New Zealand Society of Animal Production online archive

This paper is from the New Zealand Society for Animal Production online archive. NZSAP holds a regular annual conference in June or July each year for the presentation of technical and applied topics in animal production. NZSAP plays an important role as a forum fostering research in all areas of animal production including production systems, nutrition, meat science, animal welfare, wool science, animal breeding and genetics.

An invitation is extended to all those involved in the field of animal production to apply for membership of the New Zealand Society of Animal Production at our website www.nzsap.org.nz

View All Proceedings Next Conference Join NZSAP

The New Zealand Society of Animal Production in publishing the conference proceedings is engaged in disseminating information, not rendering professional advice or services. The views expressed herein do not necessarily represent the views of the New Zealand Society of Animal Production and the New Zealand Society of Animal Production expressly disclaims any form of liability with respect to anything done or omitted to be done in reliance upon the contents of these proceedings.

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License.

You are free to:

Share— copy and redistribute the material in any medium or format

Under the following terms:

Attribution — You must give appropriate credit, provide a link to the license, and indicate if changes were made. You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use.

NonCommercial — You may not use the material for commercial purposes.

NoDerivatives — If you remix, transform, or build upon the material, you may not distribute the modified material.

http://creativecommons.org.nz/licences/licences-explained/

PRINCIPLES OF MODELLING ANIMAL SYSTEMS

R. L. BALDWIN

Department of Animal Science, University of California, Davis, California

SUMMARY

The use of modelling techniques in pursuit of greater understanding of animals and animal production systems is currently in its infancy. Naive and improper applications of this approach have led to doubt among many experimentalists about the usefulness of these techniques. If a negative attitude towards mathematical models persists among experimentalists and, as a result, models are constructed without associated experimentation, the usefulness of a powerful technique will be limited. If, on the other hand, experimentalists accept and utilize these techniques, contributions to the advancement of knowledge could soon rival the contributions of conventional statistical techniques. Certainly, methods which complement intuition are required for analysis of the complex, dynamic systems we seek to understand.

INTRODUCTION

FOUR OBJECTIVES were set in development of this introductory paper to the symposium on applications of modelling in the animal sciences. The first was identification of some of the general and specific objectives one seeks to achieve through modelling. The second was discussion of several principles which underlie the construction and use of models in practical agriculture and in research with emphasis on the fact that modelling is an orderly, rigorous and scientific process. Another objective was identification of some modelling approaches or methods appropriate to achievement of the several modelling objectives. The final objective was to develop, through the use of examples, the concept that modelling is a powerful technique when used in support of research.

MODELLING OBJECTIVES

The use of modelling techniques in animal science and production is based on the concept that the complex interactions within and among the environmental, digestive, physiological and metabolic elements that determine animal performance cannot be feasibly evaluated in a quantitative and dynamic fashion by either the human mind or traditional research methods. Thus, the statement of Forrester (1971) that "the objective in modeling is to combine the power of the human mind with the power of computers", applies. While expanding on this statement, Forrester (1971) explained that, while only the human mind can formulate a structure or set of concepts into which data can be fitted, the mind is limited in its ability to analyse or anticipate the quantitative and dynamic behaviour of the system described.

The computer is ideal for the latter function. When supplied with mathematical statements and numerical inputs which incorporate concepts, hypotheses and assumptions of how the components of a complex system interact, the computer can readily trace the behaviour of these (Forrester, 1971). Thus, modelling simply involves formalization of current knowledge of a system in the form of equations, solution of the equations using, usually, a computer, and evaluation of the computed results.

If the concepts which comprise the model are valid and adequate, computed results will reflect reality. If not, computed results will reveal inadequacies in current knowledge. The latter result is a valid outcome of modelling and can be very useful in the selection and design of experiments undertaken to improve our knowledge of the system.

Models can be based on empirical equations, theoretical equations or both. Riggs (1963) defined empirical equations as those which have been fitted to experimental data to describe a relationship which has been observed between two or more variables. These equations imply nothing about the underlying reason for the relationship. Also, the terms in these equations do not reflect specific biological entities or functions other than the identified variables for which data were input. Theoretical equations were defined as those which derive not from a particular set of data, but from some theory or hypothesis about the fundamental nature of a biological system. While an empirical equation may describe a particular set of data with great precision, a well founded theoretical equation should describe all such sets of data and explain why the relationship exists (Riggs, 1963).

