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CHAPTER 17

Evaluation and use of a growth and lactation model

with Lane Ely and K. C. Donovan

There has been a tendency to apply excessively simple economic and applied mathematics to complicated biological problems and, in the process, lose the richness that's implicit in the biology. And, the potential economic gains that are available if the richness is taken into account are lost too.

J. R. Black (personal communication)

17.1 INTRODUCTION

The objectives of this chapter are to illustrate the behavior of the lactating dairy cattle model described in Chapter 16, present sensitivity analyses of effects of varying some key parameter values in the digestion and animal elements and, finally, illustrate the types of data that a dynamic, mechanistic model can generate in support of risk analyses appropriate to evaluations of alternate feeding management strategies as a component of enterprise management.

17.2 BEHAVIORAL ANALYSES

As discussed in previous chapters, behavioral analyses of models are normally undertaken for two reasons. The first is to determine whether or not a model contains provisions adequate to simulation of variance observed in reality. The second is to determine whether or not a model can accurately simulate reality or, as it stands, be used for predictive purposes. Both positive and negative examples will be considered in this section, which illustrate limitations and strengths of the model. Effects of diet and feeding management strategies will be considered in the final section of the chapter. Sensitivity analyses, similarly, can be used for several purposes. One of these is to determine what data are required to estimate parameters not directly measurable using current methods. A related use of sensitivity

analyses is evaluations of possible effects errors in specifying input parameter values can have upon behavior of not only the specific metabolic equation in which it is used, but also behavior of the total system modeled. This later use of sensitivity analyses will be illustrated in this section.

The digestive element of the Baldwin *et al.* (1987b,c) model was expressly developed to provide best estimates of rates of nutrient availability to the animal element (Baldwin *et al.*, 1987a,c), which was the primary focus of that modeling study. It was clearly stated (Baldwin *et al.*, 1987b) that when experimental data on rumen digestion coefficients, microbial growth yields and digestible and metabolizable energy values of feeds used in a specific study, proportions of volatile fatty acid (VFA) formed, etc., were available, model parameters should be adjusted accordingly to provide more accurate estimates of nutrient availabilities to the simulated animal. Several specific limitations of the digestion element were identified. One was that rate constants for hydrolysis of hemicellulose and cellulose were based on data for dry legumes and may not apply to dried grasses, silages or fresh forages. A second was that rumen digestion coefficients for starch on high concentrate diets were too high. The stoichiometric coefficients for high concentrate diets did not account for systematic errors in predicting molar proportions of acetate and propionate production as percentage of concentrate in the diet increased. This source of systematic error was identified by Murphy *et al.* (1982), as discussed in Chapter 8.

Addition of provisions for monitoring rumen pH in the model and representing effects of pH upon fermentation rates and patterns in the model (Chapter 16; Argyle and Baldwin, 1988; Baldwin and Argyle, 1988) helped correct errors in predicting rumen digestion coefficients at high concentrate intakes. As rumen pH decreased (Fig. 17.1a) from 6.25 to 5.5, the respective rumen digestion coefficients for cellulose, starch and organic matter decreased from 0.52, 0.69 and 0.73 to 0.0, 0.56 and 0.59. As a result of these changes and a direct effect of pH on microbial maintenance requirements, microbial growth (Fig. 17.1b) decreased from 2.55 to 1.43 kg/day. Also, cellulose passage increased from 1.54 to 3.24 kg/day (not shown) and the overall ME value of the feed decreased from 10.9 to 9.4 MJ/kg.

Estimates of digestible and urinary energy output by the model (Chapter 16) contain a systematic error due to the simplified representation that microbial nucleic acids are all output in feces rather than a portion in urine and the remainder in feces. This simplification is canceled out in estimates of ME output by the model. Thus, it is valid to challenge ME but not DE values produced by the model. The result of such a challenge is presented in Fig. 17.2(a). There are a number of possible reasons for differences between observed and predicted values in a comparison of this type, including experimental and animal variance, errors in evaluating data on diet composition in formulating diet inputs to the model and model errors. In view of these potential sources of error, the r^2 value of 0.85 indicates acceptable agreement and the lack of discernible systematic error of prediction is

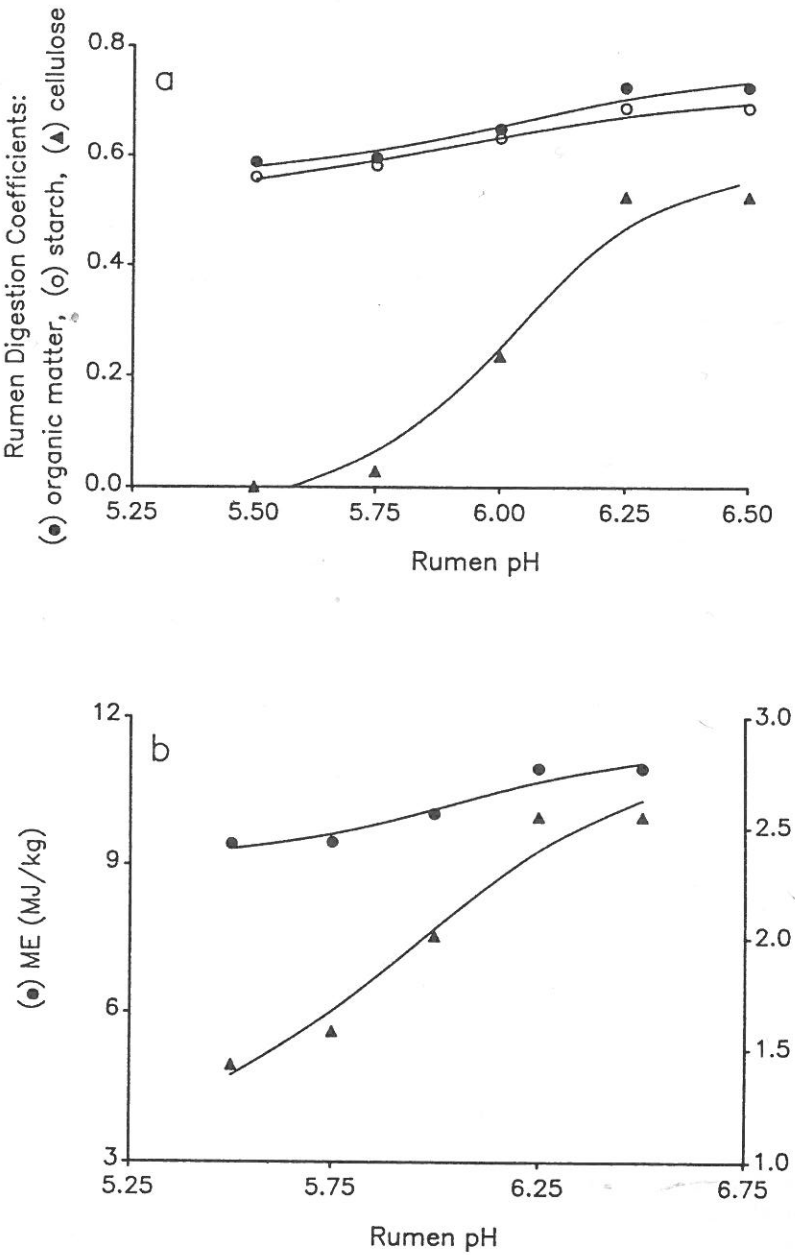


Figure 17.1 Effect of rumen pH on several digestive functions. Effects of pH were simulated by setting FIXPH (Chapter 16) to values specified on the *x*-axis. The model was for a 600 kg lactating cow fed 18.0 kg of the default diet specified in Chapter 16. Data are for day 14 of simulation.

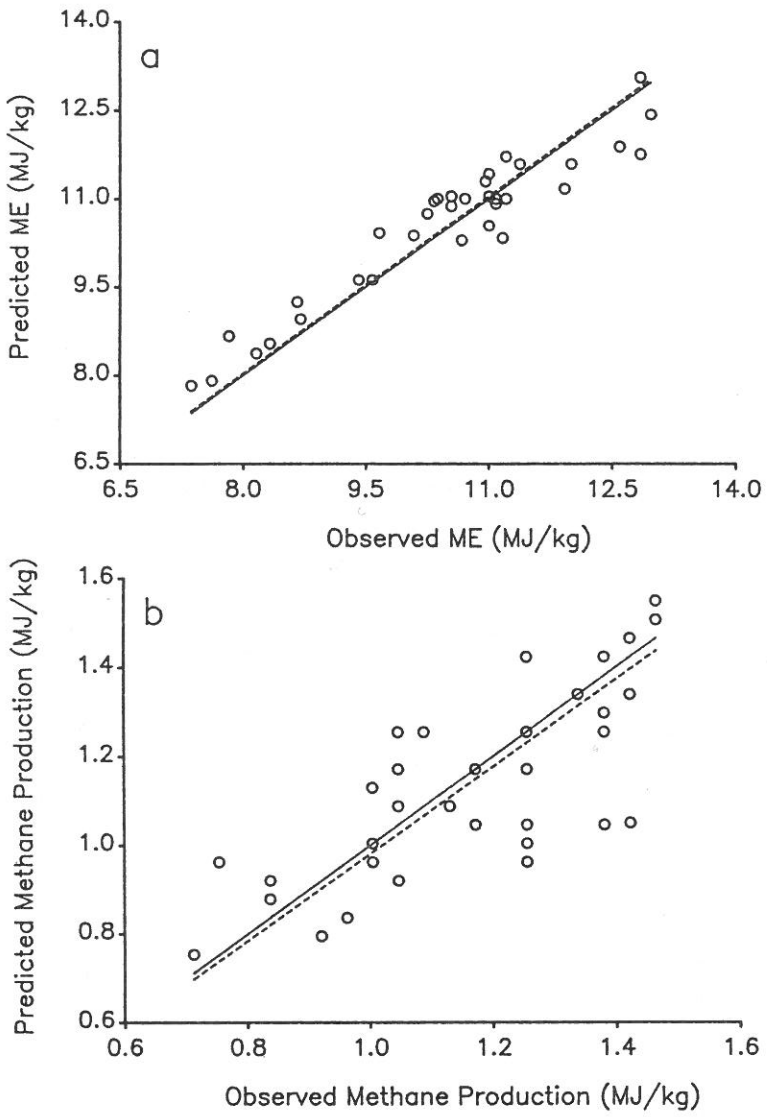


Figure 17.2 Comparisons of predicted versus observed estimates of (a) metabolizable energy and (b) methane production. Regression equations for best fit lines (—) were $y = a + bx$ *with* r^2 values for ME and CH_4 of 0.85 and 0.60, respectively. Regression equations for lines of equality (- - -) were $y = bx$. The 34 experimental estimates were reported by Armsby and Fries (1915), Armstrong (1964), Armstrong *et al.* (1958, 1964), Blaxter (1967), Blaxter and Clapperton (1965), Colovos *et al.* (1970, 1979), Coppock *et al.* (1964), Flatt *et al.* (1967), Graham, *et al.* (1958), Moe *et al.* (1972), Moe and Tyrrell (1976, 1979a,b), Moe *et al.* (1973a,b), Tyrrell and Moe (1972) and Tyrrell *et al.* (1976) for diets including high and low quality legume, corn silage, corn meal, soybean meal, and high and low quality grass hays.

gratifying. The addition of provisions for the use of different hydrolytic rate constants for cell-wall constituents of legumes, grasses and silages, for pH effects, and for the separate consideration of hemicellulose and cellulose clearly contributed to an improvement in model behavior, since r^2 values over the range of diets depicted in Fig 17.2(a) in the absence of these changes were in the 0.4–0.5 range.

Estimates of methane emissions across feeds are influenced by a number of factors, including diet composition, digestion in the rumen, patterns of VFA formed and microbial growth yields. Because of the complex interplay of factors that influence methane emissions, a comparison of observed and predicted estimates for the diets used to formulate Fig. 17.2(a) was undertaken. The results are presented in Fig. 17.2(b). Causes of differences among observed and predicted values are the same as those noted for ME estimates above, although it should be noted that animal variance expressed as coefficients of variation are significantly greater for methane as compared to ME estimates. Percentages of digestible energy lost as methane range from 6 to 13% and are calculated in the model (Chapter 16) based upon hydrogen left over after VFA patterns and yields and microbial growth are computed. As a result, small errors in computing rumen digestion coefficients and fermentation products other than methane can have major (percentage) effects upon estimates of methane loss. In view of these considerations, the r^2 value of 0.60 with only a small bias from the line of equality (Fig. 17.2b) is very encouraging. The semi-empirical equations (e.g. the equations contain mechanistic elements but were fit statistically) of Blaxter and Clapperton (1965) and Moe and Tyrrell (1979b) are commonly utilized to estimate methane emissions by ruminant livestock. When these equations are applied to predict methane emissions for the same data set used in Fig. 17.2(b), r^2 values of prediction were significantly below 0.6. Exact r^2 values are not presented because direct comparisons are inappropriate. The Blaxter and Clapperton (1965) equation was fit to forage diets and the Moe and Tyrrell (1979b) equation was fit to mixed, (largely) dairy cattle diets. Thus, these should not be challenged using rations beyond those within range with the data sets used to fit the equations.

Diets containing whole and cracked corn were excluded from the comparisons presented in Fig. 17.2(a and b). The model presented in Chapter 16 incorporates the concept that starch solubility influences rate of starch hydrolysis. This was implemented by specifying as an input the fraction of dietary starch that is water soluble (StSol), different rate constants for hydrolysis of soluble and insoluble starch, and differing rate constants for passage of soluble nutrients, including starch with water (StSol * k_{WaP}) and small particle (Sp) material (SpSt * k_{SpP}). The rate terms k_{WaP} and k_{SpP} were constants in the original model. Modifications in water dynamics (Argyle and Baldwin, 1988) and addition of dry matter intake as an effector of k_{SpP} (Chapter 16; Knapp, unpublished) enabled adequate simulations of RDCHa estimates obtained at moderate intakes of corn, barley and wheat

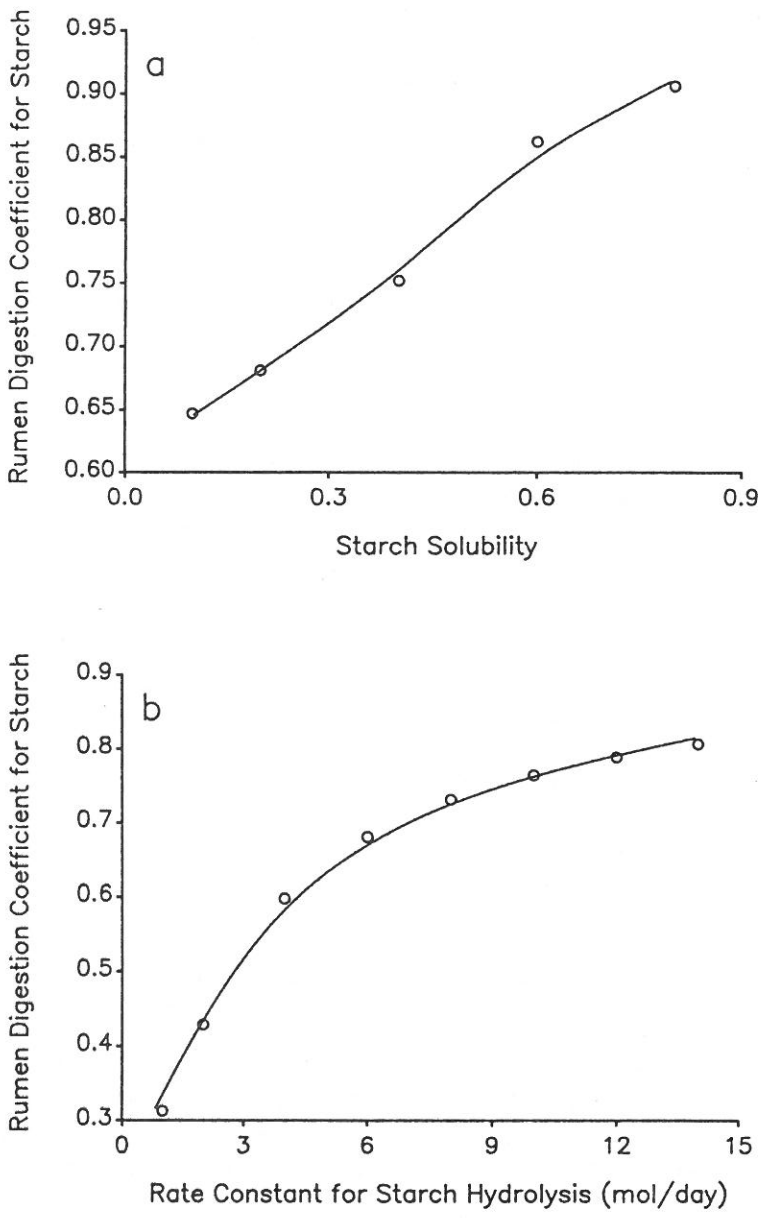


Figure 17.3 Effects of (a) starch solubility (StSol) and (b) changes in the rate constant for particulate starch hydrolysis (k_{HaCs}) on the rumen digestion coefficient for starch (RDCHa). Estimates of starch solubility were obtained using the default value of 6.0 for k_{HaCs}. Effects of varying k_{HaCs} were estimated using a StSol value of 0.2 for the default diet (Chapter 16). Other simulation inputs were as described for Fig. 17.1.

