The assessment of supplementation requirements of grazing ruminants using nutrition models

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ABSTRACT: This paper was aimed to summarize known concepts needed to comprehend the intricate interface between the ruminant animal and the pasture when predicting animal performance, acknowledge current efforts in the mathematical modeling domain of grazing ruminants, and highlight current thinking and technologies that can guide the development of advanced mathematical modeling tools for grazing ruminants. The scientific knowledge of factors that affect intake of ruminants is broad and rich, and decision-support tools (**DST**) for modeling energy expenditure and feed intake of grazing animals abound in the literature but the adequate predictability of forage intake is still lacking, remaining a major challenge that has been deceiving at times. Despite the mathematical advancements in translating experimental research of grazing ruminants into DST, numerous shortages have been identified in current models designed to predict intake of forages by grazing ruminants. Many of which are mechanistic models that rely heavily on preceding mathematical constructions that were developed to predict energy and nutrient requirements and feed intake of confined animals. The data collection of grazing (forage selection, grazing behavior, pasture growth/regrowth, pasture quality) and animal (nutrient digestion and absorption, volatile fatty acids production and profile, energy requirement) components remains a critical bottleneck for adequate modeling of forage intake by ruminants. An unresolved question that has impeded DST is how to assess the quantity and quality, ideally simultaneously, of pasture forages given that ruminant animals can be selective. The inadequate assessment of quantity and quality has been a hindrance in assessing energy expenditure of grazing animals for physical activities such as walking, grazing, and forage selection of grazing animals. The advancement of sensors might provide some insights that will likely enhance our understanding and assist in determining key variables that control forage intake and animal activity. Sensors might provide additional insights to improve the quantification of individual animal variation as the sensor data are collected on each subject over time. As a group of scientists, however, despite many obstacles in animal and forage science research, we have thrived, and progress has been made. The scientific community may need to change the angle of which the problem has been attacked, and focus more on holistic approaches.

Key words: computer, grazing, mathematical, modeling, predictability, ruminants, simulation

INTRODUCTION

Computer models have been used for the last century to translate experimental agricultural research into quantifiable measurements using rigorous mathematical notations (Black, 2014). Humankind has in many ways benefited from the evolution of digital computers in developing mathematical models to assist with production challenges for agricultural decision support through in silico experimentation (Tedeschi and Fox, 2018). Nonetheless, the collection of data is still needed to calibrate and improve the predictability of mathematical models.

Accurate supplementation of energy or nutrients (e.g., protein) to ruminant animals depend on the accurate determination of the nutritive value (**NV**) of the forage, which is a function of how much nutrients can be extracted from the forage by the ruminant animals. In a nutshell, Figure 1 schematizes the major anatomical, physiological, and metabolic loops that control satiety and hunger. We define feed value as a function of its quality (NV), usually digestible energy or metabolizable energy (**ME**), and quantity (voluntary feed intake [**VFI**]), as shown in the loop B1 in Figure 1. However, these variables interact with many other variables to alter VFI (Pulina et al., 2013; Allen, 2014; Oltjen and Gunter, 2015). Therefore, feed values are based on the VFI (i.e., dry matter intake [**DMI**]) and an assessment of the digestibility of the feed.

To some extent, however, VFI also affects digestibility of the feed via changes in the mean retention time, i.e., the reciprocal of passage rate in which as intake increases the faster the passage rate becomes, as shown in the loop R1 in Figure 1. Energy and nutrient requirements are the major drivers of forage intake (i.e., VFI) and it is determined by the level of production of the animal (e.g., growth rate, days pregnant or milking), as shown in the loop B3 in Figure 1. Similarly, the energy (or other nutrients) balance might also affect VFI via metabolic factors as shown in the loop B2 in Figure 1. The energy balance can provide stimulatory (when negative) or inhibitory (when positive) signal to the ruminant animals to eat to meet their energy requirement unless physical bulkiness of the diet prevents the consumption (Conrad et al., 1964).

The VFI depends on the palatability of the forage (i.e., acceptance or edibility by the ruminant animal) and it depends on forage's physical (i.e., bulkiness) and chemical (e.g., oils and tannins contents) characteristics that may alter animal's appetite. Many indexes have been developed to predict the NV of forages, but few have taken into account the explicit mechanisms that dictate VFI and digestibility of the feedstuff. In general, the following characteristics affect the NV of feeds: potential digestibility and ability to support high rates of fermentation digestion, balance between rates of microbial protein synthesis and volatile fatty acids absorbed by the
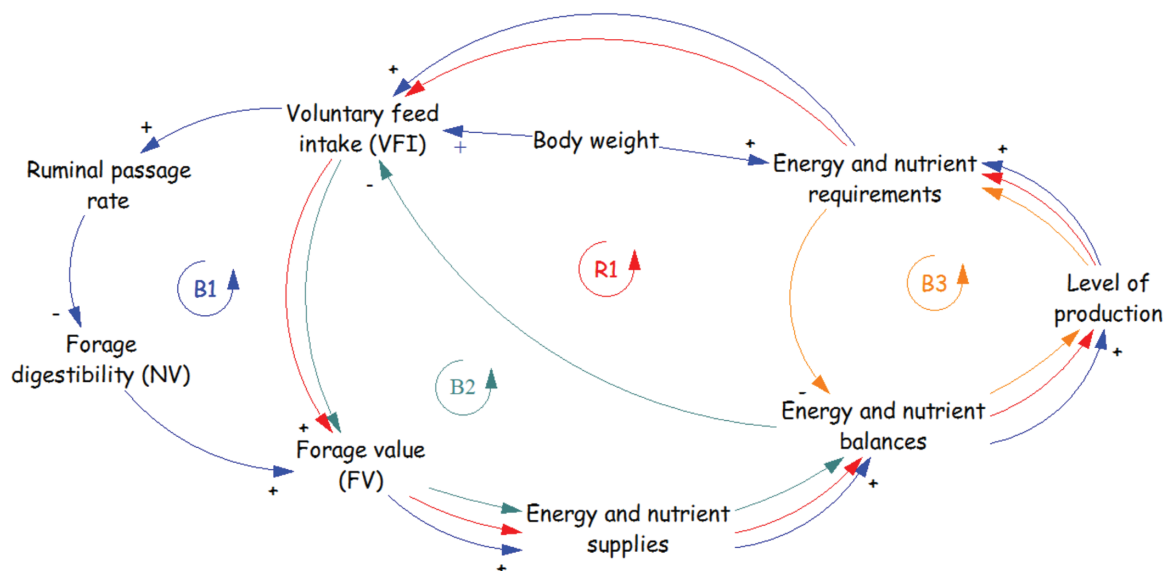

Figure 1. Feedback loops of variables that alter voluntary feed intake. Self-reinforcing (R) and self-correcting (B) loops are shown within the semicircle arrows. Positive and negative signs near the arrowheads indicate that the effect if positively or negatively related to the cause. Different colors represent different feedback loops for ease of identification.

ruminant animal, VFA profile (gluconeogenic versus fat formatting acetate), the bypass of nutrients for intestinal absorption, and VFI per se (Norton, 1994).

Therefore, feed value is not only about quantity and about quality per se, but it also involves other factors that interact among themselves and with the ruminant animal. The NV depends on the concentration of the feed nutrient, availability of the nutrient to the animal (bioavailability), efficiency of use of the absorbed nutrient, and factors that may influence the VFI (Coleman and Henry, 2002). Digestibility trial is usually assumed to be the gold standard to determine NV (Schneider and Flatt, 1975). There are many other methods (in vivo and in vitro) that can be used to determine NV (Coleman et al., 1999), such as bioassays (enzymatic assays), feed chemical and structural characteristics, and near-infrared reflectance spectroscopy. However, these methods are prone to limitations and specificity (e.g., microbial accessibility, fermentation rates, passage rate, postruminal absorption) that prevents a direct comparison, often yielding crude assessments of NV via indirect methods.

The objectives of this paper were to 1) summarize essential concepts needed to comprehend the intricate interface between the ruminant animal and the pasture when predicting animal performance, 2) review current efforts in the mathematical modeling domain of grazing ruminants, and 3) highlight current thinking and technologies that can guide the development of advanced mathematical modeling tools for grazing ruminants.

IMPLICATION OF NUTRITIONAL DIFFERENCES AMONG DOMESTIC RUMINANTS TO ASSESS PASTURE SUPPLEMENTATION REQUIREMENTS

Differences in the Digestive Capacity and Feeding Behavior

The development of models to predict the pasture supplementation requirements for ruminants need to consider the effect of body size of different domestic ruminant species and breeds in terms of digestive capacity and selectivity. Small ruminants are, in general, 10 to 12 times smaller than large domestic ruminants. Body size also changes within species by breeds and sex in which males are approximately 40% bigger than females. As ruminants increase in size, the wet fermentation contents of the gastrointestinal tract increase proportionally to body weight (**BW**) (Demment and Van Soest, 1985). However, as BW increases, there is a lower proportional increase in energy requirement for maintenance, which is usually proportional to $BW^{0.75}$. An index of the fermentative capacity may be estimated by dividing the liquid contents of the gastrointestinal tract by the maintenance energy requirements. In general, this index increases as BW increases, large ruminants have more fermentative volume and contents per unit of energy required for maintenance than small ruminants. This general mechanism is valid across ruminants of different species, breed, and sex. This implies that large ruminants compared to small ruminants can retain larger amounts of feedstuffs in their rumen per unit of requirements or that they can retain feedstuffs with low degradability for longer times. These differences result in the fact that large ruminants have a better general ability to ferment the feeds fractions with low degradation rates, such fiber and insoluble cytoplasmic or fiber linked proteins.

These facts have important practical implications, which should be accounted for when predicting supplementation of grazing animals. Indeed, to compensate for their lower fermentative capacity, small ruminants need to eat more feed per day (as % of BW) than large ruminants to satisfy hunger. For instance, high-producing lactating ewes and goats may have levels of dry matter (**DM**) intake between 6 and 7% of BW, while in high-producing cows this value does not usually exceed 4% of BW. The very high intake of small ruminants leads to shorter rumen feed retention times (Udén et al., 1982) and lower digestibility coefficients of slowly degraded feed fractions but higher daily supply of digested nutrients in small compared to large ruminants (Van Soest, 1994). For equal pasture characteristics, not even considering the effect of diet selectivity, sheep and goats have higher escape of nutrients to the intestine and, thus, would need a different nutrient composition of the supplements used to integrate the pasture eaten.

Another way small ruminants compensate for their lower fermentative capacity is by exercising greater feed selection than cattle (Van Soest, 1994). When allowed they choose feeds or parts of feeds (young stems, leaves, and buds) of good quality and whose digestibility is less affected by rumen retention time. They are helped by their narrow muzzle and by the high mobility of their tongue and lips. Langlands and Sanson (1976) demonstrated the difference in selectivity between small and large ruminants in which sheep fed in the same pasture at the same time of cattle selected a diet much richer in crude protein (**CP**: 24 vs. 18.2%, DM basis), more digestible (70.3 vs. 58.3%), and with a higher percentage of green parts (89 vs. 69.7%). In addition, the rumen liquor of

the cattle contained more acetic acid and proportionally less other volatile fatty acids than the sheep, suggesting that cattle had a fiber-rich diet (not measured in the experiment). However, feed selection cannot be explained only in terms of body size. For example, even though sheep and goats have similar body size, when fed on the same mixed (grassland and shrubs) pasture, they show quite different behavior, with goats preferring shrubs and sheep eating off of herbs (Leclerc, 1985). In addition, when fed on mixed pastures goats preferentially selected grasses and sheep did legumes (Fedele et al., 1993) likely because grasses have a higher content of sugars than legumes and goats have a higher requirement of glucose than of sheep due to their high milk yield and lactose output. This browsing behavior poses another challenge in the prediction of the nutrients actually eaten by these animals on pasture and thus on their supplementation needs.

