Mathematical absurdities in the California net energy system

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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 (\( H_p \)) 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:

\[
\text{ME intake (MEI)} = \text{NE}_m + \text{NE}_g + \text{heat increment of feeding (H}_p\text{E)}
\]

therefore:

\[
\text{MEI} = \text{ME}_m + \text{NE}_g + \text{H}_p\text{E}
\]

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 (\( \Delta G^\circ \)) and transfer of electrons from reactants to products, reactions proceed as written. An example of this is the oxidation of glucose to \( \text{CO}_2 \) and \( \text{H}_2\text{O} \) (\( \Delta G^\circ = -686 \text{ kcal/mol} \)) in which 24 mol of electrons are transferred to \( \text{O}_2 \) for each mol of glucose oxidized; C atoms in glucose are the source of electrons.

Thermodynamically unfavorable reactions are characterized by a positive \( \Delta G^\circ \), reactions will not proceed as written unless coupled with a thermodynamically favorable reaction. The magnitude of \( \Delta G^\circ \) for ATP synthesis (ADP\(^{3-}\) + P\(^{2-}\) + H\(^+\) →
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 $\Delta G^0$ 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; $\Delta G^0$ is much closer to 0 (equilibrium) for these reactions than for the oxidation of glucose to CO$_2$ and H$_2$O (products more oxidized than reactants).

Given the amino acid composition of muscle protein (Rossow, unpublished data) and the heat of combustion ($\Delta H_c$) for each amino acid, it is possible to calculate the energy input of amino acids to muscle protein synthesis. Our estimate of $\Delta H_c$ for amino acid input is 5.03 kcal/g; estimated $\Delta H_c$ 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$_E$. 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$_E$) was estimated as the intercept for log HE = f(MEI) in a single variable OLS framework:

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

as reported by Lofgreen and Garrett (1968)

$$\log HE (\text{cal} \text{EBW}^{0.750} \times d^{-1}) = 1.88659 + 0.0016466 \text{MEI (cal} \text{ME/EBW}^{0.750} \times d^{-1});$$

same data using lm package in R; (R Core Team, 2013) and H$_E$ 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 $k_i$ 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 $k_i$ are variable and essentially are $f(ME, Mcal/kg)$. It is important to note that, as determined by Lofgreen and Garrett (1968), $H_E$, $ME_m$, $k_m$ and $k_i$ 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 $H_E/ME_m$ (NRC, 1981); Lofgreen and Garrett (1968) first estimated $H_E$ 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:

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

Efficiency of ME utilization for maintenance is then:

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

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

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

$k_i$ is estimated as the ratio of $NE_k$ (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 $H_E$ is fixed, $k_m$ is variable. Similarly, $k_i$ is a variable $f$(feed required for energy equilibrium). Koong et al. (1983) suggested that $H_E$ 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 ($k_i$) 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 $k_i$ contrasts with the lability of proteins (Biddle et al., 1975), an indication of model misspecification (Mason et al., 2003). Classically derived OLS estimates of $k_i$ 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

$$ADF_i = a + b_1 \times EBW_i^{0.75} + b_2 \times ADG_i + r_i$$

where $ADF_i$ is ADFI (kg DM) by the $i$th individual, the vector $ADF = (ADF_1, ADF_2, ..., ADF_i)$, $a$ is the intercept (kg DM/d), $b_1$ is a coefficient (kg DM/d × EBW$^{-0.75}$), $b_2$ is a coefficient (kg DM/d × ADG$^{-1}$), $EBW_i^{0.75}$ is the average EBW for an individual raised to the 0.75 power, and $r_i$ is the residual for the $i$th 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 (ADF, kg DM); such a result indicates cattle in that study, when both EBW$^{0.75}$ and ADG 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} × d^{-1}) are likely to result in inflated variances about the estimate H_{E}. 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_{E}, determined in a Bayesian framework, indicated poor model specification (inflated variance); variability about the slope was also inflated in either an OLS or Bayesian framework.

Lofgreen and Garrett (1968) reported H_{E} ± s_x, or ± (root mean square residual), as bounds. Parameter estimates (slope and H_{E}) 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_{E}, variability (95% prediction interval) about the estimate 77.4 kcal /EBW^{0.750} × d^{-1} is from 66.0 to 90.7 kcal /EBW^{0.750} × 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_{E} + b × ME intake^{a,b,c,d}

| Source of estimate | log H_{E} | b |
|-------------------|-----------|---|
| Lofgreen and Garrett (1968) | 1.885 (76.8) | 0.00166 |
| Reported range | 72 to 82 | — |
| OLS | 1.88659 (77.4) | 0.001647 |
| 95% CI | 71.5 to 83.7 | 0.001486 to 0.001807 |
| Bayesian | 1.889 (77.4) | 0.001647 |
| 95% Credible interval | 59.4 to 100 | 0.001487 to 0.001807 |
| Bayesian | 1.889 (77.4) | 0.001647 |
| 95% Credible interval | 71.5 to 83.7 | 0.001099 to 0.002195 |

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a HE = heat energy (kcal/EBW^{0.750} × d^{-1}).
b HE = heat energy at ME intake = 0 (kcal/EBW^{0.750} × d^{-1}).
c b = parameter estimate (no dimension).
d Data from table 1 in Lofgreen and Garrett (1968).

As reported by Lofgreen and Garrett (1968)

Parenthetical values are H_{E} (kcal/EBW^{0.750} × d^{-1})

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

Informed priors were such that Bayesian solutions for H_{E} and b were identical to OLS solutions and variability about b identical to OLS solutions.

