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

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4

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12

13 Short title: Ingestive behaviour of grazing ruminants meta-analysis

14

15 **Abstract**

16 This meta-analysis shed light on the quantitative adaptive responses of feeding
17 behaviour of Cattle (C) and Small Ruminants (SR), facing variations of sward
18 characteristics, notably of sward height (SH, 18.7 ± 13.9 cm) and herbage bulk density
19 (HBD, 1.73 ± 1.30 kg DM / m³). All responses expressed a plateau stressing an
20 adaptive limit with extreme values of SH and HBD. The minimum plateau of BR (46.9
21 ± 14.6 min⁻¹) is around 40 min⁻¹, while IR values (different for C and SR , respectively
22 69.1 ± 38.1 vs. 99.9 ± 45.7 g/min/kg BW) ranged between a minimum and maximum
23 plateau around 50 and 100 g/min/kg BW. Two other pasture management factors affect
24 IR, namely forage allowance (10.16 ± 6.0 , DM % BW) and daily proportion of time
25 spent grazing (0.30 ± 0.08). The results obtained confirm the specifically key role of

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

32

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

34

35 **Implications**

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

45

46 **Introduction**

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

51 for increasing the profitability of livestock (Llonch *et al.*, 2018; Shalloo *et al.*, 2018).
52 Moreover, a ruminant's robustness partly comes from its ability to adapt IB to the
53 diversity of resources to be grazed. In addition, chewing behaviour provides
54 information about digestive comfort and indicators of appetite, gut health and welfare.
55 Numerous studies have focused on the IB of grazing ruminants. However, beyond the
56 problems linked with the diversity of the methodologies applied, the items measured
57 are very heterogeneous across publications. Likely for this reason, no synthetic
58 statistical interpretation of published IB data for ruminant grazing has been carried out
59 and published so far. However, there is a need to better understand the various
60 aspects of animal IB, as it is now becoming possible to measure some of them in field
61 conditions thanks to advances in electronic/computer technologies (Anderson *et al.*,
62 2014; Fogarty *et al.*, 2018). Indeed, animal behaviour documented by tools employed
63 in precision livestock farming, such as sensors, video cameras, accelerometers or
64 pedometers, should greatly help in designing efficient management strategies for
65 livestock production systems (di Virgilio *et al.*, 2018). A recent meta-analysis focused
66 on bite mass (BM) and its main determining factors linked to major animal and sward
67 characteristics (Boval and Sauvant, 2019). In this current paper, we will analyse the
68 components affecting BM which are determining for intake rate and daily dry matter
69 intake. Some studies differentiate between jaw movements due to harvesting forage
70 and those processing the forage before swallowing. We have therefore attempted to
71 better understand the function of these different types of jaw movements.

72

73 **Material and methods**

74 *Literature review and dataset construction*

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

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

86

87 *Intermediary calculations*

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

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

104

105 *Treatment encoding*

106 Beyond specific codes assigned to each publication and to each experiment, additional
107 codes were applied to identify specifically the factors of variation tested in the papers:
108 the forage species, sward height, herbage bulk density or herbage allowance and the
109 animal species. All of these codes were specific to the factors of variation studied in
110 the publication; therefore, not all rows have values in the corresponding columns. For
111 some experiments, in addition to the intra-experimental factors, some key criteria
112 varied significantly, although they were not the factors tested intra-experiment. In this
113 case, another code was added to specify these criteria, as a secondary factor of
114 variation. For example, we identified experiments for which the intra-experiment sward
115 height varied largely despite not being announced as a factor in the publications, but
116 which can then be considered as a factor of variation for 62% of papers instead of the
117 32% we had identified at first approach.

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

121

122 *Statistical analysis*

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

129

130 **Results**

131 *Statistical parameters of the ingestive behaviour components*

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

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

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

145

146 *Modelling factors of variation of the ingestive behaviour components*

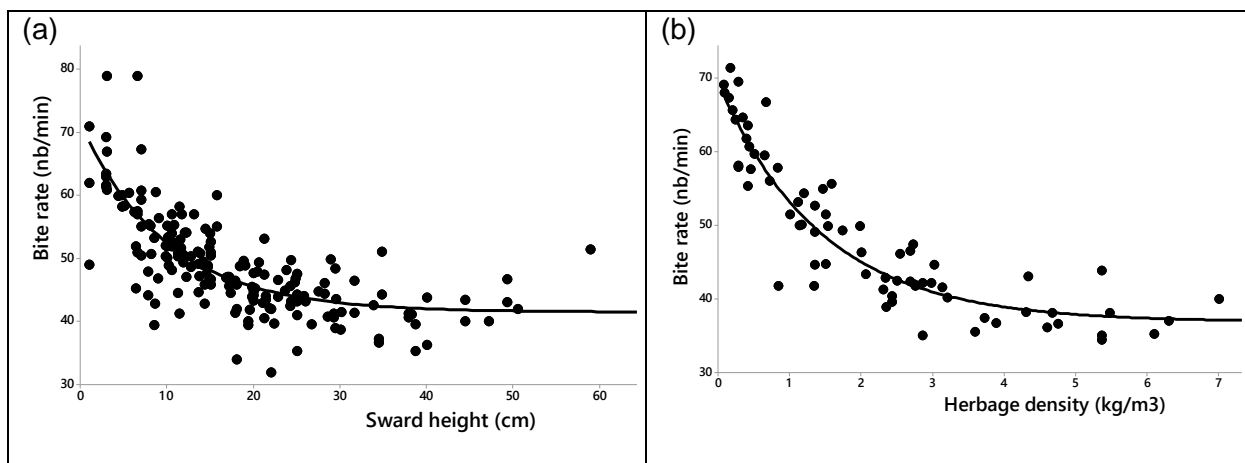
147 *Bite rate*

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

152

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

154



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

157

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

162

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

164

165 An acceleration of BR occurs when the HBD decreases below a threshold between
166 2 and 3 kg DM/m³. The regression in Equation 2 is a little more accurate than Equation
167 1 (RMSE = 3.9 vs 5.8).

