input. Milk production and intake curves of the Cow-Model were rigid with a fixed lactation length of 305 days weeks and a calving interval of one year. Therefore, it was not possible to simulate different culling and breeding strategies which affect the length of the lactation cycle. The Cow-Model had a limited biological and physiological meaning, since the complex relations in the model were based on assumptions from experts or were described with simple algorithms (Hijink and Meijer, 1987). For example, to describe the partitioning of ingested net energy to either milk production and body energy reserves, it was assumed that all body reserves mobilized in early lactation are completely restored at the end of lactation (Hijink and Meijer, 1987). Another limitation of the dairy cow model is that the model was based on a dataset with a limited number of observations (n = 157) from cows fed ad libitum grass silage supplemented with concentrates. An alternative for the Cow-Model of Hijink and Meijer (1987), must be at least more flexible, better suited to simulate a wide range of diets, feeds and farm management options, easier to maintain, expand or up-date, provide a better biological explanation and be more accurate. This without compromising the fields of application and the easiness to operate.

Therefore, the aim of this study was to develop a flexible dairy cow model able to simulate a variety of feeding management practices (i.e. forage composition, different forage options, diet composition, forage to concentrates ratio) in Holstein Friesian cows using input variables that are easy to obtain. The model is intended as a decision support tool that allows a rapid and practical exploration of different animal and feeding management strategies and their effects on DM and energy intake (NEL, van Es (1978), milk energy output (MEO), fat and milk corrected milk (FPCM) production and changes in body reserves. These model outputs can be used as inputs for separate models to calculate required feed budgets, feed costs, milk revenues, and the excretion of manure, minerals ammonia and greenhouse gases.

6.2. *Modelling approach*

The concepts of models for the prediction of animal performance can range from empirical to mechanistic and in between models that feature both empirical and mechanistic components. The choice between an empirical or mechanistic modelling approach depends on the purpose of the model and the availability of datasets with sufficient information for model development. Empirical models give a mathematical description of the relationships between inputs and outputs derived from a data set. However, these relationships are not necessarily a realistic representation of the underlying biological processes. Mechanistic models are more complicated than empirical models. Mechanistic animal models explain animal performance on the basis of a realistic description of the underlying biological processes. A mechanistic model contains at least two levels of description, the upper level phenomena (e.g. the organism) and the lower level mechanisms (e.g. organs) (Thornley and France, 2007). Mechanistic animal models may have the potential to predict a cows' feed intake and milk performance (upper level phenomenon) from a causal relationship with series of underlying metabolic and physiologic processes such as feed digestion, nutrient absorption and milk synthesis (lower level mechanisms). Theoretically, in contrast to empirical models, mechanistic models are not restricted to the limits of the underlying datasets. Therefore, mechanistic models are potentially better suited for a theoretical exploration of novel feeding strategies and diet options than empirical models. For example, Baldwin et al. (1987a) generated series of realistic lactation curves while simulating different planes of nutrition using a combined mechanistic model for nutrient digestion and utilisation and udder metabolism in dairy cows. So far, mechanistic models have been described for simulation of rumen digestion, liver and udder development and metabolism (e.g. Baldwin et al. (1994), Baldwin et al. (1987a), Baldwin et al. (1987b), Baldwin et al. (1987c), Danfaer (1990), Dijkstra et al. (2008), Dijkstra et al. (1992), Hanigan and Baldwin (1994), and Maas et al. (1998)). It is a promising prospect that future integration of the models representing different organs and tissues can finally result in a fully mechanistic whole cow-model.

However, for use in agriculture practice, a mechanistic modelling approach will meet some obstacles. At present, there is incomplete understanding of feed intake regulation. Feed intake regulation involves many mechanisms such as feedbacks from chemo- and mechanoreceptors in the gastrointestinal tract, hormonal and chemostatic control and aspects of behaviour, perception and learning, as has been extensively reviewed by Forbes (2007). However, the existing mechanistic models for prediction of feed intake for ruminants (e.g. Chilibroste et al. (1997), Hackmann and Spain (2010) and Illius and Gordon (1991)) give a greatly simplified view on feed intake regulation mechanisms since they address only a few of the aspects of intake regulation. The models of Illius and Gordon (1991) and Chilibroste et al. (1997) predict feed intake from digesta flow kinetics, which implies that intake is determined by the physical capacity of the rumen and the rate of disappearance of the rumen contents. Hackmann and Spain (2010) proposed a mechanistic intake model with a simultaneous integration of two intake regulating feedback mechanisms: a distention feedback described by the fill of the reticulo-rumen with NDF (% of body weight) and a chemostatic feedback described by absorption of net energy (NE) as % of body weight (BW). However, these feedback mechanisms regulate intake at a gross level, and not by the specific hormonal and neuronal processes by which the intake regulating effects are mediated. This simplification prohibits investigation and further understanding of feed intake regulation (Hackmann and Spain, 2010). Another limitation of these mechanistic models is that they consider a specific type of animal and do not describe the intake control mechanisms related to the animals' physiological status. This implies that these models cannot be applied to simulate long term effects of feeding management and feed supply, because the cows' physiological state changes continuously during the course of the lactation cycle and throughout life span. So far, only simple adjustments have been made to account for the size and physiological status of the cow. Illius and Gordon (1991) used scaling factors related to BW as a measure for the size of the animal whereas, Chilibroste et al. (1997) used BW to scale for animal size and table values (ARC, 1980) to scale for month of lactation.

At the current state of science, mechanistic models do not provide an add-on to the understanding of feed intake regulation and the prediction of feed intake over the existing empirical fill-unit systems (e.g. Jarrige et al. (1986) and Kristensen and Ingvartsen (1986)) which explain the mechanisms of intake regulation at a similar gross level. Additionally, in general, the precision of current empirical intake models is still superior to mechanistic models (Poppi, 1996; Yearsley et al., 2001). On the short term, development of mechanistic models that provide an understanding of regulation of feed intake at a more detailed level than the current mechanistic and empirical models would be too problematic. In the first place, a mechanistic model requires detailed and adequate data sets for development and model testing. Establishment of such data sets is expensive and time consuming. The second point of consideration is that comprehensive mechanistic models may require inputs which are not available on commercial farms.

The advantage of empirical models is in their relative simplicity. In general, empirical models require only a limited number of input data and they are easy to operate. However, extrapolation beyond the limits of the dataset is not appropriate. Empirical models can only be used with confidence if the predictions are performed for conditions and circumstances (e.g. diet, feeds, the cows genetic potential, climate, housing, etc.) which are similar as those used for model parameterization (Yearsley et al., 2001). Inherently, empirical models cannot be used to explore complete new situations (e.g. new feeds, different genetic potential) and novel feeding strategies. Fortunately, applied feeding research in the Netherlands has intensified during the last decades. The intensification of applied research has yielded large data sets with information on feed intake, feed composition and performance of individual cows covering a broad variety of feeding regimes. Although, these datasets may lack the detail that is required for modelling the biological processes that predicts animal performance, they are detailed enough to provide a basis for the calibration and validation of sound empirical dairy cow-models applicable for a wide range of feeding management situations.

As discussed above, both mechanistic and empirical models have their advantages and disadvantages. The desire to create a flexible model able to explore the effects of novel feeding strategies and diet options on feed intake and performance as the result of metabolic and physiologic processes in the cow argues for a mechanistic approach. However, a desire for a simple, robust, easy to operate model for simulation of feed intake and dairy cow performance under practical conditions, together with presence of large datasets covering a wide range feeding practices argues for an empirical approach. The aim of the Wageningen DCM has been to predict feed intake and animal performance under practical conditions, which enables evaluation of diet composition, feed supply and feeding management strategies at a gross level. For this purpose it is more important to quantify the effects on animal output rather than to provide an explanation of the mechanisms behind these effects. Taking these advantages and disadvantages of mechanistic and empirical models in to account, an empirical approach was chosen to develop a dairy cow-model, because at present it can be expected that an empirical model will give the best fit to the objectives and requirements of the users and to the data available for model calibration and validation.

However, this thesis also challenged to reduce the main disadvantages associated with empirical models such as a low flexibility, lack of biological explanation and limitations with regard to the field of application. Minimizing these disadvantages was attempted in several ways. Flexibility was created by the modular structure of the model. The relationships between inputs and outputs in the model are not solely based on statistical criteria or the best fit, but must also allow reasonable logical or biological explanation. The use of a large dataset covering a wide variety of diets and feeding practices may broaden the range in which the predictions are valid. Nevertheless, model predictions, in particular those who are made with empirical models, should be put in the right perspective and managed with common sense.

6.3. Model structure

The Wageningen DCM has a modular design in order to create a model that is flexible with regard to different feeding conditions, types of animal and future adjustments and extensions. This modular design consists of two connected sub-models which separately predict feed intake and the partitioning of ingested net energy, respectively. The separate sub-models for feed intake (Figure 6.1, box with dashed line) and energy partitioning (Figure 6.1, box with dotted line) are connected in a one-way direction. Theoretically, the separate modules of the Wageningen DCM are interchangeable which creates a high degree of flexibility. This flexible structure allows future refinements and extension of the Wageningen DCM without reconstructing the whole system. In case, there are other feed intake or energy partitioning models available which are better suited to a specific situation, it is possible to replace a sub-models with more appropriate ones.

The feed intake model is based on the principles of a fill-unit system (Jarrige et al., 1986; Kristensen and Ingvartsen, 1986). An important feature of fill-unit systems is that they include separate equations describing intake constraining effects of feeds and separate equations describing the feed intake capacity (FIC) which is the cows' ability to process the "fill". This means that the feed intake model is also constructed from two sub-modules.

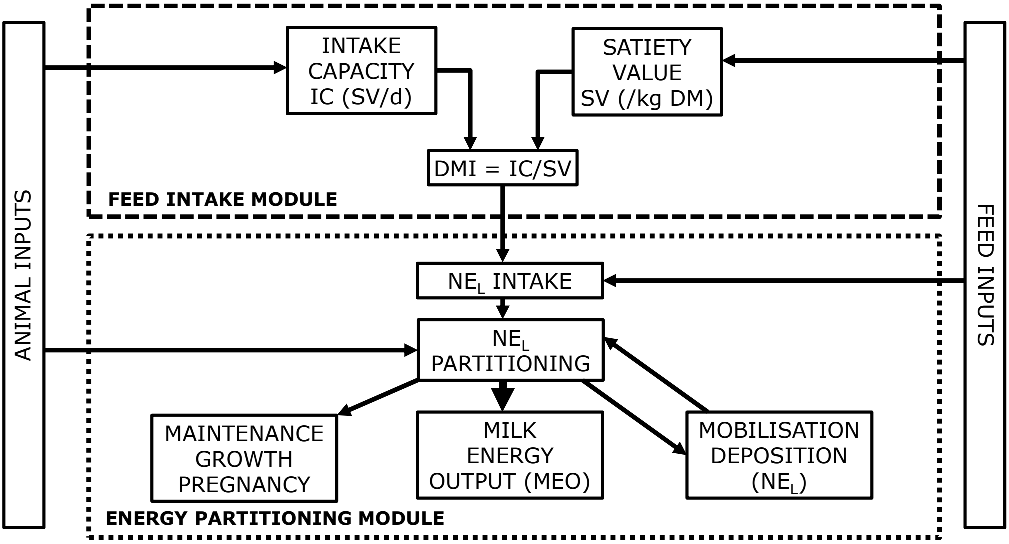


Figure 6.1 Schematic representation of the Wageningen UR Dairy Cow Model Wageningen DCM. The upper box with the dashed line (- -) is the feed intake sub-model (DMI = dry matter intake, Satiety value is calculated from feed inputs (dry matter content, crude fibre, crude protein, digestible organic matter concentration). Intake capacity and energy partitioning is predicted from lactation number, days in milk, days pregnant. The box with the dotted line is energy partitioning sub-model.

