Ingestive behaviour of grazing ruminants: meta-analysis of the components of bite mass

Maryline Boval, Daniel Sauvant

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M. Boval[a*], D.Sauvant[a]

[a]*UMR ModélisationSystémiqueAppliquée aux Ruminants, INRA, AgroParisTech, Université Paris-Saclay, 75005, Paris, France*

*Corresponding author. Tel: 0677519951; EM:maryline.boval@agroparistech.fr

Abstract

Bite mass (BM) is the main parameter determining intake, production level and efficiency for grazing ruminants. Various data have been published concerning BM and its components bite diameter, bite area, bite depth and bite volume (BDiam, BA, BD and BV). However, it was not yet possible to have a clear quantitative view of the relationships between BM and its related components. The sward factors and animal traits influencing BM have only partially been studied previously. To progress on this topic, we performed a meta-analysis of a large set of 96 publications (776 treatments).

Bite volume is closely linked with BM, and when linear components of BV are considered, BDiamis much more determining than BD. Among the sward characteristics, sward height (SH) is a key factor of BM through its strong and almost linear influence on BD and BV. On this aspect, SH is more determining than herbage mass/ha. Herbage bulk density (HBD) is also an influencing factor, notably at low HBD, which induces an adaptive behaviour consisting of increasing BDiam and BA. A significant interaction was observed between SH and HBD in determining BM;for low values of SH, the positive influence of HBD on BM was distinct.

The measured parameters were diversely scaled with BW. For BM, the power coefficient was 1, while it was 0.346 for incisor arcade (IA) and of 0.20 for bite depth. Incisor arcade is an accurate determining factor for BM via BDiam and BA.

Analysis of the various factors of variation in bite mass and its components studied in the literature facilitates our understanding of the adaptive strategies of the animals.

Keywords: Pasture, sward height, herbage density, bite characteristics, review

1. Introduction

Studies on ingestive behaviour (IB) of ruminants at grazing have always been seen as a way to better understand their environmental conditions and to improve grassland management, as this system is the most viable source for ruminant production (Steiner et al., 2014; Tedeschi et al., 2017). Numerous studies have been published on IB of grazing ruminants, domestic as well as wild ones, and the first reviews of studies focused on IB were published more than 60 years ago (Handcock, 1953). Later, thanks to the accumulated results, conceptualisations on the spatiotemporal organisation of IB have been proposed (Kondo et al., 2011; Brink and Soder, 2011). All these publications conclude that bite mass (BM) is the key variable for dry matter (DM) acquisition by animals. It represents the smaller amount of DM taken per bite and is often considered as the smallest scale process in foraging, providing information about larger scales (as reviewed by Shipley et al., 2007 and Allen et al., 2011). However, despite of the large number of publications, there is no synthetic view of the main determinants of bite mass.

In this context, the aim of this study is to develop a generic quantitative description of the main components of BM for grazing ruminants (i.e. bite depth, bite area and bite volume) and their main determinants, namely the characteristics of the sward and of the animals.When possible, the impacts of the methods of measurement implemented were also analysed. This study was based on meta-analyses of a database pooling publications focused on IB in grazing ruminants. A subsequent publication will develop links between bite mass and items based on longer terms and larger scales to explain daily intake.

2. Material and methods

2.1.Literature review and database construction

This meta-analysis was carried out by considering published studies measuring components of the feeding behaviour of ruminants on pastures (cattle, sheep or goats) in various production systems (milk or meat) in temperate or tropical contexts. Literature searches were carried out using the key words "Web of Knowledge", "Science Direct", "EDP Sciences" and "Cambridge Journals", in addition to using the reference lists cited by the bibliographic reviews on the subject. For each publication, we integrated only experiments and treatments for which there were documented values of at least one of the criteria cited in Figure1. A list of data sources used in the study is provided in the “Data sources” section.

2.2.Intermediary calculations

Beyond the measured components of BM in the publications, other components to enrich the analysis were calculated (Fig.1). Thus, assuming that the shape of the bite area (BA)is approximately a circle, we calculated the diameter of the bite (BDiam) as sqrt2BA/π. We also calculated the bite volume (BV) when possible, assuming that the mouthful is shaped in the form of a cylinder of a given depth and area.

The mean area of a bite (BA) was calculated in all publications by dividing the measured total defoliation area by the total number of bites made for the same area considered, and the volume of the bite was then the product of bite depth (BD) by BA (Burlison et al., 1991). Also, the product of BV by herbage bulk density (HBD) of the sward is equal toBM. We then calculated bite density (BDens),when possible, as the ratio of BM toBV. The units of BM, BD and BV, expressed variously in the publications, were harmonised within the whole dataset. Afterwards, these components were also expressed per kg of body weight (BW) to simultaneously analyse the entire dataset, including the maximum degrees of freedom (with data coming from different species and genotypes of ruminants).

For each publication retained,beyond the bite components, we recorded information on animal characteristics (breed, sex, age, body weight) as well as forage characteristics (species, herbage mass, surface sward height and herbage bulk density, morphological and chemical composition, etc...). Other information related to the experimental conditions (in pastures or in artificial environments) and to the methods used to measure feeding behaviour and forage characteristics were registered.

A total of 96 publications (npub) were selected, including 239 experiments (nexp) and 776 treatments (n). The list of the references used to build the database in presented in “Data sources”.

2.3.Treatment encoding

Beyond specific codes assigned to each publication and to each experiment, additional codes were appliedto identify specifically the factors of variation tested, i.e. the variations in forage species (35% of the treatments), sward height (35%),season (21%),herbage allowance (18%) or herbage bulk density (11%). All of these codes were specific to the factors of variation studied; therefore, not all rows have values in the corresponding columns. For some experiments, in addition to the studied factors, some key criteria varied significantly, although they were not the factors *a priori* tested intra-experimentally. In this case, another code was added to consider these criteria as a secondary factor of variation. For example, we identified experiments for which sward height (SH) largely varied intra-experimentally, although it was not announced as a factor in these publications. In these cases, SH can be considered as a causal covariate. This way, variations in SH concerned 62% of papers instead of the 32% which were identified at the first approach.

2.4.Statistical analyses

The statistical analysisof the data was performed by meta-analyses according to the recommendations of Sauvant et al. (2008).This method was chosen because methods such as PCA (Principal Components Analysis) cannot be applied to this dataset because there were too many missing data for most of the variables in the database. Consequently, the various relationships between variables were analysed two by two, using subsets of data to obtain the maximum number of treatments. Another reason for applying meta-analysis is the relatively high experimental heterogeneity. Therefore, it was necessary to split variations existing inter- and intra-experimentally to primarily study the intra-experiment relationships between variables considered two by two and successively through the major factors of variations.

3. Results

3.1.Statistical parameters of bite mass components

The major statistical parameters of the bite components are reported in Table 1 for cattle and small ruminants. The data volume is more important for BM than for its components. The BD and BDiam were about two times higher for cattle than for small ruminants, while logically, the ratio between both species for BA (cm^2) was 4. The mean value of BD was higher by 10% compared to that of BDiam and that for both species. The resulting BV (liter) and BM were seven to eight times higher for cattle.

3.2.Animal factors influencing bite mass or its components

The effects of animal characteristics were assessed with asub-dataset of 40 experiments (90 treatments), allowing to test the effects of body weight differences on behavioural components. A log transformation of BM and of BW allowed obtaining the following intra-experiment relationship:

Log10 BM = 0.20 + 0.97 Log10 BW (n=90, nexp=40, RMSE=0.12) (1)

The slope of this regressionis not statistically different from 1 (student test). When sward height was also considered to control BM, the number of treatments strongly decreased(49 vs. 90), but the slope linked with BW (1.06 vs. 0.97) was not different from 1. These results indicate that BM can be scaled on BW. Therefore, this principle wassystematically applied o pool results from cattle and small ruminants.

A linear relationship between BDiam (cm) and incisor arcade (IA, cm) appeared from a small subset of five available papers (22 experiments) where the incisor arcade showed significant differences. The intra-experiment relationship (Fig.2a) is as follows:

BDiam= 1.21 + 1.10 IA (n=48, nexp=22, RMSE=1.00) (2)

Values of BDiam were closely related to IA, with a mean increase close to 1 cm/cm. The ratio BDiam/IA decreased from 1.58 to 1.25 when IA increased in the range of the measured values. There was no influence of the species on the residuals of this regression [2]. Interestingly, there was no influence of IA on BD, and therefore, the impact of IA on BM was most likely related with its simultaneous effects on BDiam, BA and BV. The intra-experiment regression between BM (g) and IA (cm) is as follows (Fig.2b):

$BM = 0.015\ IA^{1.88}$ (n=45, nexp=21, RMSE=0.10) (3)

In agreement with Eq.(2),BM is curvilinearly related with IA, with a coefficient of power>1.The incisor arcade is also related to BW (Fig.3):

$IA=0.91\ BW^{0.346}$ (n=20, RMSE=0.27) (4)

3.3.Sward factors influencing bite mass and its components

3.3.1.Statistics of the main sward factors

The basic statistics of the main characteristics of the swards measured in the publications of the databaseare given in Table 2.