168

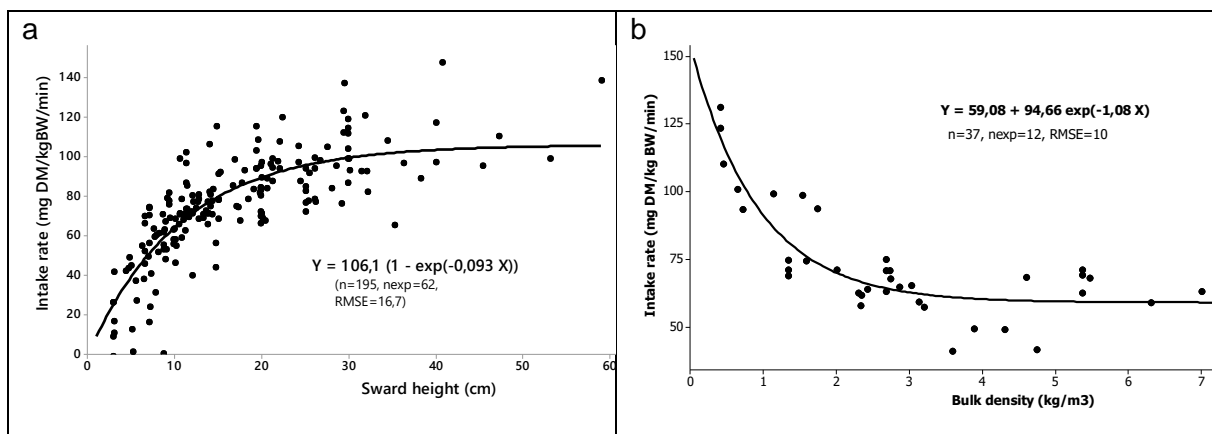
169 *Intake rate*

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

175

176
$$\text{IR} = 100.1 (1 - \exp(-0.093 \text{ SH})) \quad (n = 195; n_{\text{exp}} = 62; \text{RMSE} = 16.7) \quad [3]$$

177



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

180

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

184 (Figure S1). In these papers, the maximum values of IR ranged between about 115 and
185 160 mg DM/kg BW while the corresponding values of SH ranged between about 10
186 and 30 cm.

187

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

190

$$191 \quad \mathbf{IR = 59.08 + 94.66 \exp(-1.08 \text{ HBD})} \quad (n = 37; n_{\text{exp}} = 12; \text{RMSE} = 10) \quad [4]$$

192

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

199

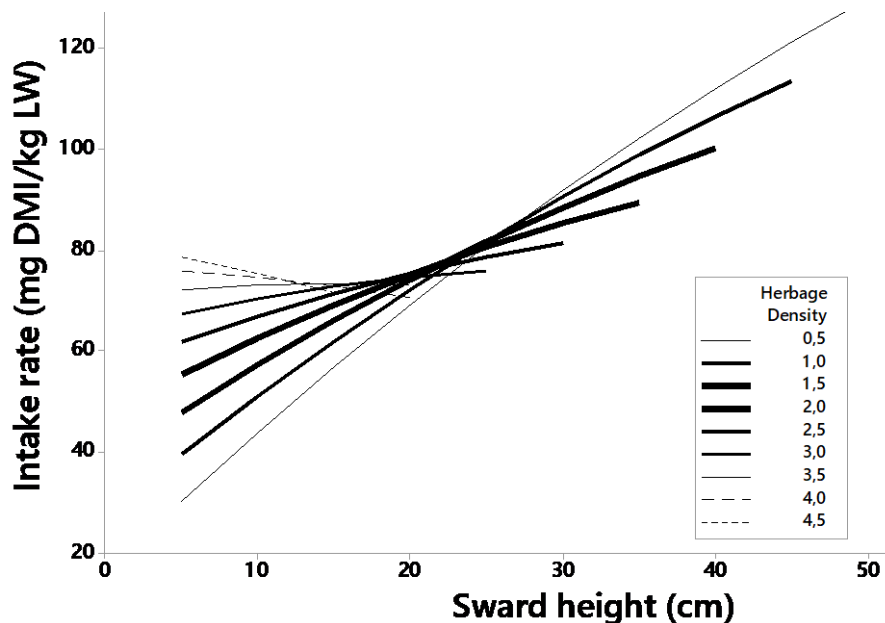
$$200 \quad \mathbf{IR = (3.74) + 3.336 \times SH - 0.01279 \times SH^2 + 25.4 \times HBD - 1.816 \times HBD^2 - 0.842 \times}$$
$$201 \quad \mathbf{SH \times HBD}$$

$$202 \quad (n = 227; n_{\text{pub}} = 30; \text{RMSE} = 21.1) \quad [5]$$

203

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

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



214
215 **Figure 3** Interactions between sward height (cm) and herbage bulk density (kg DM/m³)
216 on intake rate (mg DM/kg BW/min).