As discussed in Chapter 2, this allows also flexible extension or modification of the feed intake model (e.g. extension with alternative feeds or inclusion of additional animal factors). Fill unit systems are not restricted to one specific diet type or feed option (Chapter 2) and are therefore more flexible than multiple regression models which are unable to simulate a large variety of feed management conditions.

6.4. Feed characteristics and feed intake

The Wageningen DCM applies specific separate equations for calculation of the satiety values ("fill"; SV) of the most common feeds (Chapter 2). The most relevant feed factors for calculating the SV of feeds are the concentrations of dry matter, crude fibre, crude protein, and digestible organic matter F(igure 6.2). The concentrations of dry matter, crude protein, and crude fibre can be related to bulk volume, metabolic and physical limitation. The concentrations of crude fibre and digestible organic matter are factors which can be linked to digestibility, ruminal outflow and ruminal degradability and to metabolic regulation (Chapter 2). This approach, with separate equations for calculation of the SV of feeds, differs from other fill unit systems (Jarrige et al., 1986; Kristensen, 1986; Volden, 2011). The French INRA Fill Unit system (Jarrige et al., 1986) provides a comprehensive table with fill values (UEL) of fresh and preserved (silage and hay) forages from different species, regional origins, botanical compositions, cutting cycles, cutting dates, dry matter classes and stages of maturity at harvest. The table values are derived from a large set of intake and digestibility data from sheep (Baumont et al., 2007). The Danish Fill Unit system calculates the Fill Value of forages from Digestible Energy (DE) (MJ/kg DM) and crude fibre content (%) with correction factors for the proportion of legumes and DM content of grass silage (Kristensen, 1986). In the NorFor system (Volden, 2011) the fill value of forages is calculated from NDF content (and organic matter digestibility. Although, different approaches and equations are used to calculate "fill" , the ranking of the "fill" of different commonly used feeds is fairly the same for the different systems as shown in Table 6.1.

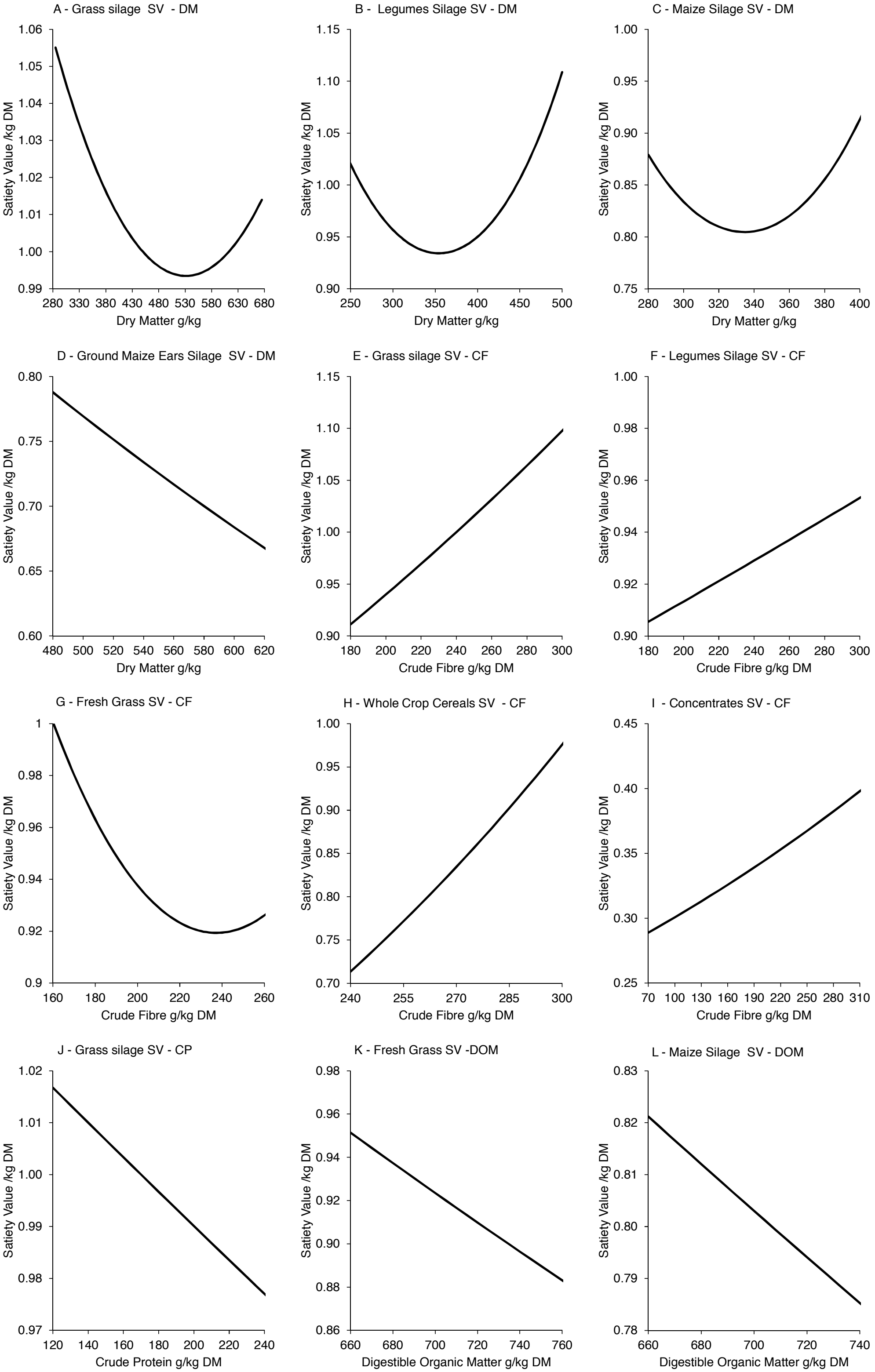
Table 6.1 Fill and satiety values of forages absolute values and values relative to grass silage (=100) derived from different fill-unit systems.

	Netherlands[1]		France[2]		Denmark[3]		Nordic[4]	
	SV[1]	Relative	UEL	Relative	FFk	Relative	FV	Relative
Grass silage (=100)	1.00	100	1.06	100	0.46	100	0.50	100
Fresh grass	0.89	89	0.98	92	0.44	96	0.41	82
Maize silage	0.80	80	0.98	92	0.39	85	0.39	78
Legumes silage	0.96	96	0.98	92	0.43	93	0.48	96
Fodder beet	0.69	69	0.60	57	0.25	54	0.28	56
Straw	1.66	166	1.60	151	0.90	196	0.68	136
Concentrates	0.33	33			0.22	48	0.22	44

1) SV satiety value Wageningen DCM (Zom et al., 2012); 2) UEL fill units for dairy cattle, INRA fill unit system (Baumont et al., 2007); 3) FFk Fill value for dairy cattle Danish Fill Unit system (Møller et al., 2000); 4) Fill Value NorFor System (Volden, 2011)

The total amounts of lactic and acetic acids, ammonia and bioamines affects the palatability and intake (Dulphy and van Os, 1996). For silages, the NorFor system includes a multiplicative correction factor for the concentrations of volatile fatty acidsNH$_3$N (Volden, 2011)></EndNote>, but does not include DM content in the equation of the fill value. The developmental dataset of the Wageningen DCM did not contain information on the concentrations of fermentation products in silages. Therefore, the Wageningen DCM does not include a correction for silage fermentation products, however it includes DM content in the equations of the SV of silages. Silage DM content is an important indicator of silage fermentation (Wieringa, 1958; Wieringa and de Haan, 1961; McEniry et al., 2011). Increased DM content in grass silages results in a higher osmotic pressure and restricted silage fermentation, in association with a higher pH and higher lactic acid concentration relative to the butyric acid concentration (Wieringa, 1958; Wieringa and de Haan, 1961). The concentrations of total fermentation products (lactic acid, acetic acid, propionic acid, butyric acid ethanol and NH$_3$-N) are reduced with increasing DM concentrations (McEniry et al., 2011). Therefore, when DM is included in the equations to predict SV of silages, an adjustment for silage fermentation characteristic is probably not required.

Figure 6.2 Graphical display of the relationship between the composition of feed and satiety value (SV) Panel A, B, C, D displays the relationship between the concentration of dry matter on the SV of grass silage, legumes silages maize silage and ground maize ears silage, respectively. Panel E, F, H. H and I displays the relationship between concentration of crude fibre (CF) on the SV of grass silage, legumes silages, fresh grass, whole crop cereal silage and concentrate, respectively; Panel J displays the relationship between the concentration of crude protein on the SV of grass silage Panel K and L displays the relationship between the concentration of digestible organic matter on the SV of fresh grass and maize silage respectively.


A - Grass silage SV - DM
Satiety Value /kg DM
1.06
1.05
1.04
1.03
1.02
1.01
1.00
0.99
280 330 380 430 480 530 580 630 680
Dry Matter g/kg
B - Legumes Silage SV - DM
1.15
1.10
1.05
1.00
0.95
0.90
250 300 350 400 450 500
Dry Matter g/kg
C - Maize Silage SV - DM
1.00
0.95
0.90
0.85
0.80
0.75
280 300 320 340 360 380 400
Dry Matter g/kg
D - Ground Maize Ears Silage SV - DM
0.80
0.75
0.70
0.65
0.60
480 500 520 540 560 580 600 620
Dry Matter g/kg
E - Grass silage SV - CF
1.15
1.10
1.05
1.00
0.95
0.90
180 200 220 240 260 280 300
Crude Fibre g/kg DM
F - Legumes Silage SV - CF
1.00
0.98
0.96
0.94
0.92
0.90
180 200 220 240 260 280 300
Crude Fibre g/kg DM
G - Fresh Grass SV - CF
1
0.98
0.96
0.94
0.92
0.9
160 180 200 220 240 260
Crude Fibre g/kg DM
H - Whole Crop Cereals SV - CF
1.00
0.95
0.90
0.85
0.80
0.75
0.70
240 255 270 285 300
Crude Fibre g/kg DM
I - Concentrates SV - CF
0.45
0.40
0.35
0.30
0.25
70 100 130 160 190 220 250 280 310
Crude Fibre g/kg DM
J - Grass silage SV - CP
1.02
1.01
1.00
0.99
0.98
0.97
120 140 160 180 200 220 240
Crude Protein g/kg DM
K - Fresh Grass SV -DOM
0.98
0.96
0.94
0.92
0.90
0.88
0.86
660 680 700 720 740 760
Digestible Organic Matter g/kg DM
L - Maize Silage SV - DOM
0.83
0.82
0.81
0.80
0.79
0.78
660 680 700 720 740
Digestible Organic Matter g/kg DM

6.4 Associative effects of feeds and feeding methods

The proposed system of satiety values in the Wageningen DCM assumes that the SV of different feeds in the diet are additive. Thus, it is assumed that neither intake nor supply of nutrients and energy to the cow are influenced by associative feed effects. However, it is known that associative effects between feeds occur (Doyle et al., 2005; Niderkorn and Baumont, 2009), which could affect feed intake and hence nutrient supply and animal performance. Associative effects of feeds can be either positive or negative. Positive associative effects may occur when a nitrogen deficiency is alleviated and cellulolytic activity is stimulated by supplementing low nitrogen diets with high protein supplements (Niderkorn and Baumont, 2009). Increased cellulolytic activity in the rumen results in increased fibre digestibility and feed intake (Huhtanen, 1991). A synergetic effect on cow performance may also occur when an excess of dietary nitrogen is reduced because energy requirement to synthesise and excrete excess nitrogen as urea would be reduced (Doyle et al., 2005). Negative associative effects may occur when large quantities of readily-fermentable carbohydrates in the diet causes a drop of rumen pH which impairs cellulolytic activity thereby reducing feed intake (Huhtanen, 1991). Since concentrates are often the main source or readily fermentable carbohydrates, this effect is considered as a ‘concentrate effect’ which causes substitution of forage. Volden (2011) argued that it is difficult to define feeds as strictly ‘concentrates’ or ‘forages’ and that substitution should not be related to ‘concentrates’, but that composition of the whole ration should be considered. Therefore, the NorFor system includes a substitution rate factor to adjust the fill value for the amount and concentration of readily degradable carbohydrates in the diet. An increased proportion of starch and sugar in the ration results in an increased substitution rate factor, which subsequently predicts a reduced forage intake (Volden, 2011).

