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**ESTIMATIVA DA INGESTÃO DE FORRAGEM EM PASTEJO E  
FORRAGEAMENTO DE EQUINOS E BOVINOS EM SISTEMA DE HERBIVORIA  
MISTA**

**Porto Alegre (RS), Brasil**

**Abril, 2021**

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MISTA**

Tese apresentada como requisito para obtenção do Grau de Doutor em Zootecnia, na Faculdade de Agronomia, da Universidade Federal do Rio Grande do Sul.

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**Coorientador:** Olivier Jean François Bonnet

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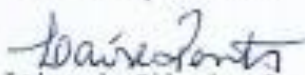
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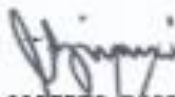
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# ESTIMATIVA DO CONSUMO DE FORRAGEM EM PASTEJO E FORRAGEAMENTO DE EQUINOS E BOVINOS EM SISTEMA DE HERBIVORIA MISTA<sup>1</sup>

Autor: Anderson Michel Soares Bolzan

Orientador: Paulo César de Faccio Carvalho

**Resumo:** O documento de tese está apresentado em três capítulos. No capítulo I, a revisão da literatura sobre métodos de medida do consumo de animais em pastejo e efeitos da herbivoria mista em sistemas pastoris. No capítulo II, apresentamos o estudo que objetivou verificar a concordância do método de monitoramento contínuo dos bocados (CBM) e a técnica de dupla pesagem para estimativa da ingestão de forragem por herbívoros em pastejo, sob a hipótese de que a metodologia CBM permite estimar a quantidade consumida em pastejo, por meio da descrição das ações alimentares realizadas durante o pastejo e a simulação da quantidade consumida das mesmas em diferentes condições de pasto. Os resultados asseguram a capacidade de estimar o consumo de animais em pastejo por meio da observação direta dos bocados. As correlações das estimativas pelos métodos de dupla pesagem e CBM foram na ordem de  $r = 0,86$  mesmo com exposição dos herbívoros a diferentes espécies e estruturas da vegetação, bem como diferentes avaliadores. Os limites de precisão entre o CBM e a dupla pesagem são coerentes, e creditamos ao CBM a vantagem de avaliação dos animais com menor intervenção, além de qualificar o processo de ingestão em tempo real. Amparados pela maior clareza dos limites da capacidade de descrever e quantificar a dieta elaborada pelos herbívoros (Cap. II), buscamos compreender a construção bocado a bocado de dois modelos animal (equinos e bovinos) em pastos geridos sobre três sistemas de herbivoria: mista, com equinos e bovinos em coexistência, monoespecífica com equinos e monoespecífica com bovinos. No capítulo 3, o estudo objetivou identificar as ações alimentares (códigos de bocados) de equinos e bovinos e verificar a composição da dieta, fluxos de ingestão e padrões de seleção de ambos os modelos simpátricos em um mesmo sistema pastoril ou em sistemas com herbivoria monoespecífica. Nossos resultados mostram a vantagem do sistema com herbivoria mista em relação ao sistema monoespecífico para ambas as espécies no que tange as oportunidades para forrageamento. O sistema misto permite potencialmente otimizar o forrageamento, pois oferece maior abundância de ações alimentares rentáveis disponíveis no recurso forrageiro (estrutura do pasto), permitindo a seleção potencial de bocados com maior taxa de ingestão instantânea, refletida na composição da dieta selecionada pelos animais. Este efeito é positivamente significativo para bovinos e indiferente para equinos, denotando facilitação proporcionada pelos equinos aos bovinos quando em coexistência.

**Palavras-chave:** Forrageamento, biodiversidade, ecossistemas pastoris, nicho alimentar, consumo em pastejo.

# ESTIMATE OF FORAGE INTAKE AND FORAGING BEHAVIOUR BY GRAZING EQUINE AND CATTLE UNDER MIXED HERBIVORY SYSTEM<sup>1</sup>

Author: Anderson Michel Soares Bolzan

Advisor: Paulo César de Faccio Carvalho

**Abstract:** This thesis is presented in three chapters. Chapter I brings a literature review on methods for measuring the consumption of grazing animals and the effects of mixed herbivory on pastoral systems. In chapter II, we present the study that aimed to verify the agreement of the continuous bite monitoring method (CBM) and the double weighing technique to estimate the forage intake by grazing herbivores, under the hypothesis that the CBM method allows estimating the amount consumed in grazing, through the description of the feeding actions performed during grazing and the simulation of the amount consumed in different grazing conditions. The results ensure the ability to estimate the consumption of grazing animals through direct observation of the bites. The correlations of the estimates obtained through the double weighing technique and the CBM were given by the coefficients  $r = 0.87$ ,  $0.86$ , and  $0.87$ , even with exposure of herbivores to different species and vegetation structures, as well as different evaluators. The precision limits between the CBM and the double weighing technique are consistent, and we credit the CBM with the advantage of being less invasive, besides qualifying the ingestion process in real-time. Supported by the greater clarity of the limits of the ability to describe and quantify the diet elaborated by herbivores, we seek to understand the construction bite by bite of two animal models (horses and cattle) in pastures managed under three herbivory systems: mixed, with horses and cattle in coexistence, monospecific with horses and monospecific with cattle. In chapter 3, we aimed to identify the feeding actions (bite codes) of horses and cattle and to verify the composition of the diet, intake flows and selection patterns of both sympatric models in the same pastoral system or systems with monospecific herbivory. Our results show the advantage of the mixed herbivory system compared to both monospecific systems in terms of foraging opportunities. The mixed system potentially allows optimizing foraging, as it offers a greater abundance of profitable feeding actions available in the forage resource (sward structure), allowing for the potential selection of bites with higher instantaneous intake rate, reflected in the composition of the diet selected by the animals. This effect is positively significant for cattle and indifferent for horses, denoting facilitation by horses towards cattle when in coexistence.

**Keywords:** Foraging, biodiversity, pastoral ecosystems, food niche, grazing consumption

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<sup>1</sup> Doctoral thesis in Animal Science, Faculty of Agronomy, Federal University of Rio Grande do Sul, Porto Alegre, RS, Brazil. (124 p.). April, 2021.



## SUMÁRIO

<b>1. CAPÍTULO I</b> .....	<b>188</b>
1.1 INTRODUÇÃO .....	199
1.2 REVISÃO BIBLIOGRÁFICA .....	23
1.2.1 <i>Quantificação e qualificação de dietas</i> .....	23
1.2.2 <i>Ecosistemas pastoris e herbivoria mista</i> <b>Erro! Indicador não definido.</b>	7
1.3 HIPÓTESES .....	30
1.4 OBJETIVOS .....	30
<b>2. CAPÍTULO II</b> .....	<b>31</b>
<b>What, how and how much do herbivores eat? The Continuous Bite Monitoring method for assessing forage intake of grazing animals.</b> .....	<b>32</b>
Abstract.....	33
Introduction.....	33
Material and Methods.....	35
<i>Site, treatments and experimental design</i> .....	35
<i>Sward measurements</i> .....	36
<i>Intake and grazing behaviour evaluations</i> .....	36
<i>Animals and experimental procedures</i> .....	36
<i>Continuous bite monitoring</i> .....	37
<i>Short-term intake rate</i> .....	38
<i>Statistical Analysis</i> .....	39
Results.....	39
Discussion.....	40
Implications.....	42
Acknowledgements.....	42
Competing Interests .....	43
Author Contributions.....	43
Data availability statement.....	43

References.....	43
Figures and Tables.....	49
<b>3. CAPÍTULO III .....</b>	<b>53</b>
<b>Foraging behaviour of bovines and equines under mixed herbivory.....</b>	<b>54</b>
Abstract.....	54
Introduction.....	54
Materials and Methods.....	56
Study area and experimental design.....	56
Vegetation resource.....	56
<i>Vegetation structure and the availability of bites</i> .....	56
<i>Herbage biomass and growth</i> .....	57
Animal measurements.....	57
Continuous bite monitoring.....	57
<i>Design of the bite-coding grid</i> .....	58
<i>Sampling of feed Items and evaluation of bite mass</i> .....	58
Nutritive value of each bite-code.....	59
Calculations of variables and statistical analysis.....	59
<i>Bite mass and nutritive value</i> .....	59
<i>Bite profitability</i> .....	59
<i>Potential intake available in each herbivory system management</i> .....	59
<i>Intake rate, diet composition and selection</i> .....	60
Results.....	61
Discussion.....	65
Conclusion.....	69
References.....	70
Figures and Tables.....	77
<b>4. CAPÍTULO IV .....</b>	<b>86</b>

4.1	CONSIDERAÇÕES FINAIS.....	87
	<b>REFERÊNCIAS.....</b>	<b><u>89</u></b> 89
	<b>APÊNDICES .....</b>	<b><u>89</u></b> 94
	<b>VITA.....</b>	<b><u>125</u></b>

## RELAÇÃO DE TABELAS

### **CAPÍTULO II What, how and how much do herbivores eat? The Continuous Bite Monitoring method for assessing forage intake of grazing animals.**

Table 1 Table for the potential sources of variation of the error in the estimation of fresh matter intake through CBM. *Day* refers to the number of days with observation since the beginning of the experiment, *Period* to the period of the day evaluated (morning or afternoon) and *Total bites* to the total number of bites observed during one trial. Interactions were not significant and were removed from the final model.

### **CAPÍTULO III Foraging behaviour of bovines and equines under mixed herbivory**

Table 1	Intake rate by sward height classes of bites	81
Table 2	Intake rate by botanical types by species in each herbivory system	82
Table 3	Diet composition by Sward height classes of bites	83
Table 4	Diet composition by Botanical types of bites	84
Table 5	General variables of the intake process	85

## RELAÇÃO DE FIGURAS

### CAPÍTULO I Revisão Bibliográfica -

- Figura 1 Grade de codificação de categorias de bocados com base na natureza e estrutura das porções da planta cortadas. O ícone em forma de “U” representa as mandíbulas do pequeno ruminante. As porções da planta são indicadas por pequenos ícones que simbolizam sua fisionomia: linhas (hastes de arbustos ou lâminas de folhas e hastes de gramíneas), formas ovais (folhas de árvores e arbustos), círculos abertos (flores) e círculos preenchidos (frutas). O comprimento das folhas, dispostas, mas não esticadas, é indicado em centímetros à esquerda dos ícones de dos códigos de bocados (BCs). Os códigos monossilábicos e bissilábicos ditados durante a observação são descritos à direita dos ícones. A coluna à esquerda dá o BCs para os caules dos arbustos e as folhas de gramíneas. A segunda coluna fornece os BCs para arbustos e plantas herbáceas dicotiledôneas ramificadas. Os grupos da terceira coluna BCs na folhagem das árvores. A última coluna é para-BCs em plantas trepadeiras. (Adaptado de Agreil & Meuret, 2004) ..... 26

### CAPÍTULO II What, how and how much do herbivores eat? The Continuous Bite Monitoring method for assessing forage intake of grazing animals.

- Figura 1 Representation of the types of sheep bites with their respective codes used in the Continuous Bite Monitoring method in Experiment 1 (A) with Italian ryegrass, 2 and 3 (B) with Tall fescue. Drawing, in Experiment 2 and 3 (B), represents the codes used in all tested heights, here demonstrated for the height of 20 cm. Note: The same codes were used for the other treatments. The arrows represent the depth of the bite in bite type. Description of bites is in Table 1 in Supporting Information..... 49
- Figura 2 Relationship between the total intake of fresh matter (g FM) of ewes during grazing sessions of 45 min estimated through continuous bite monitoring assessed by the double weight technique, in Experiment 1 (A), 2 (B) and 3 (C). Solid line represents the linear model between the two methods ( $P < 0.001$ ), dashed lines represents identity ( $Y = X$ ) and gray area represent the confidence interval of the measurement through double weight with regard to scale precision..... 50

Figura 3	Bland-Altman Plots showing the paired differences against the average between CBM and DWM methods in experiment 1 (Figure A, $P = 0.1052$ in One Sample T-Test), 2 (Figure B, $P = 0.0002$ in One Sample T-Test) and 3 (Figure C, $P = 0.0001$ in One Sample T-Test). Mean bias is represented by black line and limits of agreement are shown by the dashed lines, while confidence intervals are shown by the gray areas.....	51
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### **CAPÍTULO III Foraging behaviour of bovines and equines under mixed herbivory**

Figura 1	Characterization of bite codes according to botanical types.....	77
Figura 2	Relative frequency the sward height classes of bites available accounted in sward structure. Section lines represent of the average of the height classes. Periods: 1) May and June; 2) July and August; and 3) September and October.....	77
Figura 3	Botanical composition corresponding of bites available accounted in sward structure. Periods: 1) May and June; 2) July and August; and 3) September and October.....	78
Figura 4	Herbage biomass $\text{kg DM ha}^{-1}$ of the resource available was calculated with base by the linear models were generated between herbage biomass and the average sward height observed in the quadrat with the intercept adjusted to zero to each availed period [Period 1: $y = 115.86x + 0$ , $R^2 = 0.89$ $P < 0.001$ ; Period 2: $y = 121.58x + 0$ , $R^2 = 0.77$ , $P < 0.001$ ; Period 3: $y = 236.62x + 0$ , $R^2 = 0.93$ , $P < 0.001$ ]. Subsequently, the equations and height measurements in each system were predicted the herbage biomass available. Periods: 1) May and June; 2) July and August; and 3) September and October.....	78
Figura 5	Potential intake rate of (a) organic matter (OM) and (b) crude protein (CP) predicted by the profitability of the bite-codes available in the canopy (x axis) for each herbivory system and animal model (y axis) over the stocking season. The potential OM and CP intake rates ( $\text{g min}^{-1}$ ) were calculated considering the profitability of each bite type predicted based on the nutritional value obtained by hand plucking sampling for each bite-code recorded during the Continuous Bite Monitoring evaluation. Periods: 1) May and June; 2) July and August; and 3) September and October.....	79

- Figura 6 Diet selection of the sward height classes by Jacob's index; Varies from -1 (never used) to +1 (used exclusively), with negative and positive values indicating evasion and preference, respectively, and 0 indicating that a component of the sward is used in proportion to its availability. The different letters refer to statistical difference ( $P < 0.05$ ) by the Bonferroni multiple comparison test. .... 80
- Figura 7 Diet selection of the botanical types by Jacob's index; Varies from -1 (never used) to +1 (used exclusively), with negative and positive values indicating evasion and preference, respectively, and 0 indicating that a component of the sward is used in proportion to its availability. The different letters refer to statistical difference ( $P < 0.05$ ) by the Bonferroni multiple comparison test. .... 80



## LISTA DE ABREVIATURAS

a.s.l.	above sea level
ANOVA	analysis of variance
cm	centímetros/centimeters
CV	coefficient of variation
DM	dry matter
e.g.	<i>exempli gratia</i> (por exemplo; latim)
g	gramas/grams
ha	hectares
i.e.	<i>id est</i> (isto é; latim)
LW	live weight
m	metros/meters
mm	milimeters
N	nitrogen
SE	standard error
SEM	standard error of the mean
Mixte	herbivory mixed system
Monoequi	herbivory equine system
Monobov	herbivory bovine system
Mixteequi	equines in herbivore mixed system
Mixtebov	equines in herbivore mixed system

## CAPÍTULO I

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<sup>1</sup> Doctoral thesis in Animal Science, Faculty of Agronomy, Federal University of Rio Grande do Sul, Porto Alegre, RS, Brazil. (124 p.). April, 2021.

## 1.1 INTRODUÇÃO

O desafio em compreender as interações entre o homem e o ecossistema vai além da memória criada pelas sociedades ao longo do tempo. Em uma visão mais apurada, percorremos a reflexão de que além das superfícies exploradas, conhecidas e utilizadas, o que efetivamente nos interessa nas relações ecológicas é a capacidade de interagirmos com o meio em uma visão duradoura (Gordon, 2009, Carvalho et al., 2021), a fim de garantir e/ou prover a repetibilidade dos ciclos biológicos para gerações vindouras (Gordon et al., 2021).

Nos ecossistemas campestres, selvagens ou cultivados, que perfazem 40% da superfície terrestre (Suttie, 2005), as relações de fluxos de ingestão e seleção de componentes morfológicos vegetais em pastos monoespecíficos ou diversificados coordenam a dinâmica populacional dos animais selvagens (Bukombe et al. 2017) e o desempenho animal no caso dos sistemas de produção agrícolas (FAO 2005). A domesticação dos animais pode ser considerada como uma atividade primordial (Mottet et al., 2018) no entendimento da exploração do recurso e sua abundância, e seus efeitos foram (Enri et al., 2017), e ainda são, os pilares do trabalho do homem para desfrute dos diferentes serviços de provisão (Prins & Fritz, 2008; Dumont et al., 2018).

Além disso, a compreensão das relações dos herbívoros com o ecossistema é objeto de interesse também para cientistas e técnicos para a melhor coordenação das ações de gerência nos ambientes pastoris (Sollenberger & Wallau, 2020; Dumont et al., 2020a). Assim, direcionar rebanhos em pastos naturais por trajetos profícuos ao forrageamento (Meuret & Provenza, 2015) ou dimensionar tempo de permanência, carga animal em  $\text{kg ha}^{-1}$ , e disponibilidade de recurso (i.e., pasto) (Mott & Lucas 1952), intensidade moderada do pastejo (Kunrath et al., 2020; Zubieta et al., 2020), tem sido ao curso da história a base dos pensamentos para provisão de serviços advindos da herbivoria de animais domésticos. Atualmente, a visão intimista da relação planta-animal subsidia conceitos e práticas para gestão dos recursos pastoris no intuito de propiciar condições instantâneas favoráveis à ingestão de forragem (Carvalho et al., 2013; Nunes et al., 2019; Savian et al., 2021), que refletem em desempenho animal, produtividade e rendimento em diversas atividades (e.g. produção de carne, leite, lã e

outros) e em sistemas agrícolas sustentáveis (Dumont et al., 2020b; Szymczak et al., 2020a; Jaurena et al., 2021).

Neste sentido, conhecer as relações causa-efeito na interface planta animal e o processo de ingestão (i.e., pastejo) e seus efeitos é o que pode ser entendido como o principal avanço no cenário descrito anteriormente (Carvalho et al., 2013; Savian et al., 2020; Schons et al., 2021). Entretanto, perceber e medir estas relações é uma tarefa desafiadora, uma vez que envolve processos como consumo de forragem e seleção de dietas em pastejo, fluxos de crescimento vegetal, entre outros. A ingestão de forragem pelos animais é um exemplo destes desafios. Métodos diretos [e.g. fistula esofágica (Stobbs, 1973; Geremia et al., 2018)] e indiretos foram propostos para estes fins, alguns relacionados às funções metabólicas [e.g. marcadores particularmente n-alcanos (Dove & Mayes, 2006)], sensores de movimento inercial (Andriamasinoro et al., 2017) e outros de maneira quantitativa [e.g. dupla pesagem (Penning & Hooper, 1985)].

Os métodos acima referidos fornecem um resultado satisfatório para a medida de consumo, entretanto, exigem níveis de intervenção e manipulação animal e/ou estruturas de manejo e suporte próprias, que limitam o emprego das técnicas em muitas situações, seja sobre a medida do animal na espontaneidade do processo de pastejo, ou pela impossibilidade no uso de equipamentos e estruturas de suporte (bretes de contenção ou equipos eletrônicos) no tempo e no espaço. A observação direta das ações alimentares dos animais (Agreil & Meuret et al., 2004; Bonnet et al., 2015), em contrapartida, oportuniza a um indivíduo observador descrever de maneira espontânea os eventos do forrageamento em ambientes pastoris.

A técnica de monitoramento contínuo de bocados, proposta por Agreil & Meuret (2004), qualifica e quantifica o forrageamento dos herbívoros vertebrados e permite verificar o processo de ingestão em diversas condições (e.g. pastos cultivados e nativos, monoespecíficos ou diversos). Essa metodologia propõe construir grades de bocados adequadas aos objetivos e do nível das escalas espaço-temporais desejadas nos estudos. Esta observação instantânea da dinâmica de pastejo desnuda a medida até então pouco detalhada e descrita na composição do consumo, e permite construir o processo do forrageamento detalhadamente em tempo real. A partir desse entendimento, melhores manejos podem ser propostos, visando otimizar a interação herbívoros e ambientes pastoris (Schons et al., 2021). Do ponto de vista da gestão

dos ambientes pastoris, muitas propostas visam configurar as atividades produtivas, valor paisagístico e funções ecossistêmicas metabólicas (Bonaudo et al., 2014; Ryschawy et al., 2017; Mengyuan Lia et al., 2021).

Com a multifuncionalidade dos ecossistemas pastoris em seus arranjos de biodiversidade (Bengtsson et al., 2019), muitas formas de otimizar o uso dos recursos em uma visão durável têm sido pensadas e exploradas (Dumont, Groot & Tichit 2018). A promoção da herbivoria mista é uma proposição de um saber fazer sustentável (Dumont et al., 2020), para atividades sustentáveis provedoras de serviços e autonomia (Bonaudo et al., 2014). Na configuração desses arranjos, considera-se as particularidades morfofisiológicas dos animais (Janis, 1976; Demment & Van Soest, 1985; Hofmann, 1989) em termos de diferenciação de tamanho (Brown, 1988; Fleurance et al., 2009), morfofisiologia e capacidade digestiva dos herbívoros (Duncan et al., 1990), o que reflete na competição ou compartilhamento de nichos alimentares e na seleção de dietas (Menard et al., 2002) e fluxos de ingestão e digestão (Ferreira et al., 2007). São esses fatores que, principalmente em ambientes selvagens, definem os fluxos populacionais na dinâmica entre herbívoros, a disponibilidade de recursos e o tempo de uso/permanência (Bell, 1971; Bukombe et al., 2019). No caso de ecossistemas pastoris para produção animal (i.e., animais domésticos), que visam otimizar o uso dos recursos e potencializar o desempenho animal (Martin et al., 2020), tais fatores são dependentes das limitações antrópicas impostas pela gerência.

A relação dos nichos interespecie afeta a apresentação e a disponibilidade do recurso forrageiro, interferindo nas possibilidades de seleção alimentar e elaboração da dieta destes mesmos herbívoros (Ménard et al., 2002) e evidenciando a razão causa-efeito do processo de pastejo, com efeito no consumo e desempenho animal (Illius & Gordon, 1987). Neste contexto, herbívoros de tamanho semelhante, mas com aparato digestivo com limitações e potencialidades diferentes (Janis, 1976) podem gerar expressões de forrageamento também particulares, como os equinos com aparato intestinal de digestão da fibra (Edouard et al., 2008), portanto, pouco sensíveis à limitação física (tamanho da partícula) para digestão da mesma em comparação aos bovinos, limitados pela taxa de passagem ruminal (Duncan et al., 1990). Além disso, o aparato bucal com diferenças pronunciadas entre os dois modelos animais possibilita ações distintas no forrageamento. Enquanto os bovinos ampliam a capacidade ingestiva em bocados com o auxílio da língua (Illius & Gordon, 1987), os

equinos pelos incisivos superiores e inferiores podem otimizar a ingestão em estratos inferiores do pasto (Fleurance et al., 2010).

Embora existam vantagens dos sistemas mistos em relação aos específicos, em funções de provisão (Ormunen-Cristian et al., 2012; Fraser et al., 2014) e imunidade?, como a diluição parasitária interespecie (Forteau et al., 2020), alguns aspectos sobre os fatores que provocam tais vantagens ainda não são claros. Relações ecológicas como competição, complementariedade em que a ação de um não prejudica a ação do outro e beneficia o meio, facilitação em que a ação de um promove a ação do outro e sinergia em que ambas ações são potencializadas por coexistirem (Hooper, 1998; Arsenault & Owen-Smith 2008; McNaughton, 1976; Sinclair & Norton-Griffiths, 1982) estão presentes como argumentos para avaliar estes sistemas. No caso de herbívoros pastejadores, a ingestibilidade é o fator provedor para o êxito do forrageamento, condições para ingestão em menor tempo.

Uma possibilidade para exploração multiespecie, frequente em condições ecológico-sociais (Jouven, Via & Fleurance, 2015), é a coexistência de equinos e bovinos. Considerando estes fatores, centrados nas diferentes potencialidades ingestivas dos modelos equinos e bovinos e com a possibilidade da descrição da seleção alimentar, da dieta e da exploração do recurso pelos animais, buscamos compreender as relações entre os nichos alimentares dos diferentes modelos de herbívoros em coexistência.

