GLEIDSON LUZ AGUIAR

EFFECT OF LACTATION STAGE ON QUANTITATIVE ASPECTS OF DIGESTION AND PHYSIOLOGY OF BEEF COWS

LAVRAS-MG
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Master's dissertation presented to the Universidade Federal de Lavras, as part of the requirements of the Graduate Program in Animal Science, area of concentration in Production and Nutrition of Ruminants, to obtain the title of Master.

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Approved in September 16, 2019.

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Dedico

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ABSTRACT

The lactation period is critical to the cow, since this phase is marked of greatest nutrient demand by beef cows. This demand is associated with milk yield. Information about quantitative adjustments in the uptake and utilization of nutrients according to the stage of lactation in ruminants are scarce. Our objective was to quantify the effects of the physiological status (PS, lactation) and of the stage of lactation (DIM = days in milk) on dry matter (DM) intake (DMI), total apparent, ruminal, and intestinal digestibilities, as well as on metabolism of beef cows. The experiment was conducted in the feedlot facilities of the Department of Animal Science of the Federal University of Lavras. Twelve beef heifers with an average body weight (BW) of 482 ± 129 kg fitted with rumen cannula were used. Seven lactating (LA) cows were compared with their non-lactating (NLA) pairs (n = 5, heifers from the same contemporary group) to estimate the physiological effect of lactation at different time points over time (3, 10, 35 and 100 days of lactation). Before calving the animals were housed in individual pens with 50 m² per animal, with 16 m² of covered area to facilitate animals handling from calving. At being allocated in the pens, the heifers started the adaptation phase to the experimental conditions, in which the quantities of DM offered were gradually increased until voluntary intake was reached. At calving, it was installed in the bottom of each pen, a structure that allows the calves to move to a common pasture area, without the possibility of cows to move. The animal received the same diet composed by (DM basis) corn silage (92.3%) and concentrate supplement (7.7%) prepared from soybean meal (4.55%), ground corn (0.25%), urea (1.58%) and mineral mixture (1.32%). The nutritional composition of the experimental diet was designed to allow *ad libitum* intake without large accumulation of body reserves and adequate maintenance of lactation. Data was analysed through the mixed models methodology, considering the physiological effect (lactating and non-lactating) and the days in milk (DIM) as classificatory fixed effects and the animal as the random effect. Measurements were taken repeatedly over time (animal as experimental unit). The LA group increased DMI (g/kg BW) from DIM10 to DIM35 by 26% ($P < 0.001$), following with intake relatively constant until DIM100 ($P = 0.205$), whereas the NLA group increase by 18% in DMI during all trial period ($P = 0.079$). Ruminal digestibilities of DM, organic matter (OM), and ash- and protein-free neutral detergent fiber (apNDF) were lower for the LA group than for the NLA group from DIM10 to DIM35 ($P < 0.1$). However, there were no differences in ruminal digestibilities of all nutrients until DIM100 ($P > 0.1$). Physiological status did not affect the intestinal digestibility of all nutrients ($P > 0.1$). The mean ruminal pool of DM was greater than 31.5% for LA group that NLA group during the trial period. Lactating cows increased by 6.2% their ruminal pool between DIM10 and DIM100. Non-lactating cows showed ruminal pool relatively constant until DIM100 (mean = 4.55 ± 0.38). Passage rate (kp, h^{-1}) of DM was affected by PS ($P = 0.024$). Lactating group presented greater passage rate (0.045 ± 0.0022) than NLA group (0.037 ± 0.0026). However, higher difference in passage rate between the groups was observed at DIM35 (kp, h^{-1} = 0.011). The physiological status as well as the stage of lactation should be included in performance prediction models, since early lactating beef cows are less efficient at extracting energy from feed compared to non-lactating animals, changing the feed predicted total digestible nutrients (TDN) values.

Key-words: Beef cow, lactation, metabolism, physiology, ruminants

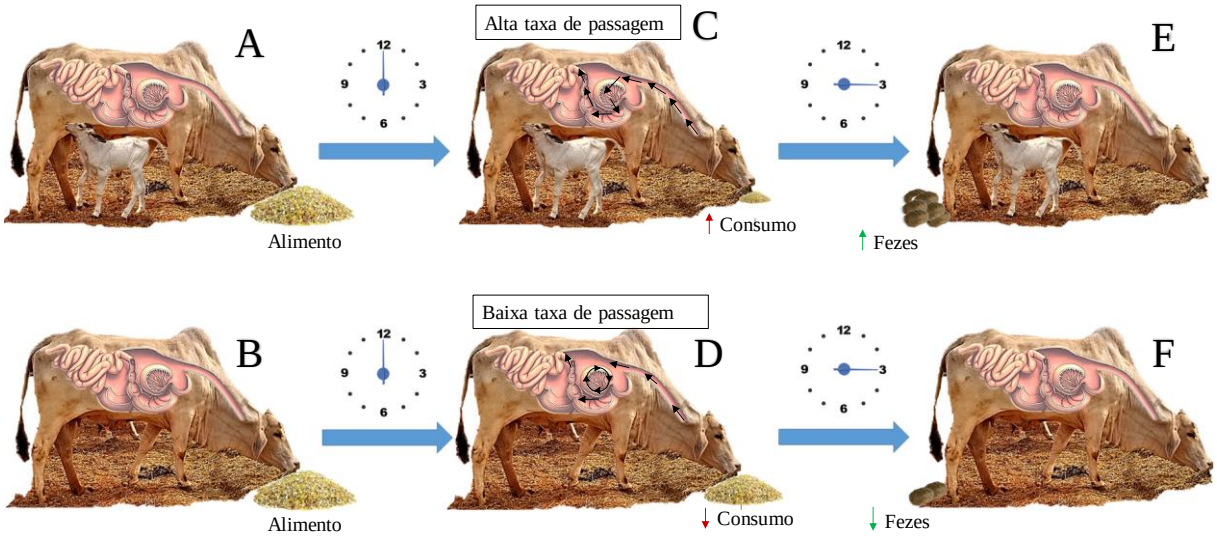
RESUMO

O período da lactação é crítico para a vaca, visto que essa fase é marcada por maior demanda de nutrientes por vacas de corte. Essa demanda está associada à produção de leite. Informação sobre ajustes quantitativos na captação e utilização dos nutrientes de acordo com o estágio da lactação em ruminantes são escassas. Nosso objetivo foi quantificar os efeitos do status fisiológico (lactação) e do estágio da lactação (DIM = dias de lactação) sobre o consumo de matéria seca (CMS), digestibilidades total aparente, ruminal e intestinal e no metabolismo de vacas de corte. O experimento foi conduzido nas instalações de confinamento do Departamento de Zootecnia da Universidade Federal de Lavras. Foram utilizadas doze novilhas de corte com peso corporal (PC) médio de 482 ± 129 kg canuladas no rúmen. Sete vacas lactantes (LA) foram comparadas com seus pares não-lactantes (NLA) (n = 5, novilhas de mesmo grupo contemporâneo) para estimar o efeito fisiológico da lactação em diferentes pontos ao longo do tempo (3, 10, 35 e 100 dias de lactação). Antes do parto os animais foram alocados em baias individuais com 50m^2 por animal, com 16m^2 de área coberta para facilitar o manejo dos animais ao parto. Ao serem alocadas em baias, as novilhas iniciaram a fase de adaptação às condições experimentais, em que as quantidades de matéria seca oferecidas foram gradualmente aumentando até que o consumo voluntário fosse alcançado. Ao parto, foi instalada na parte inferior de cada baia, uma estrutura que permitisse os bezerros se moverem a uma área de pasto comum, sem a possibilitar a locomoção da vaca. Os animais receberam dieta única composta por (base da MS) silagem de milho (92,3%), e suplemento concentrado (7,7%) preparado a partir de farelo de soja (4,44%), milho moído (0,25%), ureia (1,58%) e mistura mineral (1,32%). A composição nutricional da dieta foi planejada para permitir consumo à vontade sem grande acúmulo de reservas corporais e adequada mantença da lactação. Os dados foram analisados através da metodologia dos modelos mistos, considerando o efeito fisiológico (lactante e não-lactante) e os dias em lactação (DIM) como efeito fixo classificatório e o animal como efeito aleatório. As avaliações foram feitas como medida repetida no tempo (animal como unidade experimental). O grupo LA aumentara o CMS (g/kg PC) do DIM10 ao DIM35 em 26% (P < 0,001) seguindo com consumo relativamente constante durante até o DIM100 (P = 0,205), enquanto o grupo NLA aumentou em 18% o CMS durante todo o período experimental (P = 0,079). As digestibilidades ruminal da MS, matéria orgânica (MO) e fibra em detergente neutro corrigida para cinzas e proteína (FDNcp) foram menores para o grupo LA que para o grupo NLA do DIM10 ao DIM35 (P < 0,1). No entanto, não foram observadas diferenças nas digestibilidades ruminal de todos os nutrientes até o DIM100 (P > 0,1). o status fisiológico não afetou a digestibilidade intestinal de todos os nutrientes (P > 0,1). A média de pool ruminal da matéria seca (MS) foi 31,5% maior para o grupo LA que para o grupo NLA durante o período experimental. As vacas lactantes aumentaram em 6,2% seu pool ruminal entre o DIM10 e DIM100. As vacas não-lactantes demonstraram pool ruminal relativamente constantes até o DIM100 (média = 4,55 ± 0,38). A taxa de passagem (kp, h^{-1}) da MS foi afetada pelo status fisiológico (P = 0,024). O grupo lactante apresentou maior taxa de passagem (0,045 ± 0,0022) que o grupo NLA (0,037 ± 0,0026). No entanto, a maior diferença nas taxas de passagem entre os grupos foi observada no DIM35 (kp, h^{-1} = 0,011). O status fisiológico, bem como o estágio da lactação devem ser inclusos nos modelos de predição de desempenho, visto que vacas de corte em início de lactação são menos eficientes em extrair energia dos alimentos quando comparadas a vacas não-lactantes, alterando os valores preditos para nutrientes digestíveis totais.

Palavras-chave: Fisiologia, lactação, metabolismo, vacas de corte, ruminantes

EFEITOS DO ESTÁGIO DA LACTAÇÃO SOBRE ASPECTOS QUANTITATIVOS DA DIGESTÃO E FISIOLOGIA DE VACAS DE CORTE

A capacidade de ingestão e aproveitamento dos alimentos são os principais determinantes no desempenho dos animais. É muito importante a elaboração de modelos matemáticos que sejam precisos em predizer essas variáveis. Quanto mais preciso o modelo, maior a capacidade de aumentar o desempenho e a lucratividade dos sistemas de produção animal. O consumo de vacas de corte depende, dentre outros fatores, do status e estágio fisiológico. O objetivo com esse trabalho foi quantificar as mudanças fisiológicas e metabólicas em vacas de corte em função da lactação e do tempo em lactação (zero a 100 dias). Foi avaliada a forma como a digestão influencia o consumo alimentar em vacas no início da lactação (LA), comparando com as mesmas avaliações em vacas não-lactantes (NLA). Em geral, o alimento passa mais rápido pelo trato digestório das vacas em início de lactação quando comparado às não lactantes. Como o alimento passa mais rápido, menos é digerido. Nós observamos que essas mudanças em função da lactação ocorrem principalmente nos primeiros 35 dias após o parto. Portanto, quando pesquisadores ou nutricionistas forem elaborar dietas para vacas de corte em lactação, deverão considerar que elas aproveitam os alimentos de forma diferente das vacas que não estão em lactação. Nas vacas lactantes, os alimentos passam mais rápido pelo trato digestório. Isso as ajuda a ingerir maior quantidade de alimentos e obter mais nutrientes, mas com uma eficiência um pouco menor, pois os alimentos ficam menos tempo retidos no trato digestório e são menos digeridos.



Efeito do status fisiológico de vacas de corte sobre a ingestão, digestão e aproveitamento dos alimentos. Letras representando as diferenças entre grupos LA e NLA. A = lactante; B = não lactante; C = alta taxa de passagem e consumo; D = baixa taxa de passagem e consumo; E = baixa digestibilidade e maior produção fecal; F = alta digestibilidade e menor produção fecal.

Dissertação de mestrado em Zootecnia na UFLA, defendida em 16 de setembro de 2019.

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SUMMARY

1 INTRODUCTION

The lactation period is critical to the cow, since this phase is marked of greatest nutrient demand by beef cows (Wiltbank et al., 1962) associated with milk yield (Freetly et al., 2006). At this time, a transient state of negative energy balance (NEB) is considered natural, and the glucose production is a key factor, because at this point the maximally secreting mammary gland may require up to 80% of the total glucose turnover. Mepham (1993) affirmed that lactose is a major component in milk and that gluconeogenesis is closely linked to lactogenesis as the amount of available glucose will determine the amount of milk produced.

Information about quantitative adjustments in the uptake and utilization of nutrients according to the stage of lactation in ruminants are scarce (Bell, 1995a), especially in beef cows. The information present in the literature, usually suggests the adjustments in the uptake and utilization of nutrients as a function of the physiological stage in cows to the interaction between physical, physiological and hormonal factors (Ingvartsen and Anderson, 2000). However, the quantitative evaluation of the set of such factors and their interactions has not been established.