A simulation with the Wageningen DCM of four rations for early-lactation cows producing 25 or 40 kg FPCM based on either maize silage or grass silage, indicates that the impact of the intake and concentration of readily degradable carbohydrates is small when the simulated rations are formulated to meet the energy requirements and recommendations for the concentrations of total starch, readily degradable starch plus sugars, rumen by-pass starch (de Visser, 1993; Subnel et al., 1994), rumen degradable protein (OEB; Tamminga et al., 1994), and physical structure (DeBrabander et al., 1996). The simulations, presented in Table 6.2, indicate that in grass silage-based rations the concentration of readily degradable starch and sugars (i.e. the proportion of starch and sugars with a ruminal degradation rate >12%/h) is first limiting, whereas in maize silage-based rations the proportion of total starch is first limiting. The substitution rate correction factors calculated according to the NorFor system were close to 1. This may indicate, that when rations are formulated according to the recommendations for dietary carbohydrates concentrations (de Visser, 1993; Subnel et al., 1994) are “save” and that under these conditions, negative effects of dietary starch and sugar on fibre digestion are not to be expected.

Table 6.2 Simulation of the intake of starch and sugars of maize silage or grass silage based rations using the Wageningen Dairy Cow Model

		Grass silage-based Rations[1]		Maize silage-based Rations[1]	
FPCM yield (kg/d)		25	40	25	40
$\mathrm{NE_L}$ requirement (MJ/d)		116	166	116	166
DVE requirement (g/d)		1412	2317	1412	2317
Diet composition % of DM					
Maize silage[2]				54.9	64.0
Grass silage[3]		78.9	48.2		
Straw[4]		0.0	0.0	20.3	0.0
Concentrates		21.1	51.8	24.8	36.0
	limits				
Total Starch (%)	<22.5	12.1	12.2	22.5	22.5
RDS+S (%)[5]	<12.5	12.5	12.5	8.3	1.5
RBPS (%)[6]	<6.0	1.1	1.2	5.4	6.0
OEB (g)[7]	>0	69	30	16	10
Physical structure[8]	1.10	1.98	1.29	1.76	1.12
First limiting		RDS+S[5]	RDS+S[5]	Total Starch	Total Starch
Total Dry Matter Intake (kg/d)		19.1	24.9	18.9	25.4
Total starch + sugars intake (kg/d)		3.49	5.46	4.95	5.83
Starch + sugars (% of DM)		18.2	22.0	26.2	23.0
Substitution rate correction factor[9]		0.98	0.97	0.98	0.96

[1]Simulated grass silage and maize silage-based diets were formulated to meet the requirements for dietary carbohydrates (de Visser, 1993; Subnel et al., 1994) metabolizable protein (DVE) and rumen degradable protein balance (Tamminga et al. 1994), physical structure (DeBrabander, 1996), and net energy for lactation ($\mathrm{NE_L}$, van Es, 1978) for cows producing either 25 or 40 kg FPCM (4% fat and 3.32 % protein); [2]Maize silage: 6.5 MJ $\mathrm{NE_L}$/kg, 46 DVE, -36 OEB, DM RDS+S 10 g/kg DM, Total Starch 0 g/kg DM, RBPS 94 g/kg DM; [3]Grass silage: 6.0 MJ $\mathrm{NE_L}$/kg, 55 DVE, 40 OEB, RDS+S 120 g/kg DM, Total Starch 0 g/kg DM, RBPS 0 g/kg DM; [4]Straw:4.0 MJ $\mathrm{NE_L}$/kg, 21 DVE, -10 OEB, RDS+S 0 g/kg DM, Total Starch 0 g/kg DM, RBPS 0 g/kg DM; [5]RDS+S = readily degradable starch plus sugars, ruminal degradation rate >12%/h [6]RBPS = rumen by-pass starch (de Visser, 1993; Subnel et al., 1994); [7]OEB = rumen degradable protein balance; [8] (DeBrabander et al., 1996); [9]Substitution rate correct factor as calculated in the NorFor system (Volden, 2011).

Feeding method (TMR v.s. separate feeds) may affect intake and performance of dairy cows. Feeding TMR may promote intake when low-palatable feeds are included in the diet or compared to situations where large quantities of concentrates are fed in few meals. However, there is no advantage of feeding a TMR over separate feeding when good quality roughage is offered and when concentrates are fed in multiple meals are regularly distributed over the day (Subnel et al., 1994). Borchert et al. (2007) observed that the number of concentrate meals had no significant effect on nutrient flow from the rumen, apparent rumen degradability and microbial protein synthesis. No difference on feed digestion have been observed between TMR feeding and separate feeding (Borchert et al., 2007; De Campeneere et al., 2009). Meijs et al. (1988) observed no differences in feed intake and milk production between separate feeding and TMR feeding when concentrates were fed that were contrasting in rumen degradable protein and carbohydrate concentration.

On commercial farms where dairy cow rations are usually formulated according to standard feed evaluation systems (e.g. DVE/OEB system for metabolisable protein and rumen degradable protein, (Tamminga et al., 1994), physical structure (SW) (DeBrabander et al., 1996) and practical recommendations for dietary carbohydrates (de Visser, 1993; Subnel et al., 1994)). When these feed evaluation systems and recommendations are applied correctly, it is unlikely that major associative effects of feeds and feeding systems on feed intake and animal performance will occur. Therefore, the Wageningen DCM should be able to be used with confidence in common farm practice.

6.5. Animal factors

6.5.1. Feed intake capacity

An important novel aspect of the Wageningen DCM is that feed intake is predicted from feed and animal characteristics, excluding actual milk yield (MY) and BW. This is a crucial feature, because this enables the construction of a predictive dairy cow model able to simulate the long-term effects of animal and feed related factors on animal performance. There are only a few models for the prediction of voluntary DMI in dairy cows that do not include (actual) MY or BW as explanatory variables (Ingvartsen, 1994). An explanation for this, is that the energy status of the cow, which is affected by the energy intake and energy requirement for MY and maintenance, acts as a metabolic feedback mechanism that regulates feed intake. Indeed, the empirical relationship between DMI and milk production is to a degree observed in our database as displayed in Figure 6.3, which indicate a positive correlation between MY and DMI.

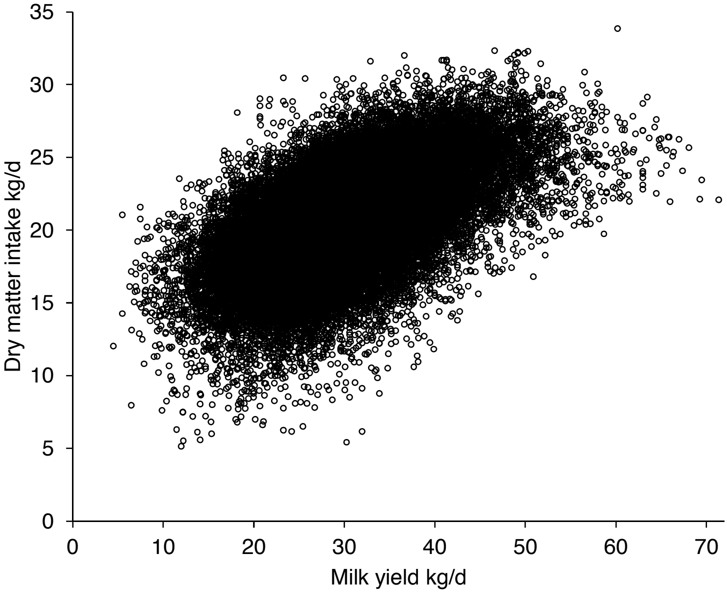


Figure 6.3 Relationship between milk yield and dry matter intake.

However, it is questionable whether a high feed intake is the result of a high energy requirement for milk production, or that a high feed intake results in high supply of energy for milk production. The positive correlation between actual MY and DMI is associated with an entanglement between diet composition, age of the cow, stage of lactation, and milk production. This entanglement is caused by the fact that dairy cow rations are usually formulated to meet the (expected) nutrient requirements. (CVB, 2012) Therefore, high-yielding and early-lactation cows are provided with rations that are composed from palatable, high quality feeds and concentrates in order to promote DM and energy intake. In contrast, low-yielding, late-lactation cows are provided with rations with lower quality forage and less concentrates in order to reduce the risk of overeating and to avoid that these cows become too fat. Another entanglement is that both milk production and DMI increase with lactation number as a result of an age-related effect on body size and hence FIC of the cow (Chapter 2 and 4). The actual MY, is highly reliant on the feeding conditions and the stage of lactation of the cow. Therefore, MY may be an indicator of the actual feed intake, but cannot be used to predict the FIC of dairy cows during the lactation. Although, feed intake models that include actual MY as explanatory variable are not suitable to predict the long-term effects of feeding strategy, they may, however, be useful for operational purposes such as calculating the amount of required concentrates supplements for individual dairy cows on farms equipped with automatic concentrates feeders (Halachmi et al., 2004).

6.5.2. Genetic merit and feed intake

Genetic correlations have been determined between MY and DMI (van Aarendonk et al., 1991; Veerkamp and Brotherstone, 1997) and between BW and DMI (Veerkamp and Brotherstone, 1997). These correlations indicate that increased MY and BW results in an increased feed intake. However, it is difficult to estimate the genetic component of feed intake, because this requires intake data of cows selected on the basis of their genetic index for milk production, subjected to similar feeding conditions, preferably during the whole lactation. The Wageningen DCM does not account for genetic differences. It was assumed that variation in feed intake is primarily attributable to variation in the physiological status (lactation number, DIM, gestation) and feed characteristics (diet and feed composition) and not to differences in genetic potential for milk production. This assumption is based on the fact that the data originate from Holstein Friesian cows which were uniformly bred for a high net milk revenue index (INET) (Hanekamp, 1993). In the experimental herds, the four highest INET-ranked and national-available Holstein Friesian sires in the Netherlands, were used each year, for breeding and the 25% lowest INET cows were mated with beef sires. This breeding practice was recommended to farmers in the Netherlands (Hanekamp, 1993). The estimated whole lactation MY of 1st, 2nd 3rd and 4th parity cows in the developmental dataset compared very well with the Dutch milk test records of 2011 (CRV, 2012) (Chapter 4). This indicate that the genetic merit for milk production of the cows present in the dataset is a reflection of the genetic merit of the Holstein Friesian population in the Netherlands, which give confidence in the assumption that differences in feed intake are not highly influenced by differences in genetic potential of the cows. However, when the model is applied to breeds or selection strains other than high-merit Holstein Friesian cows, FIC could have to be adjusted for breed or genetic potential.

Several ways have been introduced to account for the genetic merit. Faverdin et al. (2011), scale FIC according to potential milk production, which is based on a theoretical lactation curve model adjusted for metabolisable protein supply. The e-Cow model (Baudracco et al., 2012) includes a metabolic regulation of intake by the energy requirements of the cow which are based on the user-defined potential annual MY (Vetharaniam et al., 2003). Rotz et al. (1999) scale feed intake of small and large Holstein Friesian cows and other breeds relative to the BW of average Holstein Friesian cows.

