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Review: Harnessing extant energy and protein requirement modeling for sustainable beef production



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ABSTRACT

Numerous mathematical nutrition models have been developed in the last sixty years to predict the dietary supply and requirement of farm animals' energy and protein. Although these models, usually developed by different groups, share similar concepts and data, their calculation routines (i.e., submodels) have rarely been combined into generalized models. This lack of mixing submodels is partly because different models have different attributes, including paradigms, structural decisions, inputs/outputs, and parameterization processes that could render them incompatible for merging. Another reason is that predictability might increase due to offsetting errors that cannot be thoroughly studied. Alternatively, combining concepts might be more accessible and safer than combining models' calculation routines because concepts can be incorporated into existing models without changing the modeling structure and calculation logic, though additional inputs might be needed. Instead of developing new models, improving the merging of extant models' concepts might curtail the time and effort needed to develop models capable of evaluating aspects of sustainability. Two areas of beef production research that are needed to ensure adequate diet formulation include accurate energy requirements of grazing animals (decrease methane emissions) and efficiency of energy use (reduce carcass waste and resource use) by growing cattle. A revised model for energy expenditure of grazing animals was proposed to incorporate the energy needed for physical activity, as the British feeding system recommended, and eating and rumination ($H_J E_{er}$) into the total energy requirement. Unfortunately, the proposed equation can only be solved iteratively through optimization because $H_J E_{er}$ requires metabolizable energy (ME) intake. The other revised model expanded an existing model to estimate the partial efficiency of using ME for growth (k_g) from protein proportion in the retained energy by including an animal degree of maturity and average daily gain (ADG) as used in the Australian feeding system. The revised k_g model uses carcass composition, and it is less dependent on dietary ME content, but still requires an accurate assessment of the degree of maturity and ADG, which in turn depends on the k_g . Therefore, it needs to be solved iteratively or using one-step delayed continuous calculation (i.e., use the previous day's ADG to compute the current day's k_g). We believe that generalized models developed by merging different models' concepts might improve our understanding of the relationships of existing variables that were known for their importance but not included in extant models because of the lack of proper information or confidence at that time.

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Implications

The development of mathematical animal models to assist sustainable development in agriculture-related businesses might benefit drastically by merging existing animal models, more specifically those related to nutrition, given the amount of available data already collected worldwide and many different well-throughout concepts. However, problems in merging existing models include different paradigms, structural decisions, and

parameterization processes that could render the merging undertaking infeasible. Another reason is that the predictability of the merged model might increase due to offsetting errors that cannot be thoroughly studied, creating an invalid model. Combining concepts rather than calculation routines might be more achievable and promising.

Introduction

We live in a time where sustainability has dominated the conversation in every scientific field (Pretty, 1997), yet we barely

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understand its prerequisites and full potential in animal science (Tedeschi et al., 2015). Sustainability comes in many shapes and forms, given the needs of each country or region. Producing enough food to prevent hunger and eradicate poverty might be a more pressing issue than saving the environment in some places, though both might need to walk side-by-side to be effective (Anonymous, 2022). The growing demand for sustainable agricultural production systems presents complex problems that are best analyzed using mathematical modeling to assist researchers in recommending solutions to policymakers. The notion of using mathematical modeling to assist sustainable development in agriculture-related businesses is not new (Sharma et al., 2006; Gouttenoire et al., 2011; Tedeschi, 2020; Vlontzos et al., 2021).

Several mathematical animal nutrition models have been developed in the last sixty years to predict the dietary supply and animal's requirements of energy, protein, and other nutrients (Tedeschi and Fox, 2020a). These mathematical models share similar purposes, ideas, concepts, and original data. Fig. 1 depicts the chronological development and evolution of nutrition (Tedeschi et al., 2014) and grazing models (Tedeschi et al., 2019) and their derivative work (Tedeschi, 2019a). The development of animal bioenergetics, energy partitioning and utilization, and protein metabolism in the early days have been nicely documented in the past by Brody (1945), Blaxter (1962), and Kleiber (1961), and

many comprehensive reviews have been updated and expanded these traditional publications (Van Es, 1978; Moe, 1981; Garrett and Johnson, 1983; Johnson et al., 2003; Ferrell and Oltjen, 2008; Tedeschi, 2019a). Fig. 1 indicates that the development of nutrition models commenced in the mid-1960s and has since been refined and expanded vertically (i.e., released versions/editions) and horizontally (i.e., different models or schools of thoughts). These models have distinct objectives, depending on their intended development purpose, but in the end, the primary goal has usually been to improve their prediction accuracy and precision to increase the efficiency of animal production.

As Garrett and Johnson (1983) pointed out, "one of the goals of energy metabolism research with ruminants always has been the development of an accurate means for evaluating feedstuffs and stating animal requirements." Despite intrinsic relationships and dependencies among extant mathematical animal nutrition models, given their shared similarities, the supply prediction approaches have evolved further and independently of the requirement prediction approaches. For instance, the Cornell Net Carbohydrate and Protein System (CNCPS)-based model (Fox et al., 2004) developed by Tedeschi and Fox (2020a), Ruminant Nutrition System (RNS), has three levels of solution for predicting the supply of energy and nutrients but a single common calculation logic for predicting the energy and nutrient requirements. The overarching

