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A dynamical model of body composition in sheep

T.K. SOBOLEVA¹, V.H. ODDY², A.B. PLEASANTS¹, J.W. OLTJEN³, A.J. BALL⁴ AND D.G. MCCALL¹

¹AgResearch Ruakura, Private Bag 3123, Hamilton, New Zealand.

²NSW Agriculture, Cattle and Beef Industry CRC, UNE Armidale, NSW 2351, Australia

³Department of Animal Science, University of California, Davis, USA

⁴Division of Animal Science, UNE Armidale, NSW 2351, Australia

ABSTRACT

A dynamical model describing the evolution of muscle, viscera and fat in response to different levels of energy intake over time in sheep is presented. The model shows responses consistent with observations of compensatory growth in sheep and cattle over a range of energy intake levels.

Model parameters are derived from data measured by Ferrell *et al.*, (1986) to investigate compensatory growth in lambs. The model is shown to generally reproduce the behaviour of the muscle, viscera and fat components of the lambs in this trial.

The utility of the model for designing optimal nutritional management strategies for raising animals for slaughter is discussed, as well as the potential of the model to advance the understanding of animal nutrition by investigating different functional forms for relationships such as maintenance requirements.

Key words: energy intake; maintenance; compensatory growth model.

INTRODUCTION

The effect of pattern of growth in response to nutrient intake on the development of the body composition of an animal is of considerable commercial interest to farmers seeking to either find the most efficient way to grow an animal, or to develop pathways of production for specialist markets. Compensatory growth is an example of how different growth paths can alter the relative amounts of fat and muscle in an animal over time (Ryan, 1994). Models of animal growth have been developed to assist farmers to choose a suitable management strategy for raising animals. However, developing models to manipulate animal body composition through growth path has been difficult due to the dynamic and interactive nature of the growth process (Oddy *et al.*, 1997). This paper presents a dynamical systems model of the development of the viscera, muscle and fat pools of an animal under different nutritional strategies, which is suitable for describing the phenomena of compensatory growth.

MATERIALS AND METHODS

We use the following as axioms of animal growth in this model:

1. Growth is driven by energy intake. Essential elements in food intake such as protein or vitamins are not limiting.
2. Muscle and viscera each have an upper bound called the maturity of the component. The maturity of muscle is fixed (genetically?), although the possibility of reaching this level depends on both the current intake and nutritional history of the animal.
3. The maturity of viscera is affected by energy intake and depends on the previous growth path determined by the energy intake through time.

4. If energy intake is near maintenance then body protein can be gained and fat lost in the immature animal. As animals approach maturity the point at which this loss of fat and protein occurs come together. Energy intake above maintenance (net energy for gain, NE_g) is directed to viscera and muscle tissues gain in preference to fat.
5. Visceral tissues are more sensitive than muscle to changes of energy intake.
6. Maintenance requirements and heat production are related to energy intake, but changes in maintenance requirements follow changes in intake with some time delay. This depends on both the magnitude and the duration of the change in energy intake.

Based on these suppositions a system of dynamical equations expressing the changes in the muscle, viscera and fat pools was formulated as follows:

$$\begin{aligned} \frac{dm}{dt} &= k_m \left(NE_g(m, v, f, t) + \frac{c_m \left(1 - \frac{m}{m^*}\right) f}{f + f_0} \right) \cdot \left(1 - \frac{m}{m^*}\right) \\ \frac{dv}{dt} &= k_v \left(NE_g(m, v, f, t) + \frac{c_v \left(1 - \frac{m}{m^*}\right) f}{f + f_0} \right) \cdot \left(1 - \frac{v}{v^*(I)}\right)^2 \quad (1) \\ \frac{df}{dt} &= NE_g(m, v, f, t) - \frac{dm}{dt} - \frac{dv}{dt} \end{aligned}$$

where:

- m and v are masses of protein in muscle and viscera respectively, f is the mass of fat, all in energy units (kJ)
- m^* is a maximum muscle value (kJ);
- $v^*(I)$ is a maximum viscera mass (kJ) at given daily intake I (kJ/day), taken as a linear function βI here.

- NE_g is the net energy for gain expressed by $k_g \left(I - \frac{Q(m, v, f, t)}{k_{maint}} \right)$
- $\frac{Q(m, v, f, t)}{k_{maint}}$ is the daily maintenance requirement (kJ/day).
- k_m, k_v, k_g, k_{maint} and c are dimensionless coefficients, and f_0 is a coefficient with dimension of kJ.

The terms in brackets on the far right side of the first two equations in system (1) represent an upper bound on muscle and viscera, which the animal can achieve. For example, when $m = m^*$ the far right bracket of the muscle evolution equation in system (1) becomes zero and muscle growth stops. The same response occurs in the viscera evolution equation, except that the upper bound of the viscera is assumed dependent on the nutritional status represented by the energy intake I .

The energy driving the growth of muscle and viscera is given by the term NE_g which is the energy left after maintenance requirements given by function $Q(m, v, f, t)$ have been met. This function is the same for both muscle and viscera. Various forms may be used for this function. Because we have not completed this aspect of the model, we have used the form constructed by Corbett *et al.*, (1987) which partitions maintenance energy into that associated with metabolism (function of weight and age) and digestion of feed.

$$Q(m, v, f, t) = \alpha(I, t)W^{0.75} + 0.09I, \quad (2)$$

where I is the daily energy intake of the animal and W is empty body weight.

Investigations (Ferrell and Jenkins, 1985; Taylor *et al.*, 1986) show that the maintenance requirements are reduced by a history of low nutrition. Turner and Taylor (1983) review evidence that the metabolism of the animal lags behind changes in the energy intake, and that this results in lags in changes of the maintenance energy requirements. The function $\alpha(I, t)$ is constructed to model these changes in maintenance according to changes in energy intake. Let the energy intake change by an amount ΔI at time T_1 then return to the initial intake at time T_2 . The simplest form for $\alpha(I, t)$ to model the observed metabolic lags is:

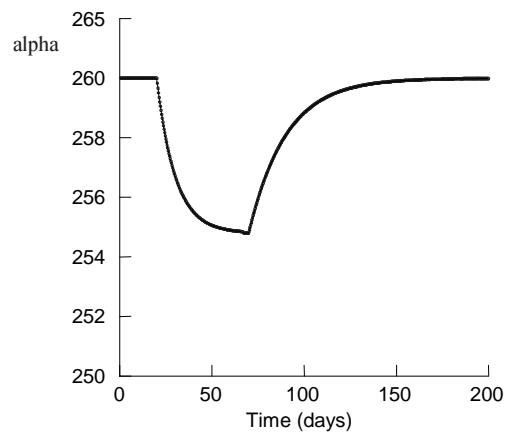
$$\alpha(I, t) = \alpha_0(I) \left[1 - b\Theta(t - T_1) \left(1 - e^{-\frac{t-T_1}{\tau_1}} \right) + b\Theta(t - T_2) \left(1 - e^{-\frac{t-T_2}{\tau_2}} \right) \right] \quad (3)$$

Here b is positive number proportional to

$a = \frac{\Delta I}{I}$ with coefficient of proportionality less than 1; τ_1, τ_2 are relaxation's times, which, generally speaking, depends

on value ΔI and duration of the period of restriction $T_1 - T_2$. The function $\Theta(t - T)$ is equal to 1 if $t - T$ is positive and to zero if $t - T$ is negative or zero. The exponential functions describe the relaxation of the animal to a new metabolic equilibrium following a rapid change in energy intake. The form of this function is shown in Figure 1. The constants $\alpha_0, k_m, k_v, k_g, c, g$ and f_0 are parameters to be estimated from data.

FIGURE 1: The form of the function $\alpha(I, t)$ which controls the delay in the response of the metabolism of the animal to a restriction in energy intake. In this case an energy restriction of 20% is applied between days 25 and 70.



Data obtained by Ferrell *et al.*, (1986) studying compensatory growth on intact male Suffolk ' Rambouillet ' Finnish Landrace lambs was used to test the model (1). In this experiment the lambs were fed in a cross-over design from 0 to 42 days on one level of nutrition, then from 42 to 84 days on a second level of nutrition. The levels of nutrition were low or steady (L or S), medium (M) and high (H). See Ferrell *et al.*, (1986) for details. Data for visceral protein alone were not available and have been combined with all non-carcass (offal and skin) protein for the example presented here. The solution of the system of non-linear differential equations (1) is given by three time dependent functions, one each giving the time evolution for muscle, viscera and fat. While the system of equations (1) cannot be solved analytically, numerical solutions can be obtained and these numerical solutions used in place of the explicit analytical solutions. In the data, measurements were made of the initial liveweight, the final liveweight and the average daily energy intake. At the end of the trial, which ran for 84 days, the weights of muscle, viscera and fat for each animal were measured.

The dynamical system (1) was solved numerically using initial conditions based on the liveweights of the animals at the beginning of the trial. The initial conditions adopted were muscle 0.078 x initial liveweight x 23800; viscera 0.06 x initial liveweight x 23800; fat 0.13 x initial liveweight x 39600. The results at day 84 from the simulation were compared to the measurements made on the animals at this time.

Values for the coefficients in the model, which were chosen empirically to fit the results reported in Tables 1

and 3 published in Ferrell *et al.*, (1986), are given in Table 1. To account for the effect of the level of energy intake on maintenance requirements as expressed in Equation (3) the value of α_0 was adjusted relative to the HH treatment. This was necessary as the average maximum energy intake differed between the groups. The value of a_0 ranged from 277(HH treatment) to 254 (LH treatment).

TABLE 1: Estimates of the Parameters in Equations (1) Based on the Data of Ferrell *et al.*, (1986).

Parameter	Units	Estimate
k_m	Dimensionless	0.17
k_v	Dimensionless	0.7
k_g	Dimensionless	0.46
k_{maint}	Dimensionless	0.68
α_0 (HH treatment)	$\text{kJ/kg}^{0.75}/\text{day}$	277
m^*	kJ	175100
β	days	7.8
c_v	kJ/day	150
c_m	kJ/day	500
f_0	kJ	5
t_1	days	10
t_2	days	20
b	Dimensionless	$0.1 \times \frac{\Delta I}{I}$

RESULTS

The model predictions of the response of the body components over time to different growth paths are shown in Figure 2. For illustration, Figure 2 shows the result of a considerable nutritional restriction of 50% of energy intake for 100 days in the restricted energy group.

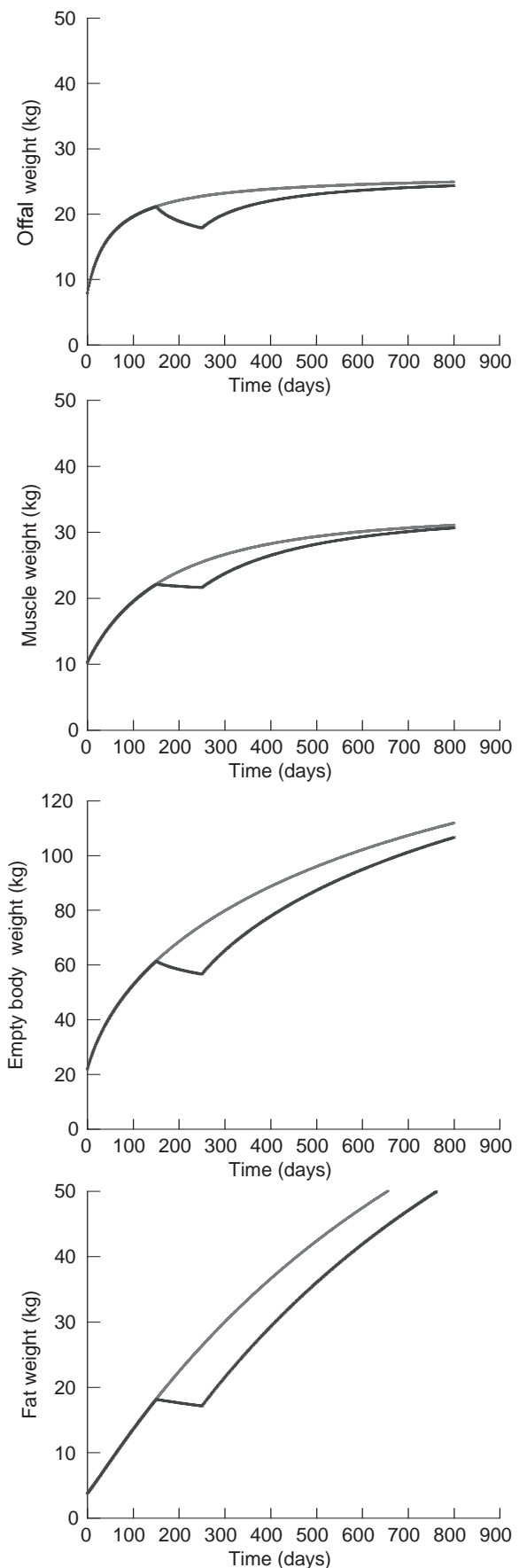
A comparison between the model predictions and the results measured by Ferrell *et al.*, (1986) for the weight of protein and fat are shown in Table 2.

TABLE 2. Comparison of the Amount of Protein and Fat Generated by the System of Equations (1) With the Results Reported by Ferrell *et al.*, (1986).