6.5.3. Physiological time as driver of cow performance

The Wageningen DCM describes the dynamic evolution of FIC, BW, MY and changes in the partitioning of ingested NE_L during successive lactation cycles. Feed intake and nutrient partitioning varies within a lactation cycle and during successive lactation cycles. These variations are the result of complex homeorhetic control mechanisms in order to support the physiological state of the cow (Bauman and

Currie, 1980). This homeorhetic control results in the typical pattern of feed intake in dairy cows characterized by an intake depression starting in late pregnancy that reaches its nadir around parturition, followed by a recovery of intake during the early lactation (Ingvartsen and Andersen, 2000). In early lactation, under influence of the same homeorhetic mechanisms, both ingested and mobilised nutrients are partitioned towards milk production. As lactation progresses, less nutrients are directed towards milk production in favour of body reserves and foetal growth (Bauman and Currie, 1980; Ingvartsen and Andersen, 2000). In ruminants, regulation of feed intake and mobilisation of body reserves are closely related. Growth hormone increases both the responsiveness of adipose tissues and the negative effect on feed intake induced by administration of β2-adrenergic agonists (Bareille et al., 1997; Faverdin and Bareille, 1999). Thus, the homeorhetic mechanisms that simulate mobilization of body reserves simultaneously reduces FIC (Faverdin and Bareille, 1999). Friggens et al. (2013) concluded that the dip in feed intake during early lactation is a consequence of the partitioning of body reserves to milk and not the cause of this partitioning. Therefore, mobilisation in early lactation is not only resulting from an inability to ingest sufficient nutrients, but also for a major part genetically driven (Friggens et al., 2007). Feed intake capacity, milk production and nutrient mobilisation vary not only within a lactation, but also between lactations (Oldenbroek, 1989; Coffey et al., 2002; Coffey et al., 2004). The hormonal and metabolic mechanisms behind the changes in feed intake and nutrient partitioning during the course of the lactation cycle are a function of physiological time. Therefore, the Wageningen DCM includes lactation number, DIM and days pregnant as the physiological time related drivers of changes in FIC, BW, MEO and partitioning of energy. Although, the Wageningen DCM is not intended to give a mechanistic description of the homeorhetic processes, it is able to generate realistic trajectories of FIC, BW, MY and energy partitioning which can be explained from the concept of homeorhetic control (Bauman and Currie, 1980).

The Wageningen DCM predicts that during early lactation ingested energy and body reserves are partitioned to milk production, and as the lactation progresses, the proportion of ingested energy partitioned towards milk declines in favour of body reserves. This shift in energy partitioning towards body reserves is enhanced in the case of pregnancy. The amount of ingested energy and body reserves partitioned to milk increases with higher lactation number, reflecting the higher FIC, the larger amount of body reserves and the reduced energy requirement for growth as the cow approaches maturity. The Wageningen DCM is able to simulate the characteristic changes in FIC and energy partitioning through lactation, pregnancy and aging (Chapter 4 and 5).

Simulation of a non-limiting feeding conditions by the Wageningen DCM showed that in early lactation mobilization of body reserves cannot be prevented (Chapter 4). This result is in accordance with Friggens et al. (2007) and Friggens et al. (2013), who concluded that mobilisation is genetically driven and would also occur under non-limiting conditions.

6.6. Limitations and further development

6.6.1. Limitations inherent to the underlying dataset

As discussed previously, empirical models should be used for conditions which are similar to those used for model parameterization (Yearsley et al., 2001). The data used for parameterization of the Wageningen DCM were obtained from indoor feeding experiments with clinical healthy, high-merit Holstein Friesian cows housed in well-ventilated and insulated cubicle barns (i.e. thermo-neutral conditions). The cows were managed according to similar experimental protocols with regard to cow handling, milking and feeding practices. The diets were formulated to meet the requirements for physical dietary structure (DeBrabander et al., 1996) and rumen degradable protein (OEB; Tamminga et al. (1994)). Drinking water and fresh feed were continuously accessible. Fresh feed was supplied once or twice a day, refusals were removed daily. *Ad libitum* intake was achieved by maintaining a refusal weight of least than 10% of the fresh weight supplied. The occupation rates of the feed access gates and weighing troughs were one cow per gate or less than two cows per weighing trough, respectively. An occupation rate of less than two cows per weighing trough was assumed to be sufficient to prevent competition for feeding space. This assumption can be justified by the results of Ferris et al. (2006) who observed that, even at an occupation rate of four cows per feeding gate DMI was not compromised.

When, the Wageningen DCM is used for conditions which differ significantly from the conditions as outlined above (for example, on farms with animal health problems, heat stress, overcrowding and competition for feed, limited access to feed and breeds other than high-merit Holstein Friesians), feed intake and milk production may be overestimated.

6.6.1.1. Health disorders

At the current stage, the Wageningen DCM does not include factors related to incidence and type of health disorders and their influence on feed intake and milk production. Health disorders can have a large negative impact on feed intake and milk production. Therefore, the Wageningen DCM may overestimate feed intake and MEO when applied to dairy herds with a high incidence of production diseases. Bareille et al. (2003) estimated the initial and cumulative effects of production diseases (diarrhoea, mastitis, ketosis, hypocalcaemia, teat injuries, foot and hock lesions) during the first 140 days of lactation. Hypocalcaemia, ketosis, mastitis, diarrhoea, hock and foot lesions had a large initial effect on DMI (-15, -11, -7, -11 -6 and -6 kg DM/d, respectively). Difficult calving, ketosis, puerpal metritis, mastitis and hock lesions had a large total effect on DMI (-43, -46, -72, -48 and 48 kg DM, respectively). Hypocalcaemia, ketosis, mastitis and diarrhoea had a large initial effect on milk production (-26, -16, -12 and 15 kg milk, respectively) and twin calvings, hypocalcaemia, ketosis, teat injuries, mastitis, and hock lesions had a large total effect on milk yield (-124, -88, -155, 160, -109 and -77 kg milk, respectively).

6.6.1.2. Climatic conditions

The Wageningen DCM assumes thermo-neutral conditions. However, in practice, occasional high humidity and ambient temperatures may induce heat stress resulting in reduced feed intake and milk production. In maritime regions, MY declined with 0.26 kg/day per unit above THI=60 (THI calculated from hourly recorded temperatures and humidities) (Brugemann et al., 2012).

6.6.1.3. Breed

As outlined previous, the Wageningen DCM is developed for high-merit Holstein Friesian cows. In the Netherlands, approximately 88% of the dairy cattle is Holstein Friesian (CRV, 2012). The remainder 12% percent of the cattle is of different breeds with the largest proportion for Maas-Rijn-IJssel (MRIJ) cows (1%). A pragmatic solution would be the inclusion of scaling factors to adjust FIC and MEO of breeds other than high-merit Holstein Friesian. These scaling factors could be derived from comparative studies with different cattle breeds (e.g. Oldenbroek (1989) and Dillon et al. (2003)). Table 6.3 presents the FIC and MEO for different breeds relative to Holstein Friesian derived from Oldenbroek (1989) and Dillon et al. (2003). These relative differences in FIC and MEO may indicate that FIC of dual purpose breeds could be scaled down with 3 to 8 % and that energy corrected MY could be scaled down with 14 to 21 %. Applying these scaling factors for FIC and MEO would theoretically result in a reduced mobilisation of body reserves in dual purpose breeds. Indeed, dual purpose breeds with a lower genetic merit for milk production tend to lose less BW and body condition score (BCS) than Holstein Friesian cattle (Koenen et al., 2001; Dillon et al., 2003).

Table 6.3 Relative feed intake capacity (FIC) and energy corrected milk production (ECM) of different breeds relative to Holstein Friesian (=100) corrected milk production derived from Oldenbroek (1989) and Dillon et al. (2003)

	FIC	ECM
Oldenbroek, 1989)		
Holstein Friesian	100	100
Maas-Rijn-IJssel	92	83
Fries Holland	97	86
Jersey	78	81
(Dillon et al., 2003)		
Holstein Friesian	100	100
Montbeliarde	94	86
Norwegian Red	87	79
Irish Friesian	94	87

6.6.2. Diet composition and nutritional history

6.6.2.1. Nutrient partitioning

The Wageningen DCM predicts the partitioning of ingested NE_L (van Es, 1978) among essential life functions (maintenance and pregnancy), MEO and mobilisation of body reserves. At the current stage of development, the Wageningen DCM is not able to predict the effects of nutrient intake on milk nutrient output. As discussed in Chapter 4, diet composition may influence energy partitioning. MEO could be impaired when dietary protein nutrient supply is limiting (Coulon and Remond, 1991; Brun-Lafleur et al., 2010). However, under practical conditions, when diets are formulated according to metabolisable protein recommendations (Tamminga et al., 1994; van Duinkerken, 2011; CVB, 2012) a limiting effect of insufficient protein supply is unlikely.

Also other nutrients may affect MEO and mobilization. Compared to cows supplemented with concentrates high in lipogenic ingredients, cows supplemented with concentrates high in glucogenic ingredients, partitioned less energy to milk and mobilized less body reserves, whereas MY and milk protein yield were similar (van Knegsel et al., 2007). Furthermore, milk revenues and nutrient use efficiency also depend on the amounts and concentrations of milk, fat and protein. Therefore, it is of interest to predict the impact of nutrient intake on milk constituent yield and milk composition. Extension of the Wageningen DCM with the possibility to predict milk constituent yield and milk composition can be considered as an item for future improvement. Therefore, it is worthwhile to investigate whether it is possible to integrate the Wageningen DCM with the mechanistic model for milk production by dairy cows as proposed by Dijkstra et al. (2008). This mechanistic model is constructed from the mechanistic rumen model of Dijkstra et al. (1992) which describes nutrient fermentation, microbial growth and production of fermentation end products, using the stoichiometric equivalents of volatile fatty acid production of Bannink et al. (2006) and a model of Mills et al. (2001) describing post-ruminal digestion in the small and large intestine. This model predicts the profiles of volatile and long chain fatty acids, glucose, and amino acids available for absorption (Dijkstra et al., 2008). Subsequently, the utilization of absorbed nutrients is described following the approach of Dijkstra et al. (1996).

The Wageningen DCM can be used to provide predictions of DMI, nutrient intake, NE_L intake, MEO, the supply of energy from mobilisation of body reserves, BW change as input for the model of Dijkstra et al. (2008). The assumptions about energy use for maintenance and BW change as made by Dijkstra et al. (2008) could be replaced by model predictions from the Wageningen DCM.

6.6.2.2. Nutritional history and body reserves

The Wageningen DCM predicts that the effects of changes in feeding management on cow performance occur immediately, denying a possible time-lag and carry-over effects of previous feeding on the predicted the response in animal performance. However, in reality carry-over effects of the nutritional history of the animal (*i.e.* previous feeding management) on feed intake and milk production, BW change and BCS have been reported (Broster and Broster, 1984; Faverdin et al., 2007; Huhtanen and Hetta, 2012). In situations when carry-over effects of previous feeding could be expected, for example when diet composition and feeding level is changed dramatically, the predictions of the Wageningen DCM should be should be interpreted with care.

A well-known example of the impact of previous feeding management on cow performance is the effect of pre-partum feeding level on the intake and performance in early lactation. In an extensive review, Remppis et al. (2011) showed that cows overfed during the pre-partum period mobilize more body reserves than cows fed according to their requirements, resulting in a higher MEO for the overfed cows. Literature data also indicate that in early lactation, feed intake is more reduced in well-conditioned cows than in thin cows followed by a greater mobilization of body reserves (Remppis et al., 2011). This argues for a future extension of the Wageningen DCM model with factors that adjust FIC and MEO for body condition score. For example, Faverdin et al. (2011) included in their model a linear adjustment factor to correct FIC for BCS. This adjustment factor indicate that for each point above or below a BCS of 3 (on a 5 point scale), FIC is reduced or increased by a factor of 0.09.

