A meta-analytical evaluation of the regulation of voluntary intake in cattle fed tropical forage-based diets

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ABSTRACT: The objective of this work was to use a meta-analytical approach to evaluate the regulation of voluntary intake in cattle fed tropical forage-based diets using dietary digestibility and bulkiness. Treatment mean values were collected from 53 studies with lactating dairy cows and 126 studies with feedlot growing and finishing cattle that were published in Brazil from 1990 to 2012. In all studies animals were fed ad libitum with diets based on tropical forages. The dataset was analyzed according to meta-analysis techniques, using linear and nonlinear mixed models. The main independent variables were the D-value and the B-value of the diets. The D-value corresponds to the dietary content of digested OM and is associated with energy content of the diet. The B-value is defined as the undigested fraction of NDF and indicates bulkiness of the diet. The DMI presented significant associations with both D-value and B-value. In the first case, DMI intake responded quadratically to the D-value \((P = 0.042)\). On the other hand, DMI decreased linearly as the B-value of the diet increased \((P = 0.004)\). Two new variables called Di and Bi were created to express the intake in terms of D-value and B-value units. A conceptual explicative model was developed from Di and Bi. This model showed that DMI is simultaneously regulated by both physical constraints and metabolic feedbacks. There were differences in the intake pattern of lactating cows and growing cattle.

Key words: dry matter intake, fiber, mixed models, physical constraints

INTRODUCTION

The main theory of intake control applied to ruminants is based on the integration of physical constraints and metabolic feedbacks, which in turn determines the maximum DMI for a specific animal under a particular feeding situation (Crampton, 1957; Blaxter et al., 1961; Conrad et al., 1964). Despite different approaches, this dual phase control theory generally states that for low-quality diets, intake would be restricted by physical limits of gastrointestinal tract (GIT) to hold the bulk from diet. Moreover, when the animals are fed with high-quality diets, the limit of DMI would be determined by metabolic feedbacks that would be responsive to dietary energy (Mertens, 1994). However, this approach has been criticized because it intrinsically assumes that both physical constraints and metabolic feedbacks are independent of each other. Such an approach would be physiologically unlikely because all regulatory signals should work in integrated manner creating a unique additive signal that determines the voluntary DMI (Weston, 1996; Pittroff and Kothmann, 1999; Fisher, 2002; Forbes, 2007a).

Most of the past investigations on the pattern and control of DMI in cattle was performed in nontropical regions. In the tropics, research has been performed to either understand (Detmann et al., 2003) or model (Azevêdo et al., 2010) the intake of feedlot cattle. In spite of this, it seems unlikely that the mechanisms of intake control would be different in the tropics compared to nontropical regions. Nevertheless, considering...
the differences concerning forages and genetic characteristics of the animals, it could be likely that the relative importance of each mechanism is different across regions.

The objective of this work was to use a meta-analytical approach to evaluate the regulation of voluntary intake in cattle fed tropical forage-based diets using dietary digestibility and bulkiness.

MATERIALS AND METHODS

Data Acquisition

Treatment mean values were collected from 53 studies with lactating dairy cows and 126 studies with growing and finishing cattle that were published in Brazil from 1990 to 2012, totaling 765 treatment means (lactating dairy cows = 226; growing and finishing cattle = 539; online supplement). In all studies, animals were fed ad libitum with diets based on tropical forages. The minimum prerequisite to include a study in the dataset was to provide information concerning DMI and NDF intake, both expressed as grams per kilogram of BW, and dietary content of NDF.

Furthermore, several additional characteristics were aggregated into the dataset including the animal category (lactating cows or growing and finishing cattle), genetic group of the animals (European, Zebu, or Crossbred), type and level of forage in the diet, in vivo total digestibility of NDF and OM, and average BW of the animals during experiment. However, not all of the above information was reported in every experiment, which resulted in some heterogeneity among the variables with regards to the total number of observations (treatment means; Table 1).

