Modeling efficiency and robustness in ruminants: the nutritional point of view

Daniel Sauvant

Feature Article

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Daniel Sauvant

UMR Modélisation Systémique Appliquée aux Ruminants, AgroParisTech, INRA, Université Paris-Saclay, 75005, Paris, France

> ### Implications
>
> - The efficiency and robustness of farm animals has been of growing interest in recent decades, particularly for ruminants which are subject to many constraints.
> - In recent times, systemic modeling approaches have been developed with promising applications in all areas of livestock production.
> - Therefore, the main challenge is to apply modeling methods to issues of efficiency and robustness. Thus, in the domain of animal nutrition, the recent systems of feeding units have proposed interesting advances that will soon be applicable in the field.

Key words: ruminants, modeling, efficiency, robustness

Introduction

Over the past decades, livestock production and breeding have been mainly focused on improving performance because more productive animals have a better feed efficiency and present a higher margin over feed cost. Efficiency is also gaining renewed interest following Food and Agricultural Organization (FAO) analysis, which shows that one of the major approaches for ensuring global food security is to increase the efficiency of processing food resources in animal products (Makkar and Beever, 2013). Nevertheless, some limitations have appeared. Selection of farm animals has resulted in better genotypes for selected traits; however, other nonselected criteria have not performed well and some traits have become more fragile when faced with environmental perturbations (Klopcic et al., 2009). Other emerging challenges in animal systems have serious repercussions in ruminant production; they concern not only feed conversion efficiency, but also composition and quality of edible products, digestive and global welfare, and emissions of elements to the environment. For the purposes of modeling our understanding of the factors involved and of the underlying mechanisms must be improved. In addition, previous models and feeding systems did not adequately take into account the diversity in dietary ingredients and feeding systems (e.g., tropical forages and intensive

production systems), which challenge the efficiency and robustness of farm ruminants. Logically a scientific debate has developed about the relationship between efficiency and robustness.

We have chosen to focus on ruminant animals that are known to be less efficient but more robust than monogastrics. This review will focus on the most recent models, particularly those feed unit systems with field applications.

Definitions

Efficiency

Efficiency is the ratio between the fluxes of output and input of a system (as a cell, an organ, a whole organism, etc.). It is assumed that input is partitioned into output of edible matter and one or several other fluxes of waste. Efficiency can have multiple expressions, a frequent criterion of feed efficiency concerns the ratio between a product (milk, average daily gain, edible matter, etc.), and a corresponding supply of feed or nutrients; these aspects have been reviewed by Wilkinson (2011).

Robustness of a living system

Robustness of a living system corresponds to its ability to maintain its life trajectory, despite external or internal disturbances. This life trajectory must be carried out, at least until reproductive capacity is mature to ensure the perpetuation of the species. Robustness is based on several underlying properties such as elasticity, plasticity, rigidity, flexibility, and resilience (Sauvant and Martin, 2010). At the biological level, robustness is an emerging property of complex systems. It cannot be easily measured and modeled by eliminating the roles of the mutual relationships between the underlying biological elements, functions, and levels of organization. Recognizing its spatio-temporal organization is a first step to progress, and the second step corresponds to study and model specific "points of view" and carry out adequate experimental measurements with respect to, as much as possible, the complexity. Small differences exist in the definitions of robustness in the literature (Strandberg, 2009). Sometimes, animal robustness has been associated with the issue of sustainability of ruminant livestock systems (Blanc et al., 2006; Phocas et al., 2014).

Regulations driving efficiency and robustness

The current INRA approach (INRA, 2018; Figure 1a) is based on the existence of two interacting regulations of flows

and partitions of nutrients. Homeorhetic regulations control functions targeted toward the reproduction and growth of the species (gestation, lactation, and growth) and defining the trajectories of life (Bauman and Currie, 1980). Under the angle of applied nutrition, homeorhetic regulations determine the kinetics of production potential, and therefore the corresponding nutritional requirements. Homeostatic regulations control adaptive functions to modifications of nutritional environment (Cannon, 1929; Ten Napel et al., 2009; Sauvant and Martin, 2010). Thus, homeostatic controls result in multiple responses to dietary practices and constitute a basin of robustness around the trajectory of life after a perturbation (Figure 1b). This perturbation, which challenges homeostatic responses, can be modeled because it can be diverse. For example, it can be a sudden and time-limited (pulse) disturbance. It may be partly random or result from specific breeding strategies. Thus, changing diets for a period of several months induces simultaneous responses (plasticity).