over the range from 0.65 to 0.9 (Fig. 17.3a). However, at the high feed intakes of high producing dairy cows fed milo and cracked corn-based rations (Herrera-Saldana *et al.*, 1990; Klusmeyer and Clark, 1991), RDCHa estimates were in the range of 0.45 and could not be simulated. These observations can be reproduced if, in addition to specifying starch solubility as a determinant of RDCHa, different values for the hydrolytic rate constants for starch (k_{HaCs}) are input for each diet (Fig. 17.3b). This is not at all satisfying from the mechanistic point of view. This is acceptable in applied models and was the approach adopted in formulating the Cornell Net Carbohydrate and Protein System (Search:Agriculture, 1990) wherein values for RDCHa are specified as input and differ dependent upon intake and the grains and processing procedures used. Ewing and Johnson (1987) developed a dynamic simulation model of corn starch digestion. In this, particulate starch digestion, passage and size reduction rates were described for five particle sizes. When *in vitro* and *in situ* (nylon bag) data were used to parameterize the model, rumen and total tract starch digestibilities were significantly underestimated, which indicated that *in vivo* estimates are essential to the development of improved representations of the digestion of not only corn but all cereal starches. These observations clearly emphasize the need to identify and quantitatively evaluate the chemical and physical properties of starch that influence degradation in the rumen and incorporate these into the model.

The use of high (added) fat diets in the dairy cattle industry is relatively recent. Initial simulations of effects of high fat intakes were compatible with early experimental data in the sense that milk yields and partial efficiencies of milk production were increased, while milk proteins yields were decreased slightly. However, as experimental data accumulated, it became apparent that the model was producing correct answers for the wrong reasons. Rumen digestion coefficients for fiber components were reduced in simulations due to decreases in amounts of microbes in the rumen, but the decreases were, generally, not as great nor variable as those observed experimentally. Further, the decreases in milk protein yields simulated were due to decreases in amounts of fermentable substrates available in the rumen and concomitant decreases in microbial growth yields, while accumulating experimental data indicated that microbial growth yields were not depressed by high fat diets. This led to modifications in the model (Chapter 16), which included addition of feed fat (FdFat) as an inhibitor of cellulose and hemicellulose (Hc, Cs) hydrolysis as in equation 17.1 and as a positive effector of microbial growth (equations 17.2 and 17.3).

$$U_{Hc,Cs} = k_{Hc,Cs} * (1.0 - (FdFat * FdLi^{-1} * k_{FaHb,Cs})) * Hc * cMiHb \quad (17.1)$$

$$Mi_G = (ATP_F - ATP_M) * Y_{ATP} * FAM_G * FFa_G \quad (17.2)$$

$$FFa_G = 1.0 + FdFat/FdLi * k_{Fa,ATg} \quad (17.3)$$

From a mechanistic point of view, these equations must be considered

arbitrary since they are not based upon direct experimentation. Direct observations are not available that FdFat effects the rate constant for hemicellulose ($k_{Hc,Cs}$) as well as cellulose hydrolysis, rather than reduces the concentration of microbes associated with cell walls (cMiHb). Similarly, well substantiated data indicate that availability of ammonia (FAM_G) is an effector of microbial growth yields, while direct FdFat effects on the efficiency of microbial growth are virtually nonexistent. One can postulate that high fat diets decrease protozoa and protozoal predation on bacteria with a result of increased net yields, however, direct measurements are not available. In view of these uncertainties, parameter values used to implement the FdFat effects were set in a very conservative fashion.

Behavior of the model with these equations incorporated is illustrated in Fig. 17.4(a and b). When the values of $k_{FaHb,Cs}$ and $k_{Fa,ATg}$ in the model were set to the default value of 0.03, fat effects were minimal, because reductions in rate constants for cellulose and hemicellulose hydrolysis were balanced or offset by the increase in microbial growth (results not presented). Results for the $k_{FaHb,Cs}$ values of 0.06 and 0.09 are presented in Fig. 17.4(a and b) to illustrate the simulated responses to feed fat. When values for $k_{FaHb,Cs}$ were set at 0.06 and 0.09, respectively, decreases in the rumen digestion coefficients for cellulose (RDCCe) were 0, 8 and 18% at the highest (8%) rate of fat addition (Fig. 17.4a). Over the same range of diets, respective reductions in concentration of blood lipids (cFA) and overall digestion of organic matter were 0, 8 and 11% and 0, 1.5 and 3.4% (Fig. 17.4a). Further, the responses were not linear with regard to dietary fat content. As expected, diet ME values, microbial growth and the transfer of blood lipids increased as dietary fat increased (Fig. 17.4b).

The characteristic depression in percentage protein in milk associated with fat feeding was not observed in the simulation analyses. Cant *et al.* (1993a,b) presented data suggesting that the depression in milk protein yields on high fat diets may be attributable, at least in part, to reduced rates of blood flow to the mammary glands. The current model is based on the concept that metabolic activities of organs and/or products of metabolism are primary determinants of local rates of blood flow (Chapter 6). The results of Cant *et al.* (1993a,b), might be compatible with this concept if one argues that the efficiency of milk fat synthesis is increased in fat-fed cows to the extent that venous bicarbonate produced per liter of milk synthesized is reduced. This causes, in turn, a decrease in blood flow per liter of milk and a decrease in amounts of amino acids available per liter of milk produced. The model, as currently configured, cannot respond to a subtle change in signal such as this. Clearly, further experimental and modeling research are essential to resolution of these issues.

The limitations in the starch and feed fat elements of the model were presented early in this chapter to emphasize that the development of research models is an evolutionary process and behavioral analyses are an important tool for use in identifying priorities for further research.

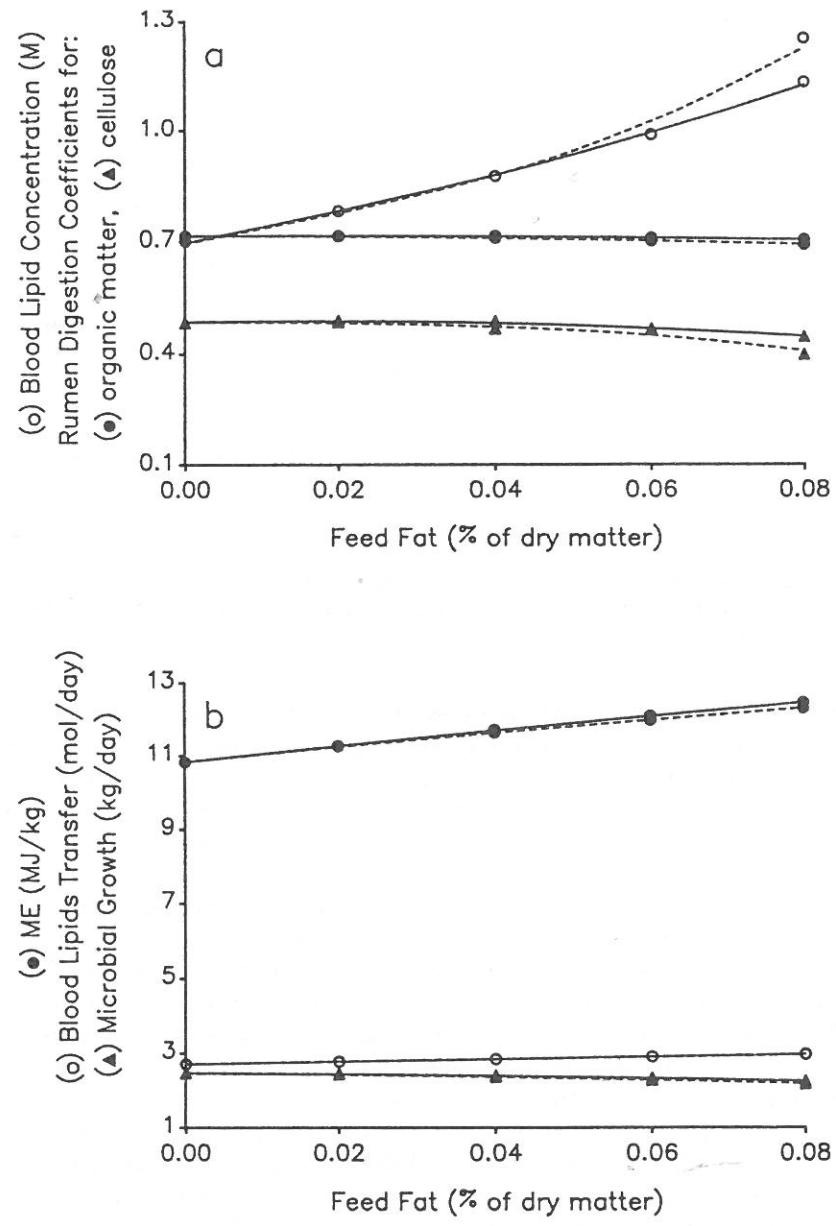


Figure 17.4 Behavior effects of dietary fat when $K_{FaHb,Cs}$ is set to 0.06 (——) and 0.09 (- - -) upon (a) rumen digestion coefficients for organic matter and cellulose and blood lipid concentration; and (b) metabolizable energy, blood lipid transfer and microbial growth. Feed fat (FdFat) inputs were calculated as substitutions of fat for starch in the default diet in Chapter 16. Other simulation conditions are as described for Fig. 17.1.

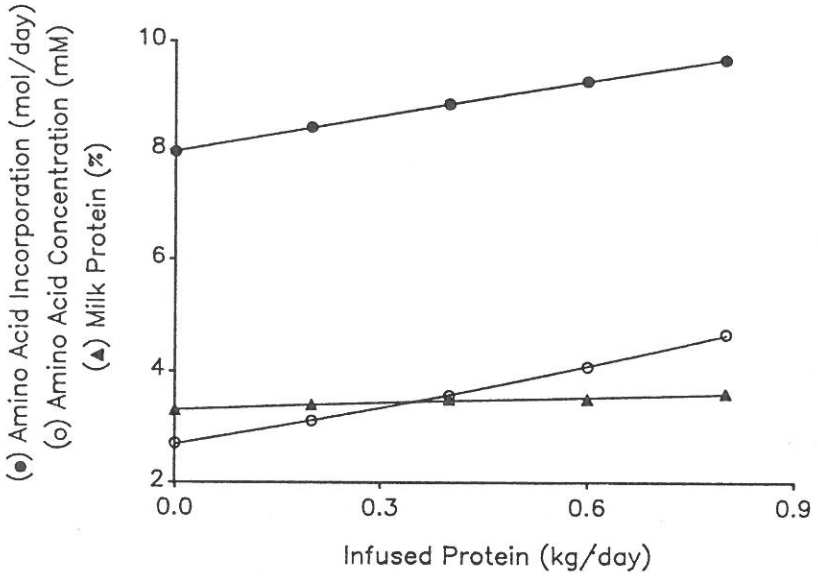
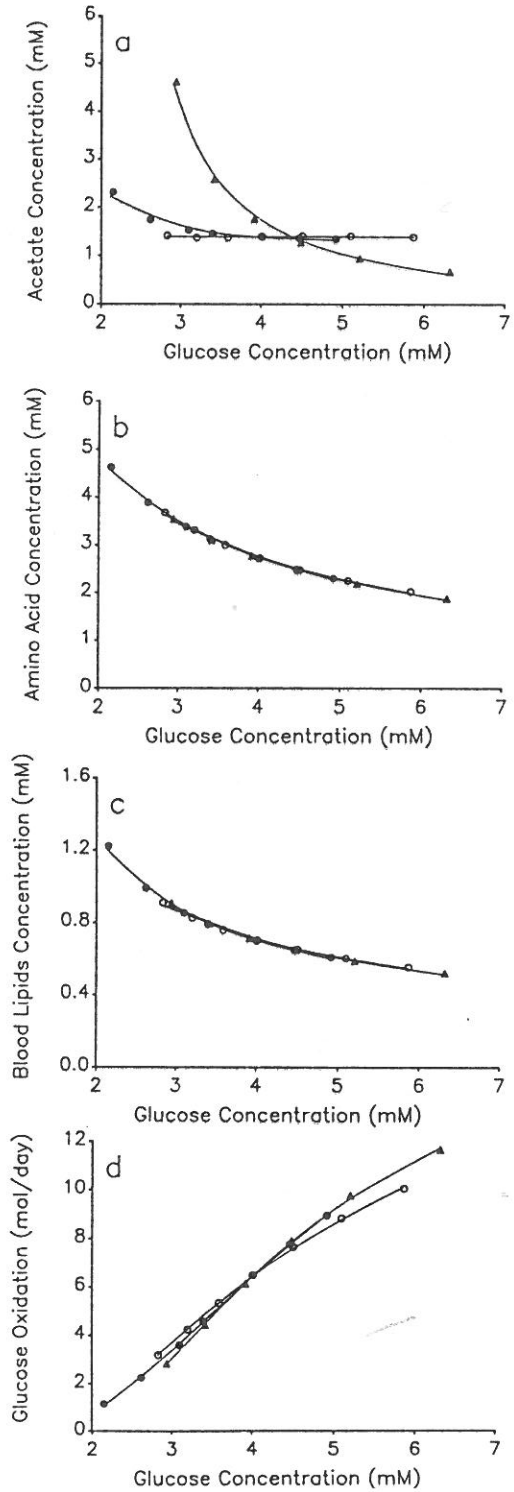
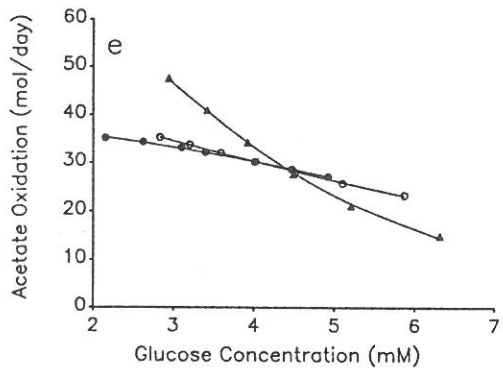


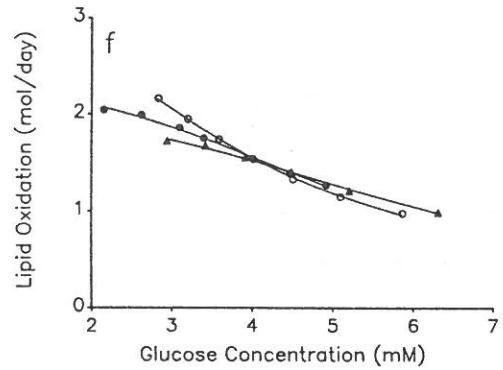
Figure 17.5 Effects of protein infusions per abomasum on milk protein synthesis. Infusions were in addition to 18 kg/day of default diet fed to a 600 kg lactating dairy cow as described in legend to Fig. 17.1.

