Mathematical absurdities in the California net energy system

Carl A. Old,[*,1] **Ian J. Lean,**[†] **and Heidi A. Rossow**[‡,○]

*A3 Cattle Company, LeGrand, CA 95333; †Scibus and the Faculty of Science, The University of Sydney, Camden 2570, Australia; and ‡School of Veterinary Medicine, University of California, Davis, Davis, CA 95616

ABSTRACT: Net energy systems, such as the California Net Energy System (**CNES**), are useful for prediction of input:output relationships not because of fidelity to the laws of thermodynamics, but because they were designed to predict well. Unless model descriptions of input:output relationships are consistent with the laws of thermodynamics, conclusions regarding those relationships may be incorrect. Heat energy (**HE**) + recovered energy (**RE**) = ME intake (**MEI**) is basic to descriptions of energy utilization found in the CNES and is consistent with the laws of thermodynamics; it may be the only relationship described in the CNES consistent with the first law of thermodynamics. In the CNES, efficiencies of ME utilization for maintenance (k_m) and gain (k_g) were estimated using ordinary least squares (**OLS**) equations. Efficiencies thus estimated using static linear models are often inconsistent with the biochemistry of processes underlying maintenance and gain. Reactions in support of oxidative mitochondrial metabolism are thermodynamically favorable and irreversible; these reactions yield ATP, or other high-energy phosphate bonds, used for what is generally termed maintenance. Synthesis of biomass (gain) is less thermodynamically favorable; reactions do not proceed unless coupled with hydrolysis of high-energy phosphate bonds and lie closer to equilibrium than those in support of oxidative mitochondrial metabolism. The opposite is described in the CNES ($k_m > k_g$) due to failure of partitioning of HE; insufficient HE is accounted for in maintenance. Efficiencies of ME utilization (k_m and k_g) as described in the CNES are variable. Further neither k_m nor k_g are uniformly monotonic f(ME, Mcal/kg); for ME (Mcal/kg) <0.512 or >4.26, k_m are inconsistent with thermodynamically allowed values for efficiencies (>1.0); k_g are a monotonically positive f(ME) concentration (Mcal/kg) for ME <3.27 Mcal/kg. For ME <1.42 Mcal/kg, k_g are not in the range of thermodynamically allowed values for efficiencies (0 to 1.0). Variable efficiencies of ME utilization require that the first law may not be observed in all cases. The CNES is an excellent empirical tool for prediction of input:output relationship, but many CNES parameter estimates evaluated in this study lack consistency with biology and the laws of thermodynamics.

Key words: beef cattle, efficiency, maintenance

INTRODUCTION

[Lofgreen and Garrett (1968)](#) described an evolutionary step in prediction of input:output relationships for growing and finishing beef cattle.

These investigators used computational tools available and concepts regarding energy utilization for maintenance and gain prevalent at the time; contemporary dogma relied extensively on parameter estimates determined using ordinary least squares (**OLS**) statistical models. Classical OLS estimates of k_m and k_g differ from theoretical and are inconsistent with laws of thermodynamics. Baldwin (1968) described theoretical efficiencies of oxidative mitochondrial metabolism and net synthesis of biomass, which fall well within the range of experimental observations. Products of oxidative mitochondrial metabolism are used to maintain ionic gradients, provide for turnover of proteins and lipids, nervous function and respiration; these service and repair functions are some of what is classically termed maintenance. Baldwin (1995) noted that efficiencies of ME utilization for maintenance (k_m) and gain (k_g) should be virtually identical to theoretical pathways. According to Schiemann (1969) and van Milgen (2002, 2006) maintenance is a requirement for ATP equivalents; k_m should be similar to the efficiency of ATP synthesis. In growing animals, k_g is determined by the composition of gain and the efficiencies of ME utilization for fat (k_f) and protein (k_p) synthesis. Differences in magnitude between empirical and theoretical estimates indicate that OLS (empirical) estimates of heat energy of product formation (H_rE) are greater than both theoretical and actual. Further, the point at which animals are calculated (OLS framework) to be in energy equilibrium (ME_m) is less than that estimated in a Bayesian framework and that value, presumed to be static in most studies, may be dynamic, varying with quantity and quality of feed consumed by an animal. We will review models and model structures used by Lofgreen and Garrett (1968) with emphasis placed on consistency of estimates reported by those investigators with biology and thermodynamics.

Energy Terms and Utilization

Animals consume feed, of which energy is a dynamic property not a nutrient; total energy intake (**IE**) is also referred to as gross energy (**GE**). Fecal energy subtracted from GE is apparent digestible energy (**DE**); DE minus energy losses as urine and gasses (primarily methane, however, hydrogen and ethane may also be lost; Flatt, 1969) equals ME. Metabolizable energy represents the physiological fuel available to the cell for metabolism (Baldwin, 1995). In the case of growing animals, net energy is utilized for either maintenance (NE_m) or gain (NE_g).

Products of digestion and absorption, volatile fatty acids, lipids and amino acids, to name a few, are either oxidized in support of mitochondrial metabolism (maintenance) or used for biomass accretion (gain). Maintenance includes repair functions such as turnover of accumulated biomass (proteins and lipids) and sodium transport in the maintenance of membrane potentials as well as service functions, including respiration, heart work, and nerve function (Baldwin, 1995). Gain in cattle, as described by Lofgreen and Garrett (1968), is the accumulation of fat and protein, both energy containing products. It is interesting to note that Moe and Tyrrell (1973) described the same products (fat and protein) as gain, yet products associated with maintenance was literally a question mark, in spite of the fact that prior reports (Baldwin, 1968; Schiemann, 1969) described maintenance as a requirement for ATP equivalents.

The NRC (1981) describes partitioning of MEI, in growing and finishing cattle as shown:

$$ME \text{ intake } (\textbf{MEI}) = NE_m + NE_g$$
$$+ \text{ heat increment of feeding } (\textbf{H}_i\textbf{E})$$

therefore:

$$MEI = ME_m + NE_g + H_rE$$

Partitioning of HE between maintenance and heat increment of product formation is a mathematical solution to a mathematical problem; unless models are properly specified, utility in those models may reside solely in prediction. Functional forms of variables must be globally consistent with mechanisms underlying calculated efficiencies of ME utilization; if not, parameter estimates will differ from the true parameters.

Thermodynamically Favorable and Unfavorable Reactions

Thermodynamically favorable reactions are characterized by a large negative Gibbs free energy change (ΔG^0) and transfer of electrons from reactants to products, reactions proceed as written. An example of this is the oxidation of glucose to CO_2 and H_2O ($\Delta G^0 = -686$ kcal/mol) in which 24 mol of electrons are transferred to O_2 for each mol of glucose oxidized; C atoms in glucose are the source of electrons.