The Wageningen DCM has no limits on the simulated amounts of body energy that can be mobilized and neither on the rate of mobilization. However, in reality, the amount of body reserves which can be mobilised depends on the BCS at calving (NRC, 2001; Schröder and Staufenbiel, 2006). Therefore, the simulated amount of mobilized energy should be used as an indicator to assess whether a feeding strategy is feasible rather than for quantification of the loss of body reserves. A future extension of the model could be the inclusion of limits for the maximum amount and rate of mobilisation of body reserves. Friggens et al. (2004) suggested a maximum fat mobilisation rate of 1.75 kg fat per day. Schröder and Staufenbiel (2006) estimated that the loss of 1 point in BCS (on a 5 point scale) compares with approximately 50 kg body fat. Thus, theoretically, when the BCS drops from 5 to 2 a cow would mobilize 200 kg of body fat. This amount of body fat equals an amount of NE_L sufficient for the production of 2000 kg of FPCM. However, such a severe loss of body reserves is associated with an increased risk for health disorders (Roche et al., 2009). In an ideal situation, cows should calf with an BCS between 3 and 3.5 and BCS should not fall below 2.5. For practical conditions, it is probably safe to use a maximum mobilisation of 2400 MJ NE_L, which compares with the mobilisation of approximately 75 kg of fat.

6.6.2.3. Grazing

Although, the proportion of cows that are grazed on pasture is declining, grazed grass is a major feed source in the Netherlands and North West Europe (CBS, 2013; Reijs et al., 2013). However, the Wageningen DCM is parameterized using data from indoor fed cows. Therefore, application of the Wageningen DCM for grazing conditions is certainly outside the conditions of the underlying datasets. Feed intake and feeding behaviour in confinement systems differs considerably from grazing. Intake at grazing is not only determined by the cows' FIC and by the properties of the grazed grass (SV, composition, digestibility), but also by the edible herbage allowance (HA) (kg DM/cow/d). The edible HA is a function of the herbage mass and the proportion of herbage that is acceptable for the cow. The effect of HA on herbage intake at grazing (HDMI) is curvilinear (Marsh and Murdoch, 1974; Zemmelink, 1980; Poppi et al., 1987; Delagarde et al., 2001). Only at very high levels of HA, HDMI is restricted by the properties of the grazed grass, the level of supplementation and the cows' FIC. When the sward is grazed down, HA declines as result of the consumption of herbage, formation of rejected areas around dung and urine spots, contamination of herbage with soil due to trampling and poaching. As HA declines, the sward becomes more difficult to graze resulting in a declining intake, and reduced substitution of grass by supplemental feeds. Zemmelink (1980) proposed the following equation to describe the curvilinear relation between HDMI and HA:

$$\mathrm{HDMI}=\mathrm{DMI_S}\times\left\{1\text{-}e^{-\left(p\times\frac{\mathrm{HA}}{\mathrm{DMI_S}}\right)^{1.23}}\right\}^{\left(\frac{1}{1.23}\right)}$$

In which, p is the proportion of edible grass (= 1-proportion rejected herbage), HA is the herbage allowance (kg DM/cow/day) above the target post-grazing sward height of 4.5 cm and $\mathrm{DMI_S}$ is the unrestricted standard DMI intake. The equation of Zemmelink (1980) can be integrated with the Wageningen DCM by calculating the $\mathrm{DMI_S}$ according to the feed intake model of the Wageningen DCM as proposed by Zom and Holshof (2011).

$$\mathrm{DMI_S}=(\mathrm{FIC}\ \text{-}\sum_{n=i}\mathrm{sDMI_i}\times\mathrm{sSV_i})/\mathrm{SV_{grass}}$$

Where FIC is the feed intake capacity and sDMI_i is the dry matter intake of supplement *i*, sSV_i is the satiety value of supplement i and $\mathrm{SV_{grass}}$ the satiety value of the grazed grass. The incorporation of the equation of Zemmelink (1980) in the Wageningen DCM would allow to simulate the effects of HA, supplementation and animal characteristics on grass utilization, substitution grass by supplementation and animal performance. This application is demonstrated in Figure 6.4 which shows the effects of HA on DMI, herbage utilisation (herbage grazed as proportion allowance) and substitution rate of a concentrates supplement. Figure 6.5 displays the results of a simulation of the impact of daily herbage allowance, concentrates supplementation and stage of lactation on grass DMI, MEO and energy balance. However, further research on the validity and accuracy of the Wageningen DCM for grazing conditions is required.

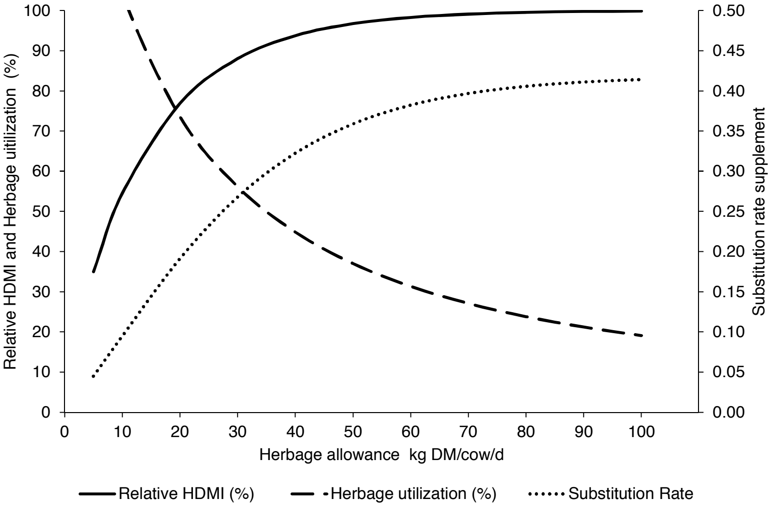


Figure 6.4 Simulation of herbage allowance on relative herbage dry matter intake (HDMI % of maximum unrestricted intake, left Y-axis), herbage utilization (herbage grazed as % of herbage allowance, left Y-axis), and substitution rate of concentrates (right Y-axis)

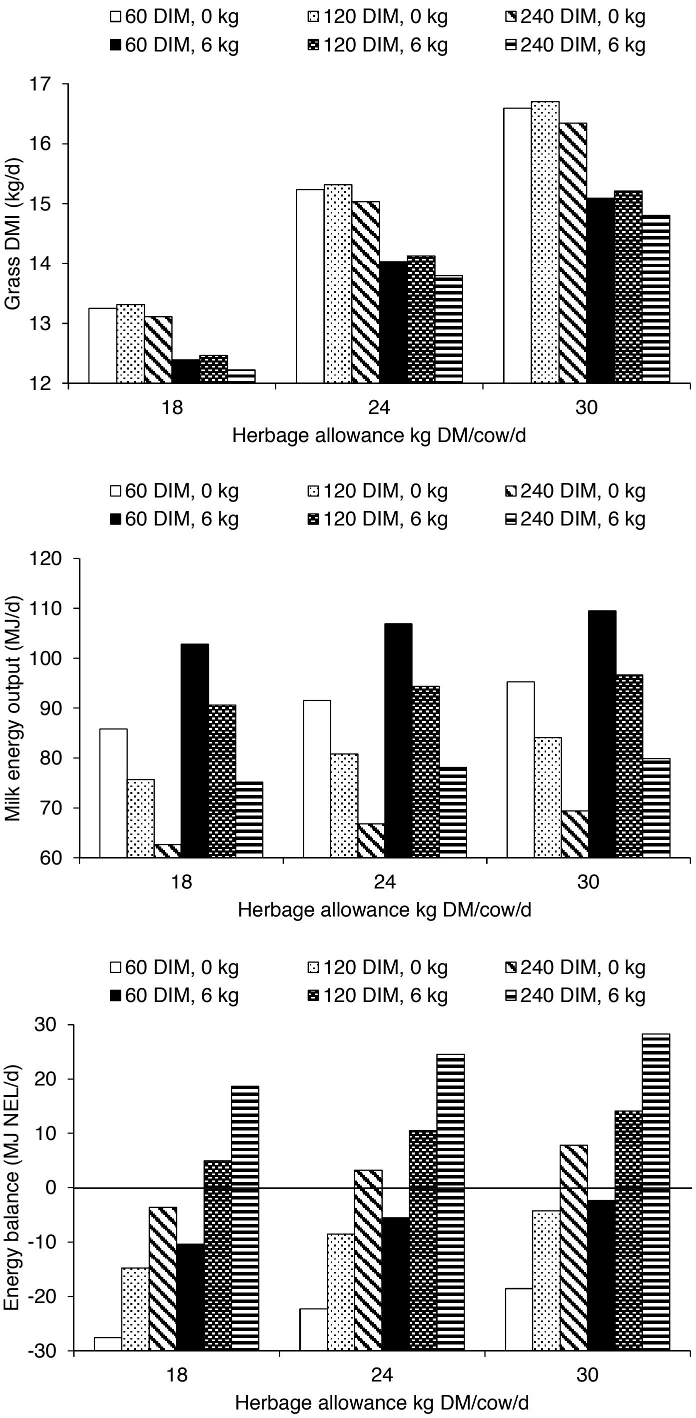


Figure 6.5 Simulation of the effect of three levels of herbage allowance (18, 24, 30 kg DM/cow/day) and two levels of concentrates supplementation (0 and 6 kg DM/day) at 3 stages of lactation (60, 120 and 240 days in milk, DIM) on Grass Dry Matter Intake (upper panel), Milk energy output (middle panel), and Energy balance (lower panel)

6.7. Practical application

6.7.1. The dairy cow as key component in a Dairy Farm system

The Wageningen DCM can be used to simulate a variety of feed and management strategies for dairy herds with the individual dairy cow as the key component. The predictions of feed, nutrient and NE_L intake and partitioning of ingested NE_L, BW and BW change are performed on a daily basis. The required feed related inputs can be obtained from different sources such as results of feed analysis, table values (e.g. (CVB, 2012)), or model predictions (e.g. grass growth model (Schils et al., 2007)). The Wageningen DCM predicts cow performance for 144 different cows representing pregnant and non-pregnant cows for individual in lactation cycles 1 to 6 and 12 different months of calving (2×6×12=144). Calving pattern (number of calvings per month), the age structure (proportion of cows per lactation number) calving interval and lactation length can be obtained from the actual herd data defined by the user. The outputs are (on daily basis) energy and nutrient intake, MEO, mobilisation of body reserves and BW.

In its current state, the Wageningen DCM performs deterministic predictions. Stochastic simulations could be also possible. However, this would require probability distribution functions with their respective parameters of input variables which are allowed to behave stochastically. Input variables which remain constant, such as composition of preserved forages, age structure and month of calving could be set stochastically at the start of each simulation run. Input variables which are variable during a time span and progress of lactation, may be allowed to behave stochastically during simulation, such as grass quality and supply, pregnancy, involuntary culling, milk and feed prices. Stochastic simulations would require multiple model runs to simulate cow and herd performance at different feed and farm strategies under variable external conditions. This can be useful to test the risks associated with feed and farm strategies.