## 1.2 REVISÃO BIBLIOGRÁFICA

### 1.2.1 *Quantificação e qualificação da dieta de herbívoros em pastejo*

Conhecer a dieta de herbívoros em ambientes pastoris é uma tarefa desafiadora, em ambos os aspectos, qualitativo e quantitativo. Entretanto, este entendimento permite compreender e interagir com alguns elementos do ecossistema pastoril a fim de favorecer o forrageamento dos animais, visando a eficiência de utilização dos recursos, e a sustentabilidade do ecossistema pastoril. O consumo de forragem pelos animais é o fator determinante para a produção animal, com efeito direto no desempenho individual (Illius & Gordon, 1987). Em herbívoros selvagens, a medida do consumo no forrageamento é importante na verificação dos efeitos presentes na interface planta–animal (e.g. altura do pasto, diversidade florística) que afetam a interação presa-predador (e.g. Belovsky, 1997; Farnsworth & Illius, 1996), o balanço da ingestão de energia, disponibilidade de recurso e deslocamento (Charnov, 1976), as respostas funcionais (e.g. Durant et al., 2003; Smallegange & Brunsting, 2002), o comportamento ingestivo (e.g. Shipley, 2007; Pretorius et al., 2016) e a seleção alimentar (Hodgson, 1979). Assim, como estudos de dinâmica de ocupação e migração (e.g. Briske et al., 2017; Bukombe et al., 2019) em estudos de modelos ecológicos em ambientes naturais, ocupação concomitante ou sucessiva de uma ou mais espécies.

A estimativa do consumo de herbívoros em pastejo continua sendo um dos maiores desafios metodológicos em estudos de ciência animal (May & Dove, 2000; Garnick et al., 2018). Em uma escala diária, o uso de marcadores de plantas, particularmente n-alcanos (Dove & Mayes, 2006) é um método objetivo, embora invasivo, para estimar o consumo individual, digestibilidade aparente e composição da dieta em condições de pastejo (Gordon, 1995; Mayes & Dove, 2000; Barcia et al., 2007). No entanto, requer manipulação intensiva dos animais e mão de obra para dosagem, coleta de amostras fecais, processamento e extração laboratorial (Garcia Gonzalez et al., 2017). Outros fatores, como custo e precisão, dependendo das condições experimentais, tornam sua aplicação menos prática.

Metodologias que fazem uso de sensores, como a medição acústica dos movimentos mandibulares durante a execução dos bocados, foram testadas com

ovelhas (Galli et al., 2011) e vacas (Galli et al., 2017). Em uma visão mais refinada sobre o processo de pastejo, para melhor compreender o efeito das diferentes estruturas do pasto no pastejo, dispositivos como “*Walk-over Weighing*” (Gonzalez Garcia et al., 2017) e no “*RumiWatch System*” (Ruuska et al., 2016; Rombach et al., 2018) foram desenvolvidos para estudos do monitoramento sensorial dos movimentos inerciais do processo de pastejo. Este último também possui um acelerômetro triaxial (Rayas-Amor et al., 2017) que pode identificar os movimentos da cabeça e classificar em mordidas de apreensão, mastigação e outros. Também, com base no movimento inercial, Andriamasinoro et al. (2017) desenvolveram um algoritmo de código aberto para smartphone que avalia o comportamento de pastejo e ruminação de vacas em pastejo, atualmente em desenvolvimento e calibração em condições de pastejo para qualificação das ações (Rosseto et al., 2021). No entanto, os sensores citados acima fornecem informações gerais sobre o processo de pastejo, o que implica em menos detalhes da dinâmica das ações dos animais frente a estrutura do pasto, altura biomassa, diversidade florística e fenológica.

Como a estrutura e a composição da vegetação afetam a taxa de ingestão de forragem, os processos que regulam a formação de um bocado (Allden & Whitakker, 1970; Laca et al., 1992; Mezzalana et al., 2017; Nadin et al., 2019) e, como resultado, a taxa de ingestão, têm repercussões na ecologia animal e vegetal (Shipley, 2007). A interação planta-animal denota um resultado anabólico com reflexo na performance no caso de animais de produção, e *fitness* no caso de animais selvagens, que é a capacidade de perpetuar o material genético (i.e., reprodução). Além disso, essa dinâmica impacta na produtividade primária do sistema, nível de heterogeneidade e biodiversidade do recurso. Herbívoros tomam decisões sobre onde olhar e que tipo de combinações fazer quando sujeitos à diversidade botânica e estrutural, através de decisões de pastejo por animais em diferentes escalas espaço-temporais (Provenza et al., 2015), o que torna o detalhamento dos componentes da dieta um fator importante para muitos estudos (Azambuja et al., 2020).

Em escalas de curto prazo, a ingestão fornece uma medida direta da interação do animal com as características da vegetação. Esta medição representa uma ferramenta para compreender as restrições de forrageamento e os mecanismos que ligam as propriedades da vegetação às escolhas alimentares e ao uso do habitat (Stephens & Krebs 1986; Spalinger & Hobbs, 1992; Shipley et al., 1994). Para



determinar o consumo em curta escala (períodos de cerca de 1 hora, i.e., uma refeição) (Bailey et al., 1996), a técnica de dupla pesagem (Penning e Hooper, 1985) é um dos procedimentos mais tradicionais e utilizados (Giovanetti et al., 2017), que estima a quantidade de ingestão através da diferença de peso do animal pré- e pós-pastejo. Essa técnica também requer que os observadores monitorem o tempo efetivo de pastejo e a taxa de bocados (o que permite calcular a massa média de bocados). Embora não seja invasivo em si, os animais treinados precisam ser equipados com aparato de coleta de excretas, o que limita o período experimental a não mais do que algumas horas.

A fistulação esofágica (Stobbs, 1973; Geremia et al., 2018) pode ser usada em diferentes condições de estrutura do pasto para determinar a ingestão e a seleção da dieta. No entanto, esta técnica é extremamente invasiva (requer procedimentos cirúrgicos). Em geral, esses métodos podem capturar apenas a massa média dos bocados, a taxa de bocados e a taxa de ingestão ao longo de sequências inteiras de pastejo ou dias, e não interferem sobre variações dessas respostas em função de diferenças locais na estrutura e composição do pasto (Bonnet et al., 2015).

A simulação de pastejo manual (i.e., *hand plucking*) tem sido usada há muito tempo para simular a ingestão e a seleção de dietas por animais em pastejo (Halls, 1954; Cook, 1964). É simples, causa perturbação mínima ao animal e pode produzir grandes conjuntos de dados a um custo mínimo. É comumente usada para estimar a massa de bocados em estudos de campo com herbívoros selvagens (Collins & Urness, 1983; Renecker & Hudson, 1985; Hudson & Frank, 1987; Okello et al., 2002) e herbívoros domésticos (Hobbs et al., 1983; Agreil & Meuret, 2004; Agreil et al., 2006).

Usando princípios semelhantes, o método de monitoramento contínuo dos bocados (*Continuous Bite Monitoring*, CBM) proposto por Agreil & Meuret (2004) representa uma ferramenta útil para uma descrição completa das atividades de forrageamento e do ambiente pastoril em nível de bocado. Com base em uma pré-avaliação da vegetação disponível e observação do processo de seleção de dieta e pastejo, bocados potenciais são classificados em categorias de códigos para compor uma grade de referência de atividades de forrageamento (ou seja, códigos de bocado, pastejo, ruminação, ócio etc.).

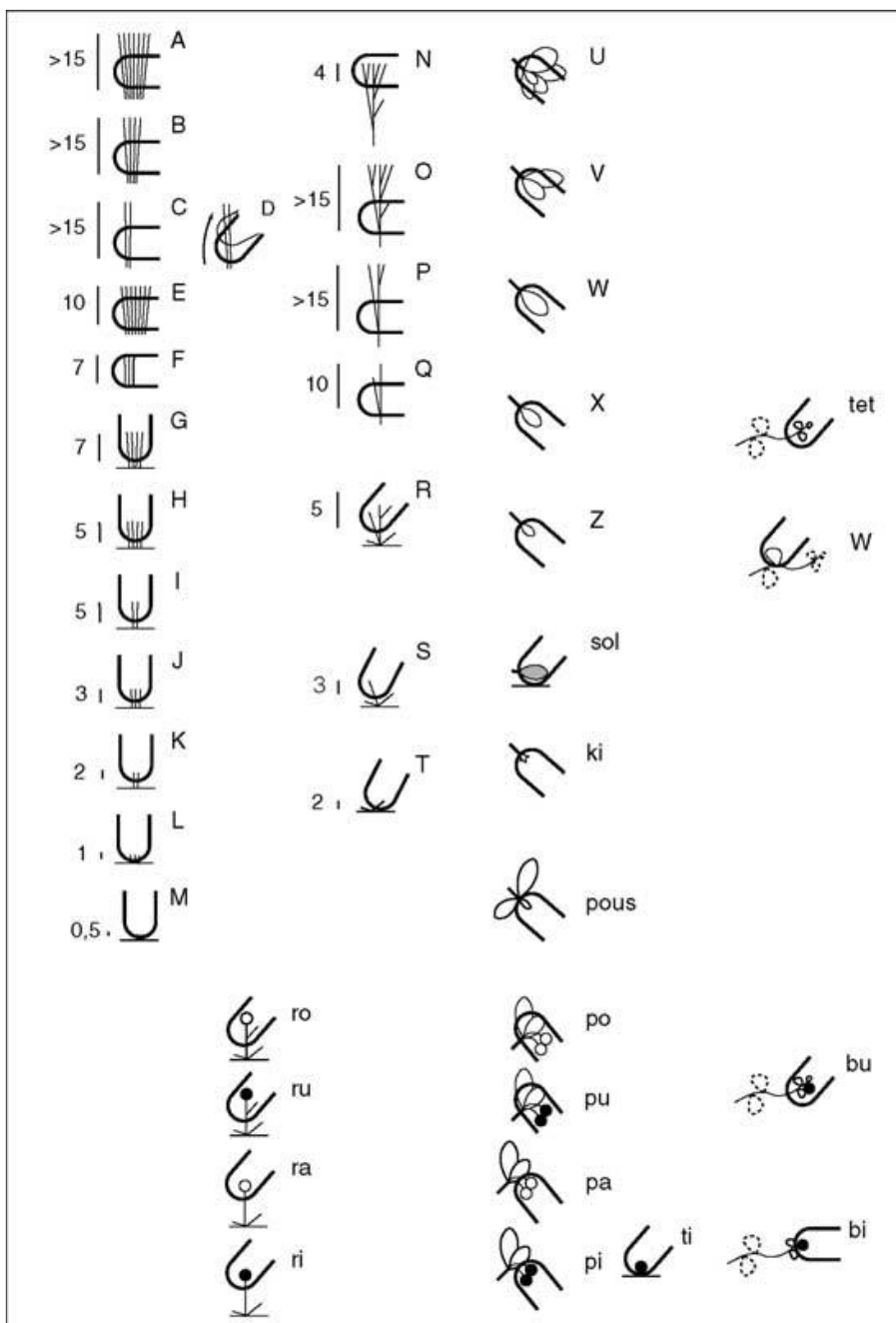


Figura 1. Grade de codificação de categorias de bocados com base na natureza e estrutura das porções da planta cortadas. O ícone em forma de “U” representa as mandíbulas do pequeno ruminante. As porções da planta são indicadas por pequenos ícones que simbolizam sua fisionomia: linhas (hastes de arbustos ou lâminas de folhas e hastes de gramíneas), formas ovais (folhas de árvores e arbustos), círculos abertos (flores) e círculos preenchidos (frutas). O comprimento das folhas, dispostas, mas não esticadas, é indicado em centímetros à esquerda dos ícones de dos códigos de bocados (BCs). Os códigos monossilábicos e bissilábicos ditados durante a observação são descritos à direita dos ícones. A coluna à esquerda dá os BCs para os caules dos arbustos e as folhas de gramíneas. A segunda coluna fornece os BCs para arbustos e plantas herbáceas dicotiledôneas ramificadas. Os grupos da terceira coluna BCs na folhagem das árvores. A última coluna é para BCs em plantas trepadeiras. (Adaptado de Agreil & Meuret, 2004)

Com isso em mãos, os observadores monitoram os animais-alvo por um determinado tempo em que todas as atividades são registradas. Os códigos de bocado observados são então simulados pelos observadores para estimar a massa e o valor nutritivo de cada bocado efetuado, para posterior cálculo da ingestão. Este método depende da eficiência do observador na interpretação da grade de codificação durante a observação visual e na capacidade de identificar o tipo de vegetação colhida pelos animais durante o processo de pastejo.

As vantagens do método CBM em relação a outros métodos residem no registro, em tempo real, de uma descrição detalhada de todos os bocados efetuados pelo animal, da estimativa do valor nutricional do tecido vegetal correspondente a cada código de bocado de cada espécie vegetal, e da dinâmica do comportamento por estação alimentar animal (Bonnet et al., 2015, Torres-Fajardo et al., 2019; Bolzan et al., 2020; Azambuja et al., 2020). Assim, este método permite um grande nível de detalhamento na descrição do processo de forrageamento. Por outro lado, sabe-se que o método CBM exige o treinamento progressivo do observador e pode possuir algum grau de viés dependendo da experiência e dedicação.

### *1.2.2 Ecossistemas pastoris e herbivoria mista*

Os ecossistemas pastoris têm grande importância, pela abrangência e pela multifuncionalidade de serviços ecossistêmicos prestados (Suttie, 2005), sendo parte deles os serviços de provisão relacionados com a produção animal. São sistemas que contemplam uma grande amplitude de arranjos de biodiversidade (Bengtsson et al., 2019), organizados em níveis tróficos horizontal (no mesmo nível trófico) e vertical (entre níveis tróficos) (Duffy et al., 2007). Isso implica em complexas relações entre a interface solo-planta-animal-ambiente, no tempo e no espaço, com efeitos na diversidade vegetal (Senft et al., 1987), distribuição espacial dos herbívoros e nichos alimentares (Bell, 1971; Shipley and Spalinger, 1995).

Na multifuncionalidade dos ecossistemas pastoris, o incremento de diversidade dentro do mesmo nível trófico (e.g. sistemas com herbivoria mista) promove em curto prazo a eficiência de utilização dos recursos (Prins and Fritz, 2008; Ormunen-Cristian et al., 2012; Fraser et al., 2014) e, posteriormente, a estabilidade da comunidade vegetal (Henning et al., 2017; Schmitz & Isselstein, 2020), melhoria da resiliência

benéfica frente a variações climáticas (Modernel et al., 2019) gerando maior autonomia dos sistemas (Thenard, 2019; Bonaudo et al., 2013) como, por exemplo, as funções imune (Jordan et al., 1998; Eysker and Mirck, 1986; Forteau et al., 2019) e metabólica (Modernel et al., 2019). Elucidar as relações da diversidade de herbivoria que conferem aumento da eficiência de uso dos recursos é um fator chave, pois está intimamente ligado à gerência dos agroecossistemas com base em práticas sustentáveis (Dumont et al., 2020; Martin et al., 2020).

Equinos e bovinos simpátricos potencialmente têm variabilidade de fluxos de ingestão e digestão (Ferreira et al., 2007) decorrentes de diferenças morfofisiológicas (Demment & Van Soest, 1985; Hofmann, 1989) e especificidades de nichos alimentares de cada espécie (Walker, 1994; Menard et al., 2002). Equinos (perissodáctilos) e bovinos (artiodáctilos) coevoluíram paralelamente desde o Paleoceno (55 milhões). No processo evolutivo, os ruminantes foram mais eficientes nas adaptações (rumem) para herbívora (Janis, 1976). Um indício desta eficiência é a riqueza e a abundância específica em espécies de herbívoros de tamanho médio com ampla distribuição global. Os equinos contrariamente são um dos poucos representantes dos fermentadores intestinais de tamanho médio potencialmente a compartilhar nichos com ruminantes de mesma escala corporal (Duncan et al., 1990).

Normalmente, os bovinos têm um hábito alimentar generalista, utilizando o movimento da língua para a ampliação da área do bocado, permitindo massas de bocado elevadas (Illius & Gordon, 1987). Os bovinos apresentam o aparato ruminal como vantagem evolutiva e adaptativa para digestão de forragem em nível de fibra moderada, bem como tolerar fatores tóxicos de plantas inertes sob à fermentação (Freeland & Janzen, 1974; Van Soest 1983; Provenza et al., 2003). Os equinos, por sua vez, usam os incisivos superiores e inferiores na apreensão do pasto, viabilizando o pastejo em estratos rasos, onde estes apresentam dossel mais jovem (Fleurance et al., 2010) e conferindo uma vantagem do ponto de vista de acesso aos estratos inferiores, que normalmente apresentam tecidos mais jovens e de maior valor nutricional (Fryxell, 1991) e que os equinos poderiam otimizar a ingestão de nitrogênio (Edouard et al., 2010). Além disso, os equinos são menos afetados por teores elevados de fibra devido à ausência de limite físico sobre a partícula, como acontece no compartimento fermentativo anterior dos bovinos (Edouard et al., 2008), uma vez que a fermentação nos equinos ocorre na porção posterior do intestino (Bell, 1971).

Dessa forma, compensam a baixa taxa de digestão ampliando a ingestão e, conseqüentemente, aumentando o tempo de pastejo (Janis, 1976; Duncan et al., 1990).

A configuração de nichos alimentares dos animais em pastejo pode ter uma relação de competição pelos mesmos itens alimentares (Murray & Illius, 2000; Lamoot et al., 2005). No entanto, as particularidades morfofisiológicas definem padrões de forrageamento com efeitos sobre o recurso disponível no ecossistema, de modo que é coerente pensar que os efeitos dos herbívoros na estrutura do pasto sejam distintos (Shiple et al., 1994; Shipley, 2007). Através dos mecanismos acima citados, estes dois modelos animais conseguem explorar com particularidades nichos alimentares diferentes em um mesmo recurso disponível (Gwyne & Bell, 1968; Putman et al., 1987; Murray & Illius, 2000; Arsenault & Owen-Smith, 2008), gerando processos de facilitação e complementaridade alimentar (Hooper, 1998; Arsenault & Owen-Smith 2002; McNaughton, 1976; Sinclair & Norton-Griffiths, 1982) devido às diferenças seletivas na exploração das estruturas do dossel do pasto (Grant et al., 1985, 1987; Lamoot et al., 2005, Dumont et al., 2010; Karmiris et al., 2011). Utilizariam, assim, os recursos disponíveis de maneira harmônica (Duffy et al., 2007), um modelo selecionando o preterido pelo outro (Sensenig et al., 2010).

A importância da estrutura do pasto sobre a taxa de ingestão dos herbívoros é bastante conhecida (Ungar & Demment, 1991). De maneira geral, o estágio fenológico (Drescher et al., 2006), densidade volumétrica, arquitetura do dossel (Gordon & Benvenuti, 2006), diversidade florística e heterogeneidade (Bailey et al., 1998; Parsons & Dumont, 2003) interferem no processo ingestivo dos animais (Shiple, 2007), por meio do efeito direto no tamanho e massa do bocado (Shiple et al., 1994). Assim, as decisões dos animais em nível de bocado, determinam a ingestão de forragem de curto e longo prazo (Mezzalana et al., 2017; Bergman et al., 2001).

Bovinos e equinos apresentam biomassa corporal semelhante, estando inseridos em diversos contextos agroecológicos e de composição de paisagem. Tanto em cenários marginais, em caráter de preservação paisagística (Celaya et al., 2011; Osoro et al., 2017), como em sistemas de produção dirigidos para provisões definidas, como leite, carne e outros produtos (Martin-Rosset & Merle 1989). A coexistência de equinos e bovinos fornece a oportunidade para a exploração versátil e durável

provedora de manutenção da biodiversidade (Putman et al., 1991; Loucougaray, 2004; Catorci et al., 2012; Nolte et al., 2017).

### 1.3 HIPÓTESES

As questões abordadas neste documento estão baseadas nas seguintes hipóteses:

- A técnica de monitoramento contínuo dos bocados e simulação manual é uma metodologia confiável para estimar o consumo por herbívoros em pastejo (Capítulo II)
- A coexistência de diferentes herbívoros (i.e., equinos e bovinos), em um mesmo ecossistema pastoril, gera melhores condições para o forrageamento para ambas as espécies pelas relações de facilitação e complementariedade (Capítulo III)

### 1.4 OBJETIVOS

Dessa maneira, nos capítulos desta tese (objetivos específicos) que visam testar o objetivo geral de verificar as razões de causa e efeito da estrutura do pasto para ingestibilidade de forragem no forrageamento a partir da visão refinada das ações alimentares dos herbívoros, os bocados e a construção da dieta.

- Capítulo II: Comparar o consumo acumulado estimado pelo monitoramento contínuo dos bocados e o consumo medido com a dupla pesagem em diferentes condições de pastejo.
- Capítulo III: i) Caracterizar e registrar as ações alimentares (bocados) realizados por diferentes modelos animal (i.e., equinos e bovinos) em pastos permanentes; ii) Estimar o rendimento dos bocados (taxa de ingestão de nutrientes por minuto) para cada modelo animal, em coexistência ou não; e iii) Quantificar o valor potencial de matéria orgânica disponível em cada sistema de herbivoria (misto ou monoespecífico).

## CAPÍTULO II

**What, how and how much do herbivores eat? The Continuous Bite Monitoring method for assessing forage intake of grazing animals<sup>2</sup>**

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1 **What, how and how much do herbivores eat? The Continuous Bite Monitoring**  
2 **method for assessing forage intake of grazing animals.**

3

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24 Running headline: A method for assessing forage intake in grazing

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30 **Abstract**

31 Determining herbage intake is pivotal for studies on grazing ecology. Direct observation  
32 of animals allows describing the interactions of animals with the pastoral environment  
33 along the complex grazing process. The objectives of the study were to evaluate the  
34 reliability of the continuous bite monitoring (CBM) method in determining herbage intake  
35 in grazing sheep compared to the standard double-weighing technique (DW) method  
36 during 45-min feeding bouts; evaluate the degree of agreement between the two  
37 techniques; and to test the effect of different potential sources of variation on the  
38 reliability of the CBM. The CBM method has been used to describe the intake behaviour  
39 of grazing herbivores. In this study, we evaluated a new approach to this method, i.e.,  
40 whether it is a good proxy for determining the intake of grazing animals. Three  
41 experiments with grazing sheep were carried out in which we tested for different sources  
42 of variations, such as the number of observers, level of detail of bite coding grid, forage  
43 species, forage allowance, sward surface height heterogeneity, experiment site, and  
44 animal weight, to determine the short-term intake rate (45 min). Observer ( $P_{exp1} = 0.018$ ,  
45  $P_{exp2} = 0.078$  and  $P_{exp3} = 0.006$ ), sward surface height ( $P_{exp2} < 0.001$ ), total number of  
46 bites observed per grazing session ( $P_{exp2} < 0.001$  and  $P_{exp3} < 0.001$ ) and sward depletion  
47 ( $P_{exp3} < 0.001$ ) were found to affect the absolute error of intake estimation. The results  
48 showed a high correlation and agreement between the two methods in the three  
49 experiments, although intake was overestimated by CBM on experiment 2 and 3 (181.38  
50 and 214.24 units, respectively). This outcome indicates the potential of CBM to  
51 determining forage intake with the benefit of a greater level of detail on foraging patterns  
52 and components of the diet. Furthermore, direct observation is not invasive nor disrupts  
53 natural animal behavior.

54

55 Keywords: Short-term intake rate, grasslands, grazing ecology, herbage intake, Italian  
56 ryegrass, foraging, Tall fescue.

57

58 **1. INTRODUCTION**

59 One of the most important processes influencing the ecology of mammalian  
60 herbivores is how vegetation structure and composition affect dry matter and nutrient  
61 intake rate. Since herbivores complete thousands of bites per day, processes regulating  
62 the formation of a bite and resulting intake rate have tremendous repercussions on

63 animal and plant ecology (Shipley, 2007). In domestic herbivore production, forage  
64 intake is well known to be the most important component affecting performance or  
65 productivity (Illius & Gordon, 1987). For wild mammalian herbivores, measurement of  
66 short-term intake is essential on the study of energy balance between forage intake,  
67 exploration and displacement (e.g., Charnov, 1976), functional responses (e.g., Durant,  
68 et al., 2003; Smallegange & Brunsting, 2002), habitat selection (Courant & Fortin, 2012),  
69 and coexistence between herbivores species (Tilman & Borer, 2015).

70         Yet, the estimation of Short-Term Intake Rate (STIR) in grazing herbivores  
71 remains one of the biggest methodological challenges in animal science studies (Mayes  
72 & Dove, 2000; Garnick et al., 2018). At a daily scale, the use of plant markers, particularly  
73 n-alkanes (Dove & Mayes, 2006) are an accurate method to estimate individual forage  
74 intake, apparent digestibility, and portion of diet composition under grazing conditions  
75 (Gordon, 1995; Mayes & Dove 2000; Barcia et al., 2007). However, it requires intensive  
76 animal manipulation and labor for dosing, fecal sample collection, processing, and  
77 laboratory extraction (González-García et al., 2017). Multiple other methods involving  
78 acoustic (e.g. Galli et al., 2011, 2017) or movement/inertia (e.g. Rayas-Amor et al. 2017;  
79 Andriamasinoro et al. 2017) sensors have been tested to various levels of success on  
80 discriminating jaw movements (i.e., bite, chew, rumination). Walk-over weighing devices  
81 (Gonzalez-Garcia et al., 2017) and the “RumiWatch System” (Ruuska et al., 2016;  
82 Rombach et al., 2018) were developed for long-term forage intake studies. For  
83 determining STIR, the double-weighing technique (Penning & Hooper, 1985) is one of  
84 the most used procedures (Giovanett et al., 2017). It estimates the amount of forage  
85 intake in grazing sessions by the difference of animal weight pre- and post-grazing.  
86 Another previously employed methodology, esophageal fistulation (Stobbs, 1973;  
87 Geremia et al., 2018), is extremely invasive and not practical in rangeland situations.

