

Energy metabolism in goats and sheep and its relationship with productive performance

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ABSTRACT

Energy metabolism in goats and sheep consists of a set of physiological and biochemical processes responsible for converting dietary nutrients into usable energy for maintaining vital functions and productive activities of the body. With that, the aim of this work is to discuss the main processes related to energy metabolism in goats and sheep and their implications for the productive performance of these animals. In small ruminants, metabolic energy primarily comes from the ruminal fermentation of structural carbohydrates, resulting in the production of short-chain fatty acids (SCFAs), like acetate, propionate, and butyrate. Propionate stands out as the main gluconeogenic precursor, supplying the glucose needed especially during critical physiological stages like lactation and pregnancy. The efficiency of energy metabolism is directly related to diet composition, ruminal microbiota, and environmental conditions, affecting animal performance and the sustainability of production systems. The energy in feed is divided into gross, digestible, metabolizable, and net energy, the latter being responsible for maintenance and production. Energy deficiencies or excesses can compromise health, fertility, and weight gain in animals. So, understanding the basics of energy metabolism is crucial for developing more efficient feeding programs that are adapted to physiological and environmental conditions, especially in semi-arid regions.

RESUMO

O metabolismo energético em caprinos e ovinos constitui um conjunto de processos fisiológicos e bioquímicos responsáveis pela conversão dos nutrientes dietéticos em energia utilizável para a manutenção das funções vitais e atividades produtivas do organismo. Com isso, o objetivo do presente trabalho é discutir os principais processos relacionados ao metabolismo energético em caprinos e ovinos e suas implicações no desempenho produtivo desses animais. Em pequenos ruminantes, a energia metabólica deriva predominantemente da fermentação ruminal de carboidratos estruturais, resultando na produção de ácidos graxos de cadeia curta (AGCCs), como acetato, propionato e butirato. O propionato destaca-se como principal precursor gliconeogênico, suprindo a glicose necessária especialmente em fases fisiológicas críticas, como lactação e gestação. A eficiência do metabolismo energético está diretamente relacionada à composição da dieta, à microbiota ruminal e às condições ambientais, impactando o desempenho zootécnico e a sustentabilidade dos sistemas produtivos. A energia dos alimentos é fracionada em energia bruta, digestível, metabolizável e líquida, sendo esta última responsável pela manutenção e produção. Deficiências ou excessos energéticos podem comprometer a saúde, a fertilidade e o ganho de peso dos animais. Portanto, a compreensão dos fundamentos do metabolismo energético é crucial para o desenvolvimento de programas alimentares mais eficientes e adaptados às condições fisiológicas e ambientais, especialmente em regiões semiáridas.

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Introduction

Goat and sheep farming has stood out in agriculture due to the animals' hardiness and adaptability, as well as their feed efficiency. The actual goat and sheep herds in Brazil are estimated at 12.8 million and 21.7 million, respectively, mainly concentrated in the Northeast region, with the state of Bahia standing out as the main national producer (IBGE, 2023). Traditionally, goat and sheep farming was directed only toward meat, milk, and hide production in the less developed areas of the country. However, this activity has become a viable option in the Semi-Arid region due to the adaptive capacity of these species under harsh environmental conditions (Santos *et al.*, 2023). Goat and sheep farming represents a major economic source, both for food production (meat products, milk, and derivatives) and for high-value commercial products (leather, wool, and inputs) for the industrial sector (Estrada, 2013).

One of the key factors for the productive performance of small ruminants is energy metabolism, which involves the uptake, transformation, and use of energy from food (Berchielli, Pires, and Oliveira, 2011). How efficiently goats and sheep convert the energy they eat into meat or milk directly affects the economic viability of the farming system (Estrada, 2013). For the nutritional needs of goats and sheep to be met, the energy and protein provided must meet this requirement, with energy being necessary for the maintenance and production of these animals (Moraes, Costa, and Araújo, 2011). Considered the biggest factor impacting animal production (representing about 85% of costs), the feed provided should be closely linked to the success and achievement of relevant zootechnical indexes (Moraes, Costa, and Araújo, 2011).

Energy plays a vital role in sustaining life and was described by Kleiber (1961) as the “flame of life,” obtained by animals through the digestion and metabolism of nutrients. Understanding energy requirements means knowing how this energy is processed and used by the body. According to the NRC - National Research Council (1981), energy requirements for maintenance include basal metabolism (or heat production during fasting), the caloric increase from food intake, and the processes needed to maintain body temperature, spontaneous physical activity, and vital metabolic functions like breathing, blood circulation, and cellular activity (Silva *et al.*, 2024). Metabolizable energy (ME) is the energy used for production, meaning it's not used for maintenance but is instead retained as tissues or products. So, this is the energy the animal uses for weight gain or milk production, for example (NRC, 1981).

Understanding the basics and specifics of energy metabolism in goats and sheep is essential for developing nutritional strategies (like using native pastures or energy supplementation) that boost production efficiency, reduce metabolic losses, and promote greater sustainability in production systems. So, this review aims to discuss the main processes

related to energy metabolism in goats and sheep and their implications on productive performance.

Zootechnical importance of goats and sheep

Agribusiness in Brazil has a considerable share in the contribution to the gross domestic product (GDP), making up 23.2% of the Brazilian economy in the last quarter of 2024, according to the Brazilian Confederation of Agriculture and Livestock (*Confederação da Agricultura e Pecuária do Brasil* - CNA) (2025). Agricultural activities grew 12.2% in the first half of 2025 compared to the last quarter of 2024, contributing to an increase from 6.7% to 7.4% (CNA, 2025). Since 1960, goat and sheep production has undergone significant changes “driven by a more favorable institutional environment, as well as the expansion of export markets,” according to Monteiro, Brisola, and Vieira Filho (2021), resulting in good zootechnical performance indicators.