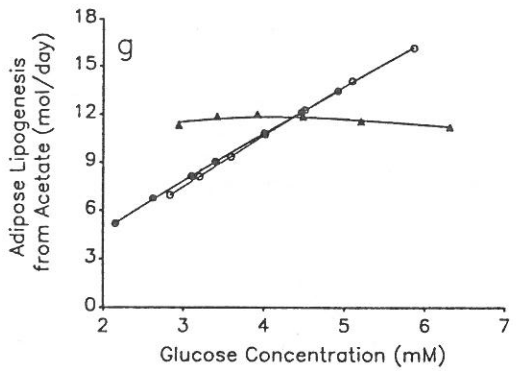
Whitelaw *et al.* (1986) among others reported that supplementation of lactating cows with formaldehyde-treated casein or casein per abomasum increased milk production 10–20%. Simulation results indicated increases in circulating amino acid concentrations and amino acid incorporation into milk protein (Fig. 17.5). The latter observation along with the indication that milk protein percentage did not change significantly indicates a milk yield increase of about 20%. In contrast, Cant *et al.* (1993a) observed a small increase in milk protein percentage when casein was infused and a lesser increase in milk production. All studies indicate an increase in milk protein yields when casein is infused. Some indicate that this is due to increases in milk yields and others that this is due to increases in milk protein percentage (Cant *et al.*, 1993a). Thus, this simulation result and the variable experimental results require further examination.

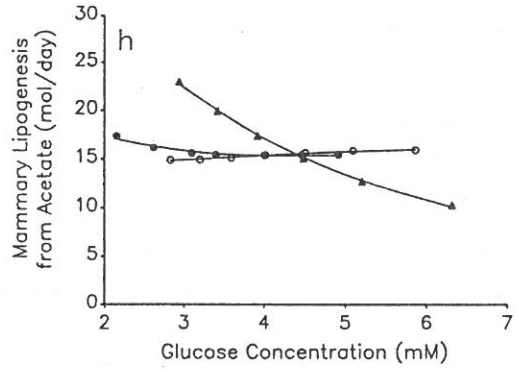
The several panels in Fig. 17.6 are different from but somewhat analogous to those presented by Baldwin *et al.* (1987a) to illustrate behavior of the original model. The analyses were repeated using the current version because of the many changes incorporated as the model evolved. Effects of three manipulations of the model were undertaken. In the first case, the differential equation for glucose was set to zero (DGl = 0.0) and glucose concentration (cGl) was specified as input. Availabilities of other nutrients were those normally produced during the digestion of 18 kg/day of the default ration (Chapter 16) fed to a 650 kg cow in mid-lactation. In the second test case, the equation for propionate absorption was set to values

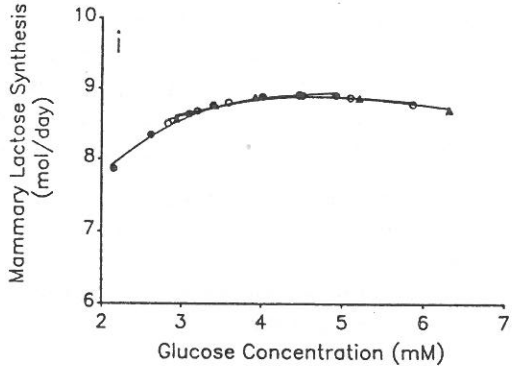












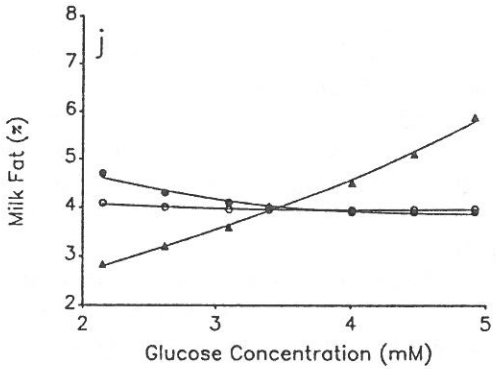


Figure 17.6 Effects of glucose concentrations (cGl) in blood produced by specifying cGl as input (case 1, ●), infusing propionate (case 2, o) and isoenergetic substitution of propionate for acetate (case 2, ▲). Other inputs were as described in text and legends to Fig. 17.1.

specified as input. This manipulation altered both propionate absorption rates and energy availability. The third test case involved specifying both acetate and propionate absorption to produce isoenergetic changes in the availabilities of these two nutrients.

Baldwin *et al.* (1980) noted that, although data compiled from radiotracer experiments conducted both *in vivo* and *in vitro* and some, but certainly not all, arteriovenous difference studies of tissue nutrient uptakes (see Chapter 13) clearly indicate that Michaelis–Menten saturation-type kinetic equations best fit most data sets, considerable variance is not accounted for when such equations are applied to data compiled from experiments with different diets, animals and conditions. By way of supporting the concept that dynamic, mechanistic simulation models can be utilized as an effective tool in research, Baldwin *et al.* (1980) suggested that interactions among nutrients contribute to the unexplained variance and that such models should/must contain provisions adequate to explain this variance. In accord with this view, Baldwin *et al.* (1987a) undertook the behavioral analyses. Similar analyses are presented in Fig. 17.6. It is impossible to generate the large number of experimental data essential to quantitative assessments of model behavior depicted in the figure. The questions addressed are:

1. Does the model contain provisions (note that most equations are based on lower level data and concepts, e.g. mechanistic) adequate to accommodate observed variance in the intact system?
3. Are the simulated interactions among nutrients consistent with both informed conceptual analyses and the sparse data sets currently available?

A redeeming virtue of the model predictions presented is that most can be challenged using existing experimental technologies and such challenges are totally appropriate. Unfortunately, the required experimental challenges are quite laborious and expensive.

The response profiles depicted in Fig. 17.6 indicate that the model contains provisions capable of accommodating a range of interactions among metabolites, hormones and energy status and can explain variance (scatter in experimental data), which was the challenge posed above. The response profiles will only be discussed in a general sense here, since detailed analyses would be redundant with concepts, interactions and responses discussed in previous chapters.

Effects of varying glucose concentrations (cGl) on concentrations of acetate (cAc), amino acids (cAa) and blood lipids (cFA) are presented in Fig. 17.6(a–c). These effects are important because concentration changes influence the rates of many reactions in the model. In the first test case, cAc decreased as glucose increased, because lipogenesis from acetate in adipose tissue (AcTsF) increased (Fig. 17.6g). This increase more than offset decreases in acetate oxidation (AcCd; Fig. 17.6e) and mammary lipogenesis from acetate (AcTm; Fig. 17.6h). The latter decrease caused a small depression of milk fat percentage (PTm) (Fig. 17.6j). In the second case, changes in AcCd, adipose (AcTsF) and mammary gland (AcTm) lipogenesis balanced out such that cAc was not altered. The isoenergetic substitution of propionate for acetate (case 3) produced, as might be expected, the greatest changes in cAc, AcCd, AcTm and PTm (Fig. 17.6a, e, h and j) and had only a minor effect on AcTsF (Fig. 17.6g). All increases in cGl caused amino acid concentrations (cAa) to decrease (Fig. 17.6b). Milk yields and milk protein content were not changed significantly by the simulated treatments (not shown). Thus, the major cause of the decrease in cAa was increased rates of synthesis of visceral and body proteins. Concentrations of blood lipids (cFA) also decreased as glucose increased in all three cases (Fig. 17.6c). Basic causes were decreased lipolysis and increased fatty acid re-esterification in adipose tissue at higher glucose concentrations. As circulating glucose concentrations increased glucose oxidation (GlCd) increased (Fig. 17.6d), while AcCd and lipid oxidation (FaCd) decreased (Fig. 17.6d, e and f). These changes were driven primarily by relative changes in concentrations, but as emphasized above, these changes clearly illustrate that the model has the capacity to explain the scatter of data observed when results of multiple experiments are compiled to evaluate effects of nutrient concentrations in blood upon rates of nutrient oxidation. Rates of lactose synthesis in mammary tissue were not very sensitive to changes in cGl (Fig. 17.6i). This lack of sensitivity reflects the fact that amino acids are required for the synthesis of α-lactalbumin, which is required for lactose synthesis (Chapter 16). As a result, the increases in glucose concentration are counterbalanced by the associated decreases in cAa.

Simulated effects of acetate concentration upon metabolism are presented in Fig. 17.7. These results were produced by setting the differential equation for acetate to zero and specifying the acetate pool size as input. Availabilities of other nutrients were simulated for a 650 kg lactating cow fed 18 kg/day of the default diet (Chapter 16). As increases in the acetate pool size were specified, energy availability to the animal increased. Thus, the responses depicted reflect both changes in acetate concentration and energy balance. As acetate concentration was increased, acetate oxidation (AcCd) and both adipose (AcTsF) and mammary gland (AcTm) lipogenic rates increased. Glucose oxidation decreased as would be expected (not shown). Rates of blood lipid incorporation into milk fat (FaTmV) were relatively unaffected, therefore the increased percentage fat in milk (PTm) is totally attributable to the increase in mammary gland lipogenesis.

Several effects of varying feed intake are presented in Fig. 17.8. Rates of body energy loss (– EB) and fatty acid oxidation (FaCd) decreased as feed intake increased. The mobilization of body energy was not adequate to sustain milk production (milk energy; NEp). The concentration of acetate in blood (cAc) increased as rates of absorption of energy (absE) and acetate (absAc) increased. These responses are consistent with what a worker in the

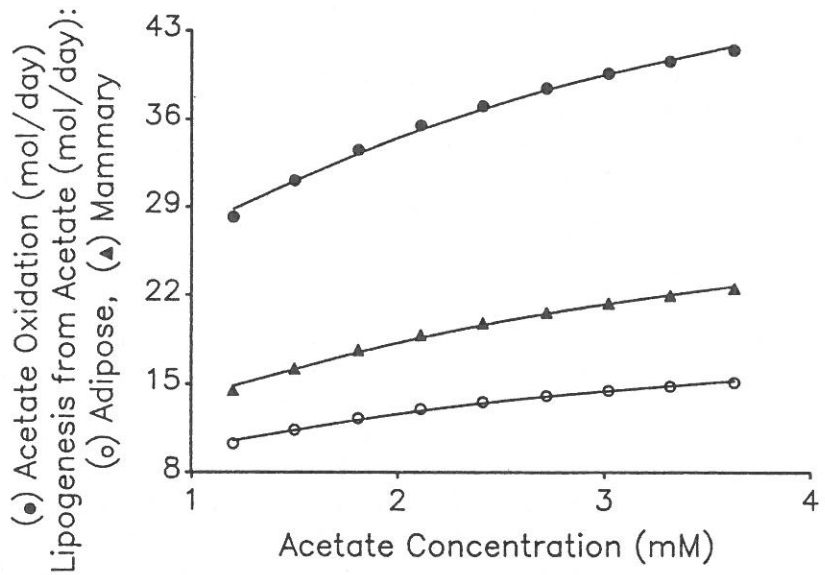


Figure 17.7 Effects of acetate concentration (cAc) in blood specified as input. Other inputs as described for Fig. 17.1.

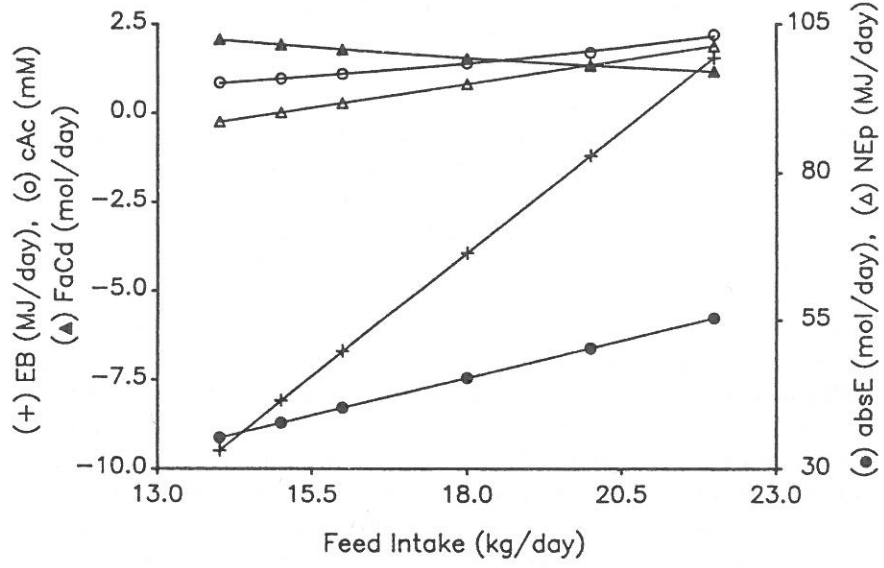


Figure 17.8 Effects of varying feed intakes of default diet. Other simulation conditions as described for Fig. 17.1. Codes are defined as body energy loss (EB), fatty acid oxidation (FaCd), energy absorption rate (absE), blood acetate concentration (cAC) and milk energy (NEp)

area would expect and agree, in general magnitude, with experimental data. However expected these results may be, it is essential that such simulations be included in behavioral analyses to assure that overall quantitative relationships are appropriate.

17.3 SENSITIVITY ANALYSES

As emphasized in Chapter 4, sensitivity analyses are undertaken for a number of reasons. An important reason is to determine whether or not and how sensitive solutions of a model are to key parameter values. This issue will be addressed in this section. A lack of (expected) sensitivity would be held suspect as would excessive sensitivity. Either of these results normally leads to re-examination of the model. Neither of these results is infrequent. They are usually unexpected and, thus, are important in model evaluations. An intermediate result is more acceptable and reassuring but, of course, does not in and of itself constitute proof that a given equation and associated parameter values adequately capture the degree of reality required by a given modeling objective. In this sense, 'undesired' results in sensitivity analyses help identify defects in concepts and data incorporated into a model and, as a result, are useful. 'Desired' results are nice but not overly informative, except for the very important fact that the accuracy with which a parameter value must be defined assures acceptable simulation outputs. 'Undesired' results of sensitivity analyses were encountered and addressed during development of the model presented in Chapter 16. Therefore, emphasis in this section will be upon the accuracy with which parameter values in the model must be known.