Numerous models for predicting dry matter intake (DMI) in ruminants have been developed as shown in reviews by Ingvartsen (1994) and Mertens (1996). The factors affecting DMI of lactating dairy cattle have received much attention for many decades. An alternative motivation for the studying of the mechanisms that regulate intake and metabolism, and particularly their integration, is their importance for the development of better concepts in predictive models for intake, production, energy balance and health of animals (Ingvartsen and Anderson, 2000), increasing the system efficiency and profitability. One of the objectives of proposing models of feeding adjustments for lactating cows is that this allows diluting the maintenance costs of the cows (Baumgard et al., 2017). In the case of beef cows, it means an increase in the production of milk with reflexes in the efficiency of production of calves per year (feed resources per kg of calves weaned per year).

At calving, the abdominal cavity is relieved by the release of the amniotic fluid, fetus and fetal membranes. That represents a decrease of 70 kg for dairy cows and 50-60 kg for beef cows. The disappearance of such a large mass in the abdominal cavity should allow a rapid increase in voluntary feed consumption in the first few days after calving. However, no rapid increase in DMI is observed shortly after calving, and the increase in feed intake is relatively slow, even in relation to the increase in milk production (Friggens et al., 1998). Therefore, it is likely that there are other physical and physiological factors interacting to regulate consumption

and partition of nutrients to various body tissues to maintain nutritional balance during the lactation period. This phenomenon was defined in two conceptual terms: "homeostasis and homeorhesis".

Cannon (1929) conceptualized homeostasis as the condition of relative uniformity that results from organismal adjustments to environmental changes. An example includes maintaining steady-state concentrations of key circulating nutrients, two of which (glucose and calcium) are especially important in lactating cows. Homeorhesis was referred by Bauman and Currie (1980), who defined as the orchestrated or coordinated changes that involve altered body tissues responses to homeostatic signals necessary to support a physiological state.

Bauman and Currier (1980) listed part of the adaptive responses mediated by metabolic changes that occur with the animals at the beginning of lactation (Table 1) showing that lactation is not just a function of the mammary gland but involves various body tissues. Same authors also pointed out the importance of understanding the partition of nutrients in the lactation period, since this physiological state is essential for the survival of species and productive interests.

Table 1 – A partial list of the metabolic changes associated with lactogenesis in ruminants[1]**.**

Physiological function	Metabolic change	Tissues involved
Milk synthesis	Increased use of nutrients	Mammary
Lipid metabolism	Increased lipolysis Decreased lipogenesis	Adipose tissue
Glucose metabolism	Increased gluconeogenesis Increased glycogenolysis	Liver
	Decreased use of glucose Increased use of lipid as energy source	Peripheral tissues
Protein metabolism	Mobilization of protein reserves	Muscle and other body tissue
Mineral metabolism	Increased absorption and mobilization of calcium	Kidney, liver, gut and bone

[1] Adapted from Bauman and Currie (1980)

The action of homeorhetic and homeostatic mechanisms of the lactation period, however, may occur differently in both high-yielding (dairy-type cow) and low-yielding cows (beef-type cow). Baumgard et al. (2017) affirmed that high-yielding cows direct a greater portion of absorbed nutrients to the mammary gland for milk synthesis and, associated with

this, they have a greater voluntary feed intake. Nevertheless, low-yielding cows have a lower feed intake and if they do consume more feed, they use it for excessive body fat accretion rather than milk synthesis.

In general, the postpartum period is marked by changes in the feed intake, digestion kinetics and partition of nutrients to the cow's body tissues in order to prioritize the nutritional supply to the mammary gland. However, these changes are triggered through complex interactions between physical and physiological factors and can be quantitatively expressed differently according to the lactation stage. Therefore, our main hypothesis is that lactating beef cows may present ways to compensate for the imbalance between nutrient intake and demand, for example, increasing ruminal passage rate, and reducing fiber digestion. In addition, a better understanding of the interactions between homeorhetic and homeostatic mechanisms with the advancement of lactation would allow us to propose better feeding models for beef cows.

2 BACKGROUND

2.1 Adjustments in DMI during lactation

Dry matter intake is positively related to animal's productive performance, so the factors affecting the behaviour of this variable has been the focus of numerous studies over years (Ingvartsen and Andersen, 2000). In practice, DMI is commonly used as an indicator of the cow's nutritional status (Grummer et al., 2004).

Cows show DMI increased postpartum when compared to non-lactating cows (Ovenell et al., 1991). This is related to the increased energy demand for milk synthesis, because according to Bell (1995) mammary demands for amino acids, glucose, and fatty acids increase several-fold within 4 d of parturition and lactating beef cows require 20 to 30% greater dietary net energy (NE) to maintain BW when compared to non-lactating cows (Neville, 1971; 1990; NRC, 2001). Furthermore, Hatfield et al. (1989) affirmed that DMI is positively correlated with increasing milk yield.

Dry matter intake is a major factor limiting milk production in early lactation (Kertz et al., 1991). However, it is known that DMI throughout the lactation period is not constant, even under similar feeding conditions. In trials with sheep, Kaske and Groth (1997) reported that during early lactation (10 - 30 d postpartum) feed intake remained on the same level as during late pregnancy (128 - 148 d post conception), but a further increase of 10% was found

during the second month of lactation. However, in beef heifers Marston and Lusby (1995) reported an increase in DMI from late gestation until 6 week postpartum, agreeing with Hunter and Siebert (1986) who reported that Brahman-cross cows had 25% greater DMI during the first month postpartum than non-lactating cows and 35% greater DMI in the third month postpartum. This variation of DMI with the advancement of lactation may be partly explained by the fact that in the first weeks of lactation there are gradual adjustments in the capacity of feed intake due to the return of the rumen to normal size (Ingvartsen and Andersen, 2000), however, DMI is influenced by a multitude of interrelated factors, which makes complex elaboration of feeding models for lactating cows based on this variable (Baile and Mclaughlin, 1987). These factors may be associated with physical, metabolic and endocrine adjustments.

2.1.1 Physical adjustments

2.1.1.1 Rumen capacity

The rumen capacity is a physical characteristic that is directly related to the capacity of feed intake. Mertens (1987) indicated that cows consume approximately 1.2% of their BW/d as neutral detergent fiber (NDF) when intake is limited by rumen capacity and suggested that this relationship was sufficiently consistent to predict DMI. It is known that ruminal capacity is associated, among other factors, to the development of rumen epithelia, and that depending on breed, diet and physiological stage. Research with sheep and beef cows (Forbes, 1968; Stanley et al., 1993) indicates that rumen capacity increases with lactation. In agreement, Park et al. (2011) assessing Holstein dairy cows during the first 90 days of lactation concluded that rumen capacity tended to increase linearly (from 160 to 171 kg), with the most substantial increases being observed by day 34. Expressed as a percentage of body weight, rumen capacity increased during lactation (31.2% by day 90 postpartum). Similarly, Stanley et al. (1993), found little change in rumen capacity between day 61 before calving (127 L) and day 22 of lactation (133 L) in crossbreed beef cattle (Hereford x Angus cows). In contrast, some studies (Hartnell and Satter, 1979; Doreau et al., 1990) showed no change in ruminal capacity as dairy cows moved from a gestating to lactating state.

The gradual increase in rumen capacity after calving and the divergence of results among studies about this event shows that there may be other mechanisms involved in rumen development in the stages of lactation besides the relief of the abdominal cavity by the release

of amniotic fluid, fetus and fetal membranes. Dado and Allen (1995) reported a reserve volume of more than 16 L in the reticulorumen of dairy cattle consuming a fill limiting diet with addition of 22.2 L of inert fill, indicating that additional capacity may exist for ruminal pool even when distension in the reticulorumen limits DMI.

2.1.1.2 Passage rate

Ruminant animals have intrinsic characteristics regarding feed degradation, mainly feeds with high fiber, because its digestive system is based on microbial degradation in the forestomachs. The range of feed degradation, however, depends on how long it is remaining in contact with microorganisms in the rumen. This influences feed consumption, because for future intake to occur, it is necessary for the content to disappear from rumen, either by digestion or passage of feed (Krizsan et al., 2010). Thus, knowledge of the factors influencing the passage rate (kp) of fiber is essential for predictions of forage utilization by lactating beef cows.

It is known that the total diet characteristic is one of the main factors that determines the digest flow through the rumen (Ellis et al., 1994), but it's not the only one. Okine and Mathison (1991) shown that the kp increases with increasing digestible energy (DE) intake and DMI. Moreover, characteristics intrinsic to the animal as a physiological stage have been associated with changes in kp. Studies with ewes (Coffey et al., 1989) and beef heifers (Vanzant et al., 1991) reported that the lactating animals had greater kp when compared with non-lactating animals and these effects were concomitant with greater DMI by lactating females. A similar result was reported by Ovenell et al. (1991), but they found only a trend for lactating beef cows to have greater particulate kp compared to non-lactating beef cows. In contrast, Stanley et al. (1993) reported a lower kp in postpartum than in prepartum.

Furthermore, Park et al. (2011) reported an increase in the solid kp when dairy cows in late lactation were fed diets with higher forage and decrease when approached calving, even reducing dietary forage, indicating the importance of physiological changes in animal metabolism. Aikman et al. (2008) related the increase in the kp as a result of feeding behavior. They observe that animals with lower ruminal capacity in proportion to the demands were more efficient in reducing the particle size of the feed. Dado and Allen (1995) also observed an increase in total time spent chewing with the addition of fiber and rumen-inert bulk to the diet and speculated that additional chewing times may have increased DM digestibility and passage

rate. Vanzant et al. (1991) determined that lactating beef heifers tended to have greater NDF digestibility (NDFD), but not organic matter (OM) digestibility (OMD), at 26 d postpartum than non-gestating, nonlactating heifers.

2.1.1.3 Neutral detergent fiber digestibility

Neutral detergent fiber digestibility is an important parameter related to DMI and consequently to animal performance, but the NDF digestibility is variable in the rumen. Grant et al. (1995) evaluated the effect of the use of silages with similar NDF and crude protein (CP) contents but different NDF digestibility on performance, ruminal metabolism, and digestive kinetics of Holstein dairy cows in midlactation and found increases in DMI and milk yield in cows consuming higher digestibility NDF.

Isolation of the specific effects of NDFD on animal performance is complex. Although many experiments have reported NDFD data, interpretation of results is difficult because of a variety of confounding factors (Oba and Allen, 1999), since the digestion of the fiber in the rumen is a dynamic process that is influenced by interrelationships both intrinsic characteristics of the feed sources (Varga and Hoover, 1983) and the physiological adaptations of the animals. About these interrelationships, Dado and Allen (1995) stated that when intake is limited by rumen fill, increases in the digestible fraction of NDF or in rates of NDF digestion and passage may enhance clearance of fill from the rumen and increase DMI.

Tyrrell and Moe (1975) indicated that the digestibility of the diet in non-lactating dairy cows may overestimate the digestibility of the same ration fed to lactating cows by 12% or more. In agree, Park et al. (2011) found a decrease of fiber digestibility between day 6 and day 20 of the lactation, and these decreases in digestion corresponded with increases in intake and ruminal solids passage rate. However, Vanzant et al. (1991) determined that lactating beef heifers tended to have greater NDFD at 26 d postpartum than non-gestating and non-lactating heifers, wich is consistent with previous studies performed with ewes (Coffey et al., 1989).

2.1.2 Metabolic adjustments

2.1.2.1 Energetic metabolism

The blood examination gives the opportunity to investigate the presence of several metabolites and other constituents in the body of animals and it plays a vital role in determining the physiological, nutritional and pathological status of an animal (Kubkomawa et al., 2015). Blood glucose, β-hydroxybutyrate (BHBA) and non-esterified fatty acids (NEFA) are the most common metabolites used to assess the energy status of cattle (Ndlovu et al., 2007).

Glucose supply is of critical importance for many tissues and physiological processes, and the performance and health of the dairy cow are dependent on the maintenance of glucose homeostasis (Bell, 1995). Glucose is a particularly important metabolite during lactation that is available primarily to the mammary gland by a series of physiological adjustments that include changes such as increased hepatic rates of gluconeogenesis, decreased glucose uptake and use by adipose tissue and muscle, and a shift in whole-body nutrient oxidation so less glucose is used as an energy source. Prioritization of glucose to the mammary gland at the onset of lactation to the mammary gland is given mainly in the function of the synthesis of lactose in this phase (Baumgard et al., 2017). Within four days postpartum, the demands for glucose, amino acids and fatty acids due to milk production, are two to five times higher than prepartum requirements (Bell, 1995), and the synthesis of lactose alone utilizes 65 to 70% of the cow's total glucose turnover (Baumgard et al., 2017).

Blood glucose has a moderate diagnostic value in the assessment of nutritional status of cattle as it varies moderately in blood. Insufficient nutrient intake may reduce circulatory glucose, which is usually associated with decreases in blood levels of glycosidic precursors (Reynolds et al., 2003).