Practical models used for prediction, diet formulation or evaluation of management alternatives are composed, largely, of empirical equations. There are several reasons for this: (1) Empirical models are cheap to solve on computers because of the aggregation or simplification achieved when underlying relationships are not considered explicitly; (2) When the concepts and data represented in the model are accurate, predictions are very precise; and (3) Current knowledge of many systems is not sufficient to support the development of causal models based on theoretical equations.

An important limitation of empirical models is that they should be used only with great care when the conditions considered extend beyond those for which data are available. This limitation must be clearly recognized when empirical models are formulated and tested; it is often feasible to identify empirical equations which either strongly affect solutions or are not generally applicable and to substitute for these causal (theoretical) equations which improve and extend the usefulness of the model.

Models constructed for use in support of a research programme are usually composed, largely, of theoretical equations since most research programmes are directed at evaluations of causal relationships determinant of system function. The researcher hopes to achieve several advantages through the use of modelling techniques. Among these are evaluations of current data and concepts for quantitative and dynamic adequacy; identification and evaluation of determinant elements; identification of critical experiments; and, rigorous evaluations and extensions of data.

APPROACHES TO MODELLING

Whether a model is being developed with practical or research goals in mind, model development must proceed systematically (Table 1). As is true in all research, the first and most important step in modelling is definition of the problem and the setting of a specific objective. The modelling objective guides the modeller in construction of a block diagram (Fig. 1) which depicts the essential elements of the system to be modelled and interactions among these; in the formulation of mathematical

TABLE 1: STEPS IN MODELLING

1. Define problem — set modelling objective.
2. Prepare block diagram representing central elements of system and interactions among them.
3. Convert concepts represented in block diagram to mathematical statements.
4. Formulate required numerical inputs based on literature data, experimental data or statistical estimation (see text).
5. Evaluate solutions and/or validate model. Return to steps 2, 3 or 4 if evaluation indicates inadequacies.

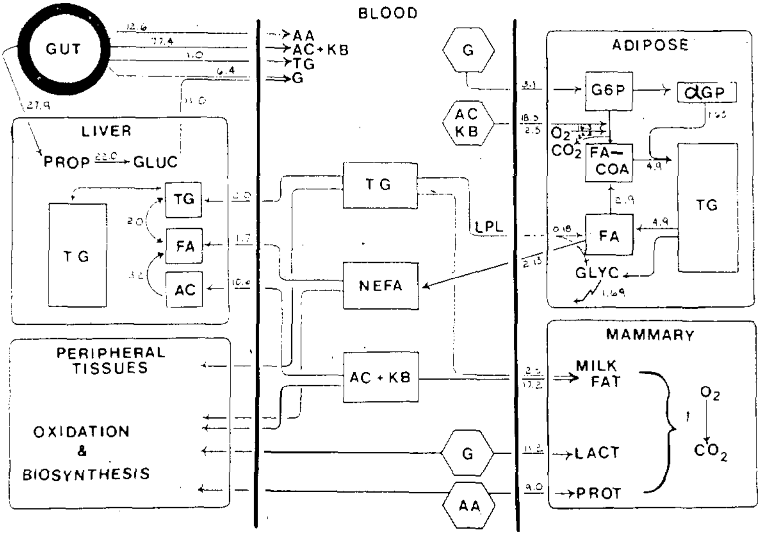

FIG. 1: *Patterns of nutrient utilization in a lactating dairy cow. Numerical entries represent rates of uptake and conversion of nutrients in moles/day for a 550 kg lactating cow in energy balance consuming a concentrate: lucerne (50:50) ration and producing 30 kg of milk daily at a gross efficiency of 48% (Smith, 1970; Baldwin and Smith, 1971b).*

statements and numerical inputs; and during evaluation and validation of the model.