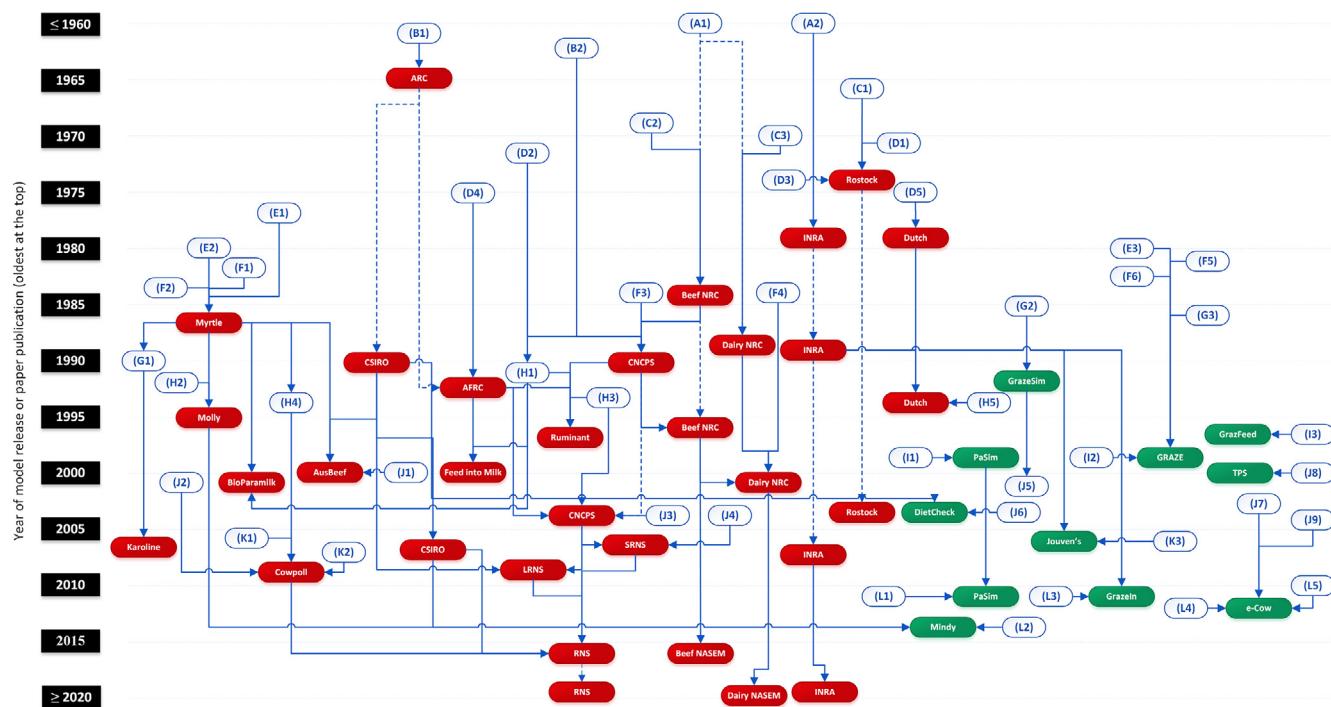


Fig. 1. Chronological evolution (older at the top to newer at the bottom) of key mathematical models whose primary goal lies within ruminant nutrition only (red squircles) or pasture/grazing ruminants (green squircles) domains. The approximate year of publication or release is shown on the left. The solid line represents a direct relationship of influence, and the dashed line represents that at least one other version or edition was released between the marks. The lack of lines connecting the same model does not imply that the model has been phased out. AFRC is Agricultural and Food Research Council; ARC is Agricultural Research Council; CNCPS is Cornell Net Carbohydrate and Protein System; LRNS is Large Ruminant Nutrition System; CSIRO is Commonwealth Scientific and Industrial Research Organisation; INRA is Institut National de la Recherche Agronomique; NASEM is the National Academies of Sciences, Engineering, and Medicine; NRC is National Research Council; RNS is Ruminant Nutrition System; SRNS is Small Ruminant Nutrition System; and TPS is Tropical Pasture Simulator. Key references (empty blue squircles) are: (A1) NRC (1945a and 1945b), (A2) Leroy (1954), (B1) (Blaxter, 1962), (B2) Van Soest (1963a) and Van Soest (1963b), (C1) Nehring et al. (1966), (C2) Lofgreen and Garrett (1968), (C3) Moe et al. (1970), (D1) Schiemann et al. (1971), (D2) Waldo et al. (1972), (D3) Hoffmann et al. (1974), (D4) Ministry of Agriculture, Fisheries and Food (1975), (D5) Van Es (1975), (E1) Baldwin et al. (1977), (E2) Baldwin et al. (1980), (E3) Loewer et al. (1980), (F1) France et al. (1982), (F2) Gill et al. (1984), (F3) Fox and Black (1984), (F4) Conrad et al. (1984), (F5) Loewer et al. (1981), (F6) Loewer et al. (1983), (G1) Danfer (1990), (G2) Mertens et al. (1985, 1987), (G3) Bridges et al. (1986), (H1) Illius and Gordon (1991), (H2) France et al. (1992), (H3) Russell et al. (1992), Sniffen et al. (1992), and Fox et al. (1992), (H4) Dijkstra et al. (1992), Neal et al. (1992), and Dijkstra (1993), (H5) Tamminga et al. (1994), (I1) Riedo et al. (1998) based on the Hurley Pasture Model (Thornley, 1998), (I2) Loewer (1998), (I3) Freer et al. (1997), (J1) Nagorcka et al. (2000), (J2) Mills et al. (2001), (J3) Fox et al. (2004), (J4) Cannas et al. (2004) and Tedeschi et al. (2010), (J5) Vazquez and Smith (2001), (J6) Heard et al. (2004), (J7) Baudracco et al. (2010), (J8) Herrero et al. (2000a, 2000b), (J9) Vetharaniam et al. (2003), (K1) Bannink et al. (2006), (K2) Bannink et al. (2008), (K3) Jouven et al. (2006b and 2006a), (L1) Graux et al. (2011), (L2) Gregorini et al. (2013), (L3) Delagarde et al. (2011a, 2011b) and Faverdin et al. (2011), (L4) Baudracco et al. (2012), and (L5) Friggens et al. (2004). The figure was replicated with permission from Tedeschi (2019a).

goal of extant animal nutrition models was in line with agriculture's mode of action at that time: increasing productivity. In the last two decades, however, agriculture's mode of action has been transitioning to a more sustainable perspective (environmental, social, and economic), and animal production systems have been placed at the forefront of the debate (Tedeschi, 2022a). Therefore, mathematical nutrition models for sustainable animal agriculture might have to be re-engineered to accommodate current needs. It may include a complete overhauling of animal nutrition models to fit the *new* expectations, but it may also need to harness specific aspects of extant animal nutrition models and seamlessly combining them into an integrated platform to represent reality more accurately and precisely.

The relative contribution of beef cattle production to the climate change phenomenon differs among countries, varying from up to 4% (Dillon et al., 2021; Tedeschi, 2022a; Tedeschi and Beauchemin, 2023) in the US to 10% in Australia (Henry et al., 2012) to 21% in Brazil (Brazilian Ministry of Science, 2021), with a perception to represent 14.5% of human-induced greenhouse gas (GHG) emissions worldwide (Gerber et al., 2013). Such discrepancies in beef cattle contribution to the anthropogenic GHG among countries are primarily due to the relative sizes of their energy, industrial, and transportation sectors (thus, diluting more or less the beef cattle production contribution) but also due to (a) our inability to accurately quantify methane (CH_4) emissions given the hurdles to applying existing methodologies to diverse production systems and large-scale regions (Tedeschi et al., 2022) and (b) controversies regarding the calculations of the global warming potential of atmospheric CH_4 about its half-life and the time horizon used in climate change models (Cain et al., 2019; Lynch et al., 2020).

Nevertheless, the question remains, what are the advancements and limitations in predicting farm animals' energy and protein requirements, specifically growing ruminants, that could improve animal agriculture sustainability? The objective of this paper was to spark discussions of two critical areas in beef cattle production (energy requirements of grazing animals and efficiency of use of energy) to ensure adequate diet formulation by borrowing concepts used in different mathematical models. Tedeschi (2022b) presented and documented the preliminary analyses of this study.

Improving the prediction of energy requirements for grazing cattle

Grazing animals produce more methane per weight gain than confined animals (Pelletier et al., 2010). In part, the discrepancy arises because low-quality, high-fiber diets (e.g., forages) yield about four times more methane than high-quality, low-fiber diets (e.g., feedlot), respectively 0.23 vs 0.07 kg CH_4 /animal/day (Harper et al., 1999). Furthermore, about 80% of total GHG emissions and 84% of methane emissions come from the cow-calf phase, whereas only 20 and 16%, respectively, come from the feedlot phase (Beauchemin et al., 2010). Therefore, accurately determining grazing animals' energy requirements is critical to ensure that strategic energy and protein supplementation is delivered to optimize animal growth and development (Tedeschi et al., 2019).

Unfortunately, most recommendations for grazing animals' energy and protein requirements were grounded on those determined for confined animals. Partly because determining energy, protein, and other nutrients for grazing animals requires special equipment and methodology, making it more challenging, expensive, and laborious. Energy and protein requirements for confined animals have been extensively studied and disseminated for over 117 years (Kellner, 1905). Digestion trials have been implemented for a bit longer: since 1860 at the Weende Experiment Station at

the University of Goettingen in Germany and since 1884 at the University of Wisconsin Agricultural Experiment State in the United States (Schneider and Flatt, 1975). For beef cattle, currently recommended energy and protein requirements stemmed from penned animal studies using the comparative slaughter technique and the California Net Energy System methodology (Oltjen, 2019), though discrepancies might exist (Tedeschi et al., 2017; Tedeschi, 2019b).

Grazing animals have an additional energy requirement associated with grazing activity compared to confined animal requirements. It comprises the additional energy needed for body movements (i.e., locomotion) and forage browsing, selection, and prehension. The non-activity maintenance requirement of energy between grazing and confined growing or finishing animals might be identical on a metabolic weight basis as long as animals are at the same degree of maturity (i.e., same composition of gain) (Tedeschi and Fox, 2015). However, because the diet consumed by grazing animals (i.e., essentially forage) has a lower partial efficiency of energy use for growth (k_g), grazing animals would require a greater DM intake (DMI) to achieve the same average daily gain (ADG). This fact becomes a significant limitation for grazing animals for two main reasons: (1) the distance traveled to reach maximum voluntary intake within a 24-h period (daily basis) may exceed the animal's locomotion or eating time capacities, worsening its energy balance; and (2) because DMI is also a function of rumen size (i.e., volume/space), low-quality forages, i.e., forage containing a higher proportion of fibrous material, may further restrict intake by triggering the negative effect of rumen fill on voluntary feed intake (Tedeschi and Fox, 2015; 2020a). Both reasons impede grazing animals from having the same ADG as confined animals. Although the energy cost of physical activities in cattle, sheep, and buffaloes has been extensively documented worldwide, a comprehensive physical activity calculation logic does not exist because the lack of information on the energy required for eating feed by the ruminant is considerably more significant for grazing animals than for confined animals (Tedeschi and Fox, 2015).