88         Although those methods provide valuable information, the grazing process is  
89 described in terms of number and distribution of jaw movements, total intake, or average  
90 bite mass, bite rate, and intake rate over entire grazing sequences or days. They offer  
91 little detail of the dynamics of foraging actions and do not infer about variations of these  
92 variables as a function of local differences in the vegetation structure and composition  
93 (Bonnet et al., 2015). Herbivores respond to the botanical and structural diversity of  
94 grasslands, making decisions on choices and combinations of forages harvested at  
95 different space-time scales (Provenza et al., 2015). Evaluating in detail the components  
96 of a diet is an essential factor for many studies of plant-animal interaction.

97 Hand plucking (Halls, 1954; Cook, 1964) has been used as a simple and cheap  
98 alternative for simulating intake and diet selection by wild (Collins & Urness, 1983;  
99 Renecker & Hudson, 1985; Hudson & Frank, 1987; Okello et al. 2002) and domestic  
100 herbivores (Hobbs et al., 1983; Agreil & Meuret, 2004; Agreil et al., 2006). By using  
101 similar principles, the continuous bite monitoring (CBM) method proposed by Agreil &  
102 Meuret (2004) represents a useful tool for a complete description of the foraging activities  
103 and grazing environment at the bite level. The advantages of the CBM method over other  
104 methods rely on real-time recording of detailed descriptions of all foraging activities  
105 performed by the animal, bites taken in each plant species or structure, the estimation of  
106 the nutritional value of the plant tissue corresponding to each bite code from each plant  
107 species, and the exploration of the dynamics of the animal feeding station behaviour  
108 (Bonnet et al., 2015, Torres-Fajardo et al., 2019; Bolzan et al., 2020; Azambuja et al.,  
109 2020; Molnár et al. 2020). Thus, it allows for a great level of detail in the description of  
110 the foraging process. On the other hand, it is known that the CBM method requires the  
111 progressive training of the observer and has a certain level of bias depending on  
112 experience and dedication (Bonnet et al., 2011).

113 Previous studies also questioned the reliability of the method as a function of  
114 different variables such as vegetation structure, period and duration of the observation  
115 and the level of detail of bite coding grid (Bonnet et al, 2015; Bolzan et al. 2020). Based  
116 on a pre-evaluation of available vegetation and observation of diet selection and grazing  
117 process, possible “bites” are classified into categories of bite codes (BC) to compose a  
118 reference grid of foraging activities (i.e., BC, grazing, ruminating, resting, etc.).  
119 Observers then monitor target animals for a determined period to record where all  
120 activities are registered. Observed BC taken are then simulated (i.e., hand-plucked) to  
121 estimate the mass and nutritive value of each bite for further calculation of intake.  
122 Therefore, our objective were: *i)* to evaluate the reliability of the CBM method in  
123 determining herbage intake in grazing sheep compared to the standard double-weighing  
124 technique (DW) method during 45-min feeding bouts, *ii)* evaluate the degree of  
125 agreement between the two techniques, and *iii)* to test the effect of different potential  
126 sources of variation (observer and animal identity, vegetation structure and period and  
127 duration of the observation) on the reliability of the CBM.

## 128 **2. MATERIALS AND METHODS**

### 129 ***2.1. Site, treatments and experimental design***

130 Three independent studies were conducted in which we tested for different  
131 sources of variation: number of observers, level of detail of BC grid (Figure 1), forage

132 species, forage allowance, sward surface height (SSH) heterogeneity, experiment site,  
133 and animal breed. Experiment 1 was carried out between 15 September and 15 October  
134 2014, on an area of approximately 0.50 ha of self-seeding Italian ryegrass (*Lolium*  
135 *multiflorum* Lam.) at the experimental farm of the Federal University of Rio Grande do  
136 Sul, Brazil (30°05'27" S, 51°40'18" W). The area was divided into two paddocks of 0.25  
137 ha (experimental areas) with salt and water freely available. In this protocol, there were  
138 no defined criteria for managing the sward pre-grazing structure. Only average sward  
139 surface height measurements were collected at the time of observation.

140 Experiments 2 and 3 were carried out at the Canguiri experimental station of the  
141 Federal University of Paraná, Brazil (25°26'30"S and 49°7'30"W). The experiments were  
142 established in a 0.3 ha experimental area of tall fescue cv. INIA Aurora (*Schedonorus*  
143 *arundinaceus* [Schreb.] Dumort) sown in June 2015 on a prepared seedbed, at 55 kg ha<sup>-1</sup>.  
144 Beginning in September 2015, the experimental area was managed under continuous  
145 stocking with sward surface height maintained between 10 and 15 cm, except just prior  
146 to and during the grazing events when the different pre-grazing SSH treatments were  
147 imposed. Experiment 2 was carried out between 24 June and 12 July 2016 and  
148 Experiment 3 was carried out between 15 and 24 November 2016. In Experiment 2, five  
149 homogeneous pre-grazing SSH (14, 17, 20, 23, and 26 cm) were evaluated in a  
150 randomized complete block design with four replicates. In Experiment 3, five levels of  
151 depletion (0, 20, 40, 60, and 70%) of average SSH (20 cm) were evaluated in a  
152 randomized complete block design with four replicates, through grazing with non-  
153 experimental animals prior to grazing sessions to measure behaviour. A more detailed  
154 description management protocol can be found in Szymczak et al. (2020).

## 155 **2.2. Sward measurements**

156 Five hundred SSH measurements were taken in the two experimental paddocks  
157 of Experiment 1 to characterize the vegetation structure. Mean SSH was 38.0 cm ( $\pm 13.12$   
158 cm) and 38.7 cm ( $\pm 12.98$  cm) for paddocks 1 and 2. For Experiments 2 and 3, 150 points  
159 pre-grazing SSH within each sampling unit were measured. Pre-grazing SSH were 14.2  
160 ( $\pm 0.19$ ), 17.3 ( $\pm 0.20$ ), 19.7 ( $\pm 0.27$ ), 22.8 ( $\pm 0.28$ ) and 25.9 ( $\pm 0.26$ ) cm, for treatment of 14,  
161 17, 20, 23 and 26 cm in experiment 2, respectively. The measured pre-grazing SSH were  
162 20.2 ( $\pm 0.18$ ), 16.5 ( $\pm 0.52$ ), 12.2 ( $\pm 0.52$ ), 8.3 ( $\pm 0.48$ ) and 5.9 ( $\pm 0.37$ ) cm, for treatments  
163 0, 20, 40, 60 and 70% of depletion in experiment 3, respectively.

## 164 **2.3. Intake and grazing behaviour evaluations**

### 165 **2.3.1. Animals and experimental procedures**

166 Procedures involving the experimental animals were conducted under the  
167 Guidelines for the Use of Animals (2012) and complied with ethical guidelines published  
168 by the International Society for Applied Ethology. All procedures involving animals were  
169 approved by the Commission for Ethics in the Use of Animals of the Sector of Agricultural  
170 Sciences of the Federal University of Paraná (024/2016).

171 Two methodologies were used simultaneously during grazing tests to measure  
172 short-term intake rate (STIR): the double weighing technique (DW) as the reference  
173 practice (Penning & Hooper, 1985) and the continuous bite monitoring (CBM) method  
174 (Agreil & Meuret, 2004; Bonnet et al., 2015). In Experiment 1, eight Texel ewes ( $42.07 \pm$   
175  $3.15$  kg LW) were used. Sixty days before the data collection, ewes were allocated on  
176 an adjacent Italian ryegrass pasture for acclimation to forage and adaptation to  
177 observers and equipment. During the experimental procedure, animals were distributed  
178 in two groups of four testers per paddock, where two testers per paddock were used for  
179 evaluation of the continuous bite monitoring and double-weighing. After the evaluations,  
180 animals were placed back on the adjacent pasture for the remaining of the day. In  
181 Experiments 2 and 3, six White Dorper x Suffolk ewes were used with an average weight  
182 of  $61.9 \pm 5.5$  kg. Two animals were chosen as testers, all previously adapted to the  
183 experimental procedure and maintained in an area similar and adjacent to the  
184 experimental paddocks.

### 185 2.3.2. *Continuous bite monitoring*

186 Experiment 1 involved three observers: one with previous experience on the  
187 methodology with wild herbivores and cattle (EO; Bonnet et al., 2015), and two new  
188 observers (TO1 and TO2) were trained by EO. Experiments 2 and 3 involved four  
189 different observers, all inexperienced. Prior to the beginning of the experiments, a mutual  
190 familiarization phase was adopted for three weeks. During this phase, animals were  
191 handled daily to acclimate to observers and protocols, and for observers to familiarize  
192 with pasture and grazing behavior. Once the tester animals were identified and  
193 familiarized with the evaluators, all bites observed were described and classified into  
194 categories based on the observation of the animals' intake behavior before the  
195 experiments under the following aspects: *i*) structural and nutritional distribution of the  
196 components in the sward; *ii*) the nature, size, density, and position of selected plant parts  
197 by animals, as a set of leaves, isolated leaves or inflorescences; and *iii*) handling  
198 (gathering herbage into the mouth, severing the herbage, ingestive mastication and  
199 swallowing, Laca et al., 1994). Simple codes were established for each bite category  
200 agreed upon by all observers, composing a grid of codes for the identification of bites in

201 real-time (Fig. 1A and 1B). The level of detail for each BC grid differed based on SSH,  
202 phenological stages, plant density heterogeneity, and species diversity. For Experiments  
203 2 and 3 the same grid was used, but the dimensions and masses varied (Annex 1 and  
204 2).

205 After three weeks of training, both experienced and naïve observers were able to  
206 codify with confidence every bite observed (Bonnet et al., 2011). The three observers in  
207 Experiment 1 (one observer per tester animal per paddock in each session evaluated)  
208 and four observers on Experiments 2 and 3 (two observers per experiment, one observer  
209 per tester animal, and one tester per paddock) collected data by standing close to the  
210 animals (within 1 m), during 45-min grazing sessions. Thirty-two (Experiment 1) and  
211 twenty (Experiments 2 and 3) sessions were conducted. These sessions were blocked  
212 into morning and afternoon periods, arranged in a completely randomized design. After  
213 each grazing session had finished and while the animals remained in a common pen for  
214 determining insensible weight losses, each bite category was simulated (minimum 22  
215 hand-plucks for each type of bite, for bite codes more frequent we replicated the  
216 samples). Samples were collected in paper bags and placed in a thermal box and  
217 weighed immediately after collection to estimate fresh matter (FM) intake. Intake was  
218 calculated as a sum of FM for all recorded bites. Data were registered using a Sony ICD-  
219 PX312 (Sony Corp., Japan) digital voice recorder and, subsequently, transcribed using  
220 the J Watcher software ([www.jwatcher.ucla.edu](http://www.jwatcher.ucla.edu)).

### 221 2.3.3. Short-term intake rate

222 During the experimental period, each day around 5:40 am (Experiment 1) or 6:30 am  
223 (Experiments 2 and 3), animals were moved to the handling area, fitted with harnesses  
224 for a total collection of urine and feces, and weighed at  $t_1$  ( $W_1$  = initial weight for  
225 estimating the rate of insensible weight losses ( $H_2O$  evaporation,  $CO_2$  and  $CH_4$  losses;  
226 RIWL pre-grazing). After being weighed, the animals remained in a common pen for 45  
227 min without access to feed or water and then weighed again at  $t_2$  ( $W_2$  = final weight for  
228 pre-grazing RIWL and pre-grazing weight). Immediately after, all the animals were  
229 conducted and allotted to their paddocks for the 45-min grazing session ( $ET$ ). Once the  
230 grazing session was finished, the animals were led to the handling area and the tester  
231 animals were weighed at  $t_3$  ( $W_3$  = post-grazing weight and initial weight for the post-  
232 grazing RIWL). The tester animals then remained in a common area without access to  
233 feed, water or shade for 45 min until being weighed at  $t_4$  ( $W_4$  = final weight for post-grazing  
234 RIWL). The harnesses were then immediately removed, and the animals returned to the  
235 adjacent area. This same procedure was repeated in the afternoon (between 2:15 pm

236 and 6:30 pm for Experiment 1 and between 2:30 and 6:30 pm, for Experiments 2 and 3).  
 237 The animals were weighed using an electronic scale (MGR-3000 Junior, Toledo,  
 238 Canoas, Brazil) with a capacity of 200 kg (5-g increments). Short-term intake rate (g FM  
 239  $\text{min}^{-1}$ ; Eq. 1) was calculated by measuring the weight change, corrected for insensible  
 240 weight loss, and the time spent grazing, according to Penning & Hooper (1985).

$$241 \quad STIR = \left\{ \left[ \frac{(W_2 - W_1)}{(t_2 - t_1)} \right] + \left[ \frac{(W_3 - W_4)}{(t_4 - t_3)} \right] \right\} \times \left[ \frac{(t_2 - t_1)}{ET} \right]$$

242 E

243 q.1

## 244 **2.4. Statistical Analysis**

245 The data were analyzed using the R software (R Development Core Team,  
 246 2016). Animal test group was the experimental unit. We systematically verified normality  
 247 and homogeneity of the residuals. Pearson correlation was used as mean accuracy  
 248 between the methods and was considered poor (<0.4), reasonable (0.4 to 0.6), good (0.6  
 249 to 0.8), or excellent (0.8 to 1.0). Bland–Altman plots were created to indicate the degree  
 250 of agreement between the two techniques (Bland and Altman, 1999). The limits of  
 251 agreement were determined by calculating the bias and standard deviation of the paired  
 252 differences. The standard deviation was multiplied by the 1.96 quantiles of a normal  
 253 distribution and then, the amount of the calculated average was added or subtracted to  
 254 provide the upper or lower limits, respectively. Thus, the agreement limits were  
 255 calculated as bias  $\pm$  standard deviation. One Sample T-Test, at a significance level of  
 256 95%, was performed to check if there was a significant difference from zero, for the  
 257 comparison between the methods.

## 258 **3. RESULTS**

259 The correlation between estimated forage intake (as FM) through the CBM and DW  
 260 methods for ewes in 45-min grazing sessions is presented in Figure 2. The overall mean  
 261 correlation over 32 observations was 0.864, in Experiment 1 (Fig. 2A), and over 20  
 262 observations was 0.867 and 0.869, in Experiment 2 and 3, respectively (Fig. 2B and C).  
 263 A significant effect of the observer on the absolute error of intake estimation (Table 1)  
 264 was found in Experiment 1. In experiments 2 and 3, we found significant effects of sward  
 265 structure (SSH and sward depletion, respectively), observer and the total number of bites  
 266 observed per grazing session (Table 1). Day of measurement, individual animals or  
 267 period of the day had no significant effect on the absolute error in none of the  
 268 experiments (Table 1).

269 The Bland-Altman analysis (Fig. 3) showed the bias between methods of 33.90,  
270 181.38, and 214.24 g FM, and the limits of agreement: 259.11 and -191.31, 533.33, and  
271 -170.56 and 201.62, and -180.93 g FM, for Experiment 1, 2 and 3, respectively. The bias  
272 value obtained in the comparison of the methods means that on average the CBM  
273 method measures 33.90, 181.38 and 214.24 more units in relation to the DW method,  
274 for Experiments 1, 2 and 3, respectively. There was a significant difference between zero  
275 and bias by One Sample T-Test, for Experiments 2 ( $P = 0.0002$ ) and 3 ( $P = 0.0001$ ).

#### 276 4. DISCUSSION

277 Direct observation has a large capacity for detailed assessment of the grazing  
278 processes, considering important factors at the plant-animal interface. Bonnet et al.  
279 (2011), using cows (*Bos taurus taurus* L.) and goats (*Capra hircus* L.), showed that the  
280 ability of different observers to evaluate short-term intake after training had a correlation  
281 greater than 85%. Similarly, our results showed correlation topping 86.4% in comparison  
282 to the standard DW technique (Penning & Hooper, 1985). However, we found significant  
283 differences in the estimate of intake between the two methodologies in Experiments 2  
284 and 3, with generally overestimation of intake by the CBM regarding to the DW (Fig 2b  
285 and 2c). Given the differences in sward pasture conditions and assuming all observers  
286 received similar levels of training, this could indicate that a greater detail of bite types in  
287 the description of the grazing process could improve the accuracy of the method.

288 Differences in estimation of intake between the two techniques may be  
289 associated with inherent error of both methodologies. Many studies in the literature  
290 reported high interindividual variability when using the DW method (Fonseca et al., 2012;  
291 Mezzalira et al., 2017; Gusati et al., 2017). Other sources of variation, such as  
292 differences between paddocks and shifts (am vs. pm) also add to the compound variation  
293 for many of the methodologies used for estimating intake (Bailey et al., 1996; Fraser,  
294 2009; Gregorini, 2012). For example, Lukuyu et al. (2014) compared two pasture  
295 disappearance-based techniques (rising-plate meter and capacitance meter) and two  
296 chemical marker-based techniques (dosed n-alkanes and chromic oxide) techniques of  
297 forage intake in steers, showing high internal variation (coefficients of variation of 28%  
298 for the capacitance meter and 44% for the plate meter) in estimates and low correlation  
299 ( $r = 0.51$ ) between chromic oxide and the plate meter. They found no correlation between  
300 disappearance-based and alkane methods. Greenwood et al. (2014) found correlations  
301 between the biomass disappearance and C32/C31 and C32/C33 n-alkane of 0.77 and  
302 0.70, respectively.



303           The correlation analysis (Fig. 2) shows only of the strength of relationship  
304 between the variables but not the agreement between them (Giavarina, 2015). A high  
305 correlation between the methods can mostly come from the large range in fresh matter  
306 intake observed during the experiment (Giavarina, 2015). The Bland-Altman analysis  
307 shows the agreement between the methods and is a parameter of greater consistency  
308 to compare techniques (Myles, 2007; Giavarina, 2015), as it is evaluated according to  
309 the data dispersion. In cases of good agreement, the scattering of points is diminished  
310 and points lie relatively close to the solid, bold line (mean bias; Fig. 3) (Myles, 2007;  
311 Giavarina, 2015). Our results had a high dispersion; however, points were mostly within  
312 the limits of agreement in all cases. This denotes agreement between methods, but with  
313 high variability in measuring intake. In addition, the Bland-Altman analysis demonstrated  
314 an intake overestimation measures for CBM compared to DW method, mostly in  
315 experiments 2 and 3 (Fig. 3B and 3C). It is important to point out that the observer's  
316 interpretation of the animal's action in the execution of the bite, along with the factors  
317 that establish the bite category (i.e., the type of tissue, position in the canopy and  
318 density), are determinants for the accuracy of the simulation. Therefore, the smaller  
319 number of bite codes on experiments 2 and 3 resulted in a greater range of bite mass  
320 for each of the BC, increasing the dispersion of the data which resulted in the  
321 overestimation of intake with CBM. Alternatively, a more detailed assessment (i.e.,  
322 experiment 1) dilutes the variations of the effects by the pasture structure (sward surface  
323 height and sward depletion), observer and the total number of bites in multiple BC  
324 (Bolzan et al., 2020), minimizing the difference between methods (Table 1).

325           Evaluating foraging behavior at the smallest scale of the grazing process, the bite  
326 (Laca & Ortega, 1995), allows us to understand each type of bite during the grazing  
327 process (Illius & Gordon, 1987). It elucidates the spatio-temporal distribution and  
328 variability of the grazing process in response to the variation in components of the  
329 vegetation structure. Our work provides evidence of the potential and limitations of the  
330 CBM technique. This tool can be used with great assurance in the estimations of STIR,  
331 considering the influence factors such as pasture structure (Allden & Whitakker, 1970;  
332 Laca et al., 1992; Mezzalira et al., 2017; Nadin et al., 2019), digestibility (Drescher et al.,  
333 2006), and selectivity (Hodgson, 1979). Both the level of observer knowledge of pasture  
334 science principles (i.e., understanding of pasture structure and botanical composition in  
335 diverse grasslands) and level of training observers receive are limiting factors for the  
336 success of this direct observation technique. The posed question to be addressed in the  
337 study directly conditions the detailing of the description of the food actions (BCs) to be  
338 evaluated, as well as other ethological standards. In addition to the intake rates, we were

339 able to know the fraction of each BC regarding what they eat, how they eat, and how  
340 much they eat of each item.

## 341 **5. IMPLICATIONS**

342 Our results indicate the accuracy of the hand plucking method and CBM as an  
343 alternative to quantify forage intake, i.e., there was agreement between the studied  
344 methods. We found an overestimated consumption when using CBM in comparison to  
345 DW in experiments 2 and 3. However, we hypothesize that the difference between the  
346 methods can decrease by increasing the detail of the BC grid. This extends the  
347 possibilities of evaluating animals during the foraging process, especially free-ranging,  
348 without significant modifications on the environment or animal manipulation. With the  
349 knowledge of quantitative reliance, we have the potential to complement other  
350 methodologies, sensor calibration and subsequent use in long-term evaluations. This  
351 reality would increase the evaluation capacity of several animals at the same time, in  
352 comparison with the CBM method, which restricts the evaluation of only one animal per  
353 observer over time, which represents a large time cost in training, evaluation, and  
354 transcription.

355 There is a high demand from the scientific community and general society for  
356 experimental protocols that promote animal welfare (Driscoll & Bateson, 1988). Non-  
357 invasive methodologies are extremely important to preserve natural animal behavioral  
358 principles, avoid diseases (e.g., chromium oxide possesses carcinogenic properties;  
359 Sedman et al., 2006) or injuries, and not alter the affective states of animal (avoid pain,  
360 fear, suffering, frustration, and distress) (Driscoll & Bateson, 1988, Sherwin et al., 2003,  
361 Fraser, 2009). We believe in the potential of the CBM methodology as an important  
362 alternative because it does not require physical contact, adaptation to unnatural  
363 conditions, or the use of equipment coupled to the animal. Thus, it has high potential for  
364 reproducing grazing animal intake in different environments and situations while  
365 maintaining animal welfare.

366

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377

#### 378 **COMPETING INTERESTS**

379 The authors declare they have no competing interests.

380

#### 381 **AUTHOR CONTRIBUTIONS**

382 **Anderson Michel Soares Bolzan:** Conceptualization (Equal); Data curation (Equal);  
383 Formal analysis (Equal); Methodology (Equal); Writing-original draft (Equal). **Leonardo**  
384 **Silvestri Szymczak:** Data curation (Equal), Formal analysis (Equal), Methodology  
385 (Equal), Writing-original draft (Equal). **Laura Nadin:** Data curation (Equal), Formal  
386 analysis (Supporting), Investigation (Equal), Methodology (Supporting), Writing-original  
387 draft (Equal). **Olivier François Bonnet:** Conceptualization (Equal), Data curation  
388 (Equal), Formal analysis (Equal), Investigation (Equal), Methodology (Equal), Writing-  
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394 Project administration (Lead), Supervision (Supporting), Writing-original draft-  
395 (Supporting). **Paulo César de Faccio Carvalho:** Conceptualization (Equal), Data  
396 curation (Supporting), Methodology (Supporting), Project administration (Lead),  
397 Supervision (Lead), Writing-original draft (Lead).