217
218 *Influence of stem and leaf mass.*

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

221
222
$$\text{IR} = 2.92 + 73.60 (1 - \exp(-2.44 \text{ SM})) \quad (n = 56; n_{\text{exp}} = 17; \text{RMSE} = 19.1) \quad [6]$$

223
224 The leaf mass (LM; 1.17 ± 0.74 t DM/ha) also affects IR according to the following
225 equation:

226

$$227 \quad \mathbf{IR = 111.46 (1 - \exp (-1.64 LM))} \quad (n = 73; n_{exp} = 19; RMS = 14.3) \quad [7]$$

228

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

237

238 *Impacts of grazing management factors.*

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

246

$$247 \quad \mathbf{IR = 41.55 + 153.8 \exp (-0.317 HA)} \quad (n = 73; n_{exp} = 25; RMSE = 7.1) \quad [8]$$

248

249 Another major factor of grazing management is the access time. In the database, only
250 10 experiments were focused on this aspect. The response of IR is negatively related
251 to the daily proportion of time spend grazing (pGT, 0.30 ± 0.08 , Figure 4b):

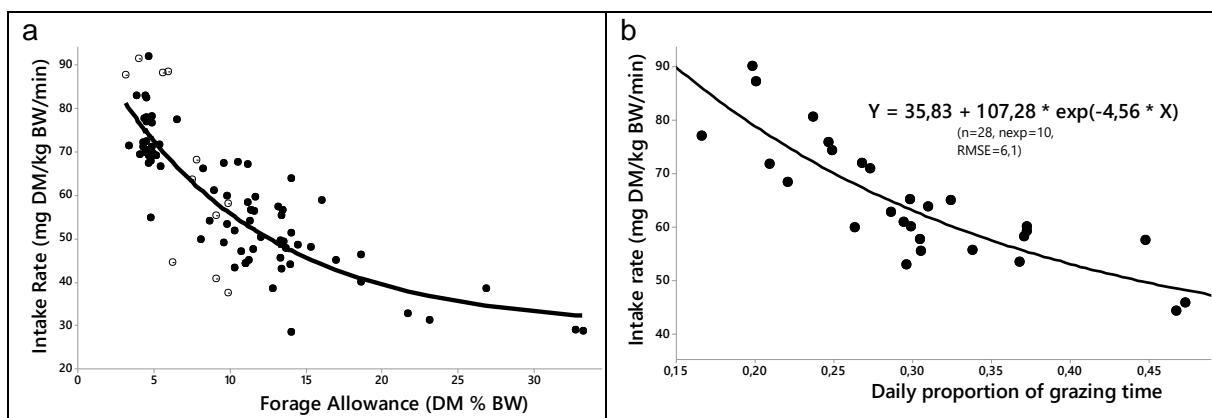
252

$$253 \quad \mathbf{IR = 35.83 + 107.28 \exp(-4.56 \text{ pGT})} \quad (n = 28; n_{\text{exp}} = 10; \text{RMSE} = 6.1) \quad [9]$$

254

255 For the same dataset, there was a trend of reducing the level of DMI/BW when pGT
256 decreased: -1.36 ± 0.81 g DMI/kg BW ($P = 0.11$) per 0.1 decrease of pGT. For a part
257 of this dataset (three experiments and nine treatments), the BM was measured and it
258 increased significantly when pGT decreased (-7.1 ± 1.3 g DM/kg BW per unit of pGT).

259 In contrast, BR was not influenced by pGT in this dataset.



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

262

263 *Grazing time*

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

266

$$267 \quad \mathbf{GT = 431.5 + 301 \exp(-0.083 \text{ SH})} \quad (n = 86; n_{\text{exp}} = 26; \text{RMSE} = 46) \quad [10]$$

268

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

271

272 *Interrelations across components*

273 *Global correlations*

274 Considering inter-experiment relationships (Table 2), the most inter-related
275 components are on one hand between BM and IR and the number of chews/bite
276 ($r = 0.75$) and on the other hand, to a lesser extent, between GT and DMI ($r = 0.328$).

277 Considering the intra-relationships (Table 2), there are two pairs of variables correlated
278 with each other, independently of BM, on the one hand inter and intra negative relations
279 between BR and chews/bite and on the other hand positive inter and intra relationships
280 between IR and DMI.

281

282 *Influence of animal species on the relationships*

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

285

$$286 \quad \mathbf{BR = 12.0 + 46.2 \exp(-0.198 \text{ BM})} \quad (n = 342; n_{\text{exp}} = 109; \text{RMSE} = 4.6) \quad [11a]$$

287

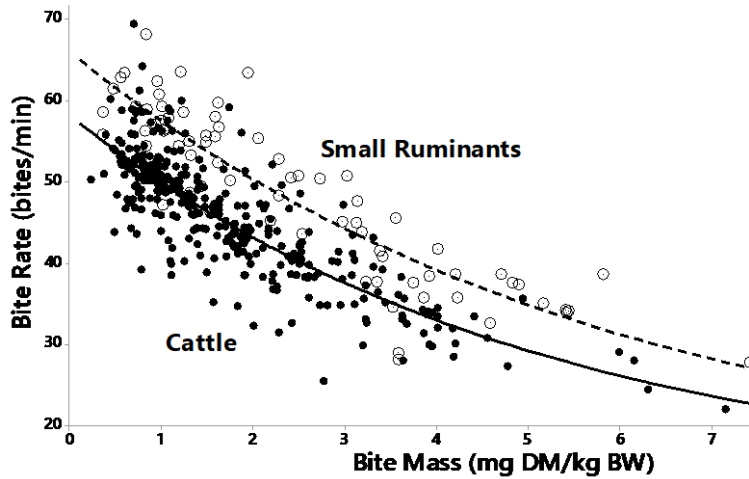
288 For small ruminants, it is:

289

$$290 \quad \mathbf{BR = 12.0 + 54.0 \exp(-0.172 \text{ BM})} \quad (n = 73; n_{\text{exp}} = 22; \text{RMSE} = 4.2) \quad [11b]$$

291

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



295
296 **Figure 5** Intra-experiment relationship between bite rate (bites/min) and bite mass
297 (mg/kg BW) for cattle (closed circles) and small ruminants (open circles).