Glucose is the main physiological regulator of insulin in mammals (Philippe, 1991) and the serum glucose concentration also is affected by the physiological status of an animal (Otto et al., 2000). In lactation, it is considered that the increase in glucose supply to the mammary gland is partially mediated by an increase in whole-body insulin resistance (Mcdowell et al., 1987). During this physiologic phase, insulin resistance inhibits glucose use in insulin-dependent tissues, such as muscle and adipose tissues and the glucose can be deviated mainly to non-insulin-dependent tissues such as the mammary gland for milk production (Contreras and Sordillo, 2011).

Previous studies have shown that the percentage of total glucose supply oxidized is reduced in lactating compared to dry cows and tissue utilization of glucose decreases while there is an increase in the use of lipid for energy (Reynolds et al., 2003).

Glucose concentration increases during the last week of pregnancy and drops to its lowest at 1 to 3 wk postpartum (Ingvartsen and Andersen, 2000). This can be explained by the 9-fold increase in glucose uptake by the mammary tissue on d 9 postpartum compared to d 2 prepartum (Bell, 1995).

In the early lactation, NEB occurs as the energy demands for milk production cannot be met by feed intake alone (Herdt, 2000). When cattle enter a NEB, stored energy reserves (commonly fat) are mobilized (lipolysis) to provide additional energy in order to meet their requirements, resulting in the production of NEFA (Adewuyi et al., 2005). In this phase, adipose lipogenesis is essentially shut down, and the sensitivity to lipolytic signals (epinephrine and norepinephrine) is greatly enhanced. Piccione et al. (2012) observed that higher NEFA values during the postpartum period indicated the activation of lipid mobilization that represented another metabolic mechanism of adaptation to the postpartum period. However, Theilgaard et al. (2002) reported greater sensitivity to lipolytic signals in early lactation compared to any other stages in lactation.

During established lactation, approximately half of the fatty acids in milk triglycerides are derived via mammary *de novo* synthesis from acetate and 3-hydroxybutyrate; the remaining half is derived preformed from plasma lipoprotein triglycerides (Bickerstaffe et al., 1974). However, during early lactation, when cows are in NEB and circulating levels of NEFA are relatively high, mammary uptake of NEFA may account for a significant fraction of milk fat synthesis (Miller et al., 1991b). Ingvartsen and Andersen (2000) found an increase in plasma NEFA approximately 2 to 3 wk prepartum with a peak 1 wk postpartum. Calculations from the data set of Reynolds et al. (1988) for cows at wk 4 of lactation indicate that uptake of NEFA by liver could supply from 20 to > 60% of O_2 utilization associated with ATP formation.

The plasma NEFA concentration is negatively correlated with DMI (Ingvartsen and Andersen, 2000). In a review by Ingvartsen (2006), he stated that feedback signals from the oxidation of NEFA in the liver are speculated to down-regulate intake in early lactation when mobilization is high, agreeing with French (2006) who affirmed that a decline in DMI was associated with an increase in plasma NEFA.

β-hydroxybutyrate is the most important indicator of NEB and the amount produced is directly linked to the intensity of mobilization of NEFA (Ospina et al., 2010). At present,

measurement of BHBA concentration is most commonly used. However, BHBA concentrations may not be sensitive enough and can come from dietary sources (Agenas et al., 2006). Circulating concentrations of BHBA will increase when the rate of acetate oxidation is slower than the incoming supply of acetate. Chapinal et al. (2012) demonstrated that serum BHBA levels of 1.4 mmol/L and 1.2 mmol/L during the first and second week after calving, respectively, were associated with considerable milk losses (1.5–2.4 kg/day).

3 HYPOTHESIS

In general, the postpartum period is marked by changes in the feed intake, digestion kinetics and partition of nutrients to the cow's body tissues in order to prioritize the nutritional supply to the mammary gland. However, these changes are triggered through complex interactions between physical and physiological factors and can be quantitatively expressed differently according to the lactation stage. Therefore, our main hypothesis is that lactating beef cows may present ways to compensate for the imbalance between nutrient intake and demand, for example, increasing ruminal passage rate and reducing fiber digestion.

4 OBJECTIVE

To quantify the effects of the physiological status (PS, lactation) and of the stage of lactation on feed intake and digestion kinetics (Total apparent, ruminal and intestinal digestibilities), and on metabolism of beef cows.

5 METHODOLOGY

All experimental procedures involving animals followed the ethical precepts for animal studies. For this purpose, this project was reviewed and approved by the Committee of Ethics in the Use of Animals of the Federal University of Lavras (Protocol number 048/2016).

5.1 Animals and facilities

The experiment was conducted in the feedlot facilities of the Department of Animal Science of the Federal University of Lavras.

Twelve Zebu heifers (6 Nellore and 6 Tabapuã breed) with an average body weight of 482 ± 129 kg, being seven lactating and five non-lactating, were used. The animals were selected in order to accurately represent the beef cattle herd (population) in Brazil.

Prior to the calving, the animals were housed in individual pens with 50 m² per animal, with 16 m² of covered area to facilitate animals handling from calving. At being allocated in the pens, the heifers started the adaptation phase to the experimental conditions, in which the quantities of DM offered were gradually increased until voluntary intake was reached. At calving, it was installed in the bottom of each pen, a structure that allows the calves to move to a common pasture area, without the possibility of cows to move.

5.2 Experimental design

The object of this study was the physiological stage of the animals (lactation) and stage of lactation (DIM, days in milk). Lactating cows were compared with their non-lactating pairs (from the same contemporary group) to estimate the physiological effect of lactation at different time points of lactation (3, 10, 35 and 100 days of lactation). Measurements were taken repeatedly over time (animal as experimental unit).

The number of replicates was defined in order to allow the use of a group of females with variable weight and distinct genetic lineages, in order to accurately represent the national herd.

The control group (non-lactating animals) was used since the nutritional composition of the diet ingredients and climate conditions could vary throughout the time. Thus the true differential value for every time point of lactation was estimated by comparing the lactating and non-lactating groups at different time points of lactation.

5.3 Diets and feeding

The experimental diet was composed by (DM basis) corn silage (92.3%) of medium quality and concentrate supplement (7.7%) prepared with soybean meal (4.55%), ground corn

(0.25%), urea (1.58%) and mineral mixture (1.32%), (Table 2). The nutritional composition of the experimental diet was designed to allow *ad libitum* intake without large accumulation of body reserves and adequate maintenance of lactation. Considering the average DMI of 1.8% of live weight and nutritional requirements for lactating Nellore cows (Valadares Filho, 2010; 2016), the planned diet meets the maintenance and lactation requirements, in addition to a 5% surplus (based on metabolizable energy). The use of 92.3% medium quality corn silage aimed to make the nutritional quality of the diet like grazing conditions with supplementation of a protein-based supplement.

The animals were fed twice a day at 07:00 a.m. and 03:00 p.m.. The refusals were weighed and sampled the following morning for feed amount of feed to be supplied for average orts of 5% of value provided. Samples of the silage were collected daily to prepare a weekly composite sample, which were processed for analysis. For the calculation of nutrient intake, the feed supplied between day 1 and day 3 of each collect period was considered. Samples of the ingredients of the concentrated supplement were obtained at each cut of the mixture.

Table 2 – Ingredients and chemical composition of the experimental diet.

Item	Experimental diet
Ingredient composition (% DM)	
Corn silage	92.3
Soybean meal	4.55
Ground corn	0.25
Urea	1.58
Mineral Mixture [a]	1.32
Chemical composition (% DM)	
TDN	61.7
Dry matter	35.1
Organic matter	93.2
Crude protein	12.9
EE [b]	2.39
apNDF [b]	51.1
NFC [b]	26.9
iNDF [b]	16.6

[a] Levels of guarantee per kilogram of product: Ca: 235g; P 45g; S 23g; Na: 80,18g; Zn: 2,38 mg; Cu: 625 mg; Fe: 1,18 mg; Mn: 312 mg: Co: 32 mg; I: 41,6 mg; Se: 11,25mg; Vit.A: 70.000 UI; Vit. D3: 5.000 UI; Vit. E: 15 UI; Niacina: 3,33 mg.

[b] apNDF = ash- and protein-free NDF; NFC = non fibrous carbohydrates; iNDF = indigestible neutral detergent fiber; EE = ether extract

5.4 Experimental period

Figure 1 - Periods for the collection of samples and measurements of parameters of the variables evaluated (cells marked in black).

Lactation stage (DIM)	**3**	**10**	**35**	**100**
Parameter				
Weigh and body condition score of animals				
Milk yield				
Feed intake				
Ruminal, intestinal and total apparent digestibility				
Ruminal pool, intake, and digestion, and passage rate				
Ruminal outflow				
Ruminal pH and ammonia nitrogen (NH3-N)				
Respiratory and heart rate				
Blood levels of metabolites				

At DIM3 punctual collections were made. However, the other collection periods (10, 35 and 100) were each 10 d in length as described later.

5.5 Body weight, body condition score, and milk yield

Cow BW and BCS as well as calf body weight were measured on d 1 and d 10 of each sample period throughout the study at T0 without restriction of feed or water. The mean values obtained for each variable between days 1 and 10 were used. Body Condition Score (BCS) was assessed on a scale ranging from 1 = severely thin at 9 = very obese, with a partial score of 0.5 and it was estimated by observation and palpation (Richards et al., 1986). The evaluation was performed by four observers in a blind quadruple scheme, in which each observer does not know the result of the evaluation of the other. The BCS of each animal was calculated as the average score of the four observers. When there was a difference greater than 1.5 points between the observers a new evaluation was carried out. Milk yield was measured on day 10 of collection period after a 12-hour cow /calf separation. Cows were manually milked after oxytocin application.

5.6 Total and partial nutrient digestibility

For quantification of the digestibility coefficients of the nutrients, spot collections of feces were performed on day 1 to 3 of each experimental period. In day 1, fecal samples were collected concurrently with defecation at 6, 12, 18 and 24 hours after the morning feeding. At days 2 and 3, the sampling periods were each delayed by two hours in relation to the previous day, thus representing a 24-h collection. Fecal aliquots were immediately frozen (-20 °C) along the collection period. Subsequently, samples were thawed, homogenized and a composite sample from each cow was formed per period. Composite fecal samples were pre-dried in a forced ventilation oven at 65 °C for 72 h and milled using a knife mill (2 mm-sieve) for further analysis. The total digestibilities of DM and nutrients were calculated by determining of the average of consumed DM and nutrients and the average amount excreted via feces during the same period.

The ruminal digestibilities of DM (DMRD) and nutrients were estimated using the omasal sampling technique. Sampling consisted of introducing into the rumen an extremity of a collection tube, leading it towards the reticule-omasal orifice, until the initial part overcomes the orifice, where it is held safely by the hand during the collection period. The other extremity of the collection tube was fitted in one of the apertures of the kitasato flask and the vacuum pump hose in the other aperture thereof. At the time of collection, the vacuum pump was triggered, and by suction, the digesta was driven through the collection tube to the kitasato flask (Leão, 2002).

For assessment of ruminal outflow, 2 indicators were utilized: Co-EDTA (Udén et al., 1980) as the fluid phase and small particles indicator and iNDF as the solid-phase indicator. The Co-EDTA was wrapped in paper cartridges, and a total of 6 g was provided daily, administered 4 times in 6-h intervals (06:00 a.m., 12:00 a.m., 06:00 p.m., and 12:00 p.m.). Administration of Co-EDTA started three days before and during omasal digesta sampling period. Omasal digesta was collected twice daily, in 12-h intervals within a day and in 16-h intervals between days to avoid possible variation in the flux of the digesta relating to collection time. Samples were collected at 06:00 a.m and 06:00 p.m. on first day, at 10:00 a.m. and 10:00 p.m. on second day, at 02:00 p.m. on third day and 02:00 a.m. on fourth day, totaling 6 collections per experimental period (Allen and Linton, 2007). Samples were frozen at −20 °C for further analysis.

At the end of each experimental period, omasal digesta samples were thawed and filtered in a 100-μm nylon precision woven screen with pore area surface of 44%, producing 2 phases: that retained in the filter (large-particle, solid phase) and the filtrate (fluid and small-particle phase). Samples were dried in a forced-air oven at 65°C for 72 h and then ground in a Wiley mill to pass through a 2-mm stainless-steel curved round-hole sieve for iNDF determination.

The iNDF concentration was quantified in triplicate on omasal digesta samples (2 phases), which were ground in a knife mill with a 2-mm sieve (Valente et al., 2011). Sample amounts of 1.5 g were added to pre-weighed polyester bags with a pore size of 12 μm and a pore area equal to 6% of the total surface. The bags were incubated for 288 h in the rumen of animals at maintenance level. After removal from the rumen, the bags were rinsed in a household washing machine, dried at 45 °C for 48 h, weighed, and residues were then analysed for NDF. Cobalt concentration was analysed by atomic absorption epectrophotometry.

The outflow of DM and the constituents of the omasal digesta were calculated as described by France and Siddons (1986). To calculate the ruminal digestibility coefficient (RDC), the average amount consumed and the estimated amount of DM and nutrients in the omasum were used. And, for the calculation of intestinal digestibility, were used the amount of DM and nutrients estimated in the omasum and the amount of DM in the feces.