398

#### 399 **DATA AVAILABILITY STATEMENT**

400 These data are available at <https://doi.org/10.5061/dryad.573n5tb73>

401

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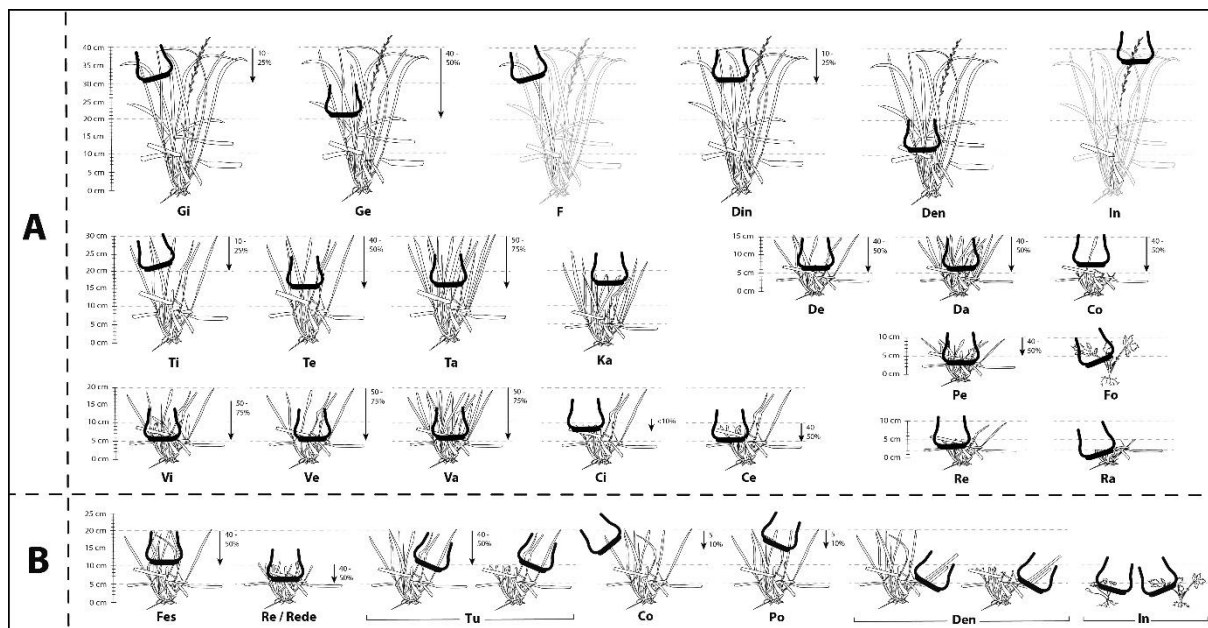
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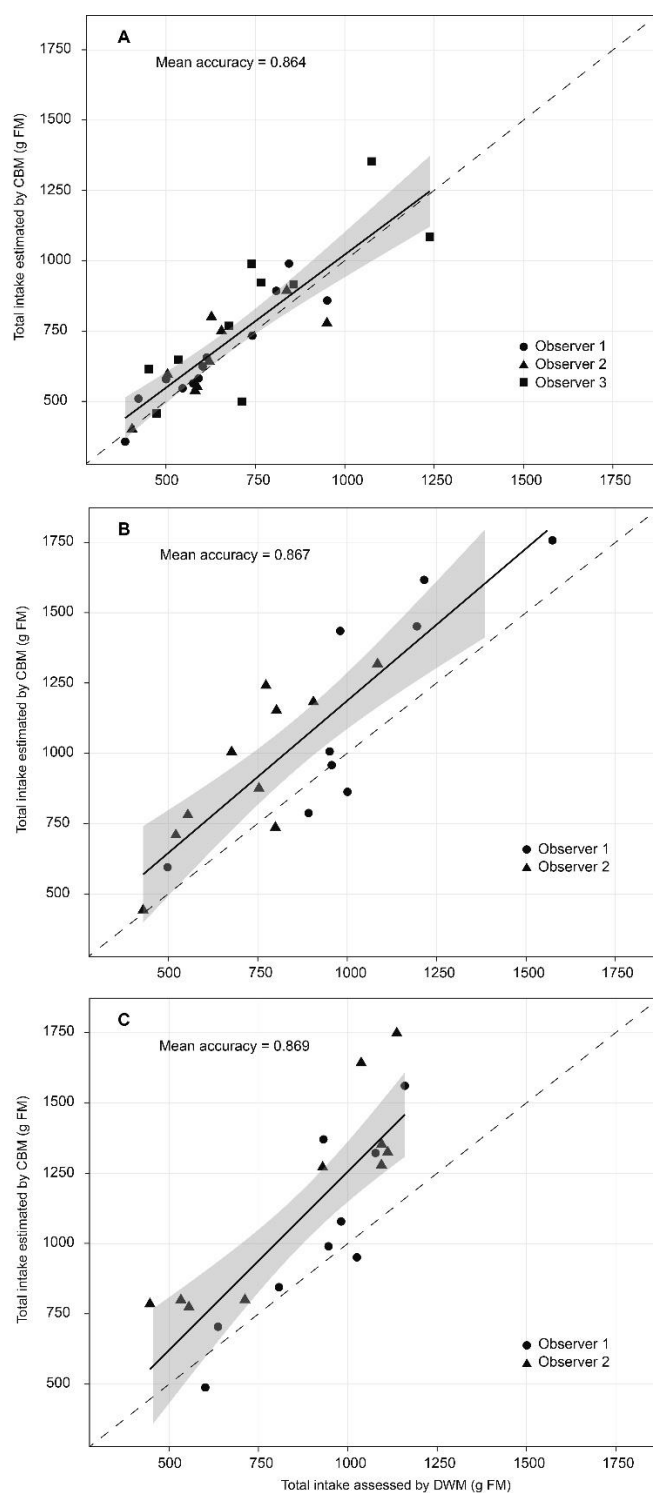
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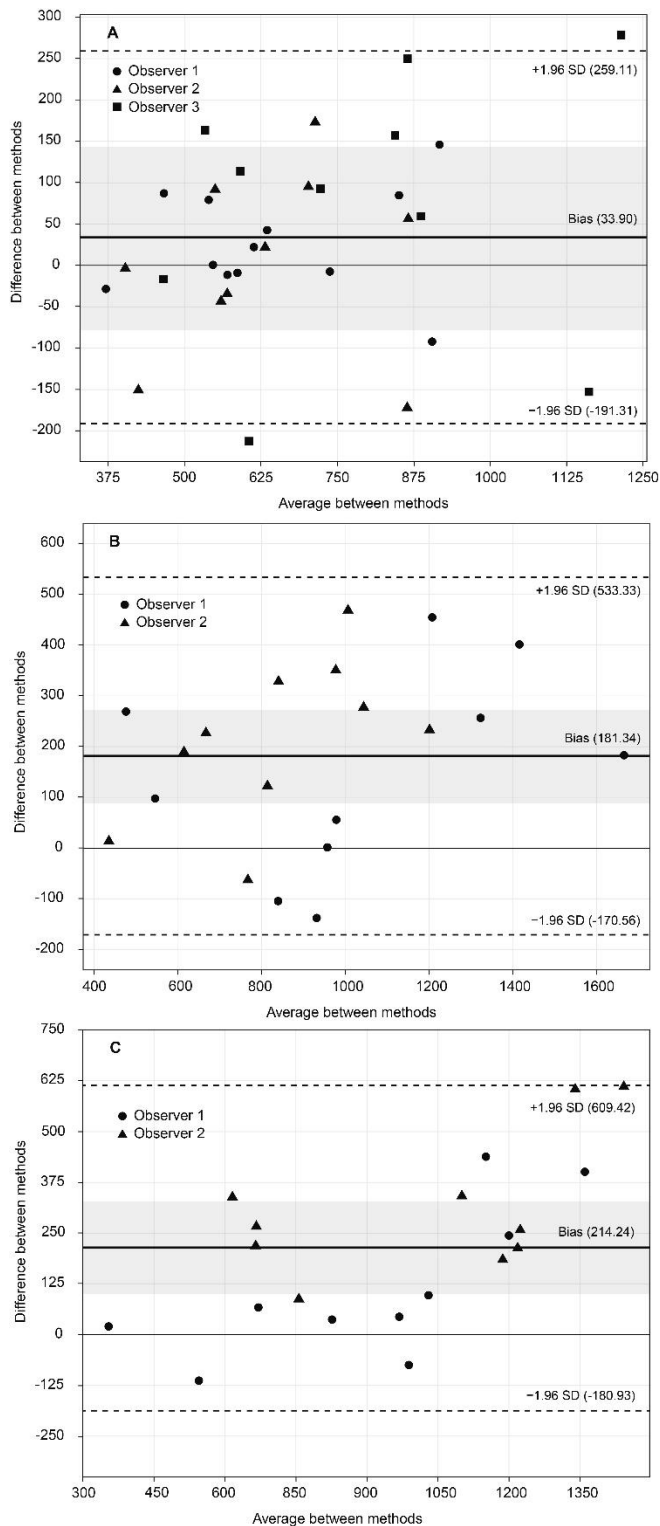
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621 Figure 1. Representation of the types of sheep bites with their respective codes used in  
 622 the Continuous Bite Monitoring method in Experiment 1 (A) with Italian ryegrass, 2 and  
 623 3 (B) with Tall fescue. Drawing, in Experiment 2 and 3 (B), represents the codes used in  
 624 all tested heights, here demonstrated for the height of 20 cm. Note: The same codes  
 625 were used for the other treatments. The arrows represent the depth of the bite in bite  
 626 type. Description of bites is in Table 1 in Supporting Information.



627

628 Figure 2. Relationship between the total intake of fresh matter (g FM) of ewes during  
 629 grazing sessions of 45 min estimated through continuous bite monitoring assessed by  
 630 the double weight technique, in Experiment 1 (A), 2 (B) and 3 (C). Solid line represents  
 631 the linear model between the two methods ( $P < 0.001$ ), dashed lines represent identity  
 632 ( $Y = X$ ) and gray area represent the confidence interval of the measurement through  
 633 double weight with regard to scale precision.



634

635 Figure 3. Bland-Altman Plots showing the paired differences against the average  
 636 between CBM and DWM methods in experiment 1 (Figure A,  $P = 0.1052$  in One Sample  
 637 T-Test), 2 (Figure B,  $P = 0.0002$  in One Sample T-Test) and 3 (Figure C,  $P = 0.0001$  in  
 638 One Sample T-Test). Mean bias is represented by black line and limits of agreement are  
 639 shown by the dashed lines, while confidence intervals are shown by the gray areas.

640 Table 1. ANOVA table for the potential sources of variation of the error in the estimation  
 641 of fresh matter intake through CBM. *Day* refers to the number of days with observation  
 642 since the beginning of the experiment, *Period* to the period of the day evaluated (morning  
 643 or afternoon) and *Total bites* to the total number of bites observed during one trial.  
 644 Interactions were not significant and were removed from the final model.

Source of variation		df	F value	P value
Experiment 1				
<i>Observer</i>		2	4.75	0.018
<i>Animal</i>		3	1.97	0.14
<i>Day</i>		1	0.06	0.81
<i>Total bites</i>		1	0.17	0.68
Experiment 2				
<i>Sward Height</i>	<i>Surface</i>	4	12.478	0.0002
<i>Observer</i>		1	3.633	0.078
<i>Day</i>		4	1.091	0.314
<i>Period</i>		1	0.083	0.777
<i>Total bites</i>		1	27.927	0.0000
Experiment 3				
<i>Sward Depletion</i>		4	91.46	0.0000
<i>Observer</i>		1	11.02	0.006
<i>Day</i>		4	7.724	0.101
<i>Period</i>		1	1.640	0.68
<i>Total bites</i>		1	15.392	0.0000

645

**CAPÍTULO III****Foraging behaviour of bovines and equines under mixed herbivory<sup>3</sup>**

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<sup>3</sup> Manuscrito elaborado conforme as normas do periódico *Oecologia* (Apêndice 4).

# 1 Foraging behaviour of bovines and equines under mixed herbivory

2

## 3 Abstract

4 Sward structure is the cause and consequence of grazing actions, affecting the intake  
5 rate of herbivores. We hypothesized that different foraging behaviors of equines and  
6 bovines in coexistence and their effects on vegetation structure would enhance the  
7 ingestion of both animals due to the inter-niche ecological relationships and the different  
8 interactions in the animal-plant interface resulting from morphophysiological differences  
9 between species. To test if their coexistence under mixed grazing affects the  
10 opportunities for diet selection compared to monospecific grazing, we characterized the  
11 feeding actions of equines and bovines in the pastoral environment by continuous bite  
12 monitoring during daily foraging behavior. We verified that the mixed herbivory system  
13 has a higher availability of bites with a higher intake rate available in the pasture structure  
14 compared with the monospecific grazing. This effect is positively evidenced in the food  
15 selection and composition of the diet for cattle and neutral for horses, conferring a  
16 condition of facilitation of horses towards cattle when in mixed herbivory condition.

17

## 18 Introduction

19 Pastoral ecosystems have a relevant distribution, ~ 40% of the global surface  
20 (Suttie 2005) and in biodiversity disposition (Bengtsson et al. 2019), organized in  
21 horizontal (at the same trophic level) and vertical (between trophic levels) trophic levels  
22 (Duffy et al. 2007). This implies complex herbivore-resource relationships in time and  
23 space, with effects on the plant community (Senft et al. 1987), spatial distribution of  
24 herbivores and food niches (Bell 1971; Jarman 1974; Shipley and Spalinger 1995). In  
25 the multifunctionality of pastoral ecosystems, increasing diversity (e.g., herbivory mixed  
26 system management, Dumont et al. 2020; Martin et al. 2020) promotes resource use  
27 efficiency in the short term (e.g., animal performance) (Prins and Fritz 2008; Ormunen-  
28 Cristian et al. 2012; Fraser et al. 2014), and subsequently the stability of the plant  
29 community (Henning et al. 2017; Schmitz and Isselstein. 2020), greater system  
30 autonomy (Thenard 2019; Bonaudo et al. 2013), such as immune (Jordan et al.1998;  
31 Eysker and Mirck 1986; Forteau et al. 2019) and metabolic functions (Modernel et al.  
32 2019).

33 Sympatric equines and bovines potentially have variability in intake and digestion  
34 flows (Ferreira et al. 2007) resulting from morphophysiological differences (Demment  
35 and Van Soest 1985; Hofmann 1989) and niches specificities (Illius and Gordon 1992;  
36 Walker 1994; Menard et al. 2002). The bovines are generalists in foraging behavior,  
37 using the movement of the tongue to enlarge the bite area (Illius and Gordon 1987) and  
38 having a ruminal apparatus as an evolutionary advantage for digesting forage at a  
39 moderate fiber level, as well as tolerating toxic factors of inert plants under fermentation  
40 (Freeland and Janzen 1974; Van Soest 1983; Provenza et al. 2003).

41 On the other hand, horses are less affected by high levels of fiber, with no  
42 physical constraint on the particle in the fermentative compartment (hindgut),  
43 compensating for the low rate of digestion by increasing intake (Edouard et al. 2008),  
44 and a consequently increasing in grazing time (Janis 1976; Duncan et al. 1990). In  
45 addition, horses can modulate intake in the food niche breadth (Bell 1971; Janis 1988)  
46 into distinct structures to balance energy and protein intake (Edouard et al. 2010), and  
47 they are more efficient grazing short swards patches (Naujeck et al. 2005), which are  
48 likely potentially rejected by cattle (Fleurance et al. 2009).

49 Accordingly, these two animal models are able to explore different food niches  
50 within the same resource (Murray and Illius 2000; Arsenault and Owen-Smith 2008), due  
51 to selective differences in the exploitation of canopy structures (Grant et al. 1985, 1987;  
52 Lamoot et al. 2005; Dumont et al. 2010; Karmiris et al. 2011) as a consequence of  
53 processes of feed facilitation and complementarity (Hooper. 1998; Arsenault and Owen-  
54 Smith. 2002; McNaughton 1976; Sinclair and Norton-Griffiths 1982).

55 Having the bite as the basis of the grazing process (Laca & Ortega. 1985; Shipley  
56 et al. 1994), and considering the morphophysiological differences of horses and cattle,  
57 which affect the form of forage selection and harvest (i.e., diversity of bites) in the sward  
58 structure (i.e., sward height and botanical composition) (Flores et al. 1993) we seek to  
59 understand the foraging of horses and cattle on this scale, the execution patterns, and  
60 the construction of the diet. These animal decisions at the bite level, determine the short  
61 and long-term forage intake (Mezzalana et al. 2017; Bergman et al. 2001). The bite  
62 diversity in the diet selection of the equine and bovine can confer relations of facilitation  
63 and complementarity during the foraging process by the bite diversity (Carvalho 2013).

64 We intend to approach the grazing process in a fine scale (i.e., bites) and assess  
65 the interactions of the pluriespecific coexistence of herbivores on the structure of the  
66 vegetation and explore the responses on forage intake comparing monospecific and  
67 mixed herbivory systems. In this context, we hypothesize that i) Sympatric equines and  
68 bovines promote the availability of more profitable feeding actions (bites), generating a  
69 facilitation process; ii) bovines and equines select by profitability and have different diets

70 when in coexistence iii) equines explore a wider range of feeding actions to compose  
71 their diet than bovines.

## 72 **Material and Methods**

### 73 **Study area and experimental design**

74 The protocol was carried out at the INRA experimental station at Le Pin-au-Haras  
75 (48°44 N; 0°08 W; 140–248 m a.s.l., Normandy, France). Three different herbivory  
76 system managements were assigned to three permanent pasture areas (paddocks) of  
77 equivalent dimensions managed under continuous stocking: a mixed-species herbivory  
78 system (“Mixte”) with two animal models (bovine and equine), consisting of six Charolais  
79 heifers ( $1.0 \pm 0.1$  years old,  $411 \text{ kg} \pm 30 \text{ kg}$  body weight (BW)) and three equines ( $2 \pm$   
80  $0.1$  years old,  $448 \pm 37 \text{ kg}$  BW) in a paddock with  $5.93 \text{ ha}^{-1}$  area; a bovine monospecific  
81 herbivory system (“Monobov”) with 12 Charolais bovines ( $1.0 \pm 0.1$  years old,  $408 \text{ kg} \pm$   
82  $26 \text{ kg}$  BW) in a paddock with  $6.0 \text{ ha}^{-1}$  area; and an Equine monospecific herbivory system  
83 (“Monoequi”) by six equines Anglo-Arab and French saddle breeds ( $3.2 \pm 0.1$  years old,  
84  $461 \pm 33 \text{ kg}$  BW) in a paddock with  $5.76 \text{ ha}^{-1}$  area. The paddocks had similar history of  
85 use (cattle grazing) and floristic composition before the allocation of treatments (see  
86 Appendix 2). The grazing season had 177 days, starting at April 25, 2018, and ending  
87 on October 18, 2018. The animals had access to half of the total paddock area in the  
88 first 68 days (Period 1, spring) whereas the other half of the area was allocated to hay  
89 production (i.e., ungrazed). Then the animals had access to the total paddock area  
90 (Periods 2 and 3, summer). The stocking density in the spring was two livestock units  
91 (LU)  $\text{ha}^{-1}$  and 1 LU  $\text{ha}^{-1}$  in the summer. The stocking densities were calculated using the  
92 INRA animal unit system for bovines [ $1.0 \pm 0.1$  years,  $500 \text{ kg} \pm 5.0 \text{ kg}$  (BW) 0.6 LU  
93 equivalent] (Inosys Réseaux d'élevage, 2018) and for equines [ $2 \pm 0.1$  years of age,  
94  $500.0 \pm 6.5 \text{ kg}$  (BW) 0.94 LU equivalent] (Martin-Rosset 2015).

95

### 96 **Vegetation resource**

#### 97 **Vegetation structure and the availability of bites**

98 To describe the vegetation in each system, 60 quadrats distributed on the surface  
99 of the paddocks were characterized before ingestive behavior assessments. At each  
100 sampling, a quadrat of  $1 \text{ m}^2$  was placed on the ground and forty-five regularly spaced  
101 canopy height measurements were taken using a sward stick (Barthram 1985). In each  
102 contact point (touch) the sward height was measured, and the type of sward structure  
103 was described according to the bite code (BC) determined for the assessment of



104 ingestive behavior. The vegetation structure was previously described in the  
105 assessments of ingestive behavior. Then the BCs (Fig. 1) (Appendix 3) were  
106 characterized in the spatial distribution of pasture available for animal selection in the  
107 different herbivory systems.

108

### 109 *Herbage biomass and growth*

110 To determine herbage mass ( $\text{kg DM ha}^{-1}$ ), the forage was cut at ground level in  
111 eight quadrats of  $0.25 \text{ m}^2$  per paddock, systematically located to represent  
112 heterogeneity. Before the cut, five points of height were taken. After cutting, the herbage  
113 samples were dried in an oven at  $55 \text{ }^\circ\text{C}$  for 72 hours and weighed (Mannetje 2000).  
114 Linear models were generated (Period 1:  $y = 115.86x + 0$ ,  $R^2=0.89$ ,  $P<0.001$ ; Period 2:  $y$   
115  $= 121.58x + 0$ ,  $R^2=0.77$ ,  $P<0.001$ ; Period 3:  $y = 236.62x + 0$ ,  $R^2=0.93$ ,  $P<0.001$ ) between  
116 herbage mass and the average sward height to predict herbage mass from sward height  
117 assessments (Kunrath et al. 2020). Thereby, the herbage mass was predicted based on  
118 approximately 1000 points measured with sward stick on each paddock (i.e., system)  
119 performed by systematic sampling in parallel transects ( $\sim 3 \text{ m}$ ) (Barthram et al. 2005).

120 The daily rate of herbage accumulation was estimated using four exclusion cages  
121 per paddock (Klingman et al. 1943). The initial herbage mass and the herbage  
122 accumulated in each subperiods (30 days) were used to calculate the total herbage  
123 production ( $\text{kg DM ha}^{-1}$ )

124

### 125 **Animal measurements**

126 The evaluations were carried out in three periods: 1) May and June; 2) July and  
127 August; and 3) September and October. For the assessment of foraging behavior, three  
128 (testers) focal individuals per animal species were evaluated in each herbivory system  
129 ( $n = 12$ ). All animals, including testers, were periodically weighed at 15-day intervals. In  
130 addition, body measurements were taken at the beginning of the season and at the end  
131 of the equine grazing season.

132

### 133 **Continuous bite monitoring**

134 We used the Continuous Bite Monitoring (CBM) method proposed by Agreil &  
135 Meuret (2004) and Bonnet et al. (2015) to investigate the grazing process, considering  
136 the botanical diversity of swards. We followed the mutual familiarization indicated to  
137 ensure the accuracy in the description of food actions (i.e., bite assessment) (Bolzan et  
138 al. 2020). The observation time of each individual was defined so that we could obtain a

139 comprehensive description of the daily scale of the foraging. In this sense, we strictly  
140 maintained 4 hours of morning observation and 5 hours in the afternoon (7:00 -12: 00  
141 and 14:00 - 19:00). Three animals of each species were observed in each period by a  
142 single observer. (3 horses - mixed, 3 mixed cattle, 3 Monoequi and 3 Monobov).

143

#### 144 *Designing of the bite-coding grid*

145 Based on the plant components in the sward and the foraging characteristics of  
146 each animal model, a grid of bite codes (BCs) was elaborated. It is worth noting that the  
147 definition of feeding actions in bite codes is an ordered representation of how the animal  
148 interprets the resource and performs the feeding action.

149 Bite codes have been defined that encompass more than one botanical type, as  
150 well as codes of isolated botanical types. As a basis for classification, we considered: 1-  
151 isolated plants, set of intra and interspecific plants (e.g., grass mixed, or grass mixed  
152 plus legume species, or others); 2- nature, size and structural characteristics that affect  
153 the bite allocation position (i.e., sward height); 3- handling and cutting behavior of the  
154 animal. The bite diversity in this study included 25 types of BCs, combined with nine  
155 classes of sward height and 35 types of BCs without height class (Annex 1). Additionally,  
156 were characterized other codes to define behavioral expressions such as interaction  
157 between individuals, mutual toilet, social grooming, or reactivity towards disturbance by  
158 flies, steps, feeding stations, the horizontal distance of feces, their effects on the intake  
159 rate. We used a Sony ICD-PX312 portable digital voice recorder to gather BC data.  
160 Records were subsequently transcribed using the JWatcher software  
161 ([www.jwatcher.ucla.edu](http://www.jwatcher.ucla.edu)).

162

#### 163 *Sampling of feed Items and the evaluation of bite mass*

164 At the end of each grazing event or its intervals (i.e., idleness and rumination),  
165 the observer performed a simulation of the BCs in the most reliable way possible to the  
166 bites made by the animal. When necessary, the observer used a cutting blade. At the  
167 end of the observation day, all BCs performed in the cumulative interval were simulated.  
168 Every BC was simulated at least 20 times, and the BCs that occurred with more  
169 frequency were simulated two or three times more than the less frequent ones. The mass  
170 of each BC was obtained by the total mass of the dry sample after 72 hours at 60 °C  
171 divided by the number of BCs in the sample, thus obtaining the value of the average  
172 mass of each BC for each animal and day of evaluation. This weighted simulation of the  
173 BCs allowed to increase the samples and represent the different moments of  
174 accumulated consumption in grazing that make up the diet.

## 175 **Nutritive value of each bite-code**

176 The nutritive value of each type of BC was obtained by NIRS spectrophotometer  
177 analysis according to laboratory protocol and equations INRA - UMRH1213. The  
178 calibration equations used for the prediction of the value is based on the following  
179 reference methods: ash content per ash at 550 °C for crude protein (CP) content  
180 combustion method (Thiex 2009), fiber fractions (neutral detergent fiber [NDF], acid  
181 detergent [ADF], acid lignin detergent [ADL]) after Van Soest (1963) and in vitro  
182 digestibility of organic matter (OMD, De Boever et al. 1986).

