

Ingestive behaviour of grazing ruminants: meta-analysis of the components linking bite mass to daily intake

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Short title: Ingestive behaviour of grazing ruminants meta-analysis

Abstract

This meta-analysis shed light on the quantitative adaptive responses of feeding behaviour of Cattle (C) and Small Ruminants (SR), facing variations of sward characteristics, notably of sward height (SH, 18.7 ± 13.9 cm) and herbage bulk density (HBD, 1.73 ± 1.30 kg DM / m³). All responses expressed a plateau stressing an adaptive limit with extreme values of SH and HBD. The minimum plateau of BR (46.9 ± 14.6 min⁻¹) is around 40 min⁻¹, while IR values (different for C and SR , respectively 69.1 ± 38.1 vs. 99.9 ± 45.7 g/min/kg BW) ranged between a minimum and maximum plateau around 50 and 100 g/min/kg BW. Two other pasture management factors affect IR, namely forage allowance (10.16 ± 6.0 , DM % BW) and daily proportion of time spent grazing (0.30 ± 0.08). The results obtained confirm the specifically key role of

BM (1.80 ± 127 mg DM/kg BW) on IR. The regressions are $IR=145 (1-\exp (-b \text{ BM}))$, b being equal respectively for C and SR and C to 0.44 vs. 0.54. This literature review has also revealed fundamental differences in behaviour between C and SR although no study to date has attempted to compare them simultaneously. SR have to chew more (2.7 ± 1.2 vs. 1.6 ± 0.5 JM/bite) to ingest the same amount of DM per bite than C, expressed in relation to BW, which allow them to ingest slightly quickly.

Keywords (5): Intake rate, Bite Rate, Sward height, Herbage bulk density

Implications

This article, following the previous one of Boval and Sauvant (2019), proposes a quantitative appraisal of the ingestive behaviour of grazing ruminants, based on studies published over 40 years, as well as well robust average values and relationships, considering inter- and intra-study effects and animal species specificities. This knowledge should contribute to a better overall understanding of the behavioural adaptation of ruminants at pasture, to the identification of key threshold values and appropriate parameters of interest to be considered, and to improve the efficiency and sensitivity of automatic devices, which are booming in the context of precision livestock farming at pasture.

Introduction

Knowledge of ingestive behaviour (IB) is determinant to better understand the strategies of animals for feeding in order to improve their management, whatever the feeding context. Ingestive behaviour determines the nutrient supply to ruminants and thus has a significant impact on performance and feed efficiency, which are essential

for increasing the profitability of livestock (Llonch *et al.*, 2018; Shalloo *et al.*, 2018). Moreover, a ruminant's robustness partly comes from its ability to adapt IB to the diversity of resources to be grazed. In addition, chewing behaviour provides information about digestive comfort and indicators of appetite, gut health and welfare. Numerous studies have focused on the IB of grazing ruminants. However, beyond the problems linked with the diversity of the methodologies applied, the items measured are very heterogeneous across publications. Likely for this reason, no synthetic statistical interpretation of published IB data for ruminant grazing has been carried out and published so far. However, there is a need to better understand the various aspects of animal IB, as it is now becoming possible to measure some of them in field conditions thanks to advances in electronic/computer technologies (Anderson *et al.*, 2014; Fogarty *et al.*, 2018). Indeed, animal behaviour documented by tools employed in precision livestock farming, such as sensors, video cameras, accelerometers or pedometers, should greatly help in designing efficient management strategies for livestock production systems (di Virgilio *et al.*, 2018). A recent meta-analysis focused on bite mass (BM) and its main determining factors linked to major animal and sward characteristics (Boval and Sauvant, 2019). In this current paper, we will analyse the components affecting BM which are determining for intake rate and daily dry matter intake. Some studies differentiate between jaw movements due to harvesting forage and those processing the forage before swallowing. We have therefore attempted to better understand the function of these different types of jaw movements.

Material and methods

Literature review and dataset construction

This meta-analysis was carried out by considering published studies measuring components of the feeding behaviour of ruminants (cattle, sheep or goats) at pasture in various production systems (milk or meat) and various climatic contexts. The search for the literature was carried out using Web of Science, Science Direct, EDP Sciences and Cambridge Journals and using the reference lists cited by some reviews on the subject.

For each publication, we have integrated experiments and treatments for which there were documented values of at least one of the following criteria: BM, biting rate (BR), intake rate (IR), grazing and ruminating times (GT and RT, respectively, min/day) and data related to dry matter intake (DMI) and BW gain. In some publications, total jaw movements and chews were also measured, and therefore were included.

Intermediary calculations

For all the characteristics, we have harmonized the units within the whole dataset. Afterwards some components were also expressed per kg of BW, such as IR, in order to analyse the whole dataset including the maximum degrees of freedom (with data coming from different species and types of domestic ruminants). Considering the BM calculation, Boval and Sauvant (2019) have shown that BM can be divided by the BW¹. When it was possible, the number of chews was calculated, considering that jaw movements (JM) = chews + bites (Galli *et al.*, 2017; Mulvenna *et al.*, 2018). When JM are expressed per bite, the number of JM/bite cannot be lower than 1 (i.e. one bite). For each publication retained in the database, the following information was recorded: the animal characteristics (breed, sex, age) as well as the forage characteristics

(species, herbage mass, surface sward height and herbage bulk density, morphological and chemical composition, etc.). Information related to the experimental conditions (at pasture or in other environments) and to the methods used to measure feeding behaviour and forage characteristics was also recorded. The season (dry or rainy), latitude and longitude have been précised as well for each experiment intra-publication, by using Köppen–Geiger classification (Peel *et al.*, 2007).

Treatment encoding

Beyond specific codes assigned to each publication and to each experiment, additional codes were applied to identify specifically the factors of variation tested in the papers: the forage species, sward height, herbage bulk density or herbage allowance and the animal species. All of these codes were specific to the factors of variation studied in the publication; therefore, not all rows have values in the corresponding columns. For some experiments, in addition to the intra-experimental factors, some key criteria varied significantly, although they were not the factors tested intra-experiment. In this case, another code was added to specify these criteria, as a secondary factor of variation. For example, we identified experiments for which the intra-experiment sward height varied largely despite not being announced as a factor in the publications, but which can then be considered as a factor of variation for 62% of papers instead of the 32% we had identified at first approach.

The final database included 98 publications (npub), 269 experiments (nexp) and 905 treatments (n). The list of the references used to build the database is presented in the Annex.

Statistical analysis

Statistical analysis of the data was performed by meta-analysis according to the recommendations of Sauviant *et al.* (2008). In particular, inter- and intra-experiment variations were split to study in the intra-experiment relationships between variables considered two by two, and successively through the various factors of variations. The numbers of data different from one variable to another explain why the interpretation must be achieved considering the variables 2 by 2.

Results

Statistical parameters of the ingestive behaviour components

The statistics of the components of feeding behaviour were calculated for cattle and small ruminants (Table 1) and according to BW when it allowed pooling of data for both species. Among the data collected in the papers analysed, BR was one of the most documented components, as well as its reverse, namely the time spent per bite. These two components have a log-normal distribution and do not differ significantly between species.

Jaw movements associated with bites were registered in only about 20% of cases, but with sufficient data for each species.

Intake rate was less much documented in the papers than BR, and distribution of the data is quite close to a Gaussian law. Otherwise, IR is largely different between cattle and small ruminants, contrary to BR (Table 1). Even when IR was expressed per kg of BW, the difference between species remained but the value in this case was a little higher for small ruminants (Table 1).

