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SPATIO-TEMPORAL HETEROGENEITY OF GRAZING SYSTEMS

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SPATIO-TEMPORAL HETEROGENEITY OF GRAZING SYSTEMS

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RESUMO

Manejo de pastagens tem sido tradicionalmente baseado em variáveis que são calculadas usando massa média de recurso e animal por unidade de área e, portanto, desconsideram a heterogeneidade presente nos sistemas de pastejo. No entanto, tais variáveis são o resultado das verdadeiras variáveis de manejo que podemos controlar: área e forma do potreiro, número, massa e espécies de animais, e tempo e duração do pastejo. Portanto, um experimento foi realizado e um modelo foi desenvolvido para explorar como os sistemas de pastejo heterogêneos funcionam quando gerenciados por meio de uma variável de manejo tradicional, mas com diferentes combinações das verdadeiras variáveis de manejo, e para demonstrar a importância de incorporar totalmente a heterogeneidade na ciência do pastejo. No capítulo II, descrevo um experimento no qual ovelhas foram expostas a dois manejos de pastejo contrastantes com altura média do pasto semelhante ao longo de todo o período de pastejo. No entanto, um teve pastos iniciais altos e alta densidade animal, esperando um alto nível de depleção; e o outro teve pastos iniciais intermediários e baixa densidade animal, esperando um baixo nível de depleção. Observamos o comportamento de forrageamento por meio do monitoramento contínuo de bocados e pareamos os registros com uma descrição detalhada da estrutura do pasto. Eu testei como a taxa de ingestão diária e os mecanismos de pastejo variaram em função das condições instantâneas do pasto e dos tratamentos de pastejo. No capítulo III, descrevo um modelo dinâmico de pastejo e crescimento do pasto como funções de uma população de pasto estruturada por altura para explorar a natureza multidimensional das situações de pastejo e determinar quais combinações de fatores levam a resultados inesperados para investigação posterior. Múltiplas condições de manejo foram simuladas para determinar a interação entre as escalas espaço-temporais inerentes de pastejo com aquelas impostas pelo manejo.

Palavras chave: heterogeneidade espaço-temporal; manejo do pasto; produção animal; pastoreio; escala; modelo de simulação.

SPATIO-TEMPORAL HETEROGENEITY OF GRAZING SYSTEMS

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ABSTRACT

Traditional grazing management has been based on variables that are calculated through average resource and animal biomass per unit area, and thus they disregard the heterogeneity present in grazing systems. However, such variables are result of the true management variables that we can control: paddock area and shape, number, mass and species of animals, and timing and duration of grazing. Therefore, an experiment was performed, and a model was developed to explore how heterogeneous grazing systems function when managed through a traditional management variable but with different combinations of the true management variables, and to demonstrate the importance of fully incorporate heterogeneity into grazing science. In chapter II, we described an experiment where sheep were exposed to two contrasting grazing management with similar average sward height over the whole grazing period. However, one had tall initial swards and high animal density, expecting a high depletion level; and the other had intermediate initial swards and low animal density, expecting a low depletion level. We observed the foraging behavior through continuous bite monitoring and paired the recordings with a detailed description of the sward structure. I tested how daily intake rate and grazing mechanisms varied as a function of the instantaneous sward conditions and grazing treatments. In chapter III, I describe a dynamic model of grazing and sward growth as functions of a sward population structured by height to investigate how the combinations of factors lead to unexpected results for further investigation. Multiple grazing management conditions were simulated to determine the interaction between the inherent spatio-temporal scales of grazing with those imposed by management.

Keywords: grazing management; resource heterogeneity; scaling; spatial ecology; mathematical modeling.

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SUMMARY

CHAPTER I

1. INTRODUCTION

Grazing management and research have revolved around recommending simple management variables. For example, quantitative variables such as herbage allowance, grazing pressure, and stocking rate; or average structural attributes of the vegetation such as light interception, height, and mass (Allen et al., 2011). The simplicity of these management variables can be important to reach the public interested, but it fails in fully predicting the dynamics and functioning of grazing systems. Grasslands are complex systems, vary over time and space, and are influenced by multiple management variables (Laca, 2009). Traditional management variables are calculated with average resource and animal biomass per unit area, disregarding the spatio-temporal heterogeneity of vegetation and the pattern of distribution of animals. On the other hand, the management variables that we can actually control are more practical and well-known to managers: paddock size and shape, number, kind and mass of animals, and timing and duration of grazing events. Thus, the purpose of the present work is to demonstrate that heterogeneous systems with similar average management descriptors can differ widely in function.

In chapter II, I report an experiment in which we exposed sheep to two contrasting grazing management treatments with similar average sward height over the whole grazing period. However, one treatment had tall initial swards and high animal density, resulting in a high depletion level and the other had intermediate initial swards and low animal density, creating a low depletion level. We observed the foraging behavior through continuous bite monitoring and paired the recordings with a detailed description of the sward structure. I performed regression modeling (and other additional statistical models) to test how daily intake rate and grazing mechanisms varied as a function of the instantaneous sward conditions. Finally, given the number of grazing management inputs and the impossibility to experimentally test a sufficient number of combinations of multiple values in all variables, we developed a dynamic model of grazing and sward growth as functions of a sward population structured by height to explore the multidimensional nature of grazing situations and determine what combinations of factors lead to unexpected results for further investigation. The model simulates grazing and sward growth from elementary processes (bite mass, intake rate, sward height distribution) to integrated consequences (intake rate over time, live weight gain per animal and per area, sward height and production). Multiple grazing management conditions were simulated to determine the interaction between the inherent spatio-temporal scales of grazing with those imposed by management, whereby a key feature is a discrete difference in the temporal scale of growth and defoliation at the individual plant level. The model and the respective simulations are presented in chapter III.

2. LITERATURE REVIEW

Grazing management research has focused on quantitative variables such as herbage allowance, grazing pressure, and stocking rate; average structural attributes of the vegetation such as light interception, height, and mass; or at controlling defoliation (i.e., frequency and intensity) through grazing methods (Allen et al. 2011). However, all these variables have in common the fact that they disregard the heterogeneity existing in grazing systems. Grazing systems are complex and vary over time and space, thus their functioning cannot be fully understood through variables that describe only an instant and part of the system properties (Laca, 2009). Nonetheless, the dynamic of grazing systems is a function of the environmental conditions and its interaction with the true management variables over which we can exert control: number, mass and species of herbivores, paddock size and shape, and timing and duration of grazing. Moreover, several other input-based management factors such as fertilization, irrigation and supplementation substantially affect the functioning of grazing systems but are not the subject of this thesis. Here, I focus on the response of heterogeneous grazing systems to the interaction between the main management factors. My goal is not to present a complete review, but simply to demonstrate the importance of heterogeneity for two key processes in these systems: grazing and sward growth.

Management descriptors such as stocking rate, herbage allowance, and grazing pressure are calculated based on average herbage and animal mass per unit area (Scarnecchia, 1994), disregarding the distribution pattern of animals and resource heterogeneity (Laca, 2009). For instance, it is assumed that 5 cows in 50 ha or 100 cows in 1000 ha grazing year-round have an equivalent stocking rate. Nonetheless, the use of space by herbivores is scale-dependent, with larger species perceiving and exploring large patches than smaller species (Laca et al., 2010; Sensenig et al., 2010). Moreover, grazing animals form groups and do not spread evenly over the pasture. A herd can likely forage more than 50 ha in a day, whereas exploring 1000 ha does not seem feasible. Moreover, because “near things are more related than distant things" (Tobler, 1970), resource heterogeneity increases with scale of observation (Palmer, 1988). In a large paddock, large overgrazed (and ungrazed) patches may be formed due to spatial selectivity, influenced by distance from shade and watering points (see below).

Swards are heterogeneous in both spatial and temporal dimensions. Sward spatial heterogeneity is mainly influenced by competition, soil characteristics such as water and nutrient availability, and disturbances such as grazing. Spatial heterogeneity can be described through two components: variance (frequency distribution) and spatial pattern (Palmer, 1988). For example, Cid & Brizuela (1998) described the structure of a fescue (*Festuca arundinacea* Schreb.) pasture grazed by cattle as a mosaic of short and tall patches (or lightly and heavily grazed patches, respectively), which can be interpreted as a bimodal frequency distribution. I will use this case to exemplify how the sward heterogeneity affects the growth and grazing processes. First, some grazing methods suggest that the proper timing of grazing is when the sward reaches 95% of the average light interception (correlated with height), because it is the peak of green biomass accumulation and from when senesce substantially increase (Congio et al. 2018). Assuming a simple bimodal frequency distribution (a mixture of two normal distributions with the same variance but different means), at the time the sward has an average light interception of 95%, almost half of the pasture has accumulated dead tissue, while the other has not reached the maximum growth rate. Besides that, growth also depends on the spatial distribution of patches because short plants near to tall patches are shaded and have lower relative growth rate (Semmartin & Oesterheld, 2001). Thus, because sward growth is nonlinear (Johnson & Parsons, 1985; Parsons & Chapman, 2000), average growth rate is not related to average sward height (or light interception) at paddock level but depends on its spatial arrangement. Second, average sward height has a very strong relationship with intake in small scales (Carvalho, 2013), but it is weak predictor in large scales (Carvalho et al. 2015). This difference can explain by the fact that animals behave according to the scale and some grazing mechanisms do not operate in small scales (Bailey & Provenza, 2008). For example, predictions of bite mass based on average height of the fescue pasture described by Cid & Brizuela (1998) probably would differ from reality, because animals through selectivity are expected to graze more tall than short swards.

Temporal heterogeneity is driven mainly by the seasonal pattern of growth as a function of environmental conditions and species phenology. Although grazing management and research have taken into account the yearly cycles of temporal heterogeneity of forage demand and supply, many times sward temporal variation in the short term has been neglected. For example, two grazing methods, one with 10 sheep in 1 ha for 10 day and other with 10 sheep grazing 10 ha for 1 days, are expected to function differently because animals will create and experience different height distributions as the sward is grazed down. However, traditional management variables accept time as a substitute of space.

Defoliation intensity and frequency are usually used as criteria to define timing and length of grazing and resting periods. Usually, the term "defoliation intensity" is used in grazing management to signify the average level of depletion at paddock scale (proportion of initial height or mass), whereas the term "defoliation frequency" express the frequency with which plants in a given area are exposed to the risk of defoliation by placing grazing animals. Whether plants are or are not defoliated in any given frequency is completely dependent on the decisions animals make given the grazing conditions. However, defoliation intensity in one biting event is a fairly constant proportion of sward height for a wide range of plant and herbivore species (Benvenutti & Cangiano, 2011; Carvalho, 2013). Defoliation frequency depends on the pattern of bite placements that animals effect and can vary widely over the available area. The probability distribution of a plant being defoliated decreases with distance from attractive points such as water and shade. For example, in a large experiment evaluating the effect of paddock size (100 ha vs 1000 ha) on vegetation structure, Oñatibia & Aguiar (2019) reported that the height of the preferred grass species increased as a function of distance from watering points. As a consequence, under the same stocking rate, larger paddocks had greater proportion of the area undergrazed because actual animal density was higher on the area actually used by the herbivores. A similar response can be observed on a smaller scale in response to the spatial distribution of the plant community. Dumont et al. (2002) observed that sheep and cattle consumed more of the less preferred fescue (Festuca arundinacea Schreb.) surrounding the preferred ryegrass (Lolium perenne L.) patches than further away. Conversely, herbivores avoid eating near patches of less preferred species. In addition to that, clearly bite density over the whole available area increases by adding more animals or then by reducing the size of the paddock (Wade & Carvalho, 2001).

Thus, grazing systems respond to multiple management dimensions, varying over time and space as a function of the interaction between the true grazing management variables and the environmental conditions. The purpose of the present work is not invalidating the current grazing management variables and concepts, but demonstrate the importance of other dimensions that have not been fully incorporated into grazing science.

CHAPTER II

Article

Low-depletion grazing outperforms traditional high-depletion method

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Abstract:

Behavioral mechanisms that determine the forage intake by herbivores have been predominantly studied and explained as a function of the abundance and spatial distribution of plants. However, as herbivores integrate the information from their body internal state and external environment, their foraging behavior can vary due to conditions imposed by grazing management. Thus, the goal of this study was to determine if low-density, low sward depletion strip grazing results in greater daily intake rate despite of both systems have similar average sward height over space and time, and to investigate whether herbivores exhibit the same foraging mechanisms for a given instantaneous sward state regardless of the grazing treatment that generated the structure. For this, sheep grazing Italian ryegrass were subjected to two contrasting sward management strategies (intermediate initial sward height – low density – low depletion and tall initial sward height - high density – high depletion), and we evaluated their foraging behavior through the continuous bite monitoring and paired the grazing observations recordings with detailed sward measurements during grazing down on a 1-day strip-grazing regime. Sward height decreased markedly during the grazing down period in both treatments, but the sward height depletion was faster under high animal density and taller initial heights, which means that sward structure was severely disrupted in the high density-high depletion treatment. The animals exhibited a markedly different herbage intake pattern for each treatment and day-shift, with animals under low density presenting greater total herbage intake. Despite of the difference in intake rate, the grazing treatments did not affect the behavioral mechanisms beyond their indirect effects on the rate of change the instantaneous sward conditions.

Keywords: grazing management; foraging behavior; behavioral mechanisms; resource heterogeneity; grazing-down; patch depression; statistical modeling;

1. Introduction

Grazing management revolves around finding the best compromise between herbage growth and animal performance, by determining a suitable combination of animal density, grazing duration and rest period (Heitschmidt & Taylor, 1991). Typical sigmoidal models of plant growth suggest that maximum growth rate is achieved at intermediate sward heights (Parsons et al., 1983ab) and that total herbage mass production is highest when resting periods allow swards to reach quasi maximum heights (Johnson & Parsons, 1985; Parsons & Chapman, 2000). However, intake rate can differ greatly between intermediate and maximum heights. Mammalian grazer models indicate that intake rate responds positively and with diminishing returns to sward height (Spalinger & Hobbs, 1992). When grazing duration is fixed, initial sward height is controlled by the rest period, and control of post-grazing sward height is achieved by changing stock density. Low animal density on swards of intermediate height achieve low levels of depletion and short periods between grazing events, while other uses high animal density on initially tall swards to achieve high levels of depletion and long resting periods (Schons et al., 2021). Therefore, there should be an optimal sward height that allows maximum sustained intake. The question is then, which grazing method is better to promote sustained animal intake, long resting periods and brief period of intense defoliation, or short, more frequent but light grazing event?