298
299 The JM and chewing associated with the bites are both positively related to BM (Table
300 2). The relationship between JM/bite and BM is significantly different for small
301 ruminants and cattle (Figure 6a). The intra-species and intra-experiment regression
302 equation for cattle is:

303
304 **JM/bite = 1.29 + 0.121 BM** (n = 79; n_{exp} = 24; RMSE = 0.16) [12a]

305
306 For sheep and goats, the corresponding regression is less accurate, and the data
307 number is lower:

308
309 **JM/bite = 1.16 + 0.72 BM** (n = 42; n_{exp} = 11; RMSE = 0.44) [12b]

310

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

316

317
$$\text{JM/bite} = 1 + 1.94 \exp(-0.0283 \text{ BR}) \quad (n = 85; n_{\text{exp}} = 28; \text{RMSE} = 0.17) \quad [13a]$$

318

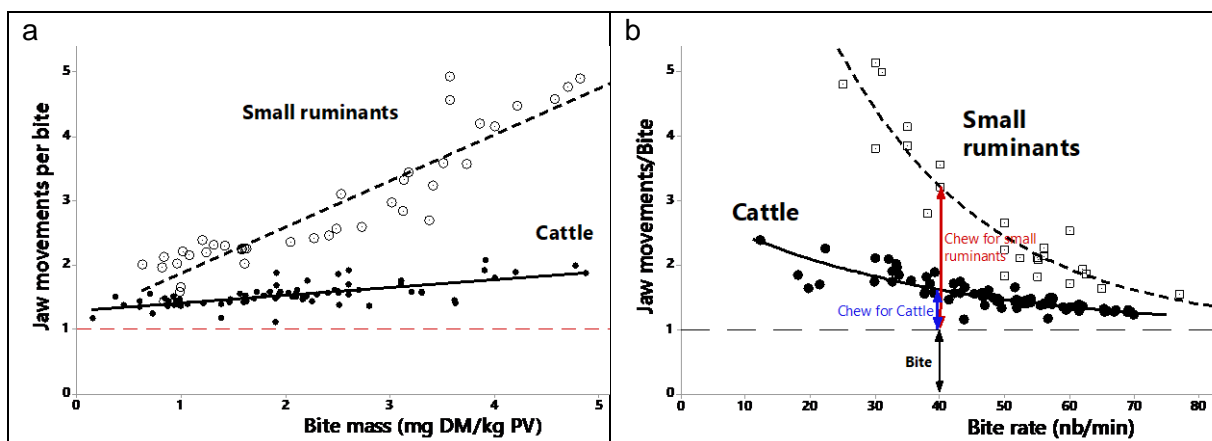
319 For sheep and goats, the corresponding regression is less accurate, and the data
320 number is lower:

321

322
$$\text{J/bite} = 1 + 12.38 \exp(-0.0428 \text{ BR}) \quad (n = 25; n_{\text{exp}} = 6; \text{RMSE} = 0.41) \quad [13b]$$

323

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



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

329

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

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

335

$$336 \quad \mathbf{JM/g\ DMI = 258/(1 + 555.4\ BM)} \quad (n = 79; n_{exp} = 23; RMSE = 1.7) \quad [14a]$$

337

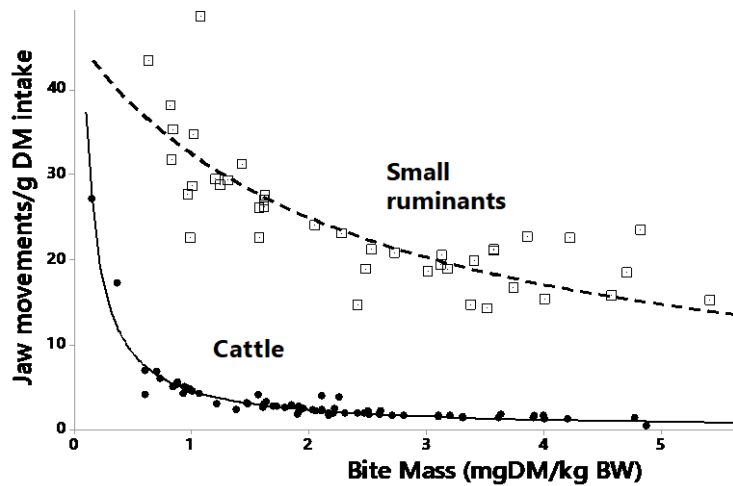
338 For small ruminants, the regression is less accurate:

339

$$340 \quad \mathbf{JM/g\ DMI = 45.8/(1 + 0.41\ BM)} \quad (n = 42; n_{exp} = 11; RMSE = 14.6) \quad [14b]$$

341

342 Figure 7 shows these two regressions; it appears clearly that for the same BM, the
343 number of JM is much higher for sheep, with an order of magnitude of about 10 ($31.1 \pm$
344 28.5 vs 3.3 ± 3.6 JM/g DMI). It must be stressed that for sheep, three high outlier values
345 of 94 to 165 JM/g DMI for a very low BM ($BM < 0.4$ mg/kg BW) from the same paper
346 (Black and Kenney, 1984) have been removed. Moreover, we were also able to verify
347 the decrease in JM with IR and significant differences that remain between small
348 ruminants and cattle.