Modelling factors of variation of the ingestive behaviour components

Bite rate

The influence of sward height (SH) on BR was evaluated from experiments that studied SH impacts. There is a negative curvilinear relation (Figure 1a) between BR (bites/min) and SH (18.7 ± 13.9 cm)). Under a threshold of SH of 15–20 cm, there appears to be an acceleration of BR. The intra-experimental regression is:

$$\text{BR} = 41.4 + 29.9 \exp(-0.100 \times \text{SH}) \quad (n = 189; n_{\text{exp}} = 63; \text{RMSE} = 5.8) \quad [1]$$

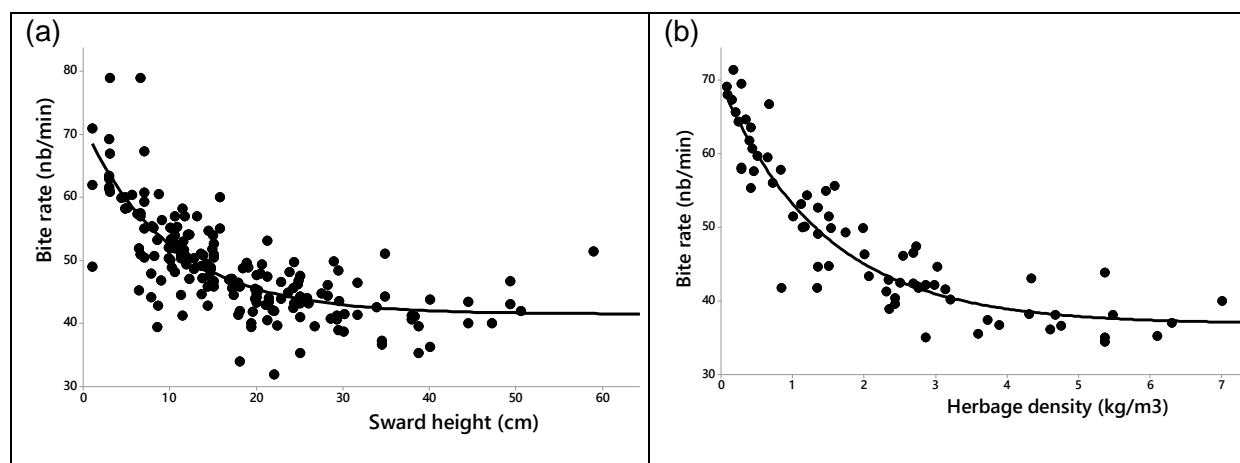


Figure 1 Intra-experiment relationships between bite rate and sward height (a) or herbage bulk density (b).

The impact of apparent forage density (HBD, 1.73 ± 1.30 kg DM/m³) on BR was assessed from experiments that tested the impacts of HBD variations. There is a negative exponential intra-experiment relationship between BR (bites/min) and HBD (Figure 1b); the regression is:

$$\text{BR} = 36.84 + 32.55 \exp(-0.692 \text{ HBD}) \quad (n = 72; n_{\text{exp}} = 25; \text{RMSE} = 3.9) \quad [2]$$

An acceleration of BR occurs when the HBD decreases below a threshold between 2 and 3 kg DM/m³. The regression in Equation 2 is a little more accurate than Equation 1 (RMSE = 3.9 vs 5.8).

Intake rate

Impact of SH. When considering the experiments dealing with SH variations, there is a positive curvilinear intra-experiment effect of SH on IR (mg DM/kg BW/min), with an asymptotic value around 100 mg DMI/min/kg BW and a rapid decline in IR under a threshold SH of about 15–20 cm (Figure 2a). The intra-experiment relationship between both variables is:

$$IR = 100.1 (1 - \exp(-0.093 SH)) \quad (n = 195; n_{exp} = 62; RMSE = 16.7) \quad [3]$$

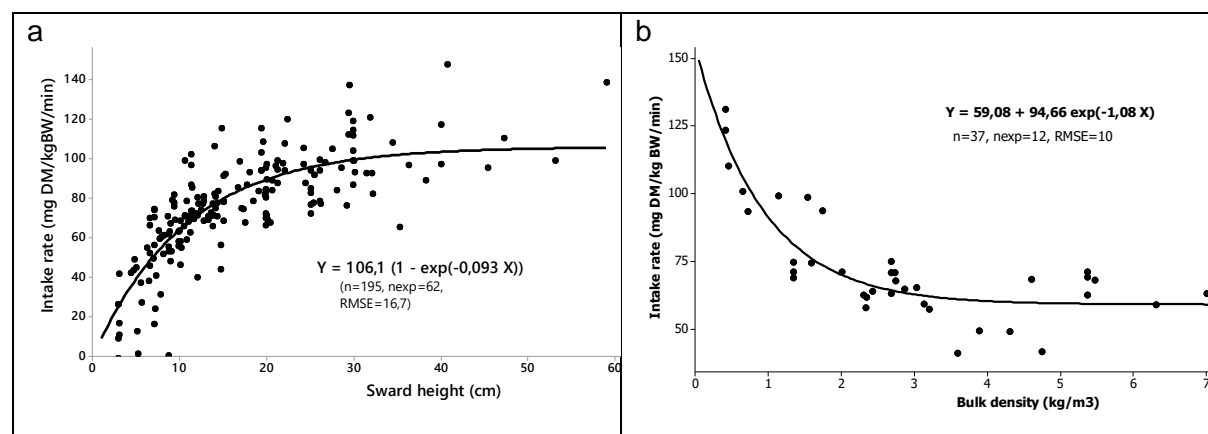


Figure 2 Impacts of sward height (cm) (a) and herbage bulk density on intake rate (mg DM/kg BW/min) (b).

It appears that for three publications (Black and Kenney, 1984; Mezzalana *et al.*, 2014 and 2017) and nine experiments, the response of IR to SH is clearly curvilinear, exhibiting a maximum value of IR followed by a decreasing IR with increasing SH

(Figure S1). In these papers, the maximum values of IR ranged between about 115 and 160 mg DM/kg BW while the corresponding values of SH ranged between about 10 and 30 cm.

Impact of HBD. As seen for BR (Figure 2b), there is an increase of IR when HBD is lower than a threshold of 2–3 kg DM/m³. The intra-experiment regression is:

$$\text{IR} = 59.08 + 94.66 \exp(-1.08 \text{ HBD}) \quad (n = 37; n_{\text{exp}} = 12; \text{RMSE} = 10) \quad [4]$$

Interaction between SH and HBD. As mentioned, Equations 3 and 4 were calculated on datasets issued from experiments that considered variations in SH and HBD, respectively, as experimental factors. As the number of data with SH and HBD is fairly high, another approach was performed to study, within publications, the effect of interactions between SH and HBD on IR (mg DM/kg BW/min). An intra-publication significant quadratic regression was calculated:

$$\text{IR} = (3.74) + 3.336 \times \text{SH} - 0.01279 \times \text{SH}^2 + 25.4 \times \text{HBD} - 1.816 \times \text{HBD}^2 - 0.842 \times \text{SH} \times \text{HBD}$$

$$(n = 227; n_{\text{pub}} = 30; \text{RMSE} = 21.1) \quad [5]$$

The three quadratic terms of this regression are highly significant, stressing the interaction between SH and HBD. Figure 3 shows the trace of this regression and illustrates the interaction with SH on the X-axis and HBD corresponding to the successive lines of iso-HBD. The thickness of the lines is proportional to the frequency of the observed situations. The interaction appears concretely in Figure 3: when SH <

about 20 cm, its negative influence on IR is compensated by an increase of HBD. Beyond the threshold value of HBD around 2–3 kg DM/m³, the influence of SH almost disappears. Otherwise in Figure 3, it can be seen that HBD has no effect on IR when SH is around 1–20 cm. Over this threshold of SH around 15–20 cm, the influence of HBD tends to be negative on IR which is then impacted mainly by the variations of SH.