Assessing the nutritional value of the feeds consumed by the animal is an essential step in determining the animal's energy and protein requirements, and it is not a trivial task. Tedeschi and Fox (2015) and Tedeschi and Dias Batista (2021) discussed existing techniques to determine feedstuffs' nutritive value. Given our inability to definitively and accurately assess the consumption of digestible energy (DE) by grazing animals when a digestibility trial cannot be carried out, some have proposed the use of mathematical modeling or empirical predictions to predict DE or its equivalent, total digestible nutrients (TDN), given the chemical composition of the diet in addition to other factors (Tedeschi and Fox, 2020a; 2020b), especially for those under grazing conditions (Tedeschi et al., 2019; Woli et al., 2020). In part, the problem arises not only because the DE content is unknown with a high degree of certainty but because of inadequate predictions of feed intake and selection. Additional problems exist when converting DE to metabolizable energy (ME) (Galyean et al., 2016; Seo et al., 2021) for grazing animals given the highly variable contribution of energy loss via methane production. Thus, the question remains, can the intake of DE be accurately determined so energy partitioning can be estimated to assess animals' energy requirements under grazing or confined conditions?

Predicting energy expenditure for grazing cattle

In the United States, comprehensive discussions about energy and protein requirements, primarily based on confined animals (Tedeschi, 2019a), have been published by the National Research

Council (NRC) and National Academies of Sciences, Engineering, and Medicine (NASEM) for beef cattle from 1945 (NRC, 1945a) to 2016 (NASEM, 2016), for dairy cattle from 1945 (NRC, 1945b) to 2021 (NASEM, 2021), and for sheep and goats from 1945 (NRC, 1945c) to 2007 (NRC, 2007). Other countries and regions around the globe have followed suit and devised their own set of recommendations to meet their needs and production conditions. Few publications have meticulously addressed the grazing animal's energy expenditure (EE) as the Australian Nutrient Requirements of Domesticated Ruminants published by the Commonwealth Scientific and Industrial Research Organization (CSIRO, 1990; 2007).

The Agricultural Research Council (ARC, 1980) developed a factorial approach to estimate the EE (kcal/d) (Eq. (1)) associated with physical activities by assigning coefficients to the number of hours animals spent standing (h/day), the number of daily body changes (laying down and standing), and walking horizontal and ascent distances (km/day). Assuming the typical values for feedlot and continuous grazing of 12 and 18 h/d for standing, 6 daily position changes, 0 and 2 km/d for horizontal distance, and no vertical distance, the EE values for animals' physical activity with 300 kg of BW, usually assumed to be shrunk BW (NASEM, 2016), are 471.6 and 1 024.6 kcal/d. If the required net energy (NE) required for maintenance is assumed to be 70 kcal/kg^{0.75} BW/d, these EE values for physical activity become an additional 9.35 and 20.3%, respectively. That means the daily required NE for maintenance becomes $1.0935 \times (70 \times \text{BW}^{0.75})$ and $1.203 \times (70 \times \text{BW}^{0.75})$ for animals under feedlot and continuous grazing conditions, respectively. Fox and Tylutki (1998) proposed to change the basal metabolic energy requirement from 77 kcal/kg^{0.75} of BW, devised by Lofgreen and Garrett (1968), to 70 kcal/kg^{0.75} of BW because of about 10% (i.e., 9.35%) needed for physical activity under typical feedlot conditions in the United States.

$$EE_{PA} = \left(\begin{array}{l} 0.1 \times \text{Standing} + 0.062 \times \text{Position changes} + \\ 0.621 \times \text{Distance}_{\text{Flat}} + 6.69 \times \text{Distance}_{\text{Vertical}} \end{array} \right) \times \text{FBW} \quad (1)$$

where $\text{Distance}_{\text{Flat}}$ is the distance traveled by the animal on a horizontal, flat surface, km/d; $\text{Distance}_{\text{Vertical}}$ is the equivalent ascending distance traveled by the animal, km/d; EE_{PA} is energy expenditure for physical activity, kcal/d; FBW is full (unshrunken) BW, kg; Position changes is the number of standing and lying changes per day; and Standing is the number of hours standing, h.

Horizontal vs sloped vs vertical distances

In practice, an animal's locomotion is either on a leveled terrain (i.e., horizontal, flat) or a sloped terrain (i.e., inclined) with a gradient or an inclination angle; animals do not "walk vertically." The main limitation of measuring the EE for sloped terrains is that the inclination angle may differ between studies, making it challenging to compare the measured EE needed for sloped distances. Thus, the EE of vertical or ascent distance removes the inclination angle as it only assumes the differences in heights to estimate EE. Because cows climbing a ladder is unheard of, the EE for "walking vertically" has to be computed mathematically.

Fig. 2 shows the graphical relationships between these distances. An animal can go from point A to point B by walking the sloped distance from A → B, or walking horizontally from A → D and then "vertically" from D → B. Given the laws of thermodynamics of conservation of energy, as shown in Eq. (2), it is assumed that the amount of energy expended for $s \times EE_{A \rightarrow B}$ is equal to the sum of the energy expended for $h \times EE_{A \rightarrow D}$ plus $v \times EE_{D \rightarrow B}$, assuming that the EE is expressed as energy per distance unit, and s , h , and v are distances.

$$EE_{A \rightarrow B} \times s = EE_{A \rightarrow D} \times h + EE_{D \rightarrow B} \times v \quad (2)$$

where EE is energy expenditure, Mcal/km.

The h and v (dashed red lines in Fig. 2) can be computed from the triangle A-B-D using trigonometric relationships, as shown in Eq. (3).

$$\begin{aligned} \cos(\alpha) &= h/s \cdot h = \cos(\alpha) \times s \\ \sin(\alpha) &= v/s \cdot v = \sin(\alpha) \times s \end{aligned} \quad (3)$$

Replacing h and v in Eq. (2) with those from Eq. (3), simplifying the equation, and re-arranging to estimate $EE_{D \rightarrow B}$, we obtain Eq. (4).

$$\begin{aligned} EE_{A \rightarrow B} \times s &= EE_{A \rightarrow D} \times (\cos(\alpha) \times s) + EE_{D \rightarrow B} \times (\sin(\alpha) \times s) \cdot \\ EE_{D \rightarrow B} &= (EE_{A \rightarrow B} - EE_{A \rightarrow D} \times \cos(\alpha)) / \sin(\alpha) \end{aligned} \quad (4)$$

where \cos is the cosine function; EE is energy expenditure, Mcal/km; \sin is the sine function; and α is the inclination angle, radians.