Behavioral mechanisms that determine the rate of herbage consumption by herbivores, such as searching, gathering and processing herbage, have been predominantly studied and explained as a function of the abundance and spatial distribution of sward resources. However, as herbivores integrate the information from their internal state (e.g. body mass, fat reserves, gut content, homeostasis) and external environment (e.g. temperature, terrain, social interactions), foraging behavior can vary due to conditions imposed by management (Laca & Ortega,1995). For example, animals can use spatial memory to adapt their searching-patterns and increases search efficiency by avoiding less profitable areas (Edwards et al., 1996; Dumont & Petit, 1998). Herbage gathering and processing are influenced by the gut content; hungry animals are capable of increasing biting rate and decreasing chewing rate to boost ingestion rate (Greenwood & Demment, 1988; Gregorini et al., 2007). Therefore, it is expected that behavioral mechanisms under imposed grazing management have greater variability and that might be affected by other effects than the sward state.

There are two contrasting approaches to grazing management when grazing duration is fixed. One applies high animal density on initially tall swards to achieve high levels of depletion and long periods between grazing events. The other applies low animal density on swards of intermediate height to achieve low levels of depletion and requires shorter periods between grazing events (Schons et al., 2021). In the first case, we should observe a rapid change in sward characteristics and the consequent responses in grazing behavior, whereas in the second case there should be less change in intake rate over time because animals are exposed to sward conditions that change little over time. The question is, if both extremes expose animals to equal or similar average sward heights over space and time, do the two methods result in different total intake per day (or average intake rate)? We hypothesize that when the average sward height selected is in the range that imposes little limitation to instantaneous intake rate in vegetative Italian ryegrass pastures (*Lolium multiflorum* Lam; 12 to 18 cm; Carvalho, 2013; Mezzalira et al., 2014; Fonseca et al., 2012), the nonlinearity of relationship between instantaneous intake rate and sward height will cause daily intake to be higher in the low-density, low depletion case.

The main mechanism that seems to dominate the explanation of responses of intake rate to changing foraging conditions is the sward structure – bite mass- bite rate triad, including the spatial distribution of local sward condition into the concept of sward structure. The focus of most explanations of the effects of changing foraging conditions converges in the triad. The goal of this work was to test if indeed the triad and the mechanisms therein are sufficient to explain changes in grazing behavior when grazers are exposed to contrasting grazing methods that generate contrasting behaviors and rates of herbage intake. Specifically, we test if grazing treatments have any additional effects beyond those that can be explained via the triad. If additional effects are found, then we either have to identify additional mechanisms or modify our understanding of the mechanisms usually cited.

Thus, our objective was two-fold: (1) to determine if indeed low-density, low depletion strip grazing results in greater daily intake rate than high-density, high depletion grazing, and (2) to investigate whether herbivores exhibit the same foraging mechanisms for a given instantaneous sward state regardless of longer-term grazing conditions imposed. To accomplish this, we exposed sheep to two contrasting strip-grazing situations, monitored their foraging behavior continuously and paired the grazing observations recordings with detailed measurements of sward conditions over grazing down.

2. Materials and Methods

This work followed all protocols for the scientific use of animals and was approved by the Ethics Committee for the Use of Animals (CEUA) of the Federal University of Rio Grande do Sul (UFRGS; protocol 3571).

Site and experimental treatments

The experiment was carried out at the Experimental Station of the Federal University of Rio Grande do Sul, Brazil (30º05 'S Lat; 51º39' W Long) over three experimental periods: period 1 was from July 19 to 22, period 2 was from August 21 to 24, and period 3 was from September 1 to 4 in 2017. Treatments were two combinations of animal density, initial sward height and level of depletion, both with the same grazing duration of 24 hours per strip. The low density – low depletion (LDLD) treatment had a nominal pre-grazing height of 20 cm and received 1.34 kg of animal mass/m^2 for 24 hours to reach a nominal 40% of height depletion or post-grazing height of 12 cm. The high density – high depletion (HDHD) treatment had a nominal pre-grazing height of 30 cm and received 5.48 kg of animal mass/m^2 for 24 hours to reach a nominal 80% of height depletion or post-grazing height of 6 cm. An area of 0.88 ha was divided into four 0.21-ha paddocks, with two paddocks receiving each treatment. Paddocks were grazed in strips that were selected based on the target height and set up daily. Strip size and number of animals were variable to achieve the desired level of depletion within each 24 h grazing period. Animals were moved to a new strip every day between 2 and 3 pm, so the first grazing period was in the afternoon and the second period was in the following morning. The reader should keep in mind that throughout this paper, the morning grazing period is the last period in each strip.

Sward

Annual ryegrass was seeded with 35 kg ha^{-1} of seed, three months before the experimental period. The area received a first fertilization at seeding (12.5 kg N/ha^{-1}, 75 kg P2O5/ha^{-1}, and 52.5 kg K2O/ha^{-1}) and a second application of 140 kg/ha^{-1} of N 30 days later.

Sward height and condition was measured at 100 points per strip using a sward stick (Bircham, 1981) four times during the grazing down at 0, 4, 19 and 24 h after the strip allocation. We call each time that the sward was measured a "moment"; therefore, each strip was measured in four moments. Each sward stick readings were classified as grazed leaves, ungrazed leaves, trampled leaves, inflorescences and stems.

Pre-grazing herbage mass was assessed by clipping at ground level four 0.153-m^2 quadrats in each strip. Five sward height measurements were made inside each quadrat and herbage was cut by stratum (0-25%, 25%-50%, and 50%-100% of the pre-grazing sward height). Post-grazing herbage mass was also evaluated by clipping four 0.25-m^2 quadrats at ground level. Herbage mass samples were dried at 55 °C for at least 72 h to determine the dry mass.

Animals

Thirteen yearling Texel x Ideal crossbred sheep, weighing 30 - 55 kg body mass, were used for foraging behavior observations. Three focal animals were allocated to each paddock. One of the animals was evaluated only in one period and had to be replaced because of health conditions; therefore, a total of 13 focal animals were observed. To provide a suitable social environment (Penning et al., 1993), additional animals were placed in each strip and paddock so that at least four individuals were together during and between experimental periods.

Grazing behavior

Foraging behavior was assessed using continuous bite monitoring (Agreil and Meuret, 2004; Bonnet et al., 2015). This methodology consists of recording continuously the observed behaviors of a focal animal. We followed the four steps described by Bonnet et al. (2015) and Bolzan et al. (2019): mutual familiarization, design of the biting-code grid, continuous bite monitoring, and bite simulations. For 45 days previous to the experimental period, four observers entered paddocks to familiarize the animals with their presence. The observers walked beside and progressively reduced the distance to the focal animals until they were closer than a meter without provoking any reaction. During the mutual familiarization period, observed bites were classified into 29 groups (i.e., bite codes). Bite codes considered (1) sward structural characteristics such as height, density, morphological components, and whether the plant was grazed, and (2) animal behavior characteristics such as time required to position the head, sever and gather herbage into the mouth. Additional codes were assigned to non-ingestive behaviors such as walking, drinking, rumination, social interaction, and resting.

Continuous bite monitoring was performed in three 3-day experimental periods (Table 1). Each observation started when the sheep were moved into a new strip at 14:00 of the first day, paused at dusk (18:00 of first day), resumed at dawn (7:00 h of next day day) and ended at 14:00 when sheep were moved to a new strip the next day. Thus, focal observations lasted ~4 hours in the first afternoon and ~7 hours in the following morning. Observers recorded bite and behavior codes with a Sony ICD-PX312 digital voice recorder and later transcribed the records using the JWatcher software (Blumstein & Daniel 2007). On the last day of the third period, the grazing observations were not completed due to a heavy rain and, therefore, were removed from the analysis. In addition, three audio recordings were corrupted and therefore were discarded from the analysis.

At least 20 bites corresponding to each code were hand-plucked, as described in Bonnet et al. (2011), between grazing bouts by each observer each day. Bite simulations mimicked the mouth placement in the sward and the tissues removed, considering the difference in the canopy before and after the biting event. Each set of 20 bites was pooled and dried at 55 °C for at least 72 h to determine dry mass in a scale with a precision of 0.0001 g.

Table 1. Organization of the grazing focal observations: numbers and letters indicate the identity of animals and observers, respectively. Each one of the four observers monitored only one focal animal per day in a different paddock. The focal animals remained in the same paddock over the three experimental periods. Bold font indicates the audio recordings that were corrupted and therefore discarded from the analysis.

		High density – High depletion		Low density – Low depletion	
		Paddock 1	Paddock 3	Paddock 2	Paddock 4
Period 1	Day 1	13 – R	31 – P	21 – G	42 – A
	Day 2	14 – G	33 – A	23 – R	43 – P
	Day 3	11 – P	32 – R	22 – A	**41 – G**
Period 2	Day 1	13 – A	**32 – G**	21 – P	42 – R
	Day 2	14 – R	33 – P	23 – A	**42 – G**
	Day 3	11 – A	32 – G	22 – R	74 – P
Period 3	Day 1	13 – P	33 – R	21 – G	74 – A
	Day 2	11 – G	31 – A	22 – P	43 – R

Calculated variables

All calculations and statistical analyses were performed using R software (R Development Core Team, 2014). Sward measurements were used to calculate average height, coefficient of variation of height, proportion of pasture area ungrazed, and proportion of pasture area trampled. Proportion of pasture area was the number of sward stick readings of each category divided by the total sward stick measurements per moment (n = 100).

Bite mass was analyzed and then predicted by using the following linear mixed-effects model: y ~ treatment + bite.code + (1|period) + (1|animal) + (1|observer). Cumulative intake was calculated as a cumulative sum of bite mass over the continuous bite monitoring time for each focal animal.

To relate foraging behavior variables to sward characteristics, we used chunks of focal data closest to the moments when swards were measured. The first chunk started at the onset of grazing in each new strip and lasted until the total number of bites per unit strip area reached approximately 3 bites m^{-2} to minimize effects of grazing on sward structure as measured before grazing. For the measurements after 4, 19, and 24 hours since strip allocation, we used chunks of 80 behavior records centered at the times of sward measurement.

Average bite mass was calculated as the sum of masses of all bites in each chunk divided by number of bites. Step rate was calculated as the sum of steps divided by the chunk duration. Similarly, bite rate was calculated as the sum of bites divided by chunk duration. Intake rate was sum of bite masses divided by chunk duration. The proportion of bites on ungrazed areas was calculated as the number of bites on intact plants (not yet defoliated) divided by the total number of bites.

Statistical analysis and modeling

We developed a structural mechanistic-empirical model to test whether short-term intake rate can be fully explained by sward variables when animals are exposed to contrasting grazing management strategies. The model is static and spatial heterogeneity is considered through the coefficient of variation of sward height. Model development proceeded by simplification of a full model, as proposed by Pinheiro & Bates (2000). The full and the final models for each grazing mechanism, expressed as a linear mixed-effects model formula for the *lmer* function of the *lme4* package (Bates et al., 2015), are presented in Table 2. The variables included in each initial model were chosen based on the known explanatory mechanisms with defined mathematical relationships, the grazing management strategies that have no direct causative relationship, and the random effects for grouping variables such as individual, paddock, period, and observer. We established an a priori order of effects into the model and tested these effects with the sequential sum of squares (Analysis of variance – Type I). Final models were obtained by removing non-significant fixed effects (p-value > 0.05) not included in a significant interaction, as well as dropping non-significant random effects. Response variables were transformed to meet distributional assumptions when needed, and the explanatory continuous variables were standardized to improve convergence of solutions. The p-value of treatment effects, after all other proximate explanatory variables were taken into account, was used to determine whether foraging mechanisms are fully explained by instantaneous sward conditions or not. The coefficient of determination, R^2 (ranging from 0 to 1), was calculated by using the variance of the predicting fitted values based on the fixed effects alone, disregarding the variance of the random effects according to the equation provided by Nakagawa & Schielzeth (2013).

Table 2. Model results showing the effect of sward variables such as average height, coefficient of variation of height, proportion of ungrazed area, proportion of trampled area, and grazing treatment on grazing behavioral mechanisms, including bite mass, step rate, bite rate and intake rate. AIC and BIC values were used to select the best fit model and non-significative effects were dropped from the models. In case of competing models with similar AIC and BIC values, the simpler model was chosen as the final model, as suggested by Pinheiro & Bates (2000).

Response	Model	Formula	AIC	BIC
Bite mass	Full	avg.height * CV.height * p.ungrazed * p.trampled * treatment + (1 ∣ animal) + (1 ∣ paddock) + (1 ∣ period) + (1 ∣ obs)	-15.574	82.622
	Final	(avg.height + CV.height + p.ungrazed)^2 - CV.height : p.ungrazed + (1 ∣ animal) + (1 ∣ paddock) + (1 ∣ obs)	-38.203	-11.664
Step rate	Full	avg.height * CV.height * p.ungrazed * p.trampled * treatment + (1 ∣ animal) + (1 ∣ paddock) + (1 ∣ period) + (1 ∣ obs)	301.05	401.90
	Final	avg.height + p.ungrazed + (1 ∣ animal) +(1 ∣ block) + (1 ∣ obs)	260.26	278.83
Bite rate	Full	bite.mass * step.rate * treatment + (1 ∣ animal) + (1 ∣ paddock) + (1 ∣ period) + (1 ∣ obs)	359.61	391.46
	Final	bite.mass * step.rate + (1 ∣ animal)	355.00	370.93
Intake rate	Full	bite.mass * bite.rate * treatment + 1 ∣ animal) + (1 ∣ paddock) + (1 ∣ period) + (1 ∣ obs)	-136.02	-100.22
	Final	bite.mass * bite.rate + (1 ∣ paddock)	-145.49	-128.97

The selectivity for previously ungrazed plants was analyzed using a generalized linear mixed model with a binomial family, with the proportion of ungrazed area available and treatment as fixed effects, and individual, period, and observer as random effects (prop.ungrazed.bites ~ prop.ungrazed.swards + treatment + (1|animal) + (1|period) + (1|observer)).

The pattern of herbage consumption over the whole grazing record was analyzed with generalized additive models (GAM) using the combination of treatment and shift (PM or AM) as fixed parametric effects, residence time in the strip (time_min) as smoothing fixed effect, and animal identity and period as random effects: cum_intake ~ s(time_min, k = 4, by = treat_shift) + treat_shift + s(animal, bs = "re") + s(period, bs = "re"). The number of knots was set to 4 to constrain the flexibility of the smoothing. Because we performed repeated measurements on the same animals over time, observations were not independent and we used the "corExp" argument of the *gam* function of the *mgcv* package (Wood, 2017) to account for the temporal autocorrelation.