The D-value of a diet (g/kg DM) was defined as the content of apparently digested OM and was calculated as

$$D-value = OM \times D_{OM} = tdOM - M,$$  \[1\]

in which OM is the dietary OM content (g/kg DM), $D_{OM}$ is the total apparent digestibility of OM (g/g), tdOM is the dietary content of truly digestible OM (g/kg DM), and M is the metabolic matter in feces expressed as a fraction of the diet (g/kg DM).

The D-value of the diet has been used to model and predict intake and to evaluate the quality of forages in nontropical conditions (Huhtanen et al., 2007, 2008). The D-value presents a direct association with the digestible energy content of the forage or diet.

To correctly understand the intake regulation, an additional measure was proposed for indicating not only the nutritive value but also the lack of capacity of the feed or diet to be used in the GIT. By contrast with the D-value, a variable called the B-value (the B was derived from “Bulk”) was also evaluated from the dataset, which was defined as the undigested fraction of NDF (g/kg DM):

$$B-value = NDF \times (1 - D_{NDF}) ,$$  \[2\]

in which NDF is the NDF content (g/kg DM) and $D_{NDF}$ is the total digestibility of NDF (g/g).

The theoretical concept of the B-value (g/kg DM) can be easily expressed in a mathematical form using first order kinetics and assuming steady state conditions in the rumen as

$$B-value = (dFE/dt)/(dCF/dt) = pdNDF \times [kp/(kp + kd)] + iNDF ,$$  \[3\]

where FE is the pool of fiber escaping from digestion, CF is the pool of consumed fiber, $pdNDF$ is the potentially digestible NDF (g ∙ kg⁻¹ DM), kp is the passage rate of fiber (h⁻¹), kd is the degradation rate of fiber (h⁻¹), $iNDF$ is the indigestible NDF (g ∙ kg⁻¹ DM), and t is the time.

<table>
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<tr>
<th>Variable¹</th>
<th>Mean</th>
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<th>Maximum</th>
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¹NDFI = NDF intake; FD = forage content in the diet; D-value = diet content of digested OM; B-value = diet content of undigested NDF.
²The dataset was not adjusted for random variation among experiments.
From Eq. [1], the relationship between the D-value and the B-value can be demonstrated as

\[ 1 - (D\text{-value}) = 1 - (\text{tdOM} - M) = (1 - \text{tdOM}) + M, \]  
\[ [4a] \]

\[ 1 - (D\text{-value}) = \text{tuOM} + M = (\text{uNDF} + \text{tuNDS}) + M, \]  
\[ [4b] \]

\[ 1 - (D\text{-value}) = \text{tuOM} + M = (\text{uNDF} + \text{tuNDS}) + M, \]  
\[ [4c] \]

in which \( \text{tuOM} \) is the truly undigested OM, \( \text{uNDF} \) is the undigested NDF (see Eq. [2]), \( \text{tuNDS} \) is the truly undigested neutral detergent soluble fraction, and \( \text{auNDS} \) is the apparently undigested neutral detergent soluble fraction. The other terms were previously defined and all of them are expressed as grams per kilogram DM.

Therefore, according to Eq. [4c], the B-value of a feed or diet is inversely proportional to D-value, as the latter indicates the fraction of the diet that can be used for energy purposes whereas the former is thought to indicate the bulk of the diet, that is, the fiber fraction that is not digested, which would present a higher fill effect.

Thereafter, 2 new variables were created to express the intake as units of the D-value and the B-value. These variables were called \( D_i \) and \( B_i \), respectively, which were calculated as follows:

\[ D_i = \text{DMI} \times (D\text{-value} / 1,000) \]  
\[ \text{and} [5] \]

\[ B_i = \text{DMI} \times (B\text{-value} / 1,000). \]  
\[ [6] \]

These new variables represent a transformation of diet characteristics into the effective intake of digestible mass (\( D_i \)) and bulk mass (\( B_i \)). The use of these variables could be seen as an inconsistent or redundant pathway to explain intake pattern, as DMI was used to produce \( D_i \) and \( B_i \). However, the main objective of this work was to understand the mechanisms of intake regulation in cattle rather than propose a new model to predict intake. It must be emphasized that energy or bulk concentration in feed only regulates intake after being consumed by the animals. Therefore, the real capacity of driving feedback signals belongs to the energy and bulk intake rather than their concentration in feeds or diets.