In this data set, when SH was less than about 30 cm, data obtained on micro-swards did not differ compared to those collected under field conditions. Beyond this threshold of 30 cm, micro-sward measurement exhibited lower values of HM for the same SH value compared to the field studies.The relationship between SH and HM was positive and curvilinear. Globally, for the same value of SH, the range of variations in HM was fairly large (± 1.3tDM/ha), and the intra-experiment relationship was relatively precise (Fig.4):

HM=5.21 (1 - exp (-0.048 (SH – 4))) (n=315, nexp = 92, RMSE=0.40) (5)

This curvilinearity is the consequence of the decrease inHBD when SH increases due to thelower density in the upper layers of the sward. Thus, 1 cm of difference in SH corresponds to 0.19, 0.12 and 0.07 t DM/ha when SH = 10, 20 and 30 cm, respectively. This relationship does not contain the origin of the graphic, suggesting that the best model could be a growth curve with a point of inflexion. However, this choice was not retained because it does not make any biological sense.

When data on micro-sward were excluded, there was an influence of the method of SH measurement on the relationship between SH and HM. More precisely, from a dataset of 286 treatments (nexp = 92, focused on the influence of SH) for which the method of SH measurement was clearly indicated, it appears that, for the average HM value of HM of 2.67 t DM/ha, SH was equal to 22 cm when the measurement was performed with a stick or ruler, whereas SH was16.5cm, when measured was made with a plate meter (RMSE = 4.3 cm). This difference of 5.5 cm/t DM in SH for the same HM is significant and does not vary with SH. Most likely, it is due to the fact that the platemeter tends to pack the grass.

3.3.2. Effectofswardheight on the components of BM

The effect of sward height (Table 2) on the components of BM were only analysed considering experiments where SH was the factor of variation studied, i.e. using a subset of 58 experiments. As the relationships between SH and various responses was calculated intra-experimentally, the influence of the method was nested in the variations between experiments, and it can be assumed that the mean effect of SH corresponds to an average of the two methods of measurement (stick/ruler vs platemeter).

When all treatments were considered, bite depth (BD, cm) was linearly and closely linked with sward height (SH).We observed two significantly different linear sub-relationships according to the type of animal, i.e. cattle (C) or small ruminants (SR) (Fig.5a). Analysis of variance-covariance of BD according to SH and animal species provided the following intra-species and intra-experiment regression, with a significant interaction between species and the covariable SH:

$$\mathbf{BD = 1.41 + [0.439\ C\ or\ 0.369\ SR]\ SH} \qquad \text{(n=149, nexp=58, RMSE = 1.40)} \qquad \text{(6a)}$$

Regarding the slopes, the marginal BD response was 0.44 cm/cm of SH for cattle (n= 109) and only of 0.37 cm/cm for small ruminants (n= 40).For cattle, the value is close to what was already suggested , while for small ruminants, the slope of the equation published by Burlison (1991) was lower than Eq.6a (0.25 vs. 0.37). It should be noted that the ratio of slopes between cattle and small ruminants, about 1.2, is relatively low compared to the ratio of BW for these species (512/58 kg BW), probably because BD is proportional to $BW^{0.20}$, according to our dataset. This low power coefficient of BW could be due to a specific difference between cattle and small ruminants in terms of bite type. Otherwise, in Figure 5a, points with values >40 cm present a significant lever effect on the regressions. When these points were removed, the intra-experiment response of $BD/BW^{0.20}$was slightly but significantly curvilinear (Fig.5b):

$$\mathbf{BD/BW^{0.20} = 0.290\ SH^{0.80}} \qquad \text{(n = 146, nexp = 89, RMSE = 0.33)} \qquad \text{(6b)}$$

The impacts of SH on BA and BDiam could only be studied for cattle. When considered intra-experimentally, BA increased with SH, according to a curvilinear relationship with a plateau of a theoretical maximum BA of 153.6cm²:

$$\mathbf{BA=153.6\ (1 - exp(-0.047\ SH))} \qquad \text{(n=65, nexp = 17, RMSE=13.5)} \qquad \text{(7)}$$

When BA was expressed on a BW basis, the intra-experimental regression presented a plateau value 0.37cm²/kg BW(Fig.6a):

$$\mathbf{BA=0.369 * (1 - exp(-0.035\ SH))} \qquad \text{(n=65, nexp = 17, RMSE=0.025)} \qquad \text{(8)}$$

The bite diameter response for cattle to an increase in SH was also curvilinear, with a plateau at 12.6cm (Fig.6b). It must be underlined that the border of the plateau of the response of

BDiamcorresponds to a value of SH ofabout 20 cm (approximately 23 cm for stick and 17 cm for platemeter).

$BDiam = 12.6 * (1 - exp(-0.109\ SH)$ (n=65, nexp = 17, RMSE=0.88) (9)

The comparison of Eqs (6a) and (9) shows that when SH<25 cm, we have BDiam>BD, while it is the opposite when SH>25 cm (see equations in Fig.6b). This illustrates the adaptations of bite shape as a function of SH to maximise BM according to the situation.

When expressed per kg BW, the Bite volume (BV, ml/kg BW), increased curvilinearly with SH (Fig. 7), and there was no difference between cattle and small ruminants. The intra-experiment regression is as follows:

$BV = 9.63\ (1 - exp\ (-0.00125\ SH))$ (n=90, nexp=34, RMSE=0.30) (10)

This curvilinear effect of SH on BV mainly results from the above evoked effect of SH on both BD and BA. The effect of SH on BM was curvilinear (Fig.8a), as established on a data set of experiments which focused on the impact of SH on behaviour components:

$BM = 3.65 * (1 - exp\ (-0.048 * SH))$ (n=296, nexp=51, RMSE=0.51) (11)

It should be noted that SH and BM were not normally distributed because of the low proportion of high values (Fig.8a). Equation 11 shows a plateau of BM, with an asymptotic value of about 3.65 mg/kg BWabove50 cm of SH. The variability of data around the regression was larger for high SH values than for the lower ones. Indeed, for some studies, there was almost no limitation of BM, which increased with SH up to40 cm (Gregorini Hodgson, 1990; Laca et al., 1992), whereas for other studies, there was a clear decrease of BM, well before a height of 40 cm (Mezzalira et al., 2017). This decrease is most likely due to tall sward species (Fonseca et al., 2012, 2013; Goncalvez et al., 2009). The Eq. 11 shows some similarities with some equations of the literature applied for a common average body weight of 400 kg (Fig.8b).

3.3.3. Effect of herbage mass compared to SH effect

The effect of herbage mass (HM, kg DM/ha) on bite area, bite depth, bite volume and bite mass was assessed on a subset of 39experiments in which SH was also measured. Two publications (Benvenutti et al., 2006 and 2009) were excluded from this dataset due to extremely high HM values in experiments performed with micro-swards.

There was a linear effect of HM on bite depth (cm), and considering the same dataset used to explore the effect of SH on BD (as in Eq.6a), the relationship was as follows:

$$\mathbf{BD=[6.39\ C\ or\ 0.69\ SR] + 2.02\ HM} \qquad (n=97,\ nexp=25,\ RMSE=3.90) \qquad (12)$$

According to this equation, there was a difference for the intercept between cattle (C) and small ruminants (SR), but not for slope. The RMSE comparison of this above equation and of Eq.6a (3.9 and 1.4, respectively) showed that the latter equation was much less accurate, suggesting that HM is a less precise predictor of BD than SH.

Besides, HM also affected BA (cm^2/kg BW) and BV(ml/kg BW). The relationship between HM and BA was curvilinear (Eq.13a), while that between HM and BV was linear (Eq. 13b). As already seen for the prediction of BD, HM also appeared as a less precise predictor than SH, for both BA (RMSE = 0.032 vs. 0.025 cm^2/kg BW for Eq. 8) and BV (RMSE = 0.8 vs. 0.5 ml/kg BW for Eq. 10).

$$\mathbf{BA = 0.229*(1-exp(-0.94\ HM)} \qquad (n=76,\ nexp=17,\ RMSE=0.032) \qquad (13a)$$

$$\mathbf{BV = 0.77 + 0.44\ HM} \qquad (n=74,\ nexp=18,\ RMSE=0.80) \qquad (13b)$$

In the case of BV, the data volume considered in Eq.13b was smaller than that for Eq. 10 (considering the effects of SH on BV). On the basis of the RMSE value, the prediction of BV was less accurate based on HM than on SH.

The effects of HM on BM, tested on the same subset as for Eq. 11, showed a plateau of BM (2.1 mg DM/kg BW) when HM increased beyond 2 t DM/ha.

BM=2.06 * (1-exp(-1.32 HM)) (n=163, nexp=39, RMSE=0.38) (14)

The influence of HM on BM was curvilinear (Fig. 9), as the effect of SH on BM (Eq. 11), while the Eq.14, established with a lower number of experiments is slightly better.

3.3.4. Effect of leaf mass compared to HM

The effect of leaf mass was tested with a subset of 45 experiments in which both leaf mass (LM) and HM were measured. In this subset, all the factors were considered, while only experiments dealing with the influence of SH were considered for the previous Eqs.(10) and (14). As the slope of the response significantly interacted with HBD, the experiments were split in two sub-groups of low HBD (LHBD= 0.98 ± 0.31 kg/m^3) or high HBD (HHBD=2.49 ± 0.91kg/m^3). The result of data fitting with HM was as follows:

BM=1.332 + (0.522 HHBD or 0.132 LHBD)*HM (n=157, nexp=45, RMSE=0.77) (15a)

When leaf mass (LM) was the explicative variable, the regression was:

BM=1.088 + (1.351 HHBD or 0.493 LHBD)*LM (n=157, nexp=45, RMSE=0.65) (15b)

Apparently, LM is slightly more accurate to predict BM than HM. Moreover, the slope is much higher when considering LM(Eq. 15a) rather than HM (Eq.15b) as explicative variable. The RMSE values of these two equations were higher than those of the Eqs.(10) and (14), which also predict BM.