Thermodynamically unfavorable reactions are characterized by a positive ΔG^0, reactions will not proceed as written unless coupled with a thermodynamically favorable reaction. The magnitude of ΔG^0 for ATP synthesis ($ADP^{3-} + P_i^{2-} + H^+ \rightarrow$

$ATP^{4-} + H_2O$) is 7.29 kcal/mol; electron flow is from the products to reactants. Coupling glucose oxidation with ATP synthesis (30 ATP/mol glucose oxidized; Rich, 2003), conserves 31.9% of ΔG^0 from glucose oxidation in ATP.

Carbon atoms in amino acids and acetate are more oxidized than C atoms in products protein and lipids therefore reactants cannot transfer electrons to products, the reactions are thermodynamically unfavorable. Coupling synthesis of proteins and lipids with ATP hydrolysis, and other thermodynamically favorable reactions, allows synthesis to occur. Because products proteins and lipids are more reduced than reactants amino acids and acetate, reactions are reversible; ΔG^0 is much closer to 0 (equilibrium) for these reactions than for the oxidation of glucose to CO_2 and H_2O (products more oxidized than reactants).

Given the amino acid composition of muscle protein (Rossow, unpublished data) and the heat of combustion (ΔH_c) for each amino acid, it is possible to calculate the energy input of amino acids to muscle protein synthesis. Our estimate of ΔH_c for amino acid input is 5.03 kcal/g; estimated ΔH_c for muscle protein output is 5.61 kcal/g, similar to the value reported by Garrett and Hinman (1969), which was 5.539 kcal/g. Baldwin (1995) reported an average molecular weight of 110 g/mol for amino acids in a protein; our estimate of 108 g/mol is similar. In much the same way that water flows downhill, not uphill, thermodynamically favorable reactions go from greater energy content to lesser energy content ($-\Delta G^0$). This analysis indicates that the condensation of amino acids to form proteins is thermodynamically unfavorable, requiring coupling with a reaction that is thermodynamically favorable.

Development of the CNES

Shortcomings of the TDN system were recognized shortly after it was introduced and by the middle of the 20th century, cattle feeders in California required a better system for prediction of input:output relationships. Studies at the University of California, Davis, conducted primarily by Glen Lofgreen and Bill Garrett, resulted in the development of a system for predicting net energy requirements and feed values for feedlot cattle; that system is still in use. In growing and finishing cattle, as described by the CNES, the fate of ME is either as heat energy (**HE**) or recovered energy (**RE**). All ME used for service and repair functions is given off as HE (HE at RE = 0 is ME_m);

ME consumed at intakes greater than maintenance is found as RE or as H_rE. Intake of ME was measured by Lofgreen and Garrett (1968); RE was determined by comparative slaughter and HE calculated as the difference between ME and RE. For animals consuming no feed, MEI = 0 and all heat energy is produced by metabolism of body reserves. Heat energy at MEI = 0 (H_eE) was estimated as the intercept for log HE = f(MEI) in a single variable OLS framework:

$$\log \text{HE (kcal EBW}^{0.750} \times \text{d}^{-1}) = 1.8851 + 0.00166 \text{ MEI (kcal ME/EBW}^{0.750} \times \text{d}^{-1});$$

as reported by Lofgreen and Garrett (1968)

$$\log \text{HE (kcal EBW}^{0.750} \times \text{d}^{-1}) = 1.888659 + 0.0016466 \text{ MEI (kcal ME/EBW}^{0.750} \times \text{d}^{-1});$$

same data using lm package in R; (R Core Team, 2013) and H_eE is assumed, in the CNES, to be equivalent to the net energy required for maintenance (NE_m), described by Lofgreen and Garrett (1968) as 0.077 Mcal/empty body mass (**EBW**, dimension = kg) raised to the 0.750 power, per day (0.077 Mcal/EBW$^{0.750} \times$ d^{-1}). As intakes of ME increase, the proportion of HE from body reserves is reduced until HE = MEI and the animal is considered to be at energy equilibrium or maintenance. Maintenance, as commonly calculated, is a mathematical solution to a mathematical problem for growing beef cattle. Bill Garrett (W. N. Garrett, University of California, Davis, late Professor Emeritus of Animal Science, personal communication) was adamant that maintenance is a state, RE = 0, and very likely to be an ephemeral condition in most production livestock and extremely unlikely to be encountered in growing and finishing beef cattle. For a mature animal at RE = 0, all metabolic processes are uniquely maintenance and include turnover of lipids and proteins, obviously at RE = 0 there is no net synthesis. Given the fact that turnover of lipids and proteins is a service and repair function in mature animals at RE = 0 it seems unlikely that turnover of lipids and proteins is not uniquely a service and repair function in growing animals as well.

Because the efficiency of metabolic processes with which ME is used for maintenance differs from that for gain (Kleiber, 1961), two values for feed energy (NE_m and NE_g, Mcal/kg) are required in the CNES; it is also necessary to determine some estimate of energy equilibrium. Lofgreen and Garrett (1968) estimated heat production at MEI = 0 and considered that value (0.077 Mcal/EBW$^{0.750} \times$ d^{-1}) to be the net energy requirement for maintenance;

k_m was estimated as f(ME, Mcal/kg) and k_g as $f(k_m)$. In keeping with popular thought regarding efficiencies of ME utilization at the time as a function of ME concentration, k_m and k_g are variable and essentially are f(ME, Mcal/kg). It is important to note that, as determined by Lofgreen and Garrett (1968), H_eE, ME_m, k_m and k_g are, again, mathematical solutions and highly unlikely to equal the true parameters. The CNES is a black box description as to how feed energy input (MEI) is converted to ATP equivalents (NE_m) and biomass gain (NE_g), not a characterization of metabolic processes.