349

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

352

353 As the JM/g DMI are linked to the process of particle comminution, the link between
354 BM and rumination time was investigated from a limited set of data for cattle with $0.5 <$
355 $BM < 2.5$ mg DM/kg BW. It appears that the two components are positively related,
356 according to the following intra-experiment regression:

357

$$358 \quad RT \text{ (min/day)} = 366 (1 - \exp(-2.92 \text{ BM} - 0.22))$$

$$359 \quad (n = 49; n_{exp} = 19; RMSE = 26.1) \quad [15]$$

360

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

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

369

$$370 \quad \mathbf{IR = 145.0 (1 - \exp(-0.440 BM))} \quad (n = 331; n_{exp} = 103; RMSE = 9.7) \quad [16a]$$

371

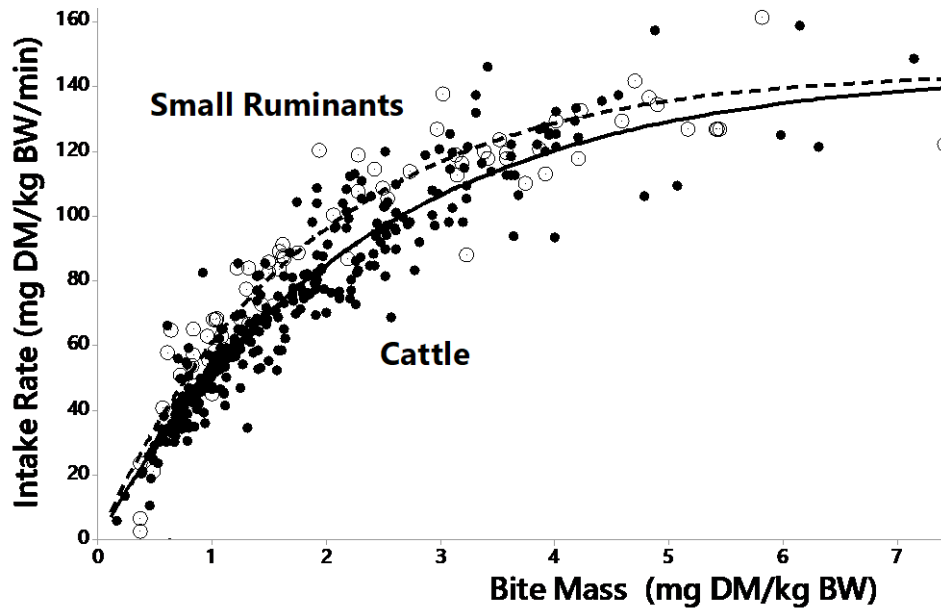
372 For small ruminants, it is:

373

$$374 \quad \mathbf{IR = 145.0 (1 - \exp(-0.543 BM))} \quad (n = 72; n_{exp} = 22; RMSE = 10.8) \quad [16b]$$

375

376 Figure 8 shows the two regressions; it appears that the differences are globally small
377 and are at the advantage of small ruminants for lighter bites, consistent with what was
378 observed for BR (Equations 11a and 11b and Figure 5). The asymptotic value of 145
379 g DM/kg BW/min is the same between both species. The maximum difference between
380 IR for the two species is observed for BM ~ 2.5 g/kg BW. It must be noted that in order
381 to have a common regression, considering all the data, the power of BW must be 0.85.
382 The curvilinearity of this relationship illustrates that BR, which is the ratio of IR to BM
383 in Figure 5, decreases with the rise of BM as already remarked. Thus, BR is
384 54 bites/min when BM is close to 0, to approximately 22–23 bites/min when BM is
385 equal to 6 mg/kg BW. This relationship is mainly the outcome of influences of both SH
386 and HBD on BM (Boval and Sauvant, 2019), and IR (Figure 2a and 2b).



387

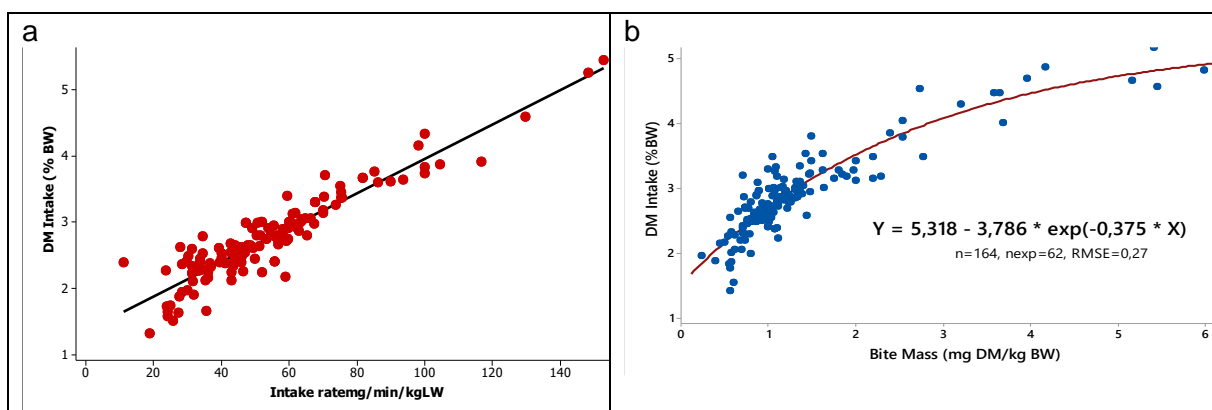
388 **Figure 8** Relationship between intake rate (mg/kg BW/min) and bite mass (mg/kg BW)
389 for cattle (closed circles) and small ruminants (open circles).