17.3.1 Digestion elements

The unique ability of ruminants, conferred by virtue of microbial digestion in the forestomachs, to convert plant fiber to human edible foods is dependent upon two rate constants in the model; the respective rate constants for cellulose (kCeCs) and hemicellulose (kHcCs) hydrolysis by microbes associated with particulate forage cell walls. Effects of varying kCeCs upon rumen digestion coefficients (RDC__) for cellulose (__Ce), hemicellulose (__Hc) and starch (__Ha) are depicted in Fig 17.9. The increase in RDCCe was, of course, expected. The lesser increase in RDCHc reflects the fact that cellulolytic microbes growing in association with small particles hydrolyze both cellulose and hemicellulose. The even more modest increase in RDCHa reflects the growth of microbes other than the cellulolytics on hydrolytic products of hemicellulose and cellulose hydrolysis. The response profiles are not linear because the positive feedback produced as a result of increased fiber digestion results in increased amounts of microbes closely associated with the cell wall fraction. These, in turn, increase rates of cellu-

lose and hemicellulose digestion and microbial growth up to a maximum determined by the rates of entry of cell wall constituents to the small particle pool, rates of hydrolysis and rates of passage (Chapter 16). Given that a positive feedback exists, one might expect that the rate constants for cellulose and hemicellulose hydrolysis would have to be specified with a high degree of accuracy for each feedstuff. This would create great difficulty in developing a generally applicable model, since a great number of data not currently available would have to be collected. In fact, collection of the large data set implied by acceptance of this notion would be economically unfeasible. The values specified for kCeCs in the current model are 6.0 for leguminous and 9.0 for grass forages. These two values were used to develop the regression relationships between observed and predicted ME estimates presented in Fig. 17.2(a). The high r^2 associated with that regression relationship indicates that errors associated with failures to specify exactly correct values for kCeCs and kHcCs probably make only a minor contribution to variance not explained by the model. Similarly, the sensitivity analyses presented indicate that reasonable but not excessive accuracy is required in specification of these two parameter values. Otherwise, a much more complex set of equations, input parameter values and descriptions of interactions among individual microbes and individual fiber types would be required.

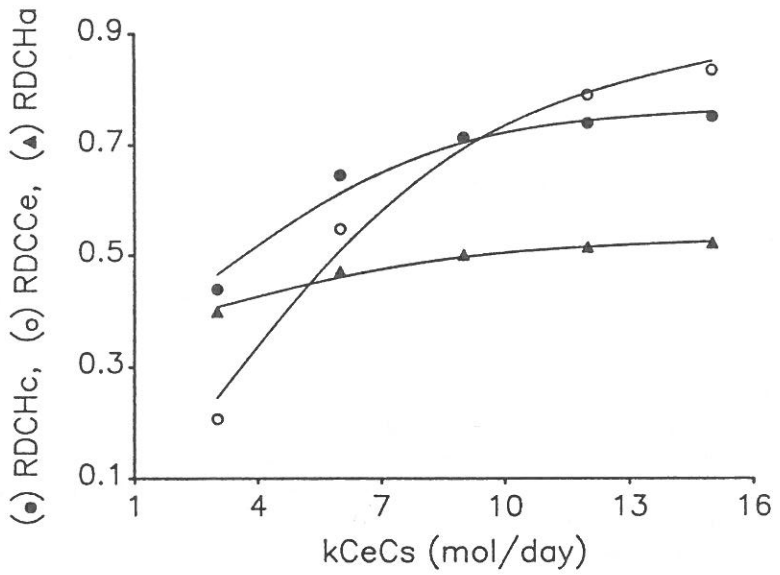


Figure 17.9 Analyses of effects of varying the hydrolytic rate constant (k_{CeCs}) on rumen digestion coefficients (RDC_) for cellulose (_Ce), hemicellulose (_Hc) and starch (_Ha). Diet and other conditions as described for Fig. 17.1.

Rates of nutrient and microbial passage from the rumen have been the subject of considerable experimental and modeling research and controversy over the years (Matis, 1972; Van Soest, 1982; Baldwin and Bywater, 1984; Chapter 11). Effects of quite a number of factors including plant species, processing, rates of particle size reduction due to rumination and hydrolysis of cell wall components, and particle density have been studied. Several issues relevant to this complexity of factors were discussed above in connection with Fig. 17.3. As a result, there is a strong motivation towards development of relatively complex equation forms to simulate passage and we have yielded to this temptation a number of times. However, none of the equation forms we devised performed better than the simple mass action equation in the current model, where passage is a function of a rate constant for small-particle passage (k_{spp}) and the mass of small particles in the rumen. There is an optional equation for scaling k_{spp} to relative feed intake in the model (Chapter 16). This can be implemented when intakes are low, e.g. during the dry period or when the model is used to simulate growth. Effects of varying k_{spp} upon several digestive processes are shown in Fig. 17.10. The range of fractional rate constants tested was 0.8 to 2.0 day^{-1}. The model default value is 1.33 day^{-1} or 5.5%/h. Solutions are clearly sensitive to changing k_{spp} over the 2.5-fold range tested. As the passage-rate constant increased, starch (HaP) and cellulose (CeP) passage increased 2.7-fold. Microbial growth (MiG), the rumen digestion coefficient for cellulose (RDCCe), absorption of acetate (absAc) and adipose tissue lipogenesis (AcTsF) decreased 30, 70, 41 and 42%, respectively. On the other hand, the model is not overly sensitive to k_{spp}, because the simulated ME value only decreased 17% and milk production (not shown) was not depressed significantly (Fig. 17.10). Based upon the sensitivity analyses presented for kCeCs in Fig. 17.9 and effects of k_{spp} in Fig. 17.10, it should be clear that when the model produces errant estimates of ME or rumen and overall digestion coefficients for fiber components, particularly for some specific forage or feedstuff, adjustments easily can be made in the model to accommodate some unusual property of the feed. However, the complexity of the interactions illustrated in Fig. 17.3 with regard to feed fat effects indicates that caution should be used in adjusting even this, highly aggregated, model.

Diet crude protein is input to the model (Chapter 16) as three fractions, i.e. non-protein nitrogen, soluble true protein and insoluble true protein. The most important rate constant defining nitrogen metabolism in the rumen is the rate constant for insoluble protein hydrolysis ($k_{Pi,Aa}$), because it influences amounts of dietary protein that pass intact from the rumen and amounts of amino acids and peptides available in the rumen (RAa) which, in turn, enhance microbial growth yields (MiG). Effects of varying $k_{Pi,Aa}$ from 3.0 to 14.0 day^{-1} are presented in Fig. 17.11. As expected, when $k_{Pi,Aa}$ is increased RAa, MiG and incorporation of amino acids and peptides into microbes (RAaMi) increase, and diet protein passage PiP decreases. The net effect of increased MiG and decreased PiP was a 10% decrease in amino

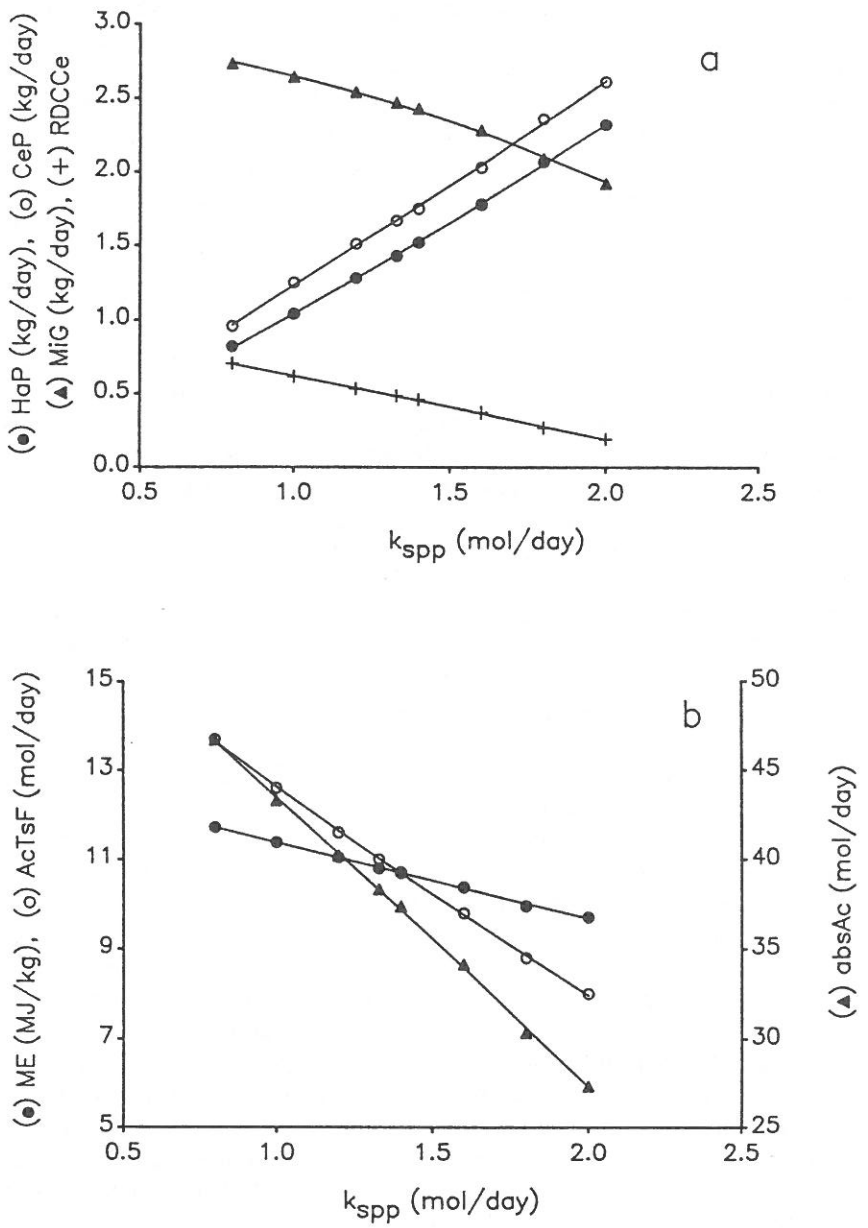


Figure 17.10 Effects of rate constant for small particle passage (k_{spp}) upon (a) starch (HaP) and cellulose (CeP) passage, microbial growth (MiG), rumen digestion coefficient for cellulose (RDCCe) and (b) ME absorption of acetate (absAc) and adipose tissue lipogenesis (AcTsF). Simulation conditions other than k_{spp} specified as input were as described for Fig. 17.1.

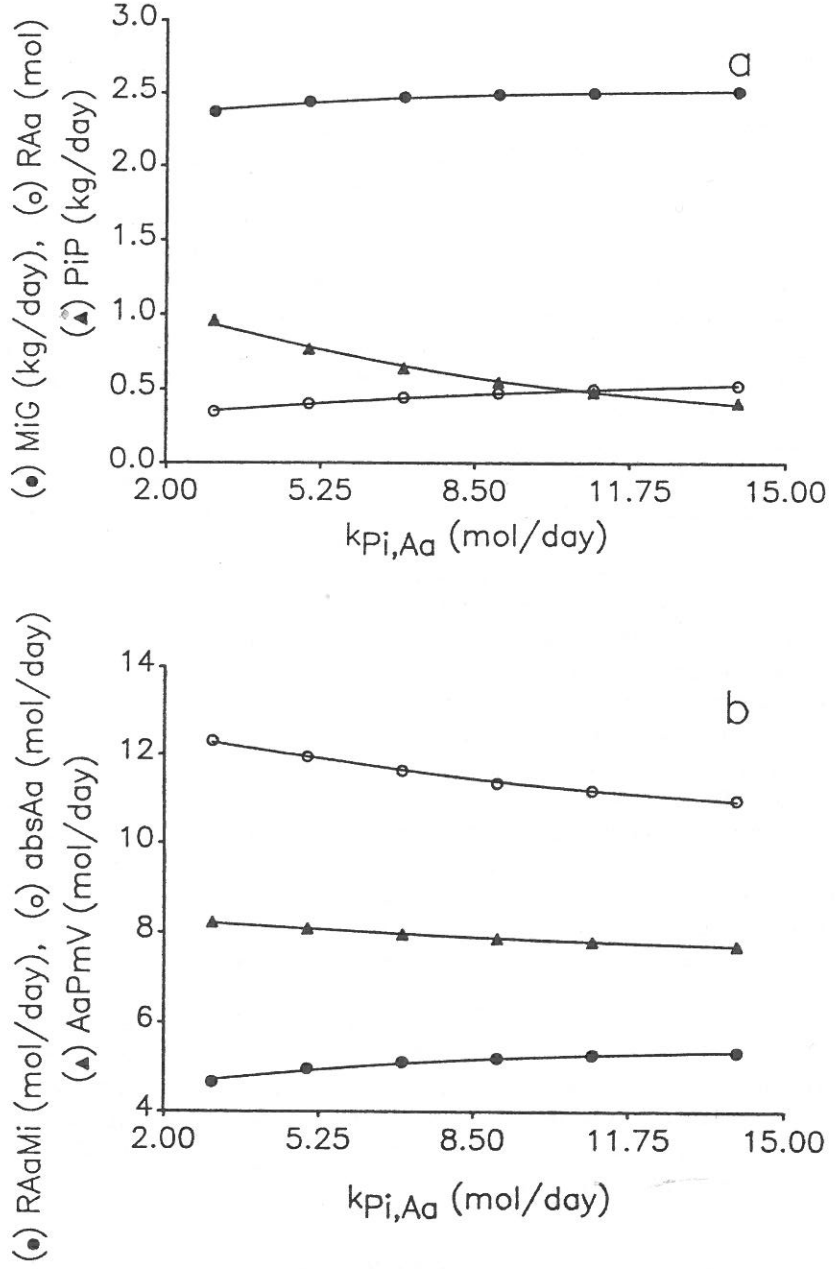


Figure 17.11 Effects of rate constant for insoluble protein hydrolysis ($k_{Pi,Aa}$) on (a) amino acids and peptides available in the rumen (RAa), microbial growth (MiG) and dietary protein passage (PiP), and (b) incorporation of amino acids and peptides into microbes (RAaMi), milk protein synthesis (AaPmV), and amino acid absorption (absAa). Excepting $k_{Pi,Aa}$ values specified as input, simulation conditions as described for Fig. 17.1.

acid absorption (absAa) by the animal and a 6% decrease in milk protein synthesis (AaPmV; Fig. 17.11b). The decrease in AaPmV was reflected in smaller decreases in milk yield and percentage of protein in milk (results not shown). This analysis indicates a relatively modest level of sensitivity that is well within range of the accuracy with which rates of hydrolysis of insoluble protein can be measured in feedstuffs.

Russell *et al.* (1992) emphasized the importance of variation in microbial maintenance requirements (MiMAd) as a determinant of microbial growth yields (MiG) and the availability of amino acids (absAa) to the host animal. Effects of varying MiMAd in the lactating cow model are depicted in Fig. 17.12. The range of values assigned MiMAd in this analysis essentially covers the range of values observed in individual microbes under various conditions, including low pH values. Increases in MiMAd over the range tested decreased ME, MiG, absAa, RDCHa and RDCHb by 6, 40, 25, 15 and 38%, respectively. The decreases in microbial growth and holocellulose and starch digestion would have been greater if rumen concentrations of amino acids and peptides (RAa) had not increased and caused a concomitant increase in the efficiency of microbial growth. The results of this sensitivity analysis emphasize the importance of MiMAd as a determinant of rumen digestion and, further, that a high priority should be assigned to research directed at augmentating the current dearth of data available on rumen microbial maintenance requirements.

In the discussion above of analyses of sensitivity of model solutions to $k_{Pi,Aa}$ and MiMAd, effects of amino acids and peptides upon microbial growth rates and yields were considered central to the responses noted. The major parameter that influences responses to amino acids and peptides is the affinity constant KYAtAa. Effects of varying KYAtAa are presented in Fig. 17.13. As this affinity constant increased, mass of microbes in the rumen (Mi) decreased 20% and microbial growth (MiG) decreased (18%). The overall effect of the changes upon the rumen digestion coefficient for organic matter (RDCOM) was modest.

The simulation results presented in Figs 17.11–17.13 illustrate behavior of the microbial component of the digestive element. The results are in general agreement with experimental data, both qualitatively and quantitatively. However, relevant experimental data are very sparse, which emphasizes an urgent need for further experimental and modeling analyses of this critical portion of the ruminant digestive elements.