Efficiency of ME utilization for maintenance (k_m) is defined as H_eE/ME_m (NRC, 1981); Lofgreen and Garrett (1968) first estimated H_eE then predicted feed required at energy equilibrium (g/d × $EBW^{-0.750}$) over the range of ME from 1.92 to 2.78 kcal/g, expressed as 90% DM. The single variable OLS solution was:

log (feed required at energy equilibrium,
$\quad$ g/d (90% DM basis) × $EBW^{-0.750}$) = 2.303 0.2455 ME (kcal/g, 90% DM basis)

Efficiency of ME utilization for maintenance is then:

$$k_m = (0.077 \text{ Mcal}/EBW^{0.750} \times d^{-1})/[(10^{(2.303\ 0.2455\ \text{ME (kcal/g, 90\% DM basis)}}) \times \text{ME (kcal/g, 90\% DM basis)}].$$

Lofgreen and Garrett (1968) estimated NE_g (kcal/g, feed) from feed required for energy equilibrium:

$$NE_g(\text{kcal/g, 90\% DM basis}) = 2.29\ 0.0254 \times (\text{feed required at energy equilibrium,} \\ \text{g/d (90\% DM basis)} \times EBW^{-0.750}.$$

k_g is estimated as the ratio of NE_g (2.29 − 0.0254 × (feed required at energy equilibrium, g/d (90% DM basis) × $EBW^{-0.750}$: ME (kcal/g, feed).

Lofgreen and Garrett (1968) overcame the common criticism that NE systems fail to give roughages greater values for maintenance than for production, relative to concentrates, by requiring ME_m to vary as f(feed required for energy equilibrium); since H_eE is fixed, k_m is variable. Similarly, k_g is a variable f(feed required for energy equilibrium). Koong et al. (1983) suggested that H_eE and ME_m are dynamic and the characterization by Lofgreen and Garrett (1968) of ME_m as dynamic is, in part, consistent with concepts put forth by Koong et al. (1983). Lofgreen and Garrett (1968) put together a system expressing animal requirements and feed values that could be used by nutritionists in the field with the tools available. Given the computational tools available at the time, a system blending empirical and mechanistic elements, may have been beyond the abilities of the investigators to create and those using the system to predict input:output relationships in growing cattle,

Mathematical Absurdities in Commonly Used Statistical Models

Kielanowski (1965) described an OLS statistical model used to estimate efficiencies of ME utilization for protein and fat synthesis. Old and Garrett (1985) used that model and estimated the efficiency of ME utilization for protein synthesis (k_p) in finishing beef cattle as 0.100. If that estimate were correct, the reaction (protein synthesis) would be considered thermodynamically favorable and lie far from equilibrium, consequently proteins would be stable and turnover minimal. Based on analysis by Baldwin (1995) for cattle described by Old and Garrett (1985), whole body protein synthesis is calculated to be from 500 to 700 g/d while net protein deposition was reported to be 100 g/d. Lobley et al. (1980) reported even greater amounts of daily protein synthesis, based on tracer flux studies in growing crossbred Hereford heifers. Estimates from the Lobley et al. (1980) study indicated that from 1.6 to 3.0 kg protein were synthesized daily and accounted for a maximum of 30% of daily HE. The magnitude of the estimator k_p contrasts with the lability of proteins (Biddle et al., 1975), an indication of model misspecification (Mason et al., 2003). Classically derived OLS estimates of k_p appear to be mathematical solutions to mathematical problems.

To estimate feed intake in growing beef cattle, Cruz et al. (2010) used a model of the form $ADFI_i = a + b_1 \times EBW_i^{0.75} + b_2 \times ADG_i + r_i$

where $\mathbf{ADFI_i}$ is ADFI (kg DM) by the ith individual, the vector $\mathbf{ADFI} = (ADFI_1, ADFI_2....ADFI_n)$, $\boldsymbol{a}$ is the intercept (kg DM/d), $\boldsymbol{b_1}$ is a coefficient (kg DM/d × $EBW^{-0.75}$), $\boldsymbol{b_2}$ is a coefficient (kg DM/d × ADG^{-1})), $\mathbf{EBW_i^{0.75}}$ is the average EBW for an individual raised to the 0.75 power, and $\boldsymbol{r_i}$ is the residual for the ith observation.

Consistent with the fact that feed, and energy in that feed, is used by growing cattle for either service and repair functions (Baldwin, 1995), collectively termed maintenance or for gain, the magnitude of the intercept reported by Cruz et al. (2010) was not different from 0. This report contrasts with that of Old et al. (2015) who calculated an intercept of −2.66 (ADFI, kg DM); such a result indicates cattle in that study, when both $EBW_i^{0.75}$ and ADG_i are equal to 0 produce feed, an observation inconsistent with the law of conservation of mass and energy. Biological irrelevance of the

intercept is noted when the true theoretical relationships between predictors and response are not described by the model An equally unlikely possibility is that, given the coefficient of maintenance 0.098 $EBW^{0.750}$ (kg DM/d) reported by Old et al. (2015), animals weighing 81.6 kg are calculated to be in energy equilibrium, while consuming no feed. It is quite likely that the model described by Old et al. (2015) is yet one more mathematical solution to a mathematical problem utilizing a model structure with no basis in biology.

Mathematical Absurdities in the CNES

Lofgreen and Garrett (1968) relied on extrapolation well outside the range of observed data for parameter estimation; the perils of extrapolation in a single variable OLS framework should be well known to the reader. Unless the model describes the true theoretical relationship between response and predictor (Imhoff and Old, 1952) estimates determined outside the observed range will be lacking in relevance. Inferences outside the observed data range (MEI ~ 0.100 to 0.335 Mcal ME/ $EBW^{0.750} \times d^{-1}$) are likely to result in inflated variances about the estimate H_eE. Heat energy for MEI < ME_m, while described as $f(MEI)$, is not solely due to MEI; from MEI = 0 to MEI = ME_m body tissue energy and MEI both contribute to HE. Variability about parameter estimates for the aforementioned function, as reported by Lofgreen and Garrett (1968), estimated in either an OLS (lm package in R; R Core Team, 2013) or Bayesian framework (WinBUGS in R; R Core Team, 2013) using Lofgreen and Garrett (1968) data, are found in Table 1. Variability about H_eE, determined in a Bayesian framework, indicated poor model specification (inflated variance); variance about the slope was also inflated in either an OLS or Bayesian framework.

Lofgreen and Garrett (1968) reported $H_eE \pm s_{y \cdot x}$, or ± (root mean square residual), as bounds. Parameter estimates (slope and H_eE) are similar and differences between Lofgreen and Garrett's (1968) reported values and those determined for this report are likely due to rounding errors, given the tools available to Glen Lofgreen for calculations.

Users of the CNES should be aware that for MEI = 0 a 95% CI about the intercept as shown in Table 1 is an appropriate measure of variability if, and only if, estimates are for data described by Lofgreen and Garrett, 1968 (table 1). For future observations, that is every other estimate of H_eE, variability (95% prediction interval) about the estimate 77.4 kcal /$EBW^{0.750} \times d^{-1}$ is from 66.0 to 90.7 kcal /$EBW^{0.750} \times d^{-1}$.

