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Integrating Sward Structure and Ingestive Behavior to Determine Intake Rate in Cattle

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TABLE OF CONTENTS

Table of contents.....	i
1. Abstract	1
2. Objectives.....	2
3. Introduction.....	3
4. Rationale	5
5. Materials and Methods	5
5.1. Hand-constructed sward methodology	5
5.1.1. Hand-Constructed Swords	5
5.1.2. Force Plate.....	7
5.1.3. Video and Sound Recording.....	8
5.1.4. Animals	9
5.1.5. Labor and Time Requirements	9
5.1.6. Procedures and Measurements.....	9
5.2. Factors and mechanisms that determine bite weight	12
5.2.1. Homogeneous swards	12
5.2.1.1. Effects of HCS height and bulk density	12
5.2.1.2. Effects of sward height, density and time within grazing bout.....	14
5.2.1.3. Effects of tiller density and tensile strength	14
5.2.1.4. Effects of sward height, density, and phenological stage.....	15
5.2.2. Heterogeneous swards	16
5.2.2.1. Vertical heterogeneity.....	16
5.2.2.2. Horizontal heterogeneity	18
5.3. Within-patch intake rate and patch depletion	20
5.3.1. Behavioral mechanisms that determine bite rate and intake rate on HCS	20
5.3.2. Patch depletion by grazers	22
5.3.2.1. Hand-constructed-sward experiment	22
5.3.2.2. Field Experiment.....	24
5.4. Models of intake rate.....	25
5.4.1. Graphical analysis of sward depletion by grazing...	25
5.5. Patch selection and intake rate in the field.....	29

5.5.1.	Effects of patch height and density, and animal experience on selection and intake rate	29
5.5.2.	Field test of the marginal value theorem with cattle.....	32
5.6.	Prediction of bite weight and intake rate in the field.....	34
6.	Results.....	35
6.1.	Hand-constructed methodology	35
6.1.1.	Sward Structure	35
6.1.2.	Evaluation of Methods for Determining Mass of Herbage Removed	35
6.1.3.	Sound and Video Recordings	36
6.2.	Factors and mechanisms that determine bite weight.....	37
6.2.1.	Homogeneous swards.....	37
6.2.1.1.	Effects of HCS height and density	37
6.2.1.2.	Effects of sward height, density and time within grazing bout	40
6.2.1.3.	Effects of tiller density and tensile strength.	40
6.2.1.4.	Effects of sward height, density and phenological stage	41
6.2.2.	Heterogeneous swards.....	42
6.2.2.1.	Vertical heterogeneity	42
6.2.2.2.	Horizontal heterogeneity.....	43
6.3.	Within-patch intake rate and patch depletion.....	44
6.3.1.	Behavioral mechanisms that determine bite rate and intake rate	44
6.3.2.	Patch depletion by grazers.....	48
6.3.2.1.	HCS Experiment.....	48
6.3.2.2.	Field Experiment	50
6.4.	Models of intake rate	51
6.4.1.	Graphical analysis of sward depletion by grazing...	51
6.5.	Patch selection and intake rate in the field	54
6.5.1.	Effects of patch height and density, and animal experience on selection and intake rate	54
6.5.2.	Field test of the marginal value theorem with cattle.....	55
6.6.	Prediction of bite weight and intake rate in the field.....	56

7.	Discussion	57
7.1.	Hand-constructed sward methodology	57
7.2.	Factors and mechanisms that determine bite weight	59
7.2.1.	Homogeneous swards	59
7.2.1.1.	Effects of HCS height and density.....	59
7.2.1.2.	Effects of sward height and density, and time within the grazing bout.....	64
7.2.1.3.	Effects of tiller density and tensile strength.....	64
7.2.1.4.	Effects of sward height, density and phenological stage.....	66
7.2.2.	Heterogeneous swards	67
7.2.2.1.	Vertical heterogeneity.....	67
7.2.2.2.	Horizontal heterogeneity	71
7.3.	Within-patch intake rate and patch depletion	72
7.3.1.	Behavioral mechanisms that determine bite rate and intake rate.....	72
7.3.2.	Patch depletion by grazers	77
7.4.	Graphical analysis of sward depletion.....	85
7.5.	Patch selection and intake rate in the field.....	88
7.5.1.	Effects of patch height and density, and animal experience on selection and intake rate.....	88
7.5.2.	Field test of the marginal value theorem with cattle	91
7.6.	Prediction of bite weight and intake rate in the field.....	92
8.	References.....	93
9.	Tables	106
10.	Figures.....	135
11.	Description of cooperation	204
11.1.	Year 1989	204
11.2.	Year 1990	204
11.3.	Year 1991	205
12.	Evaluation of research achievements	206
13.	List of publications.....	211
14.	Appendix. Reprints.....	214

1. ABSTRACT

Although intake is the key factor in animal performance and critical to intensively managed grazing systems, its prediction has been elusive. Our research incorporated a hierarchical approach to the prediction of intake: the formation of bites, intake at a feeding site (FS) or patch, and feeding in a multiple patch environment. A new experimental methodology was developed to study ingestive behavior under controlled conditions that was successful in achieving precision in the prediction of bite dimensions from sward structural characteristics. A new model of bite formation explained the mechanisms that control bite dimensions under different sward conditions. Results indicate that intake declines as an animal grazes a patch in a pattern unique to the structure of the patch. Experiments reveal that these depletion curves are the basis of animal choice at the FS level. The prediction of intake for grazing systems must integrate prediction of bite weight (a result of sward conditions) with an animal strategy to allocate its feeding effort.