390

391 $\text{DMI (\%BW)} = 1.36 + 0.026 \text{ IR}$ (n = 139; nexp = 52; RMSE = 0.30) [17]

392

393 The relationship is still significant when only the 40 experiments focused on the impact
394 of SH are considered. But, in this case the slope is higher i.e. 0.037 (n = 37; nexp =
395 14; RMSE = 0.13).



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

398

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

401

$$402 \quad \text{DMI (\%BW)} = 5.318 - 3.786 \exp(-0.375 \text{ BM})$$

$$403 \quad (n = 164; n_{\text{exp}} = 62; \text{RMSE} = 0.27) \quad [18]$$

404

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

408

409 Discussion

410 *Features of the database*

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

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

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

426

427 *Impacts of canopy characteristics and of some management strategies*

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

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

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

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

461 By increasing the HBD, BR decreased until a plateau of around 40 bites/min beyond
462 2–3 kg DM/m³ (Figure 1b), similar to the minimum plateau observed with high SH
463 (Figure 1a) in another set of experiments. We noted a similar trend with IR, which also
464 decreased globally with HBD (Figure 2b) and plateaued at about 60 mg DM/kg
465 BW/min, at the same HBD threshold of 2–3 kg DM/m³. These trends are globally
466 opposite to what were previously observed for BM, which increases with both SH and
467 HBD (Boval and Sauvant, 2019). Unfortunately, concerning GT, the effect of HBD
468 could not be analysed as for SH, as most of the experiments that tested HBD variations
469 were carried out with micro-swards, for which the duration of grazing could not be
470 measured.

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

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

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

484 While our database was not mainly focused on the influence of management strategies
485 on global responses such as DMI, some publications allowed highlighting of some IB
486 responses. Thus, ruminants are able to increase their IR until values near to 100 mg
487 DMI/kg BW/min when facing an important decrease of forage allowance (Figure 4a) or
488 of grazing access time (Figure 4b). This adaptive behaviour mainly results from
489 differences in BM (Boval and Sauvant, 2019) which appears as a key factor of animal
490 robustness as it allows ruminants to maintain, or only slightly decrease, their level of
491 DMI despite a decrease of available resource and access time. As BM is at least partly
492 explained by individual factors (Sollenberger and Vanzant, 2011; Boval and Sauvant,
493 2019), it appears useful to investigate further animals' ability to adapt to restricted
494 resources and GT.

495

496 *From BM to intake rate and daily intake*

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

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

506 Beyond analysis of the effect of sward characteristics on IB components, the major
507 relationships between these components provided further understanding. Thus, there
508 is a strong negative correlation between BM and BR (Table 2); correlations between
509 BM and chews/bite are also positive, while based on much less data (Table 2), and the
510 correlation between BM and DMI is less marked, especially inter-experiment
511 correlation. And most structuring regressions concern the link between BM and BR
512 and the influence of BM on IR (Figure 8) which are useful for modelling purposes. All
513 these correlations are consistent with previous reports (Poppi, 2011; Chilibroste *et al.*,
514 2007 and 2015) and this meta-analysis, resulting from numerous data, provides robust
515 average values of the main correlations.

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

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

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

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

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

555

556 *Animal species specificity*

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

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

574 cattle (Ungar *et al.*, 2006) and sheep (Galli *et al.*, 2011) may use discrete JM to chew
575 and bite, but also simultaneously chew and bite on the same jaw opening-closing cycle.
576 However, in our database, we had no such values of chew-bites.
577 Consequently, all of these differences imply that small ruminants have a faster IR, with
578 a maximum equal to 1.2 times higher IR expressed per kg of BW, compared to cattle
579 (Figure 8). Otherwise, Boval and Sauvant (2019) have also pointed out that, for the
580 same SH, the bite depth/kg BW is higher for small ruminants, so it was necessary to
581 use BW at power 0.20 to match the data of BD for both species. The difference of bite
582 depth between the two species is extremely low compared to their respective BW,
583 revealing that sheep chewing and biting modalities would be more effective for going
584 deeper into the sward compared to cattle, as already suggested (Gordon *et al.*, 1996;
585 Woodward, 1998; Baumont *et al.*, 2006). Indeed, it may be observed how sheep
586 perform successive chews to go deeper into the canopy sward, by mobilizing their lips
587 in quick movements.
588 All these results are well consistent with the idea that bite and chew rates decrease
589 commonly with ruminant species having greater BW and BM (Wilson and Kerley, 2003;
590 Mulvenna *et al.*, 2018). Moreover, these results emphasize the different mechanisms
591 implemented by small ruminants or cattle to adapt to the characteristics of the
592 resource, with their anatomical specificities (Baumont *et al.*, 2006; Meier *et al.*, 2016).
593 In the case of small ruminants, the most mobile lips participate in forage prehension
594 and therefore consumption, with associated movements of the jaw that can be
595 recorded. Cattle have a particularly long freely mobile tip (Meier *et al.*, 2016) that they
596 use to greatly increase the diameter and surface of each bite to compensate for limited
597 resources as with short SH (Boval and Sauvant, 2019). Although the relationships
598 between the different behavioural variables are different for these two species, the fact