3.3.5. Effect of herbage allowance

The effect of herbage allowance (HA= 2.28g DM/g BW ±1.89, n =26) on BM could be studied with a subset of seven experiments (26 treatments), with a duration of IB observations of 24 hours. We observed a significant and linear relationship between BM and HA (g DM/g BW):

BM = 0.42+ 0.088 HA (n=26, exp=7, RMSE=0.13) (16)

Figure 10 shows that BM can be doubled, ranging from 0.4 to 1 mg/mg DM/kg BW, depending on the level of HA. Therefore, HA can be considered as a significant factor in grazing ruminants. The fact that the intercept of Eq. 16 was significantly different from 0 suggests that the animals tended to compensate a decreasing of HA by maintaining thelevel of BM. It must be noted that the data volume for this subset was limited, and therefore, it was not possible to further explain this factor.

3.3.6. Effect of herbage bulk density

The effect of herbage bulk density (HBD, kg DM/m^3) on bite components was studied on a subset of 15 experiments, for which the factor of variation tested was sward bulk density, independent of the variation in sward height. The studies included in this subset were only carried out with cattle on micro-swards. A decrease in HBD had a positive effect on BA. Intra-experimental regression (Eq.17) suggested that for high values of HBD, BA presented a plateau of a minimum value of 33 cm^2in cattle, while for the lowest values of HBD, BA was close to 130 cm^2 (Fig. 11):

$$\mathbf{BA=32.5 + 102.5\ exp^{-0.486\ HBD}} \qquad (n=46,nexp=15,RMSE=9.38) \qquad (17)$$

The diameter of the bites (BDiam, cm) evolved with HBD, according to a comparable trend than the evolution of BA with HBD. In the same subset, the intra-experimental regression between BDiam and HBD was as follows:

$$\mathbf{BDiam=6.54 + 6.24exp^{-0.396\ HBD}} \qquad (n=46,nexp=15,RMS=0.64) \qquad (18)$$

There also was a negative slight linear effect of bulk density on bite depth (BD, cm), with a mean value of -0.36cm/kg of herbage bulk density (HBD, kg DM/m^3). The intra-experimental regression was as follows:

$$\mathbf{BD=12.37 - 0.36\ HBD} \qquad (n=45,nexp=15,RMSE=1.1) \qquad (19)$$

It should be noted that for a similar decrease in the lower values of bulk density (from 3 to less than 1 kg DM/m^3), the rate of increase of bite depth was considerably lower than the diameter of the bite, which then appears as the bite characteristic which is most significantly impacted by the variation in HBD (Fig.12). This impact likely reflects the adaptive work of the mouth, particularly the tongue, to expand the BA for low bulk densities, thus maximising sward removal.

Generally, for cattle, as a consequence of the evolution of BA and BD with bulk density, BV (cm^3/bite) increased curvilinearly when bulk density decreased (Fig. 13). The relationship was as follows:

$$\mathbf{BV} = 0.001*\mathbf{0.27 + 1.26\ exp^{-0.458\ HBD}} \quad \text{(n=45, nexp=15, RMSE=0.0015)} \quad (20)$$

The maximum BV value was about 1500 cm^3 for low HBD, while there was a plateau of about 270 cm^3 for high HBD values. It should be noted that all the available data for BV were obtained from micro-swards studies with cattle.

Contrary to BV, when HBD decreased, there was no significant influence on BM, because the HBD drop compensated the increasing BV. The BM depended on BV, but when BV as low, for high HBD, this did not enhance large mouthfuls and high bite masses. In particular, it is worth noting two experiments of Laca (1992, 1994), reporting contradictory results on this aspect. Comparing bite density (calculated from the equation) to HBD, we found no clear intra-experimental relationship between these two densities when experiments on HBD were pooled. In contrast, when the 14 experiments (35 treatments) focusing on SH were pooled, there was a significant relationship with a slope of 1.

The interaction between the effect of SH and HBD on BM is a key issue which has rarely been investigated. In the database, there were only three publications describing an experimental design to test this interaction (Gilloway et al., 1999; Benvennuti et al., 1986; Laca et al., 1992). When these three publications were pooled with a specific encoding, only the effect of SH was significant, despite the fact that the SH and HBD variations were not correlated (orthogonal meta design). In contrast, when all 30 publications with SH and HBD results were pooled, a significant intra-publication regression could be established to explain BM based on SH and HBD:

$$\mathbf{BM = -0.94 + 0.156\ SH - 0.0015\ SH^2 + 0.74\ HBD - 0.063\ HBD^2 - 0.012\ SH\ HBD}$$

(n=339, npub=30, RMSE=0.71) (21)

Figures14a and 14b present the predicted values of BM according to Eq. 21 within the ranges of values of SH and HBD and in the area where data were available. The accuracy of this Eq. 21 was fairly poor compared to Eqs. (11) and (14), (RMSE=0.65 vs. 0.51 and 0.38), most likely because the various experimental targets were mixed in this approach. The interaction between both predictors was clear: the influence of SH on BM was always positive (Fig.14a), confirming Eq. 11 and Figure 8a. In addition, at low SH values, BM was higher at higher HBD values, suggesting that in this case, animals were taking greater advantage of a strong HBD by increasing the amount of herbage collected per bite. The Eq. 21 and the Figure 14b allow to conclude about the influence of HBD on BM which did not appeared when considering only the HBD effect (see above).

3.4. Consequences for the relationships between BM and other components

It was important to assess the impact of each sward characteristic on each bite components (see above). It is also worthwhile to have an overall idea of the interrelations between the various components of the bite. The behavioural components, i.e. BD, BA, BV and BM, scaled by BW, were diversely inter-related and based on various numbers of treatments. Moreover, for the same couple of variables, the coefficients of correlation varied according to inter- or intra-experimental calculations (Table 3). The parameters most strongly correlated to BM were BA and BV, with significant correlations both inter- and intra-experimentally. The parameter BM was considerably less correlated with BD and BDiam, and the correlations were only intra-experimentally. In contrast, BM was not correlated with BDens. We noted a link between BA and BDiam, both inter- and intra-experimentally.

These relationships between IB components expressed per kg BW were highlighted by grouping all data, irrespective of the factors of variation. According to the available data, when considering intra-experimental relationships to avoid interferences due to methodological influences, as shown in Table 3, BV increased both with BD (cm/kg BW) and BDiam (cm/kg BW), and these variables significantly contributed to BV:

$$\mathbf{BV = - 0.58 + 2.00\ BD + 7.93\ BDiam} \quad (n = 131, nexp = 36, RMSE = 0.47) \quad (22)$$

This regression shows that a difference of 1 cm of BDiam had a higher impact (x by almost 4) on BV than BD did. The value of BM (mg/kg BW) increased curvilinearly with BV (ml/kgBW),and a non-linear fit of the data according to the following equation showeda maximum theoretical asymptotic value of BM of 8.24 mg DM/kg BW (Fig. 15):

$$\mathbf{BM}(\text{mg DM/kg BW}) \mathbf{= 8.24*(1 - exp(-0.145\ BV)} \quad (n=158, nexp=43, RMSE=0.43) \quad (23)$$

In the current dataset, this asymptotic value was never achieved, with a maximum of 5.3 mg/kg BW. According to this equation, the slope representing the adjusted bite density (BDens) evolved from 1.19 mg/ml (for smallest bites with a volume less than 1 ml/kgBW) to 0.73 mg/ml (for largest bites of up to 7.5 ml/kg BW). This evolution is consistent with the fact that larger BV values are mainly associated with taller swards (see above, Eq. 10, Fig. 7) and that bulk density decreases from the bottom to the top. However, it must be stressed that a majority of the high values of BM and BV, related to the BW, were issued from a single publication (Cangiano et al., 2002).

4. Discussion

To provide a more synthetic view of eating behaviour and its major determinants, we carried out a meta-analysis of 96 papers published between 1992 and 2017. This meta-analysis allows evaluating the already published relationships but which are only applicable in the context of each study. By grouping the data of several experiments and focusing on intra-experiment regressions this leads to widening the fields of study and to establishing laws of more general applicability. All obtained equations contribute to deepen our understanding of resource acquisition by grazing ruminants and of the components of pasture sustainability (Combes et al., 2011). This is particularly important in the context of precision livestock farming in more or less complex environments, in which it is necessary to identify which animal character is to be measured and which determining factor in the feeding environment, to automate measurement of indicators that will be really useful for practical pasture management. Indeed, recent technological advances based on measurements of behaviour, makes it increasingly possible to consider improvements in grazing management of farm animals, especially dairy grazing cows (Werner, 2018; Verdon et al, 2018). As bite mass is classically considered as the central variable of feeding behaviour in determining the acquisition of DM by grazing ruminants (Kondo et al., 2011;Carvalho et al., 2015), our analysis focused on the key components of BM and their major factors of variations. Nevertheless, this meta-analysis has several limitations, mostly because it does not take into account the vertical heterogeneity of sward density and composition (see Baumont et al., 2004; Sollenbergeret al., 2011). Moreover, we did not take into account the fact that the animals consumed the sward in successive layers (see Baumont et al., 2004; Brink and Soder, 2011; Jacobs et al., 2013). More data on these aspects are therefore needed to develop a complete mechanistic model of the feeding behaviour of ruminants in pastures to reach their daily dry matter intake.