Intake and Feeding Behavior a First Step Toward Efficiency and Robustness

Intake of dry matter is regulated by three major interacting driving forces in ruminants: 1) the fill effect of feeds and diets due to animal limitation of capacities of mastication, of long forage intake, and of particles flowing out of the rumen; 2) the regulation of homeorhesis, driving, for instance, the differences in dry matter intake linked with those of potential for production; and 3) the regulation of homeostasis, driving, for instance, the response of dry matter intake to high-concentrate supply.

Modeling intake and grazing behavior

Numerous regression models for predicting intake of dry matter intake from performance have been proposed in the literature and in several feed unit systems. These equations as such are not very useful for formulating diets as values of dry matter intake are not additive across feed resources. However, their principle has been used to study the individual variations of residual feed or energy intake and their genetic components (Yao et al., 2017). This has made it possible to identify more efficient animals and to establish links with other explicative items such as moving and chewing activities (Fisher et al., 2018). However, the heritability of residual feed intake is fairly low (Yao et al., 2017) and it remains to be seen if more efficient animals will also be more or less robust.

Domestication and selection of ruminants has dramatically improved their performance and therefore their intake capacity due to the pleïotropic effects of genes selected for enhancing performance and acting through homeorhetic regulation. However, it must be stressed that, with increased production potential, the level of fiber intake (measured as its neutral detergent fiber content) from long forage was not improved and remained limited to a maximum value of intake capacity of around 1.35% live weight (Sauvant et al., 2014).

The most aggregated mathematical models of grazing ruminants ignore the details of behavioral adaptation but mainly focus on the time available or the quantity of biomass offered (Delagarde et al., 2011). The most mechanistic models take into account either the influence of forage height on the bite mass and the rate of intake (Baumont et al., 2004, Gregorini et al., 2015) or the impact of bite depth on the removed forage parts (Boval et al., 2014). There is a place for a more mechanistic model for grazing ruminants that integrates more behavioral determinants of intake. For example, bite mass and its determinants (Boval and Sauvant, 2019) play a central role by determining the rate of intake and the daily intake either at grazing or at the trough. One of the determinants of bite mass corresponds to the measure of the incisive arch (Boval and Sauvant, 2019; Figure 2a) and it has been shown to influence the survival capacity of sheep in harsh winter conditions (Illius et al., 1995).

Digestive Efficiency and Robustness

Intensive diets challenge digestive robustness

Logically, to achieve higher levels of dry matter intake, the dietary content of fiber from forage has to be decreased
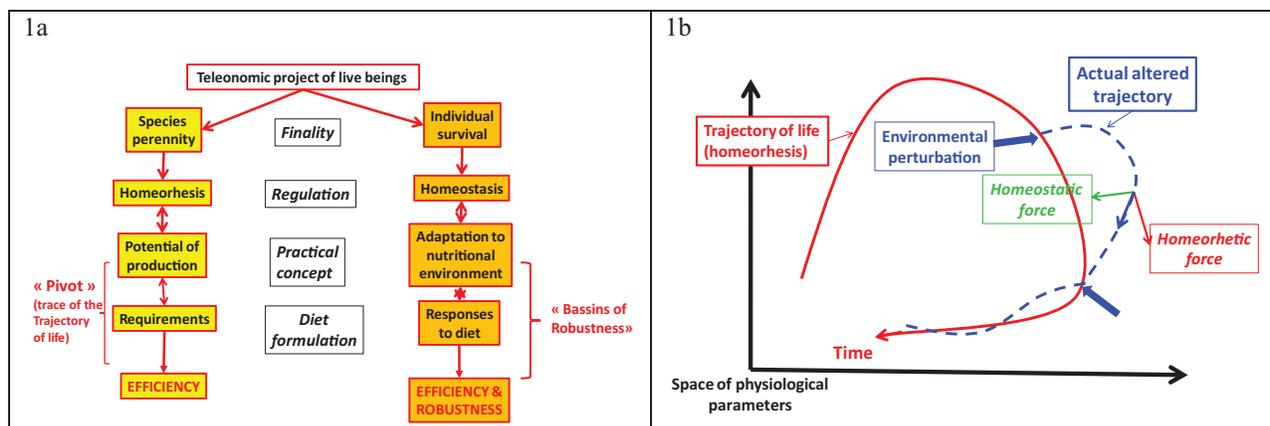

Figure 1. Conceptual organization of quantitative approaches around efficiency and robustness in nutrition of ruminants (a). Schematic representation of the relationship between homeorhesis and homeostasis around the trajectory of life (b).