Small ruminants differ from large ruminants in chewing activity as well. Indeed, small ruminants spend between 9 and 16 times more to eat and ruminate each kilogram of feed DM than large ruminants do (De Boever et al., 1990) because their chewing activity is less powerful. Sheep also have to grind the particles more finely than cattle to allow them to pass through the rumen and other compartments of the foregut (Udén and Van Soest, 1982; Clauss et al., 2015). Intense rumination in small ruminants can also be important when the diet includes grains. Rumination reduces the particle size and increases the rumen digestibility of grains, and because sheep and goats chew grains more finely than cattle the likelihood that whole grains reach the feces undigested is minimum (Cannas, 2004). Thus, the optimal physical form of the supplements for grazing sheep and goats might differ from that optimal for grazing cattle.

Differences in the Optimal NDF Intake and Concentration

The filling effect of the diet, the rumen turnover, and the physical control of DMI are mainly influenced by the rumen content of neutral detergent fiber (NDF) and by its quality, in terms of lignification and fiber degradability (Van Soest, 1994; Cannas et al., 2003; Vieira et al., 2008a, 2008b). Rumen NDF fill and forage NDF intake are closely and positively associated (Paloheimo et al., 1959; Cannas et al., 2003). For this reason, in terms of diet formulation, Mertens (1987) defined maximum concentrations of dietary NDF that would not cause DMI reduction in dairy cows due to diet's filling effect in the rumen and would also maximize milk production. In his seminal work, optimal NDF concentrations of the diet were

obtained considering an optimal daily level of NDF intake (**NDFI**), as a percent of BW (NDFI%BW), of 1.2%. This value was experimentally determined and was considered independent of milk production. The actual value used was 1.1% per day, to include safety margins. This average value can largely vary depending on milk production and the quality of the NDF, being higher for high-quality NDF sources and lower for those less fermentable (Williams et al., 1989; Rayburn and Fox, 1993). It is clear, though, that as milk production increases rumen NDF content and dietary NDFI cannot increase at the same rate. Thus, as milk production increases, a growing portion of the requirements must be covered by energy-rich concentrates. This poses the need to define optimal levels of dietary NDF concentrations. Despite all the limitations of considering a fixed optimal NDFI level, optimal NDF dietary concentrations for dairy cattle of different categories and milk production were developed assuming little variability in optimal daily NDFI (Mertens, 1987). These reference values indirectly set the optimal level of concentrate supplementation in the diet of cattle.

For small ruminants, however, the information on optimal NDFI and NDF dietary concentration is very limited (Cannas, 2004), making the assessment of optimal pasture intake and supplementation very uncertain and difficult. Because small ruminants easily reach during the peak of lactation values of DMI between 6 and 7% of BW, if their optimal average NDFI was equal to the value (1.1% of BW), their dietary concentrations of NDF would be too low (below 20% of DM) to allow a proper rumen function. Indeed, lactating ewes and goats usually have NDFI levels markedly higher than the value of 1.1% suggested for cattle. As an example, Molle et al. (2014, 2016) reported NDFI levels of 2.28% of BW for 42-kg lactating ewes, while Olsen (2016), summarizing the values of six experiments carried out on Nordic lactating ewes, found a value of 1.76% of BW for 92-kg ewes. Similarly, the intake level of NDF during pregnancy in ewes is much higher (around 1% of BW) than that usually observed in cows (around 0.6%) (A. Cannas, personal communication). Cannas et al. (2016) developed an equation to predict optimal NDFI level and dietary NDF concentration for lactating ewes using the equations of Mertens (1987). The 1.1% NDFI level suggested by Mertens (1987) was scaled to the BW of sheep BW assuming that it varied as a function of $BW^{-0.25}$, which is the result of the ratio of energy maintenance requirements, which scales at $BW^{0.75}$, and reticulum-rumen volume, which scales with BW^1 (Van Soest, 1994). This approach is coherent with

the scaling at $BW^{-0.27}$ of feed rumen passage rate reported by Illius and Gordon (1991). As shown in Equation 1, Cannas' et al. (2016) work implies that the NDFI level that would not restrict DMI due to rumen fill decreases exponentially, ranging from 2.10% for 45-kg ewes to 1.77% for 90-kg ewes.

$$NDFI = 5.4442 \times BW^{-0.25} \qquad (1)$$

where BW is body weight, kg; and NDFI is neutral detergent fiber intake, % of BW.

Tedeschi and Fox (2018, Ch. 11) provided graphical representations for DMI (% of BW) versus dietary NDF (% of DM) modulated by physical restriction and metabolism of dairy cows and ewes. Equation 1 assumed the maximum dietary concentrations of NDF to avoid rumen fill restriction on DMI were calculated for sheep of different mature BW and milk production. These values were evaluated by using the 50 individual measurements of ad libitum DMI, diet composition, and milk production of lactating ewes (Molle et al., 2014, 2016). There was a fairly close agreement between predicted and observed dietary NDF concentrations (root of the mean squared prediction error was 5.0% NDF, the concordance correlation coefficient was 0.64, and $r^2 = 0.57$) and a very close agreement between predicted and observed DMI (root of the mean squared prediction error was 0.11 kg/d, concordance correlation coefficient was 0.94, $r^2 = 0.94$). For lactating goats, it is likely that the optimal levels of intake of NDF and dietary NDF concentrations are close to those suggested for sheep. The much higher NDFI in small ruminants compared to cattle has obvious strong implications, so far not considered by existing nutritional models, in the prediction of supplementation requirements of grazing sheep and goats.

ESSENTIAL CONCEPTS TO UNDERSTAND THE INTERFACE BETWEEN RUMINANTS AND PASTURE

Accurate Determination of Forage Consumption

Predicting ruminants feed intake. The literature on feed intake of ruminants is vast as are the ideas and concepts put forward to explain it and simulation models that were developed to predict it (Tedeschi and Fox, 2018, Ch. 10). Many scientists agree that accurate prediction of forage DMI while grazing is critical in formulating and feeding supplements to improve animal performance and to reduce the excess of supplementation that is wasted, leading to nutrients excreted into the environment. This goal, however, is a typical case of easier said than done. In fact, for quite some time, we have known many of the controlling mechanisms of VFI: physical and metabolic factors (Poppi et al., 1989), but the adequate predictability of DMI in practice has not been short of deceiving attempts. Many other theoretical or practical factors that may alter VFI exist; some are partially known whereas others are simply hypothetical. For instance, it is known that variations in daily VFI are more related to the kinetics of fermentation and passage of organic matter from the rumen than shorter-term metabolic events (Illius et al., 2000). Thus, synchronization of fermentable carbohydrate in the rumen and ruminally degradable protein is believed to expedite the disappearance of organic matter from the rumen that should lead to an increased intake by freeing rumen space, but practical results have not been that clear (Herrera-Saldana et al., 1990; Henning et al., 1993; Hall and Huntington, 2008).

Empirical equations (i.e., statistical regression) might provide reliable estimates of DMI when used under similar conditions in which they were developed, such as similar animal and diet types and environmental conditions, because the correlations among independent variables are kept within an acceptable, narrow range that prevents major departures from statistical assumptions. In contrast, when animal, diet, or environmental variables deviate significantly (even temporarily) from the conditions from which empirical equations were developed, their predictive power might be significantly decreased. Grazing scenarios are classical illustrations of these conditions, and in this case, mechanistic modeling might provide better insights on VFI than empirical equations (Illius and Allen, 1994; Illius et al., 2000). Empirical equations tend to be simpler whereas mechanistic models tend to be more complex. Simplicity due to inadequate detail may lead to inadequate prediction whereas the complexity of a mechanistic model can also work against its practicality and accuracy. The complexity threshold of mechanistic models is relative and self-imposed, but clearly, an attempt to model every relationship is futile and may cause modelers to lose sight of the purpose of the model and fail miserably (Tedeschi and Fox, 2018), especially when the objective of the model is already complicated (Illius et al., 2000), and data collection is not straightforward.

Mechanistic models that use a combination of rumen fill (physical) and energy intake (metabolic) factors have been developed (Fisher, 1996; Hackmann and Spain, 2010; Tedeschi et al., 2013), but these models lack the feedback signals of specific dietary elements (micronutrient deficiency and

the presence of plant antinutritional factors also known as plant defensive chemicals [Tedeschi and Fox, 2018]) and endocrinal and physiological stages effects (Coleman et al., 1999) on feed intake. The effect of an antinutritional factor on the intake is, however, complicated and one would expect that grazing animals would minimize their impact by avoiding them. The animal's endocrinal and physiological stages could be accounted for by predicting forage DMI within specific periods. For example, Hackmann and Spain (2010) reported their model had greater adequacy in predicting VFI of different ruminant species than the National Research Council's (NRC, 2000) empirical equation, which was developed for cattle under confinement conditions and at different stages of growth.

The unanswered question still is the reliability of the measurement of forage intake for grazing animals. As stated above, the VFI of grazing and confined animals are controlled by physical and metabolic factors (Detmann et al., 2014) as well as BW, but they may have different relationships with VFI such as linear and quadratic rather than 3/4 power (Coleman et al., 2014). The VFI data of confined animals, however, may not be appropriate to predict VFI of grazing animals (Coleman et al., 2014) mainly because under confinement conditions metabolic signals are most likely to dictate VFI whereas under grazing situations physical distension of the gastrointestinal tract (primarily the rumen) is the first limiting factor of VFI. However, the opposite could occur in high-quality pasture conditions. Additionally, physical activities of walking, grazing, and forage selection are practically inexistent under confinement conditions. Wiley et al. (2016) reported the results of a comparative analysis of residual feed intake obtained for animals during confinement and grazing conditions yielded a poor ranking correlation between residual feed intake, suggesting that animals may have different priorities for VFI depending on their accessibility to feedstuffs. Therefore, using predictive equations obtained with VFI data from confined animals is likely to bias the prediction of VFI of grazing animals.

Measuring ruminants feed intake. Besides classical studies using markers to determine digestibility and feed intake of grazing animals (Mayes et al., 1986), others have relied on the detection of animal feeding behavior to assess intake through biting and chewing. Typical sensing devices for grazing animals include silicon tubes containing carbon granules (Rutter et al., 1997), acoustic monitoring systems (Ungar and Rutter, 2006), and di- or tri-axial accelerometers (Scheibe and Gromann, 2006; Oudshoorn et al., 2013) among few others. More recently, Greenwood et al. (2017) used on-animal sensor devices (accelerometers) to determine forage intake of grazing animals through grazing behaviors (time spent grazing, ruminating, walking, and resting). Though their initial assessment yielded low precision in predicting forage intake, the authors discussed several options to refine the predictions that may lead to improved modeling development. Similarly, Deniz et al. (2017) used acoustic monitoring devices to detect, classify, and quantify events of ruminant's feeding behavior (chew, bite, and chew-bite) and Rombach et al. (2018) combined pressure sensor with an accelerometer to detect a different behavioral characteristic of grazing dairy cows. These techniques are promising ways to model feeding behavior, and when associated with markers they might generate reliable data to predict forage intake more accurately.