Sward variables such as average height, coefficient of variation of height, herbage mass, proportion of area trampled and proportion of area ungrazed were analyzed using linear mixed-effects models with grazing treatment and moment as fixed effects: y ~ treatment_moment + (1 | block) + (1 | paddock) + (1 | strip). Treatment and moment were combined into a single variable called treatment_moment. Residuals of the analyses were checked for homogeneity of variance and normality using the *qplot* function of the R car package (Fox & Weisberg, 2011). Analysis of variance was conducted and then the treatment_moment means were compared with Tukey test at 95% confidence level with the *emmeans* package (Lenth, 2018).

We used a nonlinear mixed-effects model implemented by the *nlme* package (Bates et al. 2018) as an approach to estimate the vertical distribution of mass as a function of sward height. The nonlinear model was fitted with the self-starting function *SSasympOrig*, that is an asymptotic regression function through the origin: y = Asym * (1 - exp(-exp(lrc) * input)), where y is the proportion of sward mass contained below input, input is the proportion of the total sward height considered, Asym is the horizontal asymptote (no biological meaning), and lrc is a natural logarithm of the rate at which the slope tends to zero. The proportion of mass and height were calculated by dividing the mass and height of each stratum by the total mass and height of the quadrat. In the first model, grazing treatment was included as a fixed effect for both parameters (Asym and lrc), and strip and quadrat nested within strip were included as random effect on both parameters. As treatment was non-significative (p-value > 0.05), the model was updated by removing this fixed effect.

3. Results

Continuous bite monitoring was suitable for the purpose of our study. The method allowed us to calculate intake rate at multiple temporal scales, and to plot and model cumulative intake as a function of time, treatment and relevant covariables (See Figure 1 for a detailed example for each treatment). Since each bite was described by whether plants prehended were previously grazed or not, we were able to estimate indices or selectivity for grazed or ungrazed plants.

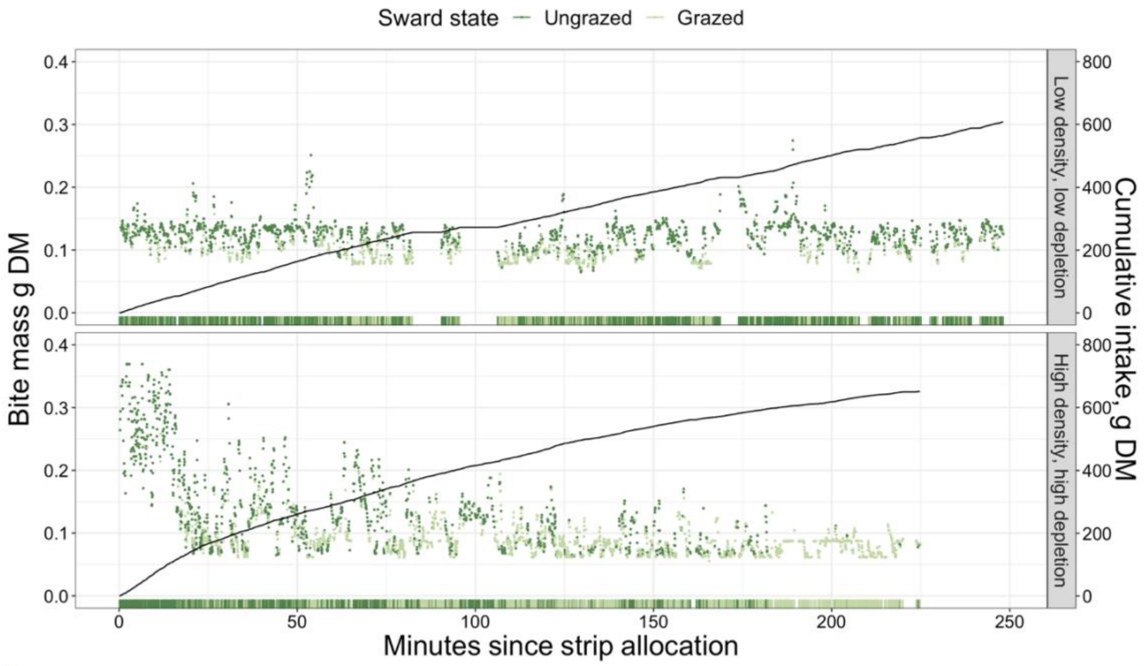

Figure 1. Examples of foraging behavior of sheep under two contrasting grazing management conditions represented by the experimental treatments: LDLD at the top and HDHD at the bottom. Both graphs represent the first four hours of grazing since animals entered a new strip. Bite mass is indicated by points (left vertical axis) and cumulative intake of herbage over time by the black line (right vertical axis). The dark and light green points represent bites on previously ungrazed and grazed plants, respectively. The slope of the cumulative intake indicates the rate of herbage consumption, which is clearly greater at the beginning of grazing and declines more over time in the lower treatment.

Sward properties

Average sward height decreased markedly during the grazing period in both treatments, but the reduction in height was faster under the HDHD treatment, with high animal density and taller initial heights (Table 3 and Figure 2). For example, the differences between initial and final sward height were 7.5 cm and 20.3 cm for LDLD and HDHD, respectively. In agreement with the pattern of statistical distributions of height, the coefficient of variation of height increased significantly over time for both treatments (Table 3).

All plants in the strip were ungrazed at the beginning of grazing and the proportion of ungrazed area decreased over time in both treatments, with the high animal density (HDHD) having much lower values when animals were moved from the strip (0.06 vs 0.35, Table 3). When animal density was high, the proportion of pasture area trampled increased significantly in the first four hours, and then it remained fairly constant until animals were removed, whereas with low animal density, no marked differences were detected in proportion trampled between the start and end of grazing in each strip (Table 3). Like sward height, herbage mass at the end of grazing was lower than pre-grazing, particularly in the HDHD treatment with high animal density (Table 3).

Sward structure was severely disrupted in the high density-high depletion treatment. Prior to grazing (Figure 3), those swards had an average height of 27.7 cm, with 37.5% (833 kg/ha) of the mass in the bottom quarter (27.7 * 0.25 = 6.7 cm). After grazing, 1544 kg/ha appeared compressed into 6.4 cm of average height. On the other hand, swards in the low density-low depletion treatment contained 75% (1278 kg/ha) of their mass in the bottom 62% (12.1 cm) of the canopy prior to grazing (Figure 3) and 1462 kg/ha in the 12.1 cm remaining after grazing.

Table 3. Means and standard errors (within parenthesis) of sward variables in each grazing management treatment at four moments after strip allocation (0, 4, 19 and 24 h). Measurements at 0 and 24 h were done

immediately before and after each grazing period, respectively. Numbers without common letters are significantly different with a probability of error type 1 equal to 5%. Comparisons of are valid only within row.

	Low density – Low depletion				High density – High depletion			
Sward variable (unit)	0h	4h	19h	24h	0h	4h	19h	24h
Height (cm)	19.6 g (0.18)	15.8 f (0.18)	14.8 e (0.18)	12.1 d (0.19)	26.7 h (0.18)	9.7 c (0.18)	8.5 b (0.18)	6.4 a (0.19)
CV of height (%)	18 a (1.43)	27 b (1.49)	29 b (1.53)	33 bc (1.67)	16 a (1.43)	39 cd (1.43)	44 de (1.53)	46 e (1.67)
Non-grazed area (%)	1.00 e (0.016)	0.49 d (0.016)	0.4 d (0.016)	0.35 c (0.017)	1.00 e (0.016)	0.16 b (0.016)	0.14 b (0.016)	0.06 a (0.017)
Trampled area (%)	0 a (0.02)	0 a (0.02)	0.01 a (0.02)	0.02 a (0.02)	0 a (0.02)	0.16 b (0.02)	0.16 b (0.02)	0.15 b (0.02)
Mass (kg DM/ha)	1704 a (98)			1462 a (117)	2223 b (102)			1544 a (119)

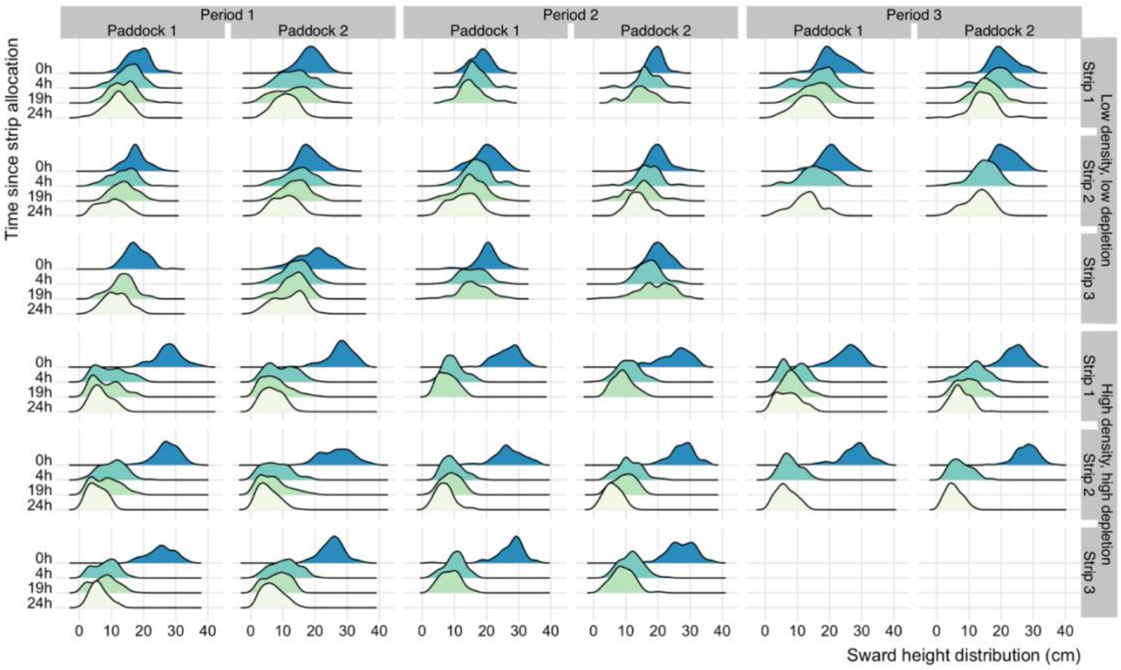

Figure 2. Distribution of sward height in each strip grazed at four moments after strip allocation (0, 4, 19 and 24 h) of sheep grazing vegetative Italian ryegrass during three evaluation periods. Note the clear difference in the impact of the first 4 hours of grazing between the low (top) and high (bottom) density treatments. The 0 and 24 h measurements were done immediately before and after each grazing observation, respectively. The experiment was conducted in four paddocks, therefore each animal density had two paddocks. Statistical differences are shown in table 3.

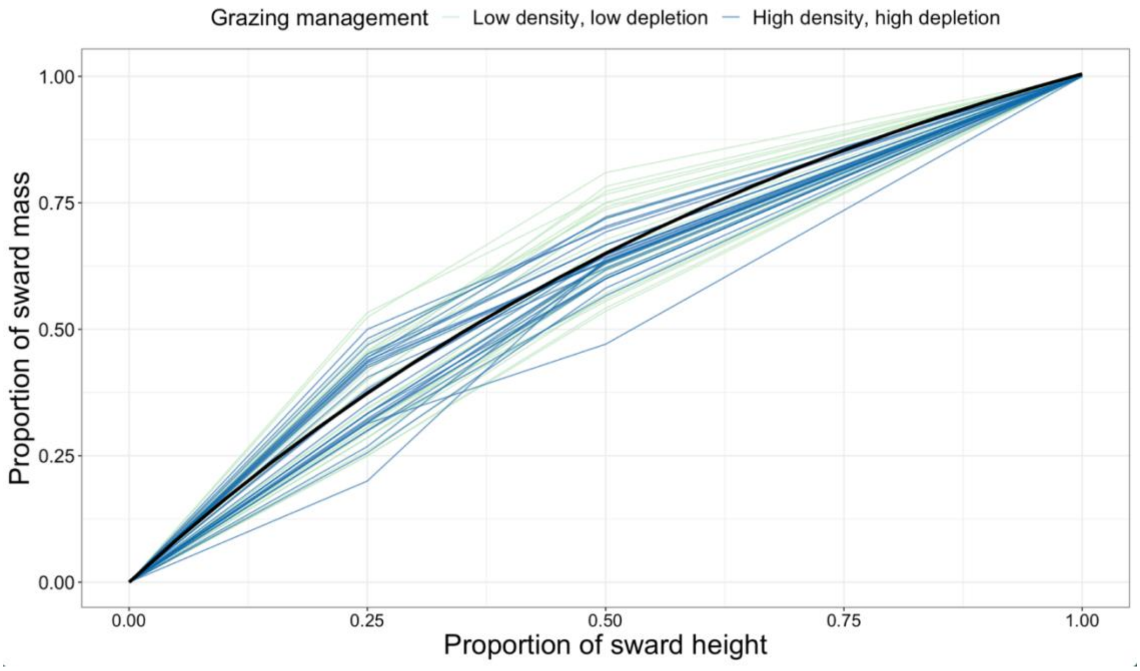

Figure 3. Distribution of sward mass over height. The curve shows the proportion of sward mass per unit area as a function of the proportion of height from the ground up. Each thin line represents one quadrat evaluated prior to grazing. There were no significant differences between grazing treatments. The nonlinear model is: proportion of sward mass = Asym * (1 - exp(-exp(lrc) * proportion of sward height)), where the estimated values for the parameters Asym and lrc are 1.424 (SE = 0.0486) and 0.191 (SE = 0.0530), respectively.

Pattern of herbage consumption

Animals exhibited a markedly different pattern of cumulative herbage consumption for each combination of treatment and day-shift (PM or AM) (Figure 4). The slope of the fitted curve represents the average intake rate over animals per unit strip occupancy time, not per unit eating time. In the afternoon when animals entered a new strip, this average intake rate was relatively constant for animals in LDLD , but it decreased over time in HDHD . Total intake in the afternoon, when first entering each strip, was 500 g per animal in LDLD and about 460 g in HDHD, in spite of the fact that the high-density treatment exhibited much greater intake rate than LDLD during the first hour of grazing. In the first 100 minutes of the following morning, total intake remained low in both treatments because animals were grazing sporadically. After that, animals in both grazing conditions had a linear increase in cumulative intake, but the slopes of the curves indicate that animals in LDLD increased the cumulative intake faster than in HDHD due to a greater rate of intake. Total intake per animal was 350 g and 170 g in the low and high animal density treatments, respectively, in the morning.