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

602

603 **Conclusions**

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

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

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

619

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

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

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

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

625

626 **Table 2** Correlations between ingestive behaviour components implied in the DMI,
 627 calculated inter- and intra-experiment (respectively the first and second value per
 628 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

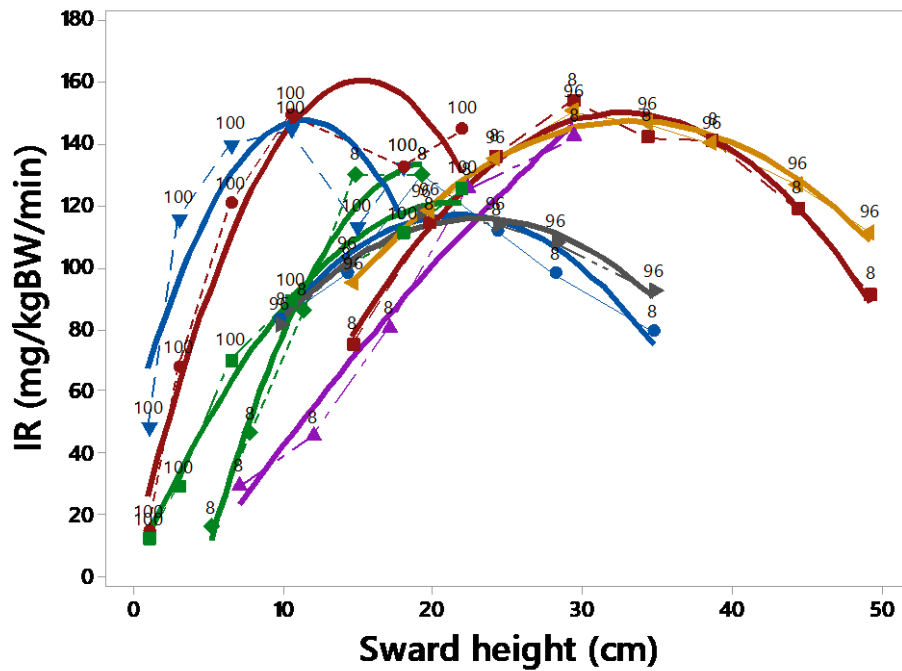
629 N = number of data; BM = bite mass; BR = bite rate; IR = intake rate; GT = grazing time.

630

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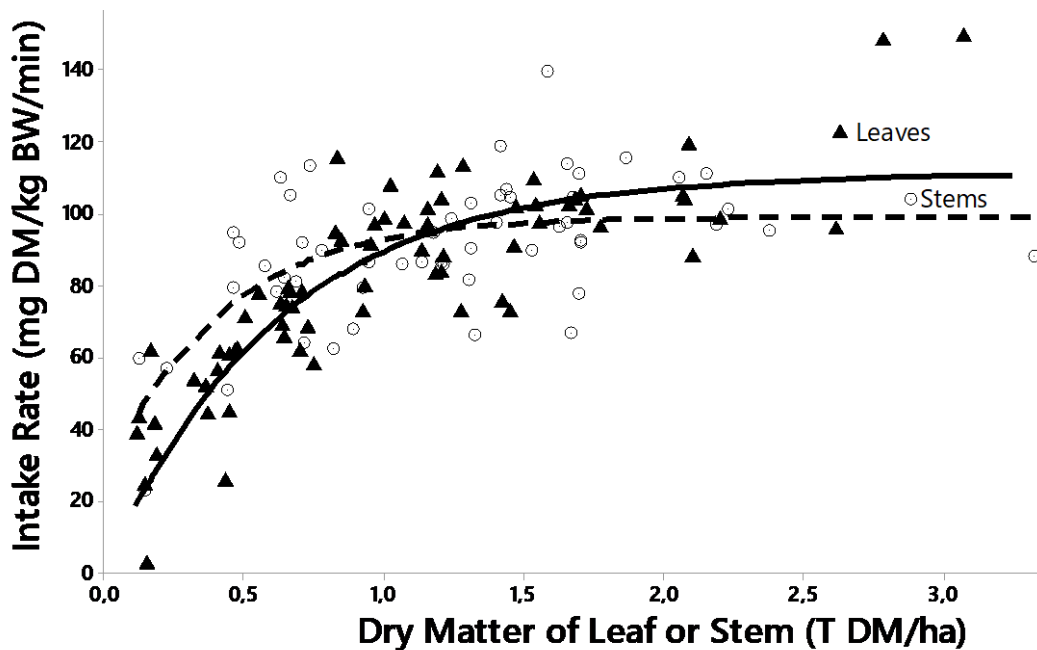
633 **Supplementary material**