Assessment of the Quantity and Quality of Pasture Herbage

Forage quality, either through its fiber content or noncell wall content, affect consumption potential (Welch and Smith, 1969). The question is how to assess the quantity and quality, ideally simultaneously, of pasture forages given that ruminant animals can be selective, i.e., select forage parts that have greater NV than the average available forage mass (Coleman and Barth, 1973). Classical methods to assess the quantity of forage mass include 1) protecting selected pasture areas with cages to avoid animal grazing and subsequent measurement of forage growth, or 2) clipping forage parts that mimic animal selectivity while grazing (Van Soest, 1994). Similarly, classical methods to assess the quality (i.e., usually digestibility) of consumed forage mass include 1) cannulate grazing animals with esophageal or rumen fistulas to collect the forage mass harvested by the animal, 2) internal (e.g., acid-insoluble ash and silica, indigestible neutral or acid detergent fibers, chromogens, waxes—alkanes) or external (stains, metal oxides, rare earths, isotopes) markers, 3) ruminal fermentation techniques (e.g., in vitro, in situ, and in sacco), or 4) enzymatic cellulases and hemicellulases procedures (Van Soest, 1994).

In the middle of the 1980s and later, other techniques were proposed for determining forage quality and quantity, including near-infrared reflectance spectroscopy (Brooks et al., 1984), light detection

and ranging (Bork and Su, 2007; Schaefer and Lamb, 2016), and satellite imagery (Milton et al., 2009; Phillips et al., 2009). Although these techniques might provide a satisfactory assessment of the quality and quantity of forage herbage mass, their practical application is currently limited due to cost, availability, and specialized labor need. Modeling and simulation decision-support tools (**DST**) might come to rescue the field of assessment of forage herbage mass quality and quantity through models that simulate plant growth under diverse ecosystems (Thornley, 1998).

Physical Activity and Grazing

The accurate assessment of energy expenditure of grazing animals for physical activities such as walking, grazing, and forage selection is a major hindrance in predicting energy requirements for grazing animals. Despite many methods available to measure energy expenditure of grazing animals such as the portable mask technique and headstall trough, double labeled water technique, carbon dioxide entry rate technique, their results vary considerably and can hardly be compared (Tedeschi and Fox, 2015). Walking is the main physical activity that requires significant amounts of energy, approx. 10.6 Kcal/$kg^{0.75}$ BW/d for standing, 21.1 Kcal/$kg^{0.75}$ BW/d for walking idle, and 23 Kcal/$kg^{0.75}$ BW/d or about 0.68 Kcal/$kg^{0.75}$ BW/km for grazing (Brosh et al., 2010). But, estimates vary widely from 0.34 to 4.45 Kcal/$kg^{0.75}$ BW/km (Tedeschi and Fox, 2015, 2018).

In developing a submodel to estimate grazing energy requirement, Tedeschi and Fox (2015) combined the recommendations of the NRC (2000), National Academies of Sciences, Engineering, and Medicine (NASEM, 2016), and Fox et al. (2004), and partitioned the energy expenditure as per the NRC (1981) in which heat production is the sum of heat for basal metabolism (H_eE), muscular activity (H_jE) required for standing, walking, grazing, drinking, and laying down; action of digestive enzymes (H_dE), fermentation as a result of ruminal microbial action (H_fE), heat associated with the metabolic processes of product formation from absorbed metabolites (H_rE), thermal regulation (H_cE), and waste formation and excretion (H_wE). Heat increment (H_iE) is the sum of H_fE, H_dE, H_rE, and H_wE. The authors further subdivided heat for muscular activities into animal physical activity (i.e., locomotion or movement) (H_jE_{pa}), and eating and ruminating (i.e., chewing) the digesta (H_jE_{er}). Assuming published energy expenditure data for chewing (Susenbeth et al., 1997, 1998) and

that feed for maintenance can be computed as the ratio between net energy required for maintenance (Mcal/d) and dietary net energy available for maintenance (Mcal/kg), Tedeschi and Fox (2015) derived Equation 2 to compute energy expenditure for eating and ruminating as a function of ME intake.

$$H_jE_{er} = \left(4.2557 \times ME_{mr}^{-0.95878}\right)$$
$$\times \frac{\left(H_eE + H_jE_{pa}\right)}{\left(NE_{ma} - 4.2557 \times ME_{mr}^{-0.95878}\right)} \quad (2)$$

where H_eE is energy expenditure for basal metabolism, Mcal/d; H_jE_{er} is energy expenditure for eating and ruminating (i.e., chewing) the digesta, Mcal/d; H_jE_{pa} is energy expenditure for physical activities, Mcal/d; ME_{mr} is ME required for maintenance, Mcal/d; and NE_{ma} is net energy available for maintenance, Mcal/d.

Unfortunately, Equation 2 can only be solved iteratively by changing ME_{mr} until ME_{mr} is equal to the sum of H_eE, H_jE_{pa}, and H_jE_{er} divided by the partial efficiency of use of ME to net energy for maintenance (Tedeschi and Fox, 2015). Based on their simulation of typical grazing conditions, animals grazing forages containing 1.5 to 1.9 Mcal/kg DM would not meet their energy need, and would lose body condition score. Further development and evaluations of such models are important in establishing the trust needed to incorporate iterative, loop-solving, models into DST for practical use.

Substitution and Associative Effects of Supplements

When a supplement is included into the diet of a ruminant fed pasture only, the total intake of DM can vary unexpectedly. This phenomenon constitutes the substitution effect, measured as substitution rate (**SR**), i.e., the ratio of the difference between herbage intake in the unsupplemented and supplemented animals to the intake of the supplement itself (Equation 3). The SR ranges between −1 and 1, and it is commonly positive, i.e., supplement intake is usually associated with a reduction of herbage intake.

$$SR = \frac{\begin{array}{c}(\textit{Forage intake when unsupplemented}) - \\ (\textit{Forage intake when supplemented})\end{array}}{\textit{Supplement intake}} \quad (3)$$

In dairy cattle, several studies have been deployed to evaluate and possibly model the substitution effect of supplements (Stockdale, 2000;

Bargo et al., 2003; Baudracco et al., 2010; Hills et al., 2015). Though most of the studies refer to perennial type pastures based on perennial ryegrass (*Lolium perenne* L.), their results support the hypothesis that SR is mainly affected by the ruminant's energy balance, being higher under conditions where the energy balance is positive. This means that SR tends to increase (i.e., decreasing herbage intake) when herbage allowance (kg DM/d) and herbage quality (i.e., ME content) are high, requirements for milk production are low, supplementation level is high, and supplements are based on starchy concentrates (e.g., cereal grain-based concentrates). The effect of the starch level is explained by the increase of rumen concentration of propionic acid, whose uptake and metabolism favors a satiation effect (Farningham and Whyte, 1993). Moreover, SR is often higher in conserved forages than concentrates due to the fill effect of the former supplements. According to Bargo et al. (2003), SR ranges as follows: 0.1 to 0.6 for concentrates, 0.4 to 1.0 for silages, and 0.3 to 2.4 for hay in cows grazing perennial pastures in different lactation stages.

Research on beef cattle, basically confirms the results in dairy cattle with a trend to positive SR with high level of supplementation (>0.7% BW) and high-quality pasture (with adequate N) and negative SR with low quality (low N) pasture but without clear differences among different types of concentrates (Moore et al., 1999). In an experiment carried out to quantify the relationship between grass supply and concentrate supplementation in steers, French et al. (2001) found an SR of 0.43 and 0.81 at medium- and high-grass allowance, respectively. Data on SR for dairy sheep follow those of cattle (Molle and Landau, 2002; Molle et al., 2008).

Recent research has shown that managerial factors may impinge on SR as well, including the number of supplementary daily meals and the supplementation timing. Pulido et al. (2009) found that SR increased with the number of daily concentrate meals: 0.65 for two, 0.76 for three, and 0.95 for four concentrate meals. Results are less clear for concentrate meal timings. In general, if the concentrate meal is close to pasture allocation, for dairy cows, herbage intake is depressed even further when the supplement is fed in the morning rather than in the afternoon (Sheahan et al., 2013). Supplementing dairy cows with 3 kg DM/d of corn silage in the morning resulted in lower SR (0.19) than in the afternoon (0.47), i.e., closer to pasture allocation (15:30 to 20:30) (Al-Marashdeh et al., 2016).

Substitution effect often goes hand in hand with the so-called "associative effect" of the supplement (Doyle et al., 2005). This is the decrease in fiber digestibility associated with the use of starchy-based supplements (cereal grains, in particular). According to Ho et al. (2013), the decline in the NDF digestibility is quadratically related with the intake of grain, with a slight linear decrease (0 to 5% less than the NDF digestibility of unsupplemented diet) up to 5 kg/d of grain supplementation. Therefore, when starch supplementation is at low to moderate level, and the diet's effective fiber not limiting, the lower digestibility of fiber does not necessarily result in a lower diet digestibility, and associative effect and SR are minimum. This explains the better milk response when the level of supplementation of starchy concentrate is low to moderate, as reported for dairy cows (Bargo et al., 2003) and dairy ewes (Molle et al., 2008), who highlighted a higher milk response in grazing ewes fed high levels of digestible fiber-based rather than starchy-based concentrates. This fact was also confirmed in stall-fed mid-lactation ewes (Cannas et al., 2013). A recent direct comparison of mid-lactation ewes and goats fed high digestible-fiber diets or high starch diets showed that the milk response might differ among species, being higher with high starch diets in goats and with high digestible-fiber diets in sheep, mainly for the different sensitivity of the two species to the insulinemic effect of starchy diets (Lunesu, 2017). Partial mixed ration has been reported to reduce associative effects of concentrate in ruminants, with a higher synchronization of nutrient intake and digestion and a better estimated economic return than the traditional combination of pasture, hay, and concentrate (Ho et al., 2013).

In general, substitution and associative effects have a synergistic negative impact on milk and meat production responses at the individual level. However, considering the grazing system rather than the individual animal, the substitution of high-quality forages with concentrates during the period of pasture shortage can be regarded as a tool for allowing 1) a delayed herbage consumption, adopting the stockpiling grazing technique; or 2) an increase of stocking rate in order to efficiently utilize the pasture saved due the substitution effect. The above consideration further emphasizes the need for accurately predicting supplementation level and its optimal composition, possibly taking into consideration both substitution and associative effects.

CURRENT NUTRITION MODELS TO PREDICT INTAKE OF GRAZING ANIMALS

Mathematical Modeling

Models, in general, are more than just an agglomeration of empirical equations obtained through statistical regressions. They are composed of concepts and input variables that are linked by meticulously validated calculation logic to yield estimates of variables of interest (Tedeschi and Fox, 2018). Some model parameters can be obtained through empirical equations (or combinations of thereof), but how they are linked (i.e., calculation logic) is what constitutes the *brain* of the mathematical model. How the calculation logic and model variables interact among themselves, dictates the nature of the mathematical model. The most common types are descriptive or predictive, empirical or mechanistic, deterministic or stochastic, static or dynamic, discrete or continuous (France and Thornley, 1984; Haefner, 2005; Tedeschi and Fox, 2018). Forbes and Gregorini (2015) have suggested the use of catastrophe theory, which deals with situations where an outcome is discontinuous (e.g., eating vs. not eating) but control variables of intake are continuous (e.g., physiological and environmental factors), to model and predict feeding behavior of grazing animals. Other types of models that have not been frequently used in ruminant nutrition, but might warrant some investigation in the future, include chaos theory (Raccoon, 1995) and fuzzy logic (Wirsam and Uthus, 1996).