**RESULTS**

Despite of a heterogeneous pattern in regards to the number of observations for each variable, the dataset broadly covered the nutritional characteristics of the Brazilian production systems in which cattle are managed under feedlot conditions (Table 1). The broad ranges of DMI, NDF intake, forage level, and D- and B-values of
Intake regulation of cattle in the tropics

The diets indicate that the dataset consists of low- to high-quality diets, which in turn represents a necessary feature for the inference of intake pattern and regulation.

There was no relationship between the dietary concentration of NDF and DMI \((P = 0.49; \text{Fig. 1})\). In addition, the D-value of the diet decreased linearly \((P < 0.001)\) as dietary NDF increased. The B-value presented a linear and positive relationship \((P < 0.001)\) with NDF concentrations in the diet (Fig. 2). There was no effect of animal category on these relationships \((P > 0.05)\).

Dry matter intake was associated with both the D-value and the B-value (Fig. 3). In the first case, DMI intake responded quadratically to the D-value \((P = 0.042)\), whose maximal estimated value was on 658 g/kg DM. On the other hand, the DMI was linearly decreased as the B-value of the diet increased \((P = 0.004)\).

The relationships of Di and Bi with the NDF concentration in the diet were found to be nonlinear, and exponential models were adjusted for describing both relationships. The responses of these variables to NDF concentration were opposite each other. The Bi increased and Di decreased as the NDF concentration in the diet increased \((P < 0.05)\). Despite this, it must be highlighted that the rates of alteration on Bi and Di according to NDF concentration were very similar (Fig. 4).

Although the pattern of Bi and Di according to dietary NDF concentration was opposite, these variables were positively and linearly \((P = 0.001)\) associated to each other (Fig. 5).

Dry matter intake presented a positive and linear relationship with both Di \((P < 0.001)\) and Bi \((P < 0.001; \text{Fig. 6})\). There was an influence of the animal category \((P < 0.001)\) on the estimates of the intercept of adjusted functions, with lactating cows having a greater intake compared to growing and finishing cattle. The alteration in DMI was more prominent in response to 1 unit of Bi when compared to 1 unit of Di. Moreover, the range of Bi values was narrower than the Di range. In addition, DMI seemed to present a stronger correlation with Di, which can be perceived through the lower residual SD, slightly higher \(R^2\), and closer distribution of the points around the regression lines.

To integrate the different mechanisms of intake control, the mathematical models described in Fig. 5 and 6 were used to describe the overall pattern of voluntary intake, which is expressed in Fig. 7 (growing cattle) and 8 (lactating dairy cows). Apart from 1 single point, there are 2 different estimates of DMI according to Di and Bi. It is proposed that voluntary intake can be interpreted according to the following equations:

\[
\hat{P}(\text{DMI}) = \max(\hat{Y}_D, \hat{Y}_B), \quad [7]
\]

\[
\hat{E}(\text{DMI}) = \min(\hat{Y}_D, \hat{Y}_B), \quad \text{and} \quad [8]
\]

\[
\text{DDI} = \hat{E}(\text{DMI}) - \hat{P}(\text{DMI}), \quad [9]
\]

in which \(\hat{P}(\text{DMI})\) is the predicted potential DMI, \(\hat{E}(\text{DMI})\) is the predicted effective DMI, \(\hat{Y}_D\) is DMI predicted according to the function based on
Di, $\hat{Y}_b$ is DMI predicted according to the function based on Bi, and DDI is the deficit on the demanded or potential intake.

Accordingly, the lowest estimate of DMI is supposed to be the effective DMI, which is the actual DMI intake considering the energy demand, the physical capacity of GIT, and the characteristics of the diet (Eq. [8]). On the other hand, the highest estimate of DMI is thought to correspond to the potential DMI with no physical or metabolic constraints to intake (Eq. [7]). The DDI (Eq. [9]) represents the portion of potential intake that does not occur due to some constraints associated with diet characteristics, physical restriction in GIT, or metabolic feedbacks. It can be noted that there is only 1 point where DDI = 0, which is the intersection between the 2 functions (Fig. 7 and 8). This point requires a different interpretation from static models of intake control. In this case, it is assumed that...
that this point represents an estimate of voluntary DMI, where both physical and metabolic mechanisms are in equilibrium rather than a threshold where the transition between mechanisms would occur. It is assumed in this work that both mechanisms are working together and with the same importance in the interception point (point of equilibrium between mechanisms [EBM]).

Considering that the description of intake pattern (Fig. 7 and 8) was originated from 3 different equations (Fig. 5 and 6), an evaluation of accuracy was performed by comparing the predicted (Eq. [8]) and the actual DMI. In general, the model described the DMI pattern well (Fig. 9). There was a small bias that seemed be caused by a slightly under predicted intake for animals with the highest values of actual DMI.

DISCUSSION

Relationships between Diet Characteristics and Intake

One of the initial objectives of this work was to evaluate the correlation between the voluntary DMI and dietary NDF content for animals fed tropical forage-based diets. Such an objective was established considering that NDF is thought to be associated with the fill effect of feeds (Mertens, 1987, 1994). On several occasions, NDF intake or diet content has been used in the tropics to define which mechanism would be regulating the voluntary intake (Detmann et al., 2003; Oliveira et al., 2011). Despite this, the results obtained here show that dietary NDF content was not directly associated to DMI regulation.

The NDF represents the insoluble fraction of the diet, which can occupy space in GIT (Van Soest, 1994). Nevertheless, the fill effect of fiber depends on several characteristics, such as the dimensions of the indigest-
ible and potentially degradable fractions and the rate of removal from the rumen (Waldo et al., 1972; Detmann, 2010). The NDF from tropical forages presents a highly heterogeneous degradation pattern in the rumen (Souza et al., 2010; Vieira et al., 2012) and that pattern is quite different amongst feeds (Valente et al., 2011). Sometimes, the separation of total NDF into iNDF and pdNDF can improve the associations with voluntary intake (Huhtanen et al., 2007), but the ratio of pdNDF to iNDF is highly variable amongst feeds (Detmann, 2010; Oliveira et al., 2011). Therefore, a single estimate of dietary NDF content would not be useful to either understand or predict the voluntary DMI in cattle.

Despite the lack of relationship with DMI, the NDF content in the diet affected D-value and B-value of the diet negatively and positively. Such a pattern seems logical since as the NDF content of the diet is increased, the neutral detergent solubles (NDS) content decreases. The NDS presents true digestibility close to the unit (Van Soest, 1994; Nousiainen et al., 2009), whereas NDF presents incomplete and highly variable digestibility (Van Soest, 1994). Considering this, the increase in NDF content decreases the highly digestible fraction of diet and increases the concentration of compounds related to the bulkiness, which gives support to the pattern obtained here.

The inverse relationship between dietary NDF content and the nutritive value of diet was also verified by evaluating Di and Bi, which varied at the same rate according to the increase in NDF content. In a specific way, the increase in Bi as NDF content increased indicates that the fill capacity of GIT (or reticulorumen) was not constant. Such a pattern agrees with previous observations in the tropics (Detmann et al., 2003) and contradicts the assumption of a fixed maximum filling capacity of GIT adopted in static models for predicting feed intake (Mertens, 1987, 1994). Variations on the filling capacity of reticulorumen have been reported in the literature as a possible adjustment of the balance between nutrient requirements and diet quality. It means that animals can increase gut capacity due to a decrease in diet nutritive value (Weston, 1996; Schettini et al., 1999; Rinne et al., 2002), an increase in nutritional requirements (Tulloh, 1966; Forbes, 2007a), or a metabolic adequacy by meeting a marginal dietary deficiency (Forbes, 2007b).