Nutritional treatment	Measured fat (kg)	Model prediction of fat (kg)	Measured protein (kg)	Model prediction of protein (kg)
HH	11.76 ± 1.068	11.5	8.04 ± 0.566	8.2
HM	10.11 ± 0.973	10.0	7.38 ± 0.528	7.1
MH	9.70 ± 0.937	9.2	6.79 ± 0.505	6.8
LS	6.38 ± 0.811	7.4	6.07 ± 0.467	6.5
HL	6.07 ± 0.738	7.2	5.98 ± 0.452	6.5
MM	7.05 ± 0.770	7.3	5.62 ± 0.441	5.6
LH	5.74 ± 0.698	5.9	5.12 ± 0.418	5.2
ML	3.76 ± 0.552	5.3*	4.18 ± 0.380	4.7
LM	4.03 ± 0.559	4.3	4.12 ± 0.378	4.7

* Difference between model prediction and experimental measurement $P < 0.05$

Given the uncertainties of the initial conditions, and lack of data on the individual energy intakes of the animals, and the pre-trial nutritional history these results show that the model reproduces well the experimental results for the H and M nutritional treatments for the chosen parameters. Nutritional treatments involving the L treatment did not show such good agreement (with the exception of LH, which did show good agreement). But only in the ML group was the difference between model and experiment statisti-



cally significant ($P < 0.05$). The model predictions of the response of the body components over time to different growth paths are shown in Figure 2. For illustration, Figure 2 shows the result of a considerable nutritional restriction of 50% of energy intake for 100 days in the restricted energy group.

The model showed that the later the nutritional restriction was imposed on the animal the less the recovery at 500 days of age. The regression of empty body weight at 500 days of age on time of nutritional restriction was -0.006 kg per day. The greater the severity of the nutritional restriction the less the recovery at 500 days of age, although the animals with the greater nutritional restriction grew faster when the nutritional level was restored.

DISCUSSION

This model of animal growth is formulated at the macro level, and is designed to incorporate those features of the relationship between muscle and viscera observed by Jenkins and Ferrell (1983). This interaction was reviewed by Ball *et al.*, (1997) in terms of the relationship to compensatory growth in animals. That is, viscera responds faster than muscle to changing energy intake by the animal, but this change has some time lag. The model predicts that changes in the maintenance requirements of the animal follow changes in the viscera pool resulting from changes in animal energy intake. This makes maintenance requirements a dynamic variable depending on the nutritional history as well as the current energy intake. The results from the model are consistent with the conjecture that the observed features of compensatory growth follow from the changes in the dynamics of body components in response to both the stage of maturity and feed intake.

The fit of the model to the data of Ferrell *et al.*, (1986) is good with some exception of those treatments including the L level of nutrition in the combination. If the lambs were on a high level of energy intake before the trial (and this is likely the case), it would account for the discrepancy in the animals placed on the L or M treatment when the trial commenced, because of the delay in the fall of maintenance described by the model. Figure 1 shows how α slowly relaxes to another value corresponding to the current level of intake. If nutritional levels were high prior to commencement of the trial this delayed response would explain the overestimation by the model of fat for the LS, MM, ML and LM groups.

The form of the maintenance function used is the traditional form adopted by nutritionists and may not be correct, especially in a dynamical situation. One of the advantages of the way the model is formulated is that the performance of different functions describing the maintenance of the animal can be investigated. That is, the fit of the model to data with different functions $Q(m, v, f, t)$ can be compared to chose the best functional description on the maintenance energy requirements and the function to describe $v^*(I)$.

The qualitative features of compensatory growth of the model illustrated in Figure 2 agree with the results given by Ryan (1994). Similarly the propensity of animals approaching maturity to show less compensatory gain in the model was also noted by Ryan (1994). However, the increased nutritional intake of animals undergoing compensation close to maturity is also a factor as noted by Nicol and Kitessa (1994). The increase in the rate of growth due to the increase in the severity of the nutritional restriction, predicted by the model, is also discussed by Ryan (1994).

This paper has established a correspondence between the model and an extensive experiment on compensatory growth suggesting that the model has captured the main features of this phenomenon. We anticipate the model can be used to design optimal feeding strategies for sheep and cattle when appropriate economic information and constraints from the external system are included.

ACKNOWLEDGEMENTS

We acknowledge the assistance of G.C. Wake, University of Canterbury, P.V. Rattray of AgResearch, T. Jenkins, C. Ferrell, J. Keele, C. Williams, D. Harris, G. Bennett and H. Freetly of the USDA Clay Centre, Nebraska.

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