5.7 Ruminal, and intake, passage and digestion rates of nutrients

Between days 7 and 9 of each collection period the rumen was emptied with the purpose of determining the ruminal fill, passage rate and nutrients digestion, according to the technique described by Allen & Linton (2007). On day 7, emptying of the rumen was made four hours after the diet supply, and the total digest was weighed, later filtered for separation of solids and liquids, which were sampled and whose aliquots were weighed for further analysis. Soon after sampling, the digest was reconstituted again and placed back in the rumen of the respective animals.

On day 8, there was a pause for feedback and rest of the animals and, on day 9, the same emptying procedure was returned, however, immediately before the diet supply when the rumen was at its lowest volume. The samples collected were weighed, dried in a forced-air oven at 65 °C by 72 h, ground in a knife mill, with a sieve containing 1 mm sieves, and one compost per animal was elaborated in each period. In this way, the composite samples were formed by

the dry samples of the solid and liquid part of the two ruminal emptyings (T0 and T4 times), based on the dry weight of each sample.

The passage rates (Kp) were calculated using the *"pool-and-flux"* method, described by Allen & Linton (2007), according to the following equation:

- Kp = omasal flow / ruminal pool

Where:

- Kp = feed passage rate (% / hour);
- Omasal flow = amount of DM in the omasum (kg / hour);
- Ruminal pool = total amount of ruminal DM (kg).

The digestion rates (Kd) were calculated as a function of the passage rate and quantity ingested per hour, using the equation:

- Kd = (ruminal intake / ruminal pool) – Kp

Where:

- Kd = feed digestion rate (% / hour);
- Intake = feed intake (kg DM / hour)

5.8 Ruminal pH and ammonia nitrogen

On day 3 of each collection period and on the predetermined dates in Figure 1, collections of ruminal content were made to evaluate the pH and concentration of ammonia nitrogen (NH3-N). Samples were collected manually from the ventral sections of the rumen immediately before feeding (T0) and four hours after feeding (T4). 50mL aliquots of ruminal fluid were used for immediate determination of ruminal pH, using potentiometer (HI 2221, Hanna Instruments Brasil Imp. E Exp.LTDA -Brasil) and 50mL aliquots of ruminal fluid were filtered through a triple layer of gauze and added to a container containing 1mL of H_2SO_4 (1:1) and frozen at -20 °C for further analysis on concentrations of NH3-N (AOAC, 2000).

5.9 Heart and respiratory rates

At T0 and T4 on day 3 of each collection period and on the predetermined dates in Figure 1, the heart (HR) and respiratory rates (RR) were measured by an experienced evaluator. For HR, the number of heart beats (beats per minute) were estimated using stethoscope (Rappaport, Premium; Ningbo Sifang Medical Instruments Co., LTD - China). For RR, the

measurement was made by visual evaluation of the respiratory movements. It was used a timer counted to measure the movements per minute.

5.10 Analysis of metabolites in the blood

Blood samples were collected at T0 and T4 times on day 3 of each period via jugular vein puncture using tubes with coagulation accelerator and vacutainer tubes containing sodium heparin. Samples were immediately centrifuged at 2700 G for 20 minutes, and then stored at -20 °C.

Blood glucose analysis were performed by the colorimetric method (Glucose PAP Liquiform, Labtest®, Lagoa Santa, Brazil, limit of photometric detection 0,41mg/dL) using God-Trinder methodology. Plasma samples were analysed for BHBA with a D-3-Hydroxybutyrate Reagent Set, Manual/RX Monza RB I007 (Randox Laoratories LTD - United Kingdom, UK) by kinetic enzymatic method.

5.11 Chemical-bromatological analysis

Non-fibrous carbohydrate (NFC) levels were calculated in accordance with proposed by Detmann and Valadares Filho (2010), with NFC = 100 - ((% CP -% CP derived from urea +% urea) +% apNDF +% EE +% ASH). The NDF was analysed according to the technique described by Mertens et al. (2002), with the addition of sodium sulfite but with the addition of thermostable α-amylase to the detergent (Ankom Technology Corp., Fairport, NY). The energy intake of the animals was obtained from the product between the DMI and the energy content of the diets, which was determined from the formula recommended by Detmann et al. (2010): TDN (%) = DCP + 2.25 x DEE + DNFC + apDNDF, where DCP, DEE, DNFC and apDNDF respectively mean digestible crude protein, digestible ethereal extract, digestible non-fibrous carbohydrates and ash- and protein-free digestible neutral detergent fiber, calculated from the digestibility coefficients to be obtained in the present study.

The chemical and bromatological analysis followed the standards of the National of Science and Technology in Animal Science (INCT-CA), published by Detmann et al. (2012). The samples of corn silage, concentrate ingredients, orts, feces and ruminal contents were analysed in the UFLA Feed Analysis Laboratory, in terms of DM, ash, CP, NDF and, EE

following INCT-CA G-003/1 methods; INCT-CA M-001/1; INCT-CA N-001/1; INCT-CA F-002/1; and INCT-CA G-004/1, respectively.

5.12 Statistical analysis

Data was analysed through the mixed models methodology (procedure MIXED of SAS 9.2, SAS Inst. Inc., Cary, NC), considering the physiological effect (lactating and non-lactating) and the days in milk (DIM) as classificatory fixed effects and the animal as the random effect. When appropriate, BW was included as covariate in the model. Once repeated measurements were taken at the same animal (for DIM), the subject animal nested to the treatment was included on the repeated measurement statement. For every DIM, the physiological effect on the measured variable was estimated using the "estimate statement" of SAS. The value of 0.10 was adopted as critical level of probability for occurrence of Type I error.

6 RESULTS

6.1 BW and BCS. Body weight and BCS data are presented in Table 3**.** We observed PS × DIM interaction ($P < 0.001$) for BW (kg). LA group demonstrated decrease in BW from DIM3 to DIM35 followed by an increase until DIM100 whereas the NLA group demonstrated increase in BW throughout the trial period. BCS was affected by PS ($P = 0.046$). At DIM35 and DIM100 LA group presented lower BCS (-1.01; -1.28) compared to the NLA group, respectively. Differences in BW and BCS between LA and NLA groups over time are presented in Figure 2.

Table 3 – Means and SEM for body weight (BW) and body condition score (BCS), according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Body weight, kg	500 ± 4.4	476 ± 3.8	0.004	<0.001	<0.001
Body condition score	6.28 ± 0.26	5.47 ± 0.22	0.046	0.884	0.080

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

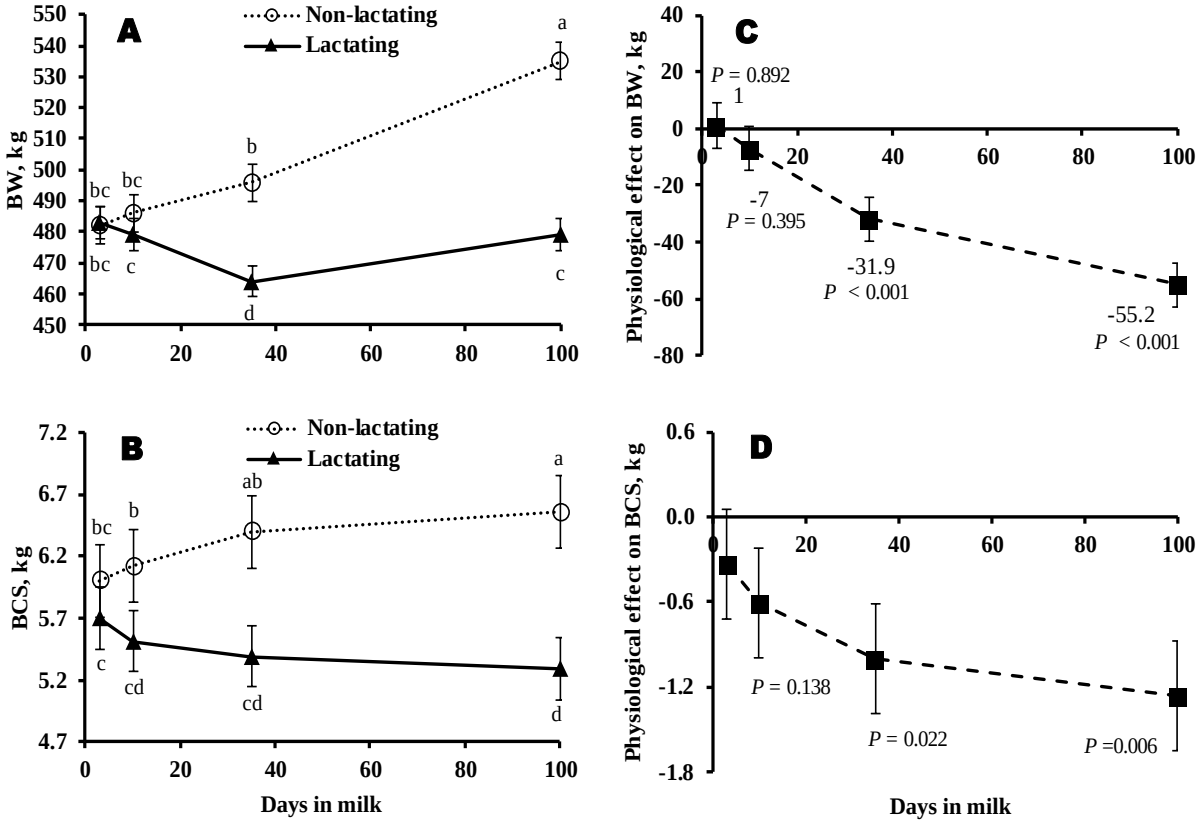

Figure 2 – Least square means for BW (A) and BCS (C) of non-lactating and lactating animals and the estimated differential physiological effect of lactation on BW (B) and BCS (D). Means followed by different letters differs at P < 0.1 (A, and C).

6.2 Milk yield and Calf body weight. Cows decreased milk yield by 13.8 g/d between DIM10 to DIM100, (Figure 3 - A). Calf presented average daily gain (ADG) by 0.825 kg/d between DIM3 to DIM100, (Figure 3 - B).

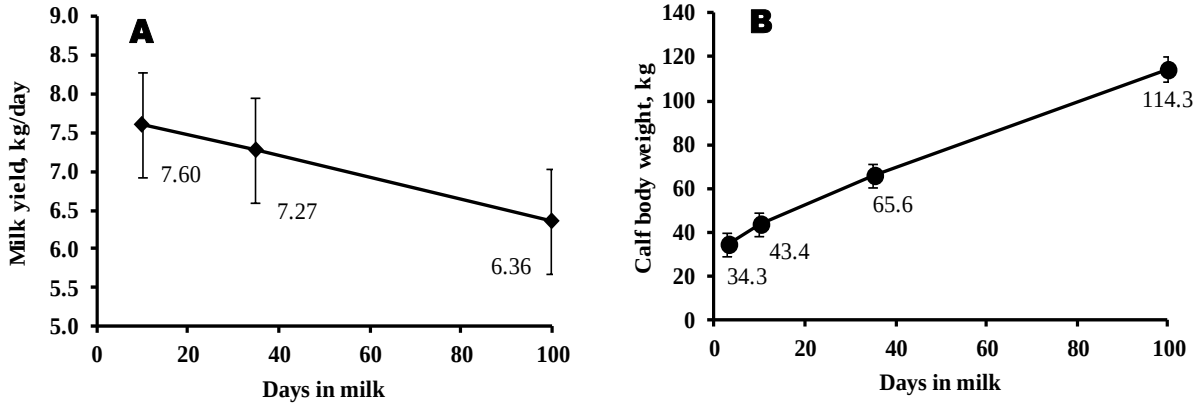

Figure 3 – Means of the milk yield (A) and calf body weight (B) from DIM10 to DIM100 of the experimental period.

6.3 DMI. Intake data are shown in Table 4. Dry matter intake (kg/day) was affected by PS (P = 0.005) and DIM (P < 0.001*)*. For DMI expressed on kg/d and BW basis (g/kg BW), it was

observed a PS × DIM interaction (P = 0.069, P = 0.029, respectively). The LA group increased DMI from DIM10 to DIM35 (P < 0.001) following with DMI relatively constant through the experiment (P = 0.205), whereas the NLA group demonstrated small increase in DMI during all trial period (P = 0.079). Dry matter intake was than 38.5% higher for LA than NLA cows until DIM100. Differences in intake between LA and NLA groups over time are presented in Figure 4.

Table 4 – Means and SEM for intake (kg/d) of the DM, OM, MM, CP, apNDF, iNDF, NFC, EE, TDN, and for intake in relation to body weight (g/kg BW) of the DM, apNDF, iNDF, and TDN, according to the experimental treatments.