Currently, in Brazil, the number of goats and sheep is estimated at 12.8 million and 21.7 million, respectively (IBGE, 2023). In 2019, the goat population was 11.3 million and the sheep population was 19.7 million, with both being more concentrated in the Northeast region due to their high adaptability to the semi-arid environmental conditions (Magalhães *et al.*, 2020).

Raising goats and sheep in tropical and semi-arid regions (Northeast) is seen as a strategy in livestock farming, since they stand out when exposed to environments with scarce water, low-quality pastures, and high temperatures due to their ability to adapt to less favorable areas, low maintenance costs, and efficiency in food conversion (Santos *et al.*, 2023). When it comes to the market for products and derivatives, the production of goats and sheep offers growing opportunities to add value to their products, like meat, milk, leather, and hides, both in the domestic and international market, supporting the development of the activity (Neres *et al.*, 2024).

Despite their hardiness, the productivity of these animals is closely linked to the proper supply of nutrients, especially energy, which highlights the importance of understanding their energy metabolism to achieve better zootechnical and economic results. Providing adequate nutrition is crucial for good productive and reproductive performance. For this, not only the nutritional value of the feed but also the animal's physiology should be considered when talking about nutrient utilization (Gomes, Leite and Ribeiro, 2007).

Physiological characteristics of small domestic ruminants

Goats and sheep are considered ruminants according to the evolutionary phylogeny of the artiodactyl genus (Melo and Silva, 2017), since the gastrointestinal tract (GIT) of these animals consists of the mouth, pharynx, esophagus, glandular stomachs, e.g., rumen, reticulum, and omasum, glandular stomach, e.g., abomasum, small intestine, e.g., the duodenum, jejunum, and ileum, large intestine, e.g., cecum, colon, and rectum, as well as the

accessory glands present in the oral cavity for saliva production, i.e., salivary glands, and the pancreas/liver complex, having as their main function the digestion of food, absorption of nutrients, and excretion of indigestible components (Silva and Leão, 1979).

The rumen and reticulum act as storage and fermentation sites, where bacteria break down cellulose and hemicellulose. The omasum absorbs much of the water and minerals present in the diet, while the abomasum is the true glandular stomach, producing hydrochloric acid and pepsin to allow enzymatic digestion. The cecum is considered a fermentation chamber for the digestion of structural carbohydrates that were not digested in the rumen, as the digesta moves through it by the action of anaerobic microorganisms. The small intestine is responsible for nutrient absorption, and the large intestine absorbs water along with electrolytes, resulting in the formation of feces. Through the course of evolution, ruminants have developed some modifications in their digestive tract, which are physical, chemical, and biochemical (Berchielli, Pires, and Oliveira, 2011).

According to Van Soest (1994), the anatomical and physiological specializations of the ruminant GI tract, especially microbial fermentation in the rumen, have led to greater efficiency in digesting the fibrous content of the diet. These adaptations have significantly reduced the need for external sources of water-soluble vitamins, like B and C complex vitamins, as well as essential amino acids, since these compounds are synthesized in sufficient amounts by the ruminal microbiota. Changes in the rumen environment can negatively affect nutrient use and cause morphological changes in the rumen lining (Costa *et al.*, 2009).

The ruminal microbiota converts the fermentable dietary content into short-chain fatty acids (SCFAs), mainly acetic, propionic, and butyric acid. These compounds are the main source of energy for small domestic ruminants. Propionic acid, and its ionic form called propionate, for example, is essential for liver gluconeogenesis, since these animals consume few monosaccharides, like glucose, directly in their diet (Cannas, Tedeschi, and Fox, 2004). So, the digestive and metabolic efficiency of these animals directly depends on a balanced supply of nutrients. Diets with too much indigestible fiber, or with energy and protein deficits, mess with the rumen microbiome's activity, lowering SCFA production and microbial protein synthesis. This limitation affects the absorption of essential nutrients, impacting energy metabolism and, as a result, productive performance (BR - Caprinos & Ovinos, 2024).

Basics of energy metabolism

Energy metabolism includes the physiological and biochemical processes through which nutrients from the diet are converted into energy available for the body's cellular functions. This energy is essential for maintaining body balance, supporting vital functions like growth, reproduction, lactation, and immune response, and also directly affects the animals' productive performance (Kozloski, 2017; NRC, 2007).

In goats and sheep, the energy in their diet mainly comes from the microbial fermentation of complex carbohydrates, e.g., starch, pectin, beta-glucan, cellulose, and hemicellulose, in the rumen. This process is carried out by bacteria, protozoa, and fungi, producing volatile fatty acids (SCFAs) as the final fermentation product, which are the main source of metabolizable energy (Van Soest, 1994). The concentrations of these SCFAs are closely related to energy use in ruminants since methane production per mmol of fermented hexose varies depending on the type of SCFAs produced.

Morgavi *et al.* (2023) review the hypothesis that reducing enteric methane emissions in ruminants would increase the animals' energy efficiency, assuming that the energy that would be “lost” through methane production could be redirected to milk, meat, and other production. Although methane is considered an energy loss when calculating the energy balance, this work shows that simply blocking methanogenesis by reducing emissions by around 25% with inhibitory additives doesn't lead to clear and consistent gains in animal production (Morgavi *et al.*, 2023).