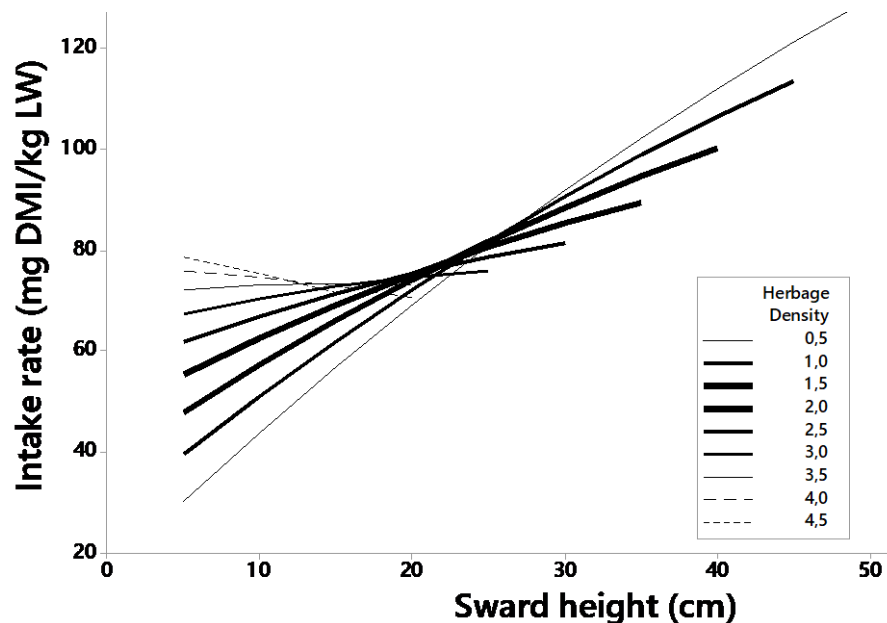


Figure 3 Interactions between sward height (cm) and herbage bulk density (kg DM/m³) on intake rate (mg DM/kg BW/min).

Influence of stem and leaf mass.

The stem mass (SM = 1.41 ± 0.80), when leaves are available, determines IR (Figure S2) according the following intra-experiment regression:

$$IR = 2.92 + 73.60 (1 - \exp(-2.44 SM)) \quad (n = 56; n_{exp} = 17; RMSE = 19.1) \quad [6]$$

The leaf mass (LM; 1.17 ± 0.74 t DM/ha) also affects IR according to the following equation:

$$\text{IR} = 111.46 (1 - \exp (-1.64 \text{ LM})) \quad (n = 73; n_{\text{exp}} = 19; \text{RMS} = 14.3) \quad [7]$$

Figure S2 presents the two regressions and illustrates the fact that LM explains a large range of IR, from 0 to 111 mg DM/kg BW/min, while for SM, the equivalent range is only 48 mg DM/kg BW/min. For the lower values of SM, there is a great variability of IR, which is only due to the impact of leaf growth. Thus, it was decided to remove these low values of SM. Figure S2 shows also that the plateau is achieved for SM beyond the threshold of about 1 t DM/ha, illustrating that the continued growth of stems does not affect IR. In contrast, leaf growth goes on impacting IR, without any precise threshold of LM/ha.

Impacts of grazing management factors.

The effect of herbage allowance (HA) on IR was analysed for experiments excluding continuous grazing. It appears that IR decreased when HA increased, until a minimum plateau close to 40 mg/kg BW/min (Figure 4a). When HA decreased under a value of around 10% BW, IR increased rapidly until values close to 100 g/kg BW/min. The values under 10% of BW come partly from experiments where the access time was only 1 h or even less (Figure 4a). This response of IR is mainly due to the increase of BM.

$$\text{IR} = 41.55 + 153.8 \exp (-0.317 \text{ HA}) \quad (n = 73; n_{\text{exp}} = 25; \text{RMSE} = 7.1) \quad [8]$$

Another major factor of grazing management is the access time. In the database, only 10 experiments were focused on this aspect. The response of IR is negatively related to the daily proportion of time spend grazing (pGT, 0.30 ± 0.08 , Figure 4b):

$$IR = 35.83 + 107.28 \exp(-4.56 \text{ pGT}) \quad (n = 28; n_{\text{exp}} = 10; \text{RMSE} = 6.1) \quad [9]$$

For the same dataset, there was a trend of reducing the level of DMI/BW when pGT decreased: -1.36 ± 0.81 g DMI/kg BW ($P = 0.11$) per 0.1 decrease of pGT. For a part of this dataset (three experiments and nine treatments), the BM was measured and it increased significantly when pGT decreased (-7.1 ± 1.3 g DM/kg BW per unit of pGT). In contrast, BR was not influenced by pGT in this dataset.

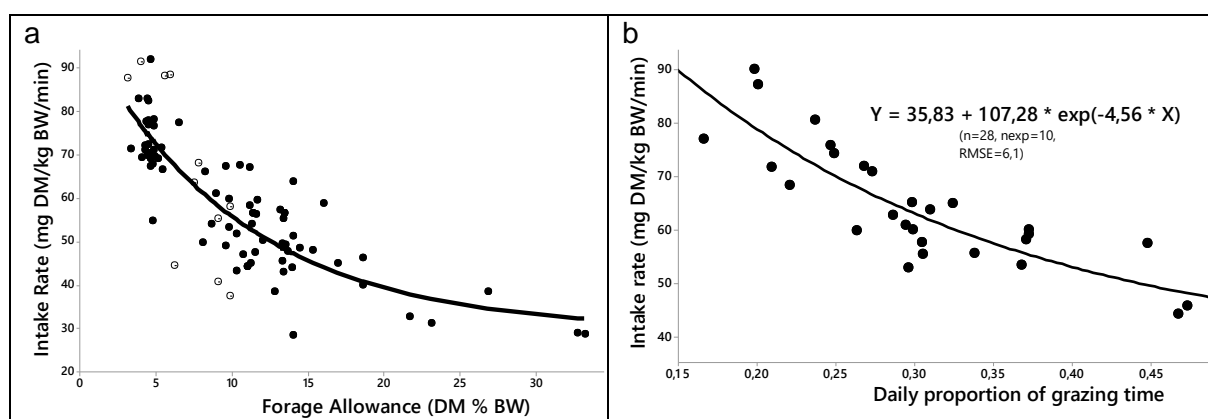


Figure 4 Effect of forage allowance (a) and proportion of time spent grazing (b) on intake rate (mg DM/kg BW/min).

Grazing time

When GT is not limited, there is a negative relationship between SH and GT (Figure S3), and the intra-experiment regression between the two parameters is:

$$GT = 431.5 + 301 \exp(-0.083 \text{ SH}) \quad (n = 86; n_{\text{exp}} = 26; \text{RMSE} = 46) \quad [10]$$

The number of data is not sufficient to study the influence of HBD on GT, or on rumination and idling times.

Interrelations across components

Global correlations

Considering inter-experiment relationships (Table 2), the most inter-related components are on one hand between BM and IR and the number of chews/bite ($r = 0.75$) and on the other hand, to a lesser extent, between GT and DMI ($r = 0.328$). Considering the intra-relationships (Table 2), there are two pairs of variables correlated with each other, independently of BM, on the one hand inter and intra negative relations between BR and chews/bite and on the other hand positive inter and intra relationships between IR and DMI.

Influence of animal species on the relationships

Whatever the type of experience, there is a negative relationship between BR and BM (Figure 5). For cattle, the intra-experiment regression is:

$$\mathbf{BR = 12.0 + 46.2 \exp(-0.198 \text{ BM})} \quad (n = 342; n_{\text{exp}} = 109; \text{RMSE} = 4.6) \quad [11a]$$

For small ruminants, it is:

$$\mathbf{BR = 12.0 + 54.0 \exp(-0.172 \text{ BM})} \quad (n = 73; n_{\text{exp}} = 22; \text{RMSE} = 4.2) \quad [11b]$$

It appears that the asymptote of 12.0 that is never achieved is not different between the two species, while the intercept is significantly higher for small ruminants compared to cattle (66.0 vs 58.2 bites/min).

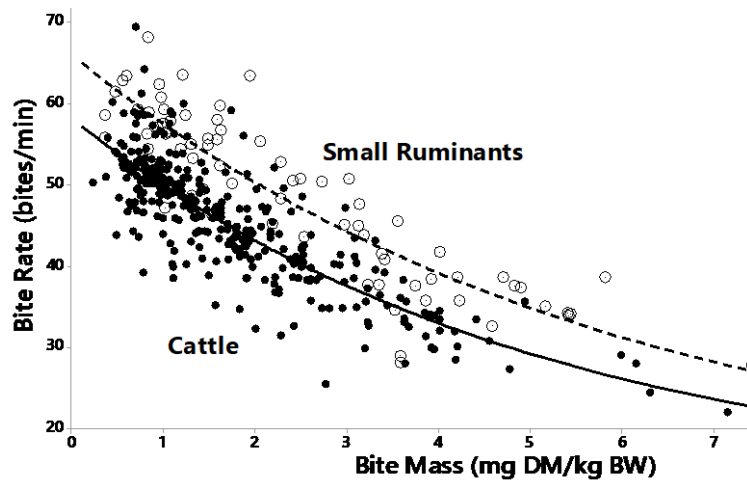


Figure 5 Intra-experiment relationship between bite rate (bites/min) and bite mass (mg/kg BW) for cattle (closed circles) and small ruminants (open circles).