An optimality model, which incorporated bite weight and depletion curves, predicted the behavior of animals in 9 different patchy environments. Field experiments in these environments measuring intake rate, choice of patch types and bites per patch type exhibited close agreement with the model's predictions. Successful prediction of intake in grazing environments can be achieved by integrating of sward structure and animal strategy. Our research demonstrates that animals profit from heterogeneity by selectivity. Selection in heterogeneous pastures is of prime importance as a determinant of intake in Mediterranean systems.

Our results make several important contributions to animal production. First, the measurement of simple parameters of sward structure and animal behaviors will predict intake with sufficient precision to improve management of grazing systems. Second, average values for sward biomass are less useful than measures of its variance to predict animal performance. Third, the incorporation of optimality principles coupled with new methodologies to study behavior provides a powerful new tool to understand performance in range production systems.

2. OBJECTIVES

1. To determine the basic mechanisms that control bite size through the interaction of the strength of sward components, their spatial arrangement, and proximate cues used by the animal toprehend and ingest the forage.

2. To test and quantify the effects of sward bulk density, and height on intake rate and ingestive behavior of cattle at different phenological stages relevant for the annual grassland system.

3. To evaluate hypotheses about the role of sward heterogeneity at the scale of individual bites on intake rate and incorporate sward characteristics which affect intake rate into experiments that determine their effects on intake rate and behavior.

4. To evaluate and amalgamate our two existing models of intake rate based on experimental results and test our experimental and mechanistic modeling conclusions on data from pasture experiments where gross characteristics of the sward are manipulated.

5. After testing, to use the mechanistic model in conjunction with statistical models to develop simple sets of rules to be used by managers to predict intake rate from behavior and sward conditions.

3. INTRODUCTION

Range livestock industries of both Israel and the United States require higher levels of management of grazing systems to improve competitiveness in global economies (Avery 1985). Greater production costs and declining cattle sales (Gillian 1985), as well as the increasing need to manage grazing lands for sustainable multiple use, make it essential to be able to predict the effect of management decisions on animal performance. Animal weight gain in grazing situations depends on intake, hence the importance of accurate monitoring and prediction of intake and intake rate. To assess the potential of management alternatives such as levels of supplement and rotation times for animals, managers require knowledge of the effect of decisions on intake rate.

The major weakness of most grazing-system models with potential management application is the plant-animal interface (Forbes *et al.*, 1985). Cafeteria-style models (e.g., SPUR: Wright 1983, ELMAGE: Pendelton *et al.*, 1983) or models based on animal requirements (e.g., BEEFEX: Seligman and Weitz 1985) have not been successful in predicting dietary intake in the range, mainly because of a lack of knowledge about limitations imposed by harvesting aspects of intake. Although NRC (1984) guidelines predict animal requirements reasonably well, their successful application in grazing situations is dependent on the linkage to the forage resource. The general goal of the research here reported is to establish this linkage and to quantify the relationships between forage characteristics and intake rate by cattle.

Bite weight is the basic unit of intake, and it is the most important determinant of intake rate (Stobbs 1973, Hodgson 1985, Spalinger *et al.*, 1988). Daily intake is the integration of intake rate over grazing time. While the physiological and digestive processes controlling intake are beyond the scope of the present research, total intake is well correlated with bite weight over a wide range of conditions (Jamieson and Hodgson 1979). Total intake is the best predictor of animal production on forage diets (Van Soest 1982). In range environments, where harvesting of the forage limits intake (Poppi *et al.*, 1987), animal production is related to ingestive behavior. Bite weight is well correlated with weight gain in steers (Chacon *et al.*, 1978).

Three problems have limited the study and understanding of the plant-animal interface. First, because sward characteristics, such as height, density and quality, are normally correlated in pastures and range, their independent

effects on intake have not been established. Without knowledge of the independent effects, effective modeling and extrapolation of results becomes tenuous.

Second, the great variability that exists in natural pastures and range has severely limited the effectiveness of experiments on the plant animal interface because the variability of the sward often overwhelms treatment effects. Researchers have constructed experiments to overcome the natural variability within and between pastures by increasing the number of replicates and making measurements at the pasture level to characterize animal response as means of pasture units. Initially, studies focused on the effect of amount of forage per animal (Hart 1972) and per area (Arnold and Dudzinski 1967) on animal performance. A large number of studies have yielded equivocal conclusions. Both linear and curvilinear relationships between daily gain and herbage per area are reported (Hart 1972, Trigg and Marsh 1979, Marsh 1979). Some researchers found no relationship between herbage mass and intake (Wheeler *et al.*, 1963, Meijs 1981, Havstad *et al.*, 1983). Others have found herbage mass to predict intake with varying levels of precision (Arnold and Dudzinski 1967, Reardon 1977, Baker *et al.*, 1981). Since a given herbage mass can be obtained by several combinations of height and density, herbage mass is too gross a measure of the sward to have general applicability. This approach is inefficient at studying the fundamental mechanisms that control the grazing process because the research is not focused at the level where the animal is interacting with the vegetation.