The setting of criteria for model evaluation and validation is a very controversial and important process. When guidelines are not provided by a well conceived modelling objective, validation may not be feasible. If the modelling objective is practical application of computed results and requires precise predictions of animal performance under a specified range of conditions, validation will require proof that model predictions of animal performance are accurate and precise. If a (research) modelling objective is evaluation of current concepts and data for quantitative and dynamic adequacy, the answer obtained during evaluation may be yes or no. Either answer is valid. When current knowledge is found inadequate, a carefully constructed causal model can be used effectively in evaluations of alternate hypotheses for potential adequacy and in the identification of critical experiments.

The research programme with which the writer is associated has as a practical objective the development of models for diet formulation and animal production system management which accommodate differences among feedstuffs in efficiencies of use for varying functions. Specific goals are more effective consideration of the nutritive value of by-product feeds in the formulation of beef and dairy cattle rations and of potential benefits obtainable from supplementation of animals grazing California's annual grasslands. In these cases, development of additional empirical relationships based on further feeding and grazing experiments is considered either too expensive because of the number of experiments required or not feasible owing to non-additive interactions among feedstuffs. Thus, current computer programs (empirical models) must be improved through the addition of theoretical equations as was discussed above. Identification of critical functions, appropriately represented by theoretical equations, and formulation of these equations requires that detailed studies be undertaken of factors which affect metabolic patterns and efficiencies of nutrient utilization.

Three types of (research) models have been used in support of these detailed studies. The first type of model used has been balance models. These are simple input/output models constrained by causal (metabolic) pathways (Baldwin, 1968; Baldwin, 1970a) and have been used to extend understanding of quantitative aspects of ruminant digestion and metabolism. They can also be used to evaluate and extend data (Reichl and Baldwin, 1975). The second type of model used has been optimization models (Reichl and Baldwin, 1976; Koong *et al.*, 1975) which provide, among other things, for statistical estimations of parameters that cannot be measured with present technology (Koong *et al.*, 1975).

Studies undertaken using balance and optimization models have the limitations that steady state is assumed. Thus, regulatory factors that determine variations in patterns of nutrient utilization over time cannot be evaluated. Dynamic models have been constructed for the latter purpose (Smith, 1970; Baldwin and Smith, 1971a). In subsequent sections, example applications of balance, optimization and dynamic models will be discussed.

BALANCE MODELS

A simplified block diagram developed to enable a detailed evaluation of energy expenditures in a lactating dairy cow is presented in Fig. 1 (Smith, 1970; Baldwin and Smith, 1971b). In developing this block diagram, estimates of amounts of nutrients absorbed per day were derived from digestion and radioisotope tracer data. Partitions of nutrients among tissues were based on knowledge of tissue functions, metabolic pathways, and a wide range of information regarding animal metabolism including: data on animal and tissue energy expenditures, blood flow rates to tissues, tissue nutrient uptakes (A-V difference), and radioisotope data (Smith, 1970; Baldwin and Smith, 1971a, b).

Initially, metabolic equations representing the uptake and usc of each nutrient by each tissue were balanced and solved by hand (Baldwin, 1968; Baldwin, 1970b; Milligan, 1971) to obtain estimates of energy expenditures for specific functions and on a tissue-by-tissue basis. Later, because solution by hand is very time-consuming and subject to error, the metabolic equations were converted to algebraic equations suitable for simultaneous solution using a computer. This conversion is straightforward in most cases. For example, the amount of glucose available for use by an animal (GLCIN) might be specified as the sum of glucose absorbed (GLCABS) plus propionate absorbed (PROPIN) times a stoichiometric coefficient (SPRGLC) plus amount of amino acid degraded (AADEG) times a stoichiometric coefficient (SAAGLC) as follows:

$$\begin{aligned} \mathrm{GLCIN} &= \mathrm{GLCABS} + \mathrm{PROPIN{*}SPRGLC} \\ &\quad + \mathrm{AADEG{*}SAAGLC} \end{aligned}$$

A number of results obtained using balance models have been published (Reichl and Baldwin, 1975; Baldwin and Smith, 1971b, 1974; Baldwin, 1970b). Example results pertaining to energy expenditures in adipose tissue are presented in Tables 2 and 3.

TABLE 2: EVALUATION OF ENERGY EXPENDITURES IN ADIPOSE TISSUES OF A LACTATING DAIRY COW

	Nutrient	*moles/day*	*MJ/day*
Input:	glucose	3.1	8.7
	acetate	18.5	16.2
	ketone bodies	2.5	5.1
	triglyceride	0.18	1.8
Output:	fatty acids	2.1	21.4
	glycerol	1.6	2.7
Heat Production:	Input-Output		7.7[1]

[1] This represents 8% of the lactating cow's total daily heat production and can be partitioned using the model into maintenance of adipose (3.0%), lipogenesis (4.5%) and lipolysis plus triglyceride resynthesis (0.5%).

TABLE 3. PARTITION OF ADIPOSE ENERGY EXPENDITURES IN FATTENING STEERS[1]

Function	*% Total Heat Production* *Normal Ration*	 *High Fat Ration*
Maintenance of adipose tissue	2.4	2.5
Lipogenesis	5.5	1.5
Lipolysis plus triglyceride resynthesis	1.2	1.4
Total	9.1	5.4

[1] Calculated using a balance model for 360 kg steers gaining 0.42 kg fat daily and fed a normal feedlot (70% concentrate) ration or a ration containing protected fat (Yang *et al.*, 1975) *ad lib.*

Unfortunately, although it may be easy to write a balance model, collection of some of the numerical inputs required for solution is not always straightforward. Two particular problems are prominent.

The first problem arises when required numerical (parameter) inputs are not available in the literature and/or cannot be measured directly. If the required parameter can be measured, the problem can be solved in the laboratory. In this case, a desired result of research modelling is attained — identification of critical experiments. If the required parameter is not directly measurable, as is sometimes the case, it is often feasible to obtain estimates using optimization models and/or statistical techniques.

A second problem encountered in using balance models is calculation of patterns or animal priorities in nutrient utilization. Such calculations usually require analyses of metabolic and physiological regulatory processes which interact in a variable fashion over time and thus cannot be accommodated in simple balance models. In this case, dynamic models are required for rigorous analyses.

OPTIMIZATION MODELS

Several types of optimization models have been used in the animal sciences (Bath *et al.*, 1972; Reichl and Baldwin, 1976; Koong and Lucas, 1976; Koong *et al.*, 1975). In this presentation only the use of optimization models to obtain estimates of parameter values not directly measurable will be considered. Koong and Lucas (1976) and Koong *et al.* (1975) considered the use of optimization models of this type for estimation of parameter values defining nutrient utilization patterns and efficiencies in lactating cows; and relationships between diet chemical composition and patterns of volatile fatty acid formation during rumen digestion, respectively.

An additional example can be constructed based on the balance model published by Canas *et al.* (1976). In this case, it was found that, because of a very high correlation between two "independent" variables, feed intake and body energy change, in an energy balance study with lactating rats, standard multiple regression techniques could not be used to estimate the maintenance requirement and lactational efficiencies of rats.

To overcome this problem, a balance model representing nutrient transformations in lactating rats was constructed. This model was used to deduce the relationship between feed intake and apparent maintenance requirement depicted in Fig. 2. It had been known for some time that maintenance requirements vary (Brody, 1945) but this had not been evaluated as a function of feed intake previously because of limitations in available statistical techniques. Further experimentation is required to reveal the underlying reason for this relationship. Modelling and pre-

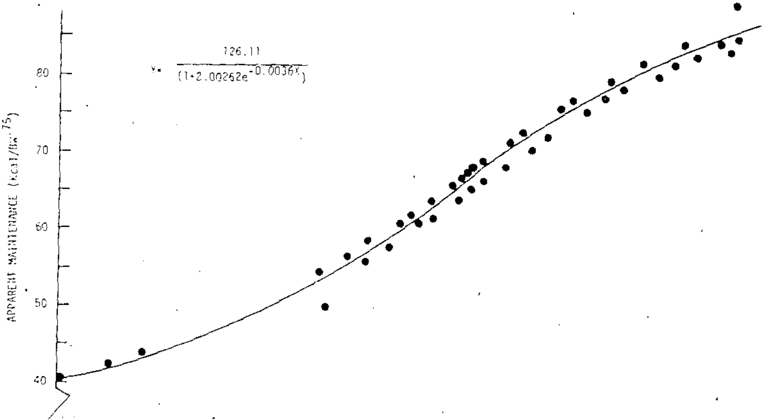

FIG. 2: *Relationship between food intake and apparent maintenance requirements. This logistic relationship was deduced using the model described by Canas (1974). The points indicated in the figure were obtained in a validation experiment with lactating rats and an experiment in which weanling rat food intakes were restricted (Walker* et al., *unpublished).*

liminary experimental analyses indicate this may be attributable to changes in relative organ weights (Canas, 1974).