The JM and chewing associated with the bites are both positively related to BM (Table 2). The relationship between JM/bite and BM is significantly different for small ruminants and cattle (Figure 6a). The intra-species and intra-experiment regression equation for cattle is:

$$\text{JM/bite} = 1.29 + 0.121 \text{ BM} \quad (n = 79; \text{nexp} = 24; \text{RMSE} = 0.16) \quad [12a]$$

For sheep and goats, the corresponding regression is less accurate, and the data number is lower:

$$\text{JM/bite} = 1.16 + 0.72 \text{ BM} \quad (n = 42; \text{nexp} = 11; \text{RMSE} = 0.44) \quad [12b]$$

For these two equations, the intercept is not different to 1, illustrating that the number of chews is negligible for very small bites, and in this extreme situation JM are only bites. The data available on jaw and chewing movements also revealed different slopes of the BR-dependent decrease, for cattle and small ruminants, respectively (Figure 6b). For cattle, the intra-experiment regression is:

$$\text{JM/bite} = 1 + 1.94 \exp(-0.0283 \text{ BR}) \quad (n = 85; n_{\text{exp}} = 28; \text{RMSE} = 0.17) \quad [13a]$$

For sheep and goats, the corresponding regression is less accurate, and the data number is lower:

$$\text{J/bite} = 1 + 12.38 \exp(-0.0428 \text{ BR}) \quad (n = 25; n_{\text{exp}} = 6; \text{RMSE} = 0.41) \quad [13b]$$

In Figure 6b, the number of JM/bite is the sum of bite + chews per bite. For instance, for a BR of 40/min, the number of JM is about 1.5 JM/bite for cattle, meaning that an animal makes a mean of half a chew/bite. In contrast, for sheep and goats, there are about 2 chews/bite when BR = 40.

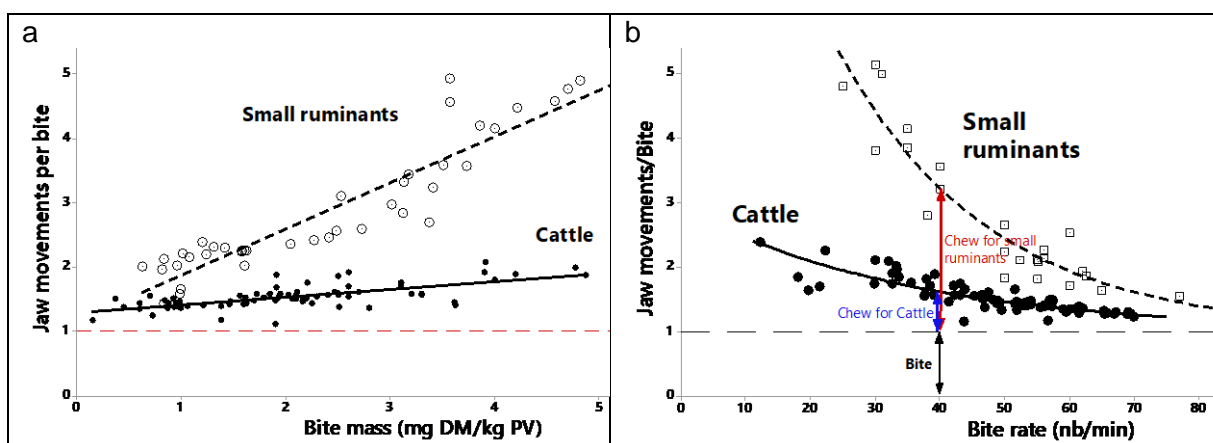


Figure 6 Influences on jaw movements/bite of bite mass (a) and bite rate (b).

It appears clearly that for the same BM, the number of JM is much higher for small ruminants, with an order of magnitude of about 10 (3.1 ± 28.5 vs. 3.3 ± 3.6).

The link between JM, expressed per gram of DMI, and BM was also analysed. For both species, the relationship is hyperbolic (Figure 7); the intra-experiment equation for cattle is:

$$\text{JM/g DMI} = 258 / (1 + 555.4 \text{ BM}) \quad (n = 79; n_{\text{exp}} = 23; \text{RMSE} = 1.7) \quad [14a]$$

For small ruminants, the regression is less accurate:

$$\text{JM/g DMI} = 45.8 / (1 + 0.41 \text{ BM}) \quad (n = 42; n_{\text{exp}} = 11; \text{RMSE} = 14.6) \quad [14b]$$

Figure 7 shows these two regressions; it appears clearly that for the same BM, the number of JM is much higher for sheep, with an order of magnitude of about 10 (31.1 ± 28.5 vs 3.3 ± 3.6 JM/g DMI). It must be stressed that for sheep, three high outlier values of 94 to 165 JM/g DMI for a very low BM ($\text{BM} < 0.4 \text{ mg/kg BW}$) from the same paper (Black and Kenney, 1984) have been removed. Moreover, we were also able to verify the decrease in JM with IR and significant differences that remain between small ruminants and cattle.

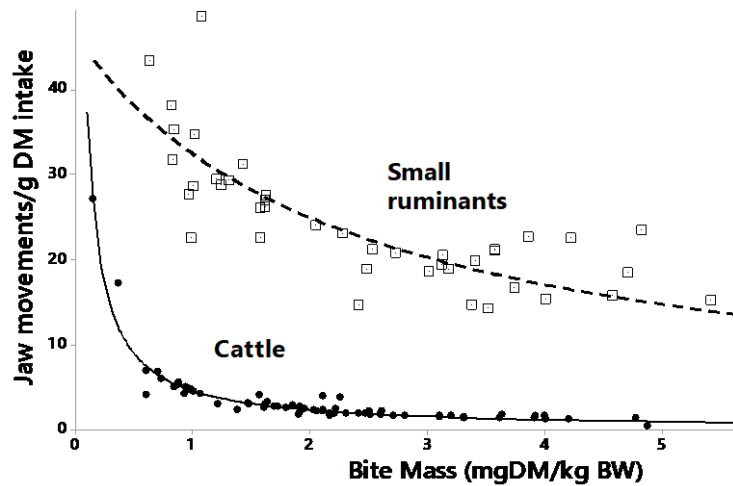


Figure 7 Influence of bite mass (BM, mg DM/kg BW) and of species on the number of jaw movements per gram of DM.

As the JM/g DMI are linked to the process of particle comminution, the link between BM and rumination time was investigated from a limited set of data for cattle with $0.5 < \text{BM} < 2.5 \text{ mg DM/kg BW}$. It appears that the two components are positively related, according to the following intra-experiment regression:

$$\text{RT (min/day)} = 366 (1 - \exp(-2.92 \text{ BM} - 0.22))$$

$$(n = 49; n_{\text{exp}} = 19; \text{RMSE} = 26.1) \quad [15]$$

This equation shows an asymptotic value of RT of 366 min/day, and RT drops markedly when BM decreases below a threshold of 1–1.5 mg DM/kg BW. It appears thus that there is a substitution in the comminution activities between intake and rumination. When the fill effect of forage in the mouth increases, the ruminant is less efficient in reducing the particle size so it must ruminate more to compensate.

The relationship between IR (mg DM/min/kg BW) and BM (mg DM/kg BW) is positive and curvilinear and, as BR was different between the two species (Figure 7), two separate fittings were performed. For cattle, the intra-experiment regression is:

$$\text{IR} = 145.0 (1 - \exp(-0.440 \text{ BM})) \quad (n = 331; n_{\text{exp}} = 103; \text{RMSE} = 9.7) \quad [16a]$$

For small ruminants, it is:

$$\text{IR} = 145.0 (1 - \exp(-0.543 \text{ BM})) \quad (n = 72; n_{\text{exp}} = 22; \text{RMSE} = 10.8) \quad [16b]$$

Figure 8 shows the two regressions; it appears that the differences are globally small and are at the advantage of small ruminants for lighter bites, consistent with what was observed for BR (Equations 11a and 11b and Figure 5). The asymptotic value of 145 g DM/kg BW/min is the same between both species. The maximum difference between IR for the two species is observed for BM ~ 2.5 g/kg BW. It must be noted that in order to have a common regression, considering all the data, the power of BW must be 0.85. The curvilinearity of this relationship illustrates that BR, which is the ratio of IR to BM in Figure 5, decreases with the rise of BM as already remarked. Thus, BR is 54 bites/min when BM is close to 0, to approximately 22–23 bites/min when BM is equal to 6 mg/kg BW. This relationship is mainly the outcome of influences of both SH and HBD on BM (Boval and Sauvant, 2019), and IR (Figure 2a and 2b).