17.3.2 Animal elements

Mammary metabolic capacity (UENZ) in the lactating cow model is the primary determinant of milk production (Chapters 13 and 16). Therefore, an analysis of effects of UENZ upon simulated patterns of nutrient use was undertaken. In other simulations, UENZ was allowed to decrease continuously throughout the 2 week simulation periods because it is a state variable

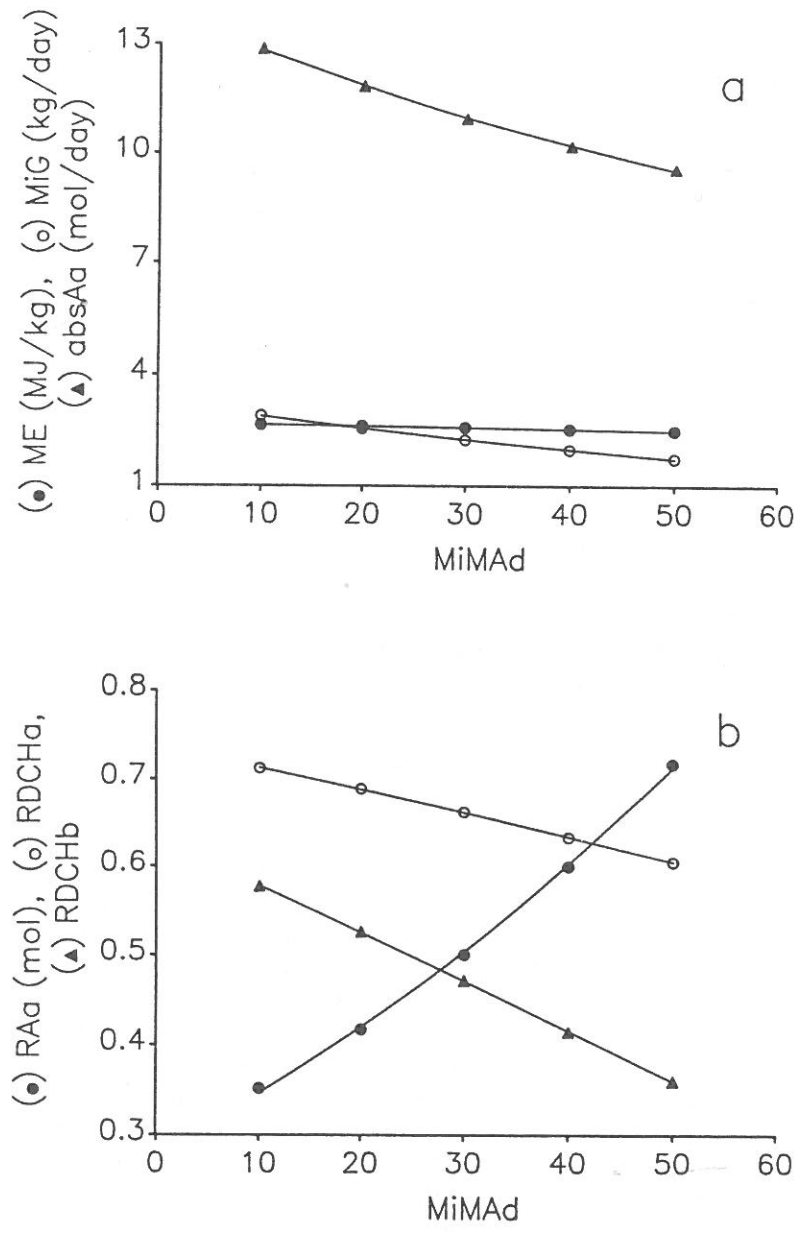


Figure 17.12 Effects of rumen microbial maintenance requirements (MiMAd) on (a) metabolizable energy (ME), microbial growth yields (MiG) and amino acid availabilty (absAa), and (b) amino acids and peptides available in the rumen (RAa) and rumen digestion coefficients (RDC_) for starch (_Ha) and holocellulose (_Hb). Simulation conditions as described for Fig. 17.1.

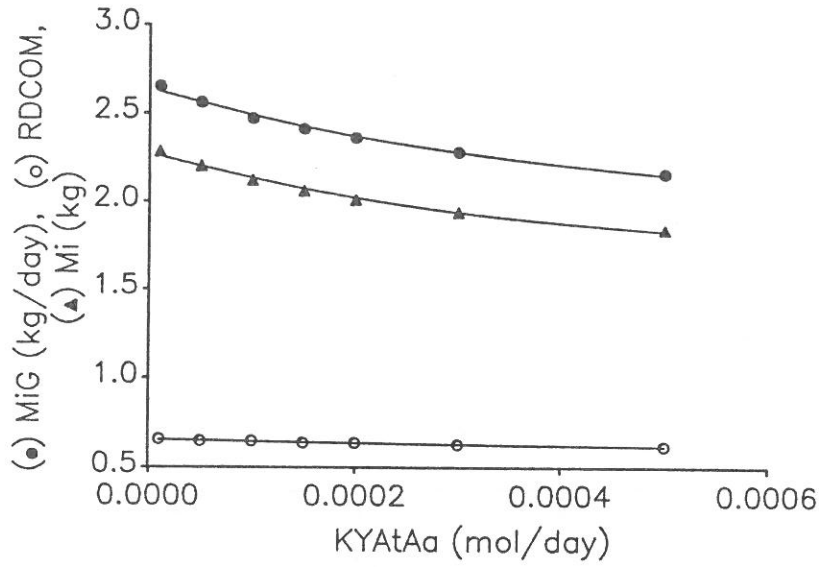


Figure 17.13 Responses to varying the affinity constant from amino acid effects (KYAtAa) upon microbial growth (MiG), microbial mass (Mi) and the rumen digestion coefficient for organic matter (RDCOM). Simulation conditions as described for Fig. 17.1.

defined by the equations of Neal and Thornley (1983), which were adopted during development of the current model. For purposes of the simulations of UENZ effects, DUENZ was set to zero such that initial values of UENZ specified as input were held constant throughout each simulation. Also, in order to simplify interpretations of the simulation results, feed intake was held constant at 18 kg/day. This means that animals were overfed at low values of UENZ and underfed when milk production (DMILK) was high. Results of the simulations are presented in Fig. 17.14. As UENZ increased from 2000 to 14 000 (7-fold), DMILK increased 4.4-fold, a curvilinear response. At the highest rate of milk production – 50.9 kg/day – the simulated animal's energy balance was –79.1 MJ/day. Clearly, DMILK would have decreased rapidly in prolonged simulations because of depletion of body energy reserves. Over the range of UENZ values tested, rate of acetate oxidation (AcCd) remained relatively constant, while the decrease in rate of lipogenesis in the mammary glands (AcTm) was essentially counterbalanced by the decrease in rates of fatty acid synthesis (AcTs) in mammary adipose tissue (Fig. 17.14a). The decrease in glucose availability for oxidation as an energy source (not shown) attributable to the increase in milk production was balanced by an increase in fatty acid oxidation (FaCd) and a decrease in rate of fatty acid re-esterification (FaTs) in adipose tissue (Fig. 17.14b).

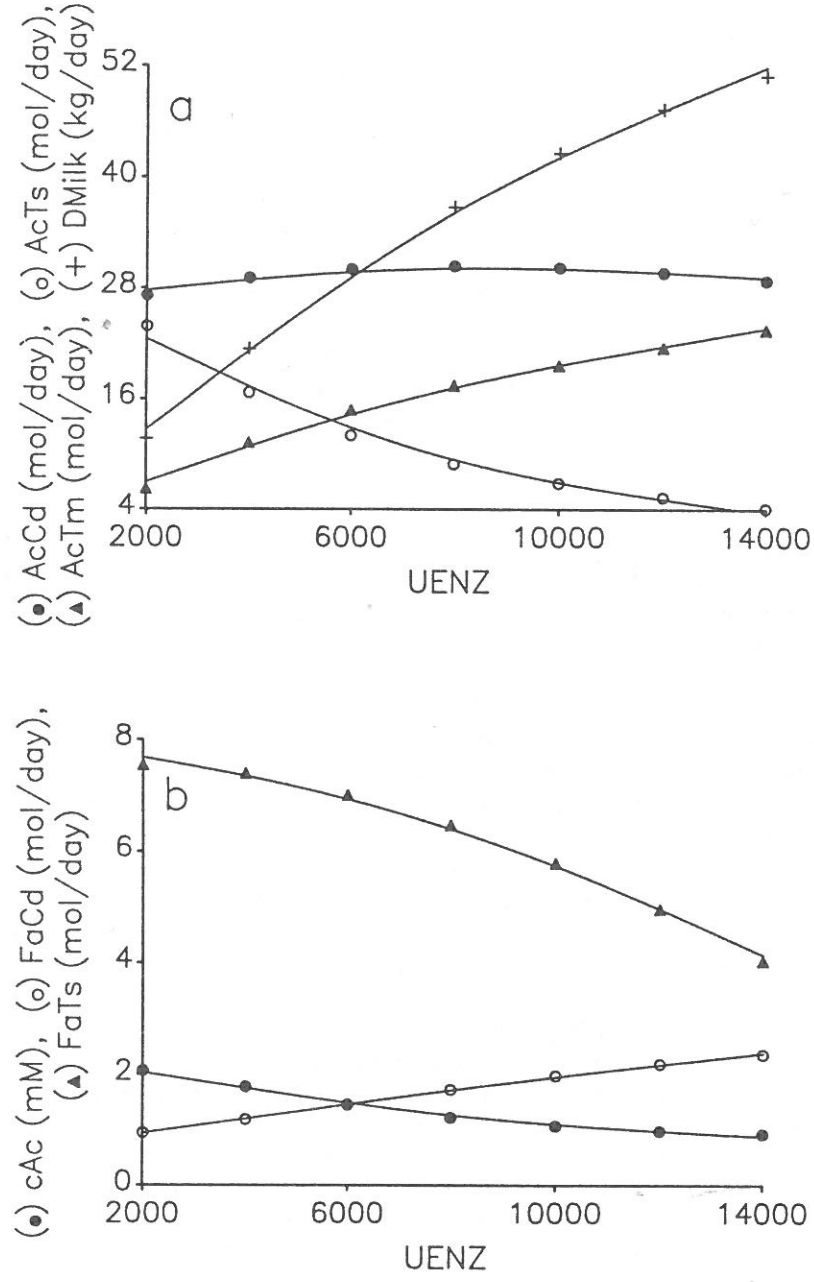


Figure 17.14 Effects of mammary gland metabolic capacity (UENZ) upon (a) acetate oxidation (AcCd), rate of mammary lipogenesis (AcTm) adipose lipogenesis (AcTs) and daily milk production (DMILK), and (b) blood acetate concentration (cAc), fatty acid oxidation (FaCd) and adipose fatty acid re-esterification (FaTs). Simulation conditions as described for Fig. 17.1.

A stated objective in formulation of the animal element of the cow model was 'to evaluate the use of *in vitro* data to parameterize mechanistic models' of metabolism. As discussed in previous chapters, it was already clear that V_{max} values determined in *in vitro* studies are usually significantly lower than those observed *in vivo*. Thus, the primary focus of this objective was on apparent affinity (k_s) values estimated *in vitro*. In a highly interactive model such as MOLLY, which was constructed for the explicit purpose of helping to explain the complex interactions among tissues that determine overall input:output relationships characteristic of real animals, relative affinities and metabolic capacities of tissues competing for common nutrients are central to model behavior and acceptability. Relative metabolic capacities of tissues can be scaled on the bases of independent data as discussed in Chapters 9, 10, 12, 13, 14 and 15. Relative affinities for nutrients are expensive, difficult and are often impossible to define *in vivo* because of the limited ranges of concentrations of nutrients that can be achieved under physiologically meaningful and acceptable conditions. A greater range of conditions can be created in studies of individual tissues *in vitro*. Thus, evaluations of effects of k_s values assigned to tissues on overall model behavior became an important focus of sensitivity analyses.

Effects of varying the apparent affinities of mammary ($k_{Ac,Tm}$) and adipose ($k_{Ac,Ts}$) tissue independently of one another are presented in Fig. 17.15. In the simulations presented both $k_{Ac,Tm}$ and $k_{Ac,Ts}$ were varied from 1.0 to 3.0 mM. The default value in both cases is 1.8 mM. Both sets of changes produced changes in concentrations of acetate (cAc); therefore, cAc was used as the independent variable in the plots presented. The response patterns depicted are essentially what one would expect. As the relative affinities of adipose and mammary tissues for acetate shifted to favor one tissue over the other, relative rates of lipogenesis and milk fat percentages (PTm) shifted accordingly. However, over the range of potential error in specifying the respective k_s values (1.8 ± 0.8 mM), effects on rates of lipogenesis in the two tissues were quite modest. Effects on acetate oxidation, glucose concentrations and milk production were all less than 5% (results not shown). Thus, model behavior is quite robust regarding these two affinity values, which supports the view that values derived from *in vitro* experiments are adequate for use in the model.

Effects of varying the affinity ($k_{Gl,Lm}$) of the lactose synthetase complex from 1.0 to 6.0 mM upon model behavior are presented in Fig. 17.16. As was noted in Chapter 13, results of arteriovenous studies indicate that glucose uptake by mammary tissue is relatively insensitive to the concentration of glucose in blood plasma. This was interpreted as indicating that glucose uptake is determined by factors other than glucose concentration, such as acetate availability from blood. Perhaps, the 6-fold range of $k_{Gl,Lm}$ tested was too large. At the extreme $k_{Gl,Lm}$ values of 1.0 and 6.0 mM, percentages of protein (PPm) and fat (PTm) in milk were too low and high, respectively (Fig. 17.16a). Comparing the full range of $k_{Gl,Lm}$ values, at higher values

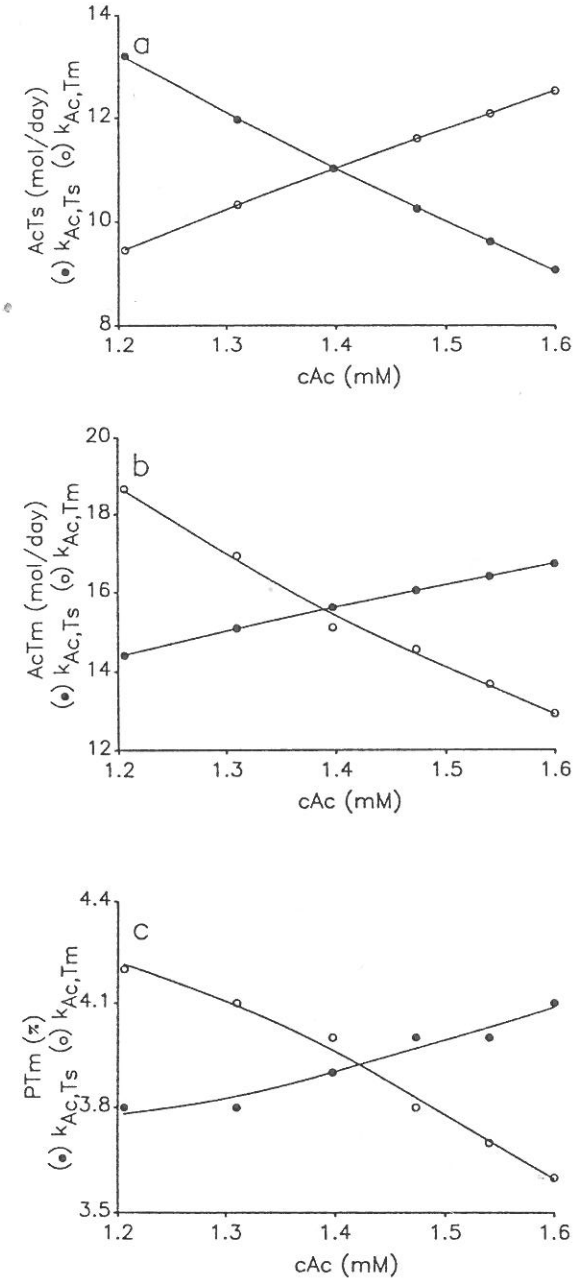


Figure 17.15 Effects of varying relative affinities of adipose ($k_{Ac,Ts}$) and mammary ($k_{Ac,Tm}$) tissues for acetate concentration (cAc) upon simulated animal performance relationships for (a) adipose tissue (AcTs), (b) lipogenesis in mammary (AcTm) and (c) milk fat percentage (PTm). Simulation conditions as described for Fig. 17.1.