Because $EE_{A \rightarrow D}$ is the same as $EE_{A \rightarrow C}$ as they are expressed as energy per distance per kilogram of BW, we can substitute $EE_{A \rightarrow D}$ with $EE_{A \rightarrow C}$ to obtain the final mathematical formulation to compute $EE_{D \rightarrow B}$ with known measurements expressed as energy per distance, as shown in Eq. (5). Note that $EE_{D \rightarrow B}$ (i.e., uphill) might

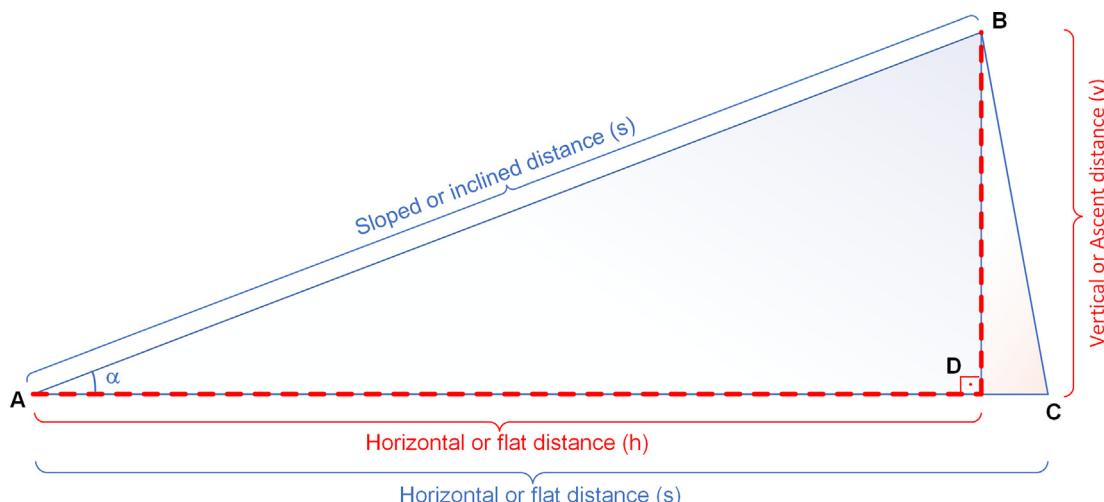


Fig. 2. Relationships among horizontal (h), sloped (s), and vertical (v) locomotion.

not be the same as $EE_{B \rightarrow D}$ (i.e., downhill) (Miwa et al., 2015; Mulvenna et al., 2022), given the EE required for maintaining equilibrium and stability to prevent falling (Hunter et al., 2010).

$$EE_{D \rightarrow B} = (EE_{A \rightarrow B} - EE_{A \rightarrow C} \times \cos(\alpha)) / \sin(\alpha) \quad (5)$$

where \cos is the cosine function; EE is energy expenditure, Mcal/km; \sin is the sine function; and α is the inclination angle, radians.

Therefore, if an animal expends 0.62 kcal/km/kg of BW for walking on a horizontal path and 1.32 kcal/km/kg of BW for walking on a 6° sloped path, the “vertical walking” EE would be 6.73 kcal/km/kg of BW, calculated using Eq. (6).

$$EE_{D \rightarrow B} = (1.32 - 0.62 \times \cos(6 \times \pi/180)) / \sin(6 \times \pi/180) \quad (6)$$

where \cos is the cosine function; EE is energy expenditure, Mcal/km; \sin is the sine function; and π is the Pi number.

For example, a 300-kg animal walking 2.5 km on a 6° sloped terrain would require 990 kcal ($300 \text{ kg} \times 2.5 \text{ km} \times 1.32 \text{ kcal/kg/kg}$). It is equivalent to a 300-kg animal walking 2.486 km horizontally ($\cos(6^\circ \times \pi/180)$) at 0.62 kcal/kg/kg plus 0.261 km “vertically” ($\sin(6^\circ \times \pi/180)$) at 6.73 kcal/kg/kg: $300 \text{ kg} \times 2.486 \text{ km} \times 0.62 \text{ kcal/kg/kg} + 300 \text{ kg} \times 0.261 \text{ km} \times 6.73 \text{ kcal/kg/kg} \approx 990 \text{ kcal}$.

Revisiting the prediction of energy expenditure for grazing cattle

The CSIRO (2007) devised a different approach to compute the EE of grazing animals by adding an assessment of animals’ DMI, grazing density (animals per ha), DM digestibility, and availability of the forage to the animals’ physical activity (horizontal locomotion). While this is a more mechanistic approach to estimating grazing animals’ EE, it requires additional information that might be neither available nor measurable. Novel methods and techniques to assess forage availability and quality (González et al., 2018) are promising, and their adoption in these situations might help our understanding of grazing animals’ EE tremendously.

Table 1 has revised literature data published by Tedeschi and Fox (2020a), which was initially reported by Tedeschi (2001) and Tedeschi and Fox (2015), who provided a detailed description of the studies. The dataset summarizes EE for different grazing ruminant species, using different techniques from 18 studies, and a summary of Israeli studies for grazing Simmental \times Hereford beef cows, using the heart rate technique and global positioning system from four studies. The average EE values for sloped (1.37, 1.33, and 1.32 kcal/kg/km) and vertical (6.59 and 6.69 kcal/kg/km) locomotions are nearly identical between the datasets (Table 1), but the EE for horizontal locomotion differs considerably from the values

adopted by ARC (1980) and CSIRO (1990) by almost six times (0.11 vs 0.62 kcal/kg/km). The variation among different techniques assessing EE of grazing animals is high, partly because of the differences in feed quality, the amount used, and types of animals under different environments in each experiment. Thus, a direct comparison of the results is complicated.

Developing a holistic energy requirement for grazing animals

Besides the basal metabolism and physical activity for grazing animals, one could include the EE for chewing (i.e., eating and ruminating), given the digestibility of the diet. The idea would be similar to CSIRO’s (2007) approach in which diet quality (i.e., digestibility) alters the EE of grazing animals. Tedeschi and Fox (2015) and Tedeschi and Fox (2020a) proposed a holistic approach to predict the increase in the NE required for maintenance due to physical activities, eating, and ruminating forages of different quality.

The prediction of EE for physical activities assumes an additive model; in other words, physical activity expenses plus the heat increment of feeding are added to basal metabolism (H_eE) (White, 1993). The heat increment due to feed type in grazing systems may be incorrectly attributed to physical activity, and the EE attributed to physical activities may overlap the heat requirement for thermoregulation in cold conditions (T_c less than the lower critical temperature). Other factors, such as eating and ruminating, may also influence the EE of grazing animals, which depends on the biting size and rate. Di Marco et al. (1996) estimated the energy cost of eating was $1.84 \text{ kcal/kg}^{0.75}/\text{h}$ for 59 bites/min (148 g DM/m² for ryegrass pasture) and $0.55 \text{ kcal/kg}^{0.75}/\text{h}$ for 28 bites/min (228 g DM/m² for oat). Osuji (1974) had previously reported the value of 7.06 cal/kg/min for eating, which is approximately $1.89 \text{ kcal/kg}^{0.75}/\text{h}$ for a 400-kg animal, nearly identical to the value of 59 bites/min measured by Di Marco et al. (1996).

A more holistic approach for partitioning the energy required (i.e., EE) of different behavior patterns of grazing animals is necessary to predict the maintenance energy needed to support physical activities and the animal’s EE for eating and ruminating forages of different quality. The submodel developed by Tedeschi and Fox (2015) proposed to partition EE for eating (i.e., mastication and ingestion of fresh feed) and ruminating (i.e., chewing the cud). The NRC (1981) defined HE as the sum of heat for basal metabolism (i.e., H_eE); heat for muscular activity (H_mE) required for standing, walking, grazing, drinking, and lying down; the heat of enzymatic digestion (H_dE); the heat of fermentation as a result of ruminal

Table 1

Summary of additional energy expenditure (kcal/kg of BW) for diverse physical activities in ruminants.¹

Items	Standing kcal/d/kg of BW	Types of walked distances		
		Horizontal kcal/km/kg of BW	Sloped	Vertical
Israeli’s dataset²				
Average	2.59	0.11	1.37	—
SD	0.22	0.03	0.23	—
CV, %	8.4	28.1	16.9	—
Tedeschi’s (2001) dataset³				
Average	—	0.11	1.33	6.59
SD	—	0.03	0.11	0.78
CV, %	—	29.3	16.2	11.9
ARC (1980)				
Average	2.39	0.62	1.32	6.69

¹ Revised from Tedeschi and Fox (2020a).

² References: Brosh et al. (2006), Aharoni et al. (2009), Brosh et al. (2010), Aharoni et al. (2013).