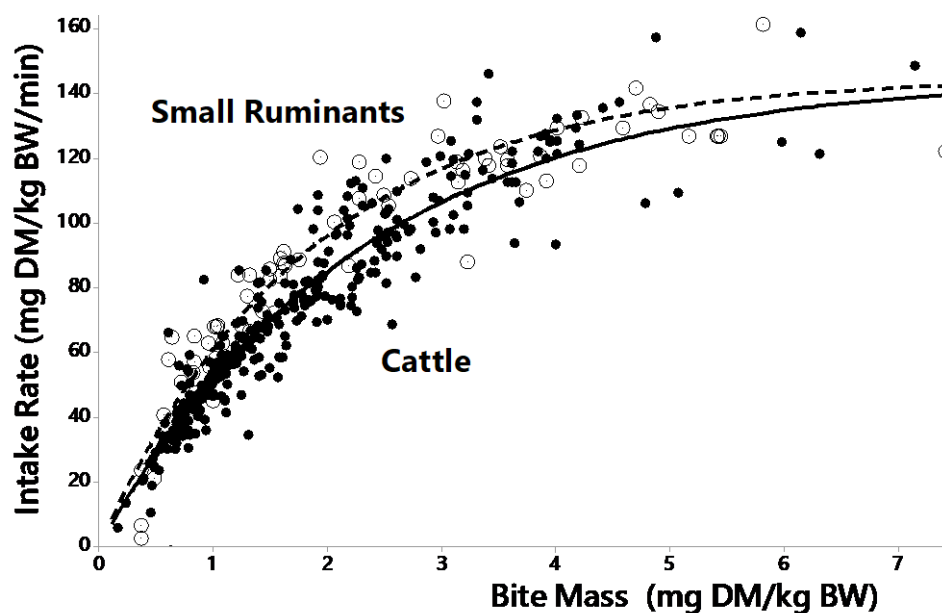


Figure 8 Relationship between intake rate (mg/kg BW/min) and bite mass (mg/kg BW) for cattle (closed circles) and small ruminants (open circles).

$$\text{DMI (\%BW)} = 1.36 + 0.026 \text{ IR} \quad (n = 139; n_{\text{exp}} = 52; \text{RMSE} = 0.30) \quad [17]$$

The relationship is still significant when only the 40 experiments focused on the impact of SH are considered. But, in this case the slope is higher i.e. 0.037 ($n = 37$; $n_{\text{exp}} = 14$; $\text{RMSE} = 0.13$).

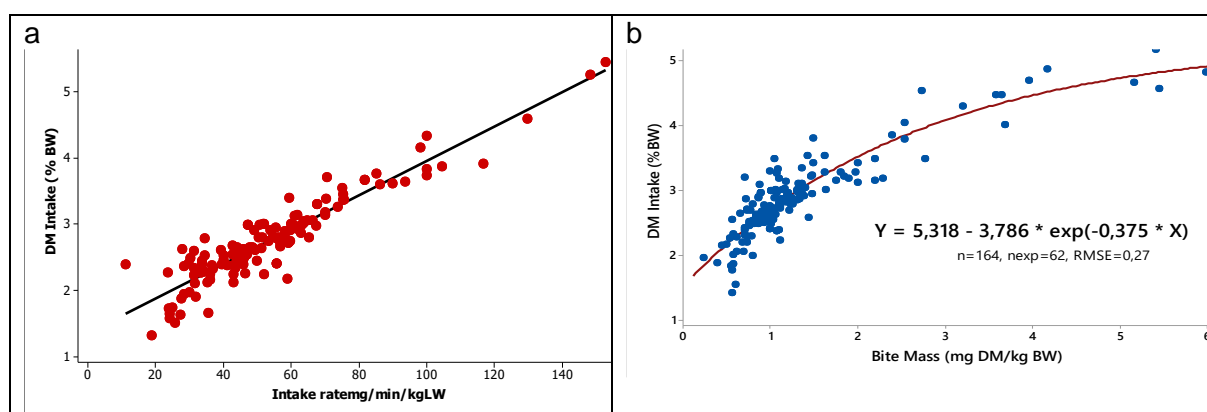


Figure 9 Relationships between daily DM intake (%BW) and intake rate (a) and between bite mass and dry matter intake (b).

There is a positive and curvilinear relationship between BM and daily DMI when treatments with an observation time longer than 1 h are pooled.

$$\text{DMI (\%BW)} = 5.318 - 3.786 \exp(-0.375 \text{ BM})$$

$$(n = 164; n_{\text{exp}} = 62; \text{RMSE} = 0.27) \quad [18]$$

Clearly, a high BM induces a saturated response of both IR (Figure 8) and daily DMI (Figure 9b) in grazing ruminants. However, the number of data determining the asymptote is low.

Discussion

Features of the database

The database made up of 98 publications shows how studies implying cattle predominate, while lines of the database related to small ruminants represent only 1/5 of the total. The publications referenced in this database are spread over the last 40 years, since 1978, with nearly 85% of publications over the last 20 years. The most studied factors of variation in the publications were SH (61 % of the treatments), then bulk density to a much lesser extent (14 % of the treatments). The other factors studied represent less treatments, and the corresponding IB components available were too scattered to allow a valuable interpretation.

Owing to the available data, this meta-analysis presents several limits such as the lack of specific consideration of the impact of some sward characteristics such as the ratio of leaves/stem and their tensile strength or the chemical composition of the sward on the behaviour components. Moreover, we did not consider the spatio-temporal behaviour characteristics of grazing ruminants (feeding stations, patches), nor the

kinetics of grazing behaviour during the nycthemeron. Therefore, the considerations done on the time budget are static.

Impacts of canopy characteristics and of some management strategies

Among the most conventional sward characteristics considered in the literature, SH and HBD mainly have been considered for their impact on BR, IR, GT and DMI. For the other sward characteristics, the IB components available were too scattered to allow a valuable interpretation. Despite the limited data available for other sward characteristics, the effects of herbage mass, LM and SM could have been studied, but only for IR. Moreover, some data were sufficient to be considered under the angle of management strategies, such as HA and access time.

Hence, by increasing SH, BR decreases to a minimum plateau value of about 40 bites/min as soon as the height reaches 20–30 cm (Figure 1a). On the contrary, IR increased with SH, as was previously reported for BM (Boval and Sauvant, 2019), and reached very rapidly a maximum plateau of about 100 mg DM/kg BW/min beyond a height of 20–30 cm (Figure 2a). This maximum plateau results from the combination of the minimum value of BR with the maximum value of BM as proposed by Boval and Sauvant (2019). These trends of response of IR to SH have already been described in the specific contexts of several experiments (Penning, 1986; Ginane and Petit, 2005; Hirata *et al.*, 2010). Notably, Delagarde *et al.* (2011) presented a synthetic response of IR with a plateau value close to that of Figure 2a; however, the response was fitted by two linear segments, and presents an elbow that we did not observe at similar values of SH of 22–23 cm. Moreover, for very low values of SH, the decrease of IR was not sufficient compared to their observed data reported in the publication (Delagarde *et al.*, 2011), nor to our model. Otherwise, the average plateau calculated

in this meta-analysis (Figure 2a) did not include data of three publications (Black and Kenney, 1984; Mezzalana *et al.*, 2014 and 2017), where a decrease of IR was observed beyond SH values ranging from 10 to 30 cm (Figure S1). For these same studies, a similar tendency has already been observed for BM (Boval and Sauvant, 2019), suggesting that in certain situations of high SH, it would become more and more difficult to assemble forage into a bite. This consistent decline in IR and BM is thought to be due to the change in the structure of tall species described by some authors (Spallinger and Hobbs, 1992; Mezzalana *et al.*, 2014 and 2017).

Regarding the influence of HS on GT, it decreased to a minimum plateau value of about 450 min when SH values exceeded 20–30 cm; while for lower HS values, GT becomes higher and can exceed 650 min/day (Figure S3). This trend is consistent with previous reports by Alvarez *et al.* (2007) and Perez-Prieto *et al.* (2011).

By increasing the HBD, BR decreased until a plateau of around 40 bites/min beyond 2–3 kg DM/m³ (Figure 1b), similar to the minimum plateau observed with high SH (Figure 1a) in another set of experiments. We noted a similar trend with IR, which also decreased globally with HBD (Figure 2b) and plateaued at about 60 mg DM/kg BW/min, at the same HBD threshold of 2–3 kg DM/m³. These trends are globally opposite to what were previously observed for BM, which increases with both SH and HBD (Boval and Sauvant, 2019). Unfortunately, concerning GT, the effect of HBD could not be analysed as for SH, as most of the experiments that tested HBD variations were carried out with micro-swards, for which the duration of grazing could not be measured.

In fact, the effects of SH and HBD cannot be disconnected from one another in natural grazing conditions, and we were opportunely able to study in our database the interaction between these two major factors, on IR (Figure 3). Globally the effect of SH

is more marked than that of HBD. At low SH, HBD positively influences IR while for high SH, HBD presents a limited negative influence on IR (Figure 3). Only a few individual studies have measured this interaction between SH and HBD consistently to our results. It has been studied actually only for short grasses and with micro-swards, as by Laca *et al.* (1992) and Benvenuti *et al.* (2006).

Aside from SH and bulk density, other characteristics are also likely to influence IR, such as LM and SM. They both have a positive effect on IR; in particular, LM explains a larger range of IR, surely linked with leaf growth, without any threshold being observed. In contrast, when the SM increases beyond 1 t of DM/ha, the IR reaches a plateau of 100 mg MS/kg BW/min.

While our database was not mainly focused on the influence of management strategies on global responses such as DMI, some publications allowed highlighting of some IB responses. Thus, ruminants are able to increase their IR until values near to 100 mg DMI/kg BW/min when facing an important decrease of forage allowance (Figure 4a) or of grazing access time (Figure 4b). This adaptive behaviour mainly results from differences in BM (Boval and Sauvant, 2019) which appears as a key factor of animal robustness as it allows ruminants to maintain, or only slightly decrease, their level of DMI despite a decrease of available resource and access time. As BM is at least partly explained by individual factors (Sollenberger and Vanzant, 2011; Boval and Sauvant, 2019), it appears useful to investigate further animals' ability to adapt to restricted resources and GT.

From BM to intake rate and daily intake

Analysis of the impact of canopy characteristics on the various IB components highlights the behavioural adaptation by ruminants to achieve satisfying BM and IR.

That appears for the low values of SH (< 20–30 cm) and of HBD (< 2–3 kg DM/m³), resulting in an acceleration of BR (Figure 1a and 1b) to compensate for the smaller bites. Consequently, the resulting IR is actually increased at low HBD (Figure 2b), while that is not the case at low SH (Figure 2a) due to the first limiting effect of SH on BM (Boval and Sauvant, 2019). In addition, for low SH, the GT is longer (Figure S3), as another way to compensate for low values of BM and IR. However, we did not have enough data to show this lengthening of GT also with low values of HBD.

Beyond analysis of the effect of sward characteristics on IB components, the major relationships between these components provided further understanding. Thus, there is a strong negative correlation between BM and BR (Table 2); correlations between BM and chews/bite are also positive, while based on much less data (Table 2), and the correlation between BM and DMI is less marked, especially inter-experiment correlation. And most structuring regressions concern the link between BM and BR and the influence of BM on IR (Figure 8) which are useful for modelling purposes. All these correlations are consistent with previous reports (Poppi, 2011; Chilubrost *et al.*, 2007 and 2015) and this meta-analysis, resulting from numerous data, provides robust average values of the main correlations.

The close negative relationship between BM and BR may be better understood by analysing JM/bite (Figure 6a) and how they increase with BM. Grazing animals perform JM, which contribute both to assembling the forage before harvesting and to chewing it in the mouth, before swallowing. Hence, larger bites require logically more processing before the next bite can be taken (Mulvenna *et al.*, 2018). Therefore, the time needed between two bites increases, representing the sum of the time devoted in the JM to biting and chewing. These additional activities mechanically slow down the frequency of bites (Figure 6b). According to Spallinger and Hobbs (1992), BR is indeed the

inverse of handling time (i.e. the time invested to bite and chew) and this occurs mainly in pastures, where potential bites are concentrated, corresponding mostly to a functional response of type 3, according to Mezzalana *et al.* (2017).

The analysis of JM expressed per gram of DM consumed (Figure 7) shows that the number of JM decreases when the bites become larger. This suggests that with larger bites of more than 1 mg/kg BW, particle fragmentation efficiency decreases (Sauvant *et al.*, 1996; Baumont *et al.*, 2000). This is consistent with our results showing how larger bites are positively correlated with longer rumination times (Figure S4, Equation 15). With larger bites, the fill effect of the forage in the mouth increases and the grazer would be less efficient in reducing the particle size and so it must ruminate more to compensate. It appears then as a substitution in the comminution activities between intake and rumination. This could be due also partly to the fact that small BM is more often composed of more fibrous removed parts. Indeed, larger bites are more often associated with the presence of leaves in the sward canopy (Drescher *et al.*, 2006; Geremia *et al.*, 2018), whereas the more fibrous stems represent a physical resistance inducing a limit to biting. Geremia *et al.* (2018) reported how BM is small at the end of the grazing period, as animals are forced to harvest grass with a higher percentage of stems and dead material.

Clearly, BM is the major determinant of IR and contributes consequently to differences of DMI. Our dataset contains some large BM, more than 4 mg/kg BW, which allows very high values of IR to be achieved, up to 140 mg/kg BW (Figure 8), while the mean asymptotic values observed for factors were around 100 mg/kg BW (Figures 2–4). Several authors had already reported these positive relationships (ref), and our results provide few data for extreme situations (low SH and HBD), as 140 mg appears as a maximum rate achievable whatever the animal species. For these few high BM and IR

values, the corresponding DM intake may exceed 5% of BW, being also influenced by the total daily duration of grazing. However, contrary to the curvilinear relationship between BM and DMI (Figure 9b), the relationship between IR and DMI (Figure 9a) appears linear, and we could not highlight any threshold of DMI. These results could be due to the low number of DMI values corresponding to high values of IR that we collected.

Animal species specificity

From our database, we were able to calculate some specific relationships for cattle or small ruminants, being unable to distinguish between sheep and goats. However, according to Mulvena *et al.* (2018) and Laca (2010), there is no marked difference between these two species of small ruminants.

It appears that for the same level of BM, small ruminants graze with a faster BR compared to cattle, by about 10 bites/min (Figure 5). Besides that, small ruminants make more JM accompanying each bite compared to cattle (Figure 6b), and the difference increases clearly when BR decreases. For very small bites less than 1 mg/kg BW, there are almost no JM/bite (Figure 6a). For small ruminants, the number of chews increases very quickly, with BM of 5 mg/kg BW, requiring about 5 JM/bite (Figure 6a). Thus when JM are expressed per gram of DMI, the number of JM is approximately 10 times higher for small ruminants compared with cattle (Figure 7). It is approximately the same scaling value when both species are compared in terms of DMI. In any case, small ruminants make many more JM to crop 1 g of DMI, likely investing more energy per gram of DMI than cattle, as already reported (Galli *et al.*, 2018). Aside from chews, another type of JM may explain the difference between species, i.e. the chew-bite that can be measured with some acoustic monitoring methods (Galli *et al.*, 2018). Indeed,

cattle (Ungar *et al.*, 2006) and sheep (Galli *et al.*, 2011) may use discrete JM to chew and bite, but also simultaneously chew and bite on the same jaw opening-closing cycle. However, in our database, we had no such values of chew-bites.