Given that MEI = MEI, MEI = RE + HE, dMEI/dMEI = 1; therefore by simple algebra, dRE/dMEI + dHE/dMEI must also be equal to 1 for animals in a positive energy balance.

Table 1. Variability about parameter estimates for log HE = H_eE + b × ME intake[a,b,c,d]

Source of estimate	Item	
	log H_eE	b
Lofgreen and Garrett (1968)[e]	1.885 (76.8)[f]	0.00166
Reported range	72 to 82	—
OLS[g]	1.888659 (77.4)[f]	0.001647
95% CI	71.5 to 83.7	0.001486 to 0.001807
Bayesian[h]	1.889 (77.4)[f]	0.001647
95% Credible interval	59.4 to 100	0.001487 to 0.001807
Bayesian[i]	1.889 (77.4)[f]	0.001647
95% Credible interval	71.5 to 83.7	0.001099 to 0.002195

[a]**HE** = heat energy (kcal/$EBW^{0.750} \times d^{-1}$).

[b]$\mathbf{H_eE}$ = heat energy at ME intake = 0 (kcal/$EBW^{0.750} \times d^{-1}$).

[c]**b** = parameter estimate (no dimension).

[d]Data from table 1 in Lofgreen and Garrett (1968).

[e]As reported by Lofgreen and Garrett (1968)

[f]Parenthetical values are H_eE (kcal/$EBW^{0.750}$ x d^{-1})

[g]**OLS** = ordinary least squares (lm package in R, R Core Team, 2013).

[h]Informed priors were such that Bayesian solutions for H_eE and b were identical to OLS solutions and variability about b identical to OLS solutions.

[i]Informed priors were such that Bayesian solutions for H_eE and b were identical to OLS solutions and variability about H_eE identical to OLS solutions.

For RE = 0, MEI = HE, therefore at ME_m dHE/dMEI is necessarily 1. The first derivative of the single variable OLS function described by Lofgreen and Garrett (1968) is dHE/dMEI = ln (10) × 0.00166 × $10^{(1.8851 + 0.00166MEI)}$. Lofgreen and Garrett (1968) did not estimate k_g as dRE/dMEI, but rather as the ratio of NE_g (feed required for energy equilibrium) to ME (kcal/g, 90% DM). Over some of the range of observed MEI for RE >0, dHE/dMEI, was >1.0, a thermodynamic impossibility; for any animal in a positive energy balance the sole source of HE is MEI. Our analysis of data described by Lofgreen and Garrett (1968) for ME (kcal/g, 90% DM) from 1.92 to 2.78 and MEI from 100 to 335 (kcal/$EBW^{0.750}$ × d^{-1}) indicates that dMEI/dMEI is poorly estimated as dRE/dMEI + dHE/dMEI. Since the laws of thermodynamics require that MEI = RE + HE, failure to describe dMEI/dMEI as the sum of dRE/dMEI and dHE/dMEI, as can be seen in Figure 1, indicates that the static linear models and methods used by Lofgreen and Garrett (1968) fail to adequately describe energy transactions in a manner consistent with the laws of thermodynamics. These observations are a clear indication that estimates of MEI at RE = 0 are less than the true parameter, therefore k_m estimated as H_eE/ME_m, is greater than the true parameter. As a result, estimates of k_g by Lofgreen and Garrett (1968) are less than the true parameter. Transformation of the response variable by Lofgreen and Garrett (1968) may have altered the relationship between predictor and response variables. It is also quite possible that the single variable OLS function log HE = f(MEI) is not the true theoretical model, the result of which is that regions of predictor variables exist for which predicted responses will be extremely inaccurate.
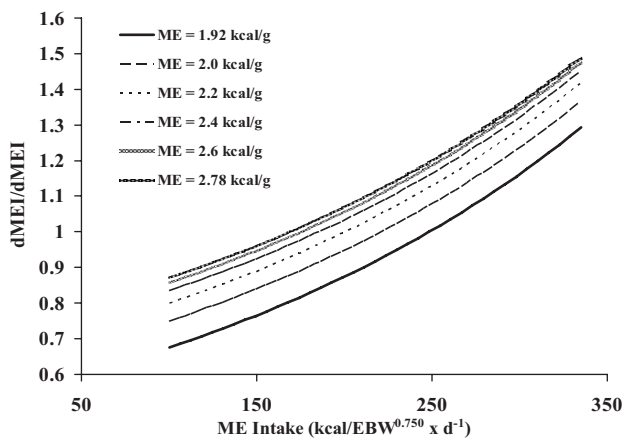

Figure 1. Rates of change of (ME intake with respect to ME intake) calculated as the rate of change of (recovered energy with respect to MEI) + the rate of change of (heat energy with respect to MEI) (dMEI/dMEI = dRE/dMEI + dHE/dMEI).

The parameter estimate H_eE, is used throughout the CNES as a basis for determination of most of the input:output relationships described by that system. Given the manner in which H_eE was determined, one may question if H_eE and other parameter estimates found in the CNES are equal to the true values. It can not be stated often enough: the methods employed by those investigators were not intended to produce parameter estimates consistent with biology and the laws of thermodynamics. Lofgreen and Garrett (1968) were presented with a mathematical problem; describe animal performance in terms of ME input. The CNES is simply a mathematical solution to that problem.

Gibbs free energy of ATP is variable and a function of tissue and substrate (Morikofer and Walter, 1992; Jibb and Richards, 2008; Siegel et al., 2012); oxidation of acetate conserves a theoretical maximum of from 32.2% to 45.8% of ΔH_c of acetate in ATP. Kennedy and Calvert (2014) updated theoretical estimates of k_f (0.71) and k_p (0.77) originally calculated by Baldwin (1968); for cattle described by Lofgreen and Garrett (1968), in which fat comprised ~40% of gain, maximum k_g is ~0.720. Theoretical estimates of efficiencies are consistent with the thermodynamic favorability of biochemical reactions; reactions in support of service and repair are thermodynamically more favorable and lie further from equilibrium than synthesis of biomass, providing further evidence that estimates of k_m and k_g within the CNES are likely to be mathematical solutions to mathematical problems.