Third, the absence of an approach that considers heterogeneity has retarded the development of concepts that integrate lower level ingestive behaviors to explain intake responses in real plant communities.. The variability being masked by this experimental approach would appear to be a strong determinant of intake rate (Illius 1986, Demment *et al.*, 1987, Ungar and Noy-Meir 1988). Feeding efficiently in a heterogeneous environment as compared to a homogeneous one, would require another layer decision-making capabilities for the animal. The inability to successfully predict intake on pasture is due to a lack of recognition of the importance of variability, an absence of appropriate experimental techniques to determine its effect on feeding and, as a result, the lack of development of conceptual models of decision making that integrate sward structure, ingestive behaviors and intake.

4. RATIONALE

Our research plan and the original proposal's stated objectives followed a hierarchical organization of grazing behavior (Figure 1). Initially we studied the mechanisms by which sward characteristics within the feeding station (FS) determine bite weight and instantaneous intake rate, (intake rate while the animal is actively grazing, IIR). We then determined the effects of grazing on the plants within the FS and therefore, on subsequent grazing on the FS. The phenomenon of patch depression (Charnov *et al.*, 1976) was described and predicted on the basis of knowledge gained in the first step. Because each bite taken from the FS changes the structure of the sward, bite weight and IIR within FS decline with time spent grazing. Finally patch depression was used, in the context of an optimality model, as the basis to test the strategy used by the animal to make feeding decisions, such as patch selection, utilization and IIR, within a heterogeneous environment.

The progression from bite weight to intake rate to patch selection was paralleled by a transition from experiments with hand-constructed swards (HCS) in a controlled stall environment, to HCS in pasture environments, to pasture experiments where patch types were created by mowing. Methodologically, this progression was very successful and extremely efficient. Additionally, it resulted in a conceptual and experimental framework that can be easily and naturally extended both within and across hierarchical levels.

5. MATERIALS AND METHODS

5.1. Hand-constructed sward methodology

5.1.1. Hand-Constructed Swards

Hand-constructed swards consisted of tillers, stems, or leaf blades threaded through a series of small modules attached to a larger base board (Figure 2). The base board was a sheet of plywood 762 mm by 1219 mm by 12.7 mm, and weighed approximately 6.8 kg. Six rows of nine 3.2 mm holes were drilled across the length of the base board, with a distance of 102 mm between holes, for the attachment of modules. The area covered by the modules was approximately the largest which animals could graze without moving their forefeet. Additional holes were drilled outside the grazing area

for the attachment of modules to be clipped for determination of DM content of the forage. Eleven 6.4 mm holes were drilled through the base board for fastening to a force plate (see below) or to a cement floor.

Each module consisted of two 95 by 95 mm sections. The upper section was 19 mm thick and made of plywood or particle board (Figure 2). The lower section was 5 mm thick and made of pre-drilled masonite (pegboard). Weight of a module ranged from 150 to 200 g. The pre-drilled pegboard had 5.6 mm holes in 4 rows and 4 columns 25.4 mm apart. The upper section was drilled with a similar pattern, such that holes ("tiller holes") in the two sections were aligned when the edges of the sections were flush. Holes in the upper section were routed so no sharp edge faced inward. Breakage of stems or leaves at the bottom during grazing was thereby reduced to less than 10%. A hole was drilled at the center of the upper section to hold a threaded bolting hole ('tee-nut'). A matching hole was drilled in the lower section that was offset 25 mm along one axis.

The materials for the boards needed to be strong and lightweight since fresh weight of herbage removed was based on the reduction in weight of the whole HCS. The thickness of the upper section of modules was the minimum that maintained tillers upright despite the bending forces imposed by clamping the forage between two offset sections. The area of a module was approximately that of one bite, calculated from preliminary measurements. This feature provides the potential for construction of swards with bite scale heterogeneity.

Fresh herbage for constructing the swards was collected early in the morning of the same day the sward was to be grazed. We searched for patches of homogeneous vegetative herbage as similar as possible to what had been used in previous days of the experiment. Tillers were clipped with hand shears as close to the ground as possible. A rough separation of undesirable tillers and dead tissue was performed in the field and the tillers were immediately placed in buckets with water. The collected herbage was brought to the laboratory where sward construction started immediately. If the herbage collected was abundant in the type of tillers desired, it was sorted directly during module construction. If the herbage was excessively heterogeneous and had abundance of dead or undesirable tillers (e.g. too short), it was sorted before construction. We estimate that in both cases time spent sorting tillers was a major component of total time to build an HCS.

Tillers for HCS assembly were kept fresh by regularly spraying with water from the time of clipping, while completed HCS were sprayed with water and enclosed in plastic. Time between herbage collection and grazing ranged between 3.3 and 6.8 hours.

HCS were assembled by a team of three to five people. The base board was mounted horizontally on a large wooden frame and 44 mm machine screws were inserted downwards into the module-attachment holes. Each worker used a small frame with a clamp which held both sections of a module with the tiller holes aligned. Plant units (tillers, leaves or stems) were threaded through the holes according to the density and height specified by the experimental treatment. Density was controlled by the number of holes filled per module, and by the number of plant units per hole. Pseudostem height was controlled by varying the length of tiller pulled through the holes. A minimum of 50 mm had to extend beneath the module for the material to be properly fastened. Once filled, the module was released from the clamp, the upper and lower sections were separated about 25 mm and shifted out of alignment such that the bolting holes were aligned and the tillers securely clamped between the sections (Fig. 2). The treatment height was obtained by clipping 50 - 100 mm from the top of plant units to ensure uniform height, and to counteract the natural reduction in bulk density towards the top of the canopy. Modules were then held upside down and bolted firmly to the underside of the base board using a power drill. Sward height was equivalent to the length to which the plant units were cut. This was due to the natural rigidity of the species used, the erectness of plant units in the HCS and the range of heights used in the experimental treatments.