³ References: Corbett et al. (1969), Ribeiro et al. (1977), Lawrence and Richards (1980), Havstad and Malechek (1982), Sanchez and Morris (1984), Thomas and Pearson (1986), Sahlu et al. (1988), Lawrence and Stibbards (1990), Nienaber et al. (1993), Méndez et al. (1996), Dijkman and Lawrence (1997), Fall et al. (1997), Prieto et al. (1997), Di Marco and Aello (1998), Herselman et al. (1998), Susembeth et al. (1998).

microbial action (H_fE); the heat associated with the metabolic processes of product formation from absorbed metabolites (H_cE); thermal regulation (H_tE), and waste formation and excretion (H_wE). Heat increment (H_iE) is the sum of H_dE , H_fE , H_tE , and H_wE . HE can be written as shown in Eq. (7) for an animal fed at maintenance.

$$HE = H_eE + H_fE + H_cE + H_iE \quad (7)$$

where H_cE is the heat for thermal regulation, Mcal/d; HE is heat production, Mcal/d; H_eE is the heat for basal metabolism, Mcal/d; H_iE is the heat increment, Mcal/d; and H_fE is the heat for muscular activity, Mcal/d.

For animals under no heat or cold stress, H_cE is assumed to be 0. Furthermore, for an animal fed at maintenance, retained energy (RE) is zero; thus, the HE is equal to ME intake ($MEI = HE + RE$). In the case of maintenance-level of intake, the MEI is the $MEmr$. We further subdivided heat for muscular activities (i.e., H_fE) into an animal's physical activity for locomotion or movement ($H_{pa}E$) and eating and ruminating the digesta ($H_{er}E$). After assuming these simplifications, Eq. (7) yields Eq. (8).

$$MEI = MEmr = H_eE + (H_fE_{pa} + H_{er}E) + H_iE \quad (8)$$

where H_eE is the heat for basal metabolism, Mcal/d; H_iE is the heat increment, Mcal/d; $H_{er}E$ is the heat for eating and ruminating, Mcal/d; $H_{pa}E$ is the heat for physical activities, Mcal/d; MEI is metabolizable energy intake, Mcal/d; and $MEmr$ is ME required for maintenance, Mcal/d.

Susenbeth et al. (1997 and 1998) reported that EE for eating was 1.91 kcal/kg^{0.75}/h for 640-kg steers, with a literature review mean of 1.78 kcal/kg^{0.75}/h from a range of 0.7 to 2.7 kcal/kg^{0.75}/h (Susenbeth et al., 1997; 1998). These authors also reported that, on average, animals expended 0.52 kcal/kg^{0.75}/h on ruminating but that the EE for eating and ruminating varied with feed quality, from 0.19 Mcal/kg DM for high-quality forage to 0.57 Mcal/kg DM for wheat straw, representing 8 and 33% of MEI, respectively (Susenbeth et al., 1997; 1998). When we regressed the EE for eating and ruminating (Mcal/kg DM) on MEI (Mcal/d), using the data reported by Susenbeth et al. (1998), we obtained Eqs. (9) (power equation) and (10) (decay equation) to predict $H_{er}E$. For instance, a 300-kg animal eating 7 kg DM/d of a diet of 16.9 Mcal ME/d would have $H_{er}E$ of 1.98 (Eq. (9)) Mcal ME/d, or about 11.7% of its energy required for maintenance. Alternatively, 2.15 Mcal ME/d is obtained with Eq. (10). Eq. (9) was adopted because it yielded a lower residual sum of squares than Eq. (10) (0.00048546 vs 0.00292620).

$$H_{er}E = (4.2557 \times MEI^{-0.95878}) \times DMI \quad (9)$$

$$H_{er}E = (0.95166 \times e^{-0.06705 \times MEI}) \times DMI \quad (10)$$

where DMI is DM intake, kg/d; e is the exponential function (i.e., e is the Napier's constant of 2.7182); $H_{er}E$ is the heat for eating and ruminating, Mcal/d; and MEI is metabolizable energy intake, Mcal/d.

As shown in Eq. (11), the heat for basal metabolism (i.e., H_eE) is computed using the equation developed by Lofgreen and Garrett (1968) adjusted for the physical activity of pen-fed animals (Fox and Tylutki, 1998) and for the energy cost of eating and ruminating, using Eq. (9). The animals in the low level of feed intake used by Lofgreen and Garrett (1968) consumed about 3.3 kg DM/d and 8 Mcal ME/d. For these values, Eq. (9) yields $H_{er}E$ of 1.9 Mcal/d. Consequently, H_eE (i.e., $NEmr$) adjusted for their animals' physical activity, eating, and ruminating EE is estimated as shown by Eq. (11). The $H_{pa}E$ (i.e., $NEmr_{Act}$) is computed with Eq. (1).

$$H_eE = NEmr_{Basal} = 0.07 \times SBW^{0.75} - 1.9 \quad (11)$$

where HE is the heat for basal metabolism (i.e., $NEmr_{Basal}$), Mcal/d; and SBW is the shrunk BW, kg.

Although the energy cost associated with physical activity is included in the observed data of Lofgreen and Garrett (1968), the physical activity adjustment proposed by Fox and Tylutki (1998) might have introduced some degree of double accounting. The reason is that physical activity cost likely varies with feed intake, and extrapolating to zero feed intake might have already adjusted for some portion of it automatically.

When animals have been starved (i.e., energy intake is zero) for some time, yielding negligible amounts of energy from the digesta, the $NEmr$ is equal to the fasting heat of production (i.e., H_eE or basal metabolism). However, when animals resume feeding (i.e., energy intake is greater than zero), the heat associated with obtaining feed (e.g., physical activity, eating, and ruminating) is added to the $NEmr$ (NRC, 1981). The physical activity ($H_{pa}E$) and eating and ruminating ($H_{er}E$) heats are included in the $NEmr$ as represented in Eqs. (12) and (13) when energy intake is greater than zero.

$$MEmr = NEmr + H_iE \quad (12)$$

$$NEmr = \begin{cases} H_eE & \text{Energy intake} = 0 \\ H_eE + H_{pa}E + H_{er}E & \text{Energy intake} > 0 \end{cases} \quad (13)$$

where H_eE is the heat for basal metabolism, Mcal/d; H_iE is the heat increment, Mcal/d; $H_{er}E$ is the heat for eating and ruminating, Mcal/d; $H_{pa}E$ is the heat for physical activities, Mcal/d; and $MEmr$ is the metabolizable energy required for maintenance, Mcal/d.

Therefore, for an animal fed at maintenance (zero energy intake), the $NEmr$ is equal to $MEmr \times k_m$ in which k_m is the partial efficiency of using ME to NE for maintenance. Consequently, replacing $NEmr$ with $MEmr \times k_m$ in Eq. (12) and solving for H_iE shows that H_iE is $MEmr \times (1 - k_m)$. Then, substituting H_iE and $NEmr$ (Eq. (13)) into Eq. (12) results in Eq. (14). Expanding Eq. (14) by replacing H_eE with Eq. (11), $H_{pa}E$ with Eq. (1), and $H_{er}E$ with Eq. (9) results in Eq. (15). Unfortunately, because $H_{er}E$ requires MEI to be computed (i.e., $MEmr$ for animals at maintenance), Eq. (15) can only be solved iteratively through optimization, highlighting the danger of adopting feedforward calculation only and ignoring feedback loops.

$$MEmr = H_eE + H_{pa}E + H_{er}E + MEmr \times (1 - k_m) \quad (14)$$

$$MEmr = (0.07 \times SBW^{0.75} - 1.9) + \frac{(0.1 \times \text{Standing} + 0.062 \times \text{PositionChanges} + 0.621 \times \text{Distance}_{\text{Flat}} + 6.69 \times \text{Distance}_{\text{Vertical}}) \times FBW}{1000} + (4.2557 \times MEI^{-0.95878}) \times DMI + MEmr \times (1 - k_m) \quad (15)$$

where $\text{Distance}_{\text{Flat}}$ is the distance traveled by the animal on a horizontal, flat surface, km/d; $\text{Distance}_{\text{Vertical}}$ is the equivalent ascending distance traveled by the animal, km/d; DMI is DM intake, kg/d; FBW is full (unshrunk) BW, kg; H_eE is the heat for basal metabolism, Mcal/d; H_iE is the heat increment, Mcal/d; $H_{er}E$ is the heat for eating and ruminating, Mcal/d; $H_{pa}E$ is the heat for physical activities, Mcal/d; k_m is the partial efficiency of the use of metabolizable energy for maintenance, Mcal/Mcal; MEI is metabolizable energy intake, Mcal/d; $MEmr$ is the metabolizable energy required for maintenance, Mcal/d; Position changes is the number of standing and lying changes per day; SBW is shrunk BW, kg; and Standing is the number of hours standing, h.