6.7.2. Target groups and potential users

The Wageningen DCM can be applied for strategic purposes to provide insight into the long term effects of single and multiple interventions in feeding and dairy herd management on the performance of specific groups of cows within a herd, for whole dairy herds and for groups of dairy herd herds within a region, rapidly. The model can be applied by farmers and advisors for planning, feed budgeting and evaluation of different farm strategies such as comparison of different forage and forage and concentrates allocation strategies (Chapter 5), the effect of replacement rates and herd structure. The Wageningen-DCM can be used to set outlines for applied research, extension and education, as it can estimate the direction and potential of different theoretical feeding and animal management options, and test the feasibility and possible limits of these strategies. The Wageningen DCM can be used by policy makers to study the effect of political interventions and spatial planning on land use, farmers income and environmental impact of dairy farming within specific regions or type of farms.

6.7.3. Practical application of the Wageningen DCM

The application of the Wageningen DCM is demonstrated by the next brief example where different feeding and farm management strategies are simulated. In the Netherlands, until 2013, dairy farmers having at least 70% of their farmland in grassland can apply for a derogation which allow them to fertilize their grassland with a maximum of 250 kg N from manure hectare. However, from 2014 onwards, farmers should have at least 80% of their farmland in grassland if they want to apply for this derogation. The average DM yields of maize silage are higher than the DM yields of grass (16286 vs. 11133 kg DM/ha, CBS (2013)). In addition, maize silage has a higher NE_L and lower protein concentration than grass silage. Therefore, it can be expected that reduction of the proportion of maize silage may have some trade-offs in terms of animal performance and feed budgets. A farmer has several options to adapt his farm strategy. One strategy could be to reduce nitrogen input from concentrates to compensate for the higher intake of nitrogen from grass silage (LNC). A second strategy could be to increase the concentrates input to compensate for the reduced energy intake in order to achieve the same level of milk production (HCI). Because of the substitution of forage by concentrates, this strategy would at same time also compensate for the reduced forage production. The third strategy is to reduce the replacement rate of dairy cattle (RRR). A lower replacement rate would result in higher MY per cow, and a lower forage consumption because of a lower number young stock. For all strategies the same fixed feeding system was used for young stock based on the recommendations of the CVB (2012). Furthermore, it was assumed that young stock received a diet with the same maize silage to grass silage ratio as the dairy cows. The summarized results show the impact of reducing silage maize production on the feed budgets, MY, and land use (Table 6.4). These results indicate that a smaller proportion of maize silage in the ration would result in a lower FPCM and a higher excretion of total N and Total Ammoniacal Nitrogen (TAN, Velthof et al., 2012) per cow. The excreted TAN, which consists of ammonium-N and N compounds that are readily broken down to ammonium, is prone to volatilization as ammonia (Velthof et al., 2012). Furthermore, because of the lower DM yield of grass compared to silage maize, the potential FPCM production per hectare will decrease. A reduction of the FPCM yield per cow and per hectare can be avoided by increasing the concentrate input (HCI). However, this is associated with an increased nitrogen intake excretion compared to the standard situation (S) and LNC. Reduction of the replacement rate from 30 to 20% results in an increased FPCM yield per cow and per hectare, and a lower feed consumption (fewer number of rearing calves and heifers), compared to LNC an HCI, without negative consequences on nitrogen excretion. This suggest that reducing the replacement rate has a high potential to improve the efficiency of dairy farms. The example of the strategies presented in table 6.4 demonstrates also that the Wageningen DCM can be applied by farmers and advisors for planning, feed budgeting and evaluation of different farm strategies to adapt changing conditions. Model simulations can be used to for education and extension to demonstrate the impact of farm management and to set priorities in applied research. The example of the Wageningen DCM also demonstrates that can be applied by policy makers to evaluate the effect of political interventions (i.e. changes in derogation legislation) on land use, farmers income and the impact of dairy farming on the environment.

Management interventions, such as reducing silage maize production, may have a cascading effect through different levels of farm system (crop production, labour requirements, housing, feed storage etc.). To investigate, these effects the model outputs could be used as inputs for other models. For example, models that calculate production of manure and nutrient excretion which in turn could be an input (fertilization) for a crop growth model and nitrate leaching models. The Wageningen DCM could also provide input for models predicting the emissions of methane and ammonia.

Table 6.4 Simulation of the effects of a reduction of the proportion of farm land used for silage maize from 30 to 20% on cow and herd level.

Strategy[1]	S	LNC	HCI	RRR
Maize silage % of farm land	30	20	20	20
Replacement rate[2]	30	30	30	20
FPCM (kg/cow/305d)[3]	8603	8469	8604	8631
Total DMI (kg/cow)[4]	7989	7878	8025	7566
Low protein concentrates (kg DM/cow)[5]	1693	1873	2121	1873
High protein concentrates (kg DM/cow)[6]	180			
Total Forage intake (kg DM/cow)	6114	6005	5904	5693
Maize silage (kg DM/cow)[7]	2385	1621	1594	1537
Grass silage (kg DM/cow)[8]	3730	4384	4310	4156
NE_L/MJ (kg DM)	6.79	6.75	6.79	6.74
dCP intake (kg)[9]	817	836	859	814
Nitrogen intake (kg/cow)[10]	200	205	210	196
Nitrogen in milk (kg/cow)[10]	45	44	45	45
Nitrogen excreted (kg/cow)[10]	69	71	72	65
Nitrogen retention (kg/cow)[10]	5	5	5	4
Total Ammoniacal N (TAN) (kg/cow)[11]	81	84	87	81
Silage maize silage hectare/cow[12]	0.15	0.10	0.10	0.10
Grass hectare/cow[12]	0.34	0.40	0.39	0.38
Potential FPCM yield/ha farm land[13]	17610	16933	17540	18305

[1] Strategy S is the standard situation with 30 % silage maize. Strategy LNC reduced nitrogen input from concentrates to compensate for the higher intake of nitrogen from grass silage. Strategy HCI increases the concentrates input to compensate for the reduced energy intake. Strategy RRR reduced the replacement rate of dairy cattle to reduce feed requirements.

[2] The percentage of dairy cows replaced by dairy heifers, [3] FPCM is fat and protein corrected milk 4% fat and 3.33% protein with an energy concentration of 3.05 MJ NE_L/kg, [4] Total dry matter intake net consumption of feed including young stock, not corrected for feeding and conservation losses. [5] Low protein concentrates 7.18 MJ NE_L, 187 g CP, 114 g DVE, 134 g dCP, 2 g OEB per kg DM, [6] High protein concentrates 7.18 MJ NEL, 329 g CP, 194 g DVE, 179 g dCP, 75 g OEB per kg DM, [7] Maize silage 6.88 MJ NEL, 337 g NDF, 360 g starch, 72 g CP, 51 g DVE, 32 g dCP, -35 g OEB per kg DM,[8] Grass silage 6.22 MJ NEL, 490 g NDF, 170 g CP, 63 g DVE, 123 g dCP, 40 g OEB per kg DM,[9] digestible crude protein intake, calculated according to CVB (2012), including 3 and 10% feed and conservation losses of concentrates and silages, respectively. [10] Calculated intake including feed and conservation losses. [11] TAN; ammonium-N + N compounds readily broken down to ammonium (Velthof et al., 2012), [12] Including 10% feed and conservation losses.[13] Calculated as FPCM yield/cow divided by the sum of acreage (ha) of silage maize and grass

It has been suggested that predicted voluntary feed intake could be used to calculate concentrates allowances at the individual cow level (Hijink and Meijer, 1987). The daily concentrates allowance could be calculated from the predicted energy intake from the diet minus the requirements based on production and BW. However, the model for prediction of voluntary DMI with Wageningen DCM accounted for 62% of the individual variation in DMI (s.d. 1.8 kg DMI), and therefore the model should be preferably used for sufficient large groups of cows (Chapter 2). In addition, André et al. (2010) showed that there is a large variation in milk response to concentrates intake between individual dairy cows. The standard feed requirement systems for dairy cattle do not account for this individual variation in biological efficiency between and within individual dairy cows. Therefore, André et al. (2011) developed an adaptive model which calculates individual concentrates supplementation based on the actual individual cow response in MY and financial returns. This approach to calculate concentrates allowances for individual cows should be preferred.

6.8. General conclusions

The thesis presents the Wageningen UR Dairy Cow Model (Wageningen DCM) which is an empirical deterministic model for the prediction of feed intake and partitioning of ingested net energy, and BW in lactating Holstein Friesian cows. The Wageningen DCM is easy to operate since it requires only easy-to-measure animal and feed related inputs and provides a rapid insight into the effects of a variety of different feeding and herd management strategies on the performance of dairy cows and dairy herds.

The modular structure of the Wageningen DCM creates a high degree of flexibility which enables easy extension and modification. The use of a large dataset with information on individual cow performance covering a wide range of different rations and individual cows different in parity and stage of lactation allowed calibration and validation of an empirical dairy cow-model which can applied in a broad diversity of cows and feeding management conditions.

Although the Wageningen DCM is not explicitly designed to describe the underlying metabolic and physiological mechanisms, the predictions of dairy cow performance allow a reasonable biological interpretation. The intake constraining characteristics of feeds, expressed in terms of satiety values, are related to the chemical composition and digestibility of the feed and can be linked to physical and metabolic factors regulating feed intake. The system assumes that there are no additive effects between feeds. This assumption is valid when diets and rations are formulated according to standard feed evaluation systems and practical recommendations for diet composition.

The Wageningen DCM uses lactation number, days in milk and days pregnant as physiological time related drivers of changes in FIC, BW and partitioning of energy to milk and body reserves. The Wageningen DCM is able to generate realistic trajectories of FIC, BW, and energy partitioning which can be explained from the concept of homeorhetic control of lactation.

Evaluation of the Wageningen DCM on the basis of statistical criteria indicate that the model is able to provide accurate predictions of feed intake and MEO for a range of various feeding and management conditions. The validity and accuracy of the Wageningen DCM for grazing dairy cows, however, remains to be tested.

At the current state of development of the Wageningen DCM, milk production is predicted as MEO. Further research is required to extent the model in order to predict MY and milk constituents yields.

The Wageningen DCM can be applied for farm planning, feed budgeting, evaluation of the effects of different farm strategies on cow and herd performance. Therefore, the Wageningen DCM can be a useful tool for assisting farmers, farm advisers extension officers and policy makers, but also for education purposes and as a tool to set outlines for applied research.

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Summary

A dairy farm is a complex system that consists of the feed production and the animal production sub-system. The feed production sub-system consists of the farmland for grass and forage crops. The animal production sub-system consists of the dairy herd, which converts on-farm produced and purchased forage and concentrates into animal growth (meat), milk, manure and gaseous emissions. Management decisions made at the level of the feed production sub-system, such as cropping plan, application of fertiliser and harvest strategies can have a large impact on the yields and nutritive values of the on-farm produced forages. In turn, the yields and nutritive values of the on-farm produced forage determines the ration, feed intake, feed budgets, essential purchase of forage and concentrates and finally the outputs in terms of milk yield, culled cattle and excretion of manure and emissions of ammonia and methane.

Balancing the supply of feeds and nutrients from the feed production sub-system with the production targets of the animal production sub-system is a crucial aspect of farm management. This involves optimization of feeding strategies, allocation of available feeds and inclusion of purchased concentrate supplements, in order to obtain the best compromise between different targets of the animal production system such as animal health and milk performance, nutrient use efficiency, mineral excretion, gaseous emissions, and profitability. Therefore, a dairy cow model which provides a rapid insight of the impact of the ration, feed quality and feeding management on feed intake and performance of dairy cows is a useful tool to optimise overall production.