Consequently, all of these differences imply that small ruminants have a faster IR, with a maximum equal to 1.2 times higher IR expressed per kg of BW, compared to cattle (Figure 8). Otherwise, Boval and Sauvant (2019) have also pointed out that, for the same SH, the bite depth/kg BW is higher for small ruminants, so it was necessary to use BW at power 0.20 to match the data of BD for both species. The difference of bite depth between the two species is extremely low compared to their respective BW, revealing that sheep chewing and biting modalities would be more effective for going deeper into the sward compared to cattle, as already suggested (Gordon *et al.*, 1996; Woodward, 1998; Baumont *et al.*, 2006). Indeed, it may be observed how sheep perform successive chews to go deeper into the canopy sward, by mobilizing their lips in quick movements.

All these results are well consistent with the idea that bite and chew rates decrease commonly with ruminant species having greater BW and BM (Wilson and Kerley, 2003; Mulvenna *et al.*, 2018). Moreover, these results emphasize the different mechanisms implemented by small ruminants or cattle to adapt to the characteristics of the resource, with their anatomical specificities (Baumont *et al.*, 2006; Meier *et al.*, 2016). In the case of small ruminants, the most mobile lips participate in forage prehension and therefore consumption, with associated movements of the jaw that can be recorded. Cattle have a particularly long freely mobile tip (Meier *et al.*, 2016) that they use to greatly increase the diameter and surface of each bite to compensate for limited resources as with short SH (Boval and Sauvant, 2019). Although the relationships between the different behavioural variables are different for these two species, the fact

remains that the make-up of the bite for both species determines the rate of intake with very similar trends (Figure 9) and with a comparable maximum threshold around 140 mg/kg BW).

Conclusions

This meta-analysis provided a set of empirical models that can serve (i) as benchmarks for future studies and models of ruminant feeding behavior and well-being (ii) to identify parameters of interest for animal management at pasture (iii) to reference values for automatic measurement devices.

Approximately 20 quantitative relationships were established within this meta-analysis, confirming that bite size is a pivotal part of the ingestive behavior of ruminants in pasture, as it is both sensitive to major sward characteristics and determining for intake rate, and daily intake.

The main response laws highlighted are valid for different domestic ruminants when expressed in relation to body weight. Nevertheless, important differences appeared between cattle and small ruminants, the latter having to chew more for the same bite mass. The literature review emphasizes the great variability of methods carried out to measure ingestive behavior components. Our database should be supplemented by data collected with animals in stalls to assess the generic relationships applying whatever the feeding context.

Table 1 Number and mean values, standard deviation, minimums and maximums of the feeding behaviour components collected in the publications

	Mean \pm SD	Min–max	n	Normality ¹
BM (mg DM/BW)	1.80 \pm 1.27	0.107–7.41	581	N(L)
Small ruminants (g DM/B)	0.11 \pm 0.09	0.09–0.63	117	N(L)
Cattle (g DM/B)	0.77 \pm 0.65	0.05–4.00	458	N(L)
BR (bites/min)	46.9 \pm 14.6	11.2–106.7	560	N
JM/bite				
Small ruminants	2.73 \pm 1.22	1.0–6.5	45	N
Cattle	1.60 \pm 0.54	1.13–5.04	97	N
Chews/bite				
Small ruminants	1.79 \pm 1.44	0.20–6.20	35	N
Cattle	0.59 \pm 0.52	0.12–3.36	92	N
IR (g DM/min)				
Small ruminants	4.34 \pm 2.0	0.5–11.3	91	
Cattle	27.6 \pm 18.9	1.3–146.3	339	
IR (mg/min/kg BW)		2.70–274.1	415	N(L)
Small ruminants	99.94 \pm 45.7	12.0–274.1	64	
Cattle	69.1 \pm 38.1	2.70–248.8	349	
Bite/g DMI				
Small ruminants	15.8 \pm 17.7	1.6–105.0	85	N(L)
Cattle	2.5 \pm 2.1	0.3–21.0	316	N(L)
GT (min)	519 \pm 146	138–1080	293	
RT (min)	366 \pm 129	31–574	140	
IT (min)	459 \pm 190	86–955	149	
DMI (%BW)	2.96 \pm 1.10	0.45–8.0	248	

BM = bite mass; B = bite; BR = bite rate; JM = jaw movements; IR = intake rate; GT = grazing time; RT = ruminating time; IT = idling time; DMI = dry matter intake.

¹ Normality of the distributions: N = non-normal; L suggests a log-normal asymmetric distribution.

Table 2 Correlations between ingestive behaviour components implied in the DMI, calculated inter- and intra-experiment (respectively the first and second value per component)

	BM	BR	Chews/bite	IR	GT
BR	-0.503*** N = 170				
	-0.576*** N = 386				
Chews/bite	0.707*** N = 43	-0.597*** N = 43			
	0.760*** N = 100	-0.701*** N = 100			
IR (mg/min/kg BW)	0.703*** N = 134	0.165** N = 134	0.100 ^{ns} N = 43		
	0.778*** N = 313	-0.244*** N = 313	0.497*** N = 100		
GT (min/day)	-0.283** N = 94	-0.039 ^{ns} N = 94	-0.463* N = 43	-0.188* N = 94	
	-0.117 ^{ns} N = 180	-0.045 ^{ns} N = 180	0.160 ^{ns} N = 100	-0.239** N = 180	
DMI %BW	0.243*** N = 86	-0.040 ^{ns} N = 86	0.645*** N = 43	0.360*** N = 86	0.408*** N = 86
	0.648*** N = 153	-0.254*** N = 153	-0.378 ^{ns} N = 100	0.793*** N = 153	0.177* N = 153

N = number of data; BM = bite mass; BR = bite rate; IR = intake rate; GT = grazing time.