Propionate is particularly important because it is the main precursor of glucose through gluconeogenesis. On the other hand, acetate, a substrate for lipogenesis important for lactating animals, and butyrate, a direct energy source for enterocytes that stimulates the growth of rumen papillae in young animals, are used as a localized energy source, applied in the GIT for transport across membranes (Berchielli, Pires, and Oliveira, 2011; NRC, 2007). It's worth remembering that these organic acids are absorbed in their ionic form, which relates to what was mentioned earlier.

In small ruminants, the energy available in the small intestine mainly comes from the digestion of starch, proteins, and long-chain fatty acids. Although glucose isn't absorbed in large amounts in adult ruminants due to pre-gastric fermentation, enzymatic starch digestion in the small intestine still matters physiologically, especially during certain productive stages, like growth and high production, when starch is a key energy source. In contrast, for non-ruminant animals, this process is a primary way to get glucose and is crucial to meet their energy needs (Resende, Texeira, and Fernandes, 2011).

In animals kept under normal feeding conditions, propionate is recognized as the main precursor of hepatic gluconeogenesis, being the primary pathway for glucose synthesis in ruminants. Besides that, glycogenic amino acids and lactate also play important roles as substrates for the formation of endogenous glucose.

Glucose metabolism in goats and sheep

In ruminants, glucose metabolism has distinct characteristics compared to monogastric animals because of the microbial fermentation that occurs in the fore-stomach. During this process, most of the carbohydrates consumed are fermented in the rumen, which prevents dietary glucose from directly reaching the small intestine in significant amounts (Van

Soest, 1994; Kozloski, 2017). As a result, circulating glucose in ruminants mainly comes from gluconeogenesis, a key mechanism for maintaining blood sugar balance.

Propionate, one of the most important products of ruminal fermentation, is the main precursor of liver glycogen in mammals. After being absorbed through the rumen wall, it is transported to the liver, where it is converted into glucose via the gluconeogenic pathway (NRC, 2007). Besides propionate, glucogenic amino acids (like alanine and glutamine) and lactate also play important roles as substrates in this process, especially in situations of higher energy demand, like late pregnancy and peak lactation (BR - Caprinos & Ovinos, 2024).

Under normal physiological conditions, gluconeogenesis in ruminants is continuous and highly regulated, since glucose is essential for glucose-dependent tissues, such as the central nervous system, red blood cells, particularly the reproductive system, and mammary tissue in lactating animals. In high-producing female goats and sheep, it is estimated that more than 60% of the synthesized glucose goes to galactopoiesis (Kozloski, 2017). This fact highlights the need for proper nutritional intake that supports propionate production in the rumen, mainly through diets with an adequate amount of fermentable carbohydrates.

There are general principles that govern how animals get energy from different metabolic substrates, as well as the pathways through which this energy is transferred across the various stages of metabolism. Additionally, the biochemical mechanisms the body uses to synthesize new molecules from the available energy and metabolic precursors are well established (Lehninger, Nelson, and Cox, 2017).

Main metabolic pathways

Energy metabolism involves a complex network of biochemical pathways that coordinate the production, storage, and use of energy in living organisms. These pathways work together to ensure a constant supply of energy for essential cellular processes like protein synthesis, muscle contraction, active ion transport, and maintaining body temperature (Lehninger, Nelson, and Cox, 2017).

Among the main pathways involved in this process, glycolysis stands out, the route responsible for breaking down glucose into pyruvic acid (or lactate under anaerobic conditions), producing small amounts of ATP.

Adenosine triphosphate - ATP

Adenosine triphosphate (ATP) is the main energy currency of biological systems, essential for carrying out cellular processes like macromolecule synthesis, active ion transport, and muscle contraction (Lehninger, Nelson, and Cox, 2017). In ruminants, ATP production is closely related to the efficiency of ruminal fermentation and the use of short-chain fatty acids (SCFAs) produced in this process. Nowadays, it is well established that in the complete

oxidation processes of a food in the body, part of the chemical energy from the food is used to form the terminal pyrophosphate bond of ATP from adenosine diphosphate (ADP) (Resende, Texeira, and Fernandes, 2011). In its simplest form, the oxidation of a food can be expressed as follows:



The absorption of a glucose molecule in the small intestine results in the production of about 36 ATP molecules, while in the rumen, the fermentation of carbohydrates produces SCFAs like acetate, propionate, and butyrate, which are also metabolized to provide energy (Di Marco *et al.*, 2007). For example, the oxidation of 1 mol of propionate can generate up to 34 ATP, while butyrate can provide up to 25 ATP, depending on rumen conditions and how efficiently these compounds are absorbed and metabolized (Di Marco *et al.*, 2007).

Also, ATP production in ruminants can vary depending on their diet and the composition of the rumen microbial flora. Diets high in fermentable carbohydrates tend to increase propionate production, which supports liver gluconeogenesis, while diets higher in fiber can result in more acetate and butyrate, which are used directly in energy processes in the body (Henriques, 2024).