183

## 184 **Calculations of variables and statistical analysis**

### 185 *Bite mass and nutritive value*

186 Bite mass (dry matter basis) was modeled and then predicted by using the  
187 following linear mixed-effects models through “lmer” function of the *lme4* package (Bates  
188 et al. 2015):  $y \sim \text{bite-code} * \text{species} + \text{paddock} + (1 | \text{period}) + (1 | \text{animal})$ . The mass of  
189 each nutrient by bite code was calculated as the dry matter multiplied by the  
190 concentration of the respective nutrient. The NDF, ADF, nitrogen and mineral matter  
191 were predicted by using the following linear model:  $y \sim \text{bite-code} * \text{species} * \text{paddock} * \text{period}$ .  
192 Organic matter was calculated as the difference between total dry matter and the  
193 mineral matter, and crude protein CP (nitrogen x 6.25). The total intake observed of dry  
194 and organic matter by animal were calculated as a sum of all bite masses.

### 195 *Bite profitability*

196 The profitability (i.e., the potential gain of intake rate of nutrients) of each bite  
197 code ( $\text{g DM min}^{-1}$ ) was calculated by species and herbivory system as the quotient of the  
198 bite mass and time per bite. To calculate time per bite, we used “chunks” (i.e. intervals  
199 with a sequence of the same bite code and divided the number of bites by the duration  
200 of each interval) of rows with sequence of a same bite code and divided the number of  
201 bites by the duration of each “chunks”. Chunks with less than 2 bites were discarded.  
202 Then, we used the calculated time per bite to parameterize the following linear mixed-  
203 effects model:  $y \sim \text{bite-code} + \text{species} + \text{paddock} + (1 | \text{period}) + (1 | \text{animal})$ . We used  
204 the “weights” argument in the “lmer” function of the *lme4* package (Bates et al. 2015) to  
205 account for the variation in chunk length.

### 206 *Potential intake available in each herbivory system*

207 In order to test whether herbivores had greater opportunity to select more  
208 profitable bites, we calculated the frequency of intake rate available (hereafter called  
209 potential intake rate) by multiplying the profitability of each bite code by their respective  
210 frequency on the resource (i.e., vegetation structure). The potential intake was analyzed

211 through the linear model formula of the “lm” function of the *lmer* package:  $y \sim \text{species} * \text{system} * \text{period}$ . Analysis of variance (ANOVA) was performed and when significant effects were detected, treatment means were compared with Bonferroni test at 95% confidence level using the *emmeans* package.

#### 215 *Intake rate, diet composition and selection*

216 Diet composition (n bites and frequency of observed bites) was verified by the sum of the performed bite, and their relative frequency according to the height classes and botanical types of the universe of bite codes for each animal in each herbivory systems and periods.

220 The intake rate for each botanical type and height classes of the bite codes were calculated by the accumulated intake of the respective botanical type or height class in each bite code, divided by the number of this bite code and the time of the same bite code. To calculate the time per bite, we used intervals with a sequence of the same bite code and divided the number of bites by the duration of each interval. Diet selection is assumed as the frequency of BCs of each height classes of bites and botanical types of bites present in the diet in relation to the BCs available in the vegetation structure. Selectivity ( $S_i$ ) for each BC was calculated using the Jacob's index (1974) derived from the Ivlev's selectivity index, where:

$$229 \quad S_i = (c_i - a_i) / (c_i + a_i - 2c_i a_i)$$

230 being ( $c_i$ ) the ratio between (0 and 1) of the component in the diet, and ( $a_i$ ) the ratio between (0 and 1) of the component (i) in the vegetation matrix.

232 For each BC ( $c_i$ ), the data of individual animals was aggregated by period, and then related to the relative abundance of this type of bite in the paddock.

234 Selectivity ( $S_i$ ) varies from -1 (never used) to +1 (used exclusively), with negative and positive values indicating avoidance and preference, respectively, and 0 indicating that a component of the sward is used in proportion to its availability. The Jacobs index was chosen for its low sensitivity to variations in the relative abundance of plant components, making it possible to classify abundant and rare plant components according to their acceptance by animals.

240 Analysis of variance (ANOVA) was performed using the linear mixed effects model using the “lmer” function of the *lme4* package (Bates et al. 2015). The fixed effect were botanical classes or heights classes, species and herbivorous systems, periods and their interactions, and animals with a random effect. When significant effects were detected, treatment means were compared with Bonferroni test at 95% confidence level using the *emmeans* package.

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248 **Results**249 **Forage resource**

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252 Sward structure did not show pronounced variations between mixed or  
 253 monospecific systems for the frequencies and patterns of sward heights (Fig. 2) and  
 254 botanical distribution in the periods of the grazing season (Fig. 3). We observed  
 255 equivalence in the herbage mass (kg DM ha<sup>-1</sup>) predicted from the sward height  
 256 measurements in each system (i.e., Mixte, Monoequi and Monobov) in each period of  
 257 the grazing season (Period 1: 2541.8 ± 772.4; 2541.2 ± 828.4; 2700.9 ± 854.6; Period 2:  
 258 2673.7 ± 681.6; 2324.9 ± 604.1; 2548.8 ± 689.1; Period 3: 2892.0 ± 529.8; 2553.1 ±  
 259 339.2; 2684.0 ± 378.9, for Monoequi, Monobov and Mixte, respectively). The daily  
 260 herbage accumulation rate was different (P <0.05) only between periods (Period 1: 52.6  
 261 ± 8.1; Period 2: 30.0 ± 4.8; Period 3: 23.1 ± 5.8 kg DM ha<sup>-1</sup> day). The total herbage  
 262 production (kg DM ha<sup>-1</sup>) in each herbivory system was 8650 ± 853.3 for Monoequi, 7550  
 263 ± 574.4 for Monobov, and 7925 ± 1043.6 for the Mixte system.

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264 **Potential intake**

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The potential intake of organic matter (OM) and crude protein (CP) min<sup>-1</sup> (Fig. 5a and 5b) depicts the density of feed actions (i.e., bite codes) and their potential intake rate (i.e., profitability) for each currency (OM or CP), for each species, in each herbivory system along the grazing season periods. A higher potential OM intake (Fig. 5a) was observed in Mixte system for bovine species (27.16 ± 0.67) compared to Monobov (19.53 ± 0.49), equines in the Mixte system (18.59 ± 0.42) and Monoequi (17.02 ± 0.42). The potential OM intake min<sup>-1</sup> did not differ between evaluations periods (P = 0.5357). For CP (Fig. 5b), there was no interaction between systems and period. There was a higher potential intake for bovines in Mixte (4.74 ± 0.12) compared to Monobov system (3.8 ± 0.11). For horses, there was no difference between Mixte (3.36 ± 0.08) and Monoequi systems (2.82 ± 0.06). The potential CP intake g min<sup>-1</sup> was higher in Periods 1 (3.86 ± 0.09) and 2 (3.97 ± 0.09) than in Period 3 (3.18 ± 0.07).

278 **Intake rate**

279 We ranked the profitability currencies of OM and CP min<sup>-1</sup> of bites by height  
 280 classes (Table 1) for each herbivory system, with no interactions with periods. We found  
 281 higher OM intake rates min<sup>-1</sup> for bovines in both Monobov and Mixte systems at sward  
 282 height classes 5-8, 9-13, 14-18 and 19-23 cm (P<0.05). In the same height classes,  
 283 bovines in the Mixte system had a higher OM intake rate compared to Monobov. For

284 equines in the Mixte system, the intake rate was equivalent in all classes for OM  
285 currency, except for the 0-2 cm sward heights. Equines in the Monoequi system had  
286 higher intake rates at sward height classes 5-8, 9-13, and 14-18 cm. Horses showed  
287 similarity in the OM intake rate for all sward height classes between Mixte and Monoequi  
288 systems. When grazing together (Mixte), bovines had higher intake rates than horses in  
289 equivalent sward heights, except for the class 24-30 cm. When verifying the interaction  
290 of height classes between systems for the currency CP, the height classes that promoted  
291 the highest OM intake rates were also the classes that most benefited CP intake for Mixte  
292 bovines. The CP intake of bovines was lower in Monobov compared to Mixte, considering  
293 the sward heights that promoted the highest CP intake rates in both systems (9-13, 14-  
294 18 and 19-23 cm). For the classes 3-4, 14-18 and 24-30 cm, the intake rate of bovines  
295 was not statistically different between systems. Equines had similar CP intake rates for  
296 all sward heights in both systems and lower than bovines.

297         The intake rate of OM and CP of equines and bovines for different botanical types  
298 (Table 2) showed interaction for periods ( $P < 0.05$ ). In Period 1, when observing the  
299 classes of botanical types in each system, we found that cattle in Mixte system had a  
300 higher rate of ingestion of OM  $\text{min}^{-1}$  in bites composed by "grass\_legu", "grass\_forbs"  
301 and "grass\_forbs\_legu", the same for Monobov that also had a higher intake of OM from  
302 these classes and in the "grass" class. Mixte bovines had a similar or higher intake rate  
303 in the most profitable categories compared to Monobov. The rate of OM intake for  
304 equines was similar for all botanical types except for "forbs", with no difference between  
305 systems. In Period 2, Mixte bovines had a similar OM intake rate in the botanical types  
306 "grass\_forbs", "grass\_legu" and "grass\_forbs\_legu". As for the classes "grass\_forbs",  
307 "grass\_legu" with the addition of the type "grass" are the most profitable for Monobov.  
308 Equines had similar intake rates for all types except the "forbs" type with no effect  
309 between systems. In the Mixte system, bovines had ingestion rates higher than equines  
310 for all items except for the "forbs" type, with an equivalent interspecies ingestion rate. In  
311 Period 3, Mixte bovines had similar intake rates for all types except "forbs" and  
312 "grass\_forbs\_legu". For Monobov, the intake rate was equivalent among botanical types.  
313 There was no difference in intake rate of bovines for types in the Mixte system. In the  
314 Monoequi system, only the "forbs" type had a lower intake.

315         The CP intake rate of bovines in the Mixte system was higher in bites with  
316 legumes in Period 1. For bovines in Monobov, the CP intake was similar for all botanical  
317 types except for "forbs", in which it was lower. The CP intake rate for equines in Monoequi  
318 was higher for the types "grass\_legu" and "grass\_forbs\_legu". For equines in the Mixte  
319 system, the highest CP intake occurred in the "grass\_legu" type. In Period 2, Mixte  
320 bovines had a higher rate of ingestion in pieces composed of two or more types. In

321 Monobov, the rates of ingestion did not differ between types. In the Mixte system,  
322 bovines had a higher intake rate than the other systems in the types "grass\_legu" and  
323 "grass\_forbs\_legu". In Period 3, bovines had similar ingestion rates between types  
324 except for the type "forbs", in which it was lower in the Mixte system, whereas in Monobov  
325 the intake rate was equivalent for all types. The CP intake rate of equines was not  
326 statistically different between types and systems. In the Mixte system, bovines had a  
327 higher intake than in Mixte and Monobov in the "grass" and "grass\_legu" types. There  
328 was a greater CP intake by Monobov for the type "forbs", with no statistical difference  
329 from the Mixte system regardless of the species.

330

### 331 **Diet composition**

332 The total number of bites observed during daily observation presented an interaction for  
333 herbivory system and period ( $P < 0.032$ ) (Table 3 and 4). In Periods 1 and 2, no  
334 differences were detected between the systems, with averages of 11582 and 10290 bites  
335 per day respectively. In Period 3, the highest total number of bites was observed in the  
336 Monobov system (18407), followed by equines in the Mixte systems (13466), bovines in  
337 the Mixte system (13092) and Monoequi (10156). The number of bites observed in each  
338 of the sward height classes and botanical types showed a species, system and period  
339 interaction ( $P < 0.001$ ). In Period 1, Mixte bovines selected the diet mainly in the classes  
340 between 5-8 and 9-13 cm, with the class 5-8 cm being the most selected by Monobov.  
341 Mixed equines distributed their diet between 3-4, 5-8, 9-13, 14-18 cm classes. Monoequi  
342 had a higher frequency of bites in the 5-8 cm class. In Period 2, Monobov, Monoequi and  
343 Mixte equines concentrated their bites in the same height classes (5-8, 9-13 and 14-18  
344 cm). Mixte bovines took more bites in classes similar to other treatments, in addition to  
345 class 3-4, 5-8, 9-13 and 14-18 cm. In Period 3, the most frequent height class in the diet  
346 of equines and bovines was 5-8 cm. As for botanical types, Mixte bovines pronouncedly  
347 selected grasses and legumes "grass\_legu" in Period 1, whereas Monobov bovines  
348 distributed their diet in all types, except for forbs. Equines preferred types "grass" and  
349 "grass\_legu" regardless of the herbivory system. In Period 2 Mixte equines took more  
350 bites on grasses than Mixte cattle, and like Monobov and Monoequi. Mixte bovines had  
351 a greater share of "grass\_forbs" in the diet than Monoequi horses, with no statistical  
352 differences from Mixte equines and Monobov bovines. In Period 3, Mixte bovines had a  
353 higher frequency of "grass", "grass\_forbs", and "grass\_legu" bites, whereas the  
354 Monoequi horses composed their diets with grasses and legumes only ("grass" and  
355 "grass\_legu" types). Equines Mixte had most bites in grass type grasses. They have  
356 more pieces in grasses than Mixte bovines and Monoequi, without differing from  
357 Monobov bovines.

358

359 **Diet selection**

360 For the selection of bites in the height classes (Fig. 6), we observed an interaction  
361 between species, system and period ( $P < 0.001$ ). In Period 1, there was a pronounced  
362 positive selection by bovines (+1) for the lowest height class (0-2cm) in both herbivory  
363 systems. For bovines, there was a difference between monospecific positive (+1) and  
364 moderate negative selection for bovines in mixed systems (-0.5). In the 2-4 cm and 5-8  
365 cm height classes, equines and bovines had strong positive selection (+1) regardless of  
366 the system. In the 9-13 cm class, the equines had a neutral index (close to 0), regardless  
367 of the system. Monobov had moderate negative selection (-0.5) and neutral for Mixte  
368 bovines (0). In classes 14-18 and 19-23 cm, horses and cattle had a moderate negative  
369 selection (-0.5). For class 24-30 cm, equines and bovines in both systems had a negative  
370 selection (-1). The 31-40 cm class showed strong negative selection (-1) for bovines  
371 regardless of the herbivory system, moderate negative selection (-0.5) for Mixte equines,  
372 and strong negative selection (-1) for Monoequi. Class 41-50 was not consumed by  
373 bovines and presented a strong negative selection (-1) for Mixte equines and Monoequi  
374 horses. In Period 2 for classes 0-2 and 3-4 cm the selection was moderately negative (0  
375 to -0.5) and did not differ for the same species between systems, nor between species  
376 in the mixed system.

377 The 5-8cm class had moderate positive selection (+0.5), classes (9-13 and 14-  
378 18) neutral selection (0) to animals in all systems. The 19-23cm class had moderate  
379 negative selection (-0.5) to animals in all systems. The 24-30, 31-40, and 41-50cm class  
380 had a negative selection in all systems. In Period 3, the selection was similar to all  
381 systems. The 0-2cm class had moderate negative, moderately positive for 3-4 and 5-8  
382 class, moderate negative for 9-13cm class, and negative for other classes (14-18, 19-23,  
383 24-30, 31-40, and 41 -50).

384 The selection of bites relative to the different botanical types did not show  
385 interaction for periods. The "forbs" type had a pronounced negative selection (-1) for  
386 bovines Intersystem and Mixte equines, and moderate negative for Monoequi (-0.5). The  
387 grass type selection was moderate negative for Mixte bovine and neutral for Monobov.  
388 For bovines, it was neutral (0) regardless of the herbivory system. The type "grass\_forbs"  
389 was slightly rejected (-0.25) by bovines in both systems. However, for equines the  
390 selection was negative in both systems. For "grass\_forbs\_legu", the selection was  
391 slightly positive between systems bovines and mild to moderate negative for Intersystem  
392 equines (-0.25 to -0.5). The type "grass\_legu" did not differ between species between  
393 system was moderately positive for all.

394



395

**396 Discussion****397 Vegetation resource**

398 The animals did not experienced forage resource constrains and therefore this  
399 condition allows to evaluate the expression of feed selection and the foraging effects of  
400 both models on the pastoral ecosystem. As in previous studies (Forteau et al. 2019;  
401 Fleurance et al. 2016) the livestock unit (LU) ha<sup>-1</sup> was used to perform the equivalency  
402 among herbivory systems (Inosys Réseaux d'élevage, 2018 – UGB-Bovine; and Martin  
403 Rosset, 2015 – UGB-Equine). Thus, we had the equivalent of 2 LU ha<sup>-1</sup> in Period 1 and  
404 1 LU ha<sup>-1</sup> in Periods 2 and 3. The difference between periods was adjusted according to  
405 the seasonality of the plant growth.

406 The resource availability in the herbivory systems was isonomic in the canopy  
407 height distribution patterns (Fig. 2), on herbage mass (Fig. 4), herbage accumulation  
408 rates, and total herbage production showing differences between the periods of the  
409 grazing season. Then, we consider the dynamics of occurrence of the potential bites as  
410 an effect of the imposed herbivory system itself since the systems were also balanced in  
411 floristic terms (Fig. 3).

412

**413 Potential Intake rate**

414 The characterization of the bites in the vegetation structure (Fig. 1) (see more  
415 details in Annex 1), and the simulation of the bites allowed us to calculate both the  
416 instantaneous intake rate and to predict the potential intake of nutrients available in each  
417 herbivory system. We found that the mixed herbivory system provided a potentially  
418 higher nutrient intake (i.e., OM and CP) for bovines than the monospecific herbivory  
419 system (Fig. 5). This is because the bites available in the sward would allow bovines to  
420 be more profitable in the bite selected, an advantage that we did not see for the equines  
421 in the same system. For the same potential bites available in the mixed system, the  
422 profitability for equines was not superior to the monospecific system. This point is  
423 consistent with our hypothesis that the mixed herbivory system favors foraging for  
424 bovines, at least in potential terms, with no disadvantage for equines.

425 With the profitability calculated for each bite code, we sought to understand how  
426 the elements that shaped the feed actions (Fig. 1) (sward height and botanical types)  
427 interfered with the intake rate (Table 1 and 2). We examined if the animals select for  
428 profitability as inferring foraging models (Stephens and Krebs 1986; Spalinger & Hobbs  
429 1992) in addition, checking if the bovines exploited the potential of the mixed system and  
430 if the equines followed the same pattern of foraging of that in monospecific systems to  
431 optimize the intake of OM and CP (Bergman et al. 2001; Edouard et al. 2010).

432           The prediction that the mixed system presents a greater availability of bites with  
433 higher potential intake rate in OM and CP (Fig. 5) currencies for bovines and indifferent  
434 for equines is a less static way of referring to the forage resource and quantifying the  
435 potential ingestive responses resulting from cause-and-effect relationship in grazing  
436 systems (Parsons & Penning 1988). Our prediction considered the different peculiarities  
437 of foraging in sympatric equines and bovines or in a monospecific system as suggested  
438 by Lamoot et al. (2005) and Karmiris et al. (2011).

439           We attributed a facilitation interaction (McNaughton 1976; Sinclair and Norton-  
440 Griffiths 1982; Arsenault and Owen-Smith. 2008) from equines to bovines by predicting  
441 the highest potential intake rate for bovines in the mixed system, with no negative effect  
442 for equines. The potential CP (Fig. 5b) intake rate was also higher for bovines, despite  
443 the reduction in the potential CP intake rate observed in Period 3 (Fig. 5b). This  
444 difference might be related to forage resource maturation (Drescher et al. 2006). No  
445 matter how much the animals have the ability to select higher than available nutritional  
446 value (Prache et al.1998), the structural limits for ingestion (Ungar and Demment. 1991)  
447 reflected in the lower levels of nutrient intake at the end of the grazing season (Fryxell  
448 1991), which was verified in the content of the observed bites that supported this  
449 prediction.

450

#### 451 **Intake rate**

452           The higher intake rates observed for bovines and equines (Table 1 and 2) in  
453 intermediate heights are consistent with other studies that considered this factor and  
454 conceived the highest intake rate within these limits, as the forage maturation theory  
455 (Drescher et al. 2006). The constrain imposed by digestibility does not seem to be the  
456 strongest in our case, but the benefits of for ingestibility do (Fryxell 1991), for this  
457 considering the morphophysiology of the bovine oral apparatus, which can expand the  
458 bite size by using the tongue (Illius and Gordon 1987) making cattle able to take bites  
459 with greater density (Shipley 2007) and therefore suffering less with the effects of the  
460 canopy dispersion at taller heights (Gordon and Benvenuti 2006).

461           The same classes that optimized the OM intake rate also optimized the CP intake  
462 for bovines in the mixed herbivory system (Table 1). Cattle in the monospecific system  
463 had a lower number of profitable classes for CP available than mixed bovines. In the  
464 lower classes (0-2 and 3-4 cm) and classes above 24-30 cm, the intake rate was  
465 equivalent for bovines in both systems. It is likely that below the lower limit the intake  
466 rate was compromised by the limited harvesting capacity of bites at excessively short  
467 swards (Allden and Whitakker 1970; Laca et al. 1992; Mezzalira et al. 2017; Nadin et al.  
468 2019), while beyond the upper limit it was compromised by the searching time and

469 manipulation of taller, sparse plants, which ended compromising bite formation as well  
470 (Wallis de Vries, Laca and Demment 1998; Gordon and Benvenuti, 2006).

471 In comparative terms, equine have an equal or lower intake rate of OM and CP  
472 than Monobov, and lower than Mixte bovines. This difference was already presented by  
473 previous authors (Bell 1971; Janis 1976; Duncan et al. 1990), as there were no major  
474 differences in the concentration of nutrients in the yield of feeding actions (to be noticed  
475 in the OM and CP contents of intake rates, Table 1 and 2). The ingestive response is  
476 more dependent on the factors previously mentioned that interfere in instantaneous  
477 intake.

478 Based on our intake rate results, the coexistence of equines and bovines shows  
479 an advantage in the intake rate of bovines, consistent in part with our hypothesis. On the  
480 other hand, the intake rate of OM and CP was similar for equines, regardless of the  
481 system. As we found a greater similarity in the interclass intake rates for Mixte bovines  
482 compared to Monoequi, we suggest that this higher intake rate in the diversity of height  
483 classes could provide a strategy for optimizing nutrient intake. However, it is not clear  
484 whether horses would have a preference for optimizing CP intake (Edouard et al. 2010;  
485 Fleurance et al. 2005), but we can infer that this optimization would not be limited by  
486 competition with bovines in the case of the Mixte system, as predicted and reflected in  
487 the composition of the diet.

488 The differentiated oral morphology of equines (lip mobility and upper incisors)  
489 gives them the capacity for greater elasticity in feeding actions by manipulating  
490 vegetation structures and allowing them to more easily adapt to the structural challenges  
491 of swards (Shipley, 2007). This characteristic could explain why equines achieve rates  
492 of ingestion in some conditions similar to bovines (e.g., classes 3-4 cm). This would be  
493 a useful strategy for coexistence when competing with another herbivore (Duncan 1990).  
494 In our case, bovines that are skilled at higher ingestion rates in the most profitable  
495 structural strata (Table 1).

496 Although the Mixte equines were exposed to the effects of competition with the  
497 bovines, they were able to explore the sward height gradient in equal or superior  
498 profitability that the Monoequi equines through their foraging elasticity, which does not  
499 denote a disadvantage of the mixed herbivory system. At this point, it would be consistent  
500 with our hypothesis that the mixed system provides an ingestion rate for both species,  
501 and that equines explore the greatest range of feeding actions for ingestion as an  
502 adaptive effect to competition (Janis and Ehrhardt 1988).

503

#### 504 **Diet Composition and Selection**

505

506 We assume that the non-harmful conditions for equines and advantageous for  
507 bovines in the mixed system predicted by the potential intake reflected in the composition  
508 of the diet. At the time of greatest stocking density, we credit the elasticity of foraging by  
509 equines on exploring the sward structure to optimize intake, which is consistent with our  
510 hypotheses (Janis and Ehrhardt 1988; Duncan 1990; Bukombe et al. 2019). At the  
511 beginning of the season, the bovine diet does not differ in botanical types of bites (Table  
512 4). More than half of the bites of Mixte bovines are in the "grass\_legu" type, which  
513 optimizes the intake rate of OM and CP and with positive selectivity for all animals. For  
514 Monobov, the diet partition is balanced between types "grass", "grass\_forbs and  
515 "grass\_legu"

516 However, although the hierarchy of types in the diet is different for bovines, the  
517 proportions are equivalent between systems. Equine diets do not differ in types. The  
518 interspecies botanical types in the Mixte system do not differ, showing a niche overlap  
519 for this period. Equines and bovines compete for the same types for the elaboration of  
520 the diet but explore different compartments in the canopy structure. We attribute this to  
521 a complementarity effect (Sinclair and Norton-Griffiths. 1982) at this moment in the mixed  
522 system, which guarantees the equivalent intake between equines between systems, and  
523 the facilitation that allows bovines to exercise preference for the profitability in bites  
524 (Arsenault and Owen-Smith 2002; McNaughton 1976).