Lactating dairy cows exhibited greater DMI per unit of Bi than growing cattle, which could be, at least partially, associated with a greater ruminal capacity when compared to growing animals. Furthermore, such a pattern seems to be logical when considering that intake is thought to be, at least partially, a response of production. It means that animals with greater nutritional requirements (e.g., energy requirements) will increase the intake as an attempt to supply the increased requirements (Hunter and Siebert, 1986; Weston, 1996; Forbes, 2007a). In addition, lactating dairy cows show a greater DMI per unit of Di, which indicates a lower digestion of dietary OM compared to growing cattle. In fact, there is a negative effect of intake on OM digestibility (Van Es, 1975; Huhtanen et al., 2009) and dairy cows presented a greater average DMI than growing cattle (32.0 vs. 21.8 g/kg BW).

Two inferences can be drawn from the relationships between Di, Bi, and DMI. First, the pattern described here contradicts one of the main assumptions of the static models of intake control, which stated that the intakes of energy units and fill units are opposite each other (Mertens, 1994). The demand for energy is one of the main mechanisms that determine voluntary intake (Weston, 1996; Forbes, 2007a,b). Considering this, it would be logical that the fill capacity of GIT can be affected by some alteration on the energy demand, which characterizes integration between mechanisms of intake regulation (Weston, 1996; Pittroff and Kothmann, 1999) and indicates that the assumption of a single opposite relationship of energy content and fill capacity is biologically unlikely. This is the first indicator that a dual phase theory of intake control is implausible, as in that theory there is an intrinsic assumption that the regulatory mechanisms (physical and metabolic) are independent of each other and the actual intake is determined by the first limiting factor (Pittroff and Kothmann, 1999).

The second inference to be taken from the relationships between Di, Bi, and DMI is associated with the dispersion pattern of both relationships of Di and Bi with DMI. The greater precision for the relationship between Di and DMI should be noted. This observation agrees with Huhtanen et al. (2002, 2007), who found that D-value predicted DMI much more precisely than bulkiness (NDF content).

Integrated Modeling of Voluntary Intake Pattern

In general, despite the small bias associate with the animals with the highest intake, the explicative model developed here described the DMI pattern well. The bias seemed be plausible because several other feed, environmental, physiological, psychogenic, health, management, production, and social characteristics can affect intake (Ingvartsen, 1994; Mertens, 1994; Forbes, 2003) and they were not considered in this work. Therefore, it can be concluded that our proposal represents a fair description of intake pattern.

The EBM point corresponded to diets with a D-value of 660 and 628 g/kg DM for lactating cows and growing cattle, respectively. These values agree with the quadratic relationship between DMI and the D-value and are close to the threshold values related in some dual phase interpretations of feed intake (Blaxter et al., 1961;
Conrad et al., 1964; Dinius and Baumgardt, 1970). In spite of this, the difference between lactating dairy cows and growing cattle brings evidence that the EBM should not be considered as a fixed point, as its position could be influenced by animal size, production level, and diet characteristics (Conrad et al., 1964; Mertens, 1994).

In spite of using a “First Limiting” mathematical structure (Eq. [8]), our explicative model is not based on the first limiting factor, as the dimensions of DDI are defined by the integration of several physical, digestion, and metabolic characteristics.

Under any feeding condition, the amount of a constraint may be considered as the difference between the quantity of feed that is eaten and the quantity of feed that would be required to meet animal requirements when constraints are absent (Eq. [9]). In general, the constraint on feed intake tends to decrease as the energy content of the diet increases (Weston, 1996), which seems to be valid for DDI(1) that represents the constraint to intake when lesser nutritive diets are considered.

The constraint in DDI(1) is the difference between the potential intake determined by the physical capacity of GIT and the effective intake restricted by the low digestibility of the diet. It seems illogical to suppose that an animal could not consume low-nutritive forages up to its GIT physical capacity, but some arguments can be used to support this pattern.