An inconsistency that arises from the factorial approach to determine HE, as shown in Eq. (7), is that the partial efficiency of using ME to NE for maintenance (i.e., k_m) is only valid to estimate

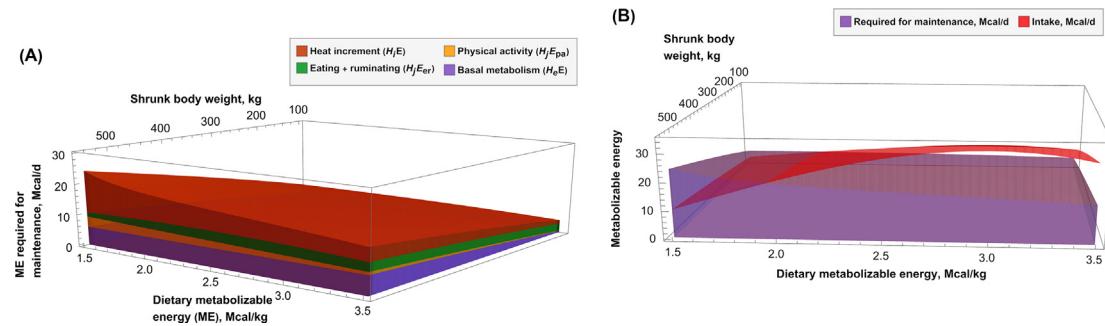


Fig. 3. (A) Metabolizable energy (ME) required for basal metabolism (H_bE), physical activity (H_pE_{pa}), eating and ruminating (H_pE_{er}), and heat increment (H_iE) of grazing cattle for different shrunk BWs and dietary ME contents calculated using Eq. (15). See [Supplementary Video S1](#). (B) Total ME required for maintenance (purple) and predicted ME intake. See [Supplementary Video S2](#). Based on [Tedeschi and Fox \(2020a\)](#).

the ME_{mr} from fasting heat production (H_eE or basal metabolism at zero energy intake). The reason is that $ME_{mr} = k_m \times H_eE$, as shown in Eqs. (12) and (13) (Garrett, 1980b). If all HE components are measured and summed up, using k_m will eventually result in double accounting. In that case, k_m needs to be “increased” to consider the HE included in estimating NE_{mr}; in other words, k_m needs to account for a smaller portion of the unaccounted HE.

Fig. 3A depicts the total daily ME required for a grazing animal, partitioned into EE for basal metabolism, physical activity, eating and ruminating, and heat increment, assuming dietary ME (1.5–3.5 Mcal/kg) and SBW (100–550 kg). The horizontal and vertical distances were assumed to vary (1 500–0 meters per day and 500–0 meters per day, respectively) for low- to high-quality dietary ME (1.5–3.5 Mcal/kg, respectively). The variable horizontal and vertical distances were used to mimic animals grazing farther on low-quality forages to meet their energy requirements for maintenance compared to those on high-quality forages (e.g., rotational grazing systems or confinement conditions). The number of hours standing was 12 h/d, and the number of body position changes was 6 times/d regardless of the diet ME and animal SBW. The proportion of MEI (i.e., ME_{mr}) lost as heat (i.e., heat increment) was identical among animals of different SBW because the k_m was computed from dietary ME, which was identical for all animals. The heat increment (H_iE) was greater for heavier than lighter animals, but the proportion of MEI that was expended for eating and ruminating was greater for lighter than heavier animals as it was a function of dietary ME. The EE for eating and ruminating was greater for low-quality forage than grain-based finishing diets (Fig. 3A). The proportion of physical activity (i.e., movement or locomotion) was similar, ranging between 7 and 14%. As expected, animals expended more energy on low-quality forage than on high-quality forage (Fig. 3A). The EE for physical activity varied from 0.16 to 0.61 Mcal/d for the 100-kg animal and 0.90 to 3.35 Mcal/d for the 550-kg animal. Animals consuming diets containing less than approximately 1.9 Mcal ME/kg are predicted not to meet their energy requirements as their MEI is below the ME required for maintenance (Fig. 3B), and they would likely lose weight and eventually succumb if dietary ME remains low. The 1.9 Mcal ME/kg DM is approximately 53% TDN, confirming the minimum threshold of forage digestibility, suggested by [Van Soest \(1994; Figures 7.8 and 7.9\)](#), of approximately 50% to support cattle at maintenance.

As shown in Fig. 3A, the EE for physical activity (H_pE_{pa}) and chewing (H_pE_{er}) accounts for nearly all the differences between confined and grazing ruminants, and yet, our incomplete understanding of these components has delayed the development of a more definitive solution. In part, data collection of plant and animal interaction (forage selection, grazing behavior, pasture growth/regrowth, pasture quality, nutrient digestion and absorp-

tion, volatile fatty acids production and profile, and energy requirement) remains a critical bottleneck for adequate knowledge of forage intake by ruminants (Tedeschi et al., 2019). Most of the data on EE for ruminants crested in the early 1960s toward the mid-1980s, boosted by many open-circuit, indirect calorimetry apparatuses and methods, but none could be decisively deemed ideal, and the development and improvement of methodologies declined. More recently, with the advancement of global positioning systems (GPS) and heart rate monitoring systems, researchers have been able to track grazing animals and estimate their EE (Brosh, 2007). The adoption of these instruments to determine grazing animals' EE was likely motivated by the desire to identify efficient animals through the residual feed intake (RFI) technique (Asher et al., 2018).

As new technologies and methodologies become available, modeling the energy requirement of grazing and confined animals will likely close the gap between model-predicted and observed performance as more factors are considered in the predictive models. Nonetheless, caution should be exercised to avoid double accounting or offsetting errors in calculating EE that could elicit false improvements in predictability.

Improving the predictability of the efficiency of the energy use for growing cattle

The second bottleneck in ensuring adequate diet formulation is the accurate determination of the efficiency of ME use for growth. There is no shortage of growth model development, but perhaps combining the quintessence of extant growth models to improve the predictability of the gain composition is warranted. Once the gain composition is known, the energy and protein requirements are straightforward calculations. The RE and ADG have been the heartbeat of many theoretical growth models (Lofgreen and Garrett, 1968; Garrett, 1980a; Loewer et al., 1983; Fox and Black, 1984; NRC, 1984; 2000; Fox et al., 1992), including stochastic models (Parks, 1973). Some growth models used ADG and specific characteristics of animal growth (Keele et al., 1992; Williams et al., 1992; Williams and Jenkins, 1998; Kilpatrick and Steen, 1999) and combined mechanistic or dynamic modeling to predict body composition (Hoch and Agabriel, 2004a; 2004b), or used DNA (deoxyribonucleic acid) accretion curves and protein-to-DNA ratio (Oltjen et al., 1986b; Bywater et al., 1988; Di Marco et al., 1989; Oltjen et al., 2000). Primary biochemistry pathways associated with the development and growth of different tissues (e.g., viscera, muscle, and adipose) have been developed for sheep (Oddy et al., 1997; Oddy et al., 2019). Most mechanistic and dynamic conceptual growth models are based on metabolic processes (Gill, 1984; France et al., 1987; Gill et al., 1989; Gill, 1996), but such models

rely heavily on the principle that substrate availability and saturation enzyme kinetics control the distribution of nutrients in body tissues (Baldwin, 1995).