The efficiency of ME utilization for maintenance is estimated, in classical systems, as the ratio H_eE/ME_m (Kleiber, 1961); efficiencies of processes are thermodynamically defined as the ratio of work done by a system to the energy supplied to that system. While ME_m represents energy supplied, it is unlikely that H_eE represents work done by MEI as MEI = 0. The magnitude of k_m, estimated as H_eE/ME_m (0.626 for table 1 data, Lofgreen and Garrett, 1968), is less than theoretical estimates of k_g. Further evidence that H_eE does not represent work done by MEI supplied; dHE/dMEI for MEI = 0 is 0.293; the expectation is that as MEI → 0, dHE/dMEI → 0 as well. The solution for energy equilibrium (ME_m) lacks uniqueness when calculated using the equation log HE = 1.8851 + 0.00166 MEI. Intake of ME = HE at MEI = 123 kcal ME/$EBW^{0.750}$ × d^{-1} and at MEI = 321 kcal ME/$EBW^{0.750}$ × d^{-1}. The former estimate is for the equality of HE and MEI; since MEI = HE +RE, for HE = MEI then RE = 0. However, since at MEI of 321 kcal ME/$EBW^{0.750}$ × d^{-1}, dHE/dMEI = 1, RE must also

equal 0. The description of log HE as a single variable OLS f(MEI) does not appear to adequately capture variability in HE; the model is misspecified.

For a subset of those data (Lofgreen and Garrett, 1968), heifers fed 100% roughage diets at either low (n = 3) or ad libitum (n = 3) intakes a crude estimate of k_g (ΔRE/ΔMEI) is 0.258; this approach is described by Lofgreen and Garrett (1968) and has been classically termed the "difference trial." Estimated k_g (ΔRE/ΔMEI) for heifers fed 2% roughage diets at either low (n = 3) or ad libitum (n = 3) intakes was 0.450. For all data (n = 31) an OLS solution RE = f(MEI) the estimate of k_g is 0.339. Lack of uniqueness of solution for k_g indicates that either one or the other or all estimates are not equal to the true parameter.

Lofgreen and Garrett (1968) estimated NE$_g$ (kcal/g, feed), as the slope ΔRE/ΔADFI, then estimated NE$_g$ (kcal/g, feed) as f(feed intake at energy equilibrium); efficiency thus calculated is not f(MEI). When estimated as ΔRE/ΔMEI for RE >0 as described by Lofgreen and Garrett (1968), that is, the change in energy deposition brought about by the increase in MEI, k_g does represent the ratio of work done by a system to the energy supplied to it. However, the magnitude of k_g, relative to k_m, is inconsistent with reversibility of reactions described by classically estimated k_m or k_g. Magnitudes of efficiencies ($k_m > k_g$), however untenable from a thermodynamic standpoint, were dogma at the time (Blaxter and Graham, 1955; Kleiber, 1961). Inappropriate magnitudes of k_m and k_g further indicate that models (and concepts) employed by Lofgreen and Garrett (1968), indeed by all classical energeticists, are merely a means to an end and fail to represent the biochemistry described by the input:output relationships in those models.

Kellner (cited by Armsby, 1903) reported that the efficiency of ME utilization was less for forages than for cereals. Analysis by Lofgreen and Garrett (1968) indicated that k_m and k_g were less for 100% forage diets than for 2% forage diets. These investigators also reported that over the range of ME, from ~1.9 to 2.8 Mcal/kg, feed required for energy equilibrium (RE = 0) was monotonically negative. The relationship was described as an OLS function in which the response variable log (feed required for energy equilibrium, g/d × EBW$^{-0.750}$) was f(ME, kcal/g). It is expected, as ME (kcal/g) → 0, feed required for energy equilibrium (g/d × EBW$^{-0.750}$) → ∞, however, Lofgreen and Garrett (1968) reported an additive constant of 201 g/d × EBW$^{-0.750}$, 90% DM basis. The additive constant was for an f(ME, kcal/g) well outside the range

of ME (kcal/g) observed by Lofgreen and Garrett (1968) and may not be equal to the true parameter. Although Lofgreen and Garrett (1968) reported the simple correlation coefficient for the relationship log (feed required for energy equilibrium, g/d × EBW$^{-0.750}$) = f(ME, kcal/g) to be −0.97 and the root mean square, residual was 2.0. While the simple correlation coefficient indicates that predictive accuracy is adequate, the magnitude of the root mean square, residual shows that parametric stability may be lacking. The root mean square, residual (2.0) is similar to that of the intercept (2.303). Given information found in Lofgreen and Garrett (1968), the minimum calculable CI, which is at mean ME (~2.35 kcal/g), for feed required for energy equilibrium is from 32.5 to 87.0 (g/d × EBW$^{-0.750}$). Hallmarks of poor model specification are inappropriate magnitude of parameter estimates and inflated variances; [log (feed required for energy equilibrium, g/d × EBW$^{-0.750}$) = 2.303 − 0.2455 × ME (kcal/g)] is unlikely to be the correct model structure.

Unlike feed required for energy equilibrium (Figure 2), ME$_m$ is not monotonically negative over the range of ME (Figure 3); maximum ME$_m$ was calculated at MEI of 131 kcal/EBW$^{0.750}$ × d^{-1}, this is also the MEI at which k_m is a minimum. If the relationship between ME$_m$ and ME was correctly specified, as ME → 0, ME$_m$ → ∞, rather than ME$_m$ = 0 at ME = 0. It is likely that estimates of ME$_m$ found in Lofgreen and Garrett (1968) are less than the true parameters.

Lofgreen and Garrett (1968, table 1) describe nine heifers fed 100% roughage diets for which ME ~2.1 kcal/g; ME$_m$ is calculated (log HE = 1.90925 + 0.001697 × MEI) to be 140 kcal/EBW$^{0.750}$ × d^{-1}. Estimated ME$_m$ for the group of
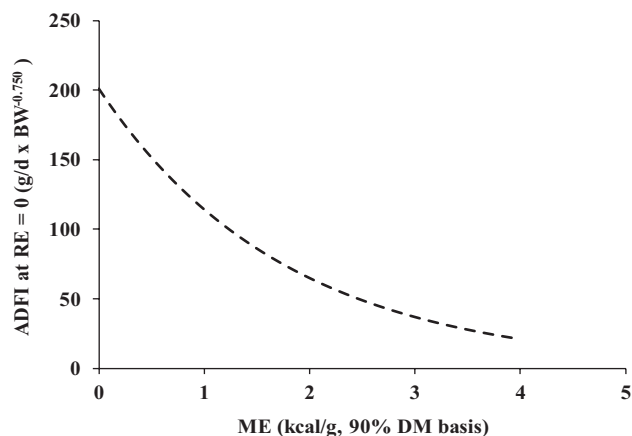