Empirical Models: Nutritive Indices

Simpler predictive systems in the form of indices have been proposed to assess the NV of forages. In general, such indices are purely empirical and have limited range of applicability and acceptability; thus, they rarely can be used outside of the boundaries (i.e., spatial region, forage species, animal species) they were developed or even evaluated. These limitations might partially explain the lack of broader utilization of nutritive indices despite the disappointment of some (Moore, 1994), who provided a comprehensive review of nutritive indices. The majority of nutritive indices provide a comparative assessment of forage quality related to a "standard" condition. Examples of nutritive indices include the NV index (Crampton et al., 1960), digestible energy intake (Heaney et al., 1966), relative feed value (Rohweder et al., 1978), quality index (Moore, 1978), fill and feed units (Jarrige

et al., 1986), and relative forage quality (Moore and Undersander, 2002). The nutritive indices have useful but limited applications, and it is unlikely that an ideal numerical index for forage NV will be developed. The main reasons lie with the simplicity by design of a nutritive index and the lack of representability of the diversity of forages that are outside of the index development boundaries.

Mechanistic Models: Integrated Systems

Table 1 shows a list of selected mechanistic nutrition models primarily aimed at the prediction of intake and performance of grazing ruminants. Most of them were published in the last decade and their base comes from previous modeling exercises such as the mechanistic model for dairy cattle fed at nonsteady conditions (Chilibroste et al., 2008), the grazing model that was focused on unsupplemented dairy cows (Brereton et al., 2005), or the partially dynamic mechanistic model that was aimed at predicting foraging behavior and intake of unsupplemented grazing sheep (Baumont et al., 2004).

The model *GrazeSim* is a simple model based on a cluster of algorithms that include equations to estimate animal requirements and nutrient supply from pasture and supplements; all expressed as energy densities. Fill intake capacity is estimated according to Mertens (1987). A coefficient is used to account for herbage intake restriction due to low herbage mass. The model has been shown to be relatively inaccurate (22% of the coefficient of variation), but this occurs particularly at high pasture allowance conditions. A new algorithm has been developed to account for this discrepancy, decreasing the coefficient of variation to 12% (Vazquez and Smith, 2001). Similarly, the model *Diet Check* (Heard et al., 2004) is comprised of two submodels (animal requirements and nutrient supply) that accounts for the substitution effect of concentrates, the energy cost of grazing activity, and weather condition effects on energy expenditures (cold stress), all overlooked by GrazeSim, but the Diet Check currently limited to localized usage in to the Northern irrigated region of Victoria, Australia.

The model *e-Cow* (Baudracco et al., 2012) includes three submodels: 1) intake prediction based on the animal (fill and metabolic) and pasture factors (herbage allowance), 2) milk production (dynamic aspect), and 3) body lipid (dynamic aspect). It was sensitive to the interaction between genotype and feeding level with a low relative prediction error (**RPE**) in an independent validation for DMI (<10%) and a moderate RPE for milk yield

Table 1. A short list of extant mathematical models to estimate intake and performance of dairy cattle under grazing conditions[1]

Name and reference	Model type	Inputs	Outputs	Evaluation (herbage intake)
GrazeSim (Vazquez and Smith, 2001)	Mechanistic: Time scale: day	Animal data inclusive of requirements; diet characteristics; and pasture characteristics	Pasture intake estimated using different algorithms accounting or not for the supplementation type and pasture selectivity	R^2 of actual vs. estimated values ranging between 0.24 and 0.50 with an average proportional bias between 2 and 23%.
Diet Check (Heard et al., 2004)	Mechanistic: Time scale: day	Animal data inclusive of requirements; diet and pasture characteristics	Pasture mass; and Pasture intake	R^2 of actual vs. estimated values = 0.87 in unsupplemented cows, and = 0.48 in supplemented cows.
e-Cow (Baudracco et al., 2012)	Mechanistic: partially dynamic time scale: day-	Animal data; diet characteristics; pasture data: HM, area per cow	Potential milk yield, potential yield of milk solids; herbage intake. Some model values can be customized	Mean prediction error of HDMI: 9.1% to 9.8% in comparison between cattle genotypes
GrazeIn (Delagarde et al., 2011a, 2011b; Faverdin et al., 2011)	Mechanistic: partially dynamic time scale: day	Animal data; diet characteristics; pasture characteristics: HM, area per cow, SSH, time at pasture	Potential milk yield, actual milk yield, and herbage DMI	Mean prediction error for HDMI: 16% for individual cows at experimental scale
Mindy (Gregorini et al., 2013)	Mechanistic: dynamic – time scale: minute-year	Data on location (to evaluate actual photoperiod). Animal data. Diet characteristics. Pasture characteristics.	Herbage intake; grazing time; searching time; meals; rumination time; distance walked; milk yield; urinary excretion; water ingested or imbibed; drinks/day	Mean prediction error of 36% for the model parametrization with 79% of random proportion. Subsequent evaluation showed a mean prediction error for HDMI equal to 4% on a per year basis
DairyMod (Johnson et al., 2016)	Mechanistic: Time scale: day	Animal data; diet characteristics; pasture characteristics: HM	Potential and actual intake (herbage, supplements, total), body weight (water, protein and fat), milk yield	Concordance correlation coefficient of 0.91 for pasture intake

[1]BCS = body condition score; DMI = dry matter intake; HDMI = herbage DMI; HM = herbage mass; NDF = neutral detergent fiber; SSH = sward surface height.

(15% to 18%). However, it has some known shortcomings, as follows: 1) only two pasture types are modeled, 2) it does not account for dietary protein nutrition and its effects on intake and performance, 3) it is not accurate for high supplementation levels, and 4) it does not incorporate the effects of weather and photoperiod.

The *GrazeIn* model (Delagarde et al., 2011a, 2011b; Faverdin et al., 2011) also entails three submodels: 1) potential milk yield (dynamic aspect), 2) VFI (based on fill value system) and nutrient partitioning, and 3) grazing non-nutritional factors affecting VFI. It has a good sensitivity concerning different variates such as BW, herbage mass, fill value of the forage, and supplementation level. The RPE in herbage DMI prediction varies from 15% to 16% (Delagarde et al., 2011b; O'Neill et al., 2013). O'Neill et al. (2014) adapted the model by increasing the intake capacity, resulting in lower RPE, particularly in mid and late lactations. The model is not sensitive enough with heavy pasture constraints such as low allowances and pasture in the reproductive phase.

Mindy is a deterministic, mechanistic, dynamic model (Gregorini et al., 2013) whose aim is to simulate diurnal grazing patterns and widen the spectrum of prediction responses by dairy cattle predominantly fed on pasture (feeding behavior, walked distance, urine excretion, intake, milk production, and BW changes). Mindy is a cluster of submodels, including 1) a modified *Molly* dairy cow digestion and metabolism model (Baldwin, 1995), 2) feeding motivation model, 3) sward canopy structure and herbage quality model, 4) feeding behavior model, and 5) foraging bioenergetics model. Because of its dynamic structure, model responses can be predicted every minute. Herbage DMI has been shown to be sensitive to changes in grazing techniques, supplementation levels, and genotypes but the RPE can be occasionally high, although consisting mainly of random components. Mindy has been subjected to an intense development since its first publication, and lately, it has incorporated another component aimed at predicting dietary preference and selection in grazing ruminants (Gregorini et al., 2015a). This model is based on the minimum total discomfort theory (Forbes, 2007) that is based on the neuro-endocrine intake control system (Ginane et al., 2015). The theory of discomfort affecting VFI has also been used in developing a dynamic model for fluxes of body reserves (Tedeschi et al., 2013). Based on these premises, a grazing ruminant having access to different feeds would prioritize (i.e., show an immediate preference for) the one richest in the

dietary component (energy, protein, or fiber) exhibiting the highest deficit in the diet at that moment (i.e., the component whose shortage cause the maximum instantaneous discomfort). Preference will be then adjusted by a coefficient (modulator), which accounts for the availability/accessibility of the preferred feed. Mindy has been challenged in several in silico tests, using different scenarios where the dietary background was imbalanced regarding energy-to-protein ratio followed by fasting or preload (breakfast) of a specific feed (Gregorini et al., 2015b). Overall, response patterns were in line with dynamics reported under experimental conditions. It is, however, noteworthy that Mindy uses only two feeds, typically a forage and a supplement or two forages. Under these conditions, the modeled pattern of preference in ruminant having free access to grass and legumes pastures soundly parallels that found during the daytime, with a preference for the legume in the morning and the grass in the evening (Rutter, 2006). Mindy has also been recently used to estimate the diurnal pattern of drinking and urination by grazing cattle, which is of great importance for predicting the environmental impact of different grazing and housing management strategies (Gregorini et al., 2018).

The model *Suckler Cow Pastoral System* (Jouven et al., 2006a, 2006b, 2008) is among the most advanced model devoted to beef cattle. This model is based on three modules: 1) pasture module that can be skipped allowing direct data entry, 2) intake module (based on the Institut National de la Recherche Agronomique's fill unit system), and 3) performance module. This model is partially dynamic and takes into account ruminant selectivity. Authors reported a good sensitivity to forage digestibility and stocking rate, with acceptable prediction errors, concerning intake and diet digestibility.

Literature is poor concerning mechanistic models to predict herbage intake and performance of cattle grazing tropical pastures. The model *Tropical Pasture Simulator* (Herrero et al., 2000a, 2000b) and the intake prediction model developed by Boval et al. (2014) are valuable DST that provide useful insights regarding grazing management of cattle allocated to *Pennisetum clandestinum*, (Herrero et al., 2000a, 2000b) or *Dichanthium* spp. (Boval et al., 2014). In both models, pasture submodels consider herbage growth under grazing, but unfortunately, Boval's (2014) model overlooks the effect of supplementation and its SR effects. There is also a lack of mechanistic and mechanistic-dynamic models encompassing both pasture and animal phases concerning dairy sheep or goat grazing Mediterranean forages (Pulina et al., 2013).

Mechanistic, but static models have been used to develop DST that allow users the rationing of ruminant fed on pasture. These applications mainly refer to dairy and beef cows, grazing temperate grassland. The Australian model *GrazFeed* (Freer et al., 1997), for instance, is an exception because it encompasses the nutrition of different species (cattle and meat sheep) grazing temperate, Mediterranean and tropical pastures but not bushland. The French's *Pasture Simulation* (Graux et al., 2011), the Irish's *Moorepark Dairy system* (Shalloo et al., 2004) and *PastureBase* (Hanrahan et al., 2017), the Australian's *Moosim* (Bryant et al., 2008), and the New Zealand's *IDEA* (Doole et al., 2013) models are mainly focused on the production system functioning rather than on animals responses. They are valuable in predicting the dynamics of key variables such as pasture growth, greenhouse gas emissions or farm economic returns, but their description and evaluation stretch beyond the scope of this review.