4.1. Features of the database

The database compiled 776 treatments and 239 experiments. The careful coding of the major factors of variation considered in the database allowed obtaining more accurate regressions issued from these factors. In contrast, the various regressions obtained from different experimental contexts are not *a priori* mutually consistent.For instance, the effects of SH and HBD on BM can be compared on the basis of RMSE, but it must be kept in mind that these equations were obtained from different datasets and therefore require different methodologies (i.e. micro-sward vs. natural grazing).The data related to sheep or the goats were significantly less abundant (11.6% of the treatments) than those for cattle. Moreover, all experiments carried out on micro-swards or with pots included cattle (26% of the treatments). Among the eight factors of variation which were *a priori*coded in the dataset, three were analysed, i.e. sward height (SH), herbage bulk density (HBD) and herbage mass (HM). The study targets and conditions were highly diverse, allowing a fairly general view of feeding behaviour components. Thus, 42% of the treatments were derived from experiments carried out in tropical or sub-tropical areas, while the other treatments were conducted in temperate zones. It should also be noted that the methods used were highly diverse, both for the measurement of forage characteristics and for the evaluation of the various components of ingestive behaviour or intake. These various methods were coded and will be considered in detail in a further analysis.

4.2. Impact of animal factors on ingestive behaviour components

Among the animal factors considered, body weight was the most important factor of bite mass variation (Eq. 1), as already stressed in previous publications (Illius and Gordon, 1987; Gordon et al., 1996). The relationship that we obtained between BM and BW^1 allowed us to scale data of BV and BM to BW^1 to obtain additional data for the calculation of regressions implicating BM components and to obtain more generic values for all types of ruminants. The Incisor Arcade (IA) is another important animal factor for both bite diameter (Eq. 2) and bite mass (Eq. 3) with the lowest error among all the predictive equations of BM that we have calculated. The power coefficient of Eq. 3 between BM and IA was higher than that for Eq.1, which is in agreement with Gordon et al., (1996) and stresses the advantage of having a larger IA for forage acquisition. This can be seen as a systematic advantage of grazing cattle compared with sheep. The Incisor Arcade was linked to BW with a power coefficient close to

0.33 which is logical because it is a linear variable (Eq. 4, Fig. 3), almost the same equation has been published previously (Gordon and Illius, 1988). In contrast, by considering the same subset, IA was not linked to bite depth. Such a scaling of BM and BW[1] has already been applied in a previous modelling approach (Woodward et al., 2008). The IA appears then as a determining animal characteristic and has long been taken into account by some authors (Illius and Gordon, 1987). Nevertheless, this characteristic is generally little measured in studies dealing with ingestive behaviour. Of the 96 publications in our database, this characteristic was measured only in eight cases. The relationships that we have highlighted suggest that in future studies, this characteristic would be extremely useful to assess various determining components of behaviour. This is particularly true for bite mass determination, for which the measurement of IA represents another method based on the animal characteristics, making it possible to assess individual variations. This characteristic appears as an important tool to estimate BA, and BV if BD is known, and has already been applied in grazing mechanistic models (Baumont et al.,2004; Gregorini et al., 2013). This method of estimating bite area based on animal characteristics may even be as accurate as the method proposed by Burlison (1991) based on the measurement of the grazed area, especially as the dental arcade can more easily be measured with a caliper (Gordon and Illius, 1988).

4.3. Impacts of sward characteristics on bite mass and its components

The analysis of the impacts of sward characteristics on ingestive behaviour components, such as sward height, herbage bulk density, or herbage mass, facilitates an understanding of how the different components contribute to BM and may interact.

As sward height increases, bite depth increases linearly when all data available are considered, with SH reaching up to 60 cm. In this case, bite depth is equivalent for cattle to almost half of the total sward height, as already reported (Laca et al., 1992, 1994; Ungar et al., 1997; Boval et al., 2007a). However, the data corresponding to SH > 40 cm are few and have a lever effect on the regressions. When these data were removed, there was a slight but significant curvilinear response, as already observed by Hirata (2010).This trend could be explained by a limitation of the physical ability of the animals to go deeper into the sward. For sheep, bite depth represents a lower part of the sward height, close to a third, rather than the quarter previously reported (Milne et al., 1982; Combes et al., 2011). The difference of bite depth between the two species is extremely low compared to their respective BW, revealing that the sheep's biting modalities would be more effective for going deeper into the sward compared to cattle, as already suggested (Woodward,1998, Gordon et al., 1996). This could be linked to some anatomical characteristics of the mouth and the tongue. For instance, Meier et al. (2016) have shown that the tongue length of small ruminants, when expressed per kg BW, is proportionally much longer than that of cattle (0.46 vs. 0.12 cm/kg BW).

When the sward becomes higher, bite diameter and bite area increase curvilinearly, characterised by a plateauing response for high swards and a drop for the lowest heights. This curvilinearity, and particularly the lowest values converging to 0 (Fig. 6), illustrates the roles of the mouth and of the tongue in the foraging process. The upper limits of BDiam and BA correspond to the greatest opening capacity of the mouth, combined with the maximum extending of the tongue to enlarge the sampling area of the herbage (Meier et al., 2016). Thus, the resulting volume of the bites cannot be strictly considered as a cylinder with a flat bottom, as suggested by Burlison et al. (1991).This bottom part presents rather a bowled shape due to the round shape of the mouth and of the tongue, sweeping grass (Woodward, 1998, Combes et al., 2011). When expressed in kg BW, the bite volume, influenced both by bite depth and bite area, increases curvilinearly up to a value of about 4.5ml/kg BW for a sward height of 50 cm. For sheep, Elston and Hutchings (cited by Woodward, 1998) have proposed a similar geometry of bite volume, except the tongue sweep, since sheep are constrained to use mainly teeth and lips in gathering herbage.

Concerning bite mass, it reaches a plateau value of around 3.65 mg/kg BW, at a sward height of 50 cm. This curvilinear response of bite mass with sward height is similar to previous findings (Fig.8b, also see Cangiano et al.,2002, Hirata, 2010 and Mezzalira et al., 2017).In contrast, other publications reported a lower response of BM to SH, such as Forbes (1988) and Boval et al. (2007a).

As with sward height, the components of feeding behaviour are sensitive to the evolution of herbage mass; the latter later being positively and curvilinearly related to sward height (see Eq. 5, Fig. 4). Thus, with the increase in HM, we have noticed the same kind of responses of the components of ingestive behaviour than with sward height; namely a positive curvilinear response of BD, BA, BDiam and BV. Bite mass also evolved curvilinearly with herbage mass, but with a plateau of around 2 mg/kg BW rather than 3.65 mg/kg BW for the higher SH. When considering the same set of data, it appears that sward height better explains the variations in the components of feeding behaviour than herbage mass. This makes sense, mainly as the animals are more able to assess SH differences rather than HM differences. Compared to HM, leaf mass (LM) also has an impact on BM, and we were able to highlight this effect in a subset where HM and LM were both measured. Thus, LM better predicted BM than HM, with a lower RMSE. Similarly, we highlighted a significantly linear positive effect of herbage allowance on BM in a small subset.

With increasing sward bulk density, all ingestive behaviour components decreased, excepted bite mass, contrary to what was observed for increasing sward height or herbage mass. These different responses of ingestive behaviour between sward height and herbage bulk density have already been reported (Laca et al., 1992; Mitchell et al., 1993; Gong et al., 1996). In fact, there was a plateau for high bulk density values for all components, suggesting that adaptation processes mostly occur at lower values of less than about 3 kg DM/m^3. Thus, when bulk density decreases, bite diameter and bite area increase curvilinearly, involving the mouth and the tongue, to compensate for and maintain the level of DM collected. The bite volume follows the same trend (Fig. 13), even in a more pronounced way, due to the simultaneous linear increase of bite depth when bulk density decreases (Fig.12). Thanks to these compensatory mechanisms, there was no significant relationship in our database between BM and HBD considered as a sole factor.

However,in natural grazing situations, sward height and bulk density interact with bite mass, although many studies consider the impacts separately for each factor. In some cases, height and bulk density evolve in the same way, for example with a maturing vegetal sward, which then becomes both higher and denser in DM (Boval et al., 2007b; Fanchone et al., 2012). In other cases, a sward may be high, but less dense in DM, as in the case of fertilised forage, which grows relatively quickly (Lemaire et al., 2009; Boval and Dixon, 2012). Therefore, knowledge of these interactions is essential, but difficult to put in evidence, and the rare experiments that focused on these interactions did not provide any consistent results. When the maximum of experiments considered in our database was analysed, pooling various factors of variation, a significant interaction between sward height and bulk density was found (Fig. 14). The study of this interaction, which is original when considering the lit erature, shows that for low values of sward height, limiting bite mass (see above), the animal is quite able to take advantage of higher bulk densities and thus to compensate the low sward heights. In contrast, for high swards, with a narrower range of bulk density, as in our dataset, the already high bite mass is not any more impacted by the increasing bulk density. It must be kept in mind that this interaction was obtained for a data set pooling all types of factors of variation, and more data would be necessary to focus on interactions between SH and HBD due to either mature or fertilised swards.

4.4. Major components determining bite mass

The various ingestive components determining BM were more or less interrelated, with some differences between inter-experiments or intra-experiments; those more marked suggest a stronger influence of the experimental conditions. A limit of ourapproach is that all factors of variation were mixed in the calculations. Thus, the relationships outlined between the components of bite mass are partly the outcome of impacts of the main factors tested in the publications, linked to animal or forage characteristics, as discussed above.

The bite volume is the component most linked to bite mass in any case (Fig. 15), as already pointed out previously (Mezzalira et al., 2017). In the present work, we obtained a slightly curvilinear relationship between bite mass and bite volume, stressing that bite density decreases when bite volume increases.