Item[b]	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Intake, kg/d					
DM	5.89 ± 0.48	8.16 ± 0.40	0.005	<0.001	0.069
OM	5.51 ± 0.43	7.57 ± 0.36	0.004	0.001	0.154
MM	0.370 ± 0.038	0.597 ± 0.030	<0.001	<0.001	0.607
CP	0.759 ± 0.070	1.061 ± 0.058	0.009	<0.001	0.363
apNDF	3.01 ± 0.23	4.11 ± 0.19	0.005	0.007	0.226
iNDF	0.936 ± 0.071	1.32 ± 0.059	0.003	0.001	0.382
NFC	1.74 ± 0.15	2.42 ± 0.12	0.008	0.038	0.246
EE	0.144 ± 0.019	0.199 ± 0.016	0.067	0.027	0.676
TDN	3.61 ± 0.20	4.79 ± 0.18	<0.001	0.002	0.342
Intake, g/kg BW					
DM	12.1 ± 0.99	17.3 ± 0.83	0.002	0.001	0.029
apNDF	6.15 ± 0.50	8.74 ± 0.42	0.002	0.010	0.160
iNDF	1.91 ± 0.16	2.79 ± 0.13	0.001	<0.001	0.245
TDN	7.72 ± 0.45	10.1 ± 0.37	<0.001	0.004	0.247

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.
[b]DM = dry matter; OM = organic matter; MM = mineral matter; CP = crude protein; apNDF = ash- and protein-free neutral detergent fiber; iNDF = indigestible neutral detergent fiber; NFC = non-fibrous carbohydrates, EE = ether extract; TDN = total digestible nutrients.

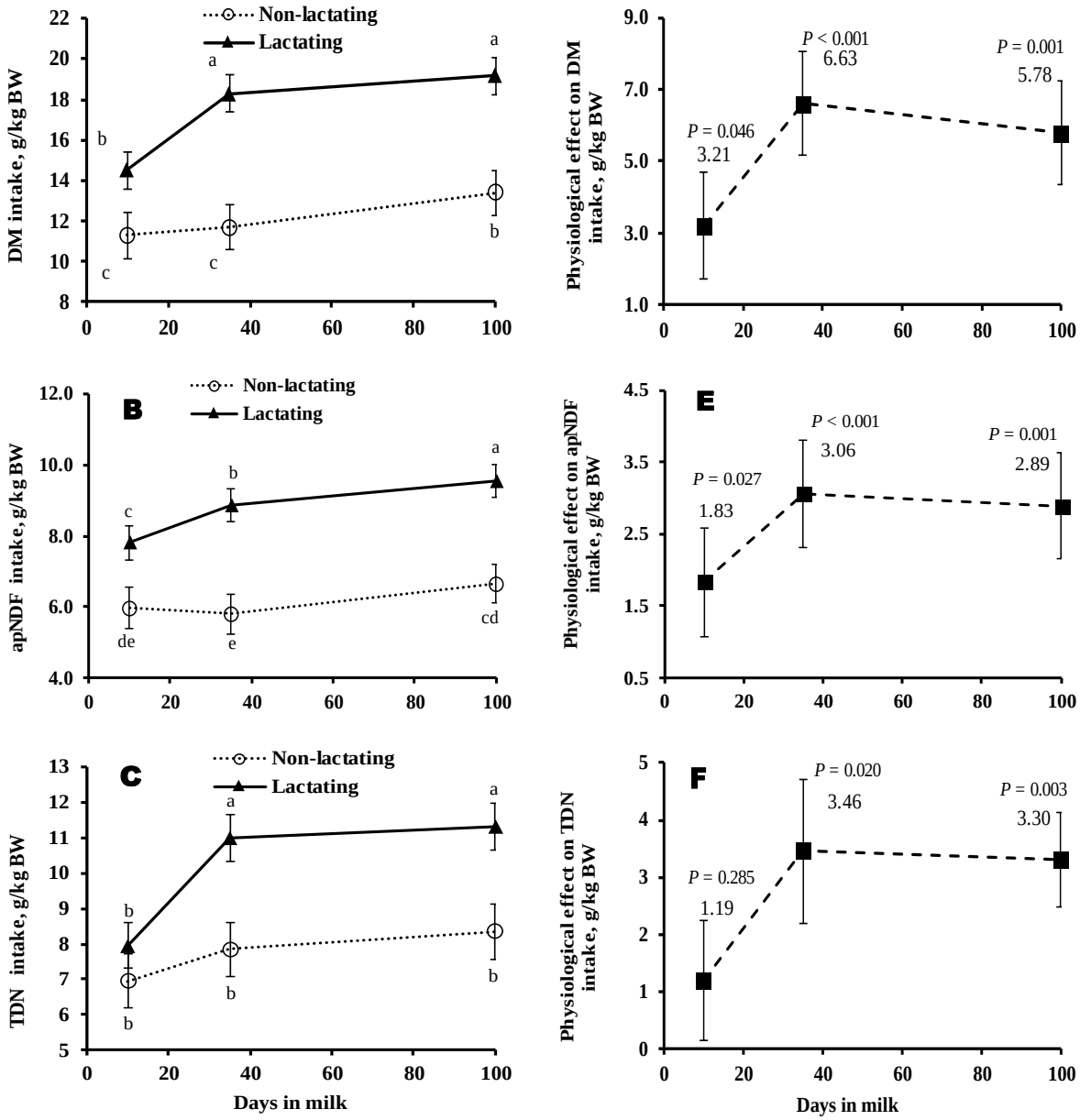

Figure 4 – Least square means for intake of DM (A), apNDF (B) and TDN (C) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on intake of DM (D), apNDF (E) and TDN (F). Means followed by different letters differs at P < 0.1 (A, B, and C).

6.4 Digestibilities. Partial and total apparent digestibilities data are shown in Table 5. Ruminal digestibilities of apNDF, OM, and DM (g/kg DM) were affected by PS (P = 0.042, 0.069 and 0.043, respectively). Ruminal digestibilities nearly all nutrients were lower for the LA group than for the NLA group from DIM10 to DIM35 (P < 0.1). However, there were no differences in ruminal digestibilities until DIM100 (P > 0.1). Physiological status did not affect (P > 0.1) the intestinal digestibilities of all nutrients. However, there was an effect (P < 0.001) of DIM in DM, OM and CP intestinal digestibilities. For total apparent digestibilities (g/kg DM) of DM, OM, apNDF, and for TDN were observed PS × DIM interactions (P = 0.074, 0.012,

0.018 and 0.004, respectively). The LA group presented increase (7%) in TDN until DIM100 ($P < 0.001$), whereas in NLA group was observed an increase in TDN between DIM10 to DIM35, followed by a decrease until DIM100. The mean TDN for LA and NLA group were 582 ± 6 and 606 ± 7, respectively. Differences on ruminal (Figure 5), and intestinal digestibility (Figure 6) as well as on total apparent digestibility, and TDN means values (Figure 7) between LA and NLA groups over time are presented following.

Table 5 – Means and SEM for ruminal, intestinal and total apparent digestibility, according to the experimental treatments.

Item[a]	Physiological status (PS)		*P*-value[b]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Ruminal digestibility, g/kg of DM					
DM	345 ± 16	300 ± 14	0.043	0.266	0.547
OM	434 ± 12	405 ± 10	0.069	0.607	0.815
CP	155 ± 29	145 ± 25	0.791	0.290	0.809
apNDF	456 ± 11	424 ± 10	0.042	0.363	0.357
NFC	556 ± 31	514 ± 27	0.324	0.936	0.996
EE	131 ± 14	123 ± 13	0.662	0.087	0.631
Intestinal digestibility, g/kg of the amount reaching the omasum					
DM	418 ± 15	436 ± 13	0.371	<0.001	0.385
OM	326 ± 15	331 ± 13	0.805	<0.001	0.406
CP	669 ± 14	657 ± 12	0.509	<0.001	0.311
apNDF	21.4 ± 15.9	10.8 ± 13.1	0.610	0.226	0.615
NFC	681 ± 29	718 ± 25	0.342	0.264	0.747
EE	597 ± 33	610 ± 28	0.768	0.354	0.436
Total apparent digestibility, g/kg of DM					
DM	625 ± 7	609 ± 6	0.076	<0.001	0.074
OM	624 ± 6	604 ± 5	0.022	<0.001	0.012
CP	715 ± 11	699 ± 9	0.261	<0.001	0.269
apNDF	468 ± 10	432 ± 18	0.014	0.067	0.018
NFC	863 ± 14	870 ± 12	0.690	0.288	0.978
EE	658 ± 34	626 ± 28	0.474	0.217	0.460
TDN	606 ± 7	582 ± 6	0.009	<0.001	0.004

[a] DM = dry matter; OM = organic matter; CP = crude protein; apNDF = ash- and protein-free neutral detergent fiber; NFC = non-fibrous carbohydrates, EE = ether extract; TDN = total digestible nutrients.

[b] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

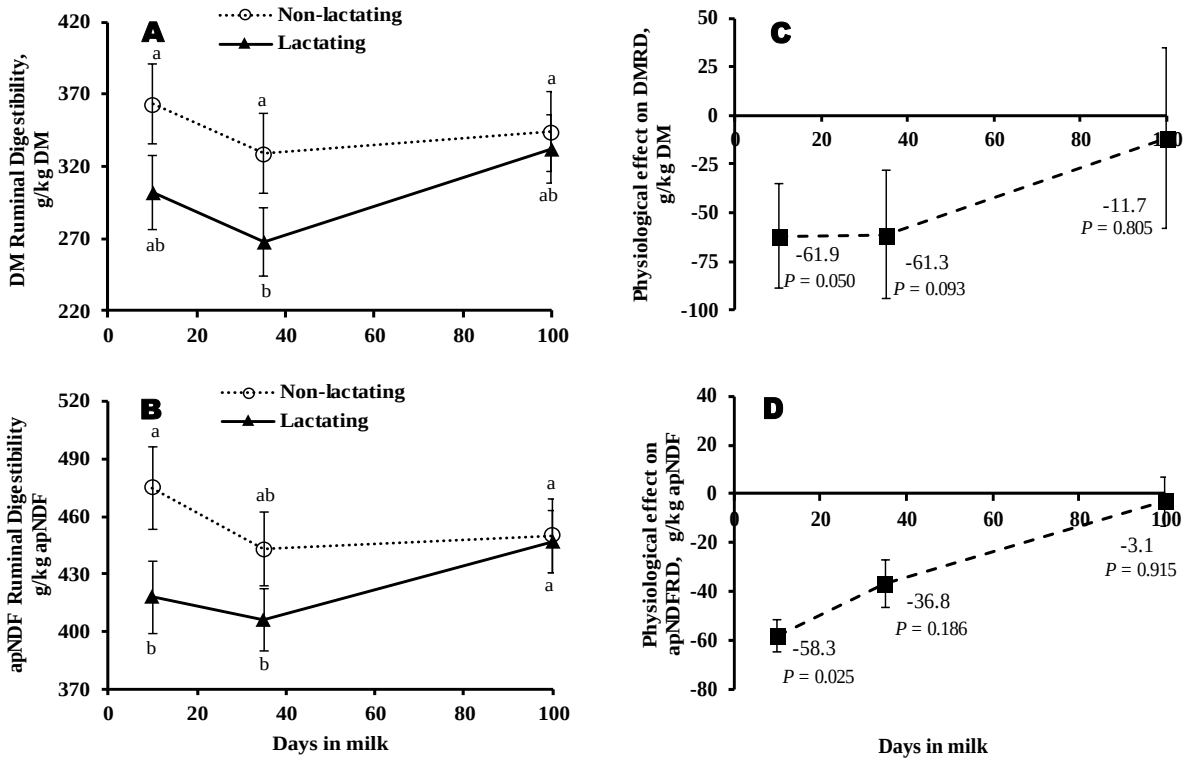

Figure 5 – Least square means for ruminal digestibility of the DM (A), and apNDF (B) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on ruminal digestibility of the DM (C) and apNDF (D). Means followed by different letters differs at P < 0.1 (A, and B).