(Figure 2b). Thus, more ingestible and digestible rations facilitate meeting the energy requirements of high-yielding animals. However, intensive rations challenge the digestive robustness as they are ingested more rapidly and are less masticated reducing saliva buffer recycling. There is also a reduction of the motility and the volume of the rumen and the increased fermentation rate facilitates a decrease in pH in the rumen juice (Sauvant and Giger-Reverdin, 2015). Figure 2b shows the trade-off between dry matter intake and rumen pH associated with the dietary proportion of fiber from forage. The sub-acidotic status frequently observed in high-yielding ruminants can alter performance and efficiency through episodes of irregular ingestion and production, and drop in rumen pH and milk fat content as was modeled by Desnoyer et al. (2009).

New interest on the key role of the rumen

As stressed above, a large part of the capacity of the adaptation of ruminants to dietary challenges is allowed by the rumen, which is a complex ecosystem in which billions of microorganisms proliferate. In the last two decades, scientific interest in this ecosystem has been renewed with the emergence of environmental issues, especially methane (CH_4) production. More recently, progress in microbiome studies has also contributed to the renewal of studies of rumen function (Zhu et al., 2018).

Mechanistic models of digestion

Modeling of ruminal digestion started in 1970 (see review of Baldwin, 2005) followed by several proposed mechanistic models (Dijkstra, 1993; Lescoat and Sauvant, 1995). These models were based on the same principles and they were able to simulate the major variations of digestive efficiency. However, these models do not provide exactly the same results when they are applied to the same diet (Offner and Sauvant, 2004). Indeed, the rumen ecosystem draws its robustness from a short-term effective elastic behavior, which is usually observed after a meal. To capture and study this interesting ability, it is necessary to increase the mechanisticiy of rumen models and to make it possible to simulate a key digestive parameter such as rumen pH (Munoz-Tamayo et al., 2016).

Empirical modeling of digestion in feed unit systems

A challenge of modern feed unit systems is to be based on simple but realistic models of digestion and to take into account major digestive events (substrate degradation, production of end products, particle transit, production of microbial biomass, volatile fatty acids and gases, etc.). Recent feeding systems tried to model precisely the production of microbial biomass (Van Duikerken et al., 2011) or endogenous protein fluxes (NorFor, 2011). The recent INRA (Institut National de la Recherche Agronomique) 2018 system was based on a digestive mechanistic model that is calibrated on structural equations of fluxes derived from meta-analysis of the literature (Sauvant and Nozière, 2012, 2016). Thus, insofar as the data and meta-analysis are representative of the feeding practices encountered in field conditions, this model is capable of application to a wide range of practical situations. In addition, it makes it possible to detect new traits linked with efficiency and robustness. Two examples are summarized below.

"Non-productive endogenous digestive losses" of proteins and organic matter have often been neglected, despite the fact that they are not negligible when compared with maintenance requirements. The empirical models of Figure 3a show that the endogenous protein fecal losses (calculated according to Sauvant et al., 2015, 2018a) in dairy cows are much more important than the basic maintenance requirements, which are mainly linked with body protein turnover. The models of Figure 3b illustrate the magnitude of nonproductive energy losses in dairy cows, which are related to digestive interactions (Sauvant and Nozière, 2016). An important consequence underlined by Figure 3a and b is that nonproductive losses increase proportionally to the level of milk yield decreases and the gain of efficiency that can be expected by increasing the level of performance (see below). Today, there is no precise information on the individual variations that are associated with these digestive losses; thus, more research is needed in this area.

"The rumen protein balance" corresponds to the difference between the crude protein fluxes ingested and passed to the
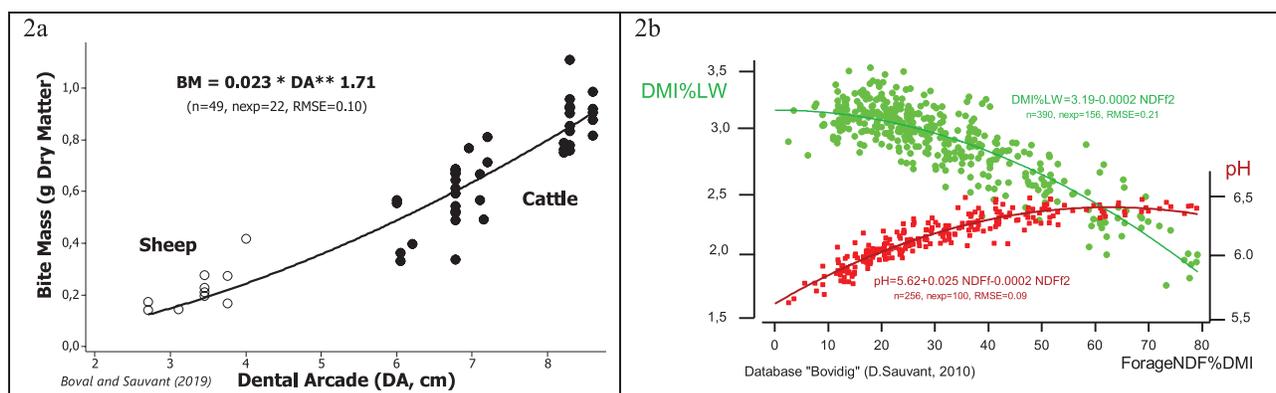
Figure 2. Influence of incisor arcade size on bite mass in grazing ruminants (a) and influence of the dietary cell wall (nondigestible fiber; NDF% dry matter) from forage on dry matter intake (DMI %live weight) and rumen pH in cattle (b).
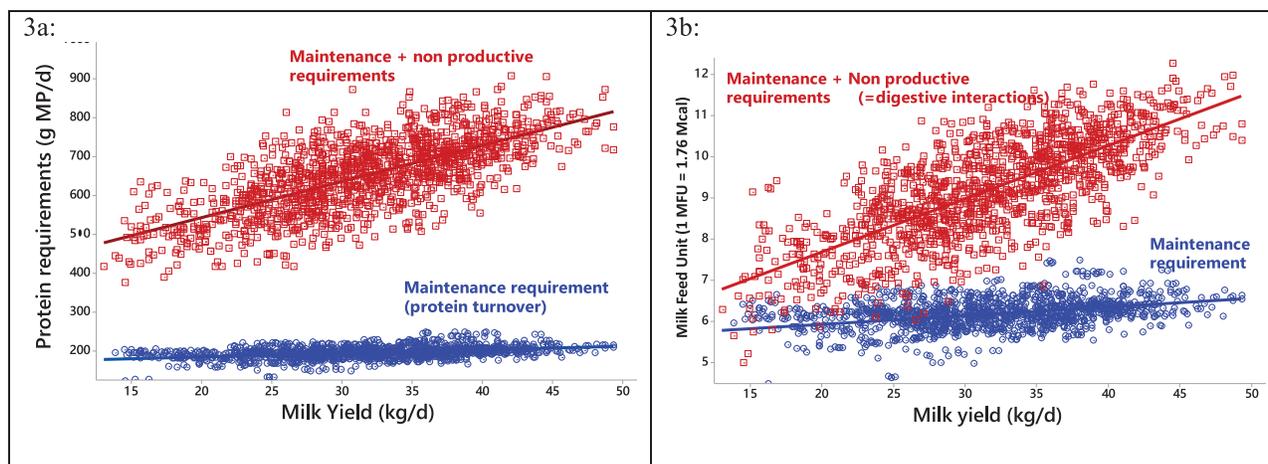
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Figure 3. Examples of increases in the maintenance requirements by taking into account (a) nonproductive requirements of protein and (b) energy (1 MFU = 1.76 Milk Mcal) in dairy cows (D. Sauvant and J. B. Daniel, unpublished data).