Figure 2. Relationship between ADFI (g/d × EBW$^{0.750}$) to maintain energy equilibrium and ME concentration (kcal/g); both expressed on a 90% DM basis, from Lofgreen and Garrett (1968). ADFI (g/d × EBW$^{0.750}$) = $10^{(2.303 - 0.2455 \times ME (kcal/g))}$.

nine heifers is greater ($P < 0.050$) than the maximum ME_m shown in Figure 3. Over the range of MEI in table 1 found in Lofgreen and Garrett (1968) using dynamic models reported in a companion paper (Old et al., 2018), a monotonically positive range of ME_m of from 113 to 194 kcal/EBW$^{0.750} \times$ d^{-1}. may be calculated. Furthermore, estimates of k_m (0.334) and k_g (0.658) reported by Old et al. (2018) are similar to previously noted theoretical estimates (k_m from 0.322 to 0.458; maximum k_g ~0.720 for ruminants) and certainly fall within the expected ranges. Static linear estimates of H_eE and variable estimates of k_m and k_g determined by Lofgreen and Garrett (1968) are likely to be different from the true parameters. Estimates of k_m (Lofgreen and Garrett, 1968 data) are >1.0 for ME <0.51 or ME >4.3 kcal/g (90% DM basis); the thermodynamically allowed range for efficiency is 0 to 1.0. Once again, log transformation of the response variable HE may have altered the relationship between predictor and response variables. In theory, Figures 2 and 3 should be identical in shape, differing only in magnitude if the systems described were consistent with thermodynamics. However, incorrect model specifications and analytical schemes employed by Lofgreen and Garrett (1968) resulted in useful estimates for predicting cattle performance that are inconsistent with the first law. Given the utility of the CNES, many have conflated that utility with correct model specification. It should be noted that a failure to equate animal utilization of feed energy with thermodynamics of the underlying mechanisms was common at the time Lofgreen and Garrett (1968) published their work. Moe and Tyrrell (1973) reported that the efficiency of ME utilizatio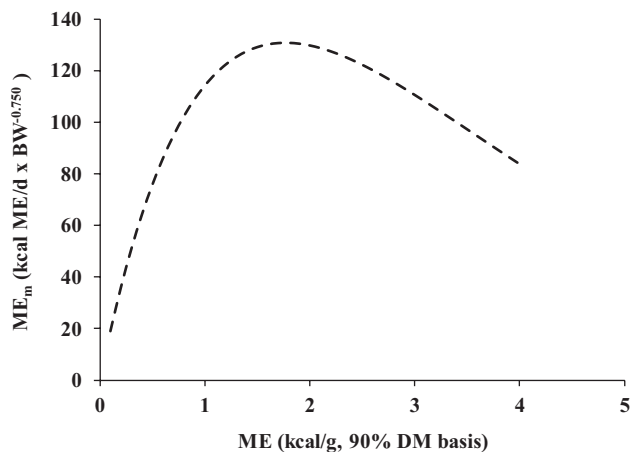n for cold stress was 100% or $k_m = 0$, an estimate that requires complete uncoupling of substrate oxidation with work. One still finds reports in the literature in which findings run counter to the laws of thermodynamics. Moraes et al. (2014) determined that k_m was not different from 1.0, in other words, nothing is happening. The true parameter is somewhere between the two estimates, if the laws of thermodynamics hold.

Work performed, for MEI < ME_m, is sparing of RE by MEI (NRC, 1981), for MEI > ME_m, work is energy gained as fat and protein; efficiencies thus estimated have no dimension. Efficiencies of metabolizable energy utilization for maintenance and gain, described by Lofgreen and Garrett (1968) have dimension, they are then rates, unlikely to represent the true parameters. As noted by Moe and Tyrrell (1973) the CNES estimate of k_m is a ratio of H_eE (fixed) to ME_m (variable) and $k_g = f(k_m)$, neither is dRE/dMEI.

How Do Cattle Know if Acetate Is from Forages or Concentrates? They Don't

In classical energetics, products of the reaction:

$$H_3CCO_2H + 2\ O_2 + 8\ ADP + 8\ P_i \rightarrow 2\ CO_2 + 2\ H_2O + 8\ ATP$$
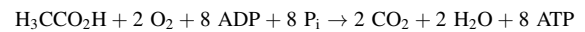
are characterized as NE_m and efficiency of the process is determined by the source of acetate; k_m is less for forages than concentrates. Classical energetics appears then to require different pathways for utilization of reactants depending on the source of those reactants. Such an approach is inconsistent with the laws of thermodynamics which require that the energy status of a system is independent of the pathway; for the same pathway outcomes must be identical. A study by Reynolds and Tyrrell (1988)
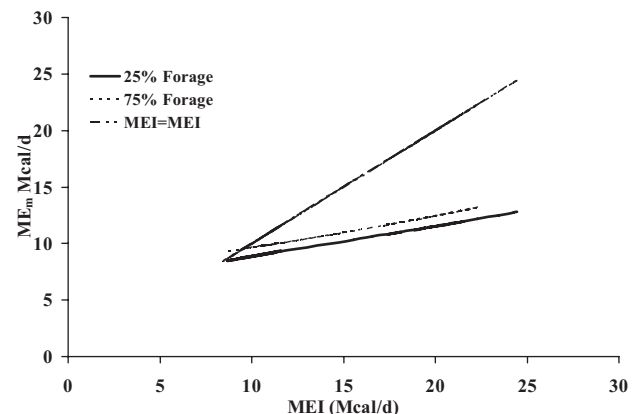

Figure 3. Relationship between ME intake (kcal/d $\times$ EBW$^{0.750}$) to maintain energy equilibrium and ME concentration (kcal/g, 90% DM basis); from Lofgreen and Garrett (1968). ME intake (kcal/d $\times$ EBW$^{0.750}$) = $10^{(2.303 - 0.2455 \times ME (kcal/g))} \times$ ME (kcal/g).

Figure 4. Metabolizable energy intake (**MEI**, Mcal/d) at maintenance (**ME_m**, Mcal/d) as f(MEI) for beef heifers fed diets containing either 25% or 75% forage for the equations: $ME_m = (7.238 \times e^{(0.2332 \times MEI)} - 4.141 \times e^{(-0.2753 \times MEI)})$ for cattle consuming 25% forage. $ME_m = (7.484 \times e^{(0.02544 \times MEI)} - 3.184 \times e^{(-2.229 \times MEI)})$ for cattle consuming 75% forage.

appears to have been designed to evaluate effects of ME concentration on energetic efficiency. Our analysis of those data in a Bayesian framework, described by Old et al. (2018), with a dynamic estimate of ME_m produced the equations:

$$RE = (MEI - (7.238 \times e^{(0.02332 \times MEI)} - 4.141 \times e^{(-0.2753 \times MEI)}))$$
$$\times 0.6434 \text{ for cattle consuming 25\% forage}$$
$$RE = (MEI - (7.484 \times e^{(0.02544 \times MEI)} - 3.184 \times e^{(-2.229 \times MEI)}))$$
$$\times 0.6434 \text{ for cattle consuming 75\% forage}$$

which indicated that k_m (0.28) and k_g (0.643) were not different for growing beef heifers fed diets containing either 25 ($n = 29$) or 75 ($n = 30$) percent forage. Estimated ME_m was greater ($P < 0.050$) for heifers fed the greater percentage of forage and RE was greater ($P < 0.050$) for heifers fed the lesser percentage of forage. Figures 4 and 5 present these data graphically and indicate that processes comprising maintenance are similar in efficiency, differing only in magnitude, for cattle fed diets containing either 25 (ME_m from 8.54 to 16.9 Mcal/d; MEI = 8.66 to 24.4 Mcal/d) or 75% forage (ME_m = from 9.11 to 16.5 Mcal/d; MEI = 8.70 to 22.4 Mcal/d); the same is noted for gain as shown in Figure 5. For a subset of the data ($n = 26$) Reynolds and Tyrrell (1988) reported an increase (26%) in O_2 uptake by the portal-drained viscera (**PDV**) for heifers fed the 75% forage diet when compared with those fed lesser amounts of forage (25%). Approximately 70% of differences in whole body heat production were explained by differences in PDV O_2 uptake, differences as a result of variability in DM intake, gut fill (Reynolds and Tyrrell, 1988) or gut mass (Ferrell et al., 1986). Classical energetics puts HE associated with these
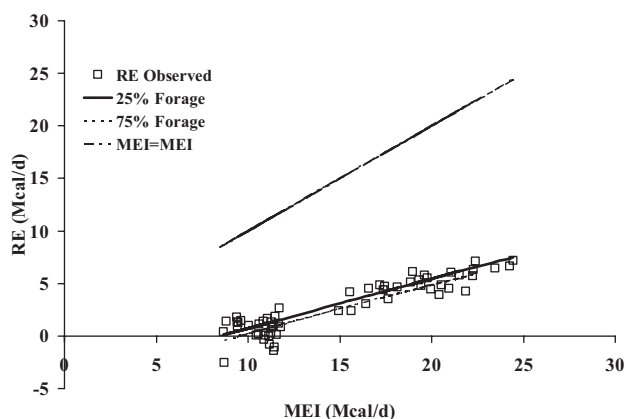

Figure 5. Recovered energy (**RE**, Mcal/d) as f(ME intake, **MEI**, Mcal/d) for beef heifers fed diets containing either 25% or 75% forage for the equations: RE = (MEI − (7.238 × e$^{(0.2332 × MEI)}$ − 4.141 × e$^{(−0.2753 × MEI)}$)) × 0.6434 for cattle consuming 25% forage. RE = (MEI − (7.484 × e$^{(0.02544 × MEI)}$ − 3.184 × e$^{(−2.229 × MEI)}$)) × 0.6434 for cattle consuming 75% forage.

energy expenditures into the gain column, as H_rE, rather than the maintenance column, as ME_m. Describing input:output relationships such that ME_m is characterized as a dynamic f(MEI) rather than the zero order approximation of H_eE found in the CNES partitions more HE to ME_m; estimates of k_m and k_g better describe the underlying mechanisms. Furthermore, estimates of k_m calculated (first order) as dRE/dMEI for MEI ~ ME_m over the range of observed MEI, are relatively constant suggesting that if k_m may be approximated by ME_m/H_eE then H_eE must also be a variable f(MEI).

SUMMARY AND CONCLUSIONS

Classical descriptions of energy utilization, such as those in the CNES, rely on observations at the level of the individual (level of aggregation = i or individual) or group ($i + 1$) and OLS functions to describe input:output relationships. Relationships thus described are often inconsistent with the laws of thermodynamics and, as such, are inappropriate descriptors of energy utilization. Mechanistic characterization of energy utilization at lesser and lesser levels of aggregation, along with integration and synthesis of that information at greater levels of aggregation, at level i and greater, improves our understanding of energy utilization.

Maintenance is fixed in the CNES, suggesting that the greatest gross efficiency should be achieved at greatest intakes of ME. However, a common feedlot practice is to feed at ADFI less than maximum; gross efficiency is often improved at lesser intakes; it has been suggested that incremental costs of maintenance reduce gross efficiency at maximum intakes (R. Pritchard, Professor Emeritus, South Dakota State University, personal communication). While digestibility is reduced as intakes of dry matter increase, metabolizability (**Q**) for Q > 0.6 is either constant or increases as intakes increase (Blaxter, 1969). As a result, MEI increases with increasing ADFI for diets typically fed to finishing beef cattle. Observations in the field may contrast with the description of maintenance in the CNES, suggesting it is not fixed, but are consistent with a model in which maintenance is a first order function of MEI, as we describe in the previous section. Our analysis does indeed indicate that the percentage of MEI partitioned to gain reaches a maximum and declines at greater MEI. Developing a more in depth understanding of energy utilization, not merely more empirical descriptions, will aid us in formulating feeds and feeding programs for cattle with ever greater energy utilization.

The CNES is an example of a system designed to do one thing well and that was to predict; in this case input:output relationships in growing and finishing beef cattle. Correct model specification and consistency of individual parameter estimates with known true parameters took back seat to prediction. As utilized since its inception, the CNES has been a good procedure for bookkeeping of energy utilization (W. N. Garrett, University of California, Davis, late Professor Emeritus of Animal Science, personal communication). Because all models are wrong, one should not question whether the relationships described in the system are true, or false, but rather are they useful.

Conflict of interest statement. C.A.O., I.J.L., and H.A.R. have no conflicts of interest.

LITERATURE CITED

Armsby, H. P. 1903. The principles of animal nutrition. New York (NY): John Wiley and Sons.

Baldwin, R. L. 1968. Estimation of theoretical calorific relationships as a teaching technique. J. Dairy Sci. 51:104–111.

Baldwin, R. L. 1995. Modeling ruminant digestion and metabolism. London (UK): Chapman and Hall.

Biddle, G. N., J. L. Evans, and J. R. Trout. 1975. Labile nitrogen reserves in the ruminant. Metabolic changes in growing cattle employing a nitrogen depletion-repletion treatment. J. Nutr. 105:1578–1583. doi:10.1093/jn/105.12.1578

Blaxter, K. L. 1969. The efficiency of energy transformations in ruminants. In: Blaxter, K. L., J. Kielanowski, and G. Thorbek, editors. Energy metabolism of farm animals. Eur. Assoc. Anim. Prod. Publ. No. 122. Newcastle upon Tyne (UK): Oriel Press Ltd; p. 21–28.

Blaxter, K. L., and N. M. Graham. 1955. Methods of assessing the energy values of foods for ruminant animals. Proc. Nutr. Soc. 14:131–139.

Cruz, G. D., J. A. Rodríguez-Sánchez, J. W. Oltjen, and R. D. Sainz. 2010. Performance, residual feed intake, digestibility, carcass traits, and profitability of angus-hereford steers housed in individual or group pens. J. Anim. Sci. 88:324–329. doi:10.2527/jas.2009-1932

Ferrell, C. L., L. J. Koong, and J. A. Nienaber. 1986. Effect of previous nutrition on body composition and maintenance energy costs of growing lambs. Br. J. Nutr. 56: 595–605.

Flatt, W. P. 1969. Methods of calorimetry. (B) Indirect. In: Cuthberson D., editor, The international encyclopedia of food and nutrition, Vol. 17: nutrition of animals of agricultural importance, Part 2. Oxford (UK): Pergamon Press. p. 1–30.

Garrett, W. N., and N. H. Hinman. 1969. Re-evaluation of the relationship between carcass density and body composition of beef steers. J. Anim. Sci. 26:1–5.

Imhoff, D. H., and C. C. Old. 1952. Extrapolation of neutron yields with increasing particle energy. California Research and Development Corporation Report CRD-T4A-126. Livermore, CA: Lawrence Research Laboratory

Jibb, L. A., and J. G. Richards. 2008. AMP-activated protein kinase activity during metabolic rate depression in the hypoxic goldfish, *Carassius auratus*. J. Exp. Biol. 211(Pt 19):3111–3122. doi:10.1242/jeb.019117

Kennedy, K. M., and C. C. Calvert. 2014. Effects of assumptions on estimating energetic efficiencies in lactating dairy cattle. J. Anim. Sci. 92(E. Suppl. 2):870.

Kielanowski, J. 1965. Estimates of the energy costs of protein deposition in growing animals. In: Blaxter K. L., editor. Energy metabolism. London (UK): Academic Press. p. 13–20.

Kleiber, M. 1961. The fire of life. New York (NY): John Wiley.

Koong, L. J., J. A. Nienaber, and H. J. Mersmann. 1983. Effects of plane of nutrition on organ size and fasting heat production in genetically obese and lean pigs. J. Nutr. 113:1626–1631. doi:10.1093/jn/113.8.1626

Lobley, G. E., V. Milne, J. M. Lovie, P. J. Reeds and K. Pennie. 1980. Whole body and tissue protein synthesis in cattle. Brit. J. Nutr. 43:491–502.

Lofgreen, G. P., and W. N. Garrett. 1968. A system for expressing net energy requirements and feed values for growing and finishing beef cattle. J. Anim. Sci. 27:793–806.

Mason, R. L., R. F. Gunst, and J. L. Hess. 2003. Statistical design and analysis of experiments with applications to engineering and science. Hoboken (NJ): Wiley Interscience.

Moe, P. W., and H. F. Tyrrell. 1973. The rationale of various energy systems for ruminants. J. Anim. Sci. 37:183–189.

Moraes, L. E., E. Kebreab, A. B. Strathe, J. France, J. Dijkstra, D. P. Casper, and J. G. Fadel. 2014. Bayesian analysis of energy balance data from growing cattle using parametric and non-parametric modeling. Anim. Prod. Sci. 54:2068–2081

Morikofer, S., and P. Walter. 1992. Binding of ADP to rat liver cytosolic proteins and its influence on the ratio of free ATP/free ADP. Biochem. J. 1992. 59:117–124.

NRC. 1981. Nutritional energetics of domestic animals and glossary of energy terms. Washington (DC): National Academy of Sciences.

Old, C. A., and W. N. Garrett. 1985. Efficiency of feed energy utilization for protein and fat gain in Hereford and Charolais steers. J. Anim. Sci. 60:766–771.

Old, C. A., H. A. Rossow, and T. R. Famula. 2015. Partitioning of feed intake into maintenance and gain in growing beef cattle: evaluation of conventional and Bayesian analyses. J. Anim. Sci. 93:4826–4842. doi:10.2527/jas.2015–9206

Old, C. A., H. A. Rossow, I. J. Lean, and T. R. Famula. 2018. Energetic efficiency and the first law: the California net energy system revisited. J. Anim. Sci. 96:4882–4901. doi:10.1093/jas/sky322

R Core Team. 2013. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Reynolds, C. K., and H. F. Tyrrell. 1988. Effects of forage to concentrate ratio and intake on whole body energy metabolism in growing beef heifers. In: van der Honing Y., and W. H. Close, editors. Proceedings of 11th EAAP Symposium. Energy metabolism of farm animals. Wageningen (The Netherlands): Pudoc; p. 151–154.

Rich, P. R. 2003. The molecular machinery of keilin's respiratory chain. Biochem. Soc. Trans. 31(Pt 6):1095–1105.

Schiemann, R. 1969. The scientific demands made of a system for evaluating feeds as an energy source and progress made toward their realization. In: Blaxter K. L., J. Kielanowski, and G. Thorbek, editors. Energy metabolism of farm

animals. Eur. Assoc. Anim. Prod. Publ. No. 122. Newcastle upon Tyne (UK): Oriel Press, Ltd. p. 31–40.

Siegel, M. P., T. Wilbur, M. Mathis, E. G. Shankland, A. Trieu, M. E. Harper, and D. J. Marcinek. 2012. Impaired adaptability of in vivo mitochondrial energetics to acute oxidative insult in aged skeletal muscle. Mech. Ageing Dev. 133:620–628. doi:10.1016/j.mad.2012.08.002.

van Milgen, J. 2002. Modeling biochemical aspects of energy metabolism in mammals. J. Nutr. 132:3195–3202. doi:10.1093/jn/131.10.3195

van Milgen, J. 2006. Nutrient flow models, energy transactions and energy feed systems. In: Gouw R., T. Morris, and C. Fisher, editors. Mechanistic modelling in pig and poultry production. Wallingford (UK): CAB International. p. 143–162.