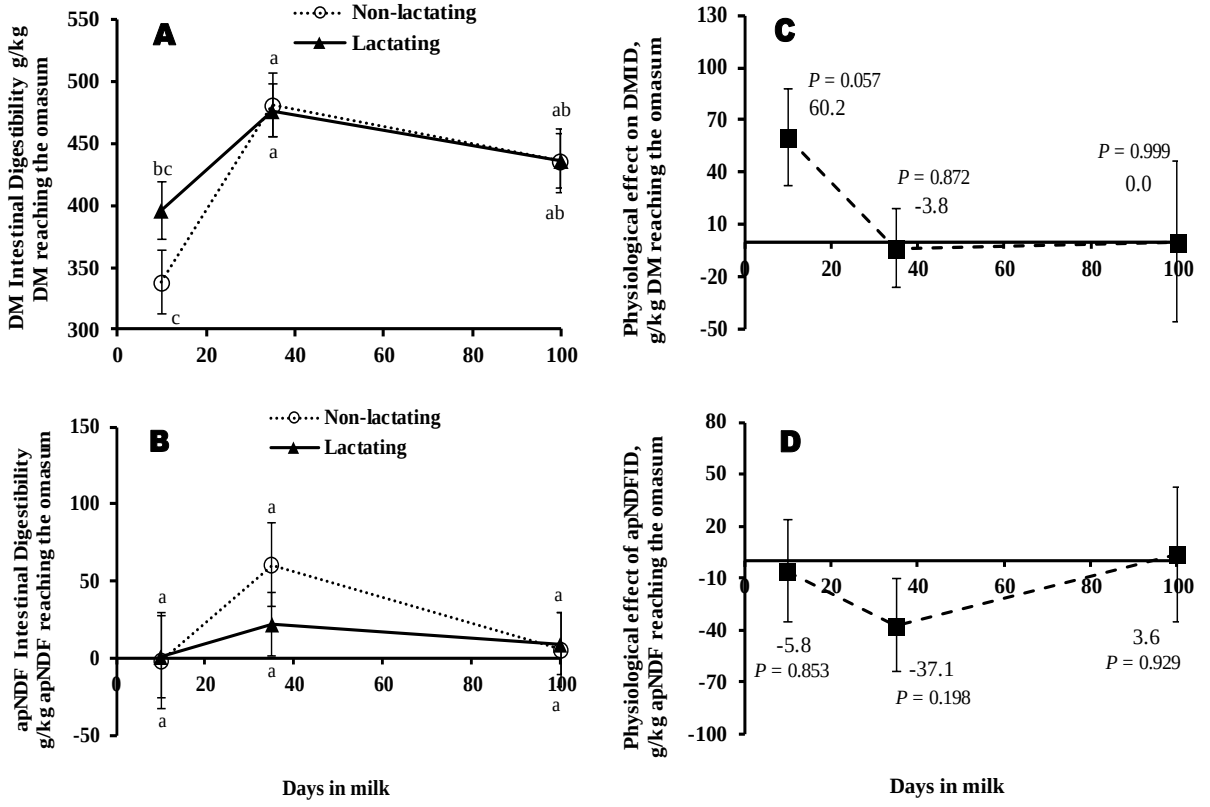

Figure 6 – Least square means for intestinal digestibility of the DM (A), and apNDF (B) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on intestinal digestibility of the DM (C) and apNDF (D). Means followed by different letters differs at P < 0.1 (A, and B)

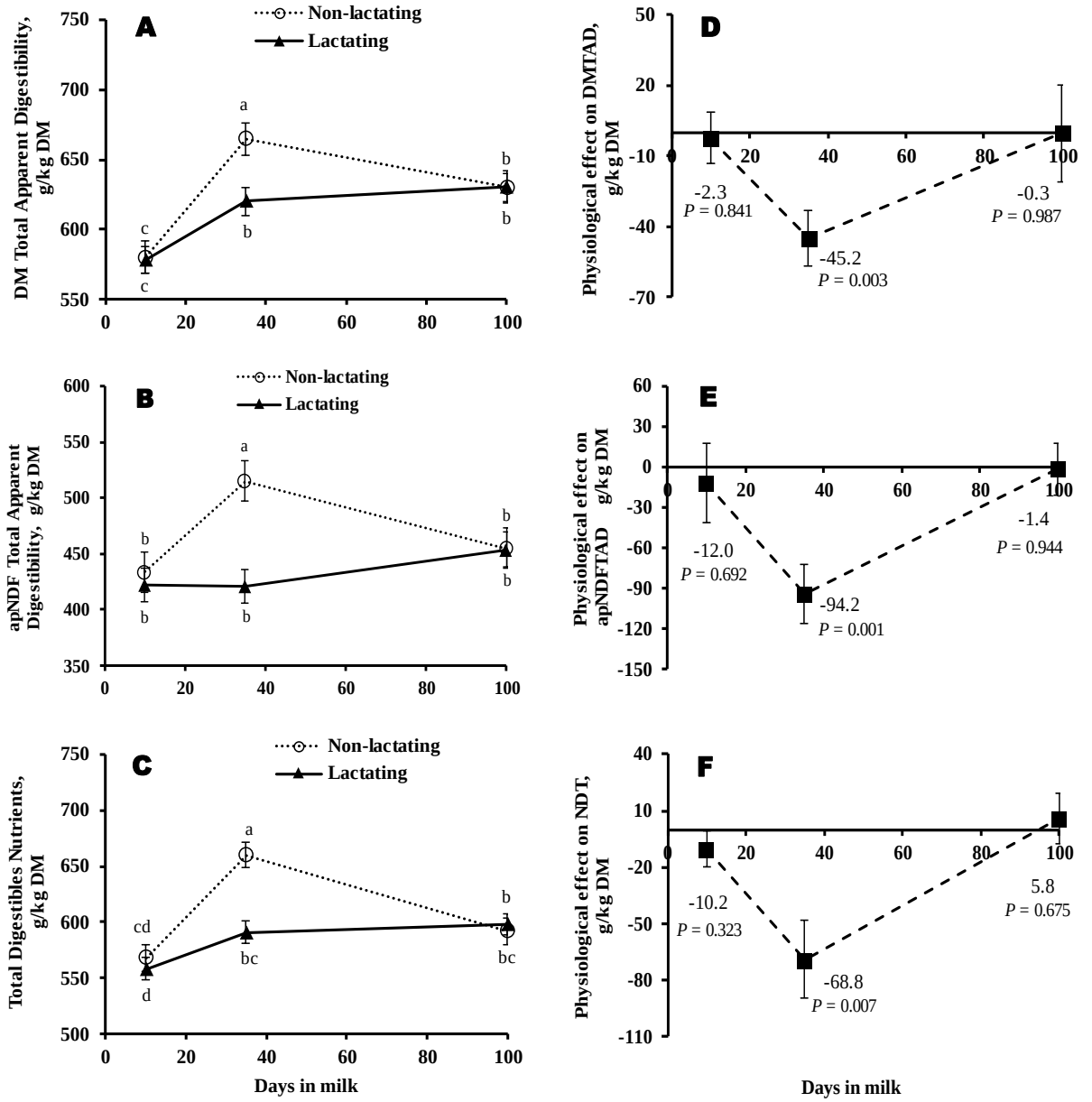

Figure 7 – Least square means for total apparent digestibility of the DM (A), and apNDF (B), and TDN means values (C) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on total apparent digestibility of the DM (D) and apNDF, and on TDN means values. Means followed different letters differs at P < 0.1 (A, B, and C).

6.5 Ruminal pool, and intake, passage and digestion rates. Ruminal pool, and Intake, passage and digestion rates data are presented in Table 6. Ruminal pool on natural matter (NM) basis (kg/day) was affected by PS (P = 0.001) and DIM (P = 0.077). The mean ruminal pool was greater than 35.2% for LA group compared to NLA group. Lactating cows increased by 10.3% their ruminal pool between DIM10 and DIM100. Non-lactating cows showed ruminal pool relatively constant until DIM100 (mean = 31.7 ± 2.4). Ruminal pool on DM basis (kg/day) was affected by PS (P = 0.014). Lactating cows presented ruminal pool mean difference by 1.3

kg/d during trial period. This difference corresponds to an increase in 28.6% for LA group compared to NLA group. Intake (ki, h^{-1}), and passage rates (kp, h^{-1}) of DM were affected ($P < 0.10$) by PS and DIM. During trial period, lactating group presented greater DMI and passage rates (0.063 ± 0.0019; 0.045 ± 0.0022) than NLA group (0.055 ± 0.0022; 0.037 ± 0.0026), respectively. However, higher differences between the groups were observed at DIM35 for the DMI rate (0.016) and passage rate (0.011). For digestion rate (kd, h^{-1}) of DM, there were no differences for both PS ($P = 0.956$) and DIM ($P = 0.377$). Differences on ruminal pool (on basis NM, and DM), as well as on intake, and passage rates between LA and NLA groups over time are presented in Figure 8, and 9, respectively.

Table 6 – Means and SEM for ruminal pool, and intake (ki, h^{-1}), passage (kp, h^{-1}) and digestion (kd, h^{-1}) rates of DM, ash- and protein-free NDF, according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Ruminal pool kg NM/day	31.7 ± 2.4	43.3 ± 2.0	0.001	0.077	0.980
DM					
Ruminal pool[b]	4.55 ± 0.38	5.92 ± 0.31	0.014	0.572	0.991
ki, h^{-1}	0.055 ± 0.0022	0.063 ± 0.0019	0.011	0.061	0.189
kp, h^{-1}	0.037 ± 0.0026	0.045 ± 0.0022	0.024	0.089	0.693
kd, h^{-1}	0.018 ± 0.0017	0.018 ± 0.0014	0.956	0.377	0.178
apNDF					
Ruminal pool[c]	3.07 ± 0.20	4.03 ± 0.17	0.001	0.874	0.883
ki, h^{-1}	0.042 ± 0.0015	0.047 ± 0.0013	0.031	0.404	0.347
kp, h^{-1}	0.023 ± 0.0010	0.027 ± 0.0008	0.042	0.270	0.331
kd, h^{-1}	0.019 ± 0.0009	0.020 ± 0.0008	0.172	0.401	0.453

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.
[b] ruminal pool, kg of DM/day
[c] ruminal pool, kg of apNDF/day

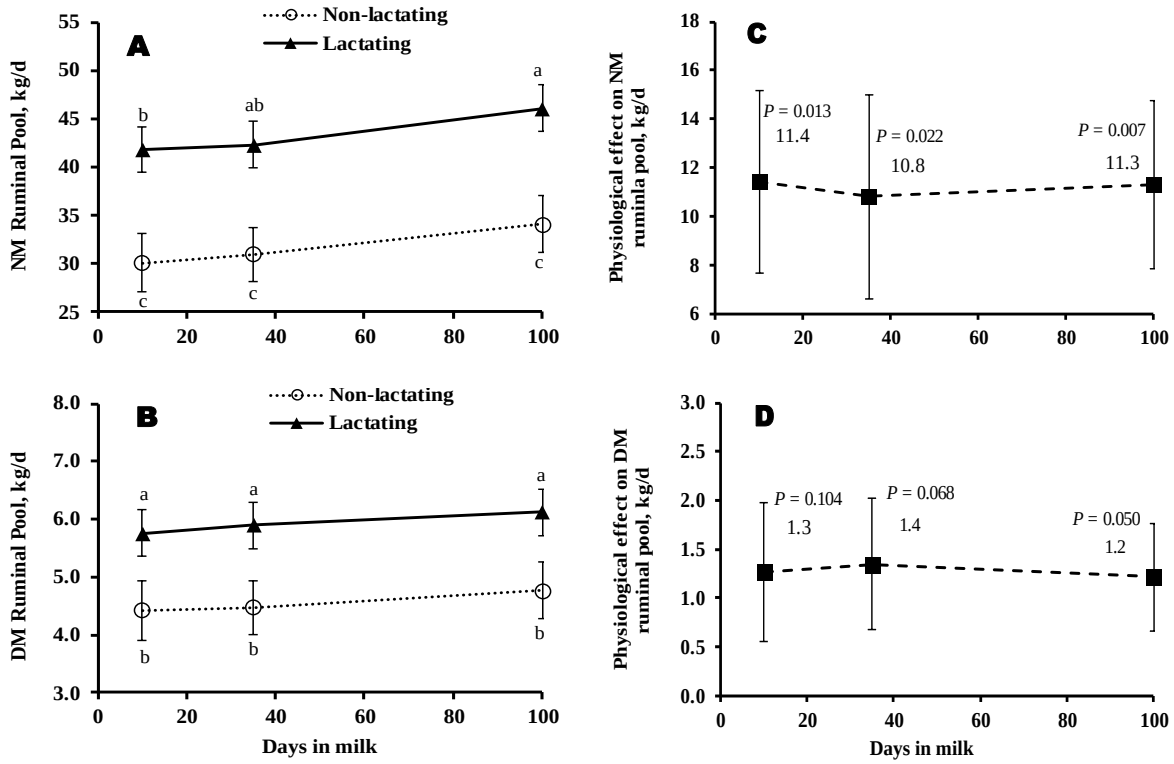

Figure 8 – Least square means for ruminal pool of NM (A), and DM (B) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation ruminal pool of NM (C), and DM (D). Means followed by different letters differs at P < 0.1 (A, and B).