Some growth models rely on empirical concepts and some elements of teleonomic behavior (Tedeschi and Fox, 2020a). Others possess some elements of mechanistic modeling, and very few or none adopted stochastic components (i.e., probabilistic theory). Because of the different modeling approaches to predict energy and protein requirements among existing growth models and their different variables, some critical limitations arise when comparing existing growth models. For instance, Arnold and Bennett (1991a and 1991b) compared four growth models developed in the early to mid-1980s: Roman L. Hruska US Meat Animal Research Center (Notter et al., 1979a; Notter et al., 1979b; 1979c), Texas A&M University (Sanders and Cartwright, 1979a; 1979b; Oltjen et al., 1986a), BEEFS156 (Loewer et al., 1983; Loewer et al., 1987), and UCDavis (Oltjen et al., 1986a; Oltjen et al., 1986b). They reported that two problems caused these models to yield inconsistent results: the definition of mature BW is different among growth models and different predictions of DMI. When these two variables were assigned independently within each model, the models simulated the animal's BW successfully but failed to predict body composition. Similarly, Garcia et al. (2008) compared the growth model developed by Institut National de la Recherche Agronomique (Hoch and Agabriel, 2004a; 2004b) and UCDavis (Oltjen et al., 1986a; Oltjen et al., 1986b), and reported that both models, developed with entirely different concepts and equations, could produce similar predictions of body composition (protein accretion), but they behaved differently under distinct growth trajectories. These evaluations reinforced the hypothesis that each model has to be evaluated within the purpose of its development, and intrinsic errors may offset each other within each model. Therefore, model comparisons should be carried out under various production conditions to accommodate each model's assumptions and purposes. Consequently, a generalized growth model is still needed.

Such limitations may hinder the predictability of growth models when different production conditions exist other than those established conditions in which the models were developed or calibrated (Tedeschi, 2022b). They may also prevent incorporating different modeling concepts from one model to another. For instance, for growing cattle, the partial efficiency of energy use for growth (i.e., k_g) in the American systems (e.g., NRC, NASEM, CNCPS, and RNS) is frequently computed based on an empirical (cubic) equation that estimates the NE for growth (NEg, Mcal/kg) based on the dietary concentration of the ME (Mcal/kg). Similarly, in the British and Australian systems (e.g., ARC, Agricultural and Food Research Council—AFRC, and CSIRO), the k_g also exclusively depends on dietary energy through the metabolizability of the diet (M/D), though a linear equation is applied. In addition to the diet characteristics, more specifically its digestibility, CSIRO (2007) proposed adjusting k_g for the legume proportion relative to grass.

Predicting the partial efficiency of the use of energy for growth

Although the dietary ME is related to the dietary contents of carbohydrates, fat, and protein and their digestibility, the efficiency to which energy is deposited in the tissue depends on the tissue gain composition (Reid et al., 1980; Tedeschi et al., 2004). Growth models rarely acknowledge this fact and still use dietary characteristics to estimate k_g and NEg; thus, incorrectly rendering k_g independent of carcass composition. If the protein proportion of RE is known, k_g can be estimated using Eq. (16), and assuming fat and protein deposition efficiencies of 75 and 20%, respectively, it yields Eq. (17) (Tedeschi, 2001; Williams and Jenkins, 2003; Tedeschi et al., 2004).

$$k_g = k_F \times k_P / (k_P + RE_P \times (k_F - k_P)) \quad (16)$$

$$k_g = 3 / (4 + 11 \times RE_P) \quad (17)$$

where k_F is the efficiency of fat deposition, Mcal/Mcal; k_g is the partial efficiency of converting metabolizable energy into net energy for growth; k_P is the efficiency of protein deposition, Mcal/Mcal; and RE_P is the proportion of protein in the retained energy.

The impact of growth rate on the deposition efficiencies of fat and protein

These deposition efficiencies are not fixed, however, Cannas et al. (2006) and Tedeschi et al. (2010) reported values of 68 and 27% for fat and protein, respectively, for growing sheep, and Chizzotti et al. (2008) reported different deposition efficiencies of fat (79%) and protein (34%) for Nellore and Nellore \times Bos taurus. Marcondes et al. (2013) empirically derived a non-linear relationship between k_g and the proportion of RE as protein (RE_P), and when solving their empirical equation, the deposition efficiencies for fat and protein are 60.7 and 21.2%, respectively. These studies suggest that deposition efficiencies of fat vary from 60.7 to 79% and of protein vary from 21.1 to 34%. Perhaps the most exciting finding elucidated by Marcondes et al. (2013) was that fat and protein deposition efficiencies are not constant; they increase linearly with ADG (Eq. (18) had r^2 of 0.916 and Eq. (19) had r^2 of 0.951). Their values suggested that fat and protein deposition efficiencies increased by about 1.84 and 1.76% for each 100 g/d increase in ADG, respectively. Interestingly, based on Eqs. (18) and (19), fat and protein deposition efficiencies are 69.1 and 19.8%, respectively, when ADG (i.e., empty weight gain, EWG) is zero. These values are close to their respective values reported above, suggesting these efficiencies are only valid when ADG approximates zero: body composition of low-gaining animals might be better estimated than high-gaining animals.

$$k_F = 0.1836 \times EWG + 0.691 \quad (18)$$

$$k_P = 0.1764 \times EWG + 0.198 \quad (19)$$

where EWG is empty weight gain, kg/d; k_F is the efficiency of fat deposition, Mcal/Mcal; and k_P is the efficiency of protein deposition, Mcal/Mcal.

Combining Eq. (16) with EWG-dependent fat (k_F) and protein (k_P) deposition efficiencies (Eqs. (18) and (19)) yields Eq. (20), which has the shape shown in Fig. 3A without restricting the maximum k_g to 79%.

$$k_g = \frac{19.0025 + EWG(21.9785 + 4.4982 \times EWG)}{27.5 + 24.5 \times EWG + RE_P(68.4722 + EWG)} \quad (20)$$

where EWG is empty weight gain, kg/d; k_g is the partial efficiency of converting metabolizable energy into net energy for growth; and RE_P is the proportion of protein in the retained energy.

Fig. 3A shows that the k_g decreases exponentially with the protein proportion in the RE and increases linearly with EWG. The direct correlation between EWG and k_g was expected because the rate of fat deposition increases as EWG increases (Owens et al., 1995), and the fat deposition efficiency is greater than protein, as discussed above. The protein requirement for growing animals can be theoretically estimated from RE and ADG (Tedeschi, 2019b); thus, improving RE (and ADG) predictions will improve the computation of protein needs.

The impact of maturity stage rate on the deposition efficiencies of fat and protein

The rate of fat accretion also increases with maturity (Owens et al., 1995; Tedeschi, 2019b), assuming empty body fat as a proxy for maturity. Thus, one would expect that k_g should also increase with maturity. Nevertheless, which variable (EWG or maturity) impacts k_g the most is unknown. The British and Australian systems (e.g., ARC, AFRC, CSIRO) developed non-linear equations to compute the proportion of protein and fat in the gain as animals mature. That means these feeding systems assumed correctly that the animals' maturity stage could be used to adjust changes in body composition, i.e., fat content increases with maturity. These feeding systems adopted the logistic (sigmoidal) function to estimate fat or protein content in the gain for large lean breeds (Charolais, Chianina, Blonde d'Aquitaine, Limousin, Maine Anjou, and Simmental) and other breeds, including crossbreds.

Therefore, combining such information (fat and protein in the gain with partial efficiency of energy use for growth) is interesting to enhance our ability to estimate the carcass composition of growing animals more accurately. Such enhancements would allow us to estimate better their requirements of energy and protein (and other nutrients), aiming to produce more resilient and sustainable production systems (i.e., less use of the resource, lower environmental pollution via an excess of nutrients, betterment of the quality of the animal product, fewer emissions of greenhouse gas due to precise nutrition and days on feed to achieve profitability).