Informed priors were such that Bayesian solutions for H_{E} and b were identical to OLS solutions and variability about H_{E} identical to OLS solutions.

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For \( \text{RE} = 0 \), \( \text{MEI} = \text{HE} \), therefore at \( \text{MEI}_m \) dHE/dMEI is necessarily 1. The first derivative of the single variable OLS function described by Lofgreen and Garrett (1968) is \( \text{dHE}/\text{dMEI} = \ln(10) \times 0.00166 \times 10^{(0.8851 + 0.00166 \times \text{MEI})} \). Lofgreen and Garrett (1968) did not estimate \( k_g \) as dRE/dMEI, but rather as the ratio of \( \text{NE}_f \) (feed required for energy equilibrium) to \( \text{ME} \) (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 \( \text{ME} \) (kcal/g, 90% DM) from 1.92 to 2.78 and MEI from 100 to 335 kcal/EBW

\[
\text{dMEI/dMEI} = \text{dRE/dMEI} + \text{dHE/dMEI}
\]

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) (dMEI/dMEI = dRE/dMEI + dHE/dMEI).

The parameter estimate \( H_{E} \), 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 \( H_{E} \) was determined, one may question if \( H_{E} \) 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 \( \Delta H_e \) of acetate in ATP. Kennedy and Calvert (2014) updated theoretical estimates of \( k_f \) (0.71) and \( k_g \) (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 \( H_{E}/\text{ME}_m \) (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 \( \text{ME}_m \) represents energy supplied, it is unlikely that \( H_{E} \) represents work done by MEI as \( \text{MEI} = 0 \). The magnitude of \( k_m \) estimated as \( H_{E}/\text{ME}_m \) (0.626 for table 1 data, Lofgreen and Garrett, 1968), is less than theoretical estimates of \( k_g \). Further evidence that \( H_{E} \) does not represent work done by MEI supplied; dHE/dMEI for \( \text{MEI} = 0 \) is 0.293; the expectation is that as \( \text{MEI} \rightarrow 0 \), dHE/dMEI \( \rightarrow 0 \) as well. The solution for energy equilibrium (\( \text{ME}_m \)) lacks uniqueness when calculated using the equation \( \log HE = 1.8851 + 0.00166 \times \text{MEI} \). Intake of \( \text{ME} = \text{HE} + \text{RE} \) at \( \text{MEI} = 123 \) kcal ME/EBW\(^{0.750} \times d^{-1} \) and at \( \text{MEI} = 321 \) kcal ME/EBW\(^{0.750} \times d^{-1} \). The former estimate is for the equality of HE and MEI; since \( \text{MEI} = \text{HE} + \text{RE} \), for \( \text{HE} = \text{MEI} \) then \( \text{RE} = 0 \). However, since at \( \text{MEI} \) of 321 kcal ME/EBW\(^{0.750} \times d^{-1} \), 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 $k_g$ (ARE/ΔMEI) is 0.258; this approach is described by Lofgreen and Garrett (1968) and has been classically termed the “difference trial.” Estimated $k_g$ (ARE/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 NEg (kcal/g, feed), as the slope $\Delta RE/\Delta MEI$, then estimated NEg (kcal/g, feed) as $f$(feed intake at energy equilibrium); efficiency thus calculated is not $f$(MEI). When estimated as $\Delta RE/\Delta MEI$ 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 $k_g$ 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](image-url). 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 × ME (kcal/g)).
nine heifers is greater ($P < 0.050$) than the maximum $\text{ME}_m$ shown in Figure 3. Over the range of $\text{MEI}$ 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 $\text{ME}_m$ 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 $k_g \sim 0.720$ for ruminants) and certainly fall within the expected ranges. Static linear estimates of $\text{HeE}$ 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 $\text{ME} < 0.51$ or $\text{ME} > 4.3$ kcal/g (90% DM basis); the thermodynamically allowed range for efficiency is 0 to 1.0. Once again, log transformation of the response variable $\text{HeE}$ 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 $\text{ME}$ utilization 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 $\text{MEI} < \text{ME}_m$, is sparing of $\text{RE}$ by $\text{MEI}$ (NRC, 1981), for $\text{MEI} > \text{ME}_m$, 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 $\text{HeE}$ (fixed) to $\text{ME}_m$ (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:

$$\text{H}_3\text{CCO}_2\text{H} + 2 \text{O}_2 + 8 \text{ADP} + 8 \text{P}_1 \rightarrow 2 \text{CO}_2 + 2 \text{H}_2\text{O} + 8 \text{ATP}$$

are characterized as $\text{NE}_m$, 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)
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:

\[
\text{RE} = (\text{MEI} - (7.238 \times e^{0.02332 \times \text{MEI}} - 4.141 \times e^{(-0.2332 \times \text{MEI}})) \times 0.6434 \text{ for cattle consuming 25\% forage}
\]

\[
\text{RE} = (\text{MEI} - (7.484 \times e^{0.02544 \times \text{MEI}} - 3.184 \times e^{(-2.229 \times \text{MEI}})) \times 0.6434 \text{ for cattle consuming 75\% forage}
\]

which indicated that \( k_m \) (0.28) and \( k_e \) (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 (MEI = 8.54 to 16.9 Mcal/d; MEI = 8.66 to 22.4 Mcal/d) or 75% forage (MEI = 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 energy expenditures into the gain column, as \( H_E \), 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 \( H_E \) found in the CNES partitions more HE to \( ME_m \); estimates of \( k_m \) and \( k_e \) 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 \( ME_m/H_E \) then \( H_E \) 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 feed-lot 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 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.

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