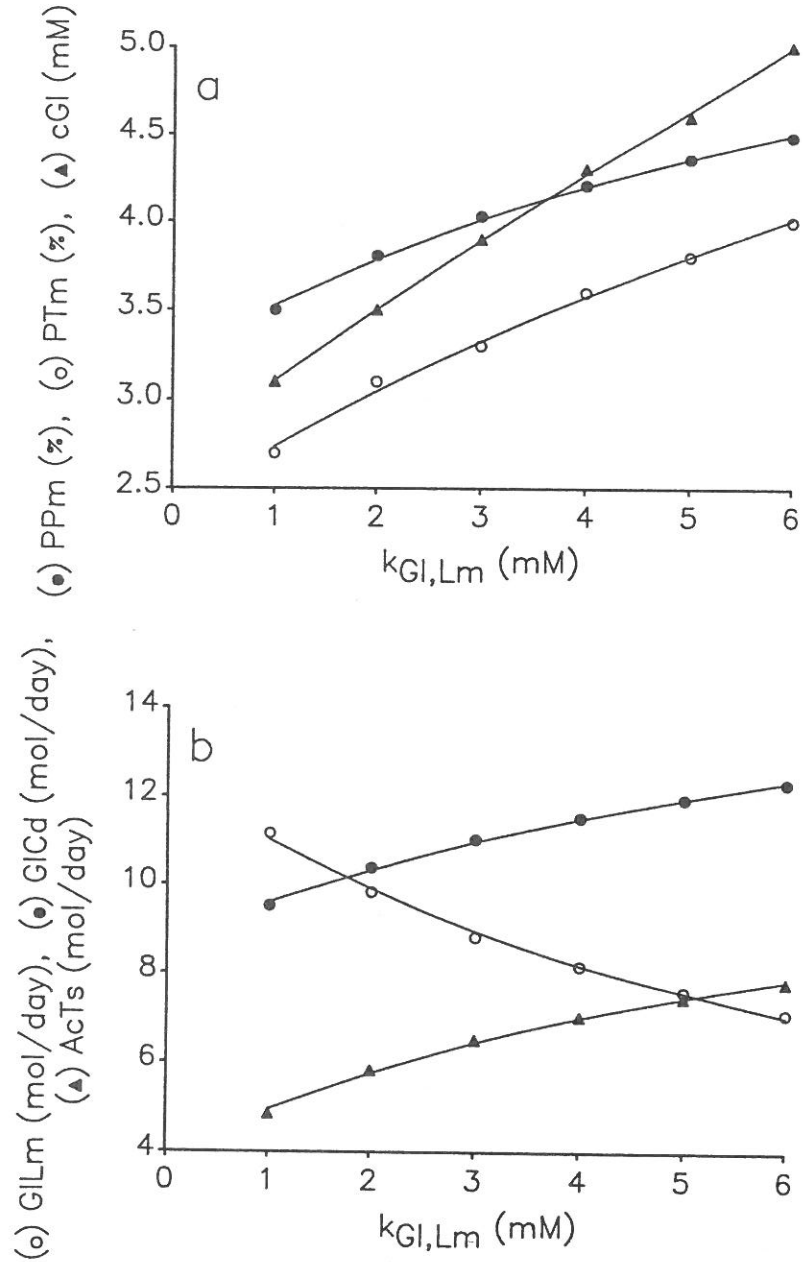


Figure 17.16 Simulated effects of affinity of the lactose synthetase complex for glucose ($k_{Gl,Lm}$) upon (a) milk protein (PPm), milk fat percentages (PTm) and glucose concentration (cGl), and (b) lactose synthesis (GlLm), glucose oxidation (GlCd) and lipogenesis from acetate in adipose tissue (AcTs). Simulation conditions as described for Fig. 17.1.

lactose synthesis (GlLm) and milk production (not shown) increased 36%, glucose oxidation (GlCd) increased 37% and lipogenesis from acetate in adipose tissue (AcTs) decreased 22.7%, indicating significant sensitivity to $k_{Gl,Lm}$ not only at the mammary gland but also at the systemic level (Fig. 17.16b). This result is in apparent conflict with the lack of a glucose concentration effect upon mammary gland arteriovenous data (Miller *et al.*, 1991). However, the range of glucose concentrations observed in that study was basically 2.5 and 4.0 mM. Effects of specifying values for $k_{Gl,Lm}$ between 2.0 and 4.0 mM were relatively modest, which suggests that if the current value of 3.0 mM is correct ± 30%, there is no conflict between the sensitivity analysis and the arteriovenous difference data. The implied requirement that $k_{Gl,Lm}$ be specified with this accuracy is clearly worthy of additional experimental and modeling analyses.

Results of the final sensitivity analysis to be presented are in Fig. 17.17. In this analysis, the affinity of the mammary gland for amino acids ($k_{Aa,Pm}$) was varied. This constant is critical to model behavior, since it has significant effects upon milk protein synthesis and percentage ($U_{Aa,Pm}$, PPm), body protein synthesis (U_{AaPb}), milk production (DMILK) and gluconeogenesis from amino acids (U_{AaGl}). Most of the responses are essentially linear. As discussed in Chapters 10, 13 and 16, both total amino acid availabilities and availabilities of specific (limiting) amino acids to the udder can increase PPm, milk production or both. A single, highly aggregated affinity constant cannot provide for simulations of these alternatives. This is why emphasis in our recent experimental research and in revision of the mammary gland (Chapter 13) and lactating cow (Chapter 16) models has been placed upon the formulation of equations that enable improved simulations of amino acid metabolism in mammary tissue. Thus, the sensitivity analyses presented in Fig. 17.17 are presented as an example of the use of models and sensitivity analyses to identify weaknesses in a model and our current data and, thus, help set research priorities.

17.4 BIOECONOMIC ANALYSES

The lactating cow model presented in Chapter 16 has been subjected to fairly extensive testing. Some results were discussed in earlier parts of this and previous chapters. Even though it was developed primarily for research purposes, the lactating cow model has a number of desirable qualities. Responses to changes in diet and intake in terms of estimates of ME and balances among products of digestion are appropriate, as are responses in blood nutrient concentrations to dietary and other perturbations and effects of these upon patterns of nutrient utilization. Nitrogen and energy balance relationships compare favorably with experimental data for a range of diets. Most importantly, the model has the capacity to simulate effects of

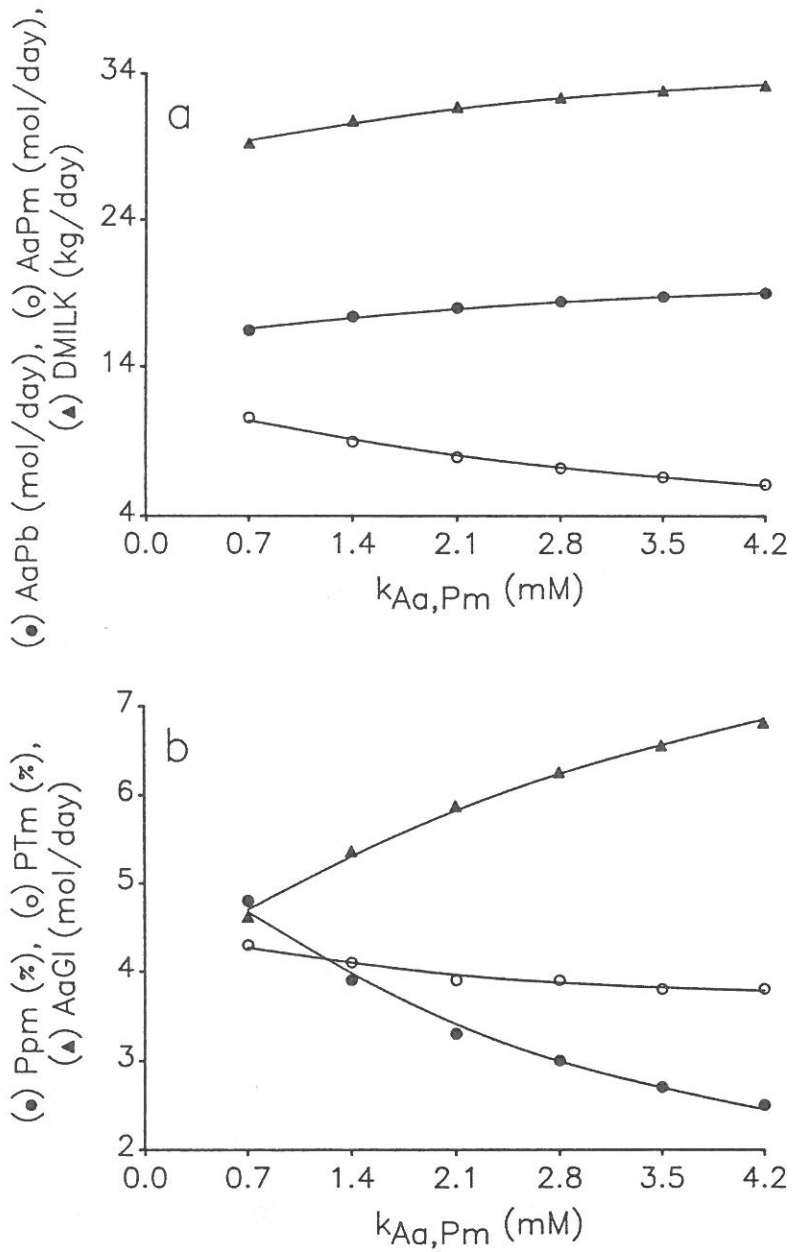


Figure 17.17 Effect of varying the aggregate mammary gland affinity constant for amino acid use for protein synthesis ($k_{Aa,Pm}$) upon (a) body protein synthesis (AaPb), protein synthesis (AaPm) and milk production (DMILK), and (b) milk protein percentage (PPm), milk fat percentage (PTm) and gluconeogenesis from amino acids (AaGl). Simulation conditions as described for Fig. 17.1.

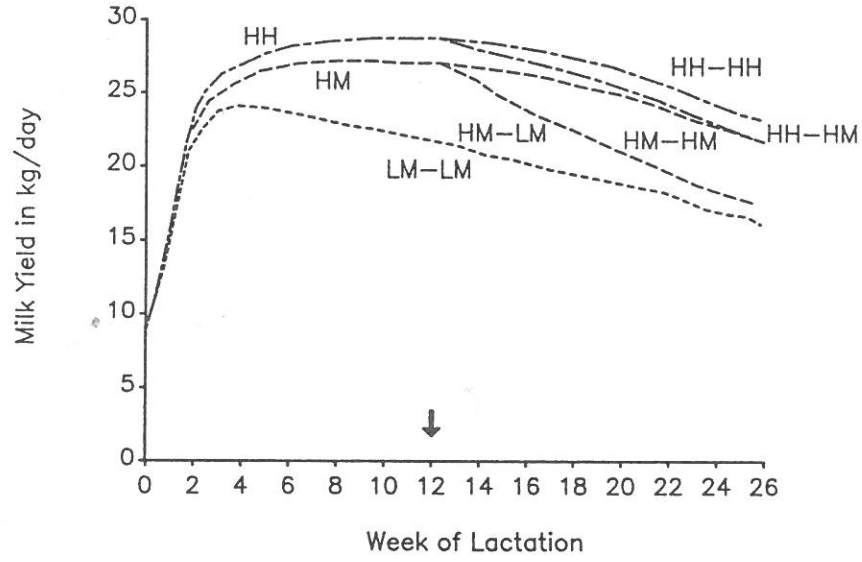


Figure 17.18 Effect of different feeding strategies upon lactational performance. L__ indicates a feeding rate of 5 kg per day plus 1 kg feed per 3 kg milk averaged over the previous 3 weeks. H__ indicates a feeding rate of 8 kg feed per day plus 1 kg feed per 3 kg average daily milk yield. __M indicates the standard forage:concentrate (50:50) ration at 15% crude protein. __H indicates standard ration was adjusted to 18% crude protein with fishmeal. Changeovers of diet and feeding strategy occurred at week 12 of lactation.

previous and current nutritional management strategies upon subsequent performance in dairy cattle. This is illustrated in Fig. 17.18.

The present lactating cow model has a number of limitations and a number of strengths, which might identify it as a prototype. It produces reasonably accurate simulations of effects of current feeding strategies upon subsequent performance, an attribute not shared with static models be they either highly empirical or highly mechanistic. Therefore, it was chosen for the bioeconomic evaluations presented in this section to illustrate applications of dynamic models in optimization of management strategies.

As an example of uses and benefits that can be gained from use of a dynamic dairy cow model, two areas will be examined. The first will be an evaluation of dry matter intake (DMI) equations. The second area will address an evaluation of feeding management strategies utilizing 100-cow herd simulations.

17.4.1 Evaluation of dry matter intake equation

A number of equations have been developed over the years to predict what a cow should eat. The NRC (1987) publication, *Predicting Feed Intake of Food*

Producing Animals, contains summaries of data for predicting dry matter intake, and factors that influence dry matter intake including milk production, body weight, environment, hormones, diet composition and physical activity. Key factors that limit dry matter intake in dairy cattle are physical fill and energy density of the feed (ME/kg). Conrad *et al.* (1964) and Conrad (1966) demonstrated that dry matter intake increased as dry matter digestibility increased until energy demands were met. Thereafter, dry matter intake remains constant or decreases as excess energy is available in relation to animal requirements. Conrad (1971) developed the following equation to describe dry matter intake:

$$DMI = 5.4W * (500 * F)^{-1} \quad (17.4)$$

where DMI is dry matter intake (kg/day), W is body weight (kg) and F is the portion of undigestible energy in the dry matter.

Several additional equations have been developed over the years (Table 17.1). The equations use various factors to determine the DMI that should be provided to support a level of milk production. The equations are static for the situation described at discrete levels of production. For evaluation, three of the equations were compared using the dynamic cow model over a full lactation.

The first of the intake equations was based upon NRC (1978) where allocations were made for maintenance and milk production. The equation used was as follows:

$$DMI = FD_{maint} + FD_{milk} \quad (17.5)$$

$$FD_{maint} = 8 \text{ kg} \quad (17.6)$$

$$FD_{milk} = 0.33 \text{ Milk} \quad (17.7)$$

where DMI is dry matter intake (kg), FD_{maint} is DMI for maintenance (kg), FD_{milk} is DMI for milk production and Milk is daily milk production (kg).