Analysing the determinism of the bite volume itself, we observed the role of bite depth, as suggested by Gong et al. (1996). However, we emphasised the predominant role of the diameter of the bite with low SH (mainly with $10<SH<20$ cm, Fig. 6b) and HBD values (<3 kg DM/m^3, Fig. 12). This component is not generally calculated in studies, yet it presents the advantage of having the same unit as bite depth. Considering both BDiam and BD allowed to better appreciate the respective impacts of the vertical and horizontal dimensions of the sward. These two dimensions are used by the animal when they push - more or less deeply – their heads into the canopy (evaluated by BD) or open their mouths while stretching their tongues (evaluated by BA or BDiam). Moreover, considering both BDiam and BD allows an understanding of the adaptation of the bite shape facing variations in SH or HBD (Figs.6a and 9) in order to maximise the bite volume. We highlight that a variation of 1 cm of BDiam impacts the bite volume four fold higher, compared to similar 1 cm variation of bite depth (Eq.22).Thus, when sward height increases, bite depth plays a major role in increasing bite volume and BM, while the role of the bite diameter is limited. In contrast, BDiam is more efficient in increasing bite volume and BM, in swards with a low sward height and bulk density. In these contexts, BDiam can contribute to increase the volume of the bite in a linear way horizontally widening the geometry of the bite (Illius et al., 1995b). This has been observed in cattle (as shown in Figures 6a and 9). The same approach could have been carried out with small ruminants, if sufficient data were available for a meta-analysis. ~~In all cases, greater volumes lead to bigger bite masses~~. Besides, the diameter of the bite is linked to the IA, as developed above, representing 1.5 to 2.4 times the IA (Fig.4a). It has been shown that IA influences the survival capacity of sheep in harsh winter conditions (Illius et al., 1995a). This link to the arcade (cf. above) represents a methodological asset, as the IA breadth is easily measurable.

4.5. Implications for modelling forage use by grazing ruminants

Models are needed to scale up from bite to meal and, ultimately, to animal performance. Several mechanistic models of grazing have already been published, generally taking into account the overall influences of SH on BD and BA and therefore on BM,as well as the impact on bite quality for grazing sheep (Woodward, 1998; Baumont et al., 2004) and cattle (Brereton et al. 2005; Gregorini et al. 2013). By another way, other models have described bite mass and composition in terms of leaf and stem based on describing the morphological growth of the forage (Boval et al., 2014). For all these models, the calculation of BD,as proportional to SH, is fairly similar. In contrast,the calculation of BA varies, according to various predictive variables, and the values estimated may then vary notably between studies. Based on this meta-analysis, we obtained considerably more equations than in the above cited models. For instance, the prediction of BA from Eqs. (8) and (17), from SH or HBD, respectively, is based on specific designs and on a higher data volume compared to previous studies.

The current challenge is now to develop a mechanistic model based on most of the equations proposed in this quantitative analysis by integrating effects of sward and of animal characteristics on ingestive behaviour. A first approach would be to assess the consistency across all these equations which were not created from a common dataset and from similar experimental contexts. The ultimate goal is to increase the predictive ability of a model of acquisition, as different authors argue that the low predictive quality of DMI by grazing animals probably result from an insufficient characterisation of the sward and its low integration in predictive models (Gunter and Cole, 2016).

5. Conclusions

This quantitative analysis of the literature provides a synthesis of the knowledge acquired in various situations and therefore offers new perspectives on the understanding of the adaptive pathways used by grazing animals benefiting to their anatomical morphology, to behave optimally facing the diversity of the structure of the sward.

As already reported in previous studies, we confirmed that SH and HBD are the major factors of variation in the IB components, that there is an almost linear influence of SH on BD, and that the BW explains the variations inIA breadth as well as those in bite mass.

Besides, we obtained various original results. First, a significant interaction was highlighted between SH and HBD on BM. Also, SH could be underlined as a more relevant predictor than HM to explain BM components, while BDiam was identified as an interesting criterion thanks to its relationships with both BA and BV and because of its connection to IA breadth. Interestingly, we observed simultaneous, but not parallel responses of BD and BDiam when SH or HBD varied. These responses allow a better understanding of the adaptive strategies of the grazing animals to sward factors to maximize BM.

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Fig 1.Functional relationship between the main components of feeding behavior

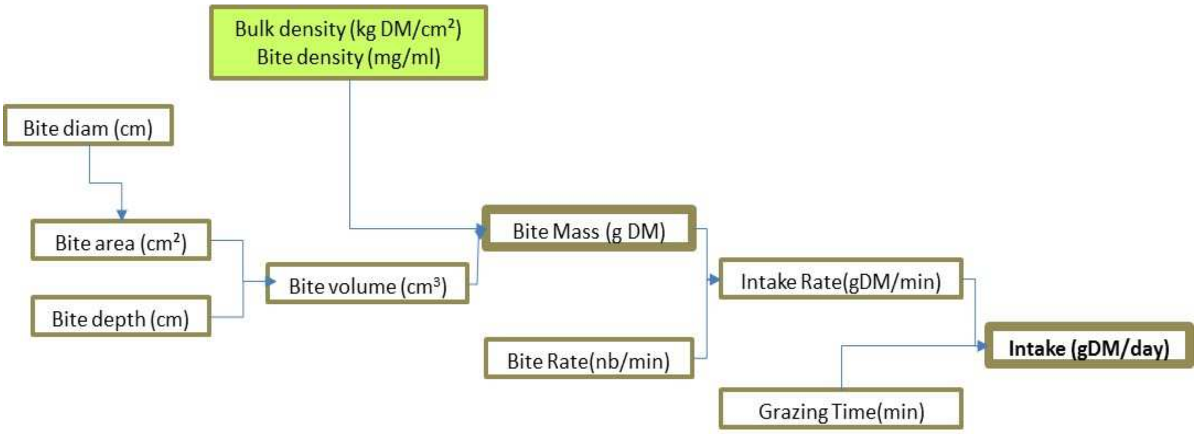

Fig2. Intra-experiment relationship between a) Bite Diameter (BDiam, cm) and Incisor Arcade (IA, cm); b) Bite mass (BM, g DM) and Incisor Arcad (IA, cm).

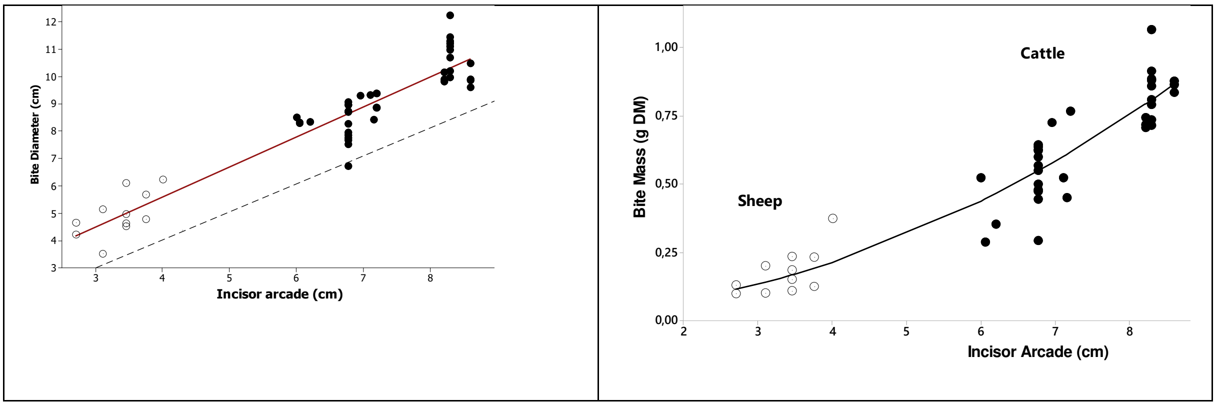

Fig 3. Intra-experiment relationships between Incisor Arcade (IA, cm) and Body Weight (BW, kg)

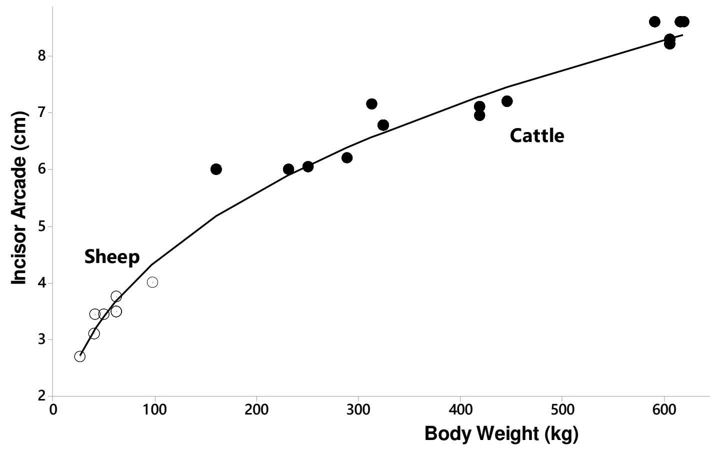

Fig 4. Intra experiment relationship between Sward Height (SH, cm) and Herbage Mass (HM, t DM/ha).

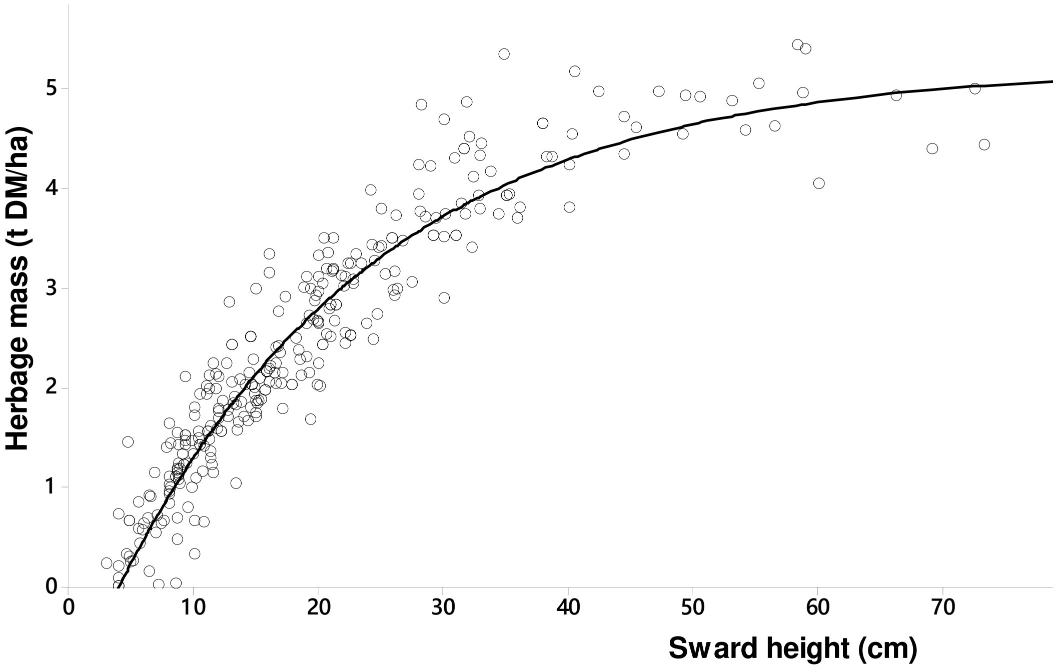

Fig5. Effect of sward height (SH, cm) on Bite Depth (BD, cm or cm/kg $BW^{0.20}$) a) in the current database for cattle ((•) and small ruminants (○) and b) with BD expressed on $BW^{0.20}$

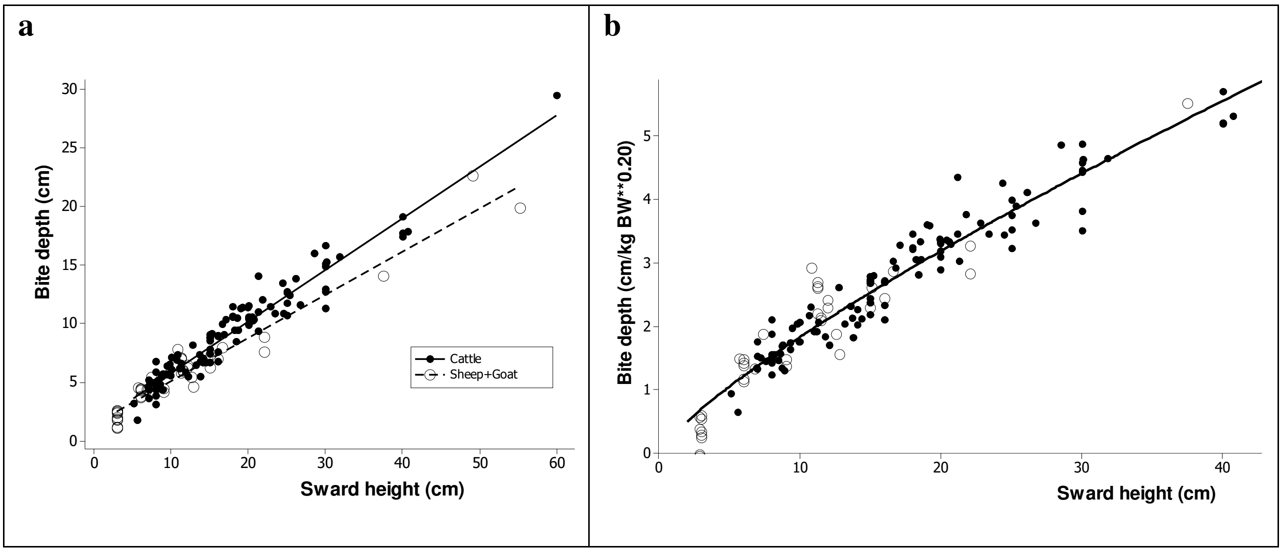

Fig 6.Influence in cattle of the sward height (SH, cm) on a) the Bite Area (BA, cm²) and b)the bite diameter (BD, cm). The dotted line being the trace of the influence of SH on BD (equation 6a for cattle)

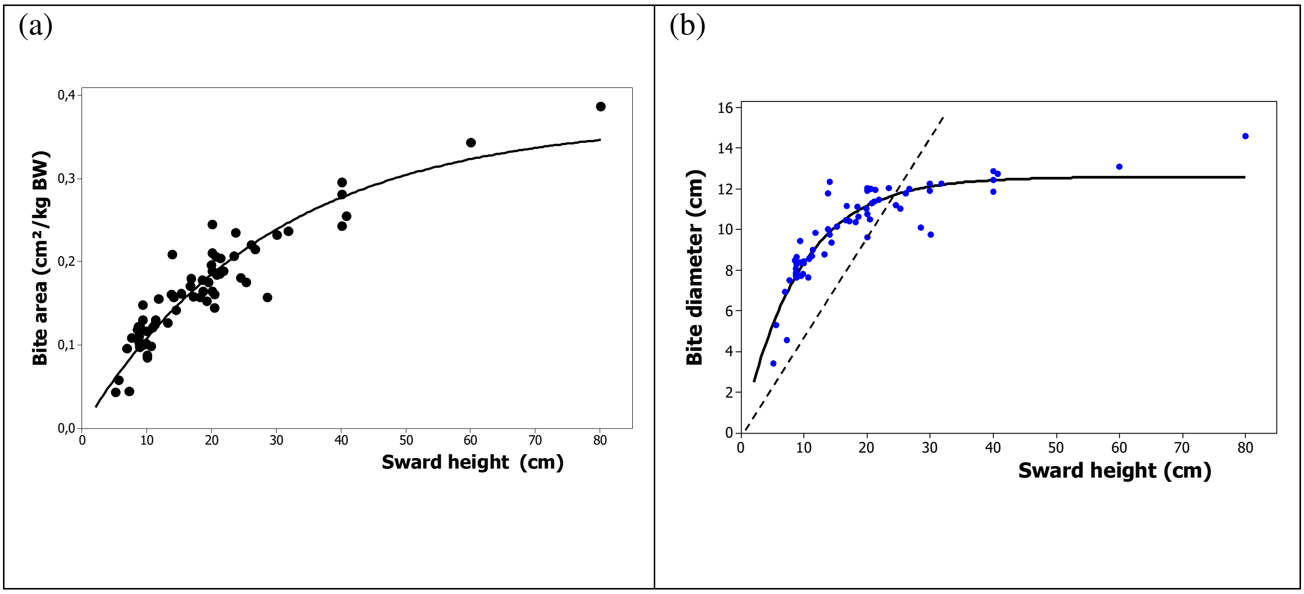

Fig 7. Influence of Sward Height (SH, cm) on the Bite Volume (BV, cm^3/kg BW), for Cattle (•) and Small Ruminants (O)

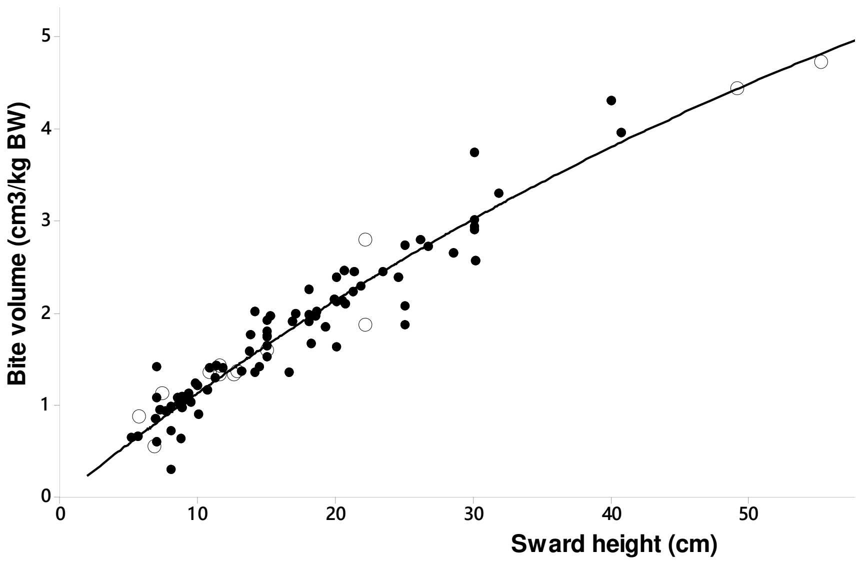

Fig 8. Influence of Sward Height (SH, cm) on the Bite Mass (BM, mg/kg BW) a) in the current data base for Cattle (•) and Small Ruminants (O) and b) in comparison with other published equations

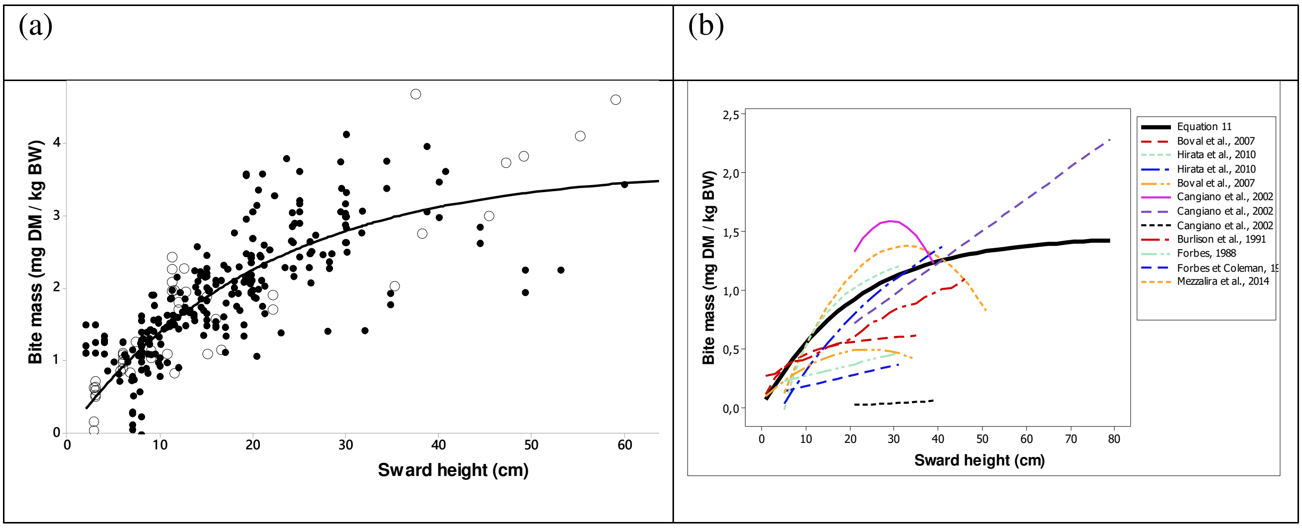

Fig 9.Intra-experiment influence of Herbage Mass (HM, t DM/ha) on the Bite Mass (BM, mg/kg BW)

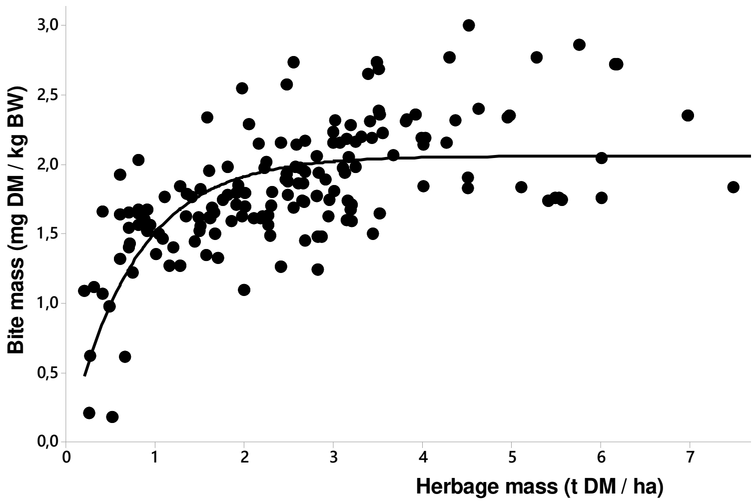

Fig 10.Effect of Herbage Allowance (HA, g DM/g BW) on Bite Mass (BM, mg DM/kg BW)

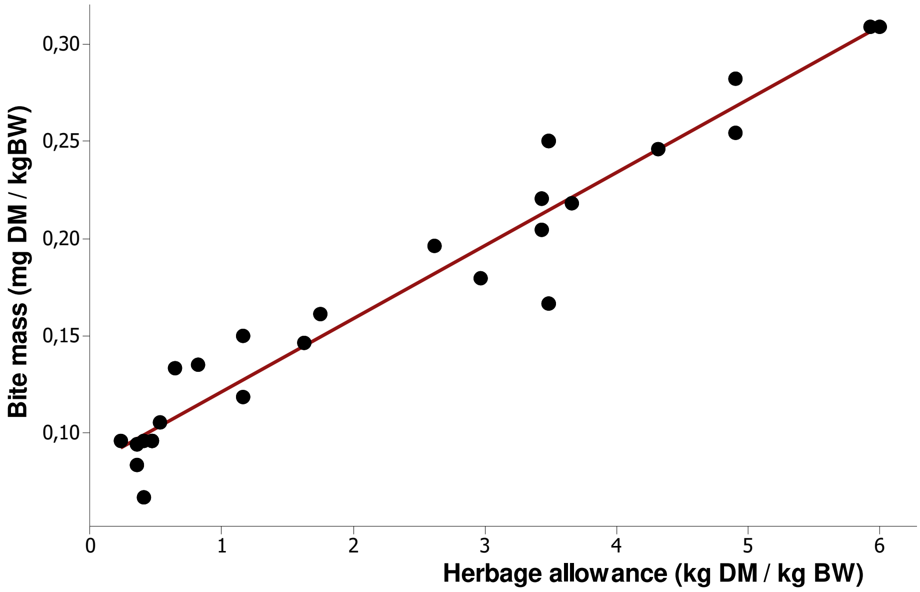

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Fig 11. Effect of Herbage Bulk Density (HBD, kg DM/m^3) on Bite Area (BA, cm²/bite) for cattle

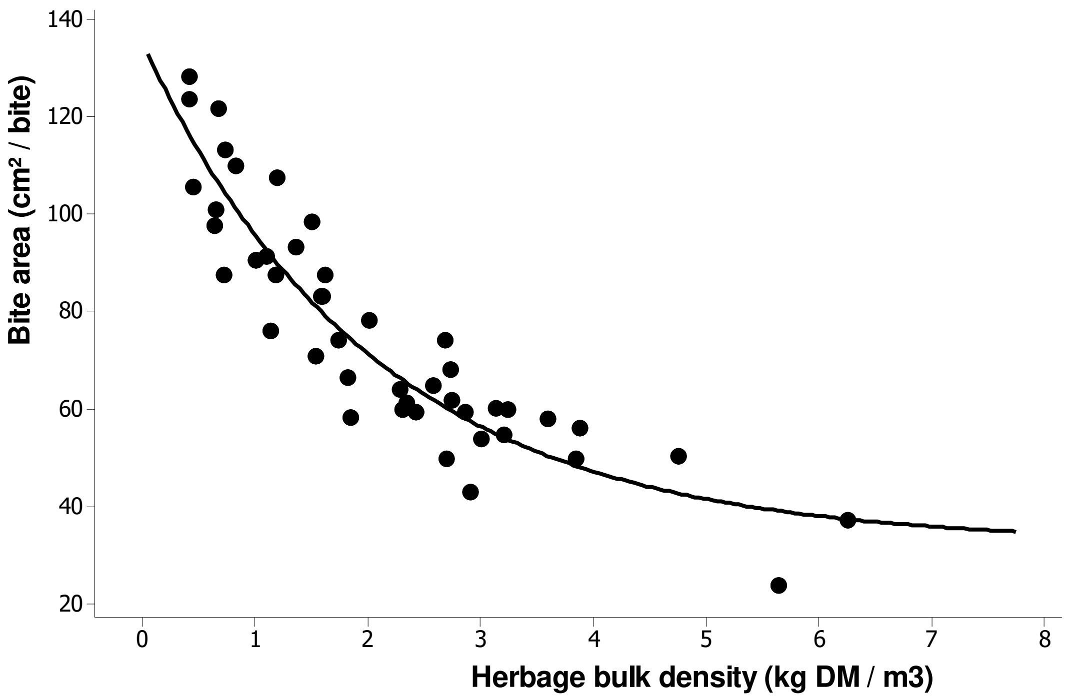

Fig 12. Traces of the fitting of the simultaneous influences of Herbage Bulk Density (HBD, kg DM/m^3) on the Bite Depth and Bite Diameter (BD and BDiam, cm) for cattle

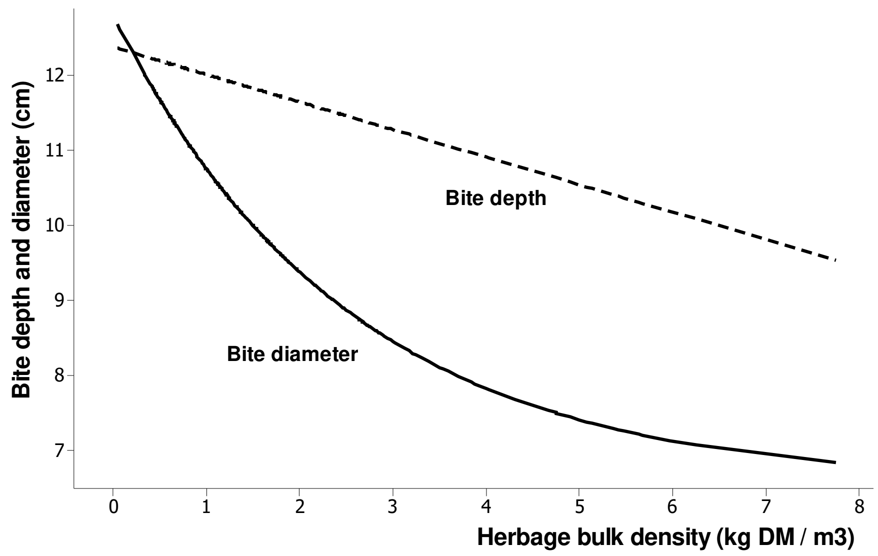

Fig 13.Influence of Herbage Bulk Density (HBD, Kg DM/m^3) on the Bite Volume (BV, cm^3/bite) for cattle.