Krebs Cycle

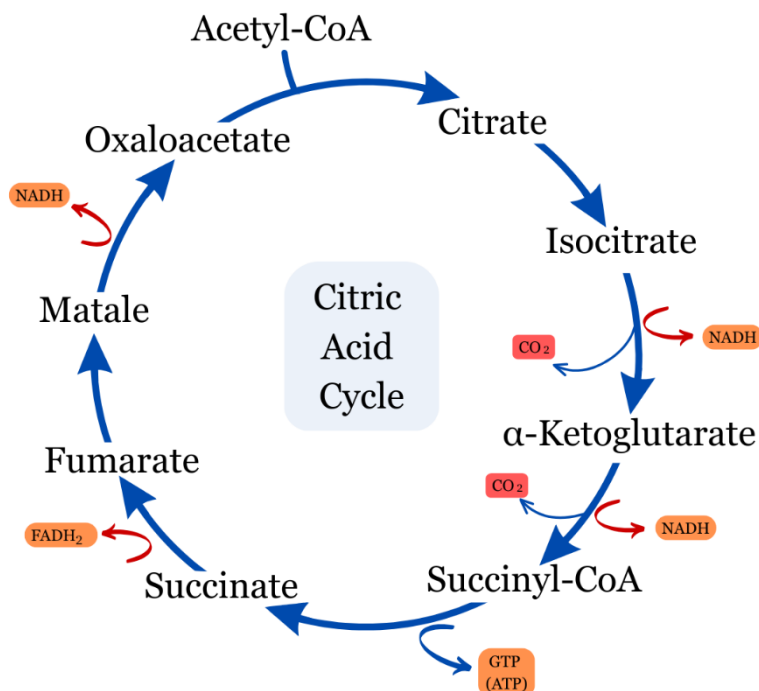
The Krebs cycle (KC), e.g., also called the citric acid cycle or the tricarboxylic acid cycle (Figure 1), is a central metabolic pathway in the aerobic breakdown of mammalian eukaryotic cells, responsible for completely oxidizing acetyl-CoA, generating chemical energy in the form of NADH, FADH₂, and GTP, which will be used in oxidative phosphorylation to produce ATP (Lehninger, Nelson, and Cox, 2017).

In ruminants, the main precursors that enter the TCA cycle are derived from SCFAs, produced by ruminal fermentation of structural or non-structural carbohydrates. Among these, acetate and butyrate are converted into acetyl-CoA due to the number of carbons in their structure, and they are metabolized in the TCA cycle by peripheral tissues, e.g., liver, skeletal muscle, and adipose tissue (Kozloski, 2017; BR - Caprinos & Ovinos, 2024).

The role of CK goes beyond simply producing energy. This mechanism acts as a convergence point between the metabolism of carbohydrates, fats, and proteins, since the cycle's intermediates also serve as precursors for the synthesis of non-essential amino acids, gluconeogenesis, and other anabolic processes. In lactating ruminants, for example, energy generation via CK is essential to support the high metabolic demand of mammary tissue.

Figure 1.

Products of a round of the nitric acid cycle.



Note: Leningher et al., 1995.

With the channeling of acetyl-CoA into the cycle, the availability of oxaloacetate is crucial for the efficiency of acetyl-CoA oxidation mechanisms, which can become limiting in situations of energy restriction or certain physiological states, like during the transition period of pregnancy and lactation, and even in fetal growth and postnatal growth. In the case of the transition period in females with energy restriction at the end of pregnancy, or in cases of twin/triple pregnancies, which is common in goats and sheep, fat mobilization leads to increased acetyl-CoA concentrations, but the lack of oxaloacetate redirects this compound toward the formation of ketone bodies, contributing to clinical or subclinical ketosis and leading to pregnancy toxemia (Kozloski, 2017; NRC, 2007).

Therefore, the mechanisms contained in CK are not only necessary for ATP production but also a central link in the metabolic integration of nutrients. Their efficient activity directly affects the productive and reproductive performance of goats and sheep, being influenced by factors such as diet composition, physiological stage, and the animal's nutritional status.

Rumen digestion and fermentation

In ruminants, like goats and sheep, digestion starts with eating food that is first stored in the rumen, the largest compartment of the non-glandular stomach. This organ hosts a complex microbial community responsible for the anaerobic fermentation of both structural

and non-structural carbohydrates, turning them into high-energy products, like SCFAs, gases, and microorganisms (Van Soest, 1994; Bergman, 1990).

As described earlier, ruminal fermentation occurs through the enzymatic action of anaerobic microorganisms in a symbiotic association, which promote the breakdown of complex polysaccharides and soluble compounds like sugars and starches (Flint *et al.*, 2008). Microbial enzymatic action converts these substrates into pyruvate, the main metabolic intermediate of ruminal fermentation. From there, various pathways lead to the formation of SCFAs (Zhang *et al.*, 2023).

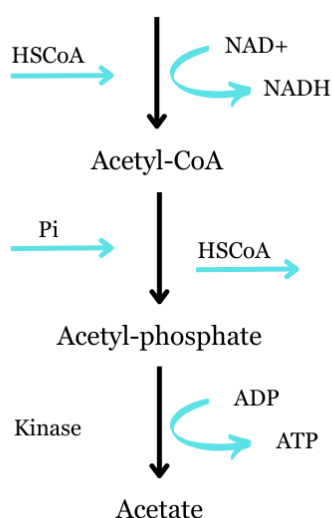
Acetate formation

Acetate is the SCFA produced in the largest amount in the rumen, especially in high-fiber diets (forages). It is mainly generated by the enzymatic action of cellulolytic bacteria, such as *Fibrobacter succinogenes*, *Ruminococcus albus*, and *Ruminococcus flavefaciens*, that break down cellulose into acetic acid, with acetate being the main product absorbed from cellulose fermentation (Van Soest, 1994).

The conversion of pyruvate to acetate can happen through different mechanisms in ruminal bacteria, with the main mechanisms shown in figure 2. Acetate is mainly formed from a metabolic pathway where pyruvate is enzymatically converted into acetyl-CoA through its connection with coenzyme A (CoA). In this process, formate is simultaneously released as a byproduct. This conversion is a key step in ruminal fermentation, especially in fiber-rich diets, and is catalyzed by enzymes like pyruvate:formate lyase, found in specialized anaerobic microorganisms (Resende, Texeira, and Fernandes, 2011).

Figure 2.

Acetate formation by ruminal bacterial fermentation.