634

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

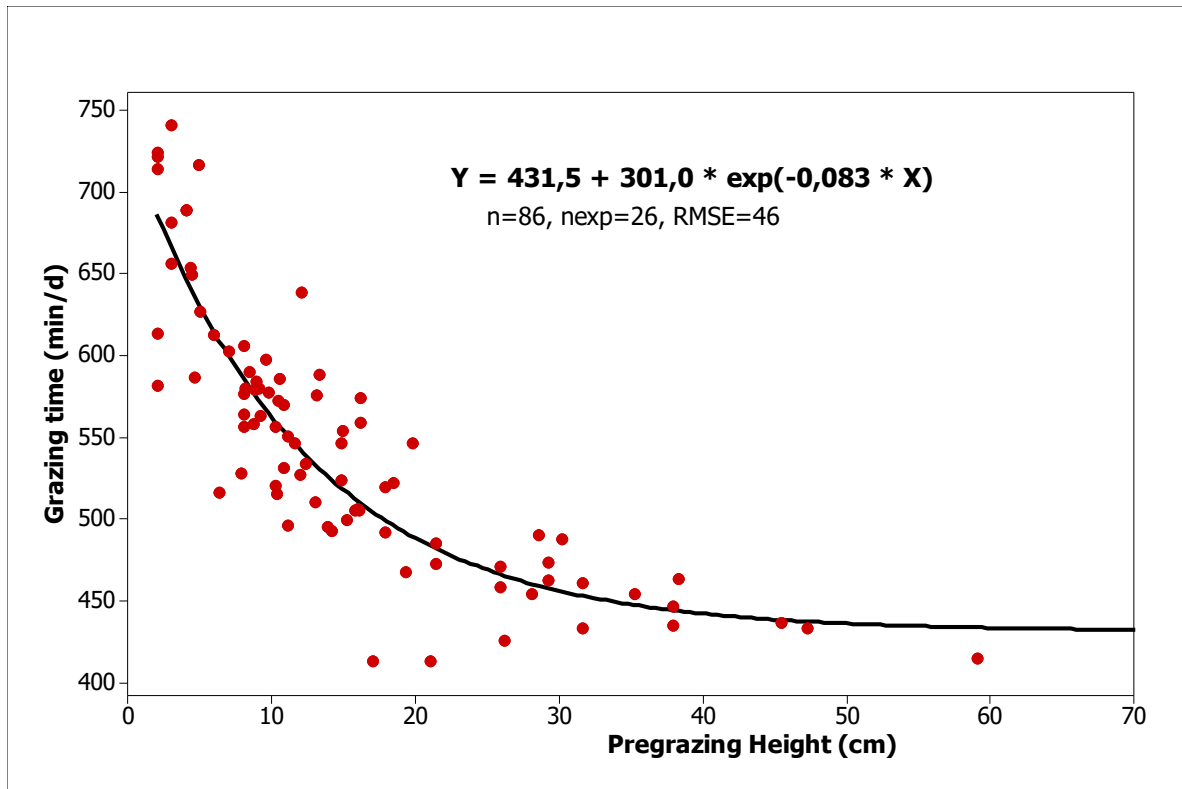
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638 **Figure S2: Respective influences of DM of leaf and stem, on intake rate.**

639

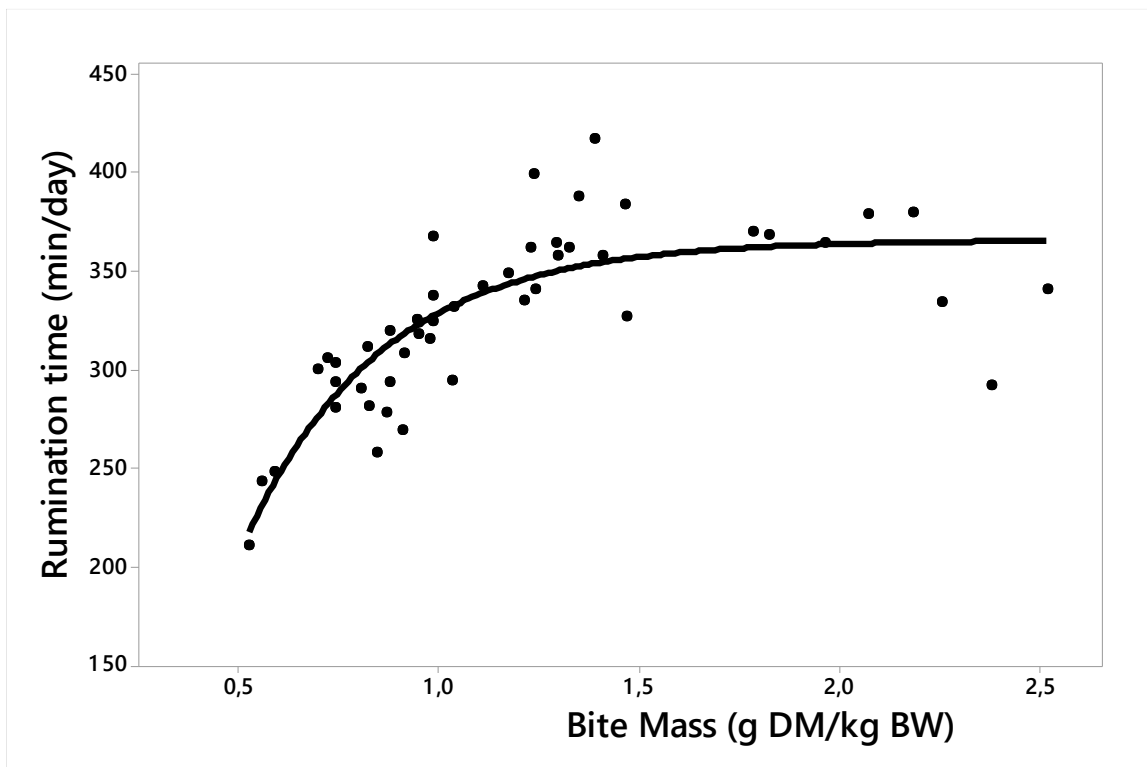


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642

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

643



644

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

646

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