Assuming a steady state condition in the rumen with regards to fiber mass and using first order kinetics, the rumen fill effect of fiber ($RF; h$) can be represented as (Waldo et al., 1972; Detmann, 2010):

$$RF = \lim_{t \to \infty} \int_{0}^{t} [R(t) \times f(t)] dt,$$  \hspace{1cm} [10a]

$$RF = \frac{pdNDF}{kd + kp} + \frac{iNDF}{kp},$$  \hspace{1cm} [10b]

in which $R(t)$ is the mathematical function that describes the undegraded NDF as a function of time and $f(t)$ is the mathematical function that describes the ruminal transit of NDF as a function of time. The other terms were previously defined. In this particular case, the pdNDF and the iNDF are expressed as grams per gram NDF and their sum must reproduce unit (pdNDF + iNDF = 1; for details, see Waldo et al., 1972).

The RF expresses the steady state fill per unit of fiber intake and means the capacity of fiber to occupy space in the reticulorumen compartment. Under normal feeding conditions (without drastic nutritional unbalance), it could be realized that $kp$ is regulated by intake (Pittroff and Kothmann, 1999). Therefore, the RF will be determined by $kd$ and by the ratio of pdNDF to iNDF (or the rate and extent of digestion respectively), which will establish the digestibility. It must be emphasized that RF is a characteristic of the fiber itself and this does not depend on the dietary fiber content.

The main problem of using a fixed physical capacity of intake is that such reference values are intrinsically static and do not take into account that the true important value is the mass flow over time (dynamic flow). A theoretical limit or capacity to “accommodate” mass in GIT can be established, but the whole use of this capacity is constrained by the variables involved in RF (Eq. [10]). It would delay the outflow of undigested material from rumen and compromise the voluntary intake. Therefore, the bulkiness of the diet must be based on dynamic measurements rather than on any static reference of intake.

Experiments where inert bulk was used to evaluate the effect of fill have shown inconsistent results, normally with minimal alterations on intake associated to great bulk volumes (e.g., Mbanya et al., 1993; Dado and Allen, 1995; Schettini et al., 1999). Such a pattern suggests that factors other than volume itself are responsible for the fill effect. It seems to corroborate that the real constraint to intake is the flow (dynamic parameters) rather than the resident mass (static parameter). Inert bulks should not be considered physiologically valid because they cannot participate in the rumen flow events. In addition, the mathematical limit for the RF of an inert bulk is infinite (Eq. [10]), which is biologically incoherent.

Conversely, the constraint in DDI(2) is the difference between the potential intake determined by the theoretical requirement of energy intake and the effective intake restricted by metabolic feedbacks and also by body size. The rate of increase of DMI according to the increase in Di becomes lower above EBM and any significant increase in energy intake can only be achieved by increasing the energy content of the diet. It is interesting to note that there is no decrease in the DMI above EBM, which is different from the assumptions of the dual-phase model (e.g., Mertens, 1994) but consistent with concepts presented by Conrad et al. (1964) and Dinius and Baumgardt (1970). As the energy content of the diet is increased, there will be an increase in the compounds in the animal metabolism that are able to generate negative feedbacks to voluntary intake (Forbes, 2007a; Allen et al., 2009). Furthermore, greater energy intake is associated with greater production and metabolism, which can increase the body heat production. The body heat dissipation capacity of an animal depends on body size and surface (Kleiber, 1961) as well as environmental conditions. Excessive body heat production can generate a negative feedback on intake and physical activities as a mechanism to allow the animal to approach a comfort condition (Poppi and McLennan, 1995). In addition,
even highly digestible diets occupy space in GIT and their intake should present some correlation with animal body size. Therefore, DDI(2) is clearly related to both physical and metabolic mechanisms of intake control.

Conclusions

The pattern of voluntary DMI in cattle fed tropical forage-based diets can be evaluated using diet characteristics, noticeably the contents of digestible OM (D-value) and undigested fiber (B-value). These variables are closely associated with the energy content and bulk capacity of the diet, respectively. A conceptual explicative model was developed based on the intake of units of the D-value and the B-value. The evaluation of intake pattern from this model brings evidence that physical constraints and metabolic feedbacks work in an integrated manner in the regulation of voluntary intake.

LITERATURE CITED