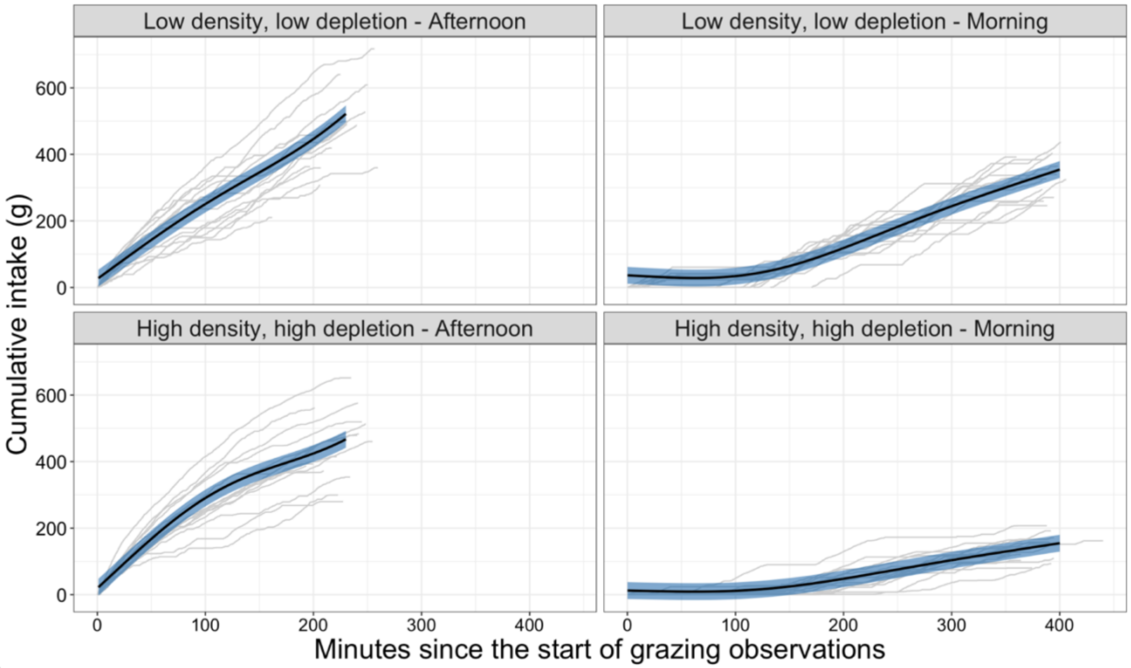

Figure 4. Cumulative intake by sheep grazing vegetative Italian ryegrass under different grazing management treatments (rows) and day-shift (columns). Thin grey lines are for individual animals. The black line and the blue ribbon are the estimated mean and 95 % confidence interval based on a GAM model parameterized with data for all animals. The slope of the curves is the rate of herbage consumption over strip occupancy time.

Foraging mechanisms

Foraging mechanisms such as searching, selection, gathering, and processing of herbage were not affected by grazing treatment ($p > 0.05$, Figures 5 and 6) beyond the effects via changes in sward conditions. At the first level of the structural equation model, 64% of the variance in bite mass was explained by average sward height and its interactions with proportion of pasture area ungrazed and coefficient of variation of height (indicative of sward heterogeneity). All final proximate explanatory variables affected bite mass positively. Forty two percent of the variance in stepping rate was explained by fixed effects, with 18% and 81% of these fixed effects directly attributable to the proportion of pasture area ungrazed and average sward height, respectively. The proportion of area ungrazed exhibited a positive effect, whereas average sward height had a negative effect on stepping rate. The proportion of pasture area trampled had no significant effect on either response variable and it was dropped from the models.

At the second level, bite mass, step rate and their interaction accounted for a total of 47% of the variance in bite rate, where the interaction having a negative impact. Finally, 96% of the variation in intake rate was explained by bite mass, bite rate, and their interaction. Bite mass, bite rate, and their interaction had a positive effect on intake rate.

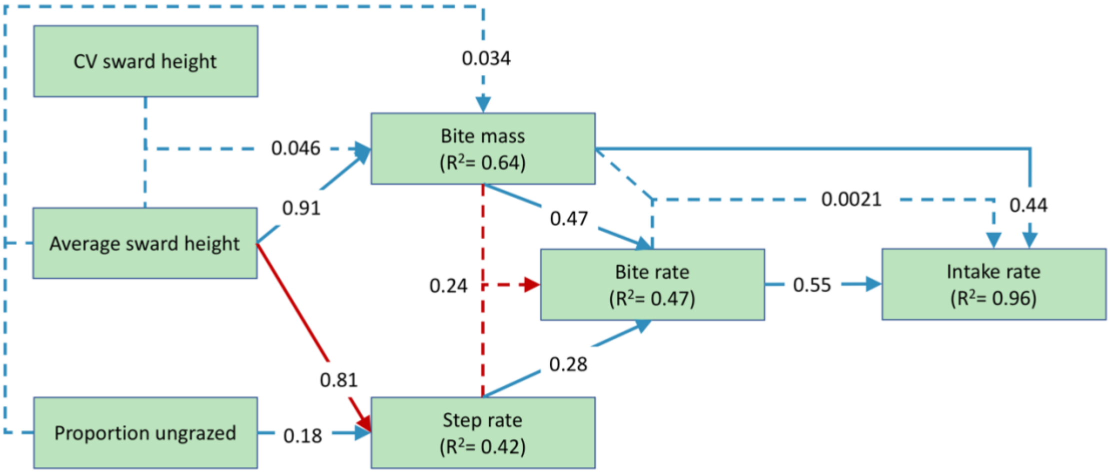

Figure 5. Structural-mechanistic modeling of the foraging behavior of sheep managed under LDLD and HDHD grazing treatments. R^2 denotes the proportion of variance explained by fixed effects. Numbers on the lines represent the proportion of the variance of the variable at the head of each arrow explained by the variable at the tail of the arrow. Interactions are represented by dashed lines. Blue indicates positive and red indicates negative effects. Only significant effects ($p < 0.05$) are shown for simplicity. Full and final models are shown in Table 2.

The proportion of bites placed in ungrazed areas as a function of the proportion of pasture area ungrazed, indicated a pattern of partial preference for intact plants (Stephens & Krebs, 1986) (Figure 6). Grazing treatment had no significant effect and it was removed from the model. When proportion of ungrazed swards was less than 80%, animals tended to select ungrazed swards. The data do not support firm conclusions about the effect of availability on preference for ungrazed areas because the ranges of proportion of pasture area ungrazed in the two treatments did not overlap, thus creating confounding between treatment and covariate, and because there was a large variability in selectivity over animals, time and strips.

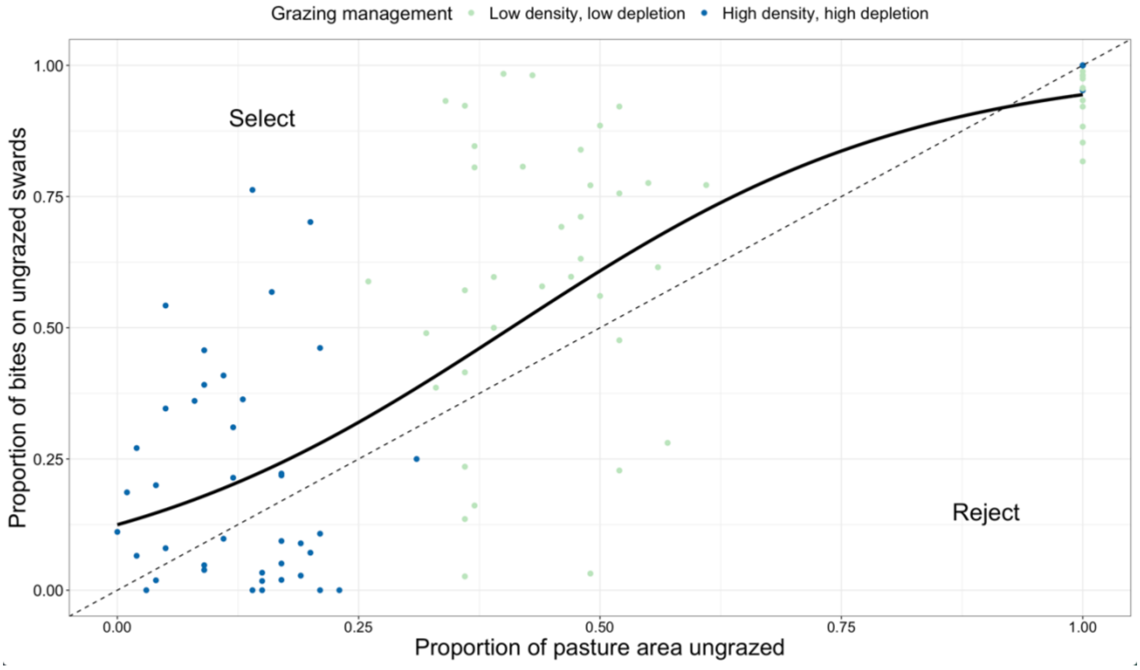

Figure 6. Selectivity pattern of herbivores grazing heterogeneous swards: proportion of bites on ungrazed swards vs proportion of pasture area covered by ungrazed swards. The black line shows the selectivity pattern by ungrazed swards as function of its availability fitted from a generalized linear

mixed model parameterized with data of all individuals' observations. There was not significantly difference for treatment effects ($p < 0.05$) for grazing management treatments. The dashed line indicates $y = x$, the area above the dashed line denotes selection by ungrazed swards whereas the area below indicates rejection.

4. Discussion

Treatment effects

The answer to our first questions is that indeed, a strategy of heavily grazing initially tall swards clearly resulted in lower daily intake rates than lightly grazing swards of intermediate height, mainly because of a rapid decline in intake rate over the first 60-100 minutes of grazing. This decline was linked to a steep decline of herbage height, which was more than expected on the basis of herbage mass consumed. Most likely, tall swards were more susceptible to trampling damage and received much more trampling than those of intermediate height because of the large differences in animal density (1.34 vs. 5.48 kg m^{-2}). This point is supported by the fact that at the end of the grazing period swards in the high density-high depletion treatment ended having about half the height of the light density-low depletion treatment but slightly more mass per area. Prior to grazing, swards did not differ in vertical distribution of mass (Figure 3) between treatments, having about 33% of their mass in the bottom 25% of their height (Table 3). Trampling more than doubled the bulk density of the bottom stratum of HDHD swards, which had about 69% of the mass in the remaining height of 6.4 cm or 24% of the original height. On the other hand, 86% of the initial mass remained in 62% of the initial height in the lightly grazed swards, which is only 11% more than expected based on the pre-grazing vertical distribution of mass.

In our study, high density of animals caused severe trampling of tall swards during the first 60 to 100 minutes of grazing, which reduced intake rate severely during the rest of the period of occupancy of each strip. Collas et al. (2020), also found that single tethered animals caused severe trampling damage to tall swards, reducing sward height from 49.2 to 15.6 cm during the first 24 h of allocation. In their experiment, individual bulls (270 kg average liveweight) were tethered with an 8 m chain, which resulted in 1.34 kg liveweight m^2, and part of the sward structure disruption was due to the chain. Authors noted that herbage allowance decreased more slowly than sward height, and that the sward resembled a carpet of lying stems.

The fact that higher animal density caused more trampling damage is not surprising, but raises the question of what would happen when initially tall swards are grazed with low animal densities. How much more susceptible to trampling damage are taller swards? A differential effect of trampling on sward structure could determine completely different state trajectories for swards of different height that are grazed with equal animal density. Silveira et al. (2013) and Congio et al. (2018) working with beef and dairy cattle, respectively, showed that taller swards are more damaged than short swards, mainly by higher animal density. In higher pre-grazing herbage masses, herbage trampling was greater when the animals started the grazing period (Carnevalli et al., 2006). In addition to that, these authors point out that taller swards result in greater herbage losses. According to Silveira et al. (2013), global grazing losses were 39% lower on short than tall swards.

Intake rate mechanisms

The second question we posed was: do herbivores exhibit the same foraging mechanisms for a given sward state, regardless of grazing management imposed? The question was approached by a model containing both direct and indirect effects of grazing treatment (LDLD vs. HDHD) on intake rate and giving priority to the proximate explanatory variables for intake rate. Measures of sward structure and availability were intervening variables between treatment and intake rate. The need for different mechanisms depending on treatment would be revealed by treatment effects or interactions that are significant even after the effects of proximate variables are accounted for.

None of the final models included treatment as a predictor, which supports the hypothesis that bite mass, bite rate and intake rate are explained by sward conditions. Most of the variance of foraging behavior mechanisms, such as searching, selectivity, gathering, and processing, can be explained by vegetation characteristics, despite the large difference between the grazing conditions imposed by the grazing treatments. The pattern of herbage consumption was remarkably different between treatments, but treatments did not affect grazing variables beyond their effects on instantaneous sward conditions and subsequently, on bite mass and rate (Figure 5). The large difference total and temporal patterns of intake between treatments (Figure 4) were caused by the different temporal patterns in sward conditions (Figure 2).

The difference in animal density, obtained by larger number of animals and smaller strip area, resulted in very different resource depletion levels (Table 3). Animals grazing in the high-density group experienced a faster resource depression, clearly demonstrated by the decreasing slope of intake over time (Figure 4). On the other hand, the low-density treatment exhibited a much smaller decline in rate of herbage consumption, indicating that patch depletion and depression were low (Laca et al., 1994).

Role of selectivity

Grazing models have described sward structure as potential bites superimposed in grazing horizons (Ungar & Noy-Meir, 1988; Ungar et al., 1992). By definition, each grazing horizon has a horizontal dimension (i.e., which is it the surface covered by such horizon across the pasture area), and also it has a vertical dimension determined by bite depth (Benvenutti et al., 2015). Thus, every time the top horizon is grazed, a new horizon is revealed. As a consequence, bite mass is constant within each horizon and potentially differs between horizons, usually decreasing from the upper top to the lower one horizon. Dynamic models (e.g., Baumont et al., 2004; Gregorini et al., 2012) suggest that use the grazing horizon approach set selectivity as a "zero–one rule", where potential bites are fully accepted or rejected as a function of their profitability (Stephens and Krebs, 1986). In this case, herbivores would only be expected to graze exclusively the top ungrazed horizon for as long as search time is not too limiting, which holds true in a wide range of conditions.

Experiments with low (Ungar et al., 2001) and high (Ungar & Ravid, 1999) levels of depletion of small patches demonstrated that heifers allocate bites systematically in the top horizon until approximately 75% of the area has been grazed. The authors argued that this grazing pattern of attack occurs because the effective bite area in the top horizon decreases and searching time increases as the horizon area decreases. Effective bite area decreases because remaining non-grazed areas left are smaller than the potential bite area. However, our results indicated that at any level of availability of previously non-grazed swards, herbivores exhibit variability in exerting a partial preference for previously ungrazed swards (Figure 6). Why are our results in disagreement with the results reported previously? A likely explanation of this discrepancy with respect to previous finding relies on the large difference in the spatial scales between experiments; whereas in Ungar et al. (1999, 2001) experiments the herbivores were exposed to small patches (0.16 to 0.53 m^2) in a short-term experiment (~ 30 min), in our experiment the animals grazed areas from 45 to 160 m^2 during a much longer period. Moreover, the use of space by herbivores has fractal properties (Garcia et al., 2005), and thus behaviors exhibited in one scale cannot be linearly translated to another. Pattern of selectivity varies with patch size and distance between patches because herbivores integrate spatial information to decide between searching for a more profitable, farther bite or for a less profitable, closer one (Utsumi et al., 2009).

Moreover, the grazing horizon approach disregards sward height heterogeneity in spite of the fact that herbivores perceive and respond to resource heterogeneity. In those theoretical models, bite dimensions result from three or four (number of horizons) combinations of sward height and density, whereas in nature multiple combinations can occur due to the resource variability, such as exemplified through the statistical distributions of sward height (Figure 2). We found a positive effect of heterogeneity on bite mass, in agreement with results previously reported by Pontes-Prates et al. (2020). By simulating short-term grazing tests with increasing levels of coefficient of variation of height, they observed a positive effect of heterogeneity on functional response due to selectivity by the taller end of the distribution.

5. Conclusions

Animals grazing in the low-density, low depletion treatment had greater daily intake rate than in the high-density, high depletion treatment. Despite of the high-density group exhibiting a higher instantaneous intake rate at the beginning due to taller initial swards, animals experienced a faster resource depression caused by the high animal density. Under the low-density, low depletion treatment, animals clearly demonstrated a more stable and higher instantaneous intake rate. Moreover, the behavioral mechanisms determining intake rate were explained by the instantaneous plant abundance and spatial distribution regardless of longer-term grazing conditions imposed.

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CHAPTER III

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Article

Mechanisms of Grazing Management in Heterogeneous Swards

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Abstract: We explored the effects of heterogeneity of sward height on the functioning of grazing systems through a spatially implicit mechanistic model of grazing and sward growth. The model uses a population dynamic approach where a sward is spatially structured by height, which changes as a function of defoliation, trampling, and growth. The grazing component incorporates mechanisms of bite formation, intake, and digestion rates, but excludes sward quality effects. Sward height selection is determined by maximization of the instantaneous intake rate of forage dry mass. For any given average sward height, intake rate increased with increasing spatial heterogeneity. Spatio-temporal distribution of animal density over paddocks did not markedly affect animal performance but it modified the balance of vegetation heterogeneity within and between paddocks. Herbage allowance was a weak predictor of animal performance because the same value can result from multiples combinations of herbage mass per unit area, number of animals, animal liveweight, and paddock area, which are the proximate determinants of intake rate. Our results differ from models that assume homogeneity and provide strong evidence of how heterogeneity influences the dynamic of grazing systems. Thus, we argue that grazing management and research need to incorporate the concept of heterogeneity into the design of future grazing systems.

Keywords: grazing management; sward height distribution; spatial heterogeneity; ecological modeling; grazing behavior; resource heterogeneity; integral projection matrix

1. Introduction

Traditional grazing management has been based on variables such as stocking rate and herbage allowance, aimed at controlling intensity and frequency of defoliation, and consequently, herbage production and animal performance. However, these approaches assume equilibrium conditions and disregard spatial heterogeneity and scaling effects present in grazing systems [1]. Herbage allowance and stocking rate may only describe an instant of a grazing system, but not its dynamics, which result from multiple processes influenced by biotic and abiotic factors. The actual management variables over which we can exert control are shape and area of paddocks, number and characteristics of animals, and timing and duration of grazing and rest periods. Additional management variables such as fertilization and irrigation timing and rate can also be used to modify the quality and dynamics of vegetation state variables. Likewise, livestock distribution and behavior can be altered through rewards like salt or supplements. These management and uncontrollable biotic and abiotic factors change over space and time and drive grazing systems into a permanent state of flux.

Defoliation intensity in one biting event is usually the proportion of the plant mass that is in the top half of the sward height at the bite location. Sheep and cattle have a remarkable constant bite depth that is about 50% of sward height, across a large variety of conditions [2,3]. Thus, the mechanism of unitary defoliation intensity is not yet directly susceptible to management. Management variables can only affect the probability that any given plant will be defoliated at any moment. Actual defoliation frequency depends not only on exposure to grazing but also on the spatial patterns of bites that animals choose [4,5]. For example, large-scale patterns of what appears to be defoliation intensity, such as the exponential increase in height with increasing distance from water [6], are most likely patterns created by the balance between plant growth and defoliation frequency. Because animals have to walk to water frequently, the actual density of livestock occupancy decreases with increasing distance from water.

Although traditional grazing management considers the temporal heterogeneity of forage demand and supply, the concept of spatial heterogeneity has not been fully incorporated, perhaps because is harder to perceive and to control. Livestock distribution has fractal properties and is in part determined by the heterogeneity of resources such as forage, water, and shade [7,8]. In addition to the inherent heterogeneity, grazing disturbance (as well trampling and excreta deposition) is an important source of variability in the vegetation [9,10] because herbivores' selectivity generates a mosaic of tall and short patches that in turn affect future grazing. Sward growth rate is nonlinear, and therefore pasture production is not fully determined by average sward height at paddock scale but also depends on the spatial distribution of sward height [11,12] (Figure A1). From an animal perspective, resource heterogeneity allows the selection of a diet that is better than the average available in the environment. Therefore, predictions of pasture production and animal intake and performance on models that assume homogeneity tend to differ from reality [13].

Grazing systems are complex and vary in time and space, requiring a broader approach than has been applied to grazing management due to their multidimensional nature. However, traditional grazing management variables such as average sward height, stocking rate, and herbage allowance disregard the effects of heterogeneity and scaling on the functioning of grazing systems. We aimed to develop a spatially implicit model of grazing and sward growth to explore the effects of spatial heterogeneity on responses to traditional grazing management variables. We simulated three grazing conditions using traditional management variables to determine the interaction between inherent spatio-temporal scales of grazing with those imposed by management in heterogeneous swards. We tested the hypotheses that (1) the functional response (instantaneous intake rate) is related not only to resource abundance but also to resource heterogeneity; (2) system performance (yield per animal and per unit area) responds to spatio-temporal distribution of animal density; and that (3) herbage allowance is not sufficient as a measure to manage animal performance because any value of herbage allowance can be obtained for any given level of forage abundance simply by changing the number of animals or the area of the paddock. This work contributes to the understanding of how heterogeneity and scaling influence the functioning of grazing systems and provides a promising platform for future research.

2. Materials and Methods

2.1. Model Description

We developed a dynamic mechanistic model of grazing where the sward is structured by height. The grazing component of the model incorporates detailed mechanisms of bite dimensions and intake rate as controlled by ingestion and digestion. Model inputs are management variables such as species and number of animals, paddock area, timing and duration of grazing and rest periods, and initial state variables: sward height distribution (amount of area in 2000 bins of sward height), rumen fill, and body mass.

The approach was to include all major grazing mechanisms known and to determine their logical consequences by integration into the model. The model is spatially implicit because it simulates the heights of a population of plants, but their positions are not specified. Diet quality is assumed to be constant and unrelated to the heights selected for grazing. This assumption is meant to eliminate quality as a factor driving selectivity in this version of the model, and it has no impact on the growth of the model swards, as we use an empirical equation based on real swards to model growth in height. The model tracks defoliation, trampling, and growth of plants in 2000 height classes, as well as selectivity and individual bite dimensions, time, and mass in a 10 min time step.

A key feature of grazing systems is the large difference in temporal scale of growth and defoliation at the individual plant level, a feature that is not contemplated in typical difference or differential equation models (e.g., [14,15]). In the present model we implement the difference in the temporal scales of grazing and growth by representing grazing as a death–birth process by which every bite "kills" an area of pre-grazing height and "gives birth" to an equal area with the corresponding post-grazing height. The integration of both spatial heterogeneity in height and pasture growth with animal behavior and productivity at a high temporal resolution, as well as the use of the integral projection matrix technique, are the main novel features that distinguish this model from similar grazing models that include resource heterogeneity (e.g., [4,16–21]).

Sward structure is represented in the model by the horizontal and vertical distribution of plant mass. The horizontal structure is represented by the frequency distribution of heights, and the vertical structure is described by an exponential decline in bulk density from the bottom to the top of the canopy [22,23]. Sward height distribution is updated every 10 min using an integral projection matrix model (a modeling approach that uses transition matrices to calculate the change in state of a population structured by a continuous variable) adapted from Ellner et al. [24]. Sward areas increase in height according to a temperature-dependent logistic growth process [25] and decrease in height by grazing and trampling with rates that depend on sward height and animal density. Using the original population dynamics view of the integral projection method, the process can be viewed as discrete areas growing into adjacent bins of taller height, or "dying" due to being grazed and trampled and being instantly "reborn" in a bin with a shorter height equal to the remaining stubble. Grazed areas are reborn at half (or another selected proportion) of the original height, whereas trampling effects are simulated by reducing 7.5% of the searched area to a height of 25 mm. Area trampled is commensurate with hoof area and number of steps per unit area searched [26], whereas trampled height is based on measurements of ryegrass plants lodged after grazing (Carvalho, unpublished data). The effect of excreta deposition on area available for grazing is partly accounted for by the trampled area, but the model does not currently focus on the effects of excreta on animal selectivity, and it does not include excreta effects on plant growth. Relative growth rate, height of trampled sward, and nutritive value were parameterized for annual ryegrass (*Lolium multiflorum* L.), whereas vertical distribution was parameterized with both annual and perennial ryegrass (*Lolium perenne* L.) data. The actual hourly temperature used for simulations was obtained from the experimental station in Federal University of Rio Grande do Sul, Brazil, for the growing period.

The beginning and end of grazing bouts are determined by rumen fill and an empirical circadian rhythm of grazing motivation. The circadian rhythm is an empirical function that defines the proportion of time that the animals are actually grazing within feeding bouts [27]. Rumen fill is a state variable whose rate of change is the difference between intake rate and digestion and passage rates. Digestion rate is constant, whereas passage rate is a linear function of instantaneous intake rate [28,29]. Grazing ceases when the rumen becomes full and it resumes when rumen fill falls below 90% of rumen capacity and circadian motivation is on. Rumen capacity is an isometric function of body mass [30] and it increases by 30% between 16 and 24 h as a mechanism to avoid nocturnal grazing [31]. Only one canonical animal is simulated, and the results are simply multiplied by the number of animals.

Instantaneous intake rate is the product of the amount of herbage mass consumed divided by the sum of searching and handling time, assuming that searching and handling are mutually exclusive behaviors. Herbage mass consumed is calculated from elementary processes that define bite dimensions as functions of sward height and vertical mass distribution. Bite volume is the product of bite depth and bite area, where bite depth is a constant proportion of 50% of sward height [2,3] and bite area is a function of sward height, herbage bulk density, and incisor arcade width [20]. The incisor arcade is determined by an allometric relationship with body mass [32]. Handling time, the sum of bite prehension time and chewing time, is a linear function of bite mass where the intercept is the time associated with prehension and chewing time is proportional to bite mass [3,33]. Searching time is determined by search path width and linear speed while walking during grazing [34].

The pattern of attack (i.e., the proportion of area of each height encountered that is selected for biting) is determined by maximization of the instantaneous intake rate [35]. At each time step, potential bites available are ranked according to profitability and incorporated into the selected diet in decreasing rank until the maximum intake rate is achieved. A sigmoidal curve centered at the shortest height selected serves to introduce "errors" or variability in the discrimination of bites, whereby some proportion of suboptimal bites is selected and some proportion of optimal bites is rejected.

Animal body mass is a state variable whose rate of change is determined by energy balance. Energy consumed is partitioned into maintenance and growth. The maintenance requirement is allometrically related to body mass, and energy expenditure increases by 30% during grazing [36,37]. Depending on its sign, remaining net energy is either met by weight loss or used for weight gain [38,39].

2.2. Simulations

In order to test whether the model gives reasonable results, we compared predicted instantaneous intake rate values with observed values according to the procedure proposed by Piñeiro et al. [40]. We set up the simulation with the management variables used by Orr et al. [41]: 12 yearling cattle weighing 248 kg, and average sward height ranging between 77 and 376 mm. Sward height was assumed to have a coefficient of variation of 10%. Simulations lasted 1 h such as in the experiment. The paddock area was set at 0.5 ha.

Three additional sets of simulations were performed. First, we examined the role of the heterogeneity of sward height on the functional response in 450 kg cattle by simulating 1 h of grazing in 300 m^2 paddocks, with average sward height ranging between 25 and 300 mm and different coefficients of variation representing levels of heterogeneity. The simulations took place between 16:00 and 17:00, when circadian motivation is high, and the initial state of rumen fill was 70% of the maximum capacity to ensure grazing activity. Paddock size was dimensioned to avoid sward depletion greater than 5% of the average initial height. The response variable was the average intake rate over the grazing session.

Second, we tested the hypothesis that different spatio-temporal distributions of animal density result in different productivity by simulating a gradient of an increasing number of pasture strips (1, 2, 3, 6, and 30 strips) and an increasing number of sheep (180, 270, and 360) in a 6 ha pasture. Each strip had a fixed period of occupation equal to the total grazing period of 30 days divided by the number of strips. The length of the resting period for each treatment was 30 days minus the period of occupation. All simulations started with a sward height distribution of 100 ± 15 mm and sheep weighing 50 kg. The response variables calculated were average daily gain and gain per unit area.

Third, we studied the impact of the "put-and-take" technique [42] to control herbage allowance when herbage mass per unit area changes when a single paddock is grazed continuously. Herbage allowance is defined as herbage mass per unit animal mass at an instant [43]. The "put-and-take" technique consists of varying the number of animals in the paddock to meet pre-established herbage allowance targets [42]. This simulation focuses on the consequences of adjusting herbage allowance by changing stocking density through changes in paddock size. We simulated a factorial arrangement of three herbage allowances (0.7, 1, and 1.5 kg DM $(kg\ BW)^{-1}$) with three paddock sizes (1, 2.5, and 5 ha) grazed for 120 days. Herbage allowance treatments were chosen based on the range usually recommended for cool-season grasses [44]. All treatments started with 12 cattle weighing 250 kg. Herbage allowance targets were maintained by adjusting the number of animals every 30 days. The response variables were body mass over time and cumulative relative gain per unit area, calculated by multiplying body mass by number of animals and dividing by paddock area.

3. Results

The model simulated instantaneous intake rate reasonably well, agreeing with experimental results by Orr et al. [42]. Observed and predicted intake rate values (Figure 1) were similar for intermediate values. Predictions underestimated high intake rates.

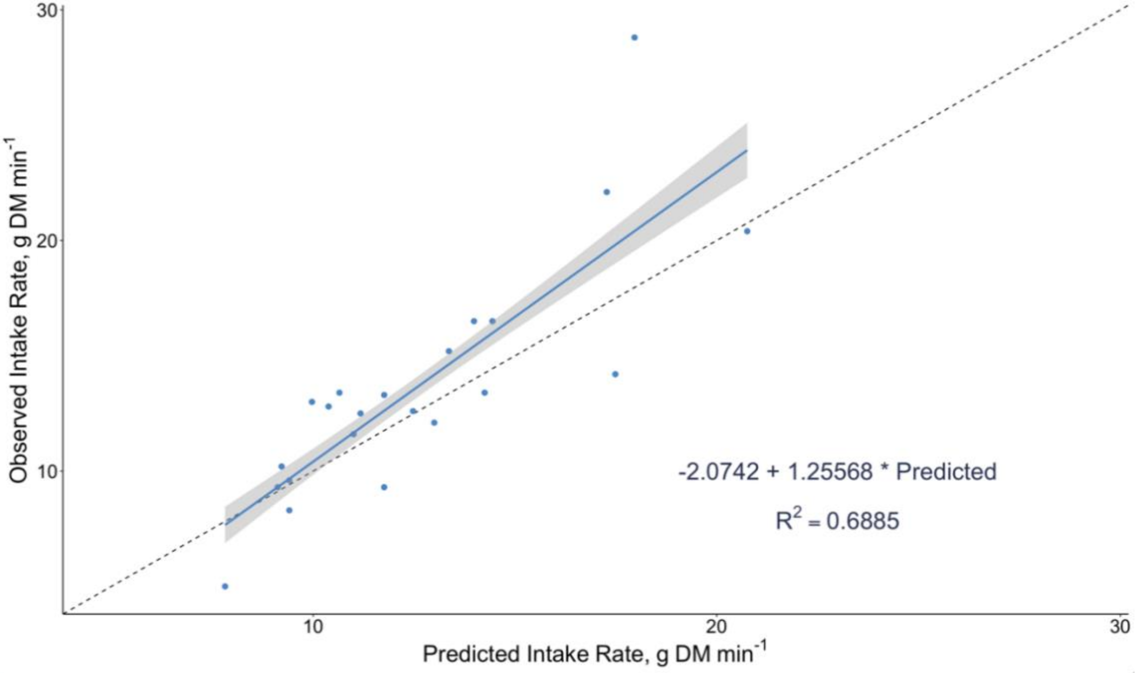

Figure 1. Relationship between observed intake rate and predicted values. Observed values are from Orr et al. [41].

This test is not a validation, but simply demonstrates the ability of the model to generate realistic results. We chose intake rate as the response variable because it plays a central role in the rate of herbage consumption and disappearance, and in animal performance. These results and multiple comparisons between observed and predicted values for several other experiments indicate that the model is suitable for our goals.

3.1. Functional Response and Sward Heterogeneity

In the first simulation set, the intake rate increased faster with increasing average sward height in swards with a greater coefficient of variation of height (Figure 2). The effect of heterogeneity was greatest for intermediate sward heights. For example, when the average height was 100 mm, the intake rate in a homogeneous sward was about 21 g DM min^{-1}, whereas a sward with a coefficient of variation of 100% resulted in an intake rate of 35 g DM min^{-1}. The size of the effect of sward heterogeneity first increased and then declined with increasing sward height because at low average height, all heights available severely constrain bite mass, whereas in the tallest swards, intake rate is constrained by the rate of chewing and it becomes saturated.

The differences are explained by the pattern of attack or selectivity over height (Figure 3). As a result of the maximization of the intake rate, grazing swards with low heterogeneity, animals exhibited little selectivity and took bites from most of the heights available. In swards with greater heterogeneity, they selected the taller end of the distribution. For example, when average sward height was 125 mm with a coefficient of variation of 10%, the shortest selected height was 108 mm and the intake rate was 26 g DM min^{-1}, whereas with a coefficient of variation of 50% the shortest selected height was 120 mm and the intake rate was 29 g DM min^{-1}.

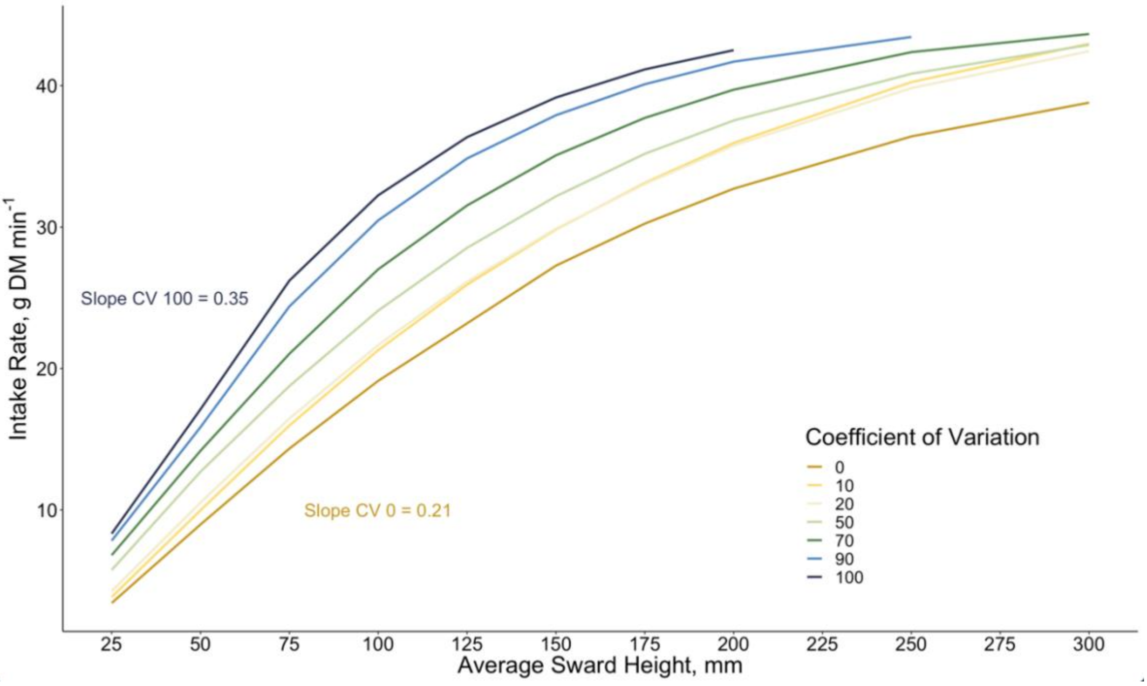

Figure 2. Functional response in cattle grazing swards with an increasing coefficient of variation of sward height distribution. The slopes were calculated between 25 and 75 mm for simulations with coefficients of variation of 0 and 100.

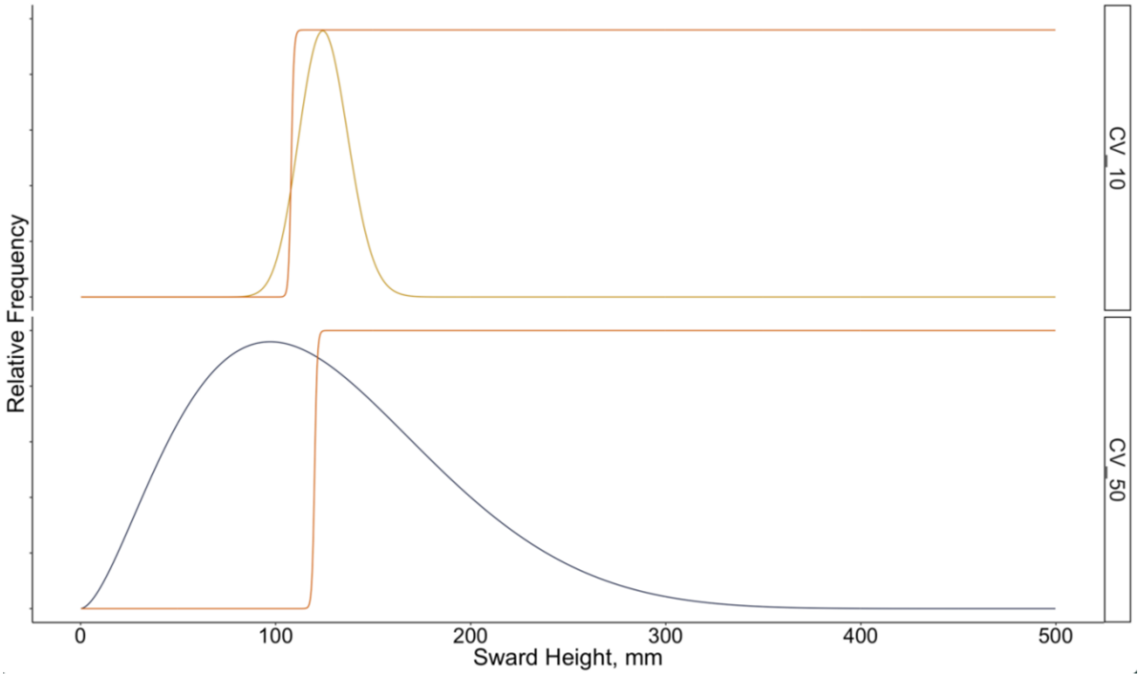

Figure 3. Sward height distribution and pattern of attack with average sward height of 125 mm and coefficients of variation of 10 and 50%. Both distributions (top and bottom) have the same average height but different coefficients of variation. The pattern of attack (sigmoidal orange curve) indicates the probability that an encountered area of a given height will be selected and bitten. On the top plateau of the line 100% of heights are selected, whereas at the bottom plateau 100% are rejected. The center of the almost vertical part of the curve indicates the shortest height that should be selected based on the maximization of the intake rate.

3.2. Spatio-Temporal Distribution of Grazing

In the second simulation set, intake and body mass responses over time were influenced by the interaction of the number of strips and stocking density. The two highest numbers of animals clearly exceeded the pasture capacity and animals started losing weight shortly after the initial standing crop was depleted, regardless of the resting period allowed for each strip (Figure 4).

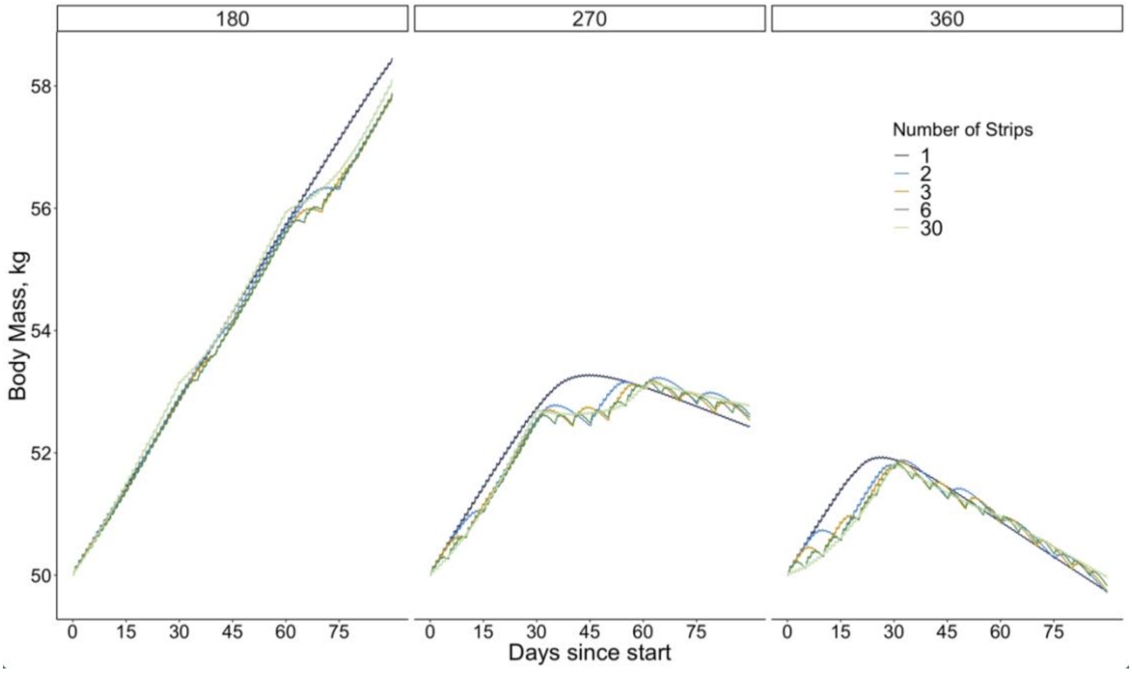

Figure 4. Effect of spatial distribution of animal density (number of strips) on body mass throughout the 90-day grazing season with 180, 270, and 360 sheep in 6 ha pastures. Different lines represent the different number of strips into which each grazing area was subdivided. Curves represent three grazing cycles wherein each strip was grazed a total of three times.

Although animals in continuous stocking (one strip) exhibited slightly higher body mass during certain periods, average daily gain and total gain per ha were fairly similar for all treatments within each stocking rate (Figure 5). For instance, at the lowest number of animals the relative average daily gain was only 7% less with six strips than with one. Average sward height (calculated for each 12 h period) for each strip was similar for each number of animals, but a greater number of strips promoted more heterogeneity among strips and homogeneity within strips (Figure 6).

3.3. Herbage Allowance and Paddock Size

In the third simulation set, average daily gain and relative gain per unit area increased with decreasing paddock size as herbage allowance was compensated by increasing herbage mass per unit area for all herbage allowances (Figure 7a,b). Even systems with lower herbage allowance had greater performance when compared to systems with greater herbage allowance but larger paddocks. For example, when herbage allowance was 0.7 kg DM kg BM^{-1} and paddock area was 1 ha, relative gain per unit area was 0.77 (unitless, because it is the ratio of the observed value and the highest absolute gain per unit area of all treatments), whereas an herbage allowance of 1.5 kg DM kg BM^{-1} and paddock size of 5 ha yielded a relative gain per unit area of 0.65. Increasing paddock area had a negative effect on relative gain per unit area and average daily gain within each herbage allowance.

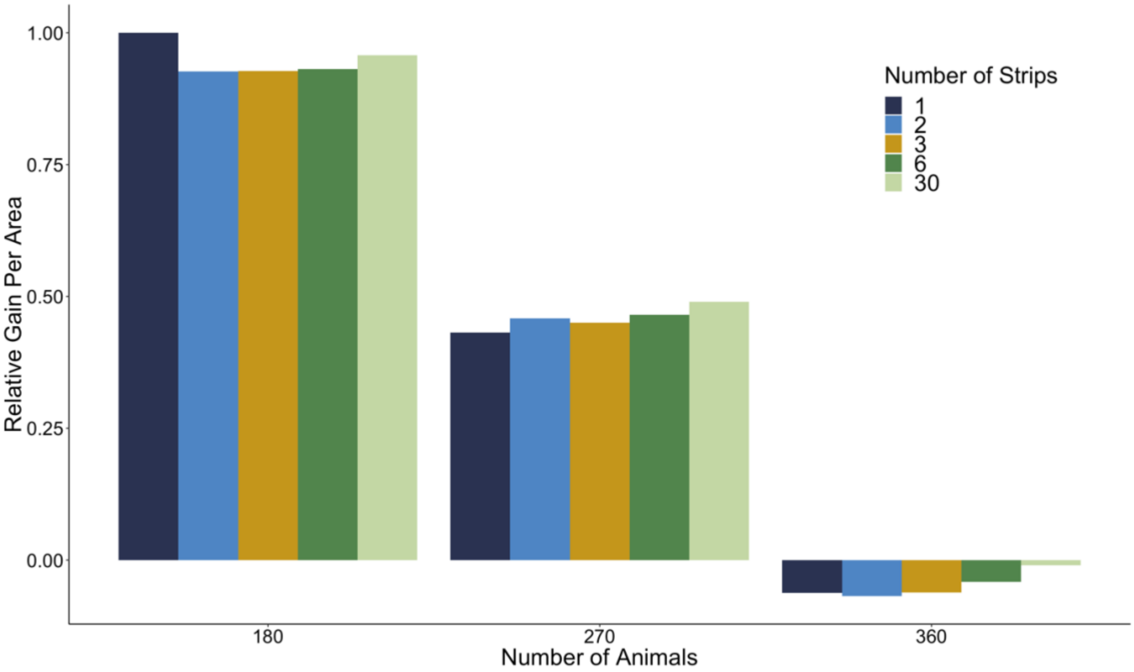

Figure 5. Effect of spatio-temporal distribution of animal density on relative gain per unit area under different numbers of sheep. Relative gain per unit area was calculated as average daily gain multiplied by number of animals per unit area, divided by the highest absolute gain per unit area of all treatments.

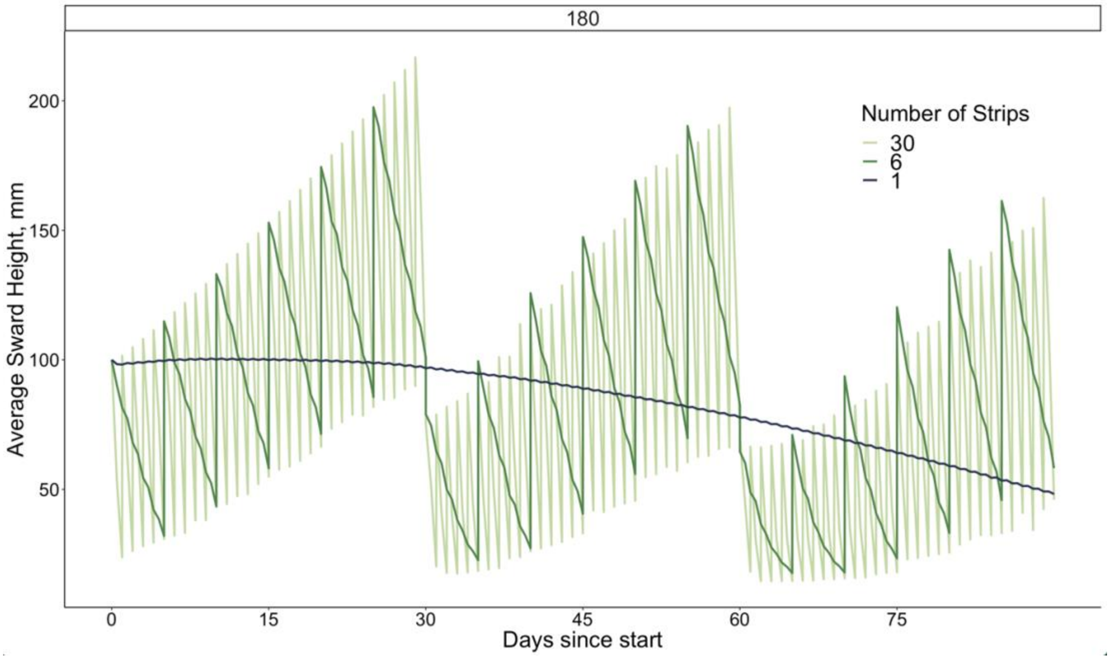

Figure 6. State of average sward height at the grazed strip every 12 h over the entire simulation period for three levels of numbers of strips for the lowest number of sheep (180). Each point on the line is the spatial average of heights within the strip.

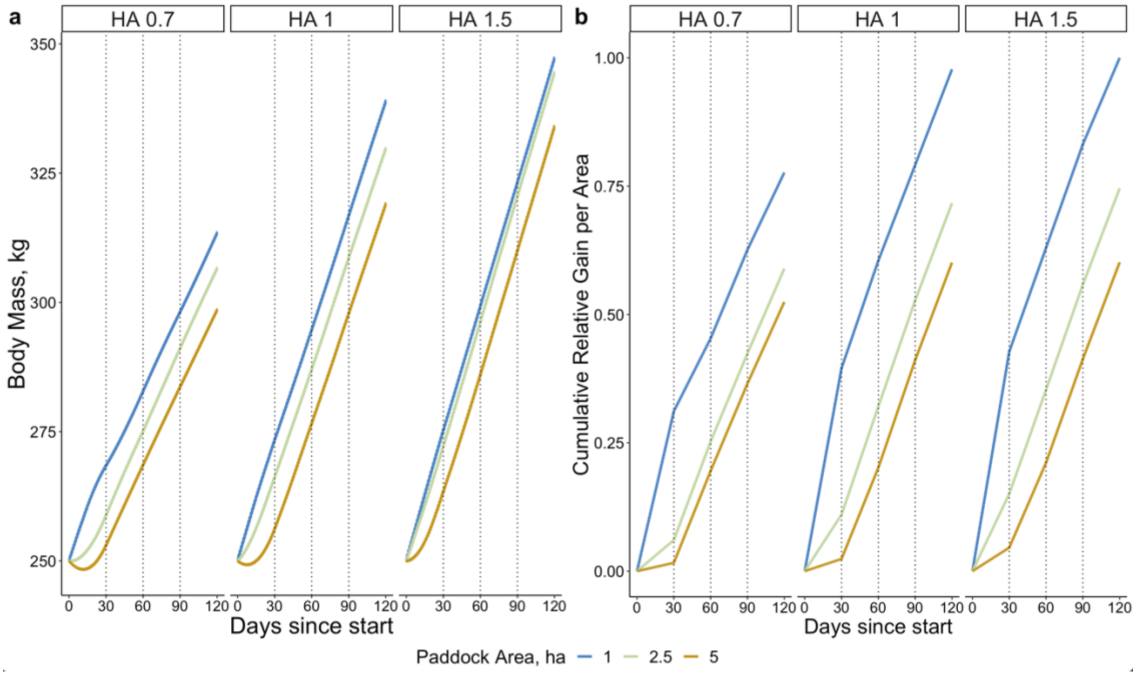

Figure 7. Effect of paddock size and herbage allowance (HA) on (a) body mass over time and (b) cumulative relative gain per unit area over time for cattle. Cumulative relative gain per unit area was calculated as the cumulative sum of average daily gain multiplied by the number of animals per unit area and divided by that of the treatment that had the highest value. All paddocks started with the same number of animals. Paddock areas were fixed over time and initial herbage allowance was achieved for each area by changing the average sward height and the corresponding distribution. As herbage mass per unit area was modified by growth and grazing, the number of animals was adjusted every 30 days (dashed line) to attain the nominal herbage allowance.

4. Discussion

4.1. Functional Response and Sward Heterogeneity

The functional response exhibited a typical type II shape (i.e., instantaneous intake rate as function of sward height exhibits asymptotic shape) [45]. However, the model could produce a type IV functional response (i.e., instantaneous intake rate as function of sward height exhibits a dome shape) with plausible values of the parameters that describe the distribution of sward mass over height. This underlines the importance of the vertical distribution of sward mass, a characteristic that is rarely measured with enough detail.

Most studies of the functional response of herbivores use plant mass per unit area as an explanatory variable or the axis of resource abundance ([46–48], but some studies have used sward height as the x axis [49,50]). However, given that bite depth is a fairly constant function of sward height, that bite area increases with sward height in a wide range of typical sward heights [51–53], and that herbage bulk density declines with increasing height in a species-specific pattern, the relationship between bite mass, intake rate, and herbage mass depends on sward structure. Furthermore, detailed models of functional responses of herbivores have been related only to average resource abundance [46,47]. Such models assume that grazers forage in a spatially homogenous resource. The present results show that greater heterogeneity, given by the horizontal distribution of height and the vertical distribution of mass, resulted in higher functional response because animals are able to select taller parts of the sward. Thus, these variables should be used as the determinant of functional response and incorporated into models with a grazing component.

Heterogeneity affords animals the opportunity to select, and thus modulates the relationship between average abundance and intake rate. Maximization of the instantaneous intake rate was done by ranking heights in decreasing order of instantaneous intake rate and adding them to the diet until the intake rate was maximized. The shortest height in the optimal diet and deviations from optimality (for example, due to imperfect discrimination of heights) was represented as a sigmoidal probability centered at the shortest height that would be selected according to the optimization of the intake rate with perfect discrimination of heights (Figure 3). Using a similar approach, Ungar and Noy-Meir [16] also reported that increases in horizontal variance at a given forage mass resulted in a higher instantaneous intake rate. Thus, functional response is not only related to average resource abundance, but also to its spatial distribution in high resolution.

The pattern of attack was set for maximization of the instantaneous intake rate based on the "zero-one rule" approach, where potential bites are fully rejected or accepted depending on their profitability [35]. However, herbivores can exhibit more pronounced partial preference [35] than what we used for the present simulations. Moreover, we ranked bite profitability using dry matter as currency. Variation in herbage quality can play a significant role in the profitability of bites and it will be included in forthcoming versions of the model.

Because the equilibrium and stability of grazing systems depend on the functional response [12,18] and sward heterogeneity can change the relationship between pasture growth and disappearance, the dynamics of heterogeneous plant–animal systems are different than homogeneous ones. The results shown for each functional response in Figure 2 apply only when sward structure and heterogeneity are constant, which would be rare in nature. In fact, longer runs of the model for any of the initial sward conditions simulated implicitly move smoothly across functional response curves, as heterogeneity changes over time. Spatial heterogeneity potentially invalidates the analysis of the stability and dynamics of grazing systems using functional responses and plant growth curves that are simple functions of average plant mass or height [12,13]. The existence of equilibrium states depends on the existence of stable height distributions where the functional response remains constant.

Our results demonstrate that spatial heterogeneity of sward height positively affects the instantaneous intake rate of herbivores because they are able to select the most profitable bites. Resource heterogeneity is an inherent characteristic of grazing systems; however, some grazing management guidelines still recommend sward homogenization through cutting and promote "non-selective" grazing. Conversely, we suggest that grazing research and management should incorporate resource heterogeneity into the design of grazing systems. Moreover, grazing experiments should include a description of the spatial heterogeneity, or at least a histogram of sward height for each treatment.

4.2. Spatio-Temporal Distribution of Grazing

Model results indicate that weight gain per animal and per unit area were not affected by the spatio-temporal distribution of animal density in a biologically significant manner within the range of conditions simulated, although there were small numerical differences. Although the sheep model in different treatments created and experienced different sward height distributions over time, sward differences did not translate to differences in animal performance across systems. Although herbivores responded positively to resource heterogeneity in the short term (Figure 2), heterogeneity effects were compensated for or diluted when the temporal scale of comparison was taken into account and increased to encompass several days. At the longer time scale of several days, mechanisms such as increased grazing time and digestive limitation interact, decreasing the effect of changes in instantaneous intake rate. Because foraging is a scale-dependent process in time and space [54], herbivores respond non-linearly to resource heterogeneity according to the temporal scale of observation. This finding is in agreement with Carvalho et al. [55], who found a weak relationship between short-term ingestive behavior variables and monthly animal performance.

Several studies argue that rotational stocking is superior to continuous stocking because it promotes resource homogeneity within paddocks after grazing, which increases animal performance by preventing the formation of areas that are over- or under grazed. Indeed, as previously reported by Barnes et al. [56], homogeneity within and heterogeneity between paddocks increased with an increasing number of strips in our simulations. Studies of the interaction between patch burn and grazing align with our results, also demonstrating the importance of animal density to create heterogeneity in space and time [57], as well as the buffer effect of heterogeneity to stabilize livestock production under extreme climatic conditions [58]. However, in our simulations, the number of strips had very little impact on animal and system performance. On the other hand, from a resource management perspective, sward heterogeneity between strips created by differences in animal density can be a tool to promote the reseeding of desirable grasses, control weeds [59], or provide habitat for wildlife. More simply, it should be obvious that the desirable level of homogeneity or heterogeneity depends on what one is trying to achieve with the stocking method.

As sward growth rate is a function of the sward state, one of the rationales to favor rotational stocking is that it allows control of sward state, growth rate, and animal production [60]. However, this explanation disregards the fact that the intensity of defoliation at the plant level is not susceptible to management by rotation of stocking. Bites are discrete events whose intensity is closely controlled by local sward height and density, and thus any system of grazing management, even continuous stocking, is "rotational" at plant level [9]. The frequency with which a plant is defoliated depends mainly on animal density [61] and can only be partially controlled by determining the number of animals, paddock area, and timing and duration of grazing periods. Moreover, it is likely that the impact of defoliation on average plant growth per unit area depends on the specific spatial pattern of defoliation. Growth and use of resources by taller plants located near defoliated plants is boosted by competitive release, thus ameliorating the total effect of uneven defoliation on community-level productivity [62,63].

In a detailed review, Briske et al. [64] compared stocking methods and did not find consistent difference in herbage production, yield per animal, and unit of area between methods. However, most of the research reviewed was conducted at scales smaller (< 1 ha) than commercial paddocks (20–500 ha). In a large experiment aiming to compare responses of vegetation and cattle to stocking methods in ranch-scale paddocks (130 ha), Augustine et al. [65] reported that neither animal performance nor desirable grass production resulted in rotational stocking surpassing continuous stocking. These works compared stocking methods by changing animal density and paddock size simultaneously, although these factors are in fact independent. To our knowledge, the hypothesis that stocking methods cause differences in performance when paddock size is kept constant has not yet been tested experimentally.

While our results indicate that spatial distribution of animal density over paddocks does not affect animal performance, some models that assume defoliation and growth as spatially homogenous processes found differences between stocking methods. Using a differential equation model with two functions (growth and consumption rates), Noy-Meir [66] compared continuous stocking to rotational stocking with different combinations of timing and duration of grazing and resting periods, as well as under different animal densities. Daily intake was largely determined by the timing and duration of grazing periods, and rotational was better than continuous stocking with high animal density. In an extended version of Noy-Meir's model, Wang et al. [67] found that a multiple-paddock system yielded higher forage intake per animal than continuous stocking in a single paddock. The question that emerges is: Why do our results differ from predictions of non-spatial models? The fundamental difference is caused by a scaling error, because growth and consumption rates are not strictly related to the average state of the vegetation at paddock scale as is assumed in spatially homogenous models [19].

In our model each biting event removes 20–30% of the herbage mass at the bite location almost instantly, rapidly and drastically modifying height and growth rate in the grazed area. Although bite depth is 50% of sward height, herbage bulk density decreases exponentially as a function of height, and therefore the mass of herbage removed per unit bite area is less than 50% of the total mass per unit area available. Conversely, non-spatial models imply that the amount of mass removed by each bite is instantly spread across the entire paddock, with little impact on growth rate. The second source of differences is that the functional response varies with heterogeneity and for any given average sward height, animals can select areas more profitable than the average (Figure 2).

The model used in this paper assumes that herbage nutritive value is constant and spatially homogeneous, whereas in reality, sward chemical composition is heterogeneous in time and space. There is strong evidence that chemical composition varies with the time of day [68,69], phenological stages [70], and the vertical position in the canopy [22]. Therefore, the results of the present model are applicable to nutritionally homogeneous swards with limited phenological change. The effects of incorporating mechanisms for change in herbage quality are the subject of forthcoming work.

One of the most discussed dilemmas in grazing science are the pros and cons of managing animal density over time and space. In agreement with empirical results [64] and contrary to non-spatial model results [66,67], our simulations using a spatial model do not provide evidence of superiority in yield in favor of any method. Thus, from the point of view of the practical application of increasing production, our results do not suggest that any specific design of spatio-temporal distribution of animal density should be promoted. On the other hand, modifications to the spatio-temporal distribution of animals can be used to control vegetation heterogeneity at paddock-to-landscape scales.

4.3. Herbage Allowance and Paddock Size

As expected, when herbage mass per unit area (which in the model translates into height) is traded off with paddock size to maintain herbage allowance, animal performance is changed, particularly in swards with short average height. Herbage allowance is a result of herbage mass per unit area, number of animals, animal liveweight, and paddock area. Part of its usefulness is that it is a metric that integrates all of its components. Unfortunately, its limitations as a predictor and cause of animal performance are also caused by the integration, which hides the specific combination of its factors. Animal performance relative to individual potential is determined mostly by daily intake rate and diet quality. Intake rate is largely controlled by herbage mass per unit area over a wide range of values of this component of herbage allowance. Gregorini et al. [71] reported a similar pattern, with herbage allowance having minor effect on daily dry matter intake when compared to sward height. Thus, when herbage mass per unit area is in the range where it dominates the control of daily intake, changes in herbage allowance achieved by changing the other factors do not have much effect on animal performance unless paddock area is small relative to the expected total intake by the group of animals during the period of occupation. This is what our simulations represented clearly.

Most of the difference between systems with the same herbage allowance occurred before the first adjustment of animal density to maintain the nominal herbage allowance (Figure 7a,b), when sward height was markedly contrasting and while the systems were not in equilibrium and differed markedly in sward heights. At the beginning, the sward height distribution was unstable and moved smoothly towards equilibrium state, and after adjustment with “put-and-take” animals, the systems reached equilibria with different stable height distributions (Figure 8). The frequency distribution was fairly similar to a Gamma distribution, with increasing frequency of short swards as the animal density increases, in agreement with observations by Shiyomi et al. [72]. Each animal density had a stable state with a particular sward height distribution, whereby heterogeneity increased as animal density decreased. Previous studies with a non-spatial model suggested a “dual stability” [12]. In another spatial model, Schwinning & Parsons [18] found that dual stability occurs only for intermediate stocking density, whereas low and high stocking present one stable state.

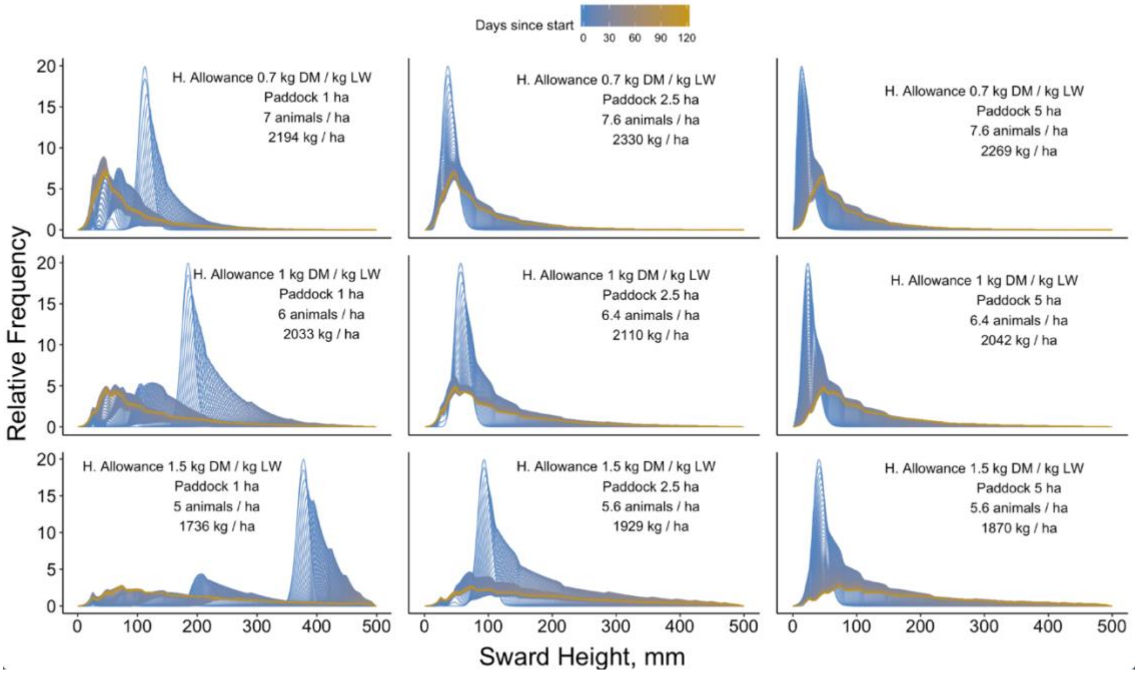

Figure 8. Sward height distribution over the entire grazing season of systems managed with herbage allowances of 0.7, 1, and 1.5 kg DM kg BW and paddock sizes of 1, 2.5, and 5 ha stocked with cattle. Each panel refers to one combination of herbage allowance and paddock size. The number of animals and kg of body mass per unit area at the end of simulations are written. Each line represents the frequency distribution of heights for one day, where day 1 is blue and day 120 is yellow. Most of the lines that appear are blue because after the systems reach equilibria, the yellow lines overlap.

Thus, herbage allowance is not sufficient as a predictor of animal performance because any value of herbage allowance can be achieved for any given vegetation state simply by changing the paddock area and number of animals. Over time, sward height will tend towards a stable height distribution determined by herbage allowance. Therefore, herbage allowance and sward height (or mass) cannot be controlled independently. This finding suggests that grazing experiments should start in conditions close to equilibrium (i.e., sward state and animal density) to avoid most differences due to factors other than herbage allowance. Moreover, these results also underline the importance of a detailed evaluation and description of sward height distribution in grazing experiments. Whereas some meta-analyses that focused on grazing behavior [73] or production [74] used herbage allowance as a predictor, we argue that herbage allowance is an insufficient metric to determine the grazing mechanisms that link pasture growth and animal performance. Finally, more than using a single variable to describe and manage systems, new approaches for grazing management should explore all management variables that can be controlled, such as number, mass and species of animals, timing and duration of grazing and rest periods, and paddock area and shape.

5. Conclusions

We created a model that integrates known mechanisms of bite formation and intake with very high temporal and spatial resolution and used it to determine how those mechanisms mediate responses to some typical factors of grazing management in realistic swards with spatial heterogeneity in height. Sward height heterogeneity resulted in higher short-term intake rate and determined the height of the resulting type II functional response. Studies of effects of sward height in grazing systems should, at the very least, include a description of the statistical distribution of sward height. Spatial distribution of animal density as controlled by fencing did not affect animal performance, but it can be used to manage resource heterogeneity. Under equilibrium conditions, sward height or mass and herbage allowance cannot be controlled independently.

The model yielded realistic results for swards that are homogeneous in quality, and future improvements will represent a broader set of swards and conditions. A more detailed vegetation growth and quality model will be developed to account for differences in unit leaf rate due to age and nitrogen content. Plant mass will be structured by both height and quality, which will influence diet selection and animal performance. Finally, resource patchiness and search mechanisms will open the potential to see the effects of heterogeneity across multiple scales.

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Appendix A

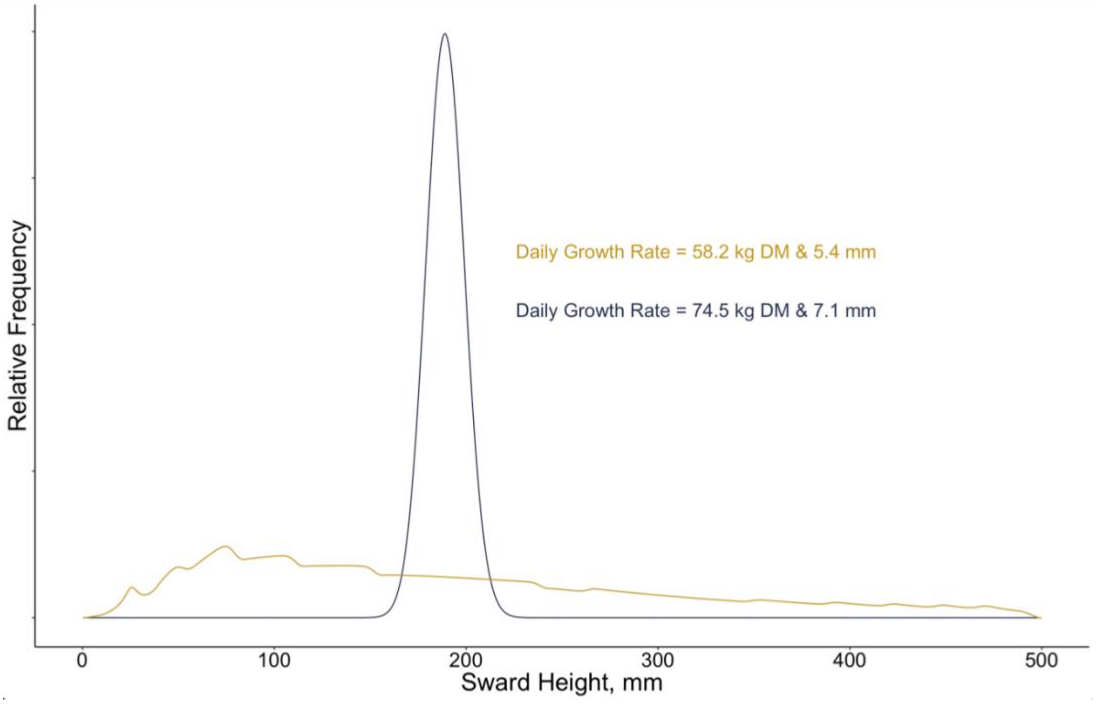

Figure A1. Effect of sward heterogeneity on growth rate. Both sward height distributions have the same average (189 mm), but different shapes. In this case, the growth rate of the more heterogeneous swards (yellow line) is lower because most paddock areas have heights that are very limiting to growth rate.

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CAPÍTULO IV

CONCLUSIONS

I proposed an experiment and a model to test the hypothesis that grazing systems managed through a given traditional grazing management descriptor, but with different combinations of paddock size, number, mass and species of animals, and timing and duration of grazing events, differ in their dynamics and functioning. The results presented in this thesis clearly support this hypothesis.

In an experiment with similar average sward height, animals grazing in the low-density, low depletion treatment had a greater daily intake rate than in the high-density, high depletion treatment. Resource was depleted faster in the high animal density treatments, and thus animal intake was limited for longer. Under the low-density, low depletion treatment, animals exhibited a more stable and higher instantaneous intake rate over time. Behavioral mechanisms determining intake rate were explained by the instantaneous plant abundance and spatial distribution regardless of longer-term grazing conditions imposed.

Besides that, we created a novel model that integrates known mechanisms of bite formation and intake with very high temporal and spatial resolution and used it to determine how those mechanisms mediate unexpected responses to some typical factors of grazing management in heterogenous swards. The model yielded realistic results for swards with homogeneous quality, but future improvements in spatio-temporal heterogeneity of quality are needed. Three sets of simulations were performed to demonstrate the model functioning. First, sward height heterogeneity resulted in a higher instantaneous intake rate and exhibited a type II functional response. Second, spatial distribution of animal density as controlled by fencing did not affect animal performance, but it can be used to manage resource heterogeneity. Finally, under equilibrium conditions, sward height or mass and herbage allowance cannot be controlled independently.

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VITA

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