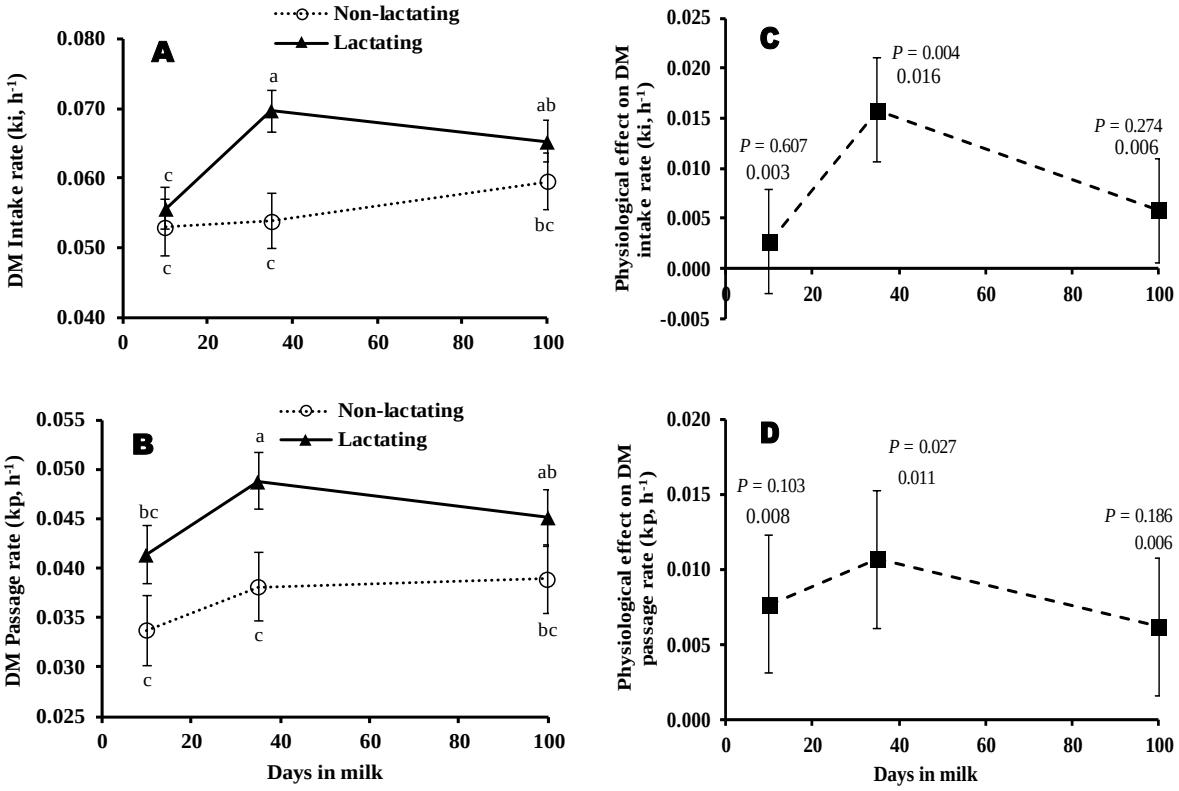

Figure 9 – Least square means for intake (A), and passage rate of DM (B) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on intake (C), passage rate (D). Means followed by different letters differs at P < 0.1 (A, and B).

6.6 Ruminal outflow. Ruminal outflows data are presented in Table 7. Dry matter ruminal outflow (kg/d) was affected by PS (P = 0.009) and DIM (P < 0.001). Dry matter outflow increased over time for LA and NLA group (P < 0.001). Mean DM outflow was greater for the LA group (5.64 ± 0.304) than for the NLA group (4.04 ± 0.353).

Table 7 – Means and SEM for ruminal outflow DM, OM, CP, ash- and protein-free NDF, NFC, and EE, according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
DM	4.04 ± 0.353	5.64 ± 0.304	0.009	<0.001	0.745
OM	3.26 ± 0.270	4.45 ± 0.232	0.010	<0.001	0.576
CP	0.673 ± 0.067	0.909 ± 0.058	0.034	0.004	0.853
apNDF	1.71 ± 0.123	2.35 ± 0.106	0.003	0.015	0.485
NFC	0.744 ± 0.082	1.05 ± 0.067	0.013	0.311	0.973
EE	0.129 ± 0.014	0.179 ± 0.012	0.024	0.066	0.915

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

6.7 Ruminal pH and ammonia nitrogen. Ruminal pH and ammonia nitrogen data are presented in Table 8. Rumen pH was not affected by PS (P = 0.784 before feeding and P = 0.416 four hours after feeding) and DIM (P = 0.877 before feeding and P = 0.949 four hours after feeding). For the ruminal NH_3, there was no difference in ruminal NH_3 as a function of physiological status (P = 0.908) at time 0. However, there was a DIM effect (P = 0.058). Both LA and NLA groups presented an increase in ruminal NH_3 over time. At time 4, neither PS (P = 0.730) nor DIM (P = 0.216) affected ruminal NH_3 concentration.

Table 8 – Means and SEM for ruminal pH and concentration of ruminal ammonia nitrogen (NH_3); at time 0 (before feeding) and time 4 (four hours after feeding), according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
pH at time 0	7.10 ± 0.11	7.05 ± 0.10	0.784	0.877	0.513
pH at time 4	6.88 ± 0.10	6.77 ± 0.08	0.416	0.949	0.361
NH_3 at time 0, mg/dL	16.7 ± 1.06	16.5 ± 0.90	0.908	0.058	0.604
NH_3 at time 4, mg/dL	22.0 ± 2.19	23.0 ± 1.76	0.730	0.216	0.453

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

6.8 Heart and Respiratory rates. Heart and respiratory rate data are depicted in Table 9. At time 0, there was no difference in HR as a function of physiological status (P = 0.895;) and DIM (P = 0.159). At time 4, the animals of the LA group tended (P = 0.076) to increase HR more than animals of the NLA group. At this time, the LA group decreased HR from DIM3 to DIM10. At DIM35 the LA group presented increase of 16,98% in HR compared to the NLA group (P = 0.044). Respiratory rate was not influenced by either PS (P = 0.596) or DIM (P = 0.191). Differences in HR between LA and NLA groups at time 4 are presented in Figure 10.

Table 9 – Means and SEM for respiratory and heart rate at time 0 (before feeding) and time 4 (four hours after feeding), according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Respiratory rate at time 0, breaths/min	23.7 ± 1.78	25.0 ± 1.43	0.586	0.191	0.457
Respiratory rate at time 4, breaths/min	30.3 ± 2.20	31.0 ± 1.80	0.799	0.139	0.930
Heart rate at time 0, bpm	72.4 ± 3.16	72.9 ± 2.57	0.895	0.159	0.642
Heart rate at time 4, bpm	77.3 ± 2.70	84.1 ± 2.29	0.076	0.032	0.499

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

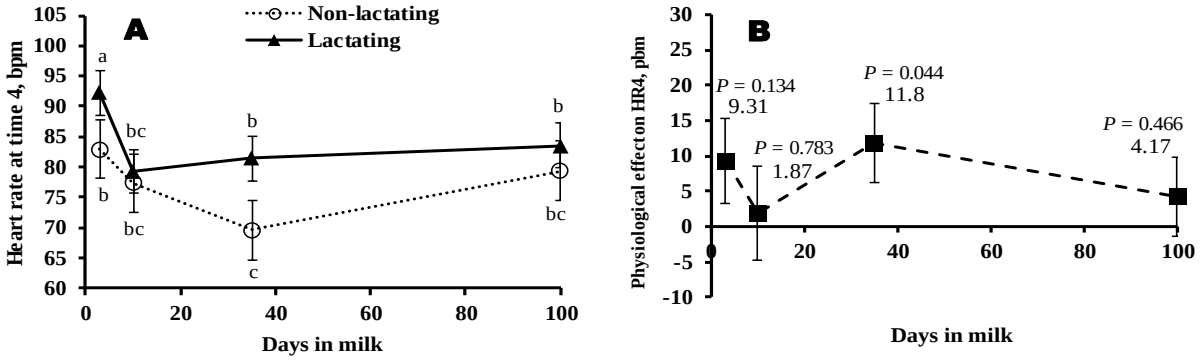

Figure 10 – Least square means for heart rate at four hours after feeding (A) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on heart rate (B). Means followed by different letters differs at P < 0.1 (A).

6.9 Plasma glucose and β-hydroxybutyrate. Plasma glucose and BHBA data are depicted in Table 10**.** At time 0, physiological status affected (P = 0.056) plasma glucose concentration (mg/dL), (Table 10). However, no differences were observed as a function of DIM (P = 0.267). Mean plasma glucose was lower for the LA group (44.5 ± 1.49) than for NLA group (49.0 ± 1.77). However, at time 4, non-lactating and lactating increased (P = 0.10) the plasma glucose concentration over time. Differences in plasma glucose between LA and

NLA groups before feeding and four hours after feeding are presented in Figure 11. Plasma BHBA (µm/l) was affected by PS ($P < 0.001$) and DIM ($P = 0.033$), (Table 10). Mean plasma BHBA was greater 139% for the LA group than the NLA group until DIM35. The lactating group presented decrease in plasma BHBA difference from 318 ± 103 to 200 ± 73.8 between DIM10 and DIM35, (Figure 11).

Table 10 – Means and SEM for plasma glucose and β-hydroxybutyrate (BHBA) concentrations at time 0 (before feeding) and time 4 (four hours after feeding), according to the experimental treatments.

Item	Physiological status (PS)		*P*-value[a]		
	Non-lactating	Lactating	PS	DIM	PS × DIM
Glucose at time 0, mg/dL	49.0 ± 1.77	44.5 ± 1.49	0.056	0.267	0.156
Glucose at time 4, mg/dL	45.9 ± 1.90	42.3 ± 1.64	0.165	0.100	0.192
BHBA at time 0, µmol/l	186 ± 45	429 ± 40	<0.001	0.033	0.185

[a] PS = physiological status; DIM = days in milk; PS × DIM = interaction between physiological status and days in milk.

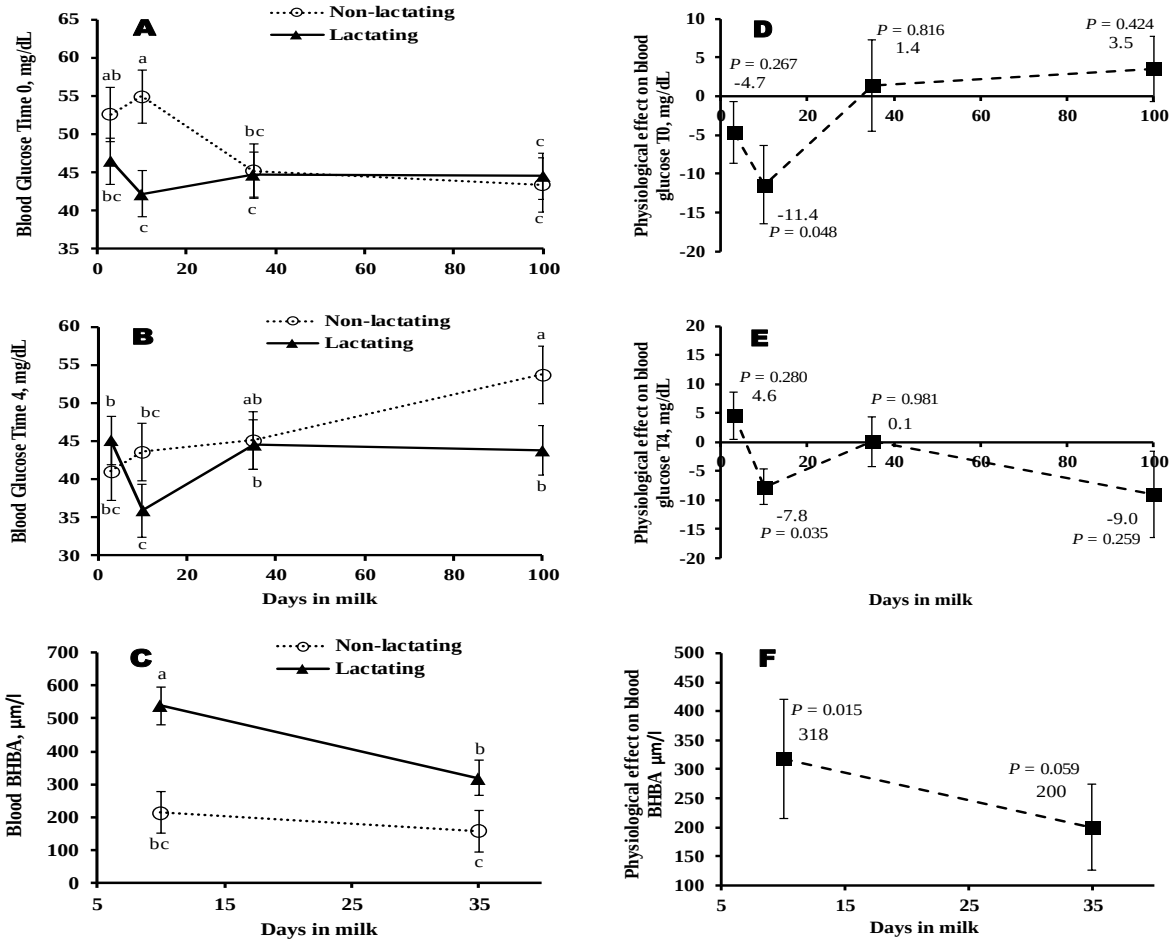

Figure 11 – Least square means for blood glucose before feeding (A), and four hours after feeding (B), and for blood BHBA (C) of non-lactating and lactating animals, and the estimated differential physiological effect of lactation on blood glucose before feeding (D), and four hours after feeding (E), and on blood BHBA (F). Means followed by different letters differs at P < 0.1 (A, B, and C).