The second equation was based upon the concept that physical fill or capacity sets an upper or maximum limit on intake. This was linked to the fiber components of the diet, especially the indigestible fiber fraction. Mertens and Ely (1979, 1982) developed a model of fiber digestion and passage from the digestive tract. Disappearance from the digestive tract was influenced by rate of digestion, the portion of indigestible and potentially digestible fiber, physical size of particles in the diet, and intake. The model indicates that rate of passage and the indigestible fiber fraction have more influence than does rate of digestion on maximum intake. Following this analysis, Mertens (1985) developed equations based on NDF (neutral detergent fiber) in feeds to predict maximum intake. The following equation was used in the evaluations:

$$NDF = (1 - A) * CNDF + A * FNDF \quad (17.8)$$

where NDF is NDF content of the total diet, A is the forage fraction of the

Table 17.1 Comparisons of intake predictions (%body weight/day) for 600 kg dairy cows with zero body weight changes

4 % fat corrected milk (kg)	Equation reference number								
	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*
10	1.87	2.2	2.53	2.12	–	2.50	2.52	2.1
15	1.94	2.4	2.69	2.42	2.25	2.82	2.79	2.5
20	2.08	2.7	2.87	2.72	2.55	3.09	3.07	2.9
25	2.27	3.0	3.03	3.02	2.84	3.32	3.34	3.2
30	2.52	3.2	3.20	3.32	3.13	3.50	3.62	3.5
35	2.82	3.4	3.37	3.56	3.43	3.64	3.89	3.8
40	3.14	3.6	3.53	–	3.72	3.74	4.17	4.1
45	3.48	3.8	3.70	–	3.94	3.79	4.44	4.4

[a]Brown *et al.* (1977).
[b]National Research Council (1987).
[c]Agricultural Research Council (1980).
[d]Mertens (1985) grass (65% NDF).
[e]Mertens (1985) legume (50% NDF)
[f]McCullough (1981).
[g]Conrad (1971).
[h]National Research Council (1989).

diet, CNDF is the NDF content of the concentrate and FNDF is the NDF content of the forage. Intake capacity (C) was assumed to be 1.1% of body weight per day of NDF. DMI is calculated as the minimum of either the fill capacity or the energy requirement of the animal based upon the energy content of the ration. (Equations implementing these concepts are identified as the MERTEN'S feeding strategy in Chapter 16).

Additional equations have been developed that utilize several factors such as body weight, milk production and nutrient density or content as variables. Brown *et al.* (1977) developed a prediction equation for DMI (kg/day) based upon live weight (W), milk fat in kg/day (FAT), milk yield in kg/day (DMILK), days in milk (DIM) and crude fiber content (CF):

$$\begin{aligned}\ln DMI = {} & 0.519 - (0.000827\ DIM) + (0.148\ LN\ DIM) + \\ & (0.33922 * LN\ Milk) + (0.099266\ FAT) + (0.000675\ W) \\ & + (0.018001\ CF) - (0.000557\ CF^2) \end{aligned} \quad (17.9)$$

The coefficients in the equations were based upon 4839 observations of 28-day intakes in university feeding trials. Field observations demonstrated that this equation predicted lower dry matter intakes than observed for high producing cows. Subsequently, Smith *et al.* (1989) adopted the equations to reflect high milk production and effects of season. Using a sine function for season, the transition from season to season (SEAF) was as follows:

$$\begin{aligned} DMI = {} & 2.7182 * (SEAF - 0.000827 * DIM + 0.14807 * LN\ (DIM) \\ & + 0.33922 * LN\ Milk + 0.0009926 * Milk * FAT \\ & + 0.0675 * BW + CFF) \end{aligned} \quad (17.10)$$

$$SEAF = -(0.24 * SIN0.0166\ (DTJ) + 1.01) + 0.586 \quad (17.11)$$

and

$$CFF = (CN\ (0.018001 - CN^2) * 0.00057) \quad (17.12)$$

where DTJ is Julian date, Fat became percent Fat; BW is body weight (kg/100), CFF is a crude fiber factor and CN is the lower limit for crude fiber. This equation is identified as the ELY equation in Chapter 16, because he programmed it for the model, and as the DART equation in this chapter. DART simply identifies the consortium of scientists who contributed to development of the equation. In the comparisons presented below, the season factor was set at a constant that would equal a March 15 feeding date.

The dairy cow model was run with the NRC, MERTEN'S and DART intake equations with four different diets (Table 17.2). The diets varied in concentrate to forage ratios to produce differences in energy density. Diet 1 was essentially a 60:40 concentrate:forage diet with a crude protein content of 15%. Diet 2 was the same as diet 1 but with an increased protein content (18%) achieved by adding fishmeal to increase bypass protein. The

Table 17.2 Diet composition (%) used in cow lactation model simulations

	Diet			
Item	*1*	*2*	*3*	*4*
Concentrate:forage	60:40	60:40	30:70	0:100
Crude protein	15	18	15	15
Soluble protein	4	2	4	4
Insoluble protein	8	13	8	8
NPN	3	3	3	3
Soluble carbohydrate	6	5	6	6
Organic acids	5	4	5	5
Pectin	6	5	6	3
Lipid	4	4	4	4
Hemicellulose	9	9	12	15
Cellulose	18	18	25	32
Lignin	4	4	4	7
Soluble ash	4	4	4	4
Insoluble ash	4	4	4	4
Starch	25	25	15	5
Soluble starch	2	2	2	2
Small particles	4	4	4	2
$/kg	0.123	0.138	0.110	0.091

forage content of diet 3 was 70% and diet 4 was 100% forage. Protein contents of diets 3 and 4 were 15%. With increasing forage content, hemicellulose, cellulose and lignin increased and starch decreased in the diets. Costs of the ration ($/kg) were calculated for a corn silage and alfalfa hay forage base.

Runs were made for average and high potential rates of production. The high production cow had a 50% greater capability for milk production than did the average cow. Each cow was simulated with each diet and intake equation for a 305 day lactation.

Because the equations for feed intake per day were devised as static equations and the evaluations were dynamic, in initial simulations body weight in the equations acted as an accelerator either upward or downward. As the simulated cow got larger she could eat more and therefore continue to increase her intake until she became overly fat. In contrast, as the simulated cow lost body weight on poor rations, she could eat less which, in turn, accelerated weight losses until simulated death occurred due to exponential overflows in the computer. To prevent this, reference body weight in the equations was set to 650 kg. This was weight at calving for the mature model cow. This was the reference for computation of maintenance requirements such that simulated body weight at a given time did not act as an accelerator either upward or downward. For the NDF equation to function properly, a maximum daily body weight gain was specified.

For the simulations, maximum daily body weight gain was set at 0.5 kg/day. This prevented the NDF equation from spiralling upward to produce a huge cow. To soften the effect of daily milk production changes upon intake, daily milk production was computed as a running 3 day average.

Diet 4 would not support full lactations for the high cow with any of the intake equations.

Total milk production and dry matter intakes for the full simulated lactations are in Table 17.3. On all diets and for all of the intake equations, the high cow produced more milk than did the average cow. The high cow had a greater dry matter intake than the average cow for each of the intake equations, but the NDF and DART equations had greater dry matter intakes for the average cow than the NRC equation had for the high cow. The NRC equation had the lowest milk productions and dry matter intakes for all combinations of diets and cows. The NDF and DART equations were similar, with the NDF equation yielding greater intakes and milk yields with some diets and DART for others. The results were confounded with milk production potential, such that no generalizations with regard to use of the two equations were evident.

Table 17.3 Milk production and dry matter intake over a full lactation for a high producing and an average cow with different intake equations

		Diet			
Intake equation	*Cow*	*1*	*2*	*3*	*4*
Milk production (kg)					
NRC[a]	AVG	6206	7106	5693	4899
NDF[b]	AVG	6788	7530	6376	4786
DART[c]	AVG	6887	7675	6353	5479
NRC	HIGH	8125	9430	7415	
NDF	HIGH	9453	10361	7877	
DART	HIGH	9106	10167	8381	
Dry matter intake (kg)					
NRC	AVG	4774	5064	4610	4359
NDF	AVG	6788	5507	5499	4547
DART	AVG	5567	5751	5387	5062
NRC	HIGH	5388	5806	5162	
NDF	HIGH	6667	6693	5785	
DART	HIGH	6349	6540	6121	

[a]National Research Council (1989).
[b]Mertens (1985).
[c]McCullough (1981)

Final body weights for each simulated cow on the diets are presented in Table 17.4. With a starting weight of 650 kg and a gain of 50 kg for pregnancy, the final weights should be 700 kg. The NRC equation with the

Table 17.4 Final body weights (kg) after a full lactation[a]

		Diet			
Intake	*Cow*	*1*	*2*	*3*	*4*
NRC	AVG	703	727	617	472
NDF	AVG	778	773	744	603
DART	AVG	806	815	714	569
NRC	HIGH	660	698	562	
NDF	HIGH	808	798	678	
DART	HIGH	780	789	683	

[a]See footnote to Table 17.3.

average cow and diet 1 yielded estimates very close to that desired, with a slight increase in diet 2. On diets 3 and 4 with the average cow and on diets 1 and 3 with the high cow, the NRC equation yielded low body weights. The NDF equation produced high body weights, except for diet 4 with the average cow and diet 3 with the high cow. The DART equation produced body weights above 700 kg in all cases, except for diet 4 with the average cow and diet 3 with the high cow. Diets 3 and 4 demonstrate the effects of lower nutrient densities in rations and the need for the cow to utilize excessive body tissue for milk production.

Traditionally, diets are evaluated economically by calculating income over feed cost (IOFC). Income is milk income. In this example, milk was priced at \$0.26/kg of 3.5% fat milk with a fat differential of \$0.0024/0.1% change of fat percent. Feed prices used for each diet are in Table 17.2. IOFC are reported in Table 17.5.

A cost for body weight change was also calculated. This was used to evaluate the use of feed for body condition gain that would be used in the next lactation. Body weight cost was calculated based upon the assumption that 1 kg body weight is equal to 8 kg milk (NRC, 1989). This value needs to be evaluated to accommodate the very large weight gains on some of the diets. Profit was calculated as milk income minus feed cost minus body weight cost. In this analysis, cows gaining weight would have a lower profit than those losing weight. Please note that for simplicity, each diet was fed for the full lactation. If the model had been interfaced with an economic optimization routine, one or more ration changes during the lactation cycle would have been indicated. Calculated profits for the lactations are reported in Table 17.5. IOFC and profit generally reflect the milk production data, with the highest profit being associated with the highest production. Diet 2 produced the highest IOFC and profit.

If diet 1 is considered to be a standard or reference production level, differences from diet 1 can be used to evaluate the effect of adding protein (diet 2) or increasing forage and decreasing energy (diet 3 and diet 4). Val-

Table 17.5 Income over feed costs (IOFC) and profit for full lactations[a]

		Diet			
Intake	*Cow*	*1*	*2*	*3*	*4*
		IOFC ($)			
NRC	AVG	983	1098	939	856
NDF	AVG	1112	1191	1089	829
DART	AVG	1133	1222	1085	987
NRC	HIGH	1411	1609	1329	
NDF	HIGH	1710	1819	1431	
DART	HIGH	1631	1775	1547	
		Profit ($)			
NRC	AVG	1234	1367	1109	965
NDF	AVG	1381	1456	1333	1008
DART	AVG	1410	1507	1334	1156
NRC	HIGH	1644	1883	1495	
NDF	HIGH	1989	2099	1649	
DART	HIGH	1901	2053	1799	

[a]See footnote to Table 17.3.

Table 17.6 Differences from diet 1 for milk production, feed, feed cost, intake over feed costs and profit for the average cow[a]

	Diet		
Intake	*2*	*3*	*4*
		Milk (kg)	
NRC	900	–513	–1307
NDF	742	–912	–2002
DART	788	–534	–1408
		Feed (kg)	
NRC	290	–164	–415
NDF	100	92	–860
DART	184	–184	–505
		Feed costs ($)	
NRC	111	–80	–190
NDF	95	–60	–251
DART	109	–92	–224
		IOFC ($)	
NRC	114	–44	–127
NDF	80	–22	–282
DART	89	–48	–146
		Profits ($)	
NRC	33	–125	–269
NDF	75	–48	–373
DART	86	–76	–254

[a]See footnote to Table 17.3.

ues for the average cow are in Table 17.6. Increasing protein (diet 2) resulted in more milk, more feed eaten, increased feed cost, increased IOFC and increased profit. Increasing forage content with decreasing energy (diet 3 and 4) resulted in less milk, less feed, lowered feed costs, lower IOFC and lower profits. Even though money is saved in feed costs with these changes, returns are actually lower with less milk and body weight. Values for the high production cow are in Table 17.7 and follow the same trend as the average cow but with differences of greater magnitude. This emphasizes the fact that production level affects the results of management decisions.

Table 17.7 Differences from diet 1 for milk production, feed, feed cost, income over feed costs and profit for high production cow[a]

	Diet	
Intake	*2*	*3*
	Milk (kg)	
NRC	1305	–710
NDF	908	–1576
DART	1061	–725
	Feed (kg)	
NRC	418	–226
NDF	26	–882
DART	191	–227
	Feed costs ($)	
NRC	138	–94
NDF	103	–184
DART	121	–107
	IOFC ($)	
NRC	198	–81
NDF	109	–279
DART	143	–83
	Profits ($)	
NRC	239	–148
NDF	110	–339
DART	151	–102

[a]See footnote to Table 17.3.

To further evaluate the equations, daily milk production and daily DMI were graphed for each of the diets and equations. Milk production for the average cow on diet 1 (Fig. 17.19), dry matter intake for the average cow on diet 1 (Fig. 17.20), milk production for the high cow on diet 1 (Fig. 17.21) and dry matter intake for the high cow on diet 1 (Fig. 17.22) show the lactation curves produced. The relative rankings for the intake equations are the same as for the full lactation data. With the high fiber diets (diet 3 and diet 4), the NDF equation differs from the NRC and DART equations. Feed intake does not peak sharply and flatten, as shown for the high cow on diet

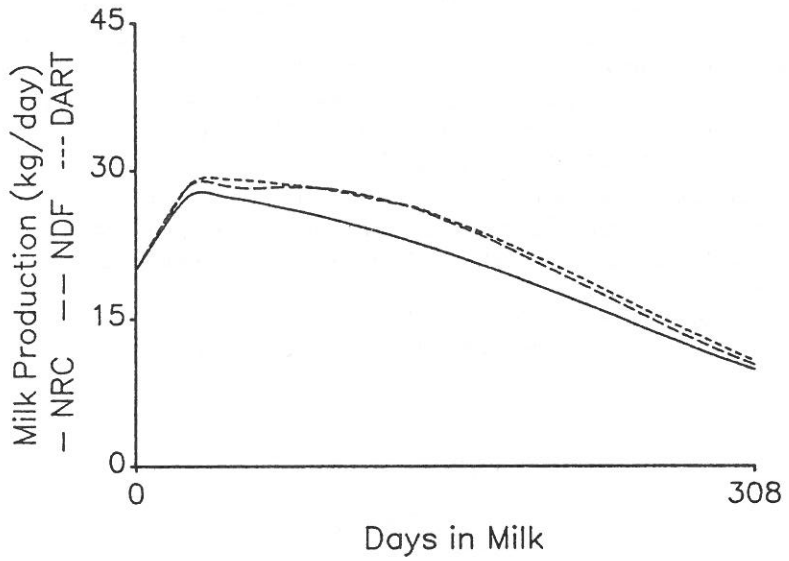


Figure 17.19 Milk production for the average cow on diet 1 (60:40 concentrate:forage ratio, 15% protein).

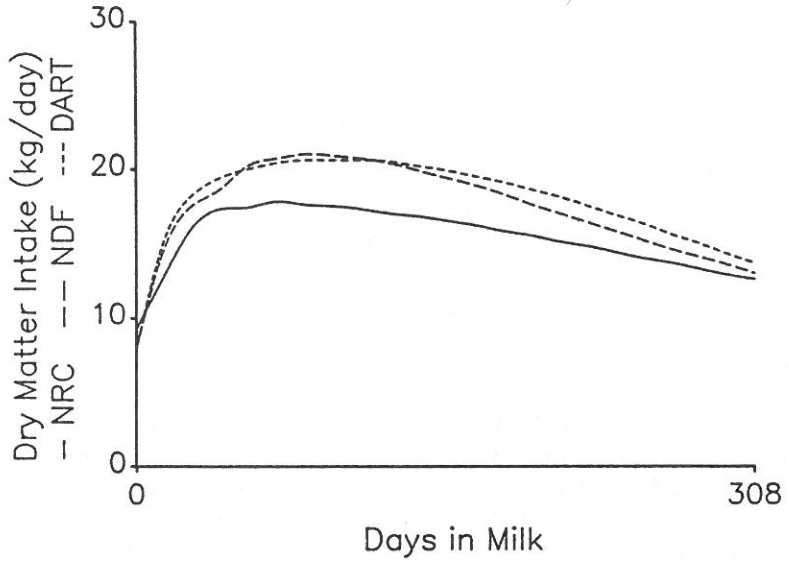


Figure 17.20 Dry matter intake of average cow on diet 1 (60:40 concentrate:forage ratio, 15% protein).