duodenum (Sauvant et Nozière, 2016). This trait, quite frequently measured with the animal fitted with duodenal fistulas, is additive and can be used in diet formulations. Rumen protein balance reflects the equilibrium between the flow of nitrogen recycling through saliva and through the rumen wall and the excess ammonia absorption in the rumen. When nitrogen recycling dominates (rumen protein balance < 0), there is an interesting recovery of nitrogen that is recycled into microbial protein available to the animal. This virtuous cycle contributes to the efficiency and robustness of ruminants receiving diets low in nitrogen, which is the case in many practical situations around the world. However, in this situation, organic matter digestibility and therefore the energy value of the diet are decreased (Sauvant et al., 2018a). In contrast, when rumen protein balance is >0, the digestive efficiency of protein decreases rapidly and about 80% of the excess nitrogen, absorbed as ammonia, is lost as urinary nitrogen (Sauvant et al., 2015). Consequently, variations in rumen protein balance largely explain overall protein efficiency. To date, the range of individual variation in rumen protein balance and their genetic control remains unknown.

Metabolic Efficiency and Robustness

Impact of level of performance on metabolic efficiency

Experimentally, the metabolic use of energy has been the most studied criterion of the efficiency of farm animals. This efficiency depends primarily on the partition of nutrients between maintenance and other expenditures. As a consequence, there is a positive relationship between the level of performance and efficiency. For example, Figure 4a illustrates this global principle for energy in the case of various growing ruminants in warm countries. The efficiency trait is the ratio of average daily gain/ingested digestible organic matter intake (ADG/DOMI). Furthermore, Figure 4b shows that, when milk performance increases, the partition of carbon evolves in favor of milk and

in disfavor of carbon dioxide–carbon, fecal–carbon, and also methane–carbon and urinary–carbon in dairy cows and goats (Sauvant and Giger-Reverdin, 2018a). The major consequence of this global and important relationship between performance and efficiency is that selection has mainly been targeted toward performance improvement.

Components of robustness attached to carbon and nitrogen metabolism

Associated with complex regulations, animals are rather well-equipped to resist variations in the dietary supply of carbon (energy is supported by carbon–hydrogen links) due to the elastic behavior of their body reserves and also because there is no adaptive excretion in response to a shortage or excess of carbon. In contrast, there is almost no undifferentiated body storage of protein (or nitrogen) and in a situation of excess, the amino acids are strongly deaminated in the liver and their nitrogen moiety is lost as urea in the urinary flow. Furthermore, a dietary protein shortage cannot be compensated, so living functions linked to protein metabolism are rapidly limited. These general principles explain why animals are much more robust toward differences in the dietary supply of carbon compared with the dietary supply of nitrogen. It is therefore necessary to ask if focusing on energy aspects in studies aimed at modeling robustness is the right direction?

Differences in robustness of metabolic pathways in response to a challenge

To assess short-term robustness, nutritional challenges of fasting have been applied to dairy females for decades (Figure 5a; Brody, 1945). Production of milk lipids, proteins, and lactose, which are supported by different metabolic pathways, does not have the same resilience to a fasting challenge. Thus, it appears that the response of lipid production is more resilient, underlining the robustness of lipid metabolism due to body reserves. In contrast, production of proteins
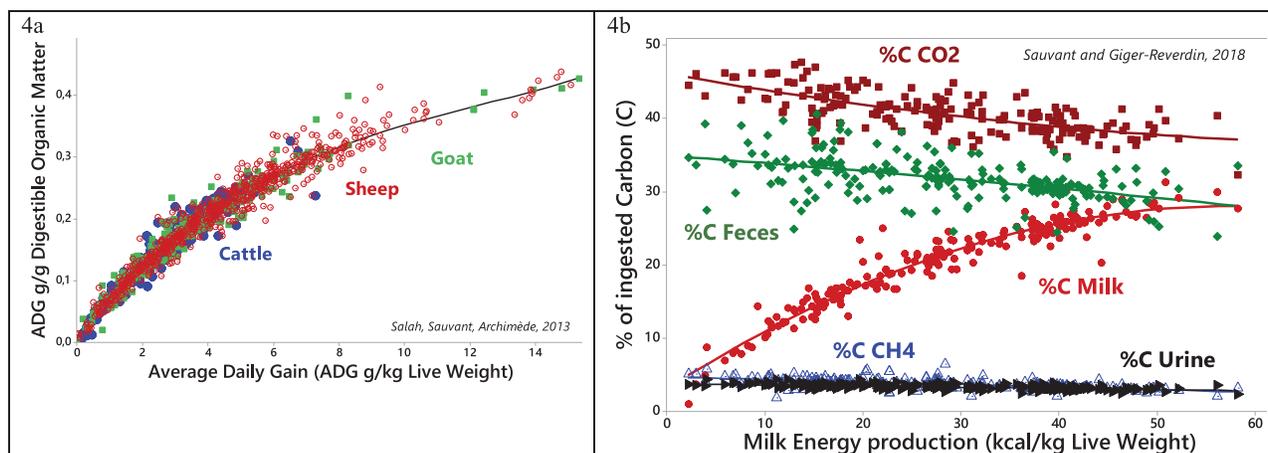
Figure 4. Intraexperimental influence in growing ruminants of the level of average daily gain (ADG) on the efficiency of digestible organic matter intake (DOMI, a). Influence, in lactating cows and goats, of the production of energy in milk and partition of carbon (C) between milk-C, carbon dioxide-C, Fecal-C, Urine-C, and CH4-C (b).
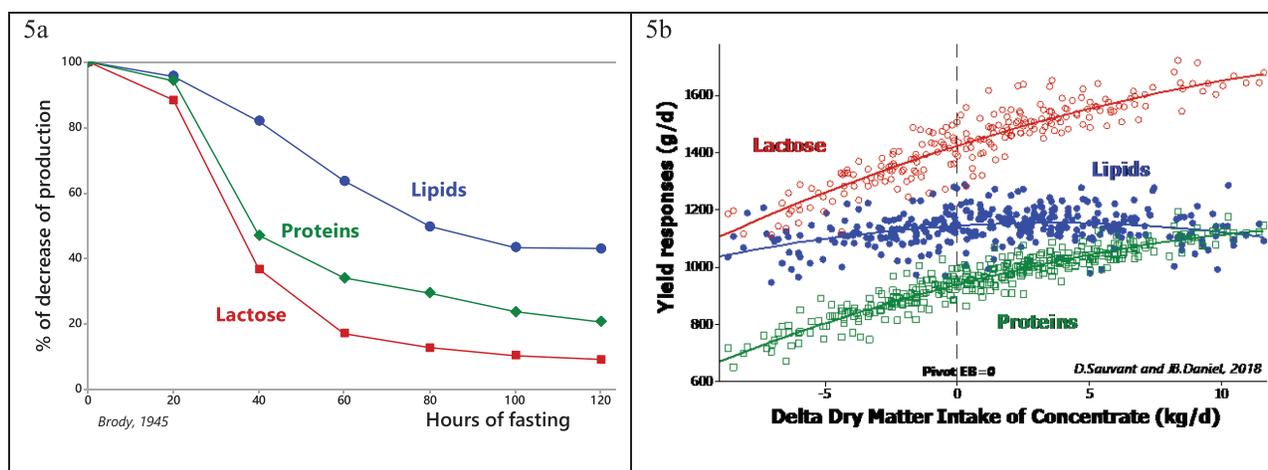

Figure 5. Influence on production of milk constituents under fasting condition (a) of concentrate intake around the pivot of energy balance = 0 on production of milk constituents (b).

and especially lactose is negatively affected, revealing a lower homeostatic capacity and robustness. These results are logical insofar as the body does not have protein reserves and there is almost no available glucose to compensate for its very low digestive input as for its precursors. Furthermore, it should be noted that milk production depends firstly on lactose (17.3 kg milk/kg lactose) and also to a lesser extent on protein (4.3 kg milk/kg protein) and not on lipids (Daniel et al., 2017a). It was reported that individual variations in response to this type of short-term challenge are significant and present a fairly good repeatability over time (Friggens et al., 2016).

Multiple responses to diets, mid-term efficiency, and robustness

The prediction of responses has been described in the INRA-2018 system, particularly for dairy cows and goats (Faverdin et al., 2018; Sauvant and Giger-Reverdin, 2018b). Each law of response corresponds to the exploration of a basin of the

homeostatic capacity where animal robustness is solicited. For all types of ruminants, standardized kinetics of performances are now proposed (INRA, 2018) and correspond to a nutritional status of energy balance = 0 and metabolizable protein (MP) efficiency = 0.67.

Models of responses to energy intake. The response of metabolic efficiency of the transformation of metabolizable energy (ME) into net energy (NE) (k = ME/NE) is better with more digestible and concentrated rations (higher values of the ratio metabolizable energy/gross energy) because they induce a lower level of heat production due to less chewing and less work for gut motility, etc. This principle is included in various ways in most current feed unit systems.

Empirical modeling of milk yield response to energy intake is not new for dairy cows (Brody, 1945). Recently, laws of response have been proposed and are a function of the supplies of concentrates (Figure 5b) or energy (Daniel et al., 2016; Faverdin et al., 2018). Interestingly, the differences of slope

responses to concentrate of lipids, proteins, and lactose production (Figure 5b) are consistent with the ranking observed after a fasting challenge (Figure 5a). This is also consistent with the data of Daniel et al. (2016) showing that, at the pivot of energy balance = 0, the marginal responses per unit of milk net energy are 2.6, 13.1, and 17.1 g/Mcal milk NE for lipids, proteins, and lactose, respectively. A similar ranking is observed with response to milk protein intake around the pivot of milk protein efficiency = 0.67 (Daniel et al., 2016) and also in dairy goats (Sauvant and Giger-Reverdin, 2018b). For energy, as there is no adaptive excretion of carbon, the response of efficiency concerns its partition between production and reserves. For instance, Figure 6b shows that changes in energy intake in dairy goats around maintenance needs result in inverse marginal responses between energy flows in milk and in reserves. Around the pivot of energy balance = 0, the marginal partition of energy between milk and reserves is about 33/67 (a lower value of around 17/83 for dairy cows), whatever the potential, was reported at the pivot by Daniel et al. (2016).

The major interest of empirical models of response laws to energy versus nutritional challenges is that they explore plausible situations of robustness and construct computer tools that can be used in diet formulation. When all these models are built, large variations can be observed from one experiment to another and also from one animal to another within a given experiment. Thus, studies aimed at identifying more robust animals are needed.

Models of responses to metabolizable protein intake. As shown in Figure 6a, changes in the supply of metabolizable protein (INRA, 2018) around the pivot value of MP_efficiency = 0.67 lead to simultaneous changes in metabolic efficiency and milk protein production in cows (similar results exist in goats) (Sauvant et al., 2018b; Faverdin et al., 2018). Figure 6a shows that the variations in MP_efficiency result in the concomitant variations in MP supply and urinary nitrogen excretion (Sauvant et al., 2015). Around the pivot of MP_efficiency of 0.67, the marginal partition between milk protein and excretion is about 20/80 (Daniel et al., 2017b). The combination of influences of rumen protein balance and MP_efficiency (Figure 6a) allows accurate prediction of urinary nitrogen excretion and therefore MP efficiency for all ruminants (Sauvant et al., 2018b).

Examples of published mechanistic models of metabolism. Many studies have addressed modeling of metabolism. One of the issues raised by these mechanistic models concerns representation of the homeorhetic and homeostatic regulations in a regulating subsystem which controls the operating subsystem (organs, metabolic pathways, etc.). In these models, regulations are based on theoretical hormones that are supposed to reflect the effects of catabolic energy and anabolic hormones (Neal and Thornley, 1983; Sauvant, 1994). More recent models have considered both energy and protein metabolism (Baldwin, 2005; Martin and Sauvant, 2007). These models essentially represented homeorhetic regulations along one lactation. More recently, a new model has made it possible to represent dynamic phenomena linked to energy over several lactations (Puillet et al., 2010). Furthermore, homeorhetic and homeostatic regulations have been simultaneously represented (Martin and Sauvant, 2010) and this is the first teleonomic model to potentially tackle issues related to energy robustness. Finally, the homeorhetic regulation subsystem has been improved to take into account the differences between the kinetics of production of lipids, proteins, and lactose in lactating cows (Daniel et al., 2017b). This is important because most studies on lactating females have focused on energy efficiency, and the associated robustness view points have focused only on lipids.