Eqs. (21) and (22) developed by CSIRO (2007) are used to predict fat and protein retained energy in the empty body gain, using the coefficients for non-large, lean animal breeds. These equations use the intake level above maintenance (L) and degree of maturity (Z), assuming that protein contains 5.7 Mcal/kg and fat contains 9.4 Mcal/kg to compute RE. Eq. (23) combined Eq. (17) with Eqs. (21) and (22).

$$E_F = 0.94 \times \left((43 + 28 \times (L - 2)) + \frac{601 - 28 \times (L - 2)}{1 + e^{(-6 \times (Z - 0.4))}} \right) \quad (21)$$

$$E_P = 0.57 \times \left((212 + 4 \times (L - 2)) + \frac{140 - 120 \times (L - 2)}{1 + e^{(-6 \times (Z - 0.4))}} \right) \quad (22)$$

$$k_g = \frac{3}{4 + 11 \times (E_P / (E_P + E_F))} \quad (23)$$

where E_F is the retained energy as fat, Mcal/d; E_P is the retained energy as protein, Mcal/d; k_g is the partial efficiency of converting metabolizable energy into net energy for growth; L is the level of

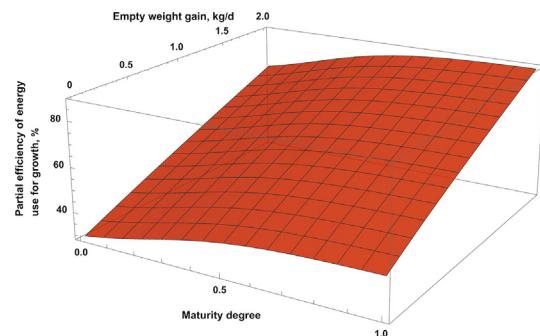


Fig. 5. Relationship between empty weight gain (kg/d) and degree of maturity on the partial efficiency of energy use for growth in cattle, assuming intake level of 2.5. See [Supplementary Video S5](#).

intake above maintenance, dimensionless; and Z is the degree of maturity, dimensionless.

Fig. 4B depicts the predicted retained energy as fat and protein, and k_g for the degree of maturity (BW basis) varying from 0 (born) to 1 (mature) and intake above maintenance varying from 2 to 4. As the degree of maturity increases, the proportion of fat and protein in the gain increases and decreases, respectively, as expected, given the shape of the non-linear logistic curve adopted by the CSIRO (2007). The k_g also increased from approximately 0.30 to 0.58 as maturity increased. The k_g values are within acceptable limits (Reid et al., 1980). However, Fig. 4B provides additional information regarding the interactions between the degree of maturity and level of feed intake above maintenance.

When we combined Eqs. (18) and (19) (growth rate effect) with Eqs. (21) and (22) (maturity stage effect) to estimate k_g (Eq. (16)), it became evident that k_g increases faster with increases in EWG (same degree of maturity) than with increases in the degree of maturity (same growth rate). Furthermore, k_g seems to increase slowly as the degree of maturity increases for animals above 50% maturity compared to those animals below 50% maturity (Fig. 5).

Combining different mathematical models

Combining submodels (i.e., model routines) obtained from distinct mathematical models, usually developed by different groups, might improve our intuition and understanding of the relationships of existing variables that were known for their importance but not included in the original models because of the lack of proper information or confidence during the development phase. The first mistake occurred by not including an essential variable in the model whose only infeasible value was zero (Tedeschi,

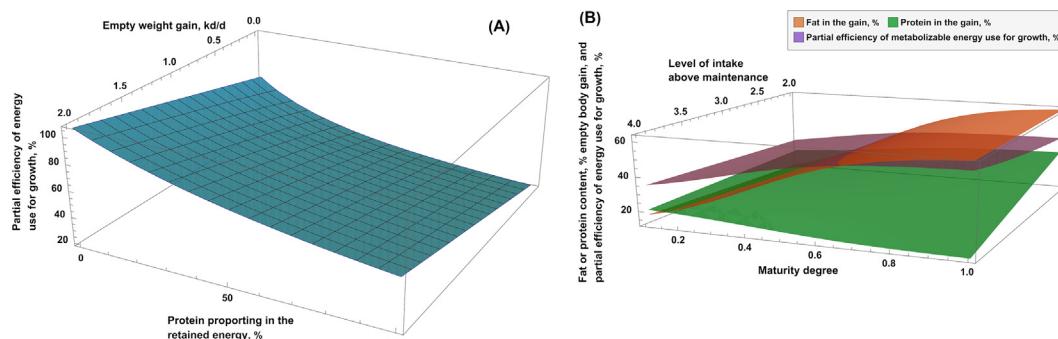


Fig. 4. (A) Relationship between empty weight gain (kg/d) and protein proportion in the retained energy on the partial efficiency of energy use for growth in cattle. Adapted from [Tedeschi \(2019b\)](#). See [Supplementary Video S3](#). (B) Relationship between fat (orange plane) or protein (green plane) content in the empty body gain (g/100 g) and the partial efficiency of use of metabolizable energy for growth (x100) (purple plane) vs degree of maturity. See [Supplementary Video S4](#). Replicated with permission from [Tedeschi \(2022b\)](#).

2023). The second mistake might happen when submodels are combined without judicious planning and evaluation. In this case, it might backfire because the *revised* model may improve the predictability; however, for the wrong reasons (e.g., offsetting errors, ill-conditioned or biased dataset)—hence no new knowledge is obtained. For instance, under specific conditions, model A overpredicts a variable of interest, whereas model B underpredicts it. Combining these models' calculation routines (i.e., submodels) may not improve the predictability because the submodels would yield different responses when changing the universe of acceptable inputs (i.e., inputs expected by a given submodel), thus, twisting or worsening the outcome by introducing systematic or slope biases. Different models have different attributes, such as paradigms (Tedeschi, 2019a, 2023), structural decisions, inputs/outputs, programming language and notation, and parameterization processes that could render them incompatible for merging into a functional model. Combining partial information from several models into a single one is known as *model merging*, and several factors make model merging a complex mission (Brunet et al., 2006), if not impractical in some situations. For instance, the many mathematical models developed recently to understand the COVID-19 pandemic are examples of such anomalies in model merging (James et al., 2021). Model merging is not to be confused with model integration, which combines different models into a whole-system approach (Ascough et al., 2019).

On the other hand, combining concepts and ideas is usually safer than combining models' routines. The two examples discussed above (EE of grazing animals and efficiency of energy use for growth) combined existing knowledge, concepts, and ideas to develop generalized or holistic predictive functional models. Although no former evaluation was conducted (lack of appropriate data), the goal was to discuss integrating existing information on these topics. Nonetheless, specific and global evaluations are necessary to establish confidence in the *revised* models.

Ensemble models

Another field in data analytics that has received greater attention lately is the development of ensemble models. Ensemble modeling is often adopted for artificial intelligence (e.g., machine learning) models to increase prediction accuracy, and it combines the outputs of unrelated models developed using different methods or algorithms but with similar scopes and purposes. Ensemble techniques include bagging (e.g., random forest, bootstrapping, decision trees), boosting (e.g., gradient boosting, adaptive boosting), stacking, and blending (Kyriakides and Margaritis, 2019). The prediction errors are expected to decrease when an ensemble approach is utilized despite contradicting the principle that the simplest solution is often the best (Elder, 2018). In the case of ensemble modeling, models (or submodels) per se are not combined or merged; their outputs are exploited. Examples of ensemble modeling exist for the impact of climate-related issues on crop (corn, wheat, soybean, and rice) yield (Jägermeyr et al., 2021), detection and management of emergent disease by integrating outputs from multiple models (Webb et al., 2017), and classification of cattle behavior (grazing, ruminating, resting, walking) using different machine learning techniques (Dutta et al., 2015) to list a few.

Summary

Because of our constant search for ways to increase the resilience and sustainability of livestock production systems, especially beef cattle production, combining different modeling concepts and ideas might help solve existing problems or limitations of modern feeding systems and meet our needs. The examples described

above showed ways to expand our knowledge, concepts, and ideas by merging extant submodels in developing generalized or holistic predictive functional models. The EE of grazing animals can incorporate the energy needed for physical activity, eating, and rumination into the energy requirement for basal metabolism. The partial efficiency of using metabolizable energy for growth could be improved by including carcass composition rather than diet characteristics alone, and the interaction between the degree of maturity and average daily gain affects the partial efficiency differently. The proposed approaches might improve our assessment of the energy requirements of growing cattle, but before implementing them into other models, they still require further evaluation to refine the inconsistencies discussed.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2023.100835>.

Ethics approval

Not applicable.

Data and model availability statement

Data or models were not deposited in an official repository. No new data were created.

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Author contributions

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Declaration of interest

The author has no perceived conflicts of interest to declare.

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Transparency Declaration

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