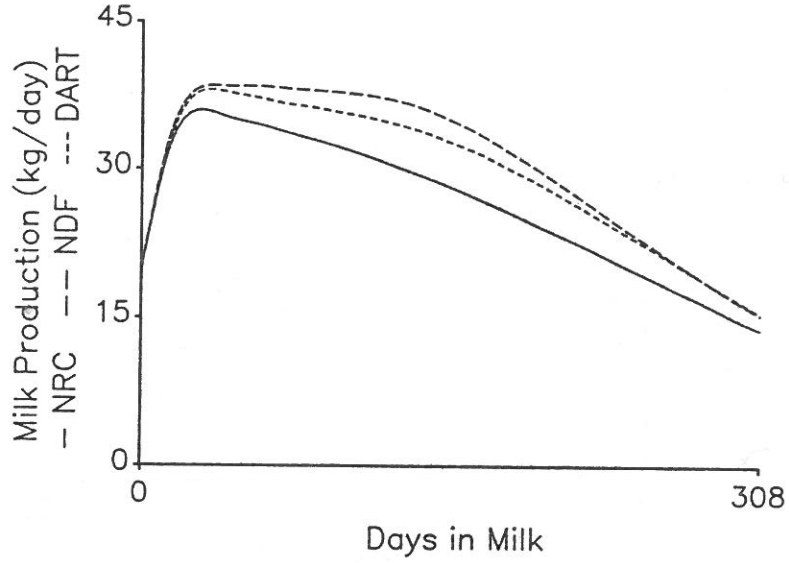


Figure 17.21 Milk production of high cow on diet 1 (60:40 concentrate:forage rati 15% protein).

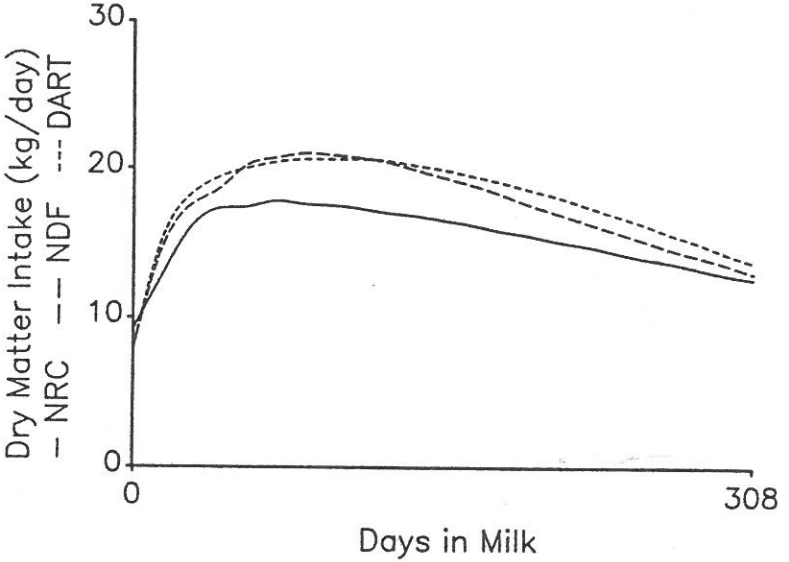


Figure 17.22 Dry matter intake of high cow on diet 1 (60:40 concentrate:forag ratio, 15% protein).

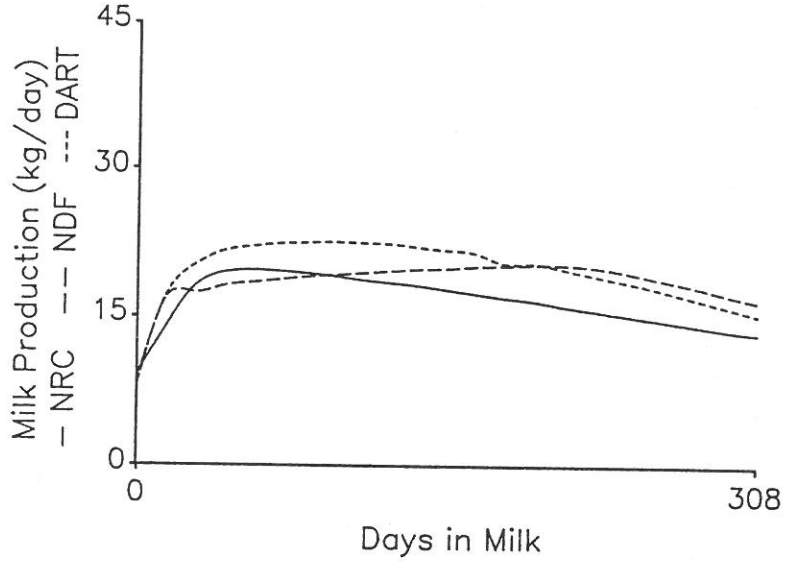


Figure 17.23 Dry matter intake of high cow on diet 3 (30:70 concentrate:forage ratio, 15% protein).

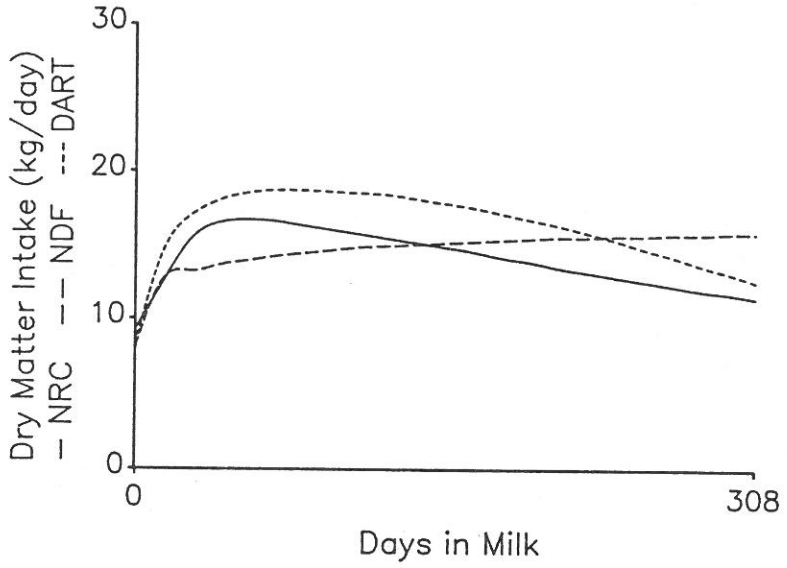


Figure 17.24 Dry matter intake of average cow on diet 4 (100 forage, 15% protein).

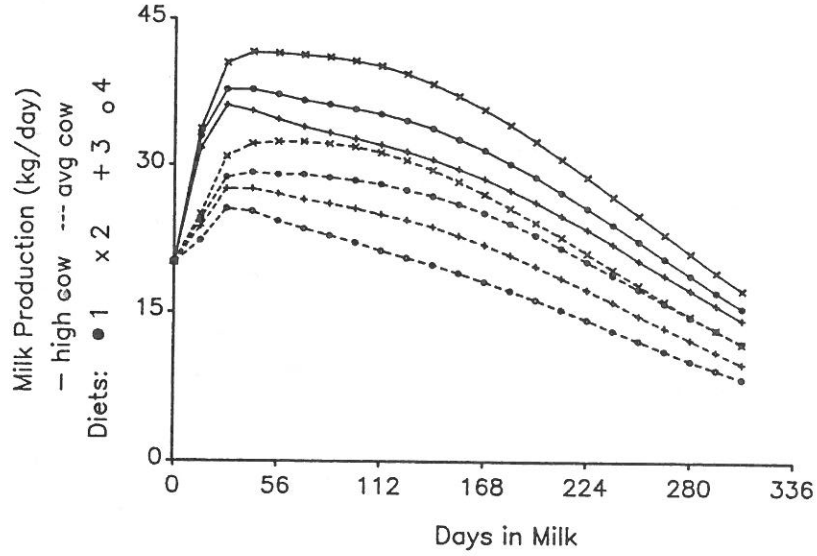


Figure 17.25 Milk production response for the DART intake equation for average cow on diets 1, 2, 3 and 4; and for high cow on diets 1, 2 and 3.

3 (Fig. 17.23) and the average cow on diet 4 (Fig. 17.24). Additional data must be generated with high fiber diets at high levels of milk production to further evaluate the NDF and DART equations and the simulated milk production responses presented in these figures.

Figure 17.25 has the milk production responses for the DART equation on all diets for both cows. The rank of the curves is the same as for lactation yields with the highest being the high cow on diet 2 followed by high cow diet 1, high cow diet 3, average cow diet 2, average cow diet 1, average cow diet 3 and average cow diet 4. The high cow's lactation curve peaks higher and decreases more sharply and faster than does the average cow as compared with lactation curve analyses of DHIA data. Comparing the three equations, the NRC equation underestimates intake while the DART and NDF equations are very similar, with the major difference occurring on high fiber diets. The DART equation may be underestimating the rumen capacity limit of these diets in early lactation.

17.4.2 Evaluation of feeding strategies

One management question that is of concern to the dairy industry is when is the best time to change rations. Using diets 1, 2 and 3, various strategies were evaluated. For these simulations, individual lactation curves for 100-cow herds were generated. The milk production potential for the herd was the same as the high cow (relative udder metabolic capacity expressed as

Table 17.8 Evaluation of alternative herd feeding strategies[a]

Strategy	*Diet*	*Milk (kg)*	*FCM (lb)*	*DMI (kg)*	*EBW (kg)*	*Profit ($)*
0	1	9044^{b}	19648^{a}	6295^{c}	690^{bc}	1888^{c}
0	2	1027^{g}	20007^{a}	6619^{e}	701^{f}	2179^{i}
0	3	8324^{e}	18155^{c}	6069^{d}	585^{g}	1708^{h}
3	1→3 T =140	9021^{b}	19593^{a}	6292^{c}	690^{b}	1884^{c}
6	1→3 T = 98	8502^{d}	18776^{b}	6123^{d}	598^{d}	1766^{g}
11	1→3 M = 20	9019^{b}	19587^{a}	6286^{c}	690^{bc}	1883^{c}
12	1→3 M = 29.5	9015^{b}	19580^{a}	6285^{c}	689^{b}	1882^{c}
7	2→1 T = 98	9899^{ac}	19761^{a}	6447^{a}	694^{c}	2061^{e}
2	2→1 T = 140	9830^{a}	19636^{a}	6381^{b}	691^{b}	2047^{ab}
8	2→3 T = 98	9397^{f}	18943^{b}	6298^{c}	605^{e}	1940^{f}
1	2→1→3 T = 98 T = 210	9829^{a}	19654a	6455^{a}	653^{a}	2022^{a}
4	2→1 M = 29.5	10079^{c}	19709^{a}	6483^{a}	690^{b}	2035^{ad}
10	2→1 M = 20	10071^{c}	19693^{a}	6475^{a}	690^{bc}	2034^{ae}
9	2→1→3 M = 29.5 M = 20	10095^{c}	19747^{a}	6483^{a}	689^{b}	2031^{ae}
Pooled standard error		63	155	21	1	14

[a]Strategies indicated by 0 involved feeding the simulated herd of 100 cows diets 1, 2 or 3 for the whole lactation. Strategy 1 involved feeding diet 2 for 98 days, diet 1 from 98 to 210 days of lactation and diet 3 from 210 days to the end of lactation. Strategies 2 and 3, respectively, involved starting lactation with diet 2 or 1 and switching to diet 1 or 3 for the remainder of the lactation. Strategy 4 simulated feeding individual cows diet 2 until their milk production dropped below 29.5 kg/day. Strategies 6, 7 and 8, respectively, involved changing from diet 1 to diet 3, diet 2 to diet 1 or diet 2 to diet 3 at day 98 of lactation. Strategy 9 involved changing individual cows from diet 2 to diet 1 when milk production dropped below 29.5 kg/day. Respective changes for strategies 10 and 11 were to change from diets 2 to 1 and 1 to 3 when milk production dropped below 20 kg/day. Strategy 12 indicated a shift from diet 1 to 3 when milk production dropped below 29.5 kg/day.

Values with differing superscripts within a column were significantly different from one another according to the Student–Newman–Kuhl test (P < 0.9\05). Strategy 1 was arbitrarily assigned the superscript 'a' for purposes of a common reference point.

Ucells [Chapter 16] was 1500). Individual cow lactation potentials were randomly generated using a range of Ucells of 1500 ± 200. The resulting herd of 100 cows had an average of 1500 Ucells±a standard deviation of 156. Everything else in the model was the same as in previous runs for individual cows. For this evaluation, only the DART intake equation was used.

Strategy 0 was feeding single diets for the whole lactation. Milk production (in kg), total volume of milk corrected to 4.0% fat (FCM in pounds), dry matter intake (DMI in kg), empty body weight (EBW in kg) and profit (in dollars) averages for the simulated 100-cow herd (Table 17.8) were slightly lower than those for the single-cow estimates presented above.

Alternative strategies evaluated were based upon diet switches at different days in milk or rates of milk production (see Table 17.8 footnote). Our purpose in formulating Table 17.8 was to illustrate the utility of using a dynamic, mechanistic model to evaluate the probable impact of alternative feeding management strategies upon profitability in herds with a known milk production potential and genetic variance. Interested readers can compare among strategies they prefer for herds with a production potential of about 9000 kg/lactation. However, we would emphasize that with herds with genetic potentials above or below this reference, rankings will differ. Therefore, our discussion of the results will be limited and should not be considered generally applicable. Two trends are evident in the simulation outputs. Starting lactations with diet 2 (higher protein strategies 7, 2, 8, 1, 4, 10, 9) instead of diet 1 (strategies 6, 3, 11, 12) resulted in higher averages for milk production, dry matter intake, profit and fat-corrected milk (Table 17.8). The increased protein input during early lactation to cows of above average genetic potential paid dividends. The second trend that was evident was that the longer a more nutrient dense diet was fed (or the die switch was made later in lactation), increased performance and profit resulted.

This limited evaluation demonstrates the value of the use of dynamic models to evaluate alternative feeding strategies and enable researchers or managers to test these in the real world. As there are an infinite number of feeding strategies, this approach could be used to identify those that are most critical. In order to improve the strategies, inclusion of body condition scores based upon body composition could be built into the decision switches illustrated in this example.

Dynamic, mechanistic lactating dairy cow models allow the generation of data for evaluations of animal performance and managerial decisions. A large number of variables can be examined to give direction to decision making for researchers and managers. As teachers of animal science and lactation courses, we wish to note that the performance evaluations presented in Tables 17.1–17.7 extend significantly beyond those one can compile from available literature to illustrate the complex matrix of decisions a dairy manager or nutritionist must address. Current practitioners may address these issues intuitively or through the use of static equation system

but both approaches are, at most, semiquantitative when used in evaluations of lactation and economic performance. In our view, dynamic models are absolutely essential to economic evaluations of risks associated with current decisions because these clearly influence subsequent performance. When a proven, dynamic, mechanistic model becomes available to students and practitioners to generate data such as those presented in Table 17.8 and, further, to enable cause-and-effect analyses of underlying reasons for the observed responses, we will have created a superior instrument for both the teaching and application of our science. This is the challenge we pose.

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