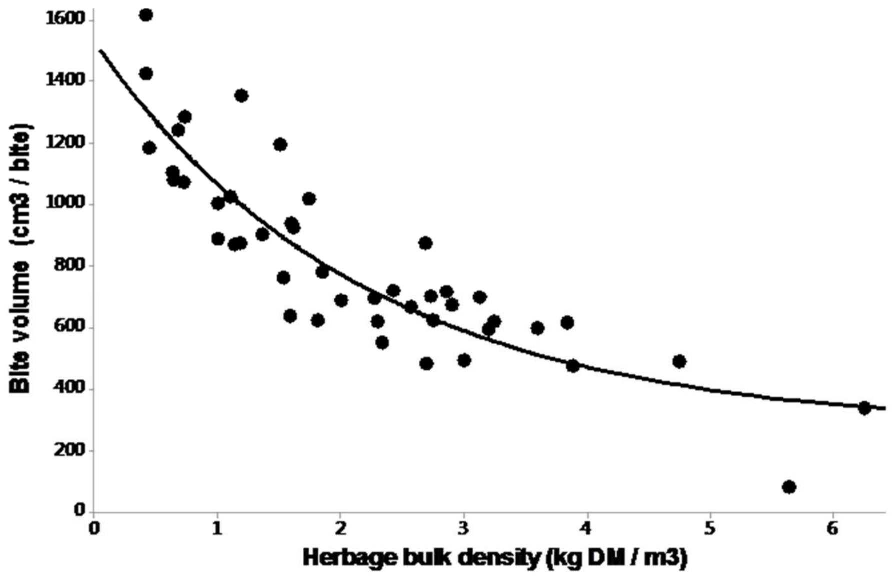

Fig14.Influence of the interactions between Sward Height (SH, cm) and Herbage Bulk Density (HBD, kg DM/m^3), on Bite Mass (BM, mg/kg BW, trace of the equation 21), seen from the angle of SH (a) or of HBD (b).

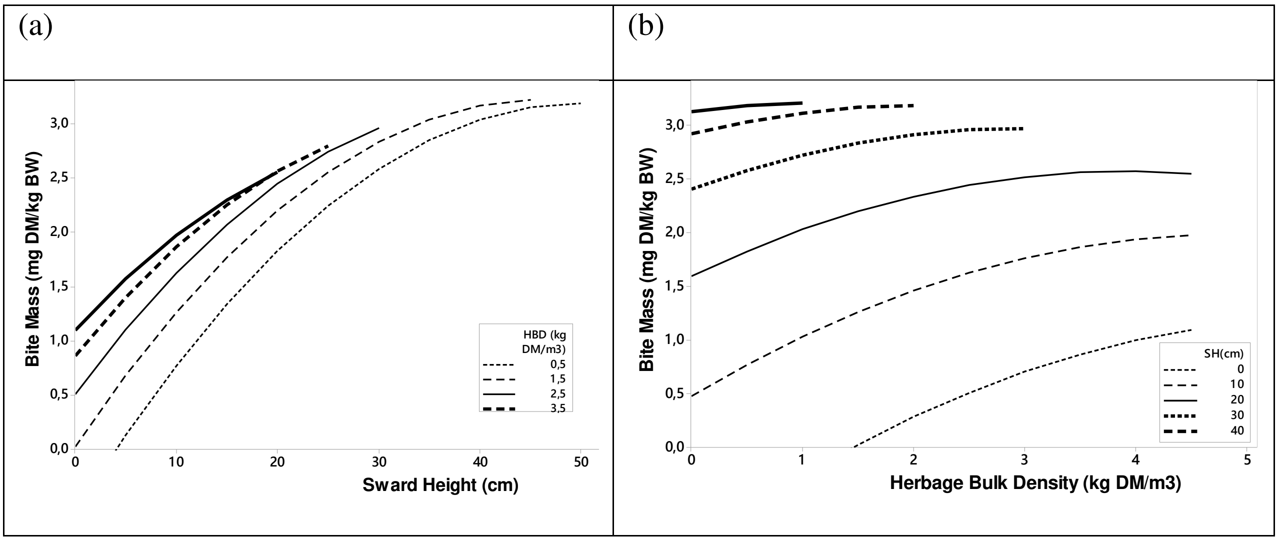

Fig 15. Relationships between Bite Mass (mg DM/kg BW), Bite volume (cm^3/kg BW) and Bite density (mg/cm^3).

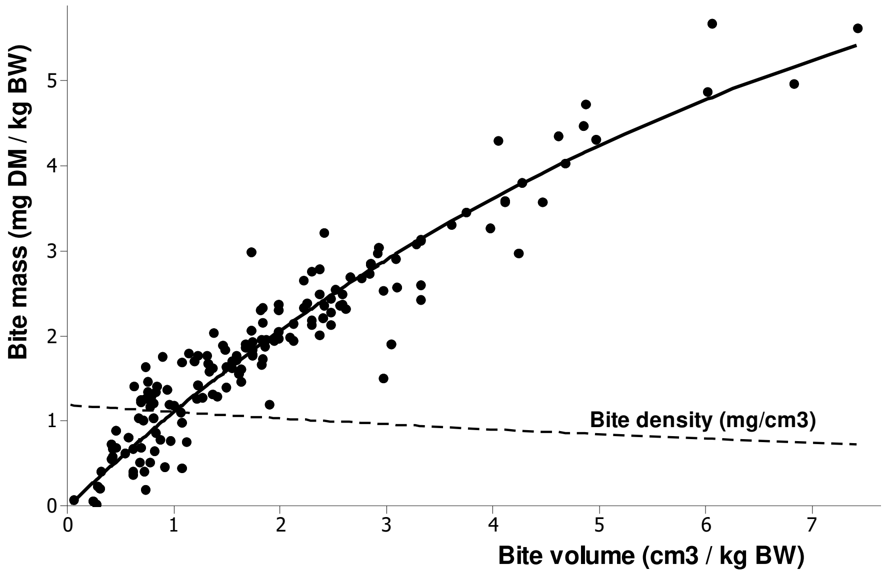

Table 1

Statistical characteristics of the feeding behavior components collected in the publications (a) units of the publications (b) units/kg BW

Components		**Mean ±SD**	**N**	**Min-Max**	**Components per kg BW**	**Mean ±SD**	**N**	**Min-Max**
Bite Area (BA, cm^2)	SR	18.12±5.26	32	9,0-35,5	(cm^2/kg BW)	0.19±0.09	197	0.01-0.52
	C	80.31±36.58	165	6,9-176,0				
Bite Diameter (BDiam, cm)	SR	4.76±0.66	32	3.4-6.7	(cm/kg BW)	0.30±0.23	197	0.06-0.98
	C	9.84±2.34	165	3.0-15.0				
Bite Depht (BD, cm)	SR	5.32±4.18	36	1.5-20.6	cm/kg BW	0.38±0.46	215	0.04-3.22
	C	10.79±5.61	179	1.6-34.1				
Bite Volume (BV, liter)	SR	0.10±0.10	32	0.02-0.43	(ml/kg BW)	2.12±1.87	194	0.03-13.64
	C	1.09±1.03	162	0.01-5.84				
	C	1.57±1.82	149	0.0-9.4				
Bite Mass (BM, g DM)	SR	0.12+0.06	34	0.0-0.3	(mg/kg BW)	1.71±1.21	437	0.00-7.14
	C	0.76+0.6	403	0.0-4.0				
Incisor arcade (cm)	SR	3,3±0,25	15	2,7-4,0				
	C	7,3±0,89	29	6,0-8,6				
Body weigh (kg)	SR	56±17	89	25-97				
	C	653±169	653	120-817				

SR:Small Ruminants; C:Cattle;

Table 2

Values of the major characteristics of the sward

Components	Mean ±SD	N	Min-Max
Sward Height (SH, cm)	18.71±12,66	576	2,00-80,00
Herbage Mass (HM, t DM/ha)	2,81±2,26	533	2,00-3,06
Herbage Bulk Density (HBD, kg DM/m^3)	1,79± 1,32	453	0,05-7,75
Leaf mass (LM,t DM/ha)	1,20 ± 0,68	285	0,08-3,43

Table 3

Inter-publication correlations (1st line) and intra-publication correlations (2nd line) between ingestive behavior components expressed per kg BW.

	Bite Area	**Bite Diameter**	**Bite Depht**	**Bite Volume**	**Bite density**
Bite Diameter (cm/kg BW)	0.777^{***} 0.667^{***} *n=114*				
Bite Depht (cm/kg BW)	0.420^{***} 0.413^{***} *n=107*	0.608^{***} 0.220^{**} *n=176*			
Bite Volume (cm^3/kg BW)	0.773^{***} 0.342^{***} *n=102*	0.282^{**} 0.502^{***} *n=135*	0.559^{***} 0.419^{***} *n=131*		
Bite Density (mg/cm^3)	-0.343^{***} -0.245^{**} *n=108*	-0.190^{*} -0.385^{***} *n=166*	-0.286^{***} -0.262^{**} *n=162*	-0.427^{***} -0.303^{***} *n=131*	
Bite Mass (mg/kg BW)	0.621^{***} 0.647^{***} *n=112*	0.150^{*} 0.624^{***} n=170	0.235^{**} 0.542^{***} *n=172*	0.608^{***} 0.669^{***} *n=132*	0.204^{**} -0.185^{*} *n=166*

Statistical significance: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$