Since many workers have reported that apparent maintenance requirements vary, it seems evident that satisfactory feeding standards must accommodate this variable. Conventional experimental approaches have not provided a suitable basis for such accommodation. Based on the progress achieved through the use of modelling in addition to experimental methods, it appears that further studies of this type will enable development of feeding standards which account for variable maintenance requirements.

In the balance model (Canas, 1974), several equivocal assumptions were required during formulation of numerical inputs. An alternative approach would have been to express these numerical inputs as unknowns within the model as in the following example:

$$\mathrm{GLCFAT} = \mathrm{X8}^{*}\mathrm{GLCBAL}/\mathrm{X9}$$

where the amount of glucose energy used to synthesize fat (GLCFAT) is represented as an unknown fraction (X8) of glucose available in excess of minimal requirements (GLCBAL) divided by an unknown efficiency of glucose conversion to fat (X9). Values for X8 and X9 could then be estimated as follows: assign initial values to unknown parameters in the model; compute, using these values and diet input data, milk production and body energy change estimates; compare these computed estimates with experimental data for each diet input and compute from this comparison, an error of estimate; and allow a computer routine to systematically adjust parameter values in sequential (iterative) solutions until differences (error) between computed and real data are minimized (optimization).

A model appropriate for this analysis has been written. However, available data were not numerous enough to obtain satisfactory estimates. The additional experiments required to support this detailed analysis of patterns and partial efficiencies of nutrient utilization in lactating animals are currently under way. The selection and design of these experiments was greatly aided by the modelling analyses undertaken demonstrating again the benefit obtained through the use of modelling along with experimental techniques in a research programme.

DYNAMIC MODELS

Important uses of dynamic models in animal research include evaluation of current data and concepts for quantitative and dynamic adequacy; identification and characterization of primary regulatory mechanisms determinant of animal performance; and, evaluation of alternative hypotheses for adequacy as explanations of observed phenomena. An early example (Smith, 1970; Baldwin and Smith, 1971b) of an application of dynamic models in an analysis of animal production involved an evaluation of then current hypotheses regarding the cause of low milk fat production in cows fed high concentrate rations. In development of the model, the data depicted in Fig. 1 for a reference cow (Smith, 1970; Baldwin and Smith, 1971a, b) were used.

A more detailed representation of adipose metabolism in the reference cow is presented in Fig. 3. This was the block diagram

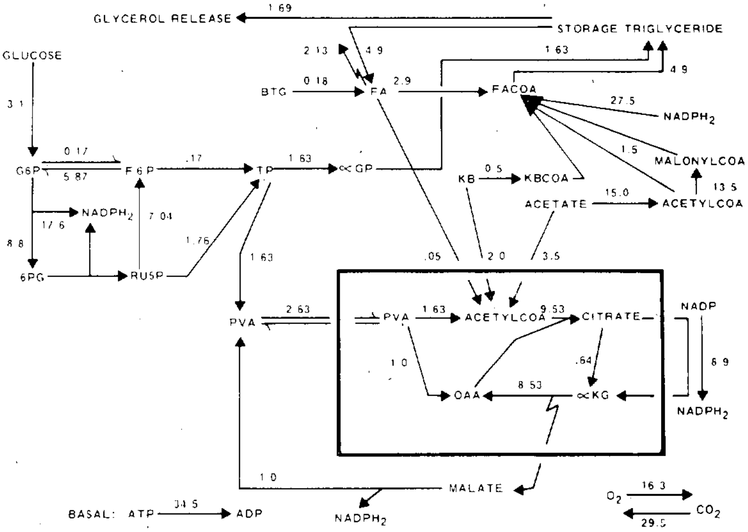

FIG. 3: *Diagrammatic representation of adipose metabolism in a lactating dairy cow. Conditions as described in legend to Fig. 1 (Smith, 1970).*

used in construction of the adipose element of the lactating cow model. Since the basic equation used to represent reaction rates in dynamic models has the form

$$\text{rate, velocity or flux} = K^*[S]$$

where K is a rate constant and [S] denotes substrate concentration, conversion of the block diagram to differential equations was quite easy. For example, the differential equation that describes the change in G6P from Fig. 3 would be:

$$dG6P/dt = K1*GLCC*ATPC - K2*G6PC + K3*F6PC - K4*G6PC*NADPC$$

where a terminal C in a codeword denotes concentration. More complex formulations can be used to represent regulatory effects if such are desired.