Supplementary material

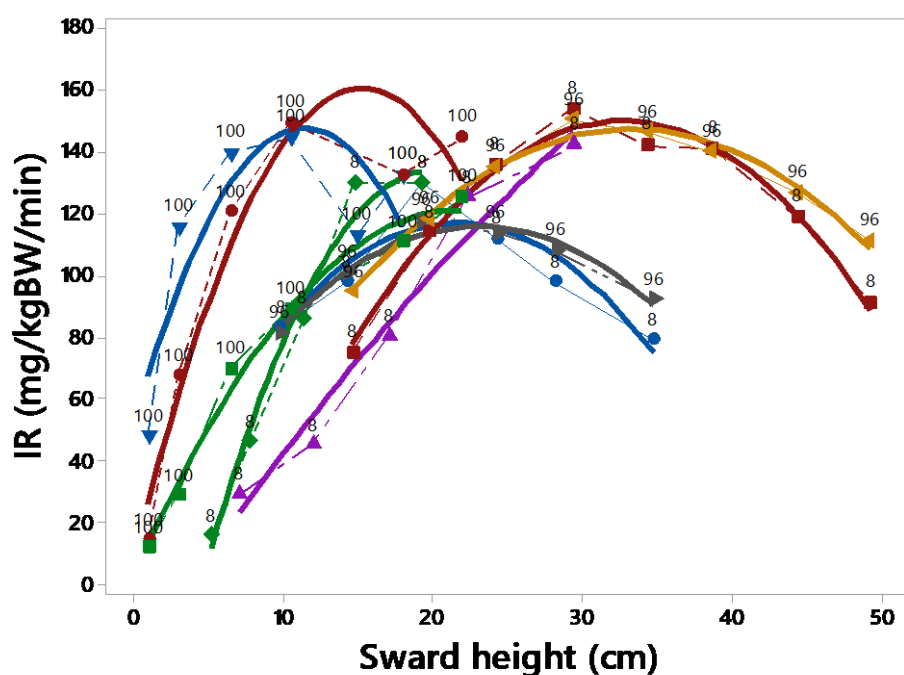


Figure S1: Impact of sward height on Intake rate for some studies

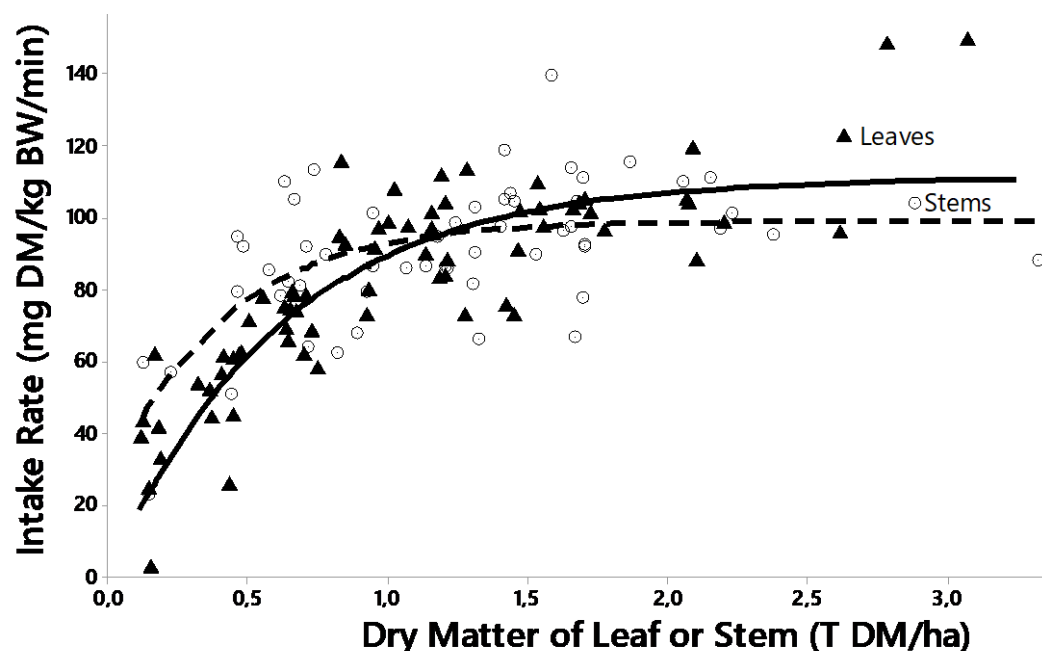


Figure S2: Respective influences of DM of leaf and stem, on intake rate.

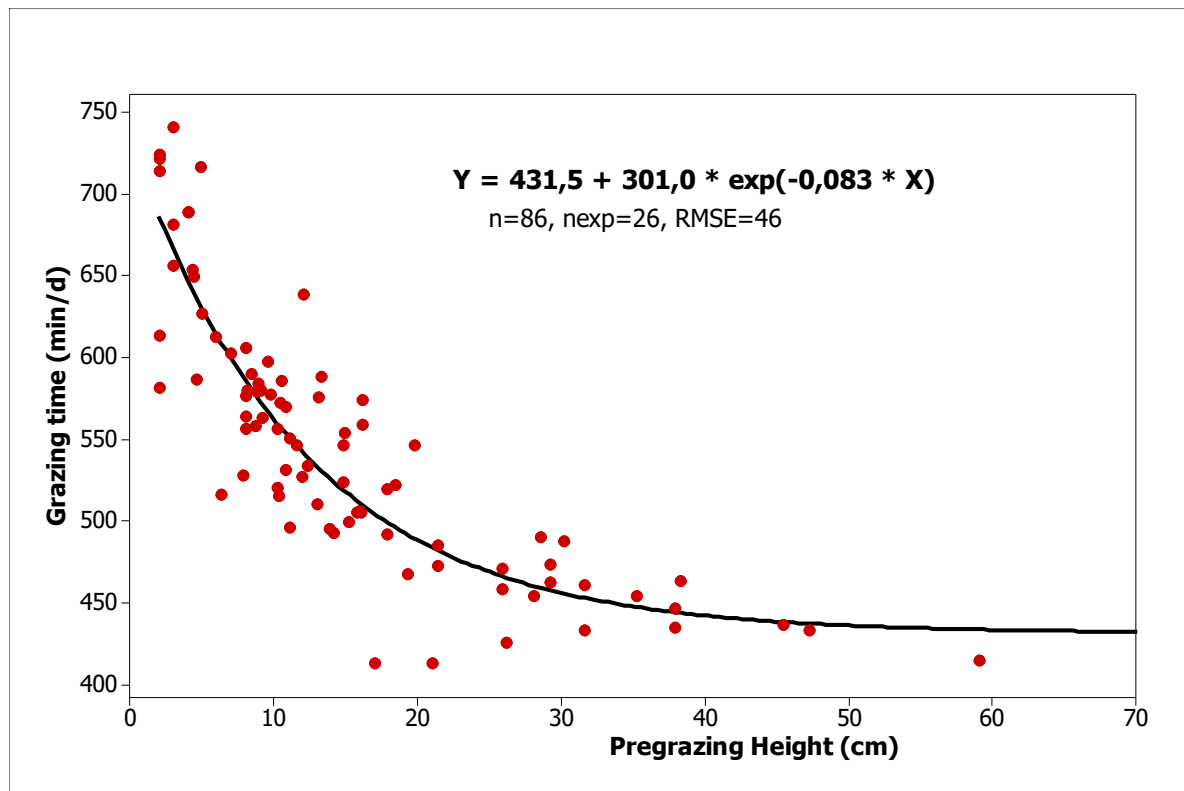


Figure S3: Effect of sward height (cm) on grazing time (min/day).

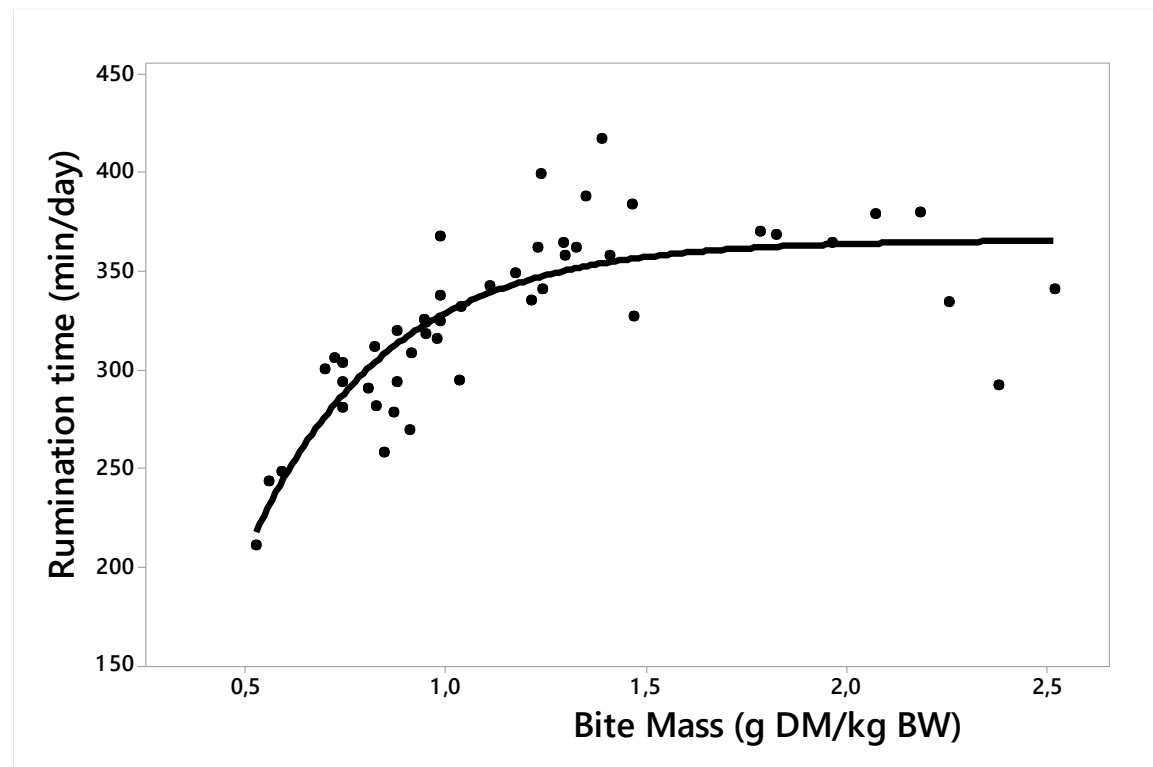


Figure S4: Relationship between rumination time (min/day) and Bite mass (mg/kg BW)

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