In the Netherlands, Hijink and Meijer were the first to recognize the value and importance of such an animal model. In 1987, Hijink and Meijer developed the Cow-model ("Koemodel") for the simulation of feed intake and energy partitioning in dairy cows. The Cow-model required only a limited number of inputs, was easy to operate and provided the user with clear interpretable information. As a result, the Cow-model has gained a widespread use as a tool to support strategic decision making on dairy farms, for extension and education, and to set the outlines of applied research. However, the Cow-model lacked flexibility and some assumptions have been disputed because they did not match practical farm situations or were not valid from a biological point of view. The major disadvantage of the Cow-Model has been that it was not a truly predictive model. Feed intake and amounts of body energy available for mobilisation were determined by the potential or target 305-d milk yield which was an input for the model. The limitations of the Cow-model called for an improved model for the prediction of feed intake and performance in dairy cows. Existing models were deemed inappropriate for various reasons amongst which that they were not tailor made to the conditions of dairy farming using high merit Holstein Friesian cows.

This PhD study was undertaken to develop an alternative animal model that could replace the Cow-model of Hijink and Meijer. This improved model, referred to as the Wageningen UR Dairy Cow Model (Wageningen DCM), should be able to provide accurate predictions of feed intake, milk production, body weight and body weight change in dairy cows under a wide range of management and feeding practices on commercial farms. In addition, the Wageningen DCM should allow a reasonable biological explanation, be flexible and easy to modify and maintain.

In order to create the desired flexibility, the Wageningen DCM was designed to have a modular structure. This modular design consists of two sub-models: a feed intake model (FIM) and a model for the partitioning of ingested net energy, respectively.

In Chapter 2, a large calibration dataset was used for the parameterization of the FIM. This dataset contained 38515 records of 1507 lactating Holstein Friesian dairy cows with the weekly means of individual voluntary feed intake, milk yield, milk composition, parity, days in lactation and days pregnant together with information on diet composition and feed analysis.

The FIM was based on the principles of a fill-unit system. Fill unit systems use separate equations to describe the feed intake capacity and separate equations to describe the intake constraining effects of feeds. The intake constraining effects of the feeds were expressed as the satiety value. Data obtained from routine feed analysis were used to estimate the satiety values for numerous commonly used feeds and forages. The feed characteristics which determine the satiety value of a feed were directly or indirectly related to digestibility, bulk volume, intake rate, palatability and other factors that play a role in physical or metabolic regulation of feed intake. The feed intake capacity expresses the cows' ability to process the intake-limiting satiety value and is predicted from parity, days in milk and days of pregnancy which are indicators of the size and physiological state of the cow. Because the model inputs to predict feed intake are not related to animal output (milk yield or body weight), the FIM can be integrated with models for the prediction of animal performance.

In Chapter 3, the accuracy and robustness of the FIM was evaluated and compared with five other commonly used feed intake models. The evaluation was performed using an independent dataset, different from the dataset used in Chapter 2 and containing 8974 weekly means of dry matter intake (DMI) from 348 individual cows observed in 6 feeding experiments including a wide range of diets and management practices. Sub-datasets were formed by combining the DMI data by experiment, lactation number, lactation week, and maize silage to grass silage ratios in order to compare the accuracy of the intake models for different feeding practices and groups of cows using mean square prediction error and relative prediction error (RPE) as criteria. Compared to five other models, the FIM was most accurate as indicated by a low mean bias, mean square prediction errors and relative prediction errors across all evaluation data subsets, indicating that the FIM is robust and can be applied to various dairy rations and cows of lactation number, stage of lactation and pregnancy. The results show that accurate predictions of DMI are possible without the use of animal performance (e.g. milk yield, body weight) as inputs. Random error as proportion of mean square prediction error for individual cows was large across all models. This may indicate that these models are likely better suited for prediction of the DMI of groups of cows than for individual cows.

In Chapter 4, the second module of the Wageningen DCM, dedicated to the partitioning of the ingested net energy (NE_L) to milk energy and body reserves, has been described. The dataset used to calibrate the energy partitioning model (EPM) comprised 20467 records with the complete weekly means of DMI, NE_L intake, diet formulation, nutrient composition, milk yield and composition, body weight, day in lactation, days pregnant and parity number from 1294 individual HF cows from 26 feeding experiments.

The EPM describes the baselines of daily NE_L intake, the unavoidable NE_L requirements, milk yield, milk fat and protein concentration, body weight and milk energy output during successive lactation cycles of the average cow with the average NE_L intake. This average cow is defined as the 'reference cow'. The deviation of NE_L intake from the baseline is used to estimate the changes in milk energy output. A NE_L intake above the baseline results in increased milk energy output and, depending on stage of lactation, reduced mobilization or increased deposition of body energy reserves. In contrast, a NE_L intake below the baseline results in a reduced milk energy output and increased mobilization or reduced deposition of body reserves. In the model, the proportion of ingested NE_L partitioned to milk increased with parity number, but declined with increasing days in lactation and energy intake, reflecting the changes in priority in energy partitioning between and within successive lactation cycles of a dairy cow. This resulted different in lactation curves and responses in milk energy output and body energy to variation in NE_L intake for cows different in lactation number, stage of lactation and pregnancy.

The EPM predicts milk energy output and changes in body reserves in response to changes in energy intake and can be predicted using easily quantifiable input parameters. Comparison of model simulations with literature data, indicated that the model predicted realistic changes in milk yield and body reserves throughout successive lactations of dairy cows. It was concluded that the EPM provides a basis for integration with feed intake models in order to develop a dairy cow model.

Chapter 5 is dedicated to the integration of the FIM and EPM into the Wageningen DCM. Dry matter and NE_L intake predicted with the FIM are used as inputs for the EPM. Simulation of different feeding strategies (different levels of concentrate feeding, distribution of concentrate and allocation of forage over the lactation) for pregnant and non-pregnant cows of different lactation number showed that the Wageningen DCM is sensitive to cow effects (stage of lactation, pregnancy and lactation number) × feeding management interactions. The Wageningen DCM was able to predict on a daily basis and for the whole lactation period, DMI, subsequent NE_L intake and simultaneously the direct effects of NE_L intake on milk energy output and changes in energy reserves in dairy cows.. The simulated effects of changes in NE_L intake and concentrate supplementation on milk energy output agrees with data from literature. External validation showed a good accuracy of the prediction of DMI and milk energy output for early and mid-lactation (0-30 weeks of lactation) dairy cows with relative prediction errors below 0.10. The overall accuracy of the prediction of DMI and milk energy output during complete lactations was acceptable with relative prediction errors of 0.10. It was concluded that the Wageningen DCM is suitable as a tool for strategic decision making, evaluation of long term feeding strategies and formulation of rations for groups of dairy cows.

The General discussion (Chapter 6) addresses several aspects of the modelling approach, model structure, assumptions, limitations, potential? improvements and the practical application of the Wageningen DCM. The desire for a simple, robust easy to operate model to simulate feed intake and performance of dairy cows under practical conditions, together with the availability of large datasets covering a wide range of feeding practices justifies the empirical modeling for the Wageningen DCM. The modular structure of the Wageningen DCM creates a high degree of flexibility which enables easy extension and modification. The use of a large dataset with information on individual cow performance covering a wide range of different rations and Holstein Friesian cows differing in parity and stage of lactation allowed calibration and validation of an empirical dairy cow-model which can be applied to a broad diversity of cows and feeding management conditions.

The Wageningen DCM is able to generate realistic trajectories of feed intake capacity, body weight changes, and energy partitioning which can be explained from the concept of homeorhetic control of lactation. The Wageningen DCM assumes that there are no additive effects between feeds. This assumption is valid when diets and rations are formulated according to standard feed evaluation systems and practical recommendations for diet composition. Evaluation of the Wageningen DCM on the basis of statistical criteria indicated that the model is able to provide accurate predictions of feed intake and milk energy output for a range of feeding and management conditions. The validity and accuracy of the Wageningen DCM under grazing conditions, however, remains to be tested.

At the current state of development of the Wageningen DCM, milk production is predicted in terms of milk energy output. It was suggested that further research is required to extent the model in order to predict milk yield and milk constituent yields. Furthermore, research is needed on aspects related to the nutritional history of the cow in the Wageningen DCM and the application for breeds other than Holstein Friesian.

It was concluded that the Wageningen DCM can be applied for farm planning, feed budgeting, evaluation of the effects of different farm strategies on cow and herd performance. Therefore, the Wageningen DCM can be a useful tool for assisting farmers, farm advisers extension officers and policy makers, but also for education purposes and as a tool to set outlines for applied research.

Samenvatting

Een grondgebonden melkveehouderijbedrijf bestaat uit een ruwvoer productie en een dierlijk productie (sub)systeem. Het ruwvoerproductiesysteem omvat de beschikbare grond voor de teelt van gras en voedergewassen. Het andere subsysteem is de veestapel, waarin het geproduceerde ruwvoer wordt omgezet in melk, dierlijke aanwas, mest en gasvormige emissies zoals ammoniak en methaan. Dit lijkt op het eerste gezicht simpel, maar het is in werkelijkheid is een stuk ingewikkelder. De teeltwijze, bouwplan, bemesting en oogsttijdstip kunnen een grote invloed de opbrengst en de voederwaarde van de ruwvoeders (gras en voedergewassen) hebben. De hoeveelheid en voederwaarde van de verschillende geproduceerde ruwvoeders is weer bepalend voor de rantsoensamenstelling, voeropname, de aankoop van krachtvoer en uiteindelijk de productie van melk, dierlijke aanwas uitscheiding van mest en mineralen en de uitstoot van ammoniak en methaan.

Het afstemmen van de ruwvoerproductie op de productiedoelstellingen van de veestapel is een cruciaal aspect van de bedrijfsvoering op een melkveebedrijf. Hierbij gaat het om optimaliseren van voerstrategieën, samenstellen van rantsoenen en verdelen van het beschikbare voer over de veestapel om het beste compromis te bereiken tussen melkproductie, diergezondheid, uitscheiding van mest en mineralen, emissies van ammoniak en methaan en de winstgevendheid. Een model van de melkkoe dat snel de effecten van het rantsoen en de voersamenstelling op de productie van de koe geeft is daarbij onmisbaar.

In Nederland, waren Hijink en Meijer de eersten die de waarde en het belang van een een dergelijk koemodel hebben ingezien. In 1987, hebben zij daarom het “Koemodel” ontwikkeld; een model waar mee de voeropname en de verdeling van de opgenomen netto energie (VEM) kon worden gesimuleerd. Het Koemodel vraagt weinig invoergegevens, is gemakkelijk te gebruiken en geeft een eenduidige, gemakkelijk te begrijpen uitvoer. Dit heeft geresulteerd in een wijd verbreide toepassing op veehouderijbedrijven, bij de landbouwvoorlichting, het onderwijs en in het praktijkonderzoek. Echter, het Koemodel was rigide en sommige aannames in het Koemodel kwamen ter discussie te staan omdat ze niet overeenstemden met de hedendaagse melkveehouderij of geen verklaarbare fysiologische achtergrond hadden. Het belangrijkste nadeel van het Koemodel was dat het niet een echt voorspellend model is. In het Koemodel zijn de voorspelde voeropname en de beschikbare hoeveelheid energie voor mobilisatie namelijk afhankelijk van de potentiële melkproductie die door de gebruiker moet worden ingevoerd.

Deze beperkingen van het Koemodel vroegen om de ontwikkeling van een verbeterd model voor het voorspellen van de voeropname en melkproductie van melkkoeien. Bestaande modellen bleken geen goed alternatief, omdat ze niet aansloten bij de hedendaagse melkveehouderij. Daarom werd een studie gestart naar de ontwikkeling van een nieuw model ter vervanging van het Koemodel. Dit alternatieve model, genaamd het Wageningen UR Melkkoe-Model (Wageningen DCM) zou goede voorspellingen moeten geven van de voeropname, melkproductie en gewichtsveranderingen van melkkoeien bij een groter variëteit in rantsoenen en voerstrategieën op melkveehouderijbedrijven. Tevens, zouden de voorspellingen met het Wageningen DCM een betere fysiologische achtergrond moeten hebben. Daarnaast zou het model flexibel moeten zijn met betrekking tot toekomstige aanpassingen en verbeteringen. Met dit pakket aan eisen is een promotieonderzoek gestart voor het ontwikkelen van het Wageningen DCM. Hierbij is gekozen voor een modulaire structuur met twee sub-modellen: een voeropnamemodel en een energieverdelingsmodel.

In hoofdstuk 2 is de ontwikkeling van het voeropnamemodel beschreven. Dit voeropnamemodel is gekalibreerd op basis van 38.515 weekgemiddelden van de voeropname, lactatienummer, dagen in lactatie en dagen drachtig van 1.507 individuele koeien met daarbij de gegevens van de rantsoensamenstelling en de samenstelling afzonderlijke voedermiddelen in het rantsoen. Het voeropnamemodel is gebaseerd op basis van het principe van de zogenaamde vulwaardesystemen. Deze systemen schatten met afzonderlijke formules de vulwaarde van het voer en de voeropnamecapaciteit van de koe. De vulwaarde geeft aan in welke mate het voer beslag legt op de voeropnamecapaciteit van de koe. Deze vulwaarde wordt in het Wageningen DCM uitgedrukt als verzadigingswaarde. Een hoge verzadigingswaarde betekent dat een voedermiddel veel beslag legt op de voeropnamecapaciteit. Een hoge verzadigingswaarde resulteert dus in een lagere opname. De verzadigingswaarde wordt geschat op basis van droge stofgehalte, ruw eiwit gehalte, ruwe celstofgehalte, en/of verteerbare organische stof. Deze voerfactoren kunnen direct of indirect worden gelinkt aan verteerbaarheid, volume van het voer, smakelijkheid en andere factoren die een rol spelen bij de fysieke en metabole regulatie van voeropname. De voeropnamecapaciteit geeft aan in welk mate een koe in staat is om de verzadigingswaarde eenheden te verwerken. De voeropnamecapaciteit is afhankelijk van het fysiologische status van de koe. De fysiologische status van de koe wordt bepaald door het lactatienummer, het stadium van de lactatie (dagen na afkalven) en dracht (dagen drachtig). Omdat de voeropnamecapaciteit niet is gerelateerd aan de melkproductie of het gewicht van koe is het mogelijk om het voeropnamemodel te integreren met een model dat de productie van melkkoeien kan voorspellen.

Hoofdstuk 3 behandelt de validatie van het voeropnamemodel. Op basis van een onafhankelijke dataset met de gegevens van 6 voederproeven met 8.974 week gemiddelden van de voeropname van 348 koeien is de voorspelnauwkeurigheid van het voeropnamemodel onderzocht en vergeleken met andere voeropnamemodellen. Het voeropnamemodel bleek in vergelijking met de andere modellen het meest nauwkeurig te zijn met de laagste gemiddelde afwijking, de laagste mean square prediction error (MSPE) en mean prediction error (MPE). De resultaten gaven aan dat nauwkeurige schatting van de voeropname mogelijk is zonder melkproductie of gewicht als verklarende variabelen.

Hoofdstuk 4 is gewijd aan de ontwikkeling van het energieverdelingsmodel, de module van het Wageningen DCM die de verdeling van de opgenomen netto energie (VEM) naar melkproductie en lichaamsreserves beschrijft. Hiervoor is een dataset gebruikt bestaande uit de 20.467 weekgemiddelden van energieopname melkproductie, gewicht, lactatienummer, dagen in lactatie en dagen drachtig van 1.294 HF koeien afkomstig van 26 voederproeven. Het energieverdelingsmodel beschrijft baselines van de energieopname, melkproductie en de onvermijdelijke energiebehoefte voor groei, onderhoud en mobilisatie gedurende opeenvolgende lactaties van de gemiddelde koe in de populatie. Deze gemiddelde koe is gedefinieerd als de referentiekoe. De afwijking in energieopname opname ten opzichte van de baseline van de referentie wordt gebruikt om de afwijkingen in meetmelkproductie ten opzichte van de referentiekoe te schatten. Neemt een koe meer energie op dan de referentiekoe, dan zal dat resulteren in een hogere voorspelde meetmelkproductie en een verminderde mobilisatie (of een hogere aanzet) ten opzichte van de referentiekoe. Wanneer een koe minder energie opneemt dan de referentiekoe, dan zal dat resulteren in een lagere hogere voorspelde meetmelkproductie en een hogere mobilisatie (of een geringere aanzet) ten opzichte van de referentiekoe. De hoeveelheid extra opgenomen energie die naar melkproductie wordt gestuurd is afhankelijk van het lactatienummer, lactatiestadium en drachtigheid. Bij hogere lactatienummers (oudere koeien) wordt een groter deel van de extra opgenomen energie richting melkproductie gestuurd. Dit komt omdat deze oudere koeien minder energie nodig hebben voor groei. Bovendien hebben oudere koeien een grotere hoeveelheid lichaamsreserves die zij kunnen aanwenden voor melkproductie. Naarmate de lactatie vordert wordt een steeds kleiner deel van de energie naar melkproductie gestuurd. Dit komt omdat in het begin van de lactatie de koe eerst lichaamsreserves mobiliseert. Deze lichaamsreserves worden later in de lactatie weer hersteld. Bij drachtige koeien gaat een geringer deel van de extra energie naar melkproductie dan bij niet-drachtige koeien, omdat ook energie nodig is voor dracht. Deze verschillen in energieverdeling tussen koeien van verschillende leeftijd, lactatiestadium en drachtigheid weerspiegelen de veranderende prioriteiten in energieverdeling als gevolg van de fysiologische status van de koe.

Een vergelijking van de resultaten van modelsimulaties met literatuurgegevens liet zien dat het energieverdelingsmodel in staat is om realistische voorspellingen van de energieverdeling te geven. Er werd geconcludeerd dat het energieverdelingsmodel een goede basis verschaft voor de verdere integratie met het voeropname model in een volledig koemodel.

Hoofdstuk 5 is gewijd aan de integratie van het voeropnamemodel met het energieverdelingsmodel in het Wageningen DCM. De energieopname voorspeld met het voeropnamemodel wordt gebruikt als een invoer voor het energieverdelingsmodel. Om na te gaan of het model een realistische beschrijving geeft van de effecten van voeropname op de productie zijn verschillende rantsoenen gesimuleerd. Hierbij werden verschillende krachtvoerniveaus en strategieën voor het verdelen van krachtvoer en ruwvoer over een lactatie gesimuleerd voor drachtige en niet-drachtige koeien, van verschillende leeftijd. Deze simulaties toonden aan dat het Wageningen DCM in staat is om de interacties tussen koe-effecten (lactatienummer, lactatiestadium, dracht) en voerstrategieën (krachtvoerniveau, verdeling van ruw en krachtvoer over de lactatie) te beschrijven. Het Wageningen DCM geeft op dag-basis voorspellingen van de voer- en energieopname en de verdeling van de opgenomen hoeveelheid energie over meetmelkproductie en lichaamsreserves.

De gesimuleerde effecten van krachtvoeropname en voerstrategie op de meetmelkproductie kwamen overeen met gegevens in de literatuur. Validatie met externe gegevens liet zien dat de droge stofopname en meetmelkproductie in het eerste deel van de lactatie (0-200 dagen) met een goede nauwkeurigheid werden voorspeld, beiden met een relatieve voorspelfout van minder dan 0.10. De voorspelnauwkeurigheid van de droge stofopname en meetmelkproductie gedurende de gehele lactatie was acceptabel met een relatieve voorspelfout van 0.10. Dit leidde tot de conclusie dat het Wageningen DCM geschikt is als een hulpmiddel voor het ondersteunen van strategische beslissingen op het melkveebedrijf, voor het samenstellen van rantsoenen en evaluatie van lange termijn voer- en managementstrategieën.

In hoofdstuk 6, de Algemene Discussie worden verschillende aspecten besproken die betrekking hebben op wijze van modelleren, de modelstructuur, aannames en beperkingen en mogelijke verbeteringen van het Wageningen DCM. Er is gekozen om een empirisch model te ontwikkelen. Deze is gebaseerd op de wens om een eenvoudig, robuust en gemakkelijk te gebruiken model te ontwikkelen, dat geschikt is om de voeropname en prestatie van melkkoeien te kunnen simuleren voor omstandigheden die ook in de praktijk voorkomen. Daarnaast waren er grote datasets beschikbaar die gedetailleerd genoeg waren voor het ontwikkelen van een empirisch model, maar niet geschikt waren voor het ontwikkelen van een mechanistisch model.

Het modulaire ontwerp van het Wageningen DCM creëert een grote mate van flexibiliteit ten aanzien van toekomstige uitbreidingen en aanpassingen. Afzonderlijke modules kunnen worden aangepast zonder een totale reconstructie van het model. Flexibiliteit wordt ook verkregen door het gebruik van datasets met grote variatie aan rantsoenen, rantsoensamenstellingen en HF melkkoeien in verschillende lactaties en lactatiestadia. Hierdoor kan het model worden toegepast op een grote diversiteit aan rantsoenen, voer- en managementomstandigheden.

Het Wageningen DCM is in staat om realistische patronen van het verloop van de opnamecapaciteit, meetmelkproductie en hoeveelheid lichaamsreserves gedurende de lactatie te genereren. Deze patronen kunnen fysiologisch worden verklaard op basis van homeorhetische controle mechanismen.

Het Wageningen DCM gaat er van uit dat de effecten van de afzonderlijke voedermiddelen optelbaar zijn. Deze aanname is geldig zolang rantsoenen worden samengesteld op basis van de standaard voederwaarderingssystemen en praktische adviezen ten aanzien van de koolhydraatsamenstelling van het rantsoen.

Evaluatie van het Wageningen DCM op basis van statistische criteria geeft aan dat het model accurate voorspellingen geeft. Echter, de geschiktheid en nauwkeurigheid van het model voor het simuleren van de opname en productie onder beweidingsomstandigheden dient nader onderzocht.

In deze fase van de ontwikkeling van het Wageningen DCM wordt de voorspelde melkproductie uitgedrukt als meetmelk. Aanvullend onderzoek is nodig naar uitbreiding van het model zodat ook voorspelling van de melksamenstelling mogelijk is. Tevens is onderzoek nodig naar aspecten met betrekking tot de effecten van de voedingshistorie van de koe en de toepassing van het Wageningen DCM voor andere melkveerassen dan het Holstein Friesian ras.

Curriculum Vitae

Ronaldus Lodewijk Gerardus (Ronald) Zom (24 april, 1962) received a basic vocational training from 1974 to 1979 at the Lagere Land en Tuinbouwschool. He continued his agricultural education at the Rijks Middelbare Land en Tuinbouwschool in Emmen. After graduation in 1983, he went to the Rijks Hogere Landbouw School Groningen and received his BSc degree in agriculture in 1987. Next to his agricultural education at different levels, he acquired farming skills at the family farm of J.H. Wolbers, Vredenheim. In 1987 he started his MSc in Animal Science at the Landbouw Universiteit Wageningen and graduated in 1991. After graduation, he worked during a period of one year as a research assistant at the department of Animal Nutrition. In 1992, he was appointed as veal calf husbandry expert at the Stichting Kwaliteitsgarantie Vleeskalversector (SKV). In 1993, he was appointed as researcher ruminant nutrition at the former Proefstation voor de Rundveehouderij, Schapenhouderij en Paardenhouderij. From 1993 onwards, he worked on many different research projects in the field of animal husbandry and dairy cow nutrition and grazing. A part of the results of these projects are included in this thesis.