525 For equines, the diet composition was similar between the hierarchy of botanical  
526 types, with the most participatory being "grass" (neutral selectivity) and "grass\_legu"  
527 (positive selectivity). Mixte equines took more bites of "grass" type than Monoequi. This  
528 would be a disadvantage of the system to bovines for the intake rate, but it is consistent  
529 with other studies that show preference of horses for grasses (Fleurance et al. 2016). In  
530 the Mixte system, bovines had more "grass\_forbs" than equines, the latter rejecting this  
531 type whereas it presented null selectivity by bovines. The equines have more "grass"  
532 bites (null selectivity) in the diet than bovines (rejected), supporting the complementarity  
533 of niches, because in the same gradient of height strata, they explore different  
534 components (Gwyne and Bell 1968; Putman et al 1987; Murray and Illius 2000; Arsenault  
535 and Owen-Smith 2008).

536 Period 3 was under the effect of canopy structure depletion (Fig. 2 and 3) and  
537 presenting the memory of the effects of grazing on the herbivory systems (Monoequi,  
538 Monobov, and Mixte). The bovines exercised their preference and composed their diet  
539 by optimizing the intake rate (5-8), however, the bovines Monobov have ~ 30% of the  
540 diet in the preferred class (3-4cm) but outside the maximum intake rate, therefore  
541 penalizing the foraging. We can understand the consumption of the types 'grass' and

542 mainly 'grass\_legu' as a compensatory selection for Monobovs since these types make  
543 up most of the diet in this period and have a null and positive selection, respectively.

544 In conditions where the pastoral ecosystem imposed constraints due to the higher  
545 stock density or resource depletion, sympatric animals explore the complementarity and  
546 facilitation of niches to optimize intake rates. We noticed that equines were able to  
547 compensate for the competition for forage resources with bovines by modulating the  
548 selection of the diet in classes of the height of the canopy and in botanical such as grass  
549 for horses and grass legu for cattle, exploring the gradient of heights (Table 3 and 4).  
550 This factor has already been mentioned in studies with equines and bovines in which the  
551 diversification of the diet allows success in equines foraging (Bell 1971) compared to  
552 cattle that potentially have higher ingestion rates. We verified this phenomenon where  
553 similar accumulated daily consumption was observed between species and systems  
554 (Table 5). Because of foraging elasticity (Belovsky 1997; Laca et al. 2010), equines had  
555 similar ingestion rates for many height classes and in different botanical types in the  
556 universe of potential bites.

557 We credit oral and lip mobility, which denotes an important tool for the challenge  
558 of the animal-plant interface in foraging (Flores et al. 1993; Naujeck, Hill and Gibb 2005),  
559 for preparation of bites (apprehension and cutting), such as exploring parts of plants in  
560 the selection (e.g., claw bites on leaf tips), or shallow bites in structural components of  
561 legumes (e.g., "grass\_legu" in which equines press the canopy against the ground).  
562 Therefore, equines, even when sharing patches (Bailey 1996), have greater possibilities  
563 to explore the diversity of feeding actions (bites), even though in the universe of equine  
564 and bovine bites they explored a similar number of bite codes.

565

## 566 **Conclusion**

567 Our results support the positive property of mixed herbivory systems for bovines  
568 and without prejudice for equines when compared to monospecific herbivory systems.  
569 The scale of observation of the study, the bites, allowed checking the animals' ability to  
570 modulate their diet selection to optimize intake rate. During the grazing season, with the  
571 effects of the variation in stock density and depletion of the advantage resource for the  
572 intake rate of bovines and horses in the mixed herbivory systems.

573

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588

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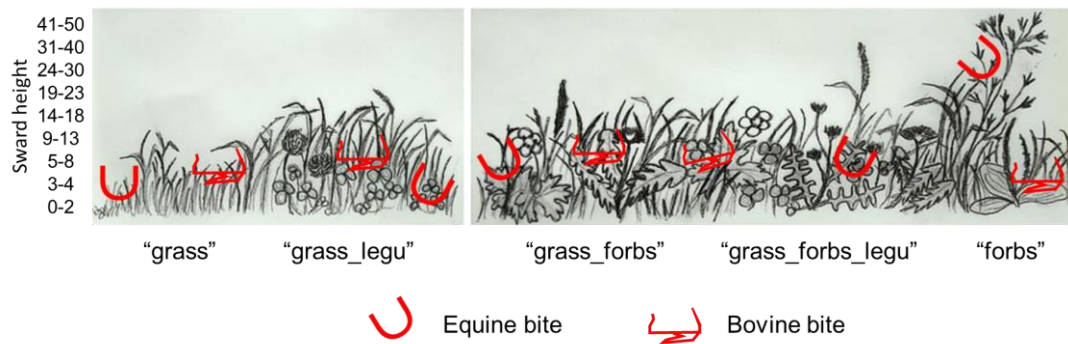
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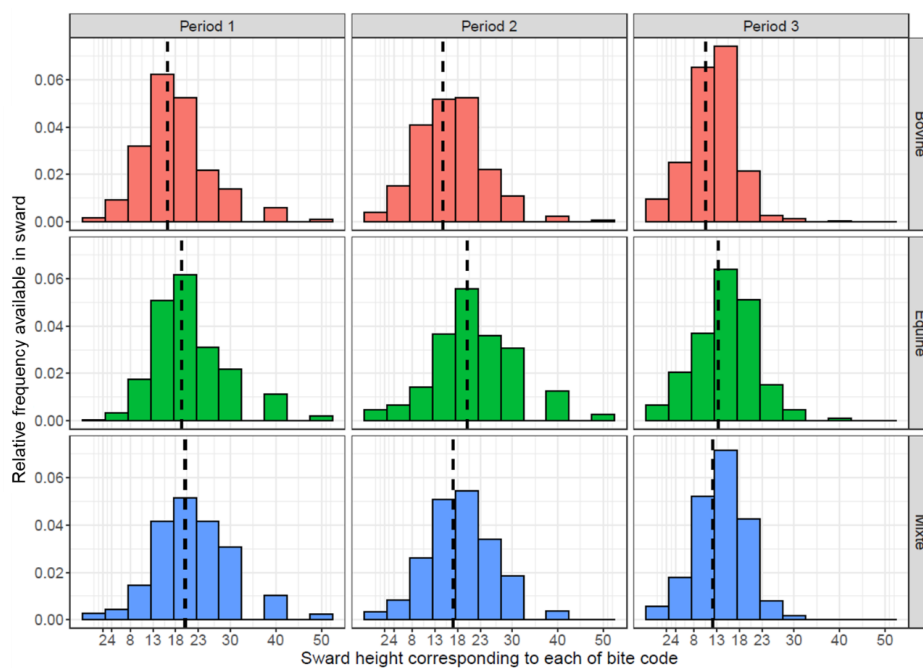
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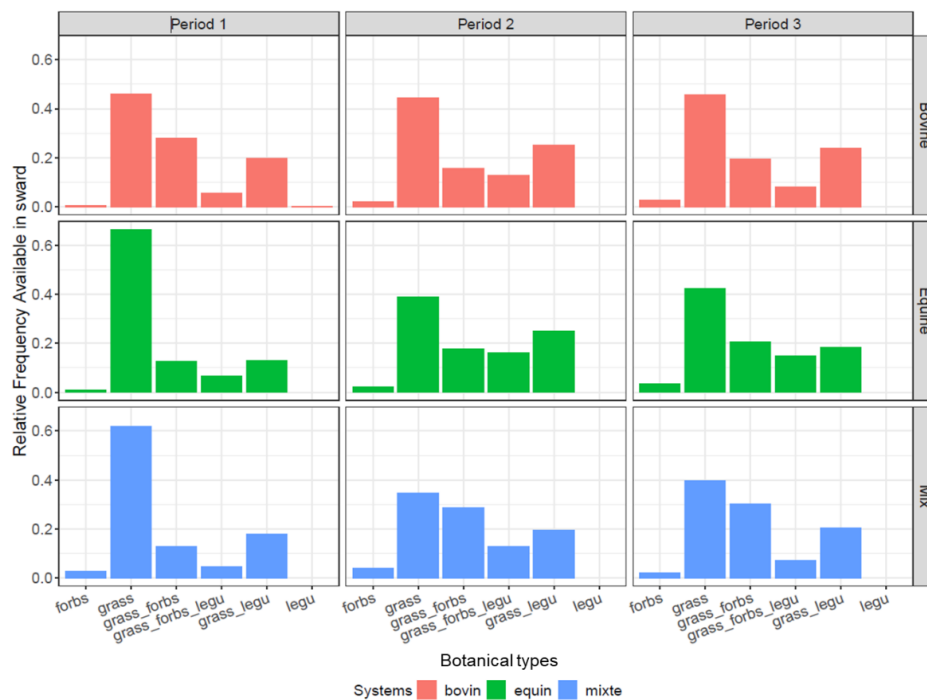
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**Fig.1** Characterization of bite codes according to botanical types



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**Fig.2** Relative frequency the sward height classes of bites available accounted in sward structure. Section lines represent of the average of the height classes. Periods: 1) May and June; 2) July and August; and 3) September and October.



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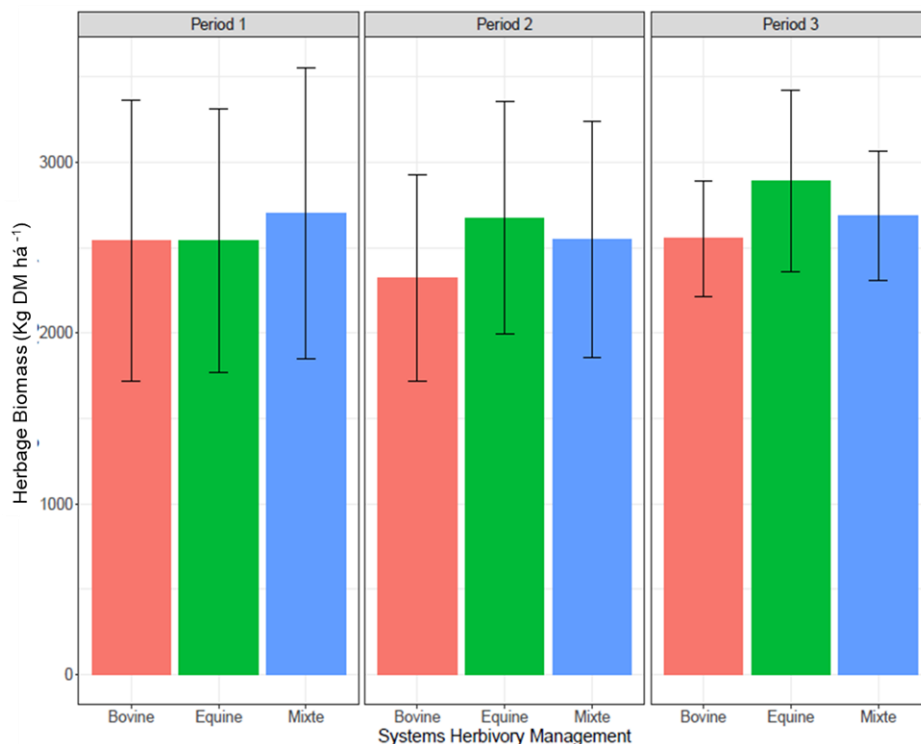
846 **Fig.3** Botanical composition corresponding of bites available accounted in sward  
 847 structure. Periods: 1) May and June; 2) July and August; and 3) September and October.

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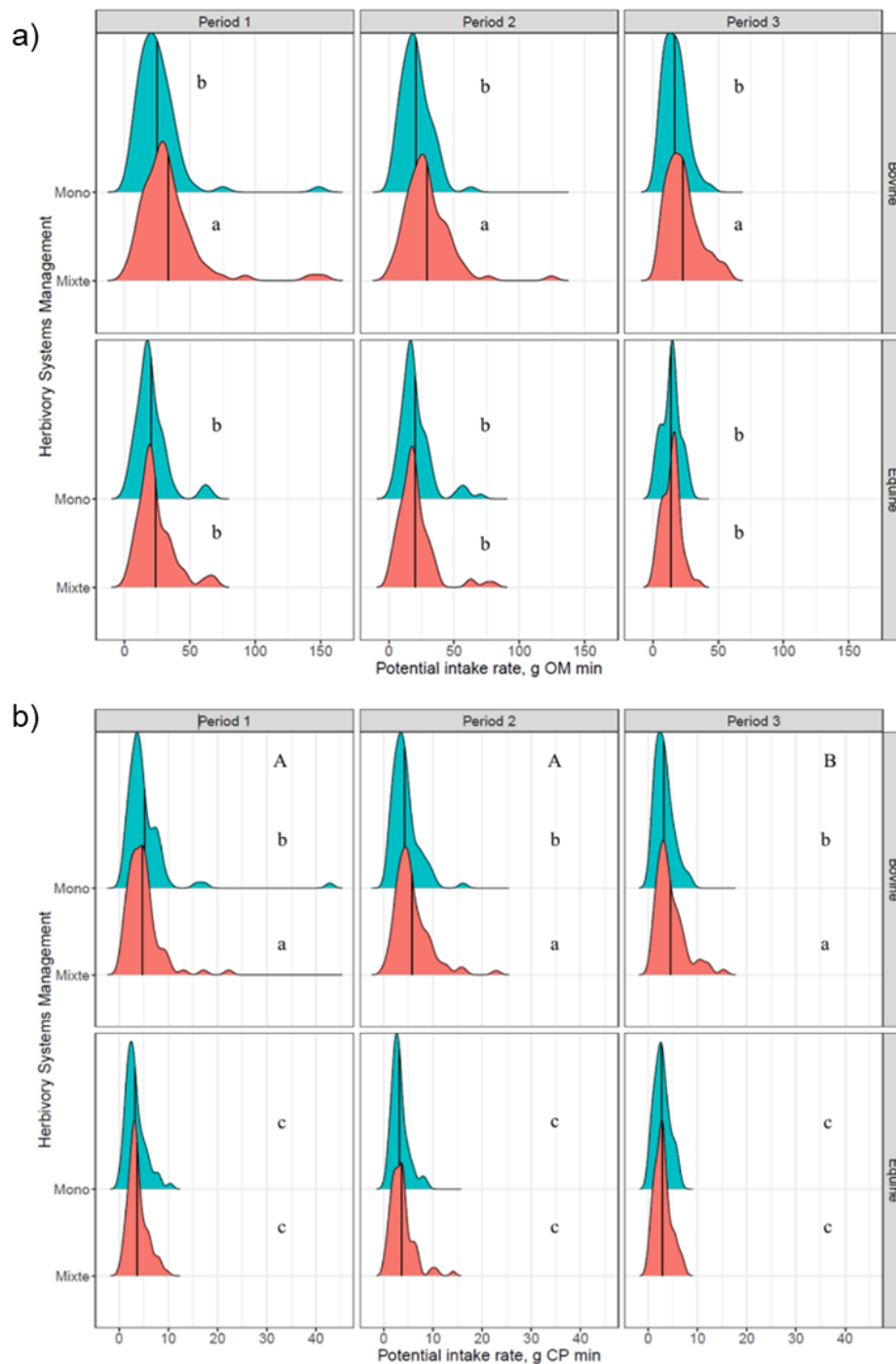
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853 **Fig.4** Herbage biomass kg DM ha<sup>-1</sup> of the resource available was calculated with base  
 854 by the linear models were generated between herbage biomass and the average sward  
 855 height observed in the quadrat with the intercept adjusted to zero to each availed period  
 856 [Period 1:  $y = 115.86x + 0$ ,  $R^2 = 0.89$   $P < 0.001$ ; Period 2:  $y = 121.58x + 0$ ,  $R^2 = 0.77$ ,  $P$   
 857  $< 0.001$ ; Period 3:  $y = 236.62x + 0$ ,  $R^2 = 0.93$ ,  $P < 0.001$ ]. Subsequently, the equations and

858 height measurements in each system were predicted the herbage biomass available.  
 859 Periods: 1) May and June; 2) July and August; and 3) September and October.  
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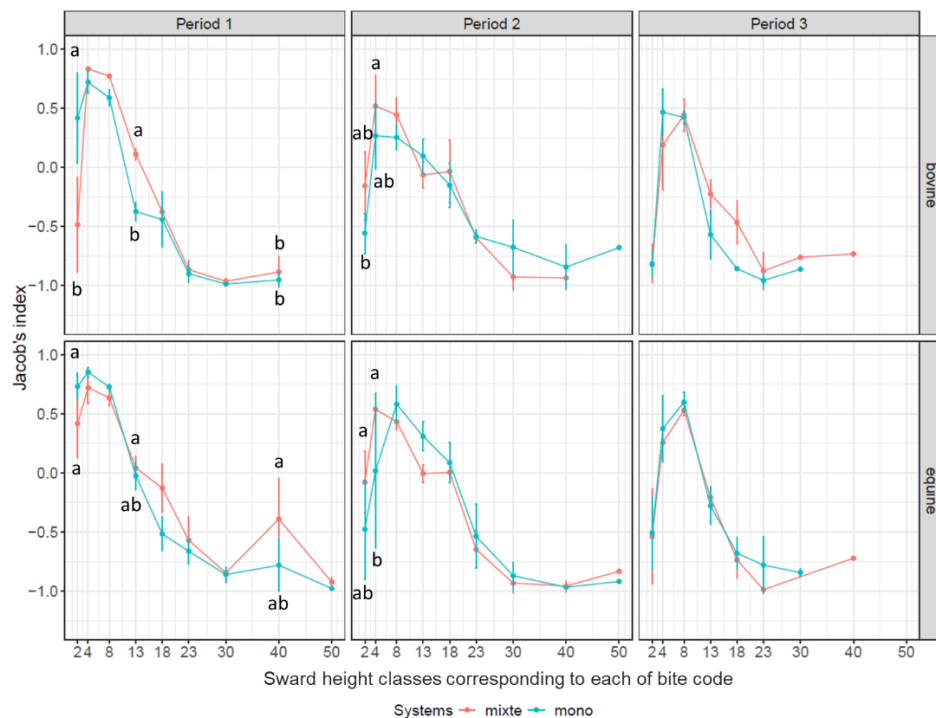


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864 **Fig.5** Potential intake rate of (a) organic matter (OM) and (b) crude protein (CP) predicted  
 865 by the profitability of the bite-codes available in the canopy (x axis) for each herbivory  
 866 system and animal model (y axis) over the stocking season. The potential OM and CP  
 867 intake rates ( $\text{g min}^{-1}$ ) were calculated considering the profitability of each bite type  
 868 predicted based on the nutritional value obtained by hand plucking sampling for each  
 869 bite-code recorded during the Continuous Bite Monitoring evaluation. Periods: 1) May  
 870 and June; 2) July and August; and 3) September and October.



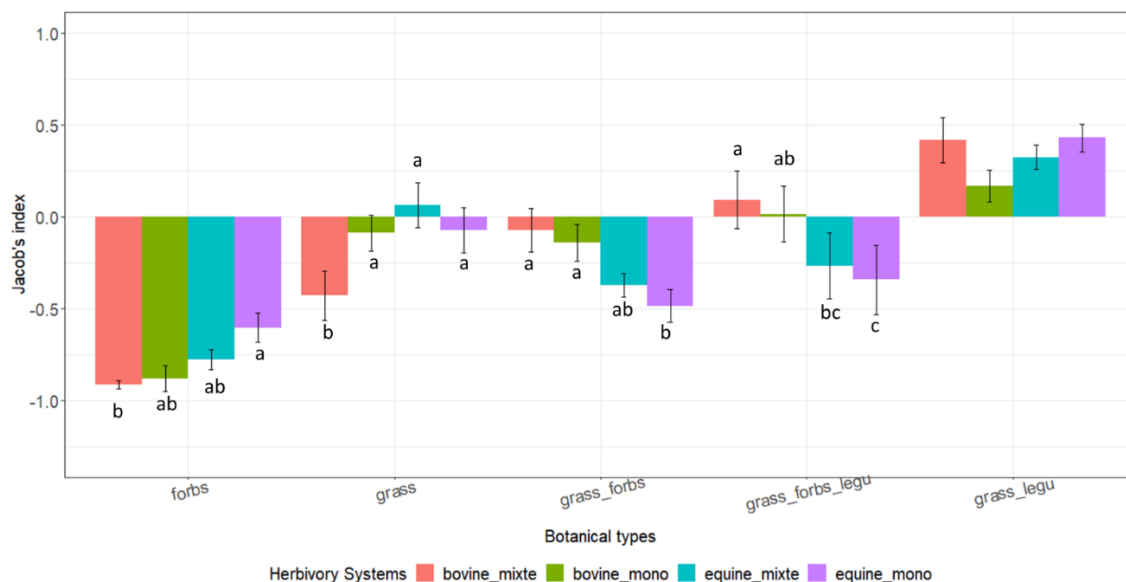


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872 **Fig.6** Diet selection of the sward height classes by Jacob's index; Varies from -1 (never  
 873 used) to +1 (used exclusively), with negative and positive values indicating evasion and  
 874 preference, respectively, and 0 indicating that a component of the sward is used in  
 875 proportion to its availability. The different letters refer to statistical difference ( $P < 0.05$ )  
 876 by the Bonferroni multiple comparison test.

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880 **Fig.7** Diet selection of the botanical types by Jacob's index; Varies from -1 (never  
 881 used) to +1 (used exclusively), with negative and positive values indicating evasion and  
 882 preference, respectively, and 0 indicating that a component of the sward is used in  
 883 proportion to its availability. The different letters refer to statistical difference ( $P < 0.05$ )  
 884 by the Bonferroni multiple comparison test.



885 **Table 1. Intake rate by sward height classes of bites**

Species	Equine		Bovine		
	Mono	Mixte	Mono	Mixte	
Currency					
Organic matter (g min <sup>-1</sup> )					
Height (cm)	0-2	6.31 (1.085) d	6.21 (0.982) b	7.55 (0.997) c	7.00 (1.165) c
	3-4	7.70 (0.773) bc	7.32 (0.707) a	8.14 (0.710) bc	9.94 (0.689) b
	5-8	10.00 (0.683) a B	9.06 (0.675) a B	10.47 (0.683) a B	13.25 (0.653) a A
	9-13	9.29 (0.651) ab B	8.75 (0.660) a B	11.50 (0.672) a B	14.21 (0.637) a A
	14-18	9.64 (0.683) ab C	9.37 (0.676) a C	12.30 (0.702) a B	15.48 (0.646) a A
	19-23	8.68 (0.813) bc B	10.25 (1.062) a B	9.80 (1.249) ab B	16.20 (0.804) a A
	24-30	6.88 (0.995) cd B	-----	9.50 (1.689) bc AB	10.42 (1.668) b A
	31-40	-----	7.54 (1.845) ab	-----	11.87 (1.816) bc
	41-50	-----	-----	-----	-----
Currency					
Crude protein (g min <sup>-1</sup> )					
Height (cm)	0-2	1.27 (0.209) bc	1.29 (0.187) b	1.65 (0.190) d	1.43 (0.226) d
	3-4	1.38 (0.141) abc B	1.49 (0.125) a AB	1.68 (0.126) cd AB	1.93 (0.121) bc A
	5-8	1.71 (0.120) a B	1.70 (0.118) a B	2.01 (0.120) bc B	2.38(0.113) ab A
	9-13	1.56 (0.112) ab B	1.65 (0.114) a B	2.29 (0.117) ab B	2.55 (0.109) a A
	14-18	1.61 (0.120) ab C	1.65 (0.118) a BC	2.28 (0.124) a AB	2.63 (0.111) a A
	19-23	1.55 (0.150) abc C	2.27 (0.204) a BC	2.25 (0.244) ab B	2.99 (0.148) a A
	24-30	1.25 (0.190) c B	-----	2.02 (0.336) bcd AB	2.06 (0.332) cd A
	31-40	-----	0.811 (0.369) c	-----	1.49 (0.363) d
	41-50	-----	-----	-----	-----

886 Letters lowercase in column refer to the statistical difference between height classes to  
887 specie. Uppercase letters in on lines refer statistical difference between species in  
888 treatments (P <0.05) by the Bonferroni multiple comparison test, (\*) mean standard error.  
889 The intake rate for each height class was calculated whit time per bite code, we used  
890 intervals with a sequence of the same bite code and divided the number of bites by the  
891 duration of each interval. After we checked the intake rate of each bite code in each  
892 height class in the sward.