Unfortunately, many DST addresses the need for local production systems in which they were originally developed to predict herbage DMI; thus, although useful, they can be relatively inaccurate. They tend to overlook several aspects that can impinge on the VFI of grazing ruminants such as diet selectivity, weather conditions, actual photoperiod, and time allocation to pasture. Some of them, such as GrazFeed, however, account for selectivity and SR, but the algorithms used have been evaluated only partially (Pittroff and Kothmann, 2001a, 2001b, 2001c). Improvement of current DST, such as incorporation of new algorithms, should be guided by explicit goals that provide a relevant standard to evaluate accuracy and precision.

FUTURE PERSPECTIVES FOR DEVELOPING HOLISTIC AND PREDICTIVE MODELS FOR GRAZING ANIMALS

Although mechanistic, dynamic models are still mainly used for exploratory research analyses, they have great scope to become core components of precision livestock farming applications, e.g., those aimed at monitoring and driving the supply of concentrates (e.g., automatic feeding systems). However, due to their low time-scale unit (min), a proper equally-scaled evaluation of these models using independent data is very difficult, if not impossible. It will be possible in the near future, under experimental conditions, if accurate and precise smart technologies can gather reference data

at the same time-scale unit of these models. This further emphasizes the value of the link between modeling and technologies to strengthen and further precision livestock farming applications.

A reasonable number of agricultural computer models (i.e., DST) exists, but because of the lack of a combination of models from different fields (animal, soil, crop, forages, and weather sciences), many believe that agricultural models are poorly coupled and difficult to integrate (Janssen et al., 2017). The integration of forage growth models with weather patterns and animal requirement models are needed for long-term prediction of production policies (Oltjen and Gunter, 2015). Many computer models for crop and pasture growth exist (Bryant and Snow, 2008), but an additional challenge is imposed to them with the inclusion of ruminant animals because they represent an additional trophic level, adding a considerable complexity of nutrients flow across the compartments (Snow et al., 2014). Besides the synchronization and flow of nutrients, the grazing and consumption of forage (e.g., grasses and legumes) by ruminant animals has been the single most constraining nutrition models to accurately predict DMI of grazing animals (Oltjen and Gunter, 2015). A model developed by Fust and Schlecht (2018) can predict forage availability and animal feed requirement for semi-arid, drought-prone regions and to simulate different management strategies and clime conditions on environmental degradation with and without ruminants. Then the question becomes, are they valid for other grassland ecosystems on the planet?

Undisturbed grasslands are ideal examples of sustainable grazing systems that support large and diverse herbivore and plant species without intensive management or resource allocation, but they are rapidly diminishing (Muir et al., 2011; Carbutt et al., 2017). Conversely, current pasture grazing systems rely on large amounts of inputs (fertilizer, seed, and pesticide) and emphasize monoculture grass and single herbivore management operations that are unsustainable, considering current and future demands for food (Muir et al., 2011; Tedeschi et al., 2015). Sustainable pasture intensification prevents the environment from being debilitated and produces more with fewer resources in a profitable, yet socially, economically, and environmentally responsible manner (Muir et al., 2011; Tedeschi et al., 2015). Implementation of innovative and heuristic approaches that utilize synergies between diverse grasses, legumes, and multiple herbivore species provide alternatives for high-input pasture systems to help overcome existing short and long-term production challenges, such as economic feasibility and resource limitations (Nicholson et al., 2001; Muir et al., 2011). However, pasture sustainability efforts have many barriers, complexity of diverse plant and animal communities and stakeholder adoption/management, which may be overcome with modeling (e.g., Sustainable Grazing Systems Pasture Model [Johnson et al., 2003]) coupled with improved technology and smart farms (Muir et al., 2014, 2017; Tedeschi et al., 2017b).

Advances in multiple technologies for improved agricultural production have led to the advent of smart farming (González et al., 2018). Smart farming harnesses sensor (e.g., livestock GPS) and communication (e.g., Wi-Fi) technologies to increase production efficiency and profitability of agricultural operations (O'Grady and O'Hare, 2017). Modeling, through DST, has been used to process and interpret large data from multiple agricultural technologies, in near-real time, to overcome environmental, technical, and economic production challenges (Le Gal et al., 2011). As discussed above, currently, a major obstacle is leveraging smart farm technology and DST to more effectively evaluate the complex interaction of livestock's physical activity and pasture composition and quantity. For example, dairy farmers rely on the accurate assessment of pasture biomass and quality to optimize productivity and manage supplemental feeding, especially when pasture is the primary feed source to meet cattle nutrient requirements (Shalloo et al., 2018). Livestock activity such as trampling, manure deposition, and grazing pressure impacts pasture quality and quantity. Bishop-Hurley et al. (2014) monitored cow feeding behavior on pasture (grazing, searching, walking, ruminating, resting, and head down) using motion sensors, accelerometer, GPS collar, and magnetometer. The authors concluded that behavior monitoring techniques might be a solution for enhancing farming systems, pasture quality and quantity, and supplemental feeding to optimize milk production and profitability. Smart farms and advancing technology combined with modeling have the potential to identify high leverage solutions (i.e., small change produces big results) that could have otherwise gone unnoticed, such as individual supplementation of dairy cattle (Bishop-Hurley et al., 2014; Milovanović, 2014). Therefore, the use of smart farms and modeling (or DST), and innovative pasture systems (e.g., multiple herbivore species and diverse plant species) is likely the next step toward improving the sustainability of livestock and pasture systems (González et al., 2018; Tedeschi et al., 2017a, 2017b).

CONCLUSIONS

The data collection on the grazing side (forage selection, grazing patterns, pasture growth/re-growth, pasture quality) as well as on the animal side (nutrient digestion and absorption, volatile fatty acids production and profile, energy requirement) remains a critical bottleneck for adequate modeling of forage intake by ruminants. The advancement of sensors might provide some insights that will likely enhance our understanding and assist in determining key variables that control forage intake. Because sensors are assigned to individual animals, they might provide additional insights on the variation associated with individual animals; thus, creating another level of sophistication for model development that can improve the predictability for each animal. The scientific knowledge of factors that affect intake of ruminants is broad and rich, and DST for modeling energy expenditure and feed intake of grazing animals abound in the literature, but the adequate predictability of forage intake is still lacking, and it has been deceiving at times. As a group of scientists, despite many obstacles in animal and forage science research, including the shortage of funding (Rouquette et al., 2009), we have thrived, and progress has been made. The scientific community may need to change the angle of which the problem has been attacked, and focus more on holistic approaches.

LITERATURE CITED

Allen, M. S. 2014. Drives and limits to feed intake in ruminants. Anim. Prod. Sci. 54:1513–1524. doi:10.1071/AN14478

Al-Marashdeh, O., P. Gregorini, and G. R. Edwards. 2016. Effect of time of maize silage supplementation on herbage intake, milk production, and nitrogen excretion of grazing dairy cows. J. Dairy Sci. 99:7123–7132. doi:10.3168/jds.2015-10681

Baldwin, R. L. 1995. Modeling ruminant digestion and metabolism. New York (NY): Chapman & Hall.

Bargo, F., L. D. Muller, E. S. Kolver, and J. E. Delahoy. 2003. Invited review: production and digestion of supplemented dairy cows on pasture. J. Dairy Sci. 86:1–42. doi:10.3168/jds.S0022-0302(03)73581–4

Baudracco, J., N. Lopez-Villalobos, C. W. Holmes, E. A. Comeron, K. A. Macdonald, T. N. Barry, and N. C. Friggens. 2012. E-cow: an animal model that predicts herbage intake, milk yield and live weight change in dairy cows grazing temperate pastures, with and without supplementary feeding. Animal 6:980–993. doi:10.1017/S1751731111002370

Baudracco, J., N. Lopez-Villalobos, C. W. Holmes, and K. A. Macdonald. 2010. Effects of stocking rate, supplementation, genotype and their interactions on grazing dairy systems: a review. N. Z. J. Agric. Res. 53:109–133. doi:10.1080/00288231003777665

Baumont, R., D. Cohen-Salmon, S. Prache, and D. Sauvant. 2004. A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. Anim. Feed Sci. Technol. 112:5–28. doi:10.1016/j.anifeedsci.2003.10.005

Bishop-Hurley, G., D. Henry, D. Smith, R. Dutta, J. Hills, R. Rawnsley, A. Hellicar, A. Timms, A. Morshed, A. Rahman, et al. 2014. An investigation of cow feeding behavior using motion sensors. In: 2014 IEEE International Instrumentation and Measurement Technology Conference (I2MTC) Proceedings. Montevideo, Uruguay. p. 1285–1290. doi:10.1109/I2MTC.2014.6860952

Black, J. L. 2014. Brief history and future of animal simulation models for science and application. Anim. Prod. Sci. 54:1883–1895. doi:10.1071/AN14650

Bork, E. W., and J. G. Su. 2007. Integrating LIDAR data and multispectral imagery for enhanced classification of rangeland vegetation: a meta analysis. Remote Sens. Environ. 111:11–24. doi:10.1016/j.rse.2007.03.011

Boval, M., O. Coppry, and D. Sauvant. 2014. Mechanistic model of intake of tropical pasture, depending on the growth and morphology of forage at a vegetative stage. Anim. Prod. Sci. 54:2097–2104. doi:10.1071/AN14542

Brereton, A. J., N. M. Holden, D. A. McGilloway, and O. T. Carton. 2005. A model describing the utilization of herbage by cattle in a rotational grazing system. Grass Forage Sci. 60:367–384. doi:10.1111/j.1365-2494.2005.00485.x

Brooks, J., III, M. Anderson, and P. J. Urness. 1984. Infrared reflectance analysis of forage quality for elk. J. Wildl. Manage. 48:254–258. doi:10.2307/3808483

Brosh, A., Z. Henkin, E. D. Ungar, A. Dolev, A. Shabtay, A. Orlov, Y. Yehuda, and Y. Aharoni. 2010. Energy cost of activities and locomotion of grazing cows: a repeated study in larger plots. J. Anim. Sci. 88:315–323. doi:10.2527/jas.2009-2108

Bryant, J., N. Lopez-Villalobos, C. Holmes, J. Pryce, J. Rossi, and K. Macdonald. 2008. Development and evaluation of a pastoral simulation model that predicts dairy cattle performance based on animal genotype and environmental sensitivity information. Agric. Syst. 97:13–25. doi:10.1016/j.agsy.2007.10.007

Bryant, J. R., and V. O. Snow. 2008. Modelling pastoral farm agro-ecosystems: a review. N. Z. J. Agric. Res. 51:349–363. doi:10.1080/00288230809510466

Cannas, A. 2004. Feeding of lactating ewes. In: G. Pulina and R. Bencini, editors, Dairy sheep nutrition. Cambridge (MA): CABI Publishing; p. 79–108.

Cannas, A., A. Cabiddu, G. Bomboi, S. Ligios, B. Floris, and G. Molle. 2013. Decreasing dietary NFC concentration during mid-lactation of dairy ewes: does it result in higher milk production? Small Ruminant Res. 111:41–49. doi:10.1016/j.smallrumres.2012.09.009

Cannas, A., L. O. Tedeschi, G. Molle, A. S. Atzori, C. Dimauro, and M. F. Lunesu. 2016. Prediction of optimal NDF intake in sheep. Can. J. Anim. Sci. 96:628–629.