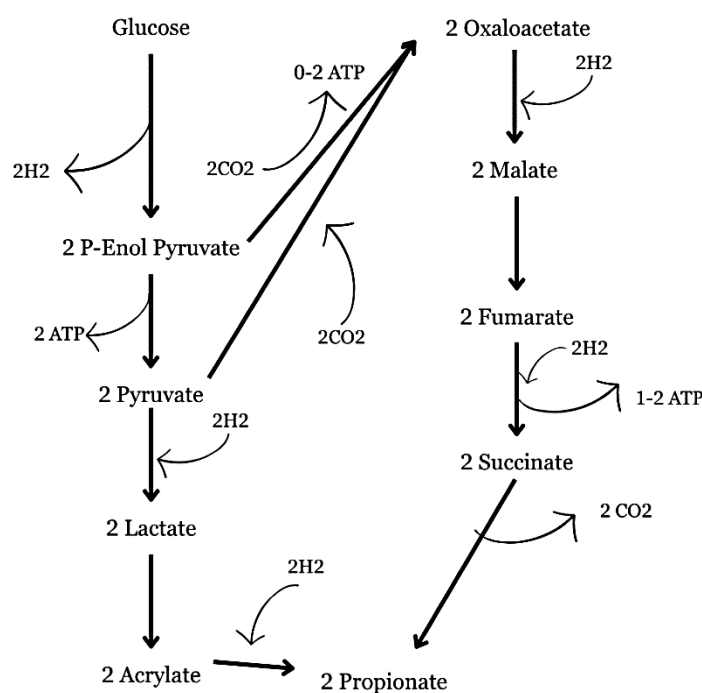
Note: Adapted from Palmquist; Mattos, 2006.

Formation of propionate

Propionic acid is mainly produced by the enzymatic action of rumen bacteria, such as *Selenomonas ruminantium*, *Succinivibrio dextrinosolvens*, and *Prevotella ruminicola*, through metabolic pathways like the succinate pathway, which converts succinate into propionate. Propionate production is favored in diets with a higher proportion of concentrates, like corn grains, which are mostly fermented into propionate (Van Soest, 1994).

The production of propionate is the main way H^+ and electrons are eliminated in the rumen, and it happens through two main mechanisms (Figure 3). The first one is related to the formation of oxaloacetate and succinate, which reacts with coenzyme-A, forming succinyl-CoA that is decarboxylated to form propionate. The second involves the formation of acrylate, where pyruvate is turned into lactate, which is converted into acrylate and then reduced to propionate (Resende, Texeira, and Fernandes, 2011).

Figure 3.
Stoichiometric pathway of propionate production in the



Note: Adapted from Ungerfeld; Kohn, 2008.

Butyrate formation

Butyric acid is produced by rumen bacteria, such as *Butyrivibrio fibrisolvens*, *Anaerovorax odorimutans*, and *Eubacterium ruminantium*, through the fermentation of

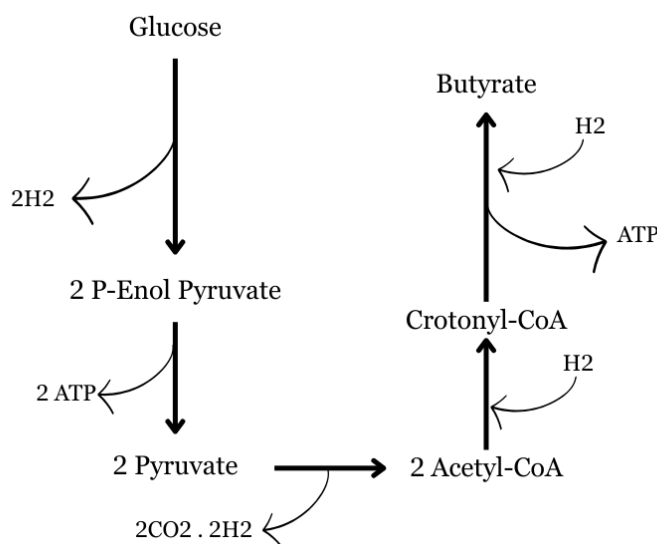
carbohydrates and proteins. Butyrate production is favored in diets with a higher proportion of fiber, like forages, which are mainly fermented into butyrate (Van Soest, 1994).

Butyrate is mainly formed from the condensation of two acetyl-CoA molecules (Figure 4), resulting in acetoacetyl-CoA, which goes through reduction and hydration reactions to form butyryl-CoA, and is finally converted into butyrate by the action of the enzyme butyrate kinase or butyryl-CoA:acetate CoA-transferase (Bergman, 1990; Zhang *et al.*, 2023).

Butyrate is quickly absorbed by the epithelial cells of the rumen, being their main energy source. Besides that, it: Stimulates rumen development, modulates gene expression, improves intestinal integrity, and reduces pathogen colonization (Baldwin *et al.*, 2004; Bento *et al.*, 2020; Zhang *et al.*, 2023)

Figure 4.

Stoichiometric route of butyrate production in the rumen.



Note: Adapted from Ungerfeld; Kohn, 2008.

Fermentative pathways and energy production

Fermentation in the rumen is mainly anaerobic, and the fate of pyruvate depends on the diet profile and microbial composition. This fermentation also produces gases like CO₂, CH₄ and H₂, which are eliminated by belching. Microbial synthesis also produces microbial protein, which is the main source of amino acids for ruminants, and is later digested in the small intestine (NRC, 2007).