When the first model of a lactating cow was challenged with a high concentrate ration, the predicted milk fat percentage increased instead of decreasing. This indicated that information incorporated into the model was inadequate. This was an acceptable result. Additional evaluations made using this model indicated that the adipose element was poorly behaved and could not be improved without additional data. Thus, studies of ruminant adipose metabolism were undertaken (Baldwin *et al.*, 1973; Yang and Baldwin, 1973a, b; Yang *et al.*, 1975). Based upon the experimental results obtained, the lactating cow model was revised. When this model was challenged with a high concentrate diet, milk fat production was reduced and expected changes in the fatty acid composition of milk fat were observed. Results of a number of additional tests of the model yielded satisfactory results also, indicating that the concepts and data incorporated in the model explain, adequately, a number of observations. This model, after over seven years of research, will soon be published and has already been made available to several interested investigators for use in support of their research programmes.

ACKNOWLEDGEMENTS

Effective modelling analyses require the participation of many persons of differing disciplines. Therefore, contributions of R. Canas, I. Hume, L. J. Koong, H. L. Lucas, J. G. Morris, J. Reichl, N. E. Smith and M. J. Ulyatt to development of the philosophy and models discussed herein are gratefully acknowledged.

Support provided by the Applied Biochemistry Division of DSIR is gratefully acknowledged.

REFERENCES

Baldwin, R. L., 1968: *J. Dairy Sci., 51*: 104.
——— 1970a: *Brody Memorial Lecture X*: 1.
——— 1970b: *Fed. Proc., 29*: 1277.
Baldwin, R. L.; Smith, N. E., 1971a: *Fed. Proc., 30*: 1459.
———; ——— 1971b: *J. Dairy Sci., 54*: 583.
———; ——— 1974: In *Control of Metabolism* (Ed. J. D. Sink), p. 17. Pennsylvania State University Press.

Baldwin, R. L.; Reichl, J. R.; Louis, S.; Smith, N. E.; Yang, Y. T.; Osborne, Elba, 1973: *J. Dairy Sci., 56*: 340.
Bath, D. L.; Hutton, G. A.; Olson, E. H., 1972: *J. Dairy Sci., 55*: 1607.
Brody, S., 1945: In *Bioenergetics and Growth*. Reinhold, New York.
Canas, R., 1974: Ph.D. thesis, Univ. Calif., Davis.
Canas, R.; Romero, J. J.; Baldwin, R. L.; Koong, L. J., 1976: *J. Dairy Sci.* (in press).
Forrester, J. W., 1971: In *World Dynamics*. Wright Allen, Cambridge, Mass.
Koong, L. J.; Baldwin, R. L.; Ulyatt, M. J.; Charlesworth, T. J., 1975: *Comp. Prog. Biomed., 4*: 209.
Koong, L. J.; Lucas, H. L., 1976: *Anim. Prod.* (in press).
Milligan, L. P., 1971: *Fed. Proc., 30*: 1454.
Reichl, J. R.; Baldwin, R. L., 1975: *J. Dairy Sci., 58*: 879.
———; ——— 1976: *J. Dairy Sci.* (in press).
Riggs, D. S., 1963: In *The Mathematical Approach to Physiological Problems*. MIT Press, Cambridge, Mass.
Smith, N. E., 1970: Ph.D. thesis, Univ. Calif., Davis.
Yang, Y. T.; Baldwin, R. L., 1973a: *J. Dairy Sci., 56*: 350.
———; ——— 1973b: *J. Dairy Sci., 56*: 366.
Yaug, Y. T.; Baldwin, R. L.; Garret, W. N., 1975: *Fed. Proc., 34*: 903.