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**Table 2. Intake rate by botanical types by species in each herbivory system**

Species	Equine				Bovine				
	Equine		Bovine		Equine		Bovine		
System	Mono	Mixte	Mono	Mixte	Mono	Mixte	Mono	Mixte	
	Currency OM g min <sup>-1</sup>				Currency CP g min <sup>-1</sup>				
Period 1	forbs	7.46 (1.220) b A	5.26 (1.332) b AB	3.30 (1.584) b B	6.99 (1.187) c A	1.220 (0.232) b A	0.928 (0.255) c A	0.757 (0.306) b B	1.681 (0.225) c A
	grass	7.55 (0.848) ab B	6.15 (0.805) a B	8.22 (0.798) a AB	10.66 (0.802) b A	1.458 (0.154) b	1.543 (0.145) b	2.040 (0.143) a	1.954 (0.144) bc
	grass_forbs	10.80 (0.835) a B	9.35 (0.721) a B	11.52 (0.753) a B	17.00 (0.697) ab A	1.410 (0.151) b B	1.395 (0.126) b B	2.405 (0.134) a A	2.148 (0.121) b AB
	grass_legu	11.33 (0.909) a B	10.92 (0.947) a B	13.08 (0.927) a B	20.76 (0.968) a A	2.452 (0.167) a	2.383 (0.175) a	2.235 (0.171) a	3.067 (0.180) a
	grass_forbs_legu	11.71 (0.850) a A B	9.24 (0.946) a B	11.45 (0.749) a AB	16.31 (0.779) ab A	1.989 (0.154) a AB	1.740 (0.175) b B	2.113 (0.133) a AB	2.443 (0.139) ab A
Period 2	forbs	4.75 (1.187) b B	5.21 (1.134) b AB	5.82 (1.965) c B	10.07 (1.584) c A	0.696 (0.225) b C	1.243 (0.214) b BC	1.630 (0.383) AB	1.861 (0.306) c A
	grass	6.26 (0.893) ab B	6.57 (0.888) ab B	8.57 (0.905) ab AB	10.30 (0.859) b A	1.213 (0.164) ab B	1.410 (0.163) ab AB	1.649 (0.166) AB	2.327 (0.157) bc A
	grass_forbs	8.66 (0.731) ab B	9.21 (0.728) a B	11.07 (0.822) ab AB	15.46 (0.714) ab A	1.601 (0.129) a B	1.557 (0.128) b B	1.751 (0.148) AB	2.612 (0.125) ab A
	grass_legu	9.17 (0.947) a B	10.83 (0.918) a B	12.69 (1.122) a B	17.00 (0.917) a A	1.511 (0.175) a B	2.063(0.169) a B	2.081 (0.169) B	3.707 (0.212) a A
	grass_forbs_legu	10.12 (0.895) a B	10.48 (0.936) a B	10.42 (0.979) bc B	15.92 (0.831) ab A	1.655 (0.164) a B	2.110 (0.173) a B	1.884 (0.182) B	3.226 (0.151) ab A
Period 3	forbs	4.53 (1.135) b AB	4.95 (1.439) AB	8.03 (1.957) A	6.35 (1.958) c AB	0.868 (0.215) b B	1.062 (0.277) b AB	2.359 (0.382) A	1.402 (0.382) b AB
	grass	6.97 (0.901) ab	7.75 (0.980)	8.58 (0.946)	9.72 (0.872) ab	1.425 (0.165) ab B	1.928 (0.182) a AB	1.405(0.175) B	2.056 (0.159) a A
	grass_forbs	9.15 (0.805) ab	9.18 (0.809)	10.30 (0.843)	10.61 (0.789) ab	1.509 (0.145) ab	1.754 (0.146) a	1.951 (0.153)	1.894 (0.141) ab
	grass_legu	9.28 (1.006) a B	9.07 (1.053) AB	11.22 (1.020) AB	13.01 (1.020) a A	1.565 (0.188) a B	1.797 (0.198) a AB	1.624 (0.191) B	2.238 (0.191) a A
	grass_forbs_legu	8.78 (1.008) ab	8.27 (0.981)	9.76 (0.919)	9.0 (0.865) bc	1.705 (0.188) a	1.631 (0.182) a	1.593 (0.169)	1.791 (0.158) ab

Letters lowercase in column refer to the statistical difference between botanical types to specie. Uppercase letters in on lines refer statistical difference between species in treatments ( $P < 0.05$ ) by the Bonferroni multiple comparison test, (\*) mean standard error.

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**Table 3. Diet composition by Sward height classes of bites**

Species		Equine				Bovine				
System		mono		mixte		mono		mixte		
Diet		bites %	bites n	bites %	bites n	bites %	bites n	bites %	bites n	
total bites observed			11864.0		9810.7		13132.7		11266.7	
Period 1	height (cm)	0-2	0.016	192.2 de	0.040	396.4 bc	0.029	379.5 de	0.006	64.2 c
		3-4	0.177	2102.3 b AB	0.144	1413.7abc B	0.241	3165.0 b A	0.201	2266.9 b AB
		5-8	0.380	4509.5 a A	0.265	2603.8 a B	0.425	5581.4 a A	0.382	4303.9 a AB
		9-13	0.247	2929.2 bc	0.224	2193.7 ab	0.171	2249.6 bc	0.248	2793.0 ab
		14-18	0.126	1494.9 cd	0.216	2120.1 ab	0.125	1637.6 cd	0.138	1555.9 bc
		19-23	0.036	429.5 e	0.069	677.9 bc	0.007	85.4 e	0.060	676.0 c
		24-30	0.009	109.1 e	0.015	147.2 c	0.001	6.6 e	0.003	37.2 c
		31-40	0.008	92.5 e	0.026	250.2 bc	0.001	9.2 e	0.003	38.3 c
		41-50	0.000	1.2 e	0.004	3.9 c	0.000	0.0	0.000	0.0
total bites observed			8303.7		11643.7		8253.5		11252.3	
Period 2	height (cm)	0-2	0.001	7.9 c	0.015	178.1 bc	0.006	48.7 c	0.013	150.8 b
		3-4	0.050	416.0 bc	0.131	1521.8 b	0.136	1121.7 bc	0.142	1596.7 ab
		5-8	0.242	2012.0 a	0.278	3235.8 a	0.304	2510.7 a	0.190	2135.7 a
		9-13	0.302	2506.0 a	0.254	2954.0 a	0.299	2470.3 a	0.233	2622.9 a
		14-18	0.319	2650.5 ab	0.275	3204.3 a	0.210	1732.4 ab	0.268	3011.1 a
		19-23	0.066	548.0 bc	0.043	499.5 bc	0.032	261.6 c	0.050	557.0 b
		24-30	0.013	107.1 c	0.004	43.1 c	0.012	94.9 c	0.040	45.0 b
		31-40	0.001	9.1 c	0.000	4.7 c	0.001	7.4 c	0.060	68.0 b
		41-50	0.001	4.2 c	0.001	9.3 c	0.001	4.1 c	0.000	0.0
total bites observed			10203.3		13481		18397.7		13077.3	
Period 3	height (cm)	0-2	0.012	123.5 d	0.011	141.6 de	0.005	90.1 d	0.003	41.8 d
		3-4	0.222	2269.2 b B	0.144	1944.0 b B	0.298	5478.8 b A	0.156	2044.0 bcB
		5-8	0.478	4880.3 aC	0.534	7202.9 a B	0.546	10041.4 a A	0.482	6303.3 aBC
		9-13	0.211	2157.0 c	0.270	3633.1 b	0.142	2606.9 c	0.262	3427.6 b
		14-18	0.062	636.7 d	0.041	552.7 cd	0.009	167.4 d	0.093	1212.3 cd
		19-23	0.011	112.2 d	0.002	2.7 e	0.000	5.5 d	0.000	3.9 d
		24-30	0.001	20.4 d	0.000	0.0 e	0.001	9.2 d	0.001	15.7 d
		31-40	0.000	0.0	0.000	0.0 e	0.000	0.0	0.001	7.8 d
		41-50	0.000	0.0	0.000	0.0 e	0.000	0.0	0.000	0.0

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Letters lowercase in column refer to the statistical difference between height classes to specie. Uppercase letters in on lines refer statistical difference between species in treatments (P <0.05) by the Bonferroni multiple comparison test.

908

**Table 4. Diet composition by Botanical types of bites**

Species	Equine				Bovine				
	System	Mono		Mixte		Mono		Mixte	
Diet	bites %	n bites	bites %	n bites	bites %	n bites	bites %	n bites	
total bites observed		11864		9810.7		13132.7		11266.7	
Period 1	forbs	0.006	68.8 c	0.002	18.6 c	0.001	7.9 b	0.002	21.4 b
	grass	0.413	4899.8 a A	0.412	4040.0 a AB	0.309	4055.4 a AB	0.138	1550.3 b B
	grass_forbs	0.074	882.7 bc	0.084	824.1 c	0.245	3210.9 a	0.11	1239.3 b
	grass_legu	0.326	3872.4 ab B	0.392	3843.8 ab AB	0.301	3955.6 a AB	0.562	6331.9 a A
	grass_forbs_legu	0.18	2137.9 abc	0.110b	1082.1 bc	0.145	1899.0 ab	0.188	2121.5 b
total bites observed		8303.7		11643.7		8253.5		11252.3	
Period 2	forbs	0.007	55.6 b	0.009	107.1c	0.005	42.1b	0.002	27.0 b
	grass	0.445	3691.8 a AB	0.439	5110.4 a A	0.476	3932.0 a AB	0.161	1813.9 ab B
	grass_forbs	0.075	622.8 b B	0.135	1566.1 bc AB	0.17	1403.1 ab AB	0.374	4203.9 a A
	grass_legu	0.423	3513.3 a	0.373	4346.6 ab	0.211	1743.1ab	0.372	4183.6 a
	grass_forbs_legu	0.05	417.7b	0.044	508.8 c	0.136	1124.1ab	0.091	1024.0 b
total bites observed		10203.3		13481		18397.7		13077.3	
Period 3	forbs	0.59	60.2b	0.003	36.4 c	0	3.7 b	0.001	7.8b
	grass	50.43	5145.5 a B	0.605	8152.0 a A	0.483	8884.2 a A	0.41	5363.0 a B
	grass_forbs	4.92	502.0 b	0.139	1871.2 bc	0.114	2091.8 b	0.205	2676.9 ab
	grass_legu	41.53	4237.4 a AB	0.228	3075.0 b B	0.363	6676.5 a A	0.324	4239.7a AB
	grass_forbs_legu	2.5	255.1 b	0.026	343.8 bc	0.04	737.7 b	0.06	130.8 b

Letters lowercase in column refer to the statistical difference between height classes to specie. Uppercase letters in on lines refer statistical difference between species in treatments ( $P < 0.05$ ) by the Bonferroni multiple comparison test.

**Table 5. General variables of the intake process**

Variables	Bovine		Equine		Period			<i>P</i> system	<i>P</i> Period	Interaction
	Mono	Mixte	Mono	Mixte	1	2	3			
Cumulative intake observed of the OM (g)	1469.5 (121)	1656.7 (112)	1521.9 (112)	1490.9 (112)	1180.9 (90)	1467.3 (96)	1596.0 (90)	0.7414	0.7584	0.1744
Intake rate DM (g min <sup>-1</sup> )	5.51ab (0.50)	8.04a (0.48)	5.42b (0.46)	5.03ab (0.48)	6.73a (0.29)	5.64ab (0.36)	5.64b (0.32)	0.0185	0.0235	0.1538
Intake rate currency. OM (g min <sup>-1</sup> )	20.72b (1.00)	28.44a (0.95)	18.09b (1.01)	19.11b (0.99)	25.55a (0.84)	22.54b (0.80)	16.69c (0.92)	<0.001	<0.001	0.5357
Bite mass (g)	0.27a (0.02)	0.33b (0.02)	0.34a (0.02)	0.30ab (0.01)	0.30b (0.01)	0.34a (0.01)	0.28c (0.01)	<0.001	<0.001	0.1501
Bite rate (bites min <sup>-1</sup> )	29.55ab (2.49)	32.40a (2.40)	21.95b (2.39)	23.87b (2.34)	29.6a (1.39)	23.33b (1.65)	27.38ab (1.51)	0.0088	<0.001	0.1501
Number of bite-code observed in grazing saeson (n)	67.6 (3.88)	74.6 (3.56)	65.3 (3.56)	66.0 (3.56)	78.0a (3.04)	72.9a (3.20)	54.1b (3.04)	0.2453	<0.001	0.6284

Different letters in the column indicate statistical difference between sward height classes for each animal species in each system ( $P < 0.05$ ). (\*) mean standard error.

## CAPÍTULO IV

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<sup>1</sup> Doctoral thesis in Animal Science, Faculty of Agronomy, Federal University of Rio Grande do Sul, Porto Alegre, RS, Brazil. (124 p.). April, 2021.

#### 4.1 CONSIDERAÇÕES FINAIS

No capítulo II, foi apresentado os limites de precisão para quantificar o consumo de herbívoros em pastejo. A metodologia CBM apresenta um detalhamento refinado para caracterização instantânea da seleção de dietas, e o respaldo com o resultado deste estudo confere uma potencialidade para a utilização desta, no estudo de fluxos de ingestão em pastos de natureza diversa. Visto que a capacitação para a metodologia é capaz de preparar avaliadores para o conhecimento do recurso forrageiro, caracterização do mesmo e capacidade de mimetizar em termos seguros ~ 0,86 a quantidade ingerida pelos herbívoros.

No capítulo III, foi apresentada a vantagem do sistema de herbivoria mista por equinos e bovinos simpátricos para oportunidades potenciais de taxas de ingestão. Esta potencialidade proveniente da rentabilidade de cada bocado para cada espécie, considerando as particularidades da interface planta – animal interespecífica.

O sistema misto apresentou maior taxa de ingestão potencial aos bovinos durante todo o período da estação de pastejo (primavera-outono), e não apresentou desvantagem para os equinos em sistema misto ao sistema monoespecífico. O sistema misto oportunizou aos bovinos a seleção de bocados de maior taxa de ingestão, refletidos na composição da dieta. E os equinos modularam a ingestão, explorando maior diversidade estrutural da estrutura do pasto (por rendimentos semelhantes em bocados em estruturas distintas) para otimizar a ingestão. Atribuímos à complementaridade interespecífica de nichos, e a facilitação dos equinos para com bovinos as melhores condições para ingestibilidade no sistema misto.

Estas respostas auxiliam no entendimento dos mecanismos pelos quais a coexistência pode prover uma interação positiva para otimizar a ingestão que é o fator determinante para performance animal. Além disso, subsidia o incremento de

diversidade para a exploração de ambientes pastoris, com as valências que o incremento de diversidade pode conferir, como melhor utilização dos recursos e potencialização das funções ecológicas destes ambientes.



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## APÊNDICES

**Apêndice 1** – Material suplementar do manuscrito “*What, how and how much do herbivores eat? The Continuous Bite Monitoring method for assessing forage intake of grazing animals.*” (Capítulo II).

### Supporting Information

Annex1. Description of the types of sheep bites with their respective codes used in the continuous monitoring of bite method in Experiment 1, 2 and 3, represented in the Figure 1.

Bite Code	Bite Category Description
Experiment 1	
Gi	Superficial bite 10 - 25 % in sward 40 cm
Ge	Bite with depth 40 - 50 % in sward 40 cm
Din	Superficial bite 10 - 25 % of sparse leaves in sward 40 cm
Den	Bite of exploration in sward 40 cm
Ti	Superficial bite 10 - 25 % of sparse leaves in sward 30 cm
Te	Bite with depth 40 - 50 % in sward 30 cm
Ta	Dense bite of leaves with depth 50 - 75 % in sward 30 cm
Vi	Bite with depth 50 - 75% in sward 15 cm
Ve	Bite of sparse leaves with depth 50 - 75 % in sward 20 cm
Va	Dense bite of leaves with depth 50 - 75 % in sward 20 cm
De	Bite with depth 40 - 50% in sward 15 cm
Da	Dense bite of leaves with depth 40 - 50% in sward 15 cm
Ci	Superficial bite < 10 % in sward 10 cm
Ce	Bite with depth 40 - 50% in sward 10 cm
Co	Bite of plant stalks
Ra	Bite in sward grazed < 8 cm

Re	Bite in sward < 8cm
Fo	Bite in other plants or plants parts (i. e., <i>Sida rhombifolia</i> L.)
In	Bite in inflorescences of Italian ryegrass
Ka	Bite superficial in leaves grazed and ungrazed in sward 20 cm
F	Single leaf Italian ryegrass

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Experiment 2

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Fes <sup>1*</sup>	Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 14 cm.
Fes <sup>2</sup>	Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 17 cm.
Fes <sup>3</sup>	Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 20 cm.
Fes <sup>4</sup>	Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 23 cm.
Fes <sup>5</sup>	Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 26 cm.
Tu <sup>1</sup>	Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 14 cm.
Tu <sup>2</sup>	Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 17 cm.
Tu <sup>3</sup>	Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 20 cm.
Tu <sup>4</sup>	Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 23 cm.
Tu <sup>5</sup>	Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at the sward surface height of 26 cm.
Den <sup>1</sup>	Bite of exploration of tall fescue leaves from lower strata or close to the ground at the sward surface height of 14 cm.

- Den<sup>2</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at the sward surface height of 17 cm.
- Den<sup>3</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at the sward surface height of 20 cm.
- Den<sup>4</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at the sward surface height of 23 cm.
- Den<sup>5</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at the sward surface height of 26 cm.
- Po<sup>1</sup> Exploration bite of 4 to 2 leaf tips at the sward surface height of 14 cm. Bite with low mass.
- Po<sup>2</sup> Exploration bite of 4 to 2 leaf tips at the sward surface height of 17 cm. Bite with low mass.
- Po<sup>3</sup> Exploration bite of 4 to 2 leaf tips at the sward surface height of 20 cm. Bite with low mass.
- Po<sup>4</sup> Exploration bite of 4 to 2 leaf tips at the sward surface height of 23 cm. Bite with low mass.
- Po<sup>5</sup> Exploration bite of 4 to 2 leaf tips at the sward surface height of 26 cm. Bite with low mass.
- Co<sup>1</sup> Exploration bite of 1 leaf tip at the sward surface height of 14 cm. Bites with less mass compared to the others.
- Co<sup>2</sup> Exploration bite of 1 leaf tip at the sward surface height of 17 cm. Bites with less mass compared to the others.
- Co<sup>3</sup> Exploration bite of 1 leaf tip at the sward surface height of 20 cm. Bites with less mass compared to the others.
- Co<sup>4</sup> Exploration bite of 1 leaf tip at the sward surface height of 23 cm. Bites with less mass compared to the others.
- Co<sup>5</sup> Exploration bite of 1 leaf tip at the sward surface height of 26 cm. Bites with less mass compared to the others.
- Re<sup>1</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at the sward surface height of 14 cm. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>2</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at the sward surface height of 17 cm. Bite made by the animal itself after intake the first grazing horizon.



- Re<sup>3</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at the sward surface height of 20 cm. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>4</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at the sward surface height of 23 cm. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>5</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at the sward surface height of 26 cm. Bite made by the animal itself after intake the first grazing horizon.
- Rede<sup>1</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at the sward surface height of 14 cm. Bite performed in places grazed by another animal.
- Rede<sup>2</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at the sward surface height of 17 cm. Bite performed in places grazed by another animal.
- Rede<sup>3</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at the sward surface height of 20 cm. Bite performed in places grazed by another animal.
- Rede<sup>4</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at the sward surface height of 23 cm. Bite performed in places grazed by another animal.
- Rede<sup>5</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at the sward surface height of 26 cm. Bite performed in places grazed by another animal.
- In<sup>1</sup> Bite in other species at the sward surface height of 14 cm.
- In<sup>2</sup> Bite in other species at the sward surface height of 17 cm.
- In<sup>3</sup> Bite in other species at the sward surface height of 20 cm.
- In<sup>4</sup> Bite in other species at the sward surface height of 23 cm.
- In<sup>5</sup> Bite in other species at the sward surface height of 26 cm.

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### Experiment 3

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- Fes<sup>A</sup> Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 0% depletion of pasture sward.

- Fes<sup>B</sup> Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 20% depletion of pasture sward.
- Fes<sup>C</sup> Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 40% depletion of pasture sward.
- Fes<sup>D</sup> Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 60% depletion of pasture sward.
- Fes<sup>E</sup> Bite with greater mass compared to the others. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 70% depletion of pasture sward.
- Tu<sup>A</sup> Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 0% depletion of pasture sward.
- Tu<sup>B</sup> Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 20% depletion of pasture sward.
- Tu<sup>C</sup> Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 40% depletion of pasture sward.
- Tu<sup>D</sup> Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 60% depletion of pasture sward.
- Tu<sup>E</sup> Bite similar to FES but with less mass. Bites depth corresponding to 40 to 50% of the sward surface height of the tall fescue (first grazing horizon) at 70% depletion of pasture sward.
- Den<sup>A</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at 0% depletion of pasture sward.
- Den<sup>B</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at 20% depletion of pasture sward.
- Den<sup>C</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at 40% depletion of pasture sward.
- Den<sup>D</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at 60% depletion of pasture sward.
- Den<sup>E</sup> Bite of exploration of tall fescue leaves from lower strata or close to the ground at 70% depletion of pasture sward.
- Po<sup>A</sup> Exploration bite of 4 to 2 leaf tips at 0% depletion of pasture sward. Bite with low mass.

- Po<sup>B</sup> Exploration bite of 4 to 2 leaf tips at 20% depletion of pasture sward. Bite with low mass.
- Po<sup>C</sup> Exploration bite of 4 to 2 leaf tips at 40% depletion of pasture sward. Bite with low mass.
- Po<sup>D</sup> Exploration bite of 4 to 2 leaf tips at 60% depletion of pasture sward. Bite with low mass.
- Po<sup>E</sup> Exploration bite of 4 to 2 leaf tips at 70% depletion of pasture. Bite with low mass sward.
- Co<sup>A</sup> Exploration bite of 1 leaf tip at 0% depletion of pasture sward. Bites with less mass compared to the others.
- Co<sup>B</sup> Exploration bite of 1 leaf tip at 20% depletion of pasture sward. Bites with less mass compared to the others.
- Co<sup>C</sup> Exploration bite of 1 leaf tip at 40% depletion of pasture sward. Bites with less mass compared to the others.
- Co<sup>D</sup> Exploration bite of 1 leaf tip at 60% depletion of pasture sward. Bites with less mass compared to the others.
- Co<sup>E</sup> Exploration bite of 1 leaf tip at 70% depletion of pasture sward. Bites with less mass compared to the others.
- Re<sup>A</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at 0% depletion of pasture sward. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>B</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at 20% depletion of pasture sward. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>C</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at 40% depletion of pasture sward. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>D</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at 60% depletion of pasture sward. Bite made by the animal itself after intake the first grazing horizon.
- Re<sup>E</sup> Bite in places where they have already been grazed (second grazing horizon) within the same feeding station at 70% depletion of pasture sward. Bite made by the animal itself after intake the first grazing horizon.

- Rede<sup>A</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at 0% depletion of pasture sward. Bite performed in places grazed by another animal.
- Rede<sup>B</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at 20% depletion of pasture sward. Bite performed in places grazed by another animal.
- Rede<sup>C</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at 40% depletion of pasture sward. Bite performed in places grazed by another animal.
- Rede<sup>D</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at 60% depletion of pasture sward. Bite performed in places grazed by another animal.
- Rede<sup>E</sup> Bite in places where they have already been grazed (second grazing horizon) outside of feeding station at 70% depletion of pasture sward. Bite performed in places grazed by another animal.
- In<sup>A</sup> Bite in other species at 0% depletion of sward surface height of the fescue.
- In<sup>B</sup> Bite in other species at 20% depletion of sward surface height of the fescue.
- In<sup>C</sup> Bite in other species at 40% depletion of sward surface height of the fescue.
- In<sup>D</sup> Bite in other species at 60% depletion of sward surface height of the fescue.
- In<sup>E</sup> Bite in other species at 70% depletion of sward surface height of the fescue.

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\* **X<sup>Y</sup> model:** X represent the bite code category and <sup>Y</sup> represent the bite class, i.e., treatment within of experiment 2 and 3, different sward surface heights and sward depletion, respectively.