The efficiency of ruminal fermentation is highly dependent on diet composition, feeding frequency, nitrogen availability, and the physico-chemical conditions of the rumen (pH, osmolarity, passage rate). For example, diets with too much starch can promote lactic acid production and lead to subacute ruminal acidosis, which harms the microbiota and energy utilization (Plaizier *et al.*, 2008).

Energy partition

Energy can be defined as the capacity to do work and involves maintaining all vital processes. This energy for ruminants can be obtained through food, such as energy-dense concentrates. These foods are defined as those that have a high content of usable energy per unit of weight, being over 60% of total digestible nutrients (TDN) and less than 20% crude protein (CP), such as corn, sorghum, molasses, fats, among others (Bonfim and Barros, 2024; EMEPA, 2018). However, it's worth noting that physiology and ruminal fermentation can vary between species, which justifies the need for prediction models for each of them.

With that, in the case of goats and sheep, there is still a gap in applying models to predict the energy value of feed, which prevents accurate diet formulation for these species. Therefore, improving these prediction models is essential for developing more precise and efficient diets. Currently, because there isn't an estimation model for TDN specifically for goats and sheep, the equation used for cattle is applied with some modifications. In this way, TDN is determined by the sum of the digestible fractions of crude protein (CP), ether extract (EE), neutral detergent fiber (NDF), and non-fibrous carbohydrates (NFC).

This estimate represents the energy potentially available after digestion, but it doesn't take into account the additional energy losses that occur during metabolism, like methane production, urinary excretion, and metabolic heat (Bonfim and Barros, 2024). That's why NDT only reflects the digestibility of the nutrients in the feed, making it a broader estimate than metabolizable or net energy. But as the name itself suggests, NDT is based solely on measuring the digestibility of the feed's nutrients, without considering energy losses (Bonfim and Barros, 2024).

However, for the purpose of formulating diets and accurately assessing energy efficiency, it is necessary to consider the progressive breakdown of food energy, from gross energy to the net energy actually used by the animals. Thus, the energy intended for ruminant nutrition is conventionally divided into gross energy (GE), digestible energy (DE), metabolizable energy (ME), and net energy (NE) (Figure 5).

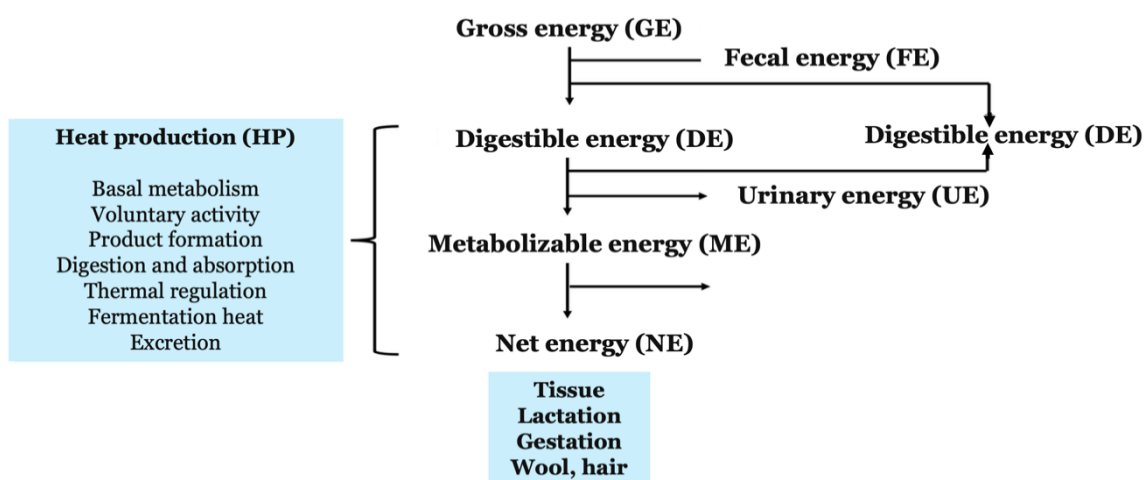
Gross energy (GE) is defined as the energy present in the food or diet. It is released as heat as an organic substance is completely oxidized to carbon dioxide (CO₂) and water (H₂O) (Berchielli, Pires, and Oliveira, 2011; Kleiber, 1972).

Digestible energy (DE) corresponds to the portion of the food's energy that is actually digested and absorbed by the animal. The first energy loss happens when undigested nutrients are excreted in the feces. So, digestible energy, also called apparently digestible energy, is calculated by the difference between the gross energy consumed and the energy lost in the feces (Berchielli, Pires, and Oliveira, 2011; Bonfim and Barros, 2024).

Metabolizable energy (ME) is determined by the energy lost through urine and gases produced in the rumen, meaning that part of the apparently digestible energy absorbed by the animal is lost due to gas production. This loss accounts for about 8% of the food's energy. Another part of the energy is excreted through urine, which includes compounds that were absorbed but not used. Thus, metabolizable energy is calculated by subtracting the energy lost through gases and urine from the apparently digestible energy (Berchielli, Pires, and Oliveira, 2011; Bonfim and Barros, 2024).

Figure 5.

Energy usage scheme by ruminants.



Note: Adapted from Berchielli et al., 2011.

Net energy (NE) is determined by the difference between the losses of metabolizable energy and the losses due to digestion, fermentation, and metabolism processes. So, it is defined as the part of the food's energy that is used by the animal, that is, the energy retained in the form of a useful product that goes into tissue production, milk production, pregnancy, fetus, among other things. NE can also be divided for maintenance (EL_M) and for lactation (EL_L) and net energy for weight gain (EL_G), referred to as net energy for production (EL_P). The energy for maintenance, which is used in basal metabolism, shows a caloric increase (CI) equivalent to 25% of metabolizable energy; the one related to production energy has a CI of 10-60% of metabolizable energy. To meet the needs of fasting metabolism, activity, and maintenance, it is used EL_P already for growth, fattening and production of milk, wool, and gestation, it is used EL_L and EL_G (Berchielli, Pires, and Oliveira, 2011; Bonfim and Barros, 2024).