7 DISCUSSION

Early lactation (4 – 5 weeks postpartum) has been recognized as the most critical phase of a cow's lactation cycle. At the onset of lactation numerous metabolic, physiological and hormonal changes must take place in a coordinated manner to sustain new demands for amino acids, glucose, and fatty acids needed for milk synthesis (Bauman and Currie, 1980). At this period the lactating beef cows experience reduced intake and typically mobilize body reserves to compensate for the negative balance between nutrient demand and consumption (Mulliniks et al., 2011). It is widely recognized the influence of environmental, plant, and management factors (Dillon, 2005) on intake variation by cows. However, apart from these factors, our hypothesis is that in early lactating beef cows the animal-dependent mechanisms are the main determinants on uptake and utilization of nutrients. Researches with cows indicate that the onset of lactation is accompanied by increase in rumen capacity (Stanley et al., 1993), and passage rate (Vanzant et al., 1991), decrease on fiber digestibility (Park et al., 2011), increase in glucose supply to the mammary gland and inhibited glucose use in insulin-dependent tissues, such as muscle and adipose tissues (Contreras and Sordillo, 2011) as well as fall on plasma glucose concentration (Ingvartsen and Andersen, 2000) and increase in plasma BHBA concentration. Uptake and utilization of nutrients according to the stage of lactation in ruminants, essentially in beef cows are scarce. Therefore, our objective is to quantify the effects of the physiological status (lactation) and the stage of lactation on dry matter intake, total digestion, partial digestion (ruminal and intestinal), the balance of nutrient usage, and metabolism of beef cows.

The absence of difference between the pH of LA and NLA groups is associated with the characteristics of the diet that was offered to the animals, which consisted of a large proportion of corn silage (92% DM basis) providing high fiber to the total diet (NDF = 51,1% DM basis). Diets with high effective fiber are responsible for stimulating chewing, which causes increased saliva flow to the rumen (Harfoot, 1981; Hoover, Stokes, 1991). Saliva's high buffering power makes rumen pH stable, despite the high consumption of fermentable material. Seymour et al. (2005) showed that rumen pH was most strongly correlated with rumen concentration of propionate ($r = -0.45$) and slightly associated with acetate ($r = -0.21$) and butyrate ($r = -0.185$). Falls in rumen pH are mostly associated with lactic acid which provides higher propionate production via the lactic acid pathway (Lucci, 1997). This can happen when rations contain large amounts of grains or sugars (Edelman, 1997).

Heart rate has been used to measure energy expenditure (EEP) (Brosh et al., 2002). In review by Brosh (2007), it was related that EEP and HR are directly affected, among other factors, by physiological status. In the same review, the production level was shown to affect feed intake. The fact that there are no differences in HR at time 0, either to PS or DIM, it is because at this time the cattle express minimal metabolic activity, once cows have a diurnal feeding pattern, both under grazing (Forbes, 1986) and feedlot (Ray and Roubicek, 1971). Higher HR at DIM3 than DIM10 to LA group may be related to the fact that on DIM3 the cow-calf manage may have stress on cows, increasing HR. Different HR at DIM35 between LA and NLA group can be explained by the higher feed intake of LA cows due to increased energy requirements for milk yield and, consequently, higher EEP. These results agree with Brosh et al. (2002) who related higher HR during lactation.

The balance between energy expenditure and nutrients intake is fundamental for the optimization of livestock systems. However, regulation of DMI in early lactation (from zero to 100 days), despite being widely discussed, it is a complex mechanism that is not fully understood (Ingvartsen and Anderson, 2000; Drackley et al., 2005). Numerous factors such as anatomical, physiological and endocrine changes contribute to reduced DMI in lactating cows (Janssen, 1994; Grant and Albright, 1995). The greater average DMI (38%) for LA than the NLA group observed during our study is related to increasing in nutritional requirements of these animals. Lactating beef cows require 20 to 30% greater metabolizable energy than non-lactating cows (Neville, 1971; Montano-Bermudez et al., 1990; NRC, 2000) to support milk yield. However, several mechanisms work together to allow this increase in consumption to achieve nutritional balance.

Despite a large increase in cow requirements at calving (Vanzant et al., 1991; Johnson et al., 2003), the DMI is increasing slower than milk production (Bewley and Schutz, 2008). At DIM10 was observed the lowest difference (28%) in DMI on a BW basis (Figure 4) between treatments. The lower DMI in LA group at DIM10 can be explained in part, by a physical impingement on ruminal volume from the growing fetus and an increasing amount of abdominal fat during gestation (Forbes, 1986; Lagerlöf, 1929), and at early lactation the rumen is still returning to normal size and therefore limiting consumption. Kessel et al. (2008) reported lower average in DMI during the first week postpartum and later increase. However, Ingvartsen and Andersen (2000) suggested that the physical limitation should be not the sole reason for the dip in the intake. Its usually assumed that the body fat mobilization during early lactation is mainly due to a shortfall in feed energy intake relative to milk energy output. However, it is

proposed that body reserves mobilization in early lactation is not a response to feed supply but rather a natural component of a safeguarding reproductive success by strategic use of body reserves (Knight, 2001, and Friggens, 2003). Thus, the reserve mobilization onset lactation also seems to be a mechanism genetically associated with dam ability to give a high priority to lactation in order to ensure the survival of their offspring (Bauman, 2000; Friggens et al., 2004), inducing high plasma NEFA and lower DMI (Grummer, 1993; Ingvartsen et al., 1995). Although we did not measure plasma NEFA, the high β-hydroxybutyrate values observed for LA group (Table 10) in early lactation may indicate high circulating NEFA in these animals, since BHBA is directly linked to the intensity of mobilization of NEFA (Ospina et al., 2010). These findings are due to increase in lipolytic signals during early lactation, which results in increase higher circulating ketones (e.g., β-hydroxybutyrate), (Herdt, 2000) and decreased BCS. Decrease in plasma BHBA and simultaneous increase in DMI over time for LA cows agree with Linden (2011), who suggested that postpartum decrease in plasma BHBA generally coincides with an increase in DMI. These results may be in response to neurohormonal signals reducing reserve mobilization and prioritizing intake.

There is normally a drop in BCS after calving (Bewley and Schutz, 2008). The use of BCS is an accurate and repeatable method to estimate body energy or fat reserves of beef cows (Wagner et al., 1988; Vizcarra and Wettemann, 1996). Body weight loss and drop in BCS observed in LA group (Figure 2) mainly from calving to DIM35 may be associated with both nutrient balance and lipolytic signals.

As mentioned before, lactating beef cows require 20% to 30% more metabolizable energy (ME) than nonlactating cows (Neville, 1971; Montano-Bermudez et al., 1990; NRC, 2000) needed to lactose synthesis. Glucose is the main precursor of lactose in cows (Bickerstaffe and Annison, 1974). Therefore, prioritization of glucose to the mammary gland at the onset of lactation to the mammary gland is given mainly in the function of the synthesis of lactose in this phase (Baumgard et al., 2017). Lowest values in plasma glucose by LA group compared to NLA group at time 0, are related to the higher glucose utilization rate required for milk yield. Furthermore, at early lactation, Insufficient nutrient intake to the detriment of demand may have reduced volatile fat acid (VFA) (mainly propionate) production, and consequently plasma glucose concentration (Reynolds et al., 2003). However, lactating cows need mechanisms acting in a coordinated manner to favor the intake and supply of nutrients to the mammary gland. These mechanisms seem to be related mainly to changes in ruminal digestion kinetics. Van Soest (1994) suggested the increase of passage rate to increase intake.

However, increases in passage rate are related to decreasing in the digestion rate (Okine and Mathison, 1991). The observed greater digesta passage rate and lower digestion rate in LA group than NLA group between DIM10 to DIM35 explain in part, the increase (from 28% to 56%) in DMI difference by LA compared to NLA group, respectively. Increased digesta passage rates and shorter digesta residence times in the gut are characteristic of high DMI and are associated with low digesta digestibility (Moe et al., 1965; Colucci et al., 1982; Edionwe and Owen, 1989). Higher digesta passage observed for LA group compared to NLA group at early lactation is associated with also higher digesta outflow in these animals (Table 7). This can be a mechanism used to increase intake given that restricted flow may result in distention of one or more segments of the gastrointestinal tract, resulting in decreased intake (Allen, 1996). Means by which changes in digesta digestibility and passage rate in lactating cows occur are still lacking, however, seem to be associated with eating behavior (Aikman et al., 2008). Deswysen et al. (1987) suggested that mastication and rumination time per kg of DM decrease with increased intake and may contribute to decreased DM digestibility (DMD). Thus, in early lactation the increase in digesta passage rate showed be part of homeostatic mechanisms to compensate for intake limitations in this period, despite relative loss of digestibility.

The NDFD may vary according to physiological status and is usually correlated with the DMI. Tyrrell and Moe (1975) indicated that the digestibility of the diet in non-lactating dairy cows may overestimate the digestibility of the same ration fed to lactating cows by 12% or more. The lack of effect of both the PS and DIM on digesta intestinal digestibility showed that changes in total digestibility kinetics happen mostly in the rumen, affecting TDN values. These findings agree with our hypothesis, that models for estimating the energy value of feed should not be the same for both cows in early lactation and non-lactating because animals in early lactation showed changes in ruminal dynamics with a consequent reduction in the utilization of feed.

There are numerous studies that attribute rumen physical limitation as the main cause in reducing early lactation intake (Ingvartsen and Anderson, 2000). However, Mertens (1994) suggested that the intake physical capacity can be modified by physiological responses, within certain limits, to achieve balance. Higher ruminal pool observed in this study for LA cows compared to NLA cows suggest that the concept the ruminal fill controlling forage intake via a distension mechanism does not adequately account for observed variation in forage intake lactation. Moreover, Dado and Allen (1995) reported a reserve volume of more than 16 L in the reticulorumen of dairy cattle consuming a fill limiting diet with addition of 22.2 L of inert fill,

indicating that additional capacity may exist for ruminal pool even when distension in the reticulorumen limits DMI.

Overall, early lactating beef cows show high glucose utilization rates decreasing the plasma glucose concentration. However, neuroendocrine signals stimulate the mobilization of body reserves, increasing the amount of circulating ketone bodies (e.g. BHBA). Reserve mobilization metabolites, coupled with physical limitation of rumen at early lactation are responsible for depressing DMI and decrease BCS, and BW. Throughout lactation cows have mechanisms to balance the uptake and nutrients utilization: increasing rumen capacity, decreasing reserve mobilization as well as reduction of metabolites that signal decreased intake, and increasing the passage rate of the digest. This last causes a reduction in digesta digestibility, decreasing the efficiency of utilization of total digestible nutrients of feed (Figure 12).

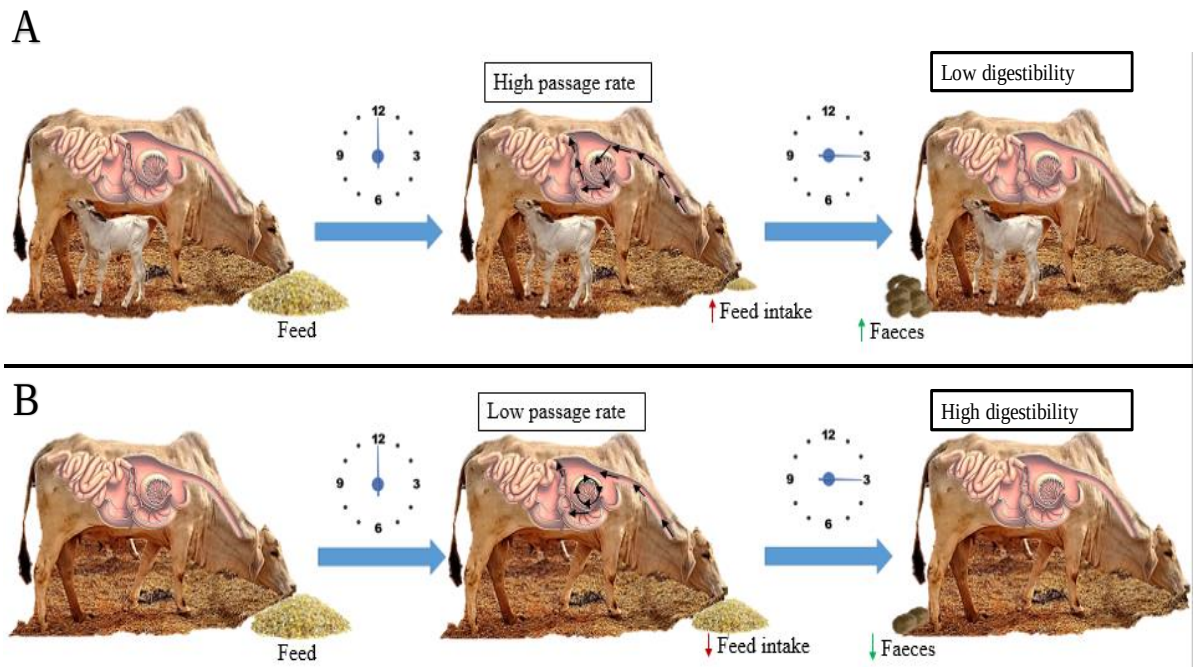

Figure 12 - Effect of physiological status on feed intake, digestion, and utilization of nutrients in early lactation. Letters represent the experimental treatments: A = Lactating group; B = Non-lactating group.

8 CONCLUSION

During the experimental period, the LA group presented, respectively, TDN and DM intake 31% and 43% greater the NLA group. The greater DMI compared to TDN intake it's because beef cows in early lactation have lower feed efficiency, having to increase feed intake to compensate for lower nutrient digestibility. However, the physiological status as well as the

stage of lactation should be included in performance prediction models, since early lactating beef cows are less efficient at extracting energy from feed compared to non-lactating cows, changing the feed predicted TDN values.

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