Cannas, A., P. J. Van Soest, and A. N. Pell. 2003. Use of animal and dietary information to predict rumen turnover. Anim. Feed Sci. Technol. 106:95–117. doi:10.1016/S0377-8401(02)00255-9

Carbutt, C., W. D. Henwood, and L. A. Gilfedder. 2017. Global plight of native temperate grasslands: going, going, gone? Biodiversity and Conservation. 26:2911–2932. doi:10.1007/s10531-017-1398-5

Chilibroste, P., J. Dijkstra, P. H. Robinson, and S. Tamminga. 2008. A simulation model "CTR Dairy" to predict the supply of nutrients in dairy cows managed under discontinuous feeding patterns. Anim. Feed Sci. Technol. 143:148–173. doi:10.1016/j.anifeedsci.2007.05.009

Clauss, M., P. Steuer, K. Erlinghagen-Lückerath, J. Kaandorp, J. Fritz, K. H. Südekum, and J. Hummel. 2015. Faecal particle size: digestive physiology meets herbivore diversity. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 179:182–191. doi:10.1016/j.cbpa.2014.10.006

Coleman, S. W., and K. M. Barth. 1973. Quality of diets selected by grazing animals and its relation to quality of available forage and species composition of pastures. J. Anim. Sci. 36:754–761. doi:10.2527/jas1973.364754x

Coleman, S. W., S. A. Gunter, J. E. Sprinkle, and J. P. Neel. 2014. Beef species symposium: difficulties associated with predicting forage intake by grazing beef cows. J. Anim. Sci. 92:2775–2784. doi:10.2527/jas.2013-7090

Coleman, S. W., and D. A. Henry. 2002. Nutritive value of herbage. In: M. Freer and H. Dove, editors, Sheep nutrition. Cambridge (MA): CABI Publishing; p. 1–26.

Coleman, S. W., H. Lippke, and M. Gill. 1999. Estimating the nutritive potential of forages. In: H.-J. G. Jung and G. C. Fahey Jr., editors. Proceedings of the 5th International Symposium on the Nutrition of Herbivores. San Antonio (TX): American Society of Animal Science; p. 647–695

Conrad, H. R., A. D. Pratt, and J. W. Hibbs. 1964. Regulation of feed intake in dairy cows. I. Change in importance of physical and physiological factors with increasing digestibility. J. Dairy Sci. 47:54–62. doi:10.3168/jds.S0022-0302(64)88581-7

Crampton, E. W., E. Donefer, and L. E. Lloyd. 1960. A nutritive value index for forages. J. Anim. Sci. 19:538–544. doi:10.2527/jas1960.192538x

De Boever, J. L., J. I. Andries, D. L. De Brabander, B. G. Cottyn, and F. X. Buysse. 1990. Chewing activity of ruminants as a measure of physical structure — A review of factors affecting it. Anim. Feed Sci. Technol. 27:281–291. doi:10.1016/0377-8401(90)90143-V

Delagarde, R., P. Faverdin, C. Baratte, and J. L. Peyraud. 2011a. GrazeIn: a model of herbage intake and milk production for grazing dairy cows. 2. Prediction of intake under rotational and continuously stocked grazing management. Gass Forage Sci. 66:45–60. doi:10.1111/j.1365-2494.2010.00769.x

Delagarde, R., H. Valk, C. S. Mayne, A. J. Rook, A. Gonzalez-Rodriguez, C. Baratte, P. Faverdin, and J. L. Peyraud. 2011b. GrazeIn: a model of herbage intake and milk production for grazing dairy cows. 3. Simulations and external validation of the model. Gass Forage Sci. 66:61–77. doi:10.1111/j.1365-2494.2010.00770.x

Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Natur. 125:641–672. doi:10.1086/284369

Deniz, N. N., J. O. Chelotti, J. R. Galli, A. M. Planisich, M. J. Larripa, H. Leonardo Rufiner, and L. L. Giovanini. 2017. Embedded system for real-time monitoring of foraging behavior of grazing cattle using acoustic signals. Comput. Electron. Agric. 138:167–174. doi:10.1016/j.compag.2017.04.024

Detmann, E., M. P. Gionbelli, and P. Huhtanen. 2014. A meta-analytical evaluation of the regulation of voluntary intake in cattle fed tropical forage-based diets. J. Anim. Sci. 92:4632–4641. doi:10.2527/jas.2014-7717

Doole, G. J., A. J. Romera, and A. A. Adler. 2013. An optimization model of a New Zealand dairy farm. J. Dairy Sci. 96:2147–2160. doi:10.3168/jds.2012-5488

Doyle, P. T., S. A. Francis, and C. R. Stockdale. 2005. Associative effects between feeds when concentrate supplements are fed to grazing dairy cows: a review of likely impacts on metabolisable energy supply. Austr. J. Agric. Res. 56:1315–1329. doi:10.1071/AR05087

Farningham, D. A. H., and C. C. Whyte. 1993. The role of propionate and acetate in the control of food intake in sheep. Br. J. Nutr. 70:37–46. doi:10.1079/BJN19930103

Faverdin, P., C. Baratte, R. Delagarde, and J. L. Peyraud. 2011. GrazeIn: a model of herbage intake and milk production for grazing dairy cows. 1. Prediction of intake capacity, voluntary intake and milk production during lactation. Gass Forage Sci. 66:29–44. doi:10.1111/j.1365-2494.2010.00776.x

Fedele, V., M. Pizzillo, S. Claps, P. Morand-Fehr, and R. Rubino. 1993. Grazing behavior and diet selection of goats on native pasture in Southern Italy. Small Ruminant Res. 11:305–322. doi:10.1016/0921-4488(93)90002-Y

Fisher, D. S. 1996. Modeling ruminant feed intake with protein, chemostatic, and distention feedbacks. J. Anim. Sci. 74:3076–3081. doi:10.2527/1996.74123076x

Forbes, J. M. 2007. A personal view of how ruminant animals control their intake and choice of food: minimal total discomfort. Nutr. Res. Rev. 20:132–146. doi:10.1017/S0954422407797834

Forbes, J. M., and P. Gregorini. 2015. The catastrophe of meal eating. Anim. Prod. Sci. 55:350–359. doi:10.1071/AN14425

Fox, D. G., L. O. Tedeschi, T. P. Tylutki, J. B. Russell, M. E. Van Amburgh, L. E. Chase, A. N. Pell, and T. R. Overton. 2004. The Cornell net carbohydrate and protein system model for evaluating herd nutrition and nutrient excretion. Anim. Feed Sci. Technol. 112:29–78. doi:10.1016/j.anifeedsci.2003.10.006

France, J., and J. H. M. Thornley. 1984. Mathematical models in agriculture: a quantitative approach to problems in agriculture and related sciences. London (UK): Butterworths.

Freer, M., A. D. Moore, and J. R. Donnelly. 1997. GRAZPLAN: Decision support systems for Australian grazing enterprises-II. The animal biology model for feed intake, production and reproduction and the GrazFeed DSS. Agric. Syst. 54:77–126. doi:10.1016/S0308-521X(96)00045-5

French, P., E. G. O'Riordan, P. O'Kiely, P. J. Caffrey, and A. P. Moloney. 2001. Intake and growth of steers offered different allowances of autumn grass and concentrates. Anim. Sci. 72:129–138. doi:10.1017/S1357729800055624

Fust, P., and E. Schlecht. 2018. Integrating spatio-temporal variation in resource availability and herbivore movements into rangeland management: RaMDry—An agent-based model on livestock feeding ecology in a dynamic, heterogeneous, semi-arid environment. Ecol. Modell. 369:13–41. doi:10.1016/j.ecolmodel.2017.10.017

Ginane, C., M. Bonnet, R. Baumont, and D. K. Revell. 2015. Feeding behaviour in ruminants: a consequence of interactions between a reward system and the regulation of metabolic homeostasis. Anim. Prod. Sci. 55:247–260. doi:10.1071/AN14481

González, L. A., I. Kyriazakis, and L. O. Tedeschi. 2018. Review: Precision nutrition of ruminants: approaches, challenges and potential gains. Animal. 12(S2):S246–S261. doi:10.1017/S1751731118002288

Graux, A. I., M. Gaurut, J. Agabriel, R. Baumont, R. Delagarde, L. Delaby, and J. F. Soussana. 2011. Development of the pasture simulation model for assessing livestock production under climate change. Agric. Ecosys. Environ. 144:69–91. doi:10.1016/j.agee.2011.07.001

Greenwood, P. L., D. R. Paull, J. McNally, T. Kalinowski, D. Ebert, B. Little, D. V. Smith, A. Rahman, P. Valencia, A. B. Ingham, and G. J. Bishop-Hurley. 2017. Use of sensor-determined behaviours to develop algorithms for pasture intake by individual grazing cattle. Crop Pasture Sci. 68:1091–1099. doi:10.1071/CP16383

Gregorini, P., F. D. Provenza, J. J. Villalba, P. C. Beukes, and M. J. Forbes. 2018. Diurnal patterns of urination and drinking by grazing ruminants: a development in a mechanistic model of a grazing ruminant, MINDY. J. Agric. Sci. 156:71–81. doi:10.1017/S0021859617000806

Gregorini, P., P. C. Beukes, A. J. Romera, G. Levy, and M. D. Hanigan. 2013. A model of diurnal grazing patterns and herbage intake of a dairy cow, MINDY: model description. Ecol. Modell. 270:11–29. doi:10.1016/j.ecolmodel.2013.09.001

Gregorini, P., P. C. Beukes, G. C. Waghorn, D. Pacheco, and M. D. Hanigan. 2015a. Development of an improved representation of rumen digesta outflow in a mechanistic and dynamic model of a dairy cow, Molly. Ecol. Modell. 313:293–306. doi:10.1016/j.ecolmodel.2015.06.042

Gregorini, P., J. J. Villalba, F. D. Provenza, P. C. Beukes, and J. M. Forbes. 2015b. Modelling preference and diet selection patterns by grazing ruminants: a development in a mechanistic model of a grazing dairy cow, MINDY. Anim. Prod. Sci. 55:360–375. doi:10.1071/AN14472

Hackmann, T. J., and J. N. Spain. 2010. A mechanistic model for predicting intake of forage diets by ruminants. J. Anim. Sci. 88:1108–1124. doi:10.2527/jas.2008-1378

Haefner, J. W. 2005. Modeling biological systems: principles and applications, 2nd edn. New York (NY): Springer.

Hall, M. B., and G. B. Huntington. 2008. Nutrient synchrony: sound in theory, elusive in practice. J. Anim. Sci. 86 (14 Suppl):E287–E292. doi:10.2527/jas.2007-0516

Hanrahan, L., A. Geoghegan, M. O'Donovan, V. Griffith, E. Ruelle, M. Wallace, and L. Shalloo. 2017. PastureBase Ireland: a grassland decision support system and national database. Comput. Electron. Agric. 136:193–201. doi:10.1016/j.compag.2017.01.029

Heaney, D. P., W. J. Pigden, and G. I. Pritchard. 1966. Comparative energy availability for lambs of four timothy varieties at progressive growth stages. J. Anim. Sci. 25:142–149. doi:10.2527/jas1966.251142x

Heard, J. W., D. C. Cohen, P. T. Doyle, W. J. Wales, and C. R. Stockdale. 2004. Diet check - a tactical decision support tool for feeding decisions with grazing dairy cows. Anim. Feed Sci. Technol. 112:177–194. doi:10.1016/j.anifeedsci.2003.10.012

Henning, P. H., D. G. Steyn, and H. H. Meissner. 1993. Effect of synchronization of energy and nitrogen supply on ruminal characteristics and microbial growth. J. Anim. Sci. 71:2516–2528. doi:10.2527/1993.7192516x

Herrera-Saldana, R., R. Gomez-Alarcon, M. Torabi, and J. T. Huber. 1990. Influence of synchronizing protein and starch degradation in the rumen on nutrient utilization and microbial protein synthesis. J. Dairy Sci. 73:142–148. doi:10.3168/jds.S0022-0302(90)78657-2

Herrero, M., R. H. Fawcett, and J. B. Dent. 2000a. Modelling the growth and utilisation of kikuyu grass (*Pennisetum clandestinum*) under grazing. 2. Model validation and analysis of management practices. Agric. Syst. 65:99–111. doi:10.1016/S0308-521X(00)00029-9

Herrero, M., R. H. Fawcett, V. Silveira, J. Busqué, A. Bernués, and J. B. Dent. 2000b. Modelling the growth and utilisation of kikuyu grass (*Pennisetum clandestinum*) under grazing. 1. Model definition and parameterisation. Agric. Syst. 65:73–97. doi:10.1016/S0308-521X(00)00028-7

Hills, J. L., W. J. Wales, F. R. Dunshea, S. C. Garcia, and J. R. Roche. 2015. Invited review: an evaluation of the likely effects of individualized feeding of concentrate supplements to pasture-based dairy cows. J. Dairy Sci. 98:1363–1401. doi:10.3168/jds.2014-8475

Ho, C. K. M., B. Malcolm, and P. T. Doyle. 2013. Potential impacts of negative associative effects between concentrate supplements, pasture and conserved forage for milk production and dairy farm profit. Anim. Prod. Sci. 53:437–452. doi:10.1071/AN12140

Illius, A. W., and M. S. Allen. 1994. Assessing forage quality using integrated models of intake and digestion by ruminants. In: G. C. Fahey Jr., M. Collins, D. R. Mertens, and L. E. Moser, editors, Forage quality, evaluation, and utilization. Madison (WI): American Society of Agronomy; p. 869–890.

Illius, A. W., and I. J. Gordon. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. J. Agric. Sci. 116:145–157. doi:10.1017/S0021859600076255

Illius, A. W., N. S. Jessop, and M. Gill. 2000. Mathematical models of feed intake and metabolism in ruminants. In: P. B. Cronjé, editor, Ruminant physiology: digestion, metabolism, growth and reproduction. New York (NY): CABI Publishing; p. 21–39.

Janssen, S. J. C., C. H. Porter, A. D. Moore, I. N. Athanasiadis, I. Foster, J. W. Jones, and J. M. Antle. 2017. Towards a new generation of agricultural system data, models and knowledge products: information and communication technology. Agric. Syst. 155:200–212. doi:10.1016/j.agsy.2016.09.017

Jarrige, R., C. Demarquilly, J. P. Dulphy, A. Hoden, J. Robelin, C. Beranger, Y. Geay, M. Journet, C. Malterre, D. Micol, et al. 1986. The INRA "fill unit" system for predicting the voluntary intake of forage-based diets in ruminants: a review. J. Anim. Sci. 63:1737–1758. doi:10.2527/jas1986.6361737x

Johnson, I. R., J. France, and B. R. Cullen. 2016. A model of milk production in lactating dairy cows in relation to energy and nitrogen dynamics. J. Dairy Sci. 99:1605–1618. doi:10.3168/jds.2015-10068

Johnson, I. R., G. M. Lodge, and R. E. White. 2003. The sustainable grazing systems pasture model: description, philosophy and application to the SGS national experiment. Austr. J. Exp. Agric. 43:711–728. doi:10.1071/EA02213

Jouven, M., J. Agabriel, and R. Baumont. 2008. A model predicting the seasonal dynamics of intake and production for suckler cows and their calves fed indoors or at pasture. Anim. Feed Sci. Technol. 143:256–279. doi:10.1016/j.anifeedsci.2007.05.014

Jouven, M., P. Carrère, and R. Baumont. 2006a. Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 1. Model description. Grass Forage Sci. 61:112–124. doi:10.1111/j.1365-2494.2006.00515.x

Jouven, M., P. Carrère, and R. Baumont. 2006b. Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 2. Model evaluation. Grass Forage Sci. 61:125–133. doi:10.1111/j.1365-2494.2006.00517.x

Langlands, J. P., and J. Sanson. 1976. Factors affecting the nutritive value of the diet and the composition of rumen fluid of grazing sheep and cattle. Austr. J. Agric. Res. 27:691–707. doi:10.1071/AR9760691

Leclerc, B. 1985. Utilisation du maquis Corse par des caprins et des ovins. II - Comparaison du regime des ovins ed des caprins. Acta Oecologia. Oecologia Aplicata. 6:303–314.

Le Gal, P. Y., P. Dugué, G. Faure, and S. Novak. 2011. How does research address the design of innovative agricultural production systems at the farm level? A review. Agric. Syst. 104:714–728. doi:10.1016/j.agsy.2011.07.007

Lunesu, M. F. 2017. Modulation of dietary energy partitioning between milk production and body reserves in sheep and goats. Dissertation, Sassari (Italy): University of Sassari.

Mayes, R. W., C. S. Lamb, and P. M. Colgrove. 1986. The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. J. Agric. Sci. 107:161–170. doi:10.1017/S0021859600066910

Mertens, D. R. 1987. Predicting intake and digestibility using mathematical models of ruminal function. J. Anim. Sci. 64:1548–1558. doi:10.2527/jas1987.6451548x

Milovanović, S. 2014. The role and potential of information technology in agricultural improvement. Econ. Agric. 61:471–485.

Milton, E. J., M. E. Schaepman, K. Anderson, M. Kneubühler, and N. Fox. 2009. Progress in field spectroscopy. Remote Sens. Environ. 113:S92–S109. doi:10.1016/j.rse.2007.08.001

Molle, G., M. Decandia, A. Cabiddu, S. Y. Landau, and A. Cannas. 2008. An update on the nutrition of dairy sheep grazing Mediterranean pastures. Small Ruminant Res. 77:93–112. doi:10.1016/j.smallrumres.2008.03.003

Molle, G., M. Decandia, V. Giovanetti, C. Manca, M. Acciaro, G. Epifani, L. Salis, A. Cabiddu, M. Sitzia, and A. Cannas. 2014. Effects of restricted time allocation to pasture on feeding behaviour, intake and milk production of dairy sheep rotationally grazing Italian ryegrass (*Lolium multiflorum* Lam) in spring. Anim. Prod. Sci. 54:1233–1237. doi:10.1071/AN14376

Molle, G., M. Decandia, V. Giovanetti, C. Manca, M. Acciaro, G. Epifani, L. Salis, A. Cabiddu, M. Sitzia, and A. Cannas. 2016. Grazing behaviour, intake and performance of dairy ewes with restricted access time to berseem clover (*Trifolium alexandrinum* L.) pasture. Gass Forage Sci. 72:194–210. doi:10.1111/gfs.12228

Molle, G., and S. Landau. 2002. SHEEP HUSBANDRY | feeding management. In: H. Roginski, editor. Encyclopedia of dairy sciences. Oxford: Elsevier; p. 2498–2507.

Moore, J. E. 1978. Forage quality and animal performance. In: Proceedings of the Forage and Grassland Conference. Raleigh (NC): American Forage and Grassland Council. p. 27–34.

Moore, J. E. 1994. Forage quality indices: development and application. In: G. C. Fahey Jr., M. Collins, D. R. Mertens, and L. E. Moser, editors, Forage quality, evaluation, and utilization. Madison (WI): American Society of Agronomy; p. 967–998.

Moore, J. E., M. H. Brant, W. E. Kunkle, and D. I. Hopkins. 1999. Effects of supplementation on voluntary forage intake, diet digestibility, and animal performance. J. Anim. Sci. 77 (Suppl 2):122–135. doi:10.2527/1999.77suppl_2122x

Moore, J. E., and D. J. Undersander. 2002. Relative forage quality: an alternative to relative feed value and quality index. In: Proceedings of the 13th Annual Florida Ruminant Nutrition Symposium. Gainesville (FL): University of Florida. p. 16–29. Available from http://dairy.ifas.ufl.edu/rns/2002/moore.pdf

Muir, J. P., W. D. Pitman, J. C. Dubeux, and J. L. Foster. 2014. The future of warm-season, tropical and subtropical forage legumes in sustainable pastures and rangelands. Afr. J. Range Forage Sci. 31:187–198. doi:10.2989/10220119.2014.884165

Muir, J. P., W. D. Pitman, and J. L. Foster. 2011. Sustainable, low-input, warm-season, grass-legume grassland mixtures: mission (nearly) impossible? Gass Forage Sci. 66:301–315. doi:10.1111/j.1365-2494.2011.00806.x

Muir, J. P., L. O. Tedeschi, J. C. B. Dubeux, Jr., M. Peters, and S. Burkart. 2017. Enhancing food security in Latin America with forage legumes. Archivos Latinoamericanos de Producción Animal. 25:113–130.

National Academies of Sciences, Engineering, and Medicine. 2016. Nutrient requirements of beef cattle. In: Nutrient requirements of domestic animals, 8th edn. Washington, DC: National Academy Press.

National Research Council. 1981. Nutritional energetics of domestic animals and glossary of energy terms. Washington, DC: National Academy Press.

National Research Council. 2000. Nutrient requirements of beef cattle. In: Nutrient requirements of domestic animals, 7th edn. Washington, DC: National Academy Press.

Nicholson, C. F., R. W. Blake, R. S. Reid, and J. Schelhas. 2001. Environmental impacts of livestock in the developing world. Environment. 43:7–17. doi:10.1080/00139150109605120

Norton, B. W. 1994. The nutritive value of tree legumes. In: R. C. Gutteridge and H. M. Shelton, editors. Forage tree legumes in tropical agriculture. Wallinford (UK): CABI Publishing; p. 177–191.

O'Grady, M. J., and G. M. P. O'Hare. 2017. Modelling the smart farm. Information Processing in Agriculture. 4:179–187. doi:10.1016/j.inpa.2017.05.001

O'Neill, B. F., E. Lewis, M. O'Donovan, L. Shalloo, T. M. Boland, F. J. Mulligan, and R. Delagarde. 2013. Evaluation of the GrazeIn model of grass dry-matter intake and milk production prediction for dairy cows in temperate grass-based production systems. 2 - Animal characteristics. Gass Forage Sci. 68:524–536. doi:10.1111/gfs.12022

O'Neill, B. F., E. Ruelle, M. O'Donovan, L. Shalloo, F. J. Mulligan, T. M. Boland, L. Delaby, R. Delagarde, and E. Lewis. 2014. Adaptation and evaluation of the grazein model of grass dry matter intake and milk yield prediction for grazing dairy cows. Animal 8:596–609. doi:10.1017/S1751731113002486.

Olsen, M. V. 2016. New models for predicting energy intake in pregnant ewes and beef cows and in nursing ewes. Dissertation, Copenhagen (Denmark): Unviersity of Copenhagen.

Oltjen, J. W., and S. A. Gunter. 2015. Managing the herbage utilisation and intake by cattle grazing rangelands. Anim. Prod. Sci. 55:397–410. doi:10.1071/AN14602

Oudshoorn, F. W., C. Cornou, A. L. F. Hellwing, H. H. Hansen, L. Munksgaard, P. Lund, and T. Kristensen. 2013. Estimation of grass intake on pasture for dairy cows using tightly and loosely mounted di- and tri-axial accelerometers combined with bite count. Comput. Electron. Agric. 99:227–235. doi:10.1016/j.compag.2013.09.013

Paloheimo, L., A. Makela, and A. Suvanto. 1959. Further studies on the retention time of food in the digestive tract of cows. Acta Agralia Fennica. 94:15–39.

Phillips, R. L., O. Beeri, E. Scholljegerdes, D. Bjergaard, and J. Hendrickson. 2009. Integration of geospatial and cattle nutrition information to estimate paddock grazing capacity in Northern US prairie. Agric. Syst. 100:72–79. doi:10.1016/j.agsy.2009.01.002

Pittroff, W., and M. M. Kothmann. 2001a. Quantitative prediction of feed intake in ruminants. I. Conceptual and mathematical analysis of models for sheep. Livest. Prod. Sci. 71:131–150. doi:10.1016/S0301-6226(01)00216-0

Pittroff, W., and M. M. Kothmann. 2001b. Quantitative prediction of feed intake in ruminants. II. Conceptual and mathematical analysis of models for cattle. Livest. Prod. Sci. 71:151–169. doi:10.1016/S0301-6226(01)00217-2

Pittroff, W., and M. M. Kothmann. 2001c. Quantitative prediction of feed intake in ruminants. III. Comparative example calculations and discussion. Livest. Prod. Sci. 71:171–181. doi:10.1016/S0301-6226(01)00218-4

Poppi, D. P., M. Gill, J. France, and R. A. Dynes. 1989. Additivity in intake models. In: A. B. Robson and D. P. Poppi, editors. Proceedings of the 3rd International Modelling Ruminant Digestion and Metabolism. Lincoln College, Canterbury (NZ): Lincoln University. p. 29–46.

Pulido, R. G., R. Muñoz, P. Lemarie, F. Wittwer, P. Orellana, and G. C. Waghorn. 2009. Impact of increasing grain feeding frequency on production of dairy cows grazing pasture. Livest. Sci. 125:109–114. doi:10.1016/j.livsci.2009.03.010

Pulina, G., M. Avondo, G. Molle, A. H. D. Francesconi, A. S. Atzori, and A. Cannas. 2013. Invited review: models for estimating feed intake in small ruminants. Rev. Bras. Zootec. 41:675–690. doi:10.1590/S1516-35982013000900010

Raccoon, L. B. S. 1995. The chaos model and the chaos cycle. ACM SIGSOFT Software Engineering Notes. 20:55–66. doi:10.1145/225907.225914

Rayburn, E. B., and D. G. Fox. 1993. Variation in neutral detergent fiber intake of Holstein cows. J. Dairy Sci. 76:544–554. doi:10.3168/jds.S0022-0302(93)77374–9

Rohweder, D. A., R. F. Barnes, and N. Jorgensen. 1978. Proposed hay grading standards based on laboratory analyses for evaluating quality. J. Anim. Sci. 47:747–759. doi:10.2527/jas1978.473747x

Rombach, M., A. Münger, J. Niederhauser, K. H. Südekum, and F. Schori. 2018. Evaluation and validation of an automatic jaw movement recorder (Rumiwatch) for ingestive and rumination behaviors of dairy cows during grazing and supplementation. J. Dairy Sci. 101:2463–2475. doi:10.3168/jds.2016-12305.

Rouquette, F. M., Jr, L. A. Redmon, G. E. Aiken, G. M. Hill, L. E. Sollenberger, and J. Andrae. 2009. ASAS centennial paper: future needs of research and extension in forage utilization. J. Anim. Sci. 87:438–446. doi:10.2527/jas.2008-1273.

Rutter, S. M. 2006. Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. Appl. Anim. Behav. Sci. 97:17–35. doi:10.1016/j.applanim.2005.11.016

Rutter, S. M., R. A. Champion, and P. D. Penning. 1997. An automatic system to record foraging behaviour in free-ranging ruminants. Appl. Anim. Behav. Sci. 54:185–195. doi:10.1016/S0168-1591(96)01191-4

Schaefer, M., and D. Lamb. 2016. A combination of plant NDVI and liDAR measurements improve the estimation of pasture biomass in tall fescue (*Festuca arundinacea* var. Fletcher). Remote Sens. 8:109. doi:10.3390/rs8020109

Scheibe, K. M., and C. Gromann. 2006. Application testing of a new three-dimensional acceleration measuring system with wireless data transfer (WAS) for behavior analysis. Behav. Res. Methods 38:427–433. doi:10.3758/bf03192796

Schneider, B. H., and W. P. Flatt. 1975. The evaluation of feed through digestibility experiments. Athens (GA): The University of Georgia Press.

Shalloo, L., P. Dillon, M. Rath, and M. Wallace. 2004. Description and validation of the moorepark dairy system model. J. Dairy Sci. 87:1945–1959. doi:10.3168/jds.S0022-0302(04)73353-6.

Shalloo, L., L. Leso, A. McDonagh, A. Geoghegan, J. Werner, and N. O'Leary. 2018. A review of big data, smart and Precision Technologies in pasture-based dairying systems. In: Sustainable meat and milk production from grasslands. Proceedings of the 27th General Meeting of the European Grassland Federation. Cork (Ireland): Teagasc, Animal & Grassland Research and Innovation Centre. p. 789–806.

Sheahan, A. J., S. J. Gibbs, and J. R. Roche. 2013. Timing of supplementation alters grazing behavior and milk production response in dairy cows. J. Dairy Sci. 96:477–483. doi:10.3168/jds.2012–5781

Snow, V. O., C. A. Rotz, A. D. Moore, R. Martin-Clouaire, I. R. Johnson, N. J. Hutchings, and R. J. Eckard. 2014. The challenges – and some solutions – to process-based modelling of grazed agricultural systems. Environ. Modell. Softw. 62:420–436. doi:10.1016/j.envsoft.2014.03.009

Stockdale, C. R. 2000. Levels of pasture substitution when concentrates are fed to grazing dairy cows in northern Victoria. Austr. J. Exp. Agric. 40:913–921. doi:10.1071/EA00034

Susenbeth, A., R. Mayer, B. Köhler, and O. Neumann. 1997. Heat production associated with eating in cattle. In: K. J. McCracken, E. F. Unsworth, and A. R. G. Wylie, editors. Proceedings of the 14th Energy Metabolism of Farm Animals. Newcastle: CABI Publishing. p. 279–282.

Susenbeth, A., R. Mayer, B. Köhler, and O. Neumann. 1998. Energy requirement for eating in cattle. J. Anim. Sci. 76:2701–2705. doi:10.2527/1998.76102701x

Tedeschi, L. O., A. K. Almeida, A. S. Atzori, J. P. Muir, M. A. Fonseca, and A. Cannas. 2017a. A glimpse of the future in animal nutrition science. 1. Past and future challenges. Rev. Bras. Zootec. 46:438–451. doi:10.1590/s1806-92902017000500011

Tedeschi, L. O., and D. G. Fox. 2015. Energy and nutrient requirements of grazing and confined growing beef cattle: refining the assessment of energy expenditure for grazing animals. In: G. R. Pereira, T. E. de Oliveira, and J. O. J. Barcellos, editors. Proceedings of the X NESPRO Meeting & II International Symposium on Beef Cattle Production Systems. Porto Alegre, (RS), Brazil: Universidade Federal

do Rio Grande do Sul. p. 21–56. Available from http://www.ufrgs.br/nespro/. Accessed May 25, 2016.

Tedeschi, L. O., and D. G. Fox. 2018. The ruminant nutrition system: an applied model for predicting nutrient requirements and feed utilization in ruminants, 2nd edn. Acton (MA): XanEdu.

Tedeschi, L. O., D. G. Fox, and P. J. Kononoff. 2013. A dynamic model to predict fat and protein fluxes and dry matter intake associated with body reserve changes in cattle. J. Dairy Sci. 96:2448–2463. doi:10.3168/jds.2012-6070.

Tedeschi, L. O., M. A. Fonseca, J. P. Muir, D. P. Poppi, G. E. Carstens, J. P. Angerer, and D. G. Fox. 2017b. A glimpse of the future in animal nutrition science. 2. Current and future solutions. Rev. Bras. Zootec. 46:452–469. doi:10.1590/s1806-92902017000500012

Tedeschi, L. O., J. P. Muir, D. G. Riley, and D. G. Fox. 2015. The role of ruminant animals in sustainable livestock intensification programs. Int. J. Sustainable Dev. World Ecol. 22:452–465. doi:10.1080/13504509.2015.1075441

Thornley, J. H. M. 1998. Grassland dynamics: an ecosystem simulation model. Wallingford (UK): CAB International.

Udén, P., T. R. Rounsaville, G. R. Wiggans, and P. J. Van Soest. 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (*Phleum pratense*) hay. Br. J. Nutr. 48:329–339. doi:10.1079/BJN19820117

Udén, P., and P. J. Van Soest. 1982. The determination of digesta particle size in some herbivores. Anim. Feed Sci. Technol. 7:35–44. doi:10.1016/0377-8401(82)90034–7

Ungar, E. D., and S. M. Rutter. 2006. Classifying cattle jaw movements: comparing IGER behaviour recorder and acoustic techniques. Appl. Anim. Behav. Sci. 98:11–27. doi:10.1016/j.applanim.2005.08.011

Van Soest, P. J. 1994. Nutritional ecology of the ruminant, 2nd edn. Ithaca (NY): Comstock Publishing Associates.

Vazquez, O. P., and T. R. Smith. 2001. Evaluation of alternative algorithms used to simulate pasture intake in grazing dairy cows. J. Dairy Sci. 84:860–872. doi:10.3168/jds.S0022-0302(01)74544-4

Vieira, R. A. M., L. O. Tedeschi, and A. Cannas. 2008a. A generalized compartmental model to estimate the fibre mass in the ruminoreticulum. 1. Estimating parameters of digestion. J. Theor. Biol. 255:345–356. doi:10.1016/j.jtbi.2008.08.014

Vieira, R. A., L. O. Tedeschi, and A. Cannas. 2008b. A generalized compartmental model to estimate the fibre mass in the ruminoreticulum: 2. Integrating digestion and passage. J. Theor. Biol. 255:357–368. doi:10.1016/j.jtbi.2008.08.013

Welch, J. G., and A. M. Smith. 1969. Influence of forage quality on rumination time in sheep. J. Anim. Sci. 28:813–818. doi:10.2527/jas1969.286813x

Wiley, L. M., L. O. Tedeschi, T. D. A. Forbes, and F. M. Rouquette. 2016. Relationships between restricted residual feed intake of Brahman bulls measured in confinement and under different stocking intensities on Coastal bermudagrass pastures. Prof. Anim. Scient. 32:605–618. doi:10.15232/pas.2015-01476

Williams, C. B., P. A. Oltenacu, and C. J. Sniffen. 1989. Refinements in determining the energy value of body tissue reserves and tissue gains from growth. J. Dairy Sci. 72:169–264. doi:10.3168/jds.S0022-0302(89)79105-0

Wirsam, B., and E. O. Uthus. 1996. The use of fuzzy logic in nutrition. J. Nutr. 126 (9 Suppl):2337S–2341S. doi:10.1093/jn/126.suppl_9.2337S