**Apêndice 2 – Foraging behaviour of bovines and equines under mixed herbivory.” (Capítulo III).**

**Supporting Information**

Annex 1. Botanical composition on different herbivory systems: mixed equine and bovine, specific equine and specific bovine. in Prairies – Normandie -France

**PAMIEBO**

4 lignes par traitement  
Points contacts (lignes de 10m, tous les 20cm : 50 points)  
% de présence

2018

Relevés du 10/04/2018

**Equins printemps**

**Bovins printemps**

**Mixte printemps**

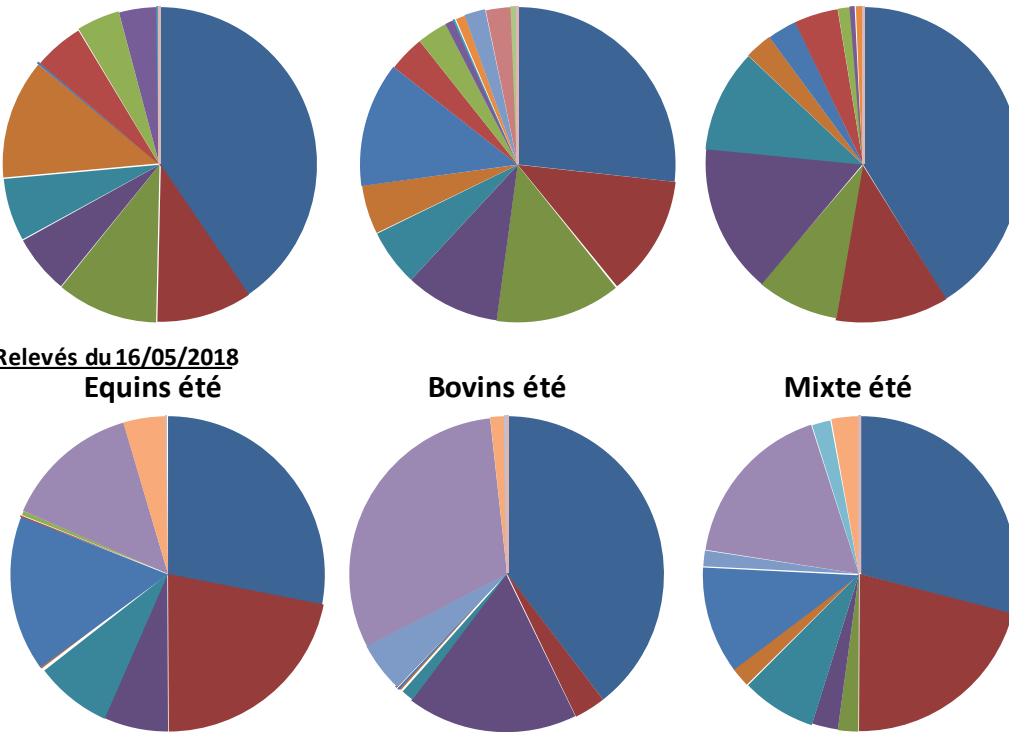
- *Lolium perenne*
- *Alopecurus pratensis*
- *Agrostis capillaris*
- *Agrostis stolonifera*
- *Trifolium repens*
- *Taraxacum officinale*
- *Ranunculus repens*
- *Phleum pratense*
- *Poa pratensis*
- *Dactylis glomerata*
- *Bromus sp*
- *Holcus lanatus*
- *Ranunculus acris*
- *Hypnum sp*
- *Bellis perennis*
- *Poa trivialis*
- *Hordeum sp.*
- *Holcus lanatus*
- *Rumex crispus*
- *Cerastium fontanum*

Relevés du 16/05/2018

**Equins été**

**Bovins été**

**Mixte été**



2018	Equins printemps		Bovins printemps		Mixte printemps		Equins été		Bovins été		Mixte été	
	moyenne %	se	moyenne %	se	Moyenne %	se	moyenne %	se	Moyenne %	se	moyenne %	se
<i>Lolium perenne</i>	<b>86,5</b>	2,6	<b>68,5</b>	2,9	<b>88,0</b>	2,5	<b>96</b>	1,6	<b>91,5</b>	3,4	<b>96</b>	2,5
<i>Alopecurus pratensis</i>	<b>21,0</b>	3,6	<b>32,0</b>	11,1	<b>24,5</b>	5,3	<b>74,5</b>	6,4	<b>7,5</b>	2,0	<b>69,5</b>	4,5
<i>Agrostis capillaris</i>	<b>22,5</b>	2,9	<b>33,0</b>	3,5	<b>18,0</b>	3,4	<b>0</b>	0,0	<b>0</b>	0,0	<b>7</b>	1,5
<i>Agrostis stolonifera</i>	<b>13,0</b>	3,5	<b>25,0</b>	9,7	<b>33,0</b>	5,7	<b>23</b>	3,3	<b>40,5</b>	11,0	<b>9</b>	4,3
<i>Trifolium repens</i>	<b>14,0</b>	6,5	<b>15,0</b>	5,4	<b>22,5</b>	13,7	<b>27</b>	5,5	<b>3</b>	2,0	<b>25,5</b>	5,8
<i>Taraxacum officinale</i>	<b>26,5</b>	4,4	<b>13,0</b>	5,2	<b>6,0</b>	2,5	<b>1,5</b>	1,7	<b>0,5</b>	0,6	<b>7</b>	4,1
<i>Ranunculus repens</i>	<b>0,5</b>	0,6	<b>32,5</b>	8,6	<b>6,5</b>	2,0	<b>54,5</b>	9,9	<b>0,5</b>	0,6	<b>36,5</b>	8,2
<i>Phleum pratense</i>	<b>11,0</b>	2,7	<b>9,5</b>	3,9	<b>9,5</b>	1,7	<b>0,5</b>	0,6	<b>0,5</b>	0,6	<b>0</b>	0,0
<i>Poa pratensis</i>	<b>9,5</b>	3,8	<b>8,0</b>	4,1	<b>3,0</b>	0,7	<b>1,5</b>	1,7	<b>0</b>	0,0	<b>0</b>	0,0
<i>Dactylis glomerata</i>	<b>8,5</b>	2,7	<b>2,5</b>	1,7	<b>1,0</b>	0,7	<b>0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0
<i>Bromus sp</i>	<b>0,5</b>	0,6	<b>0,5</b>	0,6	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0
<i>Holcus lanatus</i>	<b>0,0</b>	0,0	<b>2,5</b>	1,1	<b>1,5</b>	0,6	<b>0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0
<i>Ranunculus acris</i>	<b>0,0</b>	0,0	<b>5,5</b>	1,5	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>12</b>	5,0	<b>5,5</b>	4,1
<i>Hypnum sp</i>	<b>0,0</b>	0,0	<b>7,0</b>	6,6	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0
<i>Bellis perennis</i>	<b>0,0</b>	0,0	<b>1,5</b>	1,1	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0
<i>Poa trivialis</i>	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>47,5</b>	8,4	<b>71,5</b>	7,4	<b>58</b>	11,7
<i>Hordeum sp.</i>	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>0</b>	0,0	<b>6,5</b>	2,9
<i>Holcus lanatus</i>	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>15</b>	9,2	<b>3,5</b>	4,0	<b>10</b>	3,9
<i>Rumex crispus</i>	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0</b>	0,0	<b>0,5</b>	0,6	<b>0</b>	0,0
<i>Cerastium fontanum</i>	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,0</b>	0,0	<b>0,5</b>	0,6	<b>0</b>	0,0	<b>0</b>	0,0

### Apêndice 3 – Foraging behaviour of bovines and equines under mixed herbivory.” (Capítulo III).

#### Annex 2. Description of the bite codes to Equines and Bovines in Prairies – Normandie -France

.Code_bc	Classes	Sward_stade	Type	Description	Nom commun
mix	height	ungrazed	grass	<i>Mixed Poacea (Agrostis stolonifera, Agrostis tenuis, Alopecurus pratensis, Bromus sterilis, Cynosurus cristatus, Dactylis glomerata, Festuca pratensis, Glyceria fluitans, Holcus lanatus, Lolium perenne, Phleum pratense, Poa pratensis, Poa trivialis)</i>	Mix graminées (Agrostis stolonifère, Agrostis fin, Vulpin des prés, Flouve odorante, Brome stérile, Crételle, Dactyle aggloméré, Fétuque des prés, Fétuque rouge, Glycérie flottante, Holque laineuse, Orge faux-seigle, Ray-grass anglais, Fléole des prés, Pâturin annuel, Pâturin des prés, Pâturin commun)
mix_blanc	height	ungrazed	grass_legu	<i>Mixed Poacea + Trifolium repens</i>	mix graminées + Trèfle blanc
mix_tarax	height	ungrazed	grass_forbs	<i>Mixed Poacea + Taraxacum officinalis</i>	mix graminées + Pissenlit
mix_repens	height	ungrazed	grass_forbs	<i>Mixed Poacea + Ranunculus repens</i>	mix graminées + Ranoncule rampante
mix_acris	height	ungrazed	grass_forbs	<i>Mixed Poacea + Ranunculus acris</i>	mix graminées + Ranoncule acre
mix_corriola	height	ungrazed	grass_forbs	<i>Mixed Poacea + Convolvulus arvensis</i>	mix graminées + Liseron commun
mix_potentilla	height	ungrazed	grass_forbs	<i>Mixed Poacea + Potentilla reptans</i>	mix graminées + Potentille rampante
mix_tarax_blanc	height	ungrazed	grass_forbs_legu	<i>Mixed Poacea + Taraxacum officinalis + Trifolium repens</i>	mix graminées + Pissenlit + Trèfle blanc
mix_repens_blanc	height	ungrazed	grass_forbs_legu	<i>Mixed Poacea + Ranunculus repens + Trifolium repens</i>	mix graminées + Ranoncule rampante + Trèfle blanc
mix_acris_blanc	height	ungrazed	grass_forbs_legu	<i>Mixed Poacea + Ranunculus acris + Trifolium repens</i>	mix graminées + Ranoncule acre + Trèfle blanc
lanus	height	ungrazed	grass	<i>Holcus lanatus</i>	Holque laineuse
remix	height	grazed	grass	<i>Mixed Poacea</i>	mix graminées re-pâturage, paître sur des feuilles déjà coupées
remix_blanc	height	grazed	grass_legu	<i>Mixed Poacea + Trifolium repens</i>	mix graminées + Trèfle blanc - re-pâturage
remix_tarax	height	grazed	grass_forbs	<i>Mixed Poacea + Taraxacum officinalis</i>	mix graminées + Pissenlit - re-pâturage
remix_repens	height	grazed	grass_forbs	<i>Mixed Poacea + Ranunculus repens</i>	mix graminées + Ranoncule rampante -re-pâturage
remix_acris	height	grazed	grass_forbs	<i>Mixed Poacea + Ranunculus acris</i>	mix graminées + Ranoncule acre - re-pâturage
remix_corriola	height	grazed	grass_forbs	<i>Mixed Poacea + Convolvulus arvensis</i>	mix graminées + Liseron commun - re-pâturage
remix_potentilla	height	grazed	grass_forbs	<i>Mixed Poacea + Potentilla reptans</i>	mix graminées + Potentille rampante - re-pâturage
remix_tarax_blanc	height	grazed	grass_forbs_legu	<i>Mixed Poacea + Taraxacum officinalis + Trifolium repens</i>	mix graminées + Pissenlit + Trèfle blanc - re-pâturage
remix_repens_blanc	height	grazed	grass_forbs_legu	<i>Mixed Poacea + Ranunculus repens + Trifolium repens</i>	mix graminées + Ranoncule rampante + Trèfle blanc - re-pâturage,
remix_acris_blanc	height	grazed	grass_forbs_legu	<i>Mixed Poacea + Ranunculus acris + Trifolium repens</i>	mix graminées + Ranoncule acre + Trèfle blanc - re-pâturage
relanus	height	grazed	grass	<i>Holcus lanatus</i>	Holque laineuse - re-pâturage
dacty	height	ungrazed	grass	<i>Dactylis glomerata</i>	Dactyle aggloméré
glyceria	height	ungrazed	grass	<i>Glyceria fluitans</i>	Fétuque rouge
rubra	height	ungrazed	grass	<i>Festuca rubra Glyceria fluitans</i>	Glycérie flottante
inflorescence	without height	ungrazed	grass	<i>inflorescence of poaceae</i>	Inflorescence graminées

fleur	without height	ungrazed	forbs	<i>Flowers</i>	Fleurs
achillea	without height	ungrazed	forbs	<i>Achillea millefolium</i>	Achillée millefeuille
acris	without height	ungrazed	forbs	<i>Ranunculus acris</i>	Ranoncule acre
ajuga	without height	ungrazed	forbs	<i>Ajuga reptans</i>	Ajuga
aparine	without height	ungrazed	forbs	<i>Galium aparine</i>	Gaillet apariné
argentine	without height	ungrazed	forbs	<i>Potentilla anserina</i>	Argentine
aubepine	without height	ungrazed	shrubs	<i>Crataegus monogyna</i>	Aubepine
bellis	without height	ungrazed	forbs	<i>Bellis perennis</i>	Pâquerette
blanc	without height	ungrazed	legu	<i>Trifolium repens</i>	Trèfle blanc
cabaret	without height	ungrazed	forbs	<i>Dipsacus fullonum</i>	Cabaret aux oiseaux
cardus	without height	ungrazed	forbs	<i>Cardus nutans</i>	Chardon penché
chene	without height	ungrazed	tree	<i>Quercus sp</i>	Le Chêne
cirsium	without height	ungrazed	forbs	<i>Cirsium vulgare</i>	Chardon commun
copro	without height	ungrazed	feces	<i>Coprophagy</i>	Coprophagie - Crotin
corriola	without height	ungrazed	forbs	<i>Convolvulus arvensis</i>	Liseron commun
érable	without height	ungrazed	tree	<i>Acer campestre</i>	Érable
ficaria	without height	ungrazed	forbs	<i>Ranunculus ficaria</i>	Ranoncule ficaria
fresne	without height	ungrazed	tree	<i>Fraxinus excelsior</i>	Fresne
hypochaeris	without height	ungrazed	forbs	<i>Hypochaeris radicata</i>	Porcelle enracinée
juncus	without height	ungrazed	forbs	<i>Juncus effusus</i>	Jonc épars
lance	without height	ungrazed	forbs	<i>Plantago lanceolata</i>	Plantain lancéolé
lion	without height	ungrazed	forbs	<i>Leontodon autumnalis</i>	Liondent d'automne
major	without height	ungrazed	forbs	<i>Plantago major</i>	Plantain major
mollugo	without height	ungrazed	forbs	<i>Galium mollugo</i>	Gaillet commun
mousse	without height	ungrazed	forbs	<i>Hypnum sp</i>	Mousse
polygo	without height	ungrazed	forbs	<i>Polygonum persicaria</i>	Persicaria
potentilla	without height	ungrazed	forbs	<i>Potentilla reptans</i>	Potentille rampante
repens	without height	ungrazed	forbs	<i>Ranunculus repens</i>	Ranoncule rampante
robus	without height	ungrazed	shrubs	<i>Robus fruticosus</i>	Ronce
ronçe	without height	ungrazed	shrubs	<i>Robus sp.</i>	Ronce
rumex	without height	ungrazed	forbs	<i>Rumex crispus; Rumex obtusifolius</i>	Rumex
silaum	without height	ungrazed	forbs	<i>Silaum silaus</i>	Fenouil des chevaux



symphitum	without height	ungrazed	forbs	<i>Symphytum officinale</i>	Grande consoude
tarax	without height	ungrazed	forbs	<i>Taraxacum officinalis</i>	Pissenlit
Urtica	without height	ungrazed	forbs	<i>Urtica dioica</i>	Ortie dioïque

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## **Apêndice 4 – Normas para elaboração e submissão de trabalhos científicos ao periódico *Ecology and Evolution*.**

### **Author Guidelines**

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Ecology and Evolution requires, as a condition for publication, that data supporting the results in the paper should be archived in an appropriate public archive, such as GenBank, TreeBASE, Dryad, the Knowledge Network for Biocomplexity or other suitable long-term and stable public repositories. Data are important products of the scientific enterprise, and they should be preserved and usable for decades in the future. Authors may elect to have the data publicly available at time of publication, or, if the technology of the archive allows, may opt to embargo access to the data for a period of up to a year after publication. Exceptions may be granted at the discretion of the editor, especially for sensitive information such as a human subject data or the location of endangered species.

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- Upon submission, this statement must be included, but we are happy for authors to wait until acceptance of their paper to actually archive their data (although note that many repositories will enable authors to embargo publication of their data during the review process).
- Upon acceptance, data must be archived and the Data Accessibility statement completed including database and information such as accession numbers or DOI (as available) for all data from the manuscript.
- Note: if data, scripts, or other artefacts used to generate the analyses presented in the paper are available via a publicly available data repository, authors should include a reference to the location of the material within their paper.

Example:

"Data Accessibility:

- DNA sequences: Genbank accessions F234391-F234402; NCBI SRA: SRX0110215
- Final DNA sequence assembly uploaded as online
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
- Sampling locations, morphological data and microsatellite genotypes: Dryad doi:10.5521/dryad.12311"

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- Literature cited (see below for tips on references)
- Tables (may be sent as a separate file if necessary)
- Figure legends
- Data Accessibility Statement
- Competing Interests Statement
- Author Contributions section
- Acknowledgements, including details of funding bodies with grant numbers

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Applying an experiment that was informative for another species to a new species results in great science, as it allows us to compare the results of the new study to previous iterations of the experiment—one study acts as context for the other. This approach often results in a series of papers from a research group. At Ecology and Evolution, we wish to foster reproducibility by asking authors of replicated experiments to fully reference the original iteration of their experiment. We also strongly suggest that authors number such papers (e.g. "The Effects of Climate Change on Food Production: study 1, Tomatoes," and "The Effects of Climate Change on Food Production: study 2, Potatoes") to help highlight the similarities and differences discovered during series work.

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2. drafting the article or revising it critically for important intellectual content; and
3. final approval of the version to be published.

Authors must meet all 3 conditions. All contributors who do not meet the criteria for authorship should be listed in an acknowledgments section.

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As with the main body of text, the completeness and content of your reference list is more important than the format chosen. A clear and consistent, generic style will assist the accuracy of our production processes and produce the highest quality published work, but it is not necessary to try to replicate the journal's own style, which is applied during the production process. If you use bibliographic software to generate your reference list, select a standard output style, and check that it produces full and comprehensive reference listings. A guide to the minimum elements required for successful reference linking appears below. The final journal output will use the 'Harvard' style of reference citation. If your manuscript has already been prepared using the 'Vancouver' system, we are quite happy to receive it in this form. We will perform the conversion from one system to the other during the production process.

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Year of publication

Article title

Journal title (preferably not abbreviated)

Volume number

Issue number

Page range

##### Book

Author(s) in full

Year of publication

Book title

Place of publication

Publisher

No. Pages

##### Book Chapter

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Year of publication

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Place of publication

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Page range

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*Last updated 15 January 2021*

**Apêndice 5** – Normas para elaboração e submissão de trabalhos científicos ao periódico *Oecologia*.

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Aims and scope

Legal and ethical requirements

Manuscript submission and preparation

Manuscript contents

After acceptance

#### **Aims and scope**

*Oecologia* publishes innovative ecological research of general interest to a broad international audience. We publish several types of manuscripts in many areas of ecology:

Categories:

Concepts, Reviews and Synthesis Views and Comments

Methods

Physiological ecology – Original research

Behavioral ecology – Original research

Population ecology – Original research

Plant-animal interactions – Original research

Community ecology – Original research

Ecosystem ecology – Original research

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Special Topic

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3

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4

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7

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8

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- Discussion
- Acknowledgements** Please keep this section as short as possible. Acknowledgements of people, grants, funds, etc. should be placed in a separate section before the reference list. The names of funding organizations should be written in full. Compliance with ethical standards may be stated in the cover letter rather than the acknowledgements section.
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**Conflicts of interest/Competing interests** (include appropriate disclosures)

**Ethics approval** (include appropriate approvals or waivers)

**Consent to participate** (include appropriate statements)

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**Availability of data and material** (data transparency)

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**Authors' contributions**

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- This study follows the guidelines declared in the Declaration of Helsinki, and was approved by [ethics committee name]; Reference number XXXX.
- All animal experiments were approved by [ethics committee name], reference number XXXX
- Ethics approval for this study was waived by [ethics committee name] according to [reason/law]



Ethics approval was not required for this study according to local legislation [name of legislation]

9

**Consent to Participate:**

All patients included in this study gave written informed consent to participate in this research. If the patient was less than XXXX years old at the time of the study, written informed consent for their participation was given by their parent or legal guardian.

**Consent for publication:**

All patients included in this research gave written informed consent to publish the data and images contained within this case report.

All patients provided written informed consent to publish the data contained within this article.

**Availability of data and materials:**

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

All data produced from this study are provided in this manuscript.

The data was deposited in [repository name] under the reference number [identifier number].

The single-cell RNA sequencing clean data reported in this paper have been deposited in the [repository name] under accession number XXXX, which can be publicly accessed at [link].

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Hobson KA (2003) Making migratory connections with stable isotopes. In: Berthold P, Gwinner E, Sonnenschein E (eds) *Avian migration*. Springer, Berlin, pp 379-391

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Körner C (2003) *Alpine plant life*, 2nd edn. Springer, Berlin

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11

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12

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## VITA

Anderson Michel Soares Bolzan, filho de Iva Maria Soares Bolzan e Erli Bolzan, nasceu no dia 26 de setembro de 1985, em Santa Maria, Rio Grande do Sul, Brasil. Na cidade natal cursou ensino fundamental nos colégios Lourenço Dalla-Corte e colégio Santa Helena. O ensino médio na Escola Edna Mey Cardoso e Colégio Agrícola de Santa Maria – Universidade Federal de Santa Maria (UFSM) onde concluiu seus estudos no ano de 2003. Cumpriu serviço militar obrigatório 2004-2005 na Cia. Cmdo. da 6ª Brigada de Infantaria Blindada e no 29º Batalhão de Infantaria Blindado, com diploma de mérito, formação de Cabo de Infantaria QM 0701, Infante combatente Blindado, posição de curso 1/79 nota 9,79. Condecorado com diploma de melhor aptidão física, diploma e medalha de Praça mais distinta. Ingressou na formação acadêmica no curso bacharelado em Zootecnia UFSM (2005 – 2010) e direcionou esforços para um objeto caro do ponto de vista pessoal, os ovinos em especial os lanares que já tinha envolvimento de trabalho como esquilador. Assim durante o período de graduação participou de iniciativas de iniciação científica no setor de ovinocultura sob orientação do professor Cléber Cassol Pires, sendo monitor na mesma disciplina, e bolsista de iniciação científica CNPQ. Estas experiências subsidiaram manipular conceitos da investigação durante estágio curricular no Haras Santa Maria de Araras (2010), em Bagé RS - Brasil marcando a inserção nos estudos sobre o modelo animal equino e o processo de pastejo, o qual dedicaria atenção até hoje. Durante um período curto de atividade laboral (2012) como zootecnista, em uma empresa de nutrição animal desempenhando função de formulador e consultor. Mantive conexão com os sistemas de criação de equinos e com o cenário acadêmico na área da ciência educação, onde concluiu graduação em formação pedagógica no Centro de Ciência e Educação UFSM (2012 -2013). Com insistente dedicação e a oportunidade de ingressou domínio da pesquisa, tendo início na pós-graduação (2013) (especialização) e estudos com equinos nos campos com tutoria da Professora Adriana Pires Neves na Universidade Federal do Pampa, que posteriormente direcionou à Universidade Federal do Rio Grande do Sul para o ingresso no Grupo de Pesquisa em Ecologia do Pastejo - GPEP, coordenado pelo Professor Paulo César de Faccio Carvalho. No mestrado (2014 – 2016) sob orientação do professor Paulo César de Faccio Carvalho, evolui na visão do universalismo científico e conceitualmente nos domínios da interface solo -planta-animal. Neste período foi influenciado pelo ecólogo Olivier Bonnet, a quem refere a inquietação científica, além da apresentação e treinamento na metodologia de observação direta “Continuous bite monitoring” na qual dispenderia muitas horas de observação e descrição de ações alimentares “os bocados”, de animais em pastejo em diversos ambientes pastoris sob o propósito de variadas hipóteses totalizando mais de 894 horas de observação experienciadas. Desenvolveu com esta ferramenta o protocolo de mestrado no entendimento do processo de forrageamento de potros nos Campos da Pampa, na sequência auxiliou colegas em protocolos sobre o estudo do processo de pastejo em pastos cultivados. Na busca da compreensão das funções do forrageamento equino em coexistência com bovinos desenvolveu parte da tese (2017 -2021) no protocolo PaturEquiBov - Pâturage Mixte Equin – Bovin, nos domínios do Haras National du Pin - Normandie – France (2018-2019), em programa de cooperação Brasil – França CAPES-COFECUB. Foi orientado pelo professor Paulo Carvalho GPEP – UFRGS, Bertrand Dumont INRAE - Unité Mixte de Recherche sur les Herbivores, e Géraldine Fleurance IFCE - Institut français du cheval et de l'équitation. Atualmente além do desenvolvimento da tese, colabora em protocolos na interface solo - planta- animal no

grupo de pesquisa e outras instituições. Mantem atenção ao estudo do forrageamento, estimativas de fluxo ingestivo, composição de dieta e arranjo espaço temporal dos pastos, especialmente ecossistemas naturais. Até o momento da publicação deste documento, tem em seu currículo 5 artigos científicos e 2 capítulos de livros publicados, 2 artigos científicos em tramitação. Foi submetido à banca de defesa da Tese de Doutorado no dia 28 de Abril de 2021.