From the definitions above, it's then possible to determine the efficiency of use to understand the proportion of energy offered in the food and what is retained in the animal, using the following simple relationship:

$$\frac{\text{Total energy retained in gain} \times 100}{\text{Total energy in the food}}$$

Relationship between energy metabolism and productive performance

It is known that energy is vital for animal production, and this energy is obtained through the interaction of nutrients, like carbohydrates, lipids, and proteins when metabolized (Resende *et al.*, 2006). This energy is used for maintenance, growth, fattening, reproduction, pregnancy, and lactation, so when its supply is lacking, it can cause some problems in the animals' development, like slower growth, delayed weight gain, and delays in the onset of puberty. It also lowers fertility and makes them more susceptible to diseases. Similarly, when there's excessive energy consumption, there are also drawbacks, like high fat deposition, which can lead to imbalances of other nutrients (Estrada, 1998; 2013). So, it's essential that the animal consumes the necessary amount of energy to ensure the proper functioning of vital physiological processes according to its stage (Da Silva *et al.*, 2010).

Animals at maintenance need a minimum amount of energy so their bodily processes run without them gaining or losing weight. In other words, giving them the right amount lets them keep the proper weight and meet just their basic physiological and metabolic needs, like regulating temperature, breathing, digestion, blood circulation, keeping warm, and so on. So, it's important for animals to get diets calculated based on their needs and physiological state (Estrada, 2013; Moraes *et al.*, 2016).

For animals that are gaining weight, growing, and fattening, energy requirements are related to the deposition of protein and fat in the animal's body. Once energy intake exceeds what is spent on maintenance, energy becomes available for weight gain (Cézar and Souza, 2007). It's known that as the animal grows and develops, changes happen in the body tissues, meaning that the body tissues undergo alterations, and these intense changes depend on several factors, such as nutrition (Yáñez *et al.*, 2006). Energy requirements can also vary according to breed, gender, and other factors. According to Marcondes *et al.* (2010), females store fat more quickly compared to males, so they need more energy to gain weight. Additionally, Pereira (2017) showed in his work that females need higher amounts of energy to gain weight compared to intact and castrated males.

When it comes to reproductive issues, it is known that reproductive performance is key to production success. And when we talk about energy nutritional requirements, one of the first functions to be affected when there is a failure in nutritional management is reproduction, both for animals that are already reproducing and for animals that are about to start their reproductive life (Bonfim *et al.*, 2014). According to Scaramuzzi and Martin (2008), nutrition affects the ovaries and can either stimulate or inhibit the reproductive cycle. Likewise, nutrition also affects the hypothalamic-pituitary axis, determining whether the axis is

unlocked or not, which impacts whether ovulation occurs, and it also acts on the follicles, consequently influencing follicular growth and ovulation rate (Bonfim *et al.*, 2014).

It's widely known that pregnant females have high energy demands, since the growth of uterine tissues, fetal development, placental formation, and preparation of the mammary glands are metabolically intense processes (Berchielle *et al.*, 2006). When these females go through periods of undernutrition during pregnancy, as often happens during the dry season, there can be significant impacts on fetal development, especially in vital organs like the liver, heart, and gonads. These morphological and functional changes have long-lasting effects, affecting the offspring's productive and reproductive performance in adulthood (Greenwood *et al.*, 2000; Thomas and Kott, 1995).

During lactation, the focus of energy demands shifts to milk production, with the initial period, which includes colostrum production and the peak milk production, being particularly critical (Ferelli, 2021). Studies show that consuming diets high in non-fibrous carbohydrates can significantly improve milk production. Evidence suggests that females fed diets with higher concentrations of NFC produce more milk compared to diets with low levels of non-fibrous carbohydrates (Bovera *et al.*, 2004).

Nutritional strategies to optimize energy metabolism

Considering that optimizing energy metabolism in small ruminants is essential to improve productive performance and increase feed efficiency, there has been a focus on using nutritional strategies that optimize energy metabolism through supplementation. The goal of supplementation is to improve energy intake by adding nutrients to a basic diet, preventing drops in productive performance and animal weight, and also allowing them to reach goals faster, such as weight gain.

According to Vechiato and Ortolani (2008), diets that have high energy content allow animals to gain more weight in intensive systems. Usually, the main energy source in these systems is corn and sorghum, which is not so popular with producers due to the high cost compared to protein supplementation. However, even though it's not that popular, it has a high potential to affect the animal's performance (Silveira *et al.*, 2007). On the other hand, when these energy sources are provided in excess, they can cause health problems in animals, like digestive issues and metabolic disorders. However, using them properly and in balance has a high potential to improve the animal's performance. So, to meet producers' demands, one alternative is to use unconventional feed, such as agro-industrial by-products from grain farming and fruit growing (Deminicis *et al.*, 2012; Tigre, 2012), the forage palm, inert fats, among others.

These by-products can be included in ruminant feeding due to their ability to convert these foods into a source of energy and the subsequent production of high-quality milk or meat (Tigre, 2012). Examples of by-products include citrus pulp (Quinto and Bizzuti, 2020) and

soybean molasses (Arruda *et al.*, 2021; Rodrigues *et al.*, 2020; Pereira *et al.*, 2019), cotton seed (Maia, 2011), among others.

According to Tigre (2012), citrus pulp comes from the citrus industry and is made up of the peel, seeds, and orange pulp, and can be given to ruminants during their growth or lactation phases. In addition, it contains pectin, a non-fibrous carbohydrate (NFC), which can be absorbed more quickly by the gastrointestinal tract since it is a rapidly degradable carbohydrate in the rumen. The use of NFC in diets aims to provide energy and consequently increase productivity (Cañizares *et al.*, 2009). In this way, Tigre (2012) showed in his work that citrus pulp can be used to replace both corn and other ingredients in ruminant diets.

Soy molasses, on the other hand, is a by-product derived from soybean meal, which after some processes has a viscous texture and a sweet-and-sour taste. It has high energy quality and fits as a cheap and sustainable alternative for feeding sheep (Rodrigues, 2017). Rodrigues *et al.* (2020), when studying the effects of soy molasses concentrations on performance in feedlots and lamb meat quality, showed that replacing corn grain with soy molasses is a cost-effective option for producers, reducing the use of grains. They showed that the diet cost dropped to R\$ 0.09/kg using soy molasses compared to the control group, which was R\$ 0.10/kg. They also concluded that molasses can improve meat quality due to its high potential when included up to 300 g/kg.

In arid and semi-arid regions, finding alternatives that are efficient, meet the animals' needs, and are low-cost is still a challenge. However, there are already viable options, like using forage cactus. It's viable because of its drought resistance, being able to store up to 90% water, and it has high palatability and high biomass production. On top of that, it's considered a great energy source in animal feed (Da Frota *et al.*, 2015; Spínola *et al.*, 2020), with around 64.66% TDN (Melo, 2006). However, it's worth noting that diets for ruminants can't be based solely on palm due to deficiencies in protein and fiber, and because it can cause metabolic disorders, like diarrhea. According to Brito *et al.* (2020), palm has low dry matter content, around 10 to 13%, and about 4.2 to 6.2% crude protein. Therefore, forage palm should be offered along with other foods that provide fiber and protein (Santos, 2006; Silva and Santos, 2006).

Lipids are considered a high-energy product because of their large proportion of fatty acids, providing 2.25 times more energy than carbohydrates (Silva *et al.*, 2007). According to the NRC (2007), they have a higher energy value when compared to other nutrients and end up being considered the most important source of energy for animals. However, adding fat to ruminant feed should be done with caution, since using fat can harm the microorganisms important for fermentation (Ibrahim *et al.*, 2021). This way, the use of these lipids can't exceed more than 5% of the diet because ruminants don't have the mechanisms to digest them efficiently like they do with proteins and carbohydrates, and for this reason, it can trigger problems in the rumen environment, like reduced fiber digestion, as well as triggering the

processes of hydrolysis and biohydrogenation in the rumen (Ikwuegbu and Sutton, 1982; Silva *et al.*, 2007; Kumar, 2017; Wettstein *et al.*, 2000). To solve this problem, protected fat or inert fat has been used, which is made up of long-chain unsaturated fatty acids, saturated fatty acids, triglycerides, phospholipids, and other components (Prohmann, 2015). This protected fat, in turn, acts directly in the small intestine, where it goes through the digestion and absorption processes and is consequently used as an energy source and helps maintain the health of ruminants (Andrade, 2010; Da Freiria *et al.*, 2022).

Metabolic disorders associated with energy metabolism

Energy metabolism ensures homeostasis and synergy in cellular functions and in the overall context of the organism. However, an imbalance due to lack or excess of energy can lead to health problems in animals and, consequently, affect their production. In small domestic ruminants, metabolic disorders linked to energy metabolism are associated with females in the transition period, i.e., the last third of gestation and the beginning of lactation, as well as animals intended for reproduction.

The metabolism of pregnant and lactating goats and sheep relies on greater mobilization of glucose to the nervous tissue, fetal tissues, and mammary tissue, and the process of making this type of molecule available happens through endocrine mechanisms (Gonzalez and Silva, 2017). So, for hepatic gluconeogenesis and the use of glucose by specific tissues to occur, the phosphorylation of glycogen through the action of epinephrins triggers the release of glucose and a state of hyperglycemia (Kolnes *et al.*, 2014).

Noting that in the last third of pregnancy there is a higher energy demand and limited energy intake in female small domestic ruminants, and depending on the breed, nutrition, and genotype there is a prevalence of twin pregnancies, the need for glucose in the tissues increases, and physiological mechanisms can lead the animals to ketosis, since the energy demand is higher and glucose availability can't meet this demand, resulting in the production of β -hydroxybutyrate, which breaks down into pregnancy toxemia and increased oxidative stress (Marteniuk and Herdt, 1988; Cali, Trana and Claps, 2010; Huang *et al.*, 2021).

Under conditions of energy restriction or overnutrition, glucose metabolism in females can affect reproductive physiology, potentially keeping goats and lambs out of their cycles due to hormonal mechanisms, e.g., the effects of leptin and insulin on reproduction (Chilliard, Delavaud, and Bonnet, 2005). Monitoring nutritional needs during the reproductive phase, along with body condition scoring (BCS), helps ensure synchrony in the hypothalamus-pituitary-gonadal axis and the production of male and female gametes so that fertilization and, later, pregnancy can occur (Gallego-Calvo *et al.*, 2015).

Final considerations

Knowledge about energy metabolism in goats and sheep is essential to improve the productive performance and feed efficiency of these animals. Ruminal fermentation and the production of volatile fatty acids are key processes for energy utilization. Proper diet formulation, using alternative ingredients and nutritional balancing, contributes to metabolic health and productivity, as well as cost reduction. In this way, well-planned nutritional strategies promote more sustainable and economically viable systems.

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