Conclusion

Aspects related to effects of the nutritional environment of ruminants are interesting view points to tackle the questions concerning their efficiency and robustness. Efficiency and
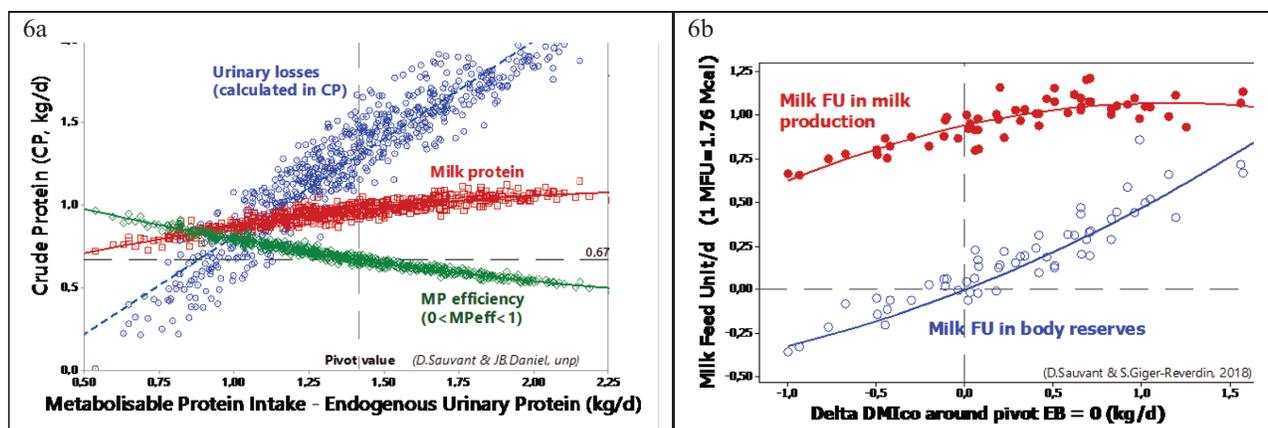

Figure 6. Intraexperimental responses (a) in dairy cows of milk protein production and metabolizable protein (MP) efficiency to its supply and (b) in dairy goats of the partition of milk net energy (in Milk Feed Unit = Milk FU = 1.76 Mcal) to concentrate supply (Delta DMIco) around the pivot of energy balance (EB) = 0.

robustness do not have the same status with respect to knowledge and application. Efficiency has been measured fairly frequently in short- and medium-term studies and it is largely empirically modeled in recent feed unit systems, such as INRA (2018). On the other hand, long-term efficiency was less studied and modeled, so it seems necessary to consider it more systematically, especially with regard to ruminant females. In contrast, robustness suffers from a lack of measurable and relevant traits given that it corresponds to a complex property. Consequently, it seemed that the traits which have been measured until now to tackle robustness have resulted more from technical possibilities than from scientific objectives. However, the models of multiple responses proposed in the INRA (2018) system make it possible to explore, through meta-analyses, certain aspects of the robustness of ruminants.

Given the importance of the requirement for maintenance, efficiency and performance is closely related and this connection has somewhat hidden many other biological aspects that are involved in feed conversion efficiency. These include aspects related to behavior, ingestion, and digestion that have been less studied than metabolic aspects. Until now the dairy cow has been a privileged object of study for issues of efficiency and robustness. This choice is understandable because of the economic importance of milk and the fact that intense selection has resulted in more obvious problems in practice. However, it is important that similar studies on all types of domestic ruminants be conducted. Furthermore, it is important that studies on efficiency and robustness involve more closely related multidisciplinary teams including geneticists, nutritionists, reproductive physiologists, and ethologists with the goal of developing interdisciplinary models that are more suited to significant progress.

About the Author

Daniel Sauvant is Professor Emeritus of Animal Science at AgroParisTech (Health and Life Sciences Department). He obtained the diploma "Ingénieur Agronome" from Institut National Agronomique (Paris) followed by MSc and PhD from the University of Paris-Sorbonne. His major scientific and technological contributions include mechanistic modeling applied to animal nutrition; meta-analysis of databases in animal nutrition; feed evaluation; updates on feed unit systems for ruminants; and recommendations and requirements for feeding goats. Dr. Sauvant served as Director of the INRA Research laboratory (UMR MoSAR [Modélisation appliquée aux ruminants]) from 1985 to 2009, Head of the Department of Animal Sciences at AgroParisTech from 1993 to 2006, and as President of the French Association of Zootechnie (AFZ) from 2000 to 2014. Dr. Sauvant is a corresponding/full member of the French Academy of Agriculture since 1996 and a corresponding member of the French Veterinarian Academy since 2016. **Corresponding author:** sauvant@agroparistech.fr

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