5.1.2. Force Plate

HCS were attached onto a force plate when grazed in order to investigate the role of the mechanical properties of the herbage in determining bite dimensions. The force plate recorded the forces applied to the herbage in three dimensions. The plate consisted of six sealed load cells (two per axis) mounted into a heavy metal frame covered by a steel plate. The cells detected the imperceptible deformations of the plate caused by forces applied to the herbage and generated changes in an analog electrical signal. A circuit box received input from the six cells and generated output to three channels (one per axis) on a Gould ES1000 chart recorder. The force plate was installed in

a pit such that the base of the sward was at ground level and animals could graze in a normal fashion.

Periodic calibrations of the force plate were performed by applying known forces in each of the axes x, y and z. Since it was impractical to ensure that the forces applied had only one component, the coefficients to transform trace displacement to force were statistically fitted. The trace displacement from an axis is proportional to the component of the total force applied that corresponds to that axis. The total force (R, known in the calibrations) is the vectorial sum of the three orthogonal components and can be expressed as: $R = [(k_x d_x)^2 + (k_y d_y)^2 + (k_z d_z)^2]^{0.5}$, where d and k are the trace displacement and proportionality coefficient for each axis, respectively. The proportionality coefficients (force per unit trace displacement) were fitted by nonlinear regression.

Force per bite (newtons, N) was defined as the value of the resultant at the time the vertical component peaked. This measure is relevant to test whether maximum force exerted by the animal has an upper limit within the range of strength of natural vegetation. A second measure, relevant to the study of the mechanism by which bites are severed, was defined as the ratio of force per bite and amount of material prehended at severance height. The amount of material at severance height (g m^{-1}) was calculated as the product of bite area and bulk density.

5.1.3. Video and Sound Recording

HCS grazing sessions were recorded using a camcorder (Panasonic AG-450). A character generator (Panasonic VW-CGIP) and a wireless microphone system (Realistic, distributed by Radio Shack cat. No. 32-1226) were connected to the camcorder. The character generator provided a stopwatch reading on each video frame to 0.1 seconds, for use in the timing of behaviors. The wireless microphone system for recording of grazing sounds consisted of an FM receiver, a battery-powered transmitter (57 x 97 x 22 mm, 82 g without 9v battery) and a small cylindrical microphone (9 mm diameter x 18 mm length). The receiver was mounted on the camera; the transmitter was clipped to the halter and the microphone tightly taped onto the forehead of the animal, facing inward.

On the basis of approximately 25 HCS grazing sessions, we found that the best sound quality was obtained when the microphone was attached on the

forehead above the eyes, where the animal cannot see it. The microphone was enclosed in a plastic suction cup and taped on an area from which hair had been clipped. This equipment did not appear to interfere with behavior.

5.1.4. Animals

The animals were tame 4-year old steers (approximately 750 kg live weight) that had been fistulated as year-olds and were used to daily handling. After approximately ten grazing sessions each, three out of five animals became well adjusted to the procedures and were used in subsequent experiments.

5.1.5. Labor and Time Requirements

A team of four people required a minimum of 1 hour to assemble an HCS of 54 modules at a density of 8 holes filled per module. When running experiments the daily schedule was approximately: 7:30-8:15 herbage collection, 8:15-11:30 HCS assembly, 12:00-15:00 HCS grazing and associated measurements. A team of 4 people worked 8 hours to assemble and run 3 HCS.

5.1.6. Procedures and Measurements

One module per worker, with a minimum of two per board were randomly selected during HCS assembly for determination of the vertical biomass profile by plant fraction. Herbage from each module was separately clipped in 50-mm horizons from the base, bagged, dried at 65 C and prior to weighing was separated into leaf, pseudostem (or stem) and inflorescence.

Three methods were available to determine the mass of herbage removed from the HCS during any grazing session. In methods 1 and 2 bite weight was calculated by dividing mass of herbage removed by number of bites taken.

Method 1. Mass of herbage removed was calculated as the product of the reduction in fresh weight of the HCS (corrected for moisture loss) and the DM content of the herbage immediately prior to grazing. Water loss from the HCS by evapotranspiration can reach 10 g per minute and thereby lead to substantial overestimation of herbage removal by the animal. To correct for this, the rate of water loss of each HCS was determined by weight difference immediately before grazing, over a timed period of about 5 minutes. A scale (Setra Systems, Model 140 CP) with an accuracy of 1 g and a range of 0-60 kg

was used (total weight of the HCS varied between 14200 and 17500 g). Water loss during grazing was estimated as the product of time between weighings and measured rate of water loss for the HCS. Fresh herbage intake was calculated as HCS weight before grazing minus HCS weight after grazing minus water loss. This measure was converted to dry matter using the DM content of herbage clipped immediately before the animal grazed the HCS. An additional module was attached to the base board for this purpose. Error will be introduced by differences in the rate of water loss between the period over which drying rate is determined and the grazing period, and by variability between modules in the DM content of herbage.

Method 2. Following grazing, all tiller holes that were grazed to any extent were counted, clipped at the base, bagged, dried and weighed. This procedure was repeated if the same HCS was grazed a second time (see below). Number and weight of all ungrazed tiller holes was similarly determined. The mass of herbage from ungrazed tiller holes together with the mass of herbage from the modules used to determine sward structure yielded an estimate of the initial mass of herbage per tiller hole. Mass of herbage removed was calculated as the product of the number of tiller holes grazed and the initial mass per tiller hole minus the residual mass of tiller holes grazed. Sources of error for this technique are variability in the measurement of area grazed and in the mean initial herbage mass per tiller hole.

Method 3. Bite weight was calculated as the product of bite area, bite depth, and bulk density of the grazed horizon. In addition to the errors introduced by each factor, this method might tend to underestimate true bite weight due to tiller breakage at the bottom. Tillers broken at the base were counted for area determination, but ignored in the calculation of bite depth.

The relation between sward structure and bite dimensions is preferably determined when each bite is selected from a uniform, previously ungrazed sward structure. Our observations indicate that steers do not graze the HCS strictly by horizons, nevertheless the probability of re-grazing an area was low for the first 6 bites. Measurements of bite dimensions were therefore taken after the removal of the first 6 bites from an HCS.

To determine bite dimensions the animal was led to the board, allowed to take six bites, and moved away. The HCS was weighed and time was recorded immediately before and after grazing (for method 1 of determining herbage mass removed).

In order to determine bite area and depth, we measured the residual height of the herbage in each grazed tiller hole and counted the number of tiller holes grazed. An area correction was needed for tiller holes that were partially grazed in the horizontal plane, i.e. the tongue sweep of the animal failed to include all plant units (tillers, leaves or stems) from the same hole. This occurrence was most common for tiller holes on the periphery of the tongue sweep. In such cases the residual height of the grazed plant units were measured and the fraction (.25, .50, .75) they represented of the total number of plant units in the hole estimated. The contribution of the tiller hole to bite area was weighted accordingly. Bite area was calculated as total number of tiller holes grazed per bite, divided by number of holes per unit area. Thus, we measured effective bite area given by the total number of tillers actually severed, which was usually smaller than the area encompassed by tongue and jaw movements. Bite depth was calculated as treatment height minus average residual height of grazed tiller holes. As grazed tillers were measured, they were clipped and bagged for drying (method 2 of determining herbage mass removed).

Following the determination of bite dimensions, the animal grazed the HCS for a second and longer period. The total area of sward presented to the animal was smaller for the second grazing session due to the removal at the base of all herbage from tiller holes that had been grazed during the first grazing session. The criteria for withdrawing the animal from the HCS depended on the purpose of the experiment, but generally the animal grazed for a period of approximately one to three minutes and grazed the vast majority of the area of the HCS at least once.

Timing commenced with the start of the first bite. The time until the last bite and the time until all material was swallowed were recorded. The HCS was weighed and time was recorded immediately before and after grazing (for method 1 of determining herbage mass removed). Grazed and ungrazed tiller holes were separately clipped (method 2) and fresh weight of the extrusa was recorded to the nearest gram (method 3). Grazing time was estimated as the time until all material was swallowed minus 'idling time' (no chewing or swallowing) after the last bite. Idling time was determined from the video recordings. IIR was defined as DM intake divided by grazing time.

Video tapes were examined by slow motion playback. The grazing movements of the jaw and tongue were described and quantified. Jaw

movements were classified in 4 categories: a) manipulation of herbage to draw it into the mouth with a tongue movement such that the tongue swept an area beyond that covered by the gape, b) manipulation of herbage to draw it into the mouth without a tongue movement as above, c) exclusive chewing motion, d) simultaneous chewing as the jaw closes as in (a) or (b). A bite was tallied when all herbage gathered in preceding motions was severed. A chew was counted when the jaws closed with a distinct grinding sound. Behaviors were defined and timed with a precision of 1/30 seconds.

We carried out two experiments on homogeneous swards to determine the effects of sward height and bulk density on grazing behavior. In experiment 1, dallisgrass (*Paspalum dilatatum* Poir.) swards of 3 densities (388, 775 and 1550 holes filled per m²) and 4 heights (80, 150, 180 and 300 mm) were replicated over three steers. Swards were constructed exclusively with leaf laminae. In experiment 2, alfalfa (*Medicago sativa* L.) swards of 3 densities (388, 775 and 1550 holes filled per m²) and 3 heights (70, 150 and 250 mm) were replicated over the same three steers.

5.2. Factors and mechanisms that determine bite weight

5.2.1. Homogeneous swards

5.2.1.1. Effects of HCS height and bulk density

Experimental swards were prepared by hand as described above. Hand-constructed swards were bolted to the floor of the pen or to a force plate at ground level. Animals were given access to the freshly prepared swards and allowed to take 6 bites after which access was blocked and bite dimensions were determined. Grazing sessions were video taped at close range for detailed study of the mechanics of grazing.

Two experiments were conducted to study the effects of sward height and density on bite weight and bite dimensions of cattle. The first experiment consisted of a factorial combination of dallisgrass (*Paspalum dilatatum* Poir.) swards of 4 heights (80, 150, 180 and 300 mm) and 3 densities (378, 775 and 1550 holes m⁻²). Swards were made exclusively of leaf lamina, resembling a vegetative stage with uniform foliage. The experiment was conducted from May 24 to July 5 (days 53 to 95 since the growing season started) and from August 9 to August 14, 1989 (days 34 to 39 after cutting). For the second

experiment, experimental swards were made of alfalfa (*Medicago sativa* L.) in a factorial combination of 3 heights (70, 150 and 250 mm) and 3 densities (378, 775 and 1550 holes m⁻²). Alfalfa swards were composed of stems and leaves, resembling the normal architecture of these plants. The experiment was carried out between July 10 and July 26, 1989 (days 12 to 28 after midsummer cut).

In both experiments, treatments were replicated over 3 steers considered to be blocks (Gill, 1978). In order to correct for effects of phenological changes in the pastures, days of regrowth was used as covariate. Effects of height and holes m⁻² as categorical treatments, and interactions were analyzed by orthogonal contrasts. General predictive equations for bite dimensions as functions of sward height and bulk density as continuous variables were derived as follows. Data from each experiment were corrected by animal and covariate effects, pooled, and then third-order response surfaces fitted. Only significant terms were kept in the equations. The nature of the response of bite area required a slightly more complex model fitted by non-linear procedures (NLIN, SAS Institute Inc., 1985).

Swards were sampled before grazing for determination of dry mass per unit area, bulk density by 50-mm horizons (starting at bottom). Each horizon of alfalfa swards was separated into stem and leaf. Concentration of NDF in alfalfa stem tissue by horizon was determined by standard procedures. Bulk density of the grazed horizon was calculated by weighting the bulk density of each horizon by the proportion of total bite depth derived from each horizon.

Residual height of each grazed hole (in 5 mm classes) was recorded. The residual herbage from grazed holes was clipped, dried, and weighed. Bite area was determined as the ratio of grazed holes per bite over density of holes per unit area. Bite depth was determined as the difference between sward height and average residual height. An indicator of incisor height was calculated as the mean residual height of the shortest grazed tillers in an area covered by incisor breadth and gape. Bite volume was calculated as the product of bite area and bite depth. Bite weight was computed as the difference between estimated pre-grazing herbage mass in the holes grazed and weight of residual herbage clipped (DM basis), divided by number of bites. Video records were played back in slow motion and the number and estimated amplitude of tongue sweeps were recorded.

Three 4-year old esophageally-fistulated steers were used in this study. Animals were familiar with the experimental protocol and diets prior to the experiments. They were collectively fed 1-1.5 bales (ca. 55 kg) of good quality alfalfa hay once a day between 6:30 and 7:00 am.

5.2.1.2. Effects of sward height, density and time within grazing bout

Leaf blades from vegetative tillers were arranged to create 0.2-m² HCS 10 and 18 cm high, each at bulk densities of 1300 and 2500 g m⁻³. Three steers (mean wt. 750 kg) given daily access to a dallisgrass pasture for 7 hr following overnight fasting were presented with HCS 0, 2, and 4 hr after the initiation of grazing. Grazing times were assumed to correspond to hunger levels. Steers grazed as a group and were allotted a new paddock area daily which supplied a mass of herbage dry matter equal to 10% of their combined body weight. Bite area, bite depth, and bite weight were determined by differences between HCS before and after grazing as described above for other experiments. Steers comprised blocks and treatment effects were tested at $P = 0.10$.

5.2.1.3. Effects of tiller density and tensile strength

Preliminary measurements indicated that dallisgrass (*Paspalum dilatatum* Poir.) leaf blades were 14% lighter (4.3 vs. 4.9 mg) and 89% stronger (11.5 vs. 6.1 Newtons/blade) than wild oats (*Avena fatua* L.). At equal bulk density, dallisgrass swards were expected to be 120% stronger than oat ones. The experiment consisted of a factorial with two species (dallisgrass and oats) and 5 densities of leaf blades (1550, 2326, 3101, 4651, and 6202 blades m⁻²). All swards were of equal homogeneous height (18 cm). Treatments were replicated on 3 steers which were treated as blocks. Swards were constructed and measurements performed as described in detail in previous sections.

Swards were mounted on a force plate and the forces exerted by the animals as they severed bites were recorded on a chart. Immediately prior to swards being grazed, strength of leaves was recorded by breaking groups of blades using a standardized procedure. Maximum breaking force per bite and the integral of force over biting time were derived from the charts. Bite area, bite depth, incisor height and bite weight were determined after the animals took 8 bites.

5.2.1.4. Effects of sward height, density, and phenological stage

This experiment was carried out in April 1990. It consisted of a factorial of two sward heights (10 and 15 cm), two densities (775 and 1550 tillers m⁻²) and two phenological stages (early and late flower). The resulting 8 treatments were replicated over two steers considered to be blocks. Swards were constructed by hand as previously described in detail. The main difference with previous experiments using this methodology is that tillers were used as units and individual tiller architecture was not modified. The two phenological stages were arbitrarily defined on the basis of tiller architecture and the material available. Tillers were collected between 0700 and 0900 hours from a seeded *Bromus mollis* L. pasture, and classified according to stage. Only tillers with total length ranging between ca. 15 and 40 cm were selected. These tillers were classified as "early flower" (early) if the panicle was emerging or about to emerge, but no culm was visible. Tillers were classified as "late flower" (late) if 5-10 cm of culm protruded above the uppermost ligule. Although this classification of phenological stages may differ from previous ones, it was used because it focuses on the proportions of plant parts, which is relevant for grazing behavior.

Swards were constructed by hand in the morning and offered to the animals the same day between 1100 and 1400 hours. Two treatments were observed each day, and treatments were randomized over time with the constraints that each day we observed both animals and both phenological stages.

Twenty eight 0.01-m² modules were built for each hand-constructed sward (HCS). Three modules were randomly sampled during construction for determination of herbage mass in 5-cm horizons. The other 25 modules formed a patch that was attached to a force plate. Immediately before the animal was offered the remaining 24 modules, the tillers in one module were broken by hand in groups of two, to estimate tensile strength of the material. Breaking forces were analyzed as described above. After breaking tillers by hand, animals were allowed to take ten bites from the HCS. Height and number of grazed tillers were determined, as well as dry weight of grazed and ungrazed tillers, for calculation of bite area, bite depth, incisor height, and bite weight.

Animals were 4.5 yr-old, esophageally fistulated steers of 680 and 770 kg live weight. Steers were stalled with three other steers and collectively fed a maintenance ration of alfalfa hay once daily between 0900 and 1000 hours.

5.2.2. Heterogeneous swards

5.2.2.1. Vertical heterogeneity

Tillers from an irrigated dallisgrass pasture in Davis, CA were clipped daily during autumn of 1989, to approximately 3 cm above ground. The dallisgrass pasture was mowed to approximately 6 cm above ground in June. Tillers retained for Exp. 1 during late September to mid-October were vegetative, while those retained for Exp. 2 in November were reproductive tillers that had set seed. Following collection, tillers were maintained in an upright position with lower ends immersed in water to maintain turgor.

Each HCS consisted of vegetative (Exp. 1) or reproductive (Exp. 2) tillers trimmed according to treatments and threaded through multiple 10- by 10-cm perforated modules. Modules were attached to a base board in sets of 36 to form continuous 0.4-m² sward in the manner described above. In each experiment, tillers were trimmed and positioned to create a factorial arrangement of swards with two lamina lengths and two sward heights (Figs. 3 and 4). A depiction of how tillers were trimmed is given in Fig. 3. Swards of 8- and 16-cm height were constructed with 5 and 8 cm of leaf lamina at the top (Fig. 4); 8-cm-tall swards had 0 or 3 cm of basal pseudostem (Exp. 1) or stem (Exp. 2), while 16-cm-tall swards had 8 or 11 cm of basal pseudostem or stem. Number of HCS module perforations filled with tissue was 775 m⁻² in all treatments. In Exp. 1, swards with pseudostems at the base had four pseudostems, each bearing one lamina, in each perforation (3100 laminae m⁻² with pseudostems at the base). Swards without pseudostems (8 cm height, 8 cm lamina length) had six laminae in each perforation (4650 laminae m⁻²). In Exp. 2, swards with stems at the base had two stems, each bearing one lamina, in each perforation (1550 lamina m⁻² with stems at the base). Swards without stems (8 cm height, 8 cm lamina length) had six laminae in each perforation (4650 laminae m⁻²). Completed HCS were kept moist and shaded to prevent wilting until offered to animals.

Experimental design was a 2 X 2 factorial (2 lamina lengths by 2 sward heights) in a randomized complete-block in which three Hereford steers

(approximately 750 kg avg. weight) were replications. The 12 HCS (3 steers X 4 treatments) in each experiment were offered sequentially in time, such that two HCS-ingestive behavior sessions were obtained daily. Grazing of HCS was completed between 19 and 28 Sep 89 for Exp. 1, and between 1 and 10 Nov 89 for Exp. 2. Assumptions included the absence of a date effect, residual effect of previous treatments on responses to the current treatment, and order of feeding effect. These assumptions are supported by the fact that animals were accustomed to feeding in similar swards and were fasted for approximately 19 hours before grazing.

Each day, tillers harvested at 0800 h were assembled into HCS that were bolted to the concrete floor of an outdoor pen and offered to steers between 1100 and 1300 h. During HCS construction four modules out of the 40 per HCS were randomly chosen; 3 were clipped for estimation of herbage DM mass (HM) and sward DM bulk density, and one was clipped immediately before grazing for estimation of herbage dry matter (DM) concentration. All values were determined on the basis of the oven-dry (60 °C) weight of herbage clipped to the module surface. Sward DM bulk density was determined for successive 4-cm vertical horizons through the sward profile. A steer familiar with the protocol was led to the HCS and allowed to harvest 10 bites. Except during observations, animals remained in an outdoor corral and were collectively fed one bale (approximately 45 kg) of sudangrass [*Sorghum bicolor* (L.) Moench] hay once daily between 1400 and 1500 h.

Each test session was video-recorded as described in the preceding methodology section, using a camera providing a stopwatch reading (0.1-s increment) on each video frame for later use in analysis of mode of prehension. Bite dimensions were determined as differences between pre- and post-grazing measurements of HCS. Bite depth was the difference between sward height and residual height. Bite area was the product of the number of module perforations grazed and area per perforation filled with herbage. Mode of prehension was characterized in terms of the proportion of prehending bites in which the tongue was used to sweep an area greater than that covered by the opening of the mouth, and number of tongue sweeps per bite. Prehension mode data were transcribed by two observers viewing video recordings and averaged. Significance of treatment effects and interactions were determined by standard analyses of variance and F-tests for the orthogonal contrasts for effects of sward height, lamina length and interaction.

5.2.2.2. Horizontal heterogeneity

Hand-constructed swards consisted of dallisgrass leaf blades in discrete patches of different height or bulk density (Exp. 1) and discrete patches of leaf blades or reproductive stems (Exp. 2) held in a series of 10- by 10-cm perforated modules. These were attached to a base board to form continuous microwards. Tillers for HCS were collected daily at ~8:00 by clipping at ≤ 3 cm above soil level from an established irrigated pasture in Davis, CA. Tiller phenological stages on each sampling date ranged from vegetative to ripe seed in 6-wk-old regrowth following mowing to ~6 cm in both experiments. Samples retained for Exp. 1 during 21 Aug. to 1 Sept., 1989 were leaf blades from vegetative tillers; those for Exp. 2 during 13 to 30 July, 1990 were leaf blades as in Exp. 1 and stems of reproductive tillers including the second and third elongated internodes above soil level, with leaf blades detached. Freshly gathered tillers were placed in an upright position with lower ends immersed in water to maintain turgor, and kept cool and shaded throughout each morning HCS construction session. Duration of each experiment was brief so that changes in herbage composition within each experiment were minimized. Completed HCS were kept moist, cool, and shaded to prevent wilting before they were delivered to an outdoor cattle holding pen, bolted to a platform flush with the pen floor, and grazed immediately.

For each grazing session, a tame Hereford steer (mean weight ~750 kg) familiar with the experimental protocols and materials was led by the same handler to the HCS and allowed to harvest 6 (Exp. 1) or 20 (Exp. 2) bites. Prior to grazing each HCS, three modules were clipped for determination of herbage mass (HM) and sward bulk density, and one was clipped for determination of herbage dry matter (DM) concentration. All values were calculated on the basis of the oven-dry (60 C) weight of herbage clipped at the module surface. Sward bulk density was determined for successive 5-cm vertical horizons through the sward profile. Grazing sessions were timed and video-recorded as previously described, which provided verification of bite number, rate, and other data. Bite dimensions, diet selection, and rate of intake were determined as differences between pre- and postgrazing measurements of HCS. Steers were permanently housed in an outdoor pen with access to shelter and received a background maintenance ration of alfalfa (*Medicago sativa* L.) hay or pellets fed once daily.

Experimental design for each experiment was a randomized complete block in which three steers were replications. The 18 HCS in Exp. 1 and 24 HCS in Exp. 2 were offered sequentially in time, such that multiple ($\leq$ three) ingestive behavior sessions were obtained daily. Assumptions included the absence of residual effects of treatments on subsequent behavior. Sward heterogeneity treatments were obtained by arranging alternating sward structures in adjacent patches each consisting of one or more modules. Scales of heterogeneity in these HCS were selected as multiples of the 0.01 m^2 module area previously found to be an approximate minimum bite area for these cattle, in order to help define the scale at which ingestive behavior is as if swards were homogeneous (Fig. 5). It was assumed that ingestive behavioral responses to adjacent patches smaller than one module would approach those found in homogeneous swards. Treatment effects were determined by analyses of variance; those described hereafter were significant at $P \leq 0.05$, unless otherwise indicated. Procedures specific to each experiment follow.

Experiment 1. Manipulation of height and density of leaf blades resulted in five treatments, one of which was a homogeneous control with all patches of equal height (15 cm) and bulk density ($1460 \pm 47 \text{ g m}^{-3}$). The other treatments, each consisting of a checkerboard arrangement of patches, were heterogeneity in height (10- and 20-cm patches) or bulk density (670 ± 50 - and 2022 ± 48 - g m^{-3} patches), each at two horizontal scales (0.01 - and 0.04 - m^2 patches). Swards with heterogeneity in height had an equal number of modules with 10-cm blades as modules with 20-cm blades, while those with heterogeneity in density had equal numbers of modules with high and low bulk densities. All treatments represented swards with mean height and bulk density equal to the control (Fig. 6). Total HCS area offered during a grazing session varied between 0.35 and 0.40 m^2 .

Animals were allowed to take six bites from an HCS, after which measurements were obtained on individual patches. Bite dimensions were compared to values predicted by equations developed for homogeneous swards of dallisgrass (Laca *et al.*, 1992b). Steers were fed their daily maintenance ration at $\sim 7:00$, then offered HCS at $11:30$ to $16:00$; most sessions were between $13:00$ and $14:30$. Selectivity for taller or higher density ('high') patches was calculated as the ratio of grazed areas of each patch type; values

exceeding 1.0 indicate selection for high patches and those below 1.0 indicate selection for 'low' patches.

Experiment 2. Leaf blades and reproductive stems were arranged in twelve 0.04- or two 0.25-m² patches alternately interspersed in 15-cm-tall, 0.5 m² HCS (Fig. 5). Tiller density was 775 stems or 1550 leaf blades m⁻², and sward bulk density was ~710 g m⁻³ in leaf patches and ~1711 g m⁻³ in stem patches. Hunger satiation levels were assumed to correspond to proportions of meal size determined during a 7-day preliminary period for steers previously maintained on an alfalfa pellet diet. Meal size was calculated as *ad libitum* consumption of alfalfa pellets, offered once daily, through the first 30-min. period in which no feeding bout exceeded 5 min. Meals lasted ~2.0 to 2.5 hr, averaged 12.3 to 15.9 kg in size, and comprised the total daily intake of each steer during periods of meal size determination and subsequent HCS grazing sessions. Hunger level and patch size comprised a factorial treatment arrangement and two HCS grazing sessions were obtained daily.

Swards were offered at ~11:00 to 12:00 each day to steers recently fed to 0, 30, 60, or 90% of meal size. Twenty bites were allowed from each HCS, after which steers received the complementary quantity of pellets necessary to provide each animal with 100% of meal size daily. Ingestive behavior variables measured were bite area, bite depth, and bite weight for leaf and stem patches; