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A dynamic model of feed intake regulation in dairy cows. Model evaluation

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ABSTRACT

The objective of this work was the evaluation of a feed intake regulation model for dairy cows described in a previous paper. Sensibility analysis revealed that the model is sensible mainly to those parameters defining the upper limit of NDF rumen digesta. The level of sensibility varies with the energy content of the diet evaluated and with the time in the lactation cycle where the sensibility analysis is done. A total of 17 treatments from a series of experiments were used to compare experimentally observed feed intake and body condition score (BCS) of dairy cows with model predictions of these variables. Feed intake, either throughout the whole lactation period or as an average for a certain period of it, is predicted by the model with an acceptable degree of accuracy for most of the treatments. Typical curves of feed intake are predicted by the model for most of the treatments. Accuracy of prediction of BCS depends on the treatment being evaluated. However, losses of BCS are predicted at the beginning of the lactation period followed by a gradual increase in BCS. The interplay between energy transactions and rumen digesta load constitutes an acceptable framework on which mechanistic models of feed intake regulation can be developed.

KEY WORDS: model, evaluation, intake regulation, prediction, body condition score, dairy cows

INTRODUCTION

A feed intake regulation model (FIRM) in dairy cows has been presented in a previous paper (Petruzzi and Danfaer, 2004). The biological concepts of feed

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intake regulation on which this model is based are explained in the model and a complete description of the model appears in the appendix of the referred paper. Briefly, the model is based on a conceptual model presented by Weston (1985, 1996) and involves an interplay between rumen functions and energy transactions. The NDF load capacity of the rumen in the dairy cow is a function of an energy variable (*E_diff_h*) defined with the following equation:

$$E\_diff\_h = E\_balance - E\_bal\_optimum + Fac\_BCS$$

E_balance is an energy balance calculated by the model, *E_bal_optimum* is an optimal energy balance which is determined from a standard curve of body condition score (BCS), and *Fac_BCS* is a factor related to the initial and actual BCS of the dairy cow.

The model is designed to simulate up to the entire lactation cycle using only information about feed composition and the animal at either the beginning of the simulation period or with daily inputs. The initial information about the animal is updated daily by the model. A final and mandatory step in the modelling process is the evaluation of the model. Evaluation has been defined as “a comparison of the model’s predictions with the real world to determine whether the model is suitable for its intended purpose” (Hoover, 1989).

The objective of this paper is to describe an evaluation of the model behaviour to assess the appropriateness of the model predictions and the adequacy of the basic model concepts.

MATERIAL AND METHODS

Two kinds of evaluations were carried out, sensitivity analysis and behavioural analysis. During the formulation of the model, energy difference as defined above and rumen digesta load are the determinants of intake regulation. Therefore, parameters related directly with the determination of these two key variables were used in the sensitivity analysis. The parameters chosen to be changed were (with the abbreviation as used in the appendix in the published model and the original value in brackets): parameters *Alfa1* (4.15), *Alfa2* (4), *Alfa3* (0.925), *Alfa4* (1.3) and *Alfa5* (1.9) as determinants of the variable upper limit of NDF digesta load in the rumen (*Upper*); difference between the upper and the lower limit of NDF digesta in the rumen (*Diff*; 0.6); eating rate (*Eating*; 3.3 kg DM h^{-1}); constant *K_BCS* (100) used in the determination of a variable related to actual body condition score (BCS) of the animal; proportion of gross energy lost as urine by the cow (*K_UE*; 0.04); constant *K_HE* (0.08) used for the determination of heat energy depending on daily milk production; constant rate of endogenous protein secretion

(K_*EP*; 0.2856). From the analysis of the rumen model on which the feed intake regulation model is based (see Petruzzi et al., 2002), it was demonstrated that the rumen model was sensitive to parameters defining the rate constant of passage of small particles (*KpSP*) and the digestion rate constant of NDF. Hence, parameters *a* (0.01), *b* (0.052) and *d* (3.2) were also included in the sensitivity analysis of FIRM.

In the sensitivity analysis, the selected parameters, one at a time, were changed by ±10, ±25 or ±50% of the original values, whereas all other variables or constants remained at their original values. The effects of changes in the selected parameters were evaluated by analysis of the response variable daily feed intake predicted by the model. As the model simulates up to an entire lactation cycle, two different simulation periods during the cycle (weeks 7 and 39 of lactation) were chosen to evaluate the impact of the changes.

The effects of changing the values were analysed using two total mixed diets with a low (LTMD) and a high (HTMD) level of concentrates. These diets correspond to those used by Friggens et al. (1998a) and information about ingredients, chemical composition and energy content of the diets, as well as initial values of the cow used by the model is presented in Tables 1, 2, 3 and 4. The chosen diets were total mixed diets composed of grass silage and concentrates differing only in the level of concentrates used.

TABLE 1

Description of diets and cows used in the sensitivity analysis of the feed intake regulation model

Indices	LTMD	HTMD
Ingredients, % of DM		
silage	73.0	41.2
concentrates	27.0	58.8
Chemical composition, g kg^{-1} of DM		
NDF	42.9	34.4
crude protein	17.5	18.5
starch	5.9	12.9
sugars	7.1	6.2
crude fat	1.0	2.2
ash	7.8	7.8
Energy content		
GE, MJ kg^{-1}	18.6	18.7
Initial inputs for the cow		
body weight, kg	624	629
BCS	3.0	3.2
parity	3[a]	3[a]

[a] - include cows in third or higher parity

TABLE 2

Description of the diets used in the behavioural analysis of the feed intake regulation model

Author	Treatments	Type of forage and concentrate	Simulation time	Treatment number
Friggens et al., 1998	H – H	Grass silage + high level of concentrates	Whole lactation	1
	H – L	Grass silage + high and low level of concentrates	Whole lactation	2
	L – H	Grass silage + low and high level of concentrates	Whole lactation	3
	L – L	Grass silage + low level of concentrates	Whole lactation	4
MEMO (Ingvartsen and Jensen, 2001)	LOW 2	Whole crop wheat silage + wheat straw + concentrates	Whole lactation	5
	NORMAL2	Whole crop wheat silage + concentrates	Whole lactation	6
	LOW 3	Whole crop wheat silage + wheat straw + concentrates	Whole lactation	7
	NORMAL3	Whole crop wheat silage + concentrates	Whole lactation	8
HEF (Kristensen, 1999)	GS-1	Grass silage + low level of concentrates	Week 3 to 15 after calving	9
	GS-2	Grass silage + medium level of concentrates	Week 3 to 15 after calving	10
	GS-3	Grass silage + high level of concentrates	Week 3 to 15 after calving	11
	WCBS-1	WCBS[a] + low level of concentrates	Week 3 to 15 after calving	12
	WCBS-2	WCBS[a] + medium level of concentrates	Week 3 to 15 after calving	13
	WCBS-3	WCBS[a] + high level of concentrate	Week 3 to 15 after calving	14
	STRAW-1	NH_3 Straw[b] + low level of concentrates	Week 3 to 15 after calving	15
	STRAW-2	NH_3 Straw[b] + medium level of concentrates	Week 3 to 15 after calving	16
	STRAW-3	NH_3 Straw[b] + high level of concentrates	Week 3 to 15 after calving	17

[a] - whole crop barley silage

[b] - ammonia treated wheat straw

TABLE 3

Chemical and physical description, on a DM basis, of diets used in the behavioural analysis of the feed intake regulation model

Treatment number	Organic mater %	Crude protein %	NDF %	DNDF[1] % of NDF	Small NDF particles %	Starch %	Sugars %	Lipids %
1	92.2	18.5	34.4	78.9	10.3	12.9	6.2	2.2
4	92.2	17.5	42.9	83.6	4.7	5.9	7.1	1.0
5 and 7	91.5	14.5	35.1	71.3	6.9	8.9	13.0	3.3
6 and 8	91.5	15.2	29.9	75.6	5.9	11.9	13.7	3.4
9	89.5	20.0	40.9	82.7	15.2	7.7	3.4	3.7
10	89.1	19.5	38.1	81.9	22.2	11.2	4.1	3.9
11	91.2	20.1	35.5	81.1	30.1	14.6	4.8	3.6
12	93.5	16.5	37.6	71.5	19.1	22.0	3.5	3.3
13	93.6	16.8	35.7	72.8	25.6	22.1	4.1	3.0
14	93.4	16.8	31.9	73.3	35.9	22.5	4.7	3.7
15	92.2	15.2	37.6	73.7	27.4	12.4	1.3	2.8
16	92.6	16.2	34.1	74.3	32.7	14.1	1.4	3.1
17	93.6	16.1	30.3	75.0	38.9	15.7	1.4	2.9

[1] - potentially digestible NDF

According to the authors (Friggens et al., 1998a), HTMD was designed to allow the animals to cover their energy requirements whereas the LTMD was designed to limit the feed intake of the cows. The same diet was supplied to the respective group of cows throughout the whole lactation cycle. Information about chemical composition and physical characteristics of these diets was obtained from the paper (Friggens et al., 1998a), by personal communication with one of the authors and from the Danish Feedstuff Table (Møller et al., 2000). Animal inputs needed to start the model were also obtained using the first two sources of diet information. BCS values as reported in the publication were originally scored on a six point scale (0 = emaciated to 5 = very fat cows) but were converted into a five point scale (Edmonson et al., 1989) as is used in FIRM. Milk yield and milk composition are daily inputs to the model.

In the behavioural analysis, three different experiments with a total of 13 different diets and 17 treatments were used to compare the outputs of the model with the experimentally observed values. A total of 361 records were evaluated, 44 records for each of the first eight treatments and one record for each of the last nine treatments (Table 2). A description of the diets used in behavioural analysis is presented in Tables 2 and 3. Initial parameter values describing the dairy cows in the model for each treatment are presented in Table 4. Chemical composition and physical characteristics of the diets as well as information about the animals

TABLE 4

Initial parameter values describing the cows used in the behavioural analysis of the feed intake regulation model as well as number of animals used in the experiments

Diet number	Body weight kg	Parity[a]	BCS[b]	Milk yield	Number of animals
1	629	3	3.2	Daily input	4
2	679	3	3.3	Daily input	5
3	656	3	3.0	Daily input	6
4	624	3	3.0	Daily input	6
5	633	2	3.2	Daily input	28
6	642	2	3.5	Daily input	24
7	677	3	3.4	Daily input	18
8	650	3	3.5	Daily input	16
9	599	3	3.2[c]	29.2[d]	7
10	597	3	3.2[c]	34.2[d]	7
11	621	3	3.2[c]	36.9[d]	7
12	620	3	3.2[c]	32.4[d]	7
13	585	3	3.2[c]	31.6[d]	7
14	629	3	3.2[c]	35.2[d]	7
15	620	3	3.2[c]	32.6[d]	7
16	610	3	3.2[c]	33.5[d]	7
17	612	3	3.2[c]	32.9[d]	7

[a] - when parity = 3, cows in third or higher parity are included

[b] - body condition score

[c] - not originally reported. Assumed for simulation purposes

[d] - daily average for the reported period

used in the experiments were obtained from the published papers or by personal communication with the authors.

The first experiment used in the behavioural analysis was carried out by Friggens et al. (1998a) and includes two diets and four treatments (Treatments 1 to 4). Diets were already described in the sensitivity analysis. Two treatments have used the same diet throughout the lactation period and two treatments have changed diet at 153 days in milk. Treatments were: H-H and L-L where the same diet (HTMD and LTMD, respectively) was fed during the whole lactation, and H-L and L-H where cows started with HTMD or LTMD, respectively, and were changed to the LTMD or HTMD at the specified time. Milk yield and milk composition inputs were entered daily to the model from an Excel spreadsheet. As was mentioned during the sensitivity analysis, original values of BCS in the experiment were converted from a six-point scale to a five-point scale as used in the model. The experiment covered the whole period of lactation.

Treatments 5 to 8 correspond to a long-term experiment named MEMO (Malkekoens Energioptagelse, Mobilisering og Sundhed) carried out by the Departments of Animal Health and Welfare and the Department of Animal Breeding and Genetics, DIAS Foulum (Ingvartsen and Jensen, 2001; Nielsen et al., 2002). From the MEMO project, only cows of the Danish Holstein breed in their second and third or higher parity were considered in the analysis. Two diets were used in the project, a low (Treatments 5 and 7) and a normal energy diet (Treatments 6 and 8). Both diets were fed as total mixed diets and were based on whole crop wheat silage with or without wheat straw (Tables 2 and 3). Treatments 5 and 6 correspond to animals in their second lactation and treatments 7 and 8 to dairy cows with three or more lactations.

Animal inputs to the model are presented in Table 4. A total of 86 animals were used in the experiment with 28, 24, 18 and 16 in treatments 5 to 8, respectively. Milk yield and composition were given as daily inputs to the model. Body condition was scored on a five-points scale. The experiment covered the whole lactation cycle.

The last experiment (HEF, 1999) includes nine treatments and was carried out by the Department of Animal Nutrition and Physiology, DIAS, Foulum (Kristensen, 1999; Weisbjerg et al., 2001) during two consecutive years, but only results from the second year were considered for analysis. Three different forage sources with three different levels of concentrates were used to define the nine diets and corresponding treatments (9 to 17). A description of the diets used is presented in Tables 2 and 3. Grass silage is the forage source in treatments 9, 10 and 11 with 34, 50 and 65%, respectively of the diet DM as concentrate. Treatments 12, 13 and 14 use whole crop barley silage with 38, 53 and 67%, respectively of the diet DM as concentrate. The last group of treatments (15, 16 and 17) uses ammonia treated barley straw as the forage source and concentrates constitute 55, 62 and 69% of DM, respectively. Animal inputs to the model are given in Table 4. The period of analysis was twelve weeks from week 3 to week 15 after calving. An average value of energy corrected milk was reported for each treatment for the period of analysis. This average milk yield was used in combination with the equation taken from Friggens et al. (1999) and included in the model (see Petruzzi and Danfaer, 2004) to produce a pattern of daily milk production that could be used as daily inputs to the model. Body condition score was not measured in the experiment, but on average the animals were in a good condition at calving (Børsting, personal communication). As a consequence, a value of 3.2 was adopted as initial BCS for the animals in all treatments.

In all treatments, experimentally obtained values of feed intake (kg DM d^{-1}) were compared with the daily feed intake predicted by the model. BCS predicted by the model and reported in the experiment are compared only for the treatments 1 to 8.

Evaluation techniques

For sensitivity analysis, a graphical display was used to show the effect of changes in the selected parameters on the resulting changes in the selected output.

For both periods of analysis, the resulting changes are presented as percentage of the results obtained with the original parameter values.

Different methods were used to estimate the ability of the model to predict values observed in the different experiments. The first one was to plot observed and predicted values as functions of time, e.g., lactation time. A second type of graph display used was to plot the observed ($\mathbf{O}_i$) against the predicted ($\mathbf{P}_i$) values, with the line $\mathbf{O}_i = \mathbf{P}_i$ indicating the position of a perfect fit. With this type of graph it is possible to see if any bias of the model is present. The goodness of fit is directly observed as the vertical deviation from the perfect fit line.

The measure of deviation was calculated using the root mean square prediction error (RMSPE) defined as:

$$\mathbf{RMSPE = \{[\sum (O_{\mathit{i}} - P_{\mathit{i}})^2\,] \,/\, n\}^{0.5}}$$

where $\boldsymbol{i}$ = 1,2…**n**; **n** is the number of experimental observations; $\mathbf{O}_i$ and $\mathbf{P}_i$ are the observed and predicted values, respectively. Decomposition of the mean square prediction error (MSPE) into error due to central tendency (ECT), error due to regression (ER) and error due to disturbance (ED) was done as defined by Bibby and Toutenberg (1977). Significance and formulas to calculate these terms were also presented in Petruzzi et al. (2002). The **RMSPE** expressed as a percentage of the observed mean is used as a measure of the prediction error. A criterion of 10% of deviation was considered as a reasonable prediction accuracy.

A dimensionless statistical test, modelling efficiency (EF) (Loague and Green, 1991) was also used to relate model predictions to observed data and is defined as:

$$\mathbf{EF = 1 - \sum (O_{\mathit{i}} - P_{\mathit{i}})^2 \,/ \sum (O_{\mathit{i}} - \bar{O})^2}$$

where the term $(\sum \mathbf{(O_{\mathit{i}} - P_{\mathit{i}})}^2)$ is the sum of squares, and $\mathbf{(\sum (O_{\mathit{i}} - \bar{O})^2)}$ is the corrected sum of squares of observed values. EF is also an indication of goodness of fit and can be compared with the widely-used coefficient of determination R^2. Values close to one indicate a “near-perfect” model. Negative values are possible for EF.

Graphical display and statistical tests were also used to evaluate results predicted by the Danish Fill Factor System (DFFS) (Kristensen, 1995) for the diets 5 to 17. DFFS predictions for treatments 5 to 8 were calculated with the fill factor values for each diet reported by Ingvartsen and Jensen (2001). For treatments 9 to 17, information about fill factors for the different diets was given by the authors of the experiment. Milk yield values used to calculate predicted feed intake according to DFFS for all treatments were the same as those used in FIRM.

RESULTS

From sensitivity analysis

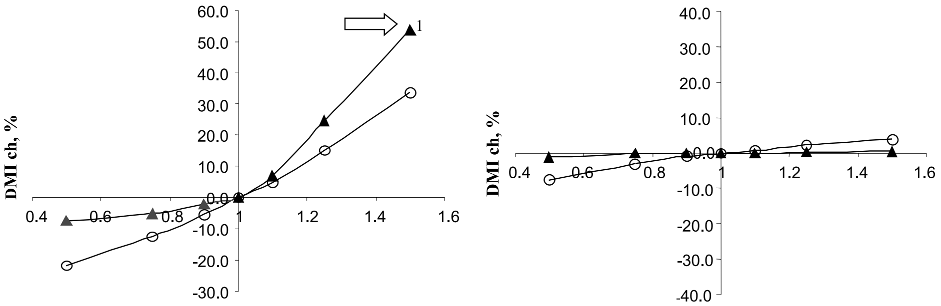
Figure 1 (a, b, c, d, e and f) presents results from the sensitivity analysis with HTMD for the parameters *Alfa1* to *Alfa 5* and the difference between upper and lower limit of NDF digesta load in the rumen (*Diff*), respectively. Results for the first period of analysis (week 7 in lactation) are plotted with (-○-) while the second period of analysis (week 39) is represented by (-▲-). Values along the X axis represent changes in the original value of the selected parameter while values on the Y axis represent changes in the response variable (expressed as % of change in feed intake obtained with the original parameter values). For example point 1 in Figure 1a means that when analysing week 39 in lactation, a 53% of increment in the predicted feed intake (response variable) is observed when *Alfa1* (selected parameter) is increased 50% of its original value.

From this group of parameters affecting directly the NDF digesta load in the rumen, FIRM is mainly sensitive to the values of *Alfa1,* which determines the lowest value of the upper limit to digesta and as a consequence also the lower limit. The effect of changing the values of *Alfa1* is not symmetric, as an increment of the original value produces a higher difference in the predicted feed intake compared to an equivalent reduction of the parameter. Changes are also dependent on the time of analysis. In late lactation, the effect of increasing the parameter value is larger than in early lactation, but the opposite is the case when the parameter value is decreased.

These differences can be explained when analysing the curves presented in Figure 2. Figure 2a shows the value of the upper limit for a cow in week 7 (X axis in hours from calving) for the original value of parameter *Alfa1*, line 1, and when the parameter was increased by 50%, line 2. Figure 2b shows the same, but in late lactation (week 39). When using the original value of *Alfa1* (line 1), the cow in early lactation has values of *E_diff* operating in the range between *Alfa1* (4.15 kg) and *Alfa1* plus *Alfa2* (8.15 kg). As a consequence of the increment in *Alfa1*, feed intake is increased. When *E_diff* becomes more positive, the upper limit moves closer to *Alfa1* and feed intake will be reduced.

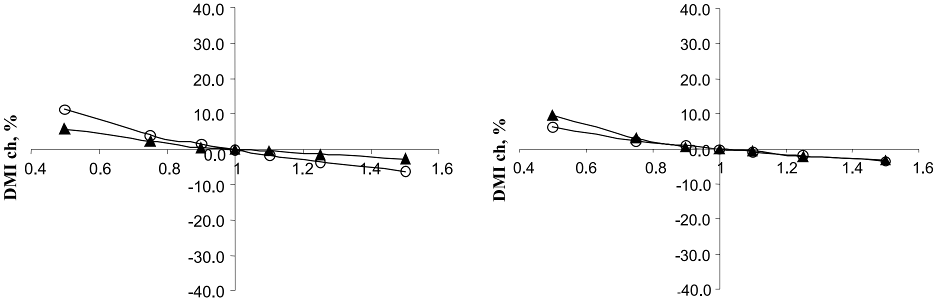
In late lactation (Figure 2b), *E-diff* values are close to *Alfa1* (4.15) and it is not possible for the model to adjust for an increment of *Alfa1* and as a consequence, feed intake is increased more than in early lactation.

Alfa2 determines the difference between the lowest and the highest value of the upper limit of rumen NDF, and the model is almost insensible to changes in this parameter. Due to the equation used to calculate *Upper* (See Apendix and Figure 2 in Petruzzi and Danfaer, 2004), differences in intake are expected if the variable *E_diff* takes values in the range were the slope of the NDF load curve is high, i.e.



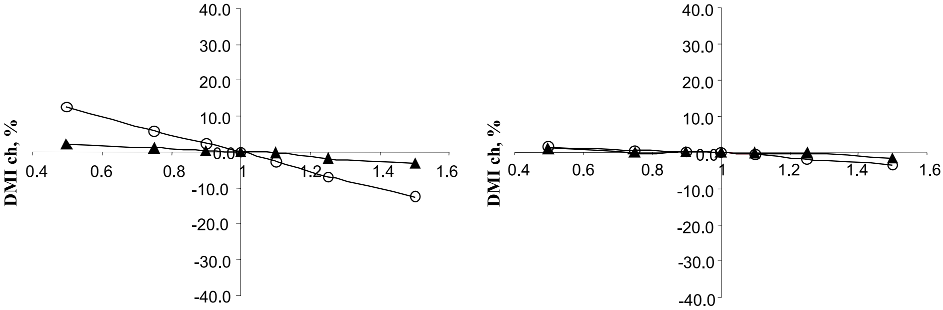
a) Alfa1

b) Alfa2



c) Alfa3

d) Alfa4



e) Alfa5

f) Diff

Figure 1 (a, b, c, d, e and f). Results from the sensitivity analysis for the different parameters evaluated using a diet with a high proportion of concentrates. Results are presented for week 7 (-○-) and week 39 (-▲-) in lactation

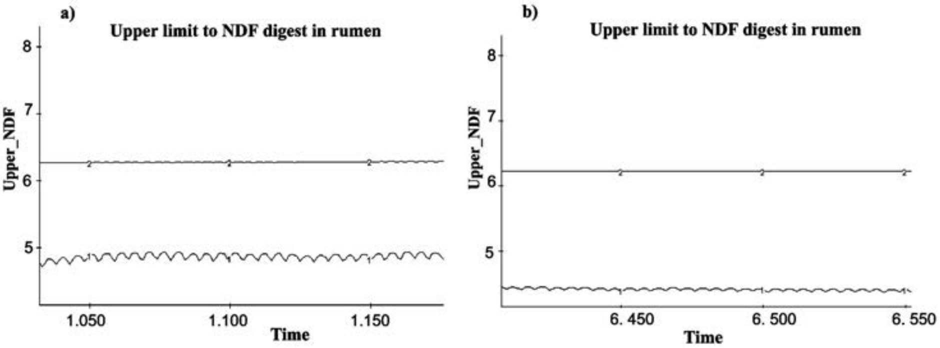


Figure 2. Upper limit of NDF digesta in the rumen in early lactation (*a*) and late lactation (*b*) determined with the original value (1) of parameter *Alfa1* or with a value increased by 50% (2)

E_diff with values below 0.5 as is the case in early lactation. In late lactation, feed intake is almost not modified when *Alfa2* is changed because values of *E_diff* is always operating in the range where the upper limit of NDF load is close to *Alfa1*, i.e. the slope of the curve is close to zero.

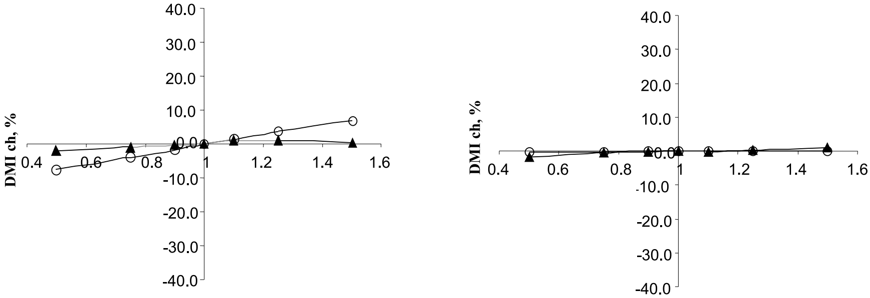
FIRM has almost the same sensibility, very low, to parameters *Alfa3, Alfa4* and *Alfa5* (Figure 1c, d and e). In all cases, an increment in the original value of the parameter produces a reduction in the predicted feed intake. Except for *Alfa5*, very small differences are observed between period of analysis. All parameters modify the shape of the curve, but with no effect on the minimum or maximum values of the upper limit of NDF digesta. The model is not sensible to changes in the parameter *Diff* (Figure 1f). Changes in D*iff* affect the number and size of meals, but not the total feed intake.

Figure 3 (a, b, c, d, e, f, g and h) shows results from the sensitivity analysis with the HTMD diet for the parameters: *Eating*, *K_BCS*, *K_UE*, *K_HE*, *K_EP*, *a*, *b* and *d*, respectively.

Sensibility of the model is very low to the eating rate constant (*Eating*) especially in late lactation. Eating rate is not necessarily related to the level of feed intake. Eating rate in dairy cows is normally influenced by the social environment and is more indicative of the degree of constraint that is exposed to the animal (Greenwood and Demment, 1988; Nielsen, 1999). Experiments have proved that animals are extremely flexible in the organization of their feeding behaviour, meaning that the same intake can be achieved through many different intake patterns (Friggens et al., 1998b; Tolkamp et al., 2002). Tolkamp et al. (2002) observed a reduction in the daily number of visits to the feeder without any changes in the average daily intake when changes in feeder construction were implemented. Grant and Albright (2000) reported that cows spend from 3 to 6 h eating meaning that for an

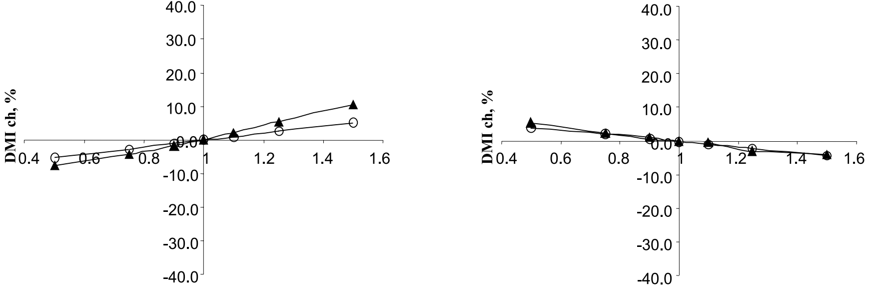
a) Eating

b) K_BCS



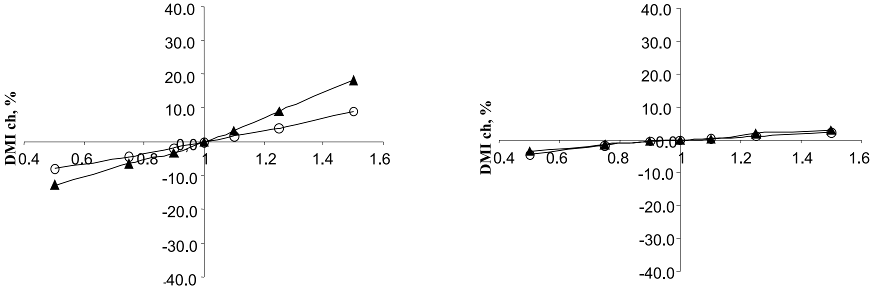
c) K_U E

d) K_HE



e) K_EP

f) a



g) b

h) d

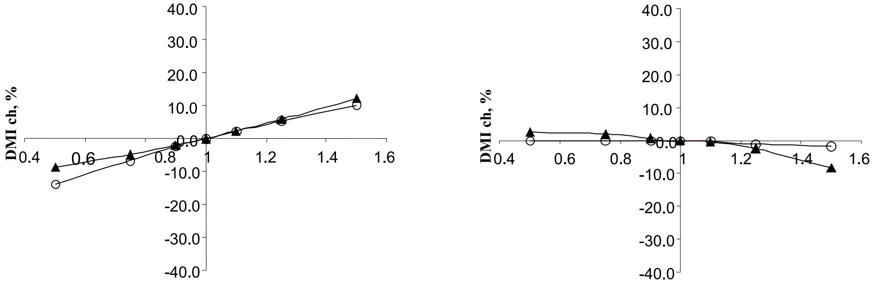


Figure 3 (a, b, c, d, e, f, g and h). Results from the sensitivity analysis for the different parameters evaluated using a diet with a high proportion of concentrates. Results are presented for week 7 (-○-) and week 39 (-▲-) in lactation intake of about 20 kg DM d^{-1}, the eating rate should be between 3 and 6 kg DM h^{-1}. These eating rate values are within or close to the range tested in the sensitivity analysis. *Eating* can be changed, without any major changes in the predicted feed intake values, if eating time is the variable to be predicted.

Factor *K_BCS* (Figure 3b) has no impact on the response variable of the model. No effect was expected for the first period of analysis because due to the variable *Sigm1*, the influence at that time is relatively small. However, as the impact of this parameter is highly dependent on the initial and actual BCS of the animal, the sensibility of the model would have been different if the initial condition of the cow was different.

Sensibility of the model to factor *K_UE* is low as presented in Figure 3c. An increment in the parameter value reduces the net energy available for the cow leading to a lower energy balance, a lower value of *E_Diff* and consequently an increased intake. The value of the parameter adopted in the model is very close to the mean value reported by Yan et al. (1997) (4.2% of GE intake, range from 3.7 to 6%) taken from more than 200 energy balance studies in dairy cows and by Ferris et al. (1999a). However, lower values have been reported by Sutter and Beever (2000) (2.5% of GE) for the first 8 weeks of lactation and by Sutton et al. (1998) (2.7 to 3.3% of GE).

The parameter *K_HE* (Figure 3d) has an equal or even smaller effect on the response variable than *K_UE*, but in the opposite direction. An increment in the original value reduces the energy lost as heat and produces a higher value of *E_balance*. The model reacts in the same way, but a little stronger to changes in parameter *K_EP* as to changes in the parameter *K_UE*. The range of values tested in the sensitivity analysis for *K_EP* is possibly out of range of the normal values found in the literature and extreme values should not be considered. Bequette (2002) estimated that a dairy cow loses 22 g of endogenous protein per kg of DM intake, whereas Ferrel (1995) estimated this loss as 30 g of crude protein per kg DMI. The value adopted in the model (0.2859 mol N kg^{-1} DMI or 25 g CP kg^{-1} DMI) is between these values and extreme values tested in the sensitivity analysis (12.5 and 37.5 g CP per kg DMI) are far away from the values cited in the literature.

The last group of parameters evaluated (*a*, *b*, *d*) were proved to have an impact on the output from the rumen model (Petruzzi et al., 2002). In general the sensibility of FIRM is low to these parameters. Only parameter *b* seems to affect the model when tested at extreme values with almost no difference between periods of analysis.

A sensitivity analysis with the diet LTMD (results not shown) produced, in general, results close to that already presented for the diet HTMD. The parameter *Alfa1* was again the most sensible parameter, but with almost no difference between early and late lactation when an increase of 50% of the original value was tested. Compared to HMTD, the model is more sensitive with LTMD to changes in *Alfa5*, especially in early lactation, and to changes in *K_EP*, *b* and *d* in late lactation.

From behavioural analysis

Figure 4 (a, b, c and d) presents observed and simulated daily dry matter intake estimated as weekly averages, corresponding to each of the four diets evaluated by Friggens et al. (1998a) during the whole lactation cycle. Table 5 summarises results from the statistical analysis of individual treatments and groups of treatments. Considering the four treatments in the experiment of Friggens et al. (1998a), DMI is well predicted by the model with an RMSPE of 1.46 kg d^{-1} which is 7.8% of the observed mean. Decomposition of the MSPE gives the largest (72%) contribution to the error resulting from random variation in the data, followed by the error attributed to bias (27%). Efficiency of modelling (EF) for the whole data set is 0.75.

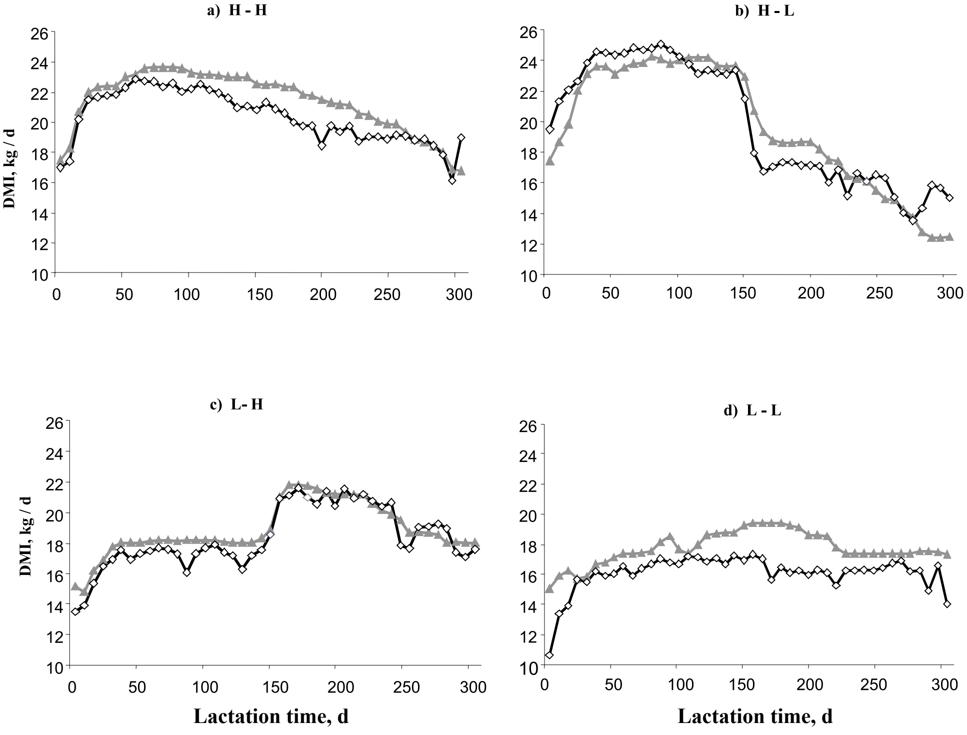


Figure 4 (a, b, c, and d). Observed (-◊-) and predicted (-▲-) weekly mean DM intake during the whole lactation in dairy cows given different levels of concentrates (Friggens et al., 1998a). For details see text and Table 2

TABLE 5

Results from statistical analysis of observed and predicted values of dry matter intake for individual treatments and experiments tested with the feed intake regulation model

Experiment	Treatments		RMSPE[a]	Prediction error[b]	Modeling efficiency
Friggens et al., 1998	H H		1.33	6.6	0.40
	H L		1.49	7.5	0.85
	L H		0.84	4.6	0.83
	L L		1.95	12.1	-1.72
	Mean		1.46	7.8	0.75
MEMO (Ingvartsen and Jensen, 2001)	LOW2		1.87	8.9	-0.24
	NORMAL2		1.55	7.1	0.37
	LOW3		2.90	13.8	-1.02
	NORMAL3		1.72	8.0	0.39
	Mean		2.38	11.2	-0.06
HEF (Kristensen, 1999)	GS-1	Mean	0.39	1.81	0.97
	GS-2				
	GS-3				
	WCBS-1	Mean	0.99	4.58	0.58
	WCBS-2				
	WCBS-3				
	STRAW-1	Mean	1.75	7.42	-11.44
	STRAW-2				
	STRAW-3				

[a] - Root Mean Square Prediction Error

[b] - as % of the observed mean

In Figure 5, the predicted DM intake is plotted against the experimentally observed values for all four treatments. The broken line indicates the perfect fit. Treatments using the same diet along the lactation period have errors of prediction of 6.6 and 12.1 as % of the observed mean, for the H-H and the L-L treatment, respectively, with the highest proportion of the error contributed by bias (60 and 74% for H-H and L-L treatment, respectively). EF for both treatments is low (0.40 and -1.72 for treatment H-H and L-L; respectively; Table 5). The H-H and L-L treatments are overpredicted during most of the lactation period with a RMSPE of 1.33 kg d^{-1} and 1.95 kg d^{-1}, respectively. DMI in the treatments with changeover of diets (H-L and L-H) is predicted with an error of 1.49 and 0.84 for H-L and L-H, respectively, and with 92 and 55% of the MSPE contributed by the disturbance part. The H-L treatment has an efficiency of modelling of 0.85 while a value of 0.83 was calculated for the L-H treatment.

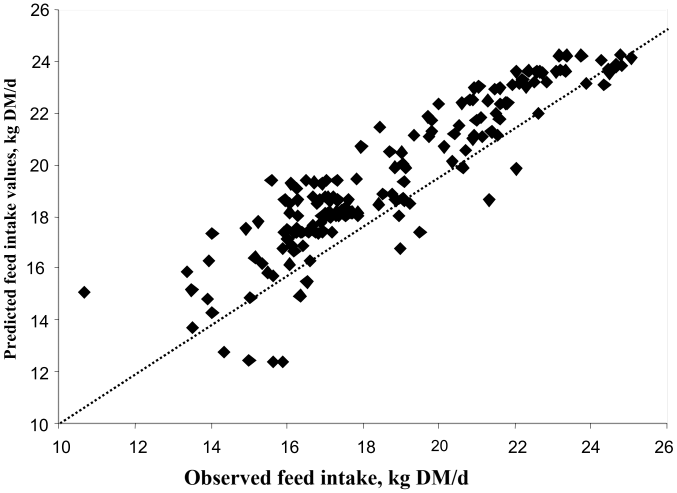


Figure 5. Dry matter intake for the whole lactation period in dairy cows. X-values are experimentally observed values (Friggens et al., 1998a) and Y-values are obtained by simulation with FIRM. Broken line Y = X

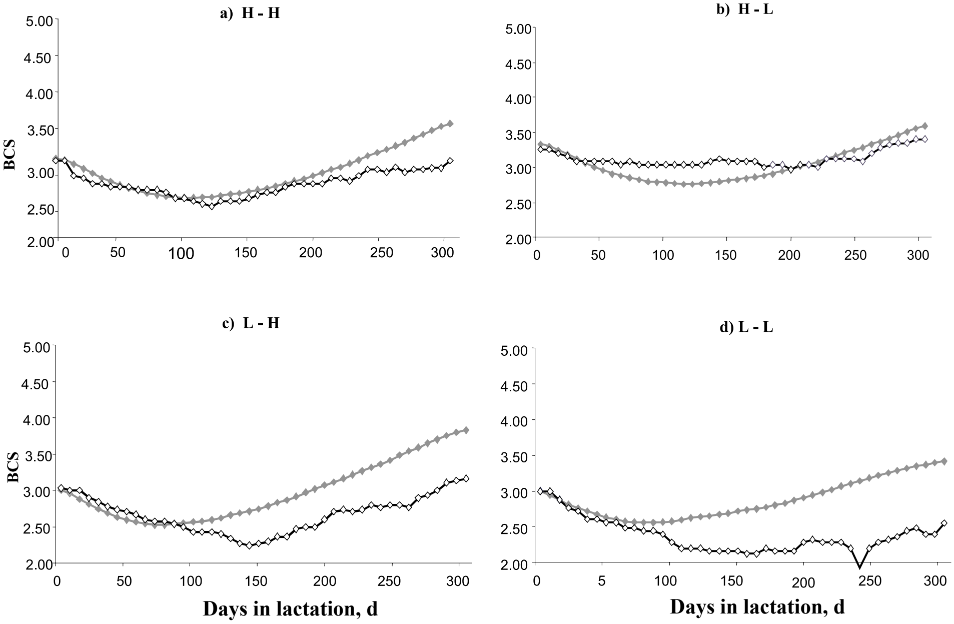


Figure 6 (a, b, c, and d). Observed (-◊-) and predicted (-▲-) weekly mean BCS during the whole lactation in dairy cows given different levels of concentrates (Friggens et al., 1998a). For details see text and Table 2

Figure 6 presents observed and predicted values of BCS for all treatments. Errors of prediction, expressed as % of the observed mean, are 9.2, 7.1, 14 and 24 for treatments H-H, H-L, L-H and L-L, respectively. In almost all cases, model predictions of BCS are higher than the observed values at the end of the lactation period. In all cases, the same pattern of BCS is predicted by the model, a low BCS is predicted from week 11 to 16, depending on the treatment, and higher values at the end of lactation reflecting changes from losses of body weight at the beginning of the lactation period to positive energy balances at the end of the period.

For the second group of treatments (5 to 8) from the MEMO project, predicted and observed values of feed intake are plotted in Figure 7 (a, b, c and d). Feed intake is predicted with an RMSPE of 2.38 kg DM d^{-1} (11.2% of the observed mean) (Table 5) with most of the error attributed to bias (47%) and random error (43%). Treatments using the low energy diet (LOW2 and LOW3) have the highest errors in prediction (RMSPE of 1.87 and 2.9 kg DM d^{-1} corresponding to 8.9 and 13.8 of the observed mean, respectively). Most of the error is attributed to bias (84% in both cases). Confirming the inadequate performance of the model with this diet, efficiency of modelling in both cases has negative values (-0.24 and -1.0 for LOW2 and LOW3, respectively) (Table 5).

The model prediction improves with the normal energy diet for both parity groups. Prediction errors for treatments NORMAL2 and NORMAL3 are 7.07 and 7.99% of the observed mean and RMSPE values are 1.55 and 1.72 kg DM d^{-1} for both treatments with 79 and 87% of the MSPE contributed by disturbance, respectively. Efficiency of modelling for NORMAL2 and NORMAL3 is estimated as 0.37 and 0.39, respectively (Table 5).

Feed intake predictions calculated by the Danish Fill Factor System (DFFS) are also plotted in Figure 7 for the four treatments considered. In general, DFFS predicts lower values than the observed ones and also than those predicted by FIRM. Errors of prediction with DFFS (20.9, 21.9, 8.77 and 8.93% of observed mean for LOW2, LOW3, NORMAL2 and NORMAL3, respectively) are higher than those computed for FIRM. In all cases, the highest proportion of the error is contributed by overall bias (values not shown). As in the case of FIRM predictions, the normal energy diet is better predicted than the low energy diet for both parity groups, and the differences of predictions between FIRM and DFFS are smaller than for the LOW diets.

Observed losses of BCS at the beginning of lactation (values not shown) are much higher than those predicted by FIRM for treatments with the normal energy diet in the MEMO experiment and hence, predicted BCS at the end of lactation are also higher than those observed experimentally for these diets. For treatments with the low energy diet, predicted losses of BCS are close to the observed ones, but the low intake predicted by the model prevents the predicted BCS at the end of the simulation period to be as high as the observed values.

Observed and predicted dry matter intake values for the last group of treatments (9 to 17 from the HEF experiment) are presented in Figure 8. For diets using grass

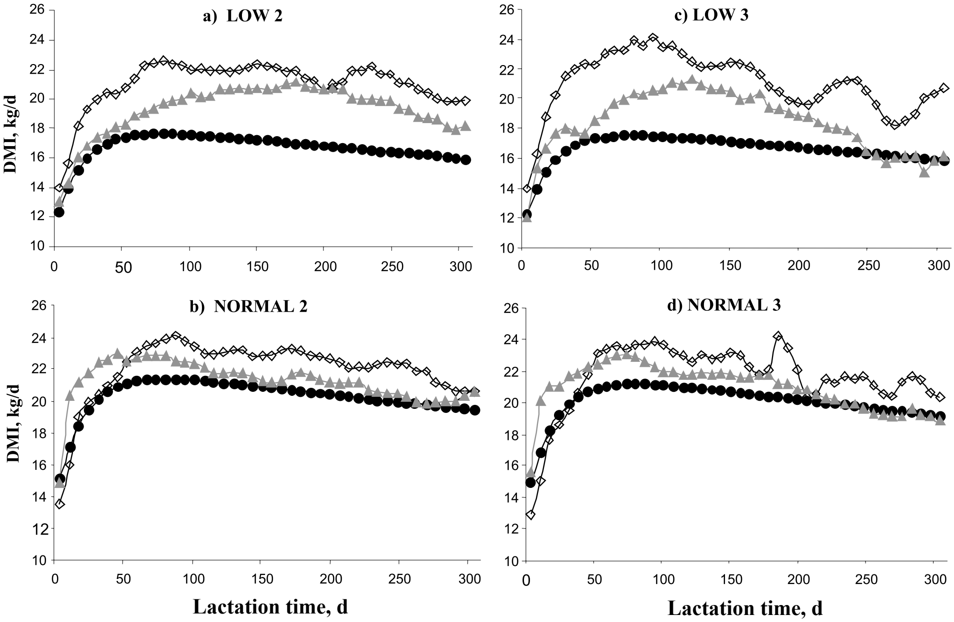


Figure 7 (a, b, c, and d). Observed (-◊-), predicted by FIRM (-▲-) and predicted by Danish Fill Factor System (-● -) weekly mean DM intake during the whole lactation in dairy cows in the MEMO experiment (Ingvartsen and Jensen, 2001). For details see text and Table 2

silage as the forage source, feed intake predicted by FIRM matches almost perfectly with the observed mean values, the error of prediction being very low (RMSPE 0.39 kg DM d^{-1}, i.e. 1.8% observed mean) with an efficiency of modelling close to one (Table 5). Intake is underpredicted, especially in diets with low or medium amount of concentrates, when WCBS or ammonia treated barley straw is used as the forage source. For treatments 12 to 14 (WCBS) (Table 2), the error of prediction is 4.6 as % of the observed mean (0.99 kg DM d^{-1}) and as a consequence, the modelling efficiency is lower (0.58) than in the group of diets with grass silage (Table 5). For the last group of treatments (15 to 17) using ammonia treated straw, the model predicts feed intake with a RMSPE of 1.75 kg DM d^{-1} corresponding to 7.4% of the observed mean, but the modelling efficiency goes to a very low negative value (-11). With grass silage as the forage source most of the MSPE (89%) is caused by error due to deviation of the regression slope from unity, while overall bias (73%) is the most important contributor for the WCBS diets. For ammonia treated straw diets, both sources of error (bias and regression) contributed equally (50%) to MSPE.

Predictions of the Danish Fill Factor System are also plotted in Figure 8 for the nine diets. Grass silage diets are underpredicted by DFFS (2.1 kg DM d^{-1}), but with almost a constant difference between observed and predicted values for

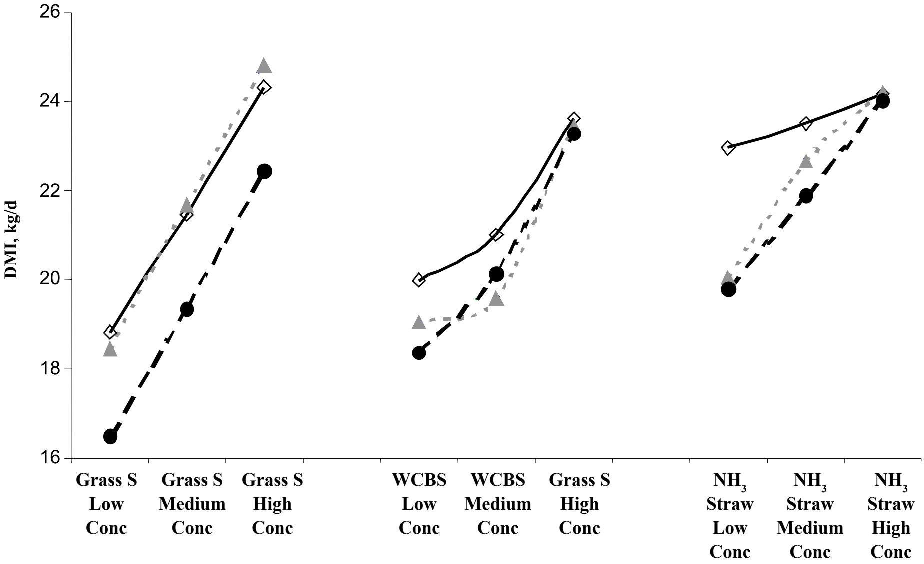


Figure 8. Observed (-◊-), predicted by FIRM (-▲-) and predicted by Danish Fill Factor System (-●-) mean feed intake in dairy cows during a 13 week period with different diets from the HEF experiment (Kristensen, 1999). Grass S = Grass silage, WCBS = Whole crop barley silage, (NH_3) Straw = Ammonia treated barley straw

the three diets. In the cases of treatments with WCBS or ammonia treated barley straw, predictions with DFFS and FIRM are close to each other. Errors of prediction with DFFS expressed as a percentage of the observed mean are 9.79, 5.02 and 8.75 for diets with grass silage, WCBS and ammonia treated barley straw, respectively.

DISCUSSION

Feed intake either throughout the lactation period or as an average for a certain period of it is well predicted by the model for most of the treatments tested. Given that a model validity depends on both the type of model and its intended uses, it would be impractical to set a single absolute value on error acceptability. However, a value of 10% prediction error has been suggested as a reasonable value for acceptance (AFRC, 1990; Volden, 1998). Most of the prediction errors found, either for groups of treatment or for individual treatments, are below the reference value of 10% error (Table 5). An exception to this is the prediction error computed for the LOW3 diet in the MEMO experiment. This also affects the prediction error for the complete data set of MEMO increasing it to 11.2%. However, although the prediction errors could be accepted as reasonable values for the low energy diet, the bias proportion as main contributor to MSPE and the negative values of modelling efficiency for both parity groups indicate inadequate predictions of feed intake for this diet.

In most of the cases when feed intake is predicted throughout the lactation period, the model predicts a typical curve of feed intake (Figures 4 and 7). In general, peak of intake is predicted at about day 90 in lactation in good agreement with observed peak of intake. Exceptions to this are again treatments 5 and 7 with the low energy diet (MEMO experiment). Apparently, this diet constraints the model too much in terms of its capacity for load or fill. This supposition is also valid when analysing the predictions with DFFS because values calculated by this system are also below those measured experimentally. A reasonable explanation for this error is the selection that cows could have made even with a TMR. If this has happened, the proportion of the consumed feed and that offered could have been completely different at least in those parameters determining load or fill, NDF content and proportion of small particles as well as in terms of energy content of the diet. Selection of dietary components in diets containing urea treated whole-crop wheat silage has been reported previously for dairy cows and this selection changed the digestibility of the diet (Hill and Leaver, 1999).

Nevertheless, as mentioned by Neal et al. (1992) differences between predicted and observed values should not be considered as entirely due to inadequacy of the model, because inadequacies of input data describing the diets or errors in experimental measurements could also contribute to these differences.

Over- and underprediction of feed intake occurs for the H-H and H-L treatment from the experiment of Friggens et al. (1998a), respectively. There is no apparent reason for the over- and underprediction of these treatment effects. Perhaps the opposite could be affirmed that there is no reason a priori to expect different intakes for the first 150 days in lactation for treatments H-H and H-L due to the fact that the cows in both treatments consume the same diet and produce almost the same amount of milk. Model predictions for this period are not very different for treatments H-H and H-L and as a consequence one of them is overpredicted and the other is underpredicted when compared with observed values. Feed intake is overpredicted in the L-L treatment especially from 130 to 220 days in lactation displacing the peak of intake from its more natural time of occurrence (around day 90 in lactation) to day 170 in lactation (Figure 4d). The only feasible explanation for this increment in intake, not observed in the experiment, is due to an increment in the milk yield produced during that period. The milk yield was 23.6 l d^{-1} around day 110 in lactation, increased gradually up to 25.9 l d^{-1} at day 170 in lactation and then started to decline. This abnormal increment in milk production induces the model to predict an increment in the feed intake with this treatment and period. However, this explanation contradicts one of the conclusions reported by Friggens et al. (1998a), that the feed intake of cows fed LTMD is not related to current milk yield and does not change with stage of lactation after the first 6 weeks of lactation. Except for the mentioned period in the L-L treatment, results from FIRM are in agreement with the cited conclusion. One of the advantages working with simulation models is the possibility to repeat the experiment as many times as desired without any extra cost, an attribute normally not possible in the real world. The model was run with a corrected data set eliminating the mentioned peak of milk yield with the L-L treatment and a close agreement between observed and predicted values of feed intake was observed. However for the statistical analysis, predictions with the original data set of milk yield are reported here.

One of the objectives when choosing the first group of treatments (1 to 4) to test FIRM, was to see if the model is able to predict changes in intake when the diet is changed during lactation. Predicted changes in DMI in response to a change in the given diet are prompt as were observed experimentally. The curve of observed feed intake when changing from LTMD to HTMD is well matched by the predicted values (Figure 4c). For the H-L treatment a reduction in feed intake is also predicted by the model at the right time, although the simulated decrease is lower than observed *in vivo* (Figure 4b).

In general, feed intake is well predicted for all experiments carried out by Friggens et al. (1998). However, FIRM was developed using different assumptions about feed intake regulation (see Petruzzi and Danfær, 2004). Friggens et al. (1998a) have used the concepts of feed intake regulation developed by Conrad et al. (1964) and later expressed mathematically by Mertens (1987) to explain the observed intakes. These concepts are based on the assumption that when cows are fed a low quality diet, the intake is a consequence of physical regulation whereas intake is determined by energy requirements or subject to physiological constraints when a high quality diet is fed. The most critical weakness of these concepts have been pointed out by Weston (1996) and dismissed through a literature review (Pittroff and Kothmann, 1999) as well as by experimental work (Huhtanen et al., 2002; Rinne et al., 2002) as a valid hypothesis to explain feed intake regulation

FIRM, using both milk yield and stage of lactation as inputs predicts a rapid decline in feed intake when the HTMD was replaced by the LTMD diet. FIRM also predicts constant intake when cows were fed the LTMD diet even when milk yield was constantly declining. Both these predictions were expected to fail by Friggens et al. (1998a) when models using milk yield or stage of lactation as inputs to control rumen fill were used to predict intake.

When increasing amounts of concentrates were included in the diet (treatments 9 to 17 from the HEF experiment), an increment in feed intake is predicted by the model for the different forage sources in agreement with observed values. Total DMI increases with increasing proportions of concentrates in the diet (Ferris et al., 1999a,b; Huhtanen et al., 2002). For dairy cows fed grass silage, Ferris et al. (1999b) reported increments in DMI from 18 to 22 kg DM d^{-1} when the proportion of concentrates increased from 0.37 to 0.7. These values are close to the predicted DMI for grass silage based diets with similar levels of concentrates (Figure 8). However, Maekawa et al. (2002) found no difference in intake when cows were fed a whole-crop barley silage with 40 to 60% of concentrates. The model predicts small increments in intake when low (38%) or medium (53%) amounts of concentrates were added to a diet based on whole-crop barley silage, but with further increment of concentrates the simulated as well as the observed DMI is increased much more. Differences between predicted and observed values for the treatments containing ammonia treated straw should be taken with precaution because in spite that the diets were fed as TMD, dietary selection in favour of the concentrate fraction was observed with the diets low in concentrates (Kristensen, 1999; Weisbjerg, personal communication).

CONCLUSIONS

The developed feed intake regulation model simulates feed intake with an acceptable degree of accuracy for a wide range of different diets and milk yields.

Concepts on which the model was developed seem to constitute an acceptable theory on which feed intake regulation can be explained. Mechanistic modelling of those principles is possible as demonstrated by the functionality of the present model.

However, additional simulation work needs to be done to improve or complete areas on which the present model has not been well developed. The inclusion of the principles of feed intake regulation of the present model into a more complete animal model, like the Karoline model (Danfær, 1998) may save both time and modeling efforts and contribute to accuracy of predictions.

Additional evaluation using results from experiments specifically designed to test the model would contribute to further improvements of the present model.

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STERSZCZENIE

Dynamiczny model regulacji pobrania paszy dla krów mlecznych. Weryfikacja modelu

Celem pracy była ocena modelu regulacji pobierania paszy przez krowy mleczne, opisanego w poprzedniej części pracy. Analiza odporności wykazała, że model jest „czuły" głównie na te parametry, które definiują górną granicę poziomu NDF w treści żwacza. Poziom odporności modelu zmienia się wraz ze zmianą zawartości energii w badanej dawce i w zależności od stadium laktacji, w którym jest przeprowadzana analiza weryfikacyjna. Całkowita liczba siedemnastu dawek z serii doświadczeń została wykorzystana do porównania obserwowanego pobrania paszy i oceny kondycji zwierzęcia (BCS) z predyktorami tych zmiennych uzyskanymi na podstawie modelu. W przypadku większości dawek, pobranie paszy w całym okresie laktacji lub w jej części (średniej wybranego okresu) jest z satysfakcjonującą dokładnością przewidywane przy użyciu tego modelu. Dla większości dawek, opierając się na proponowanym modelu, uzyskano typowe krzywe pobrania paszy. Dokładność predykcji BCS zależy od konkretnej dawki. Generalnie jednak, straty BSC przewidywane są na początku laktacji, podczas gdy w następnych fazach wartość cechy stopniowo wzrasta. Satysfakcjonujące współzależności między przemianami energii a obciążeniem żwacza procesami trawiennymi sprawiają, że modele mechanistyczne mogą być rekomendowane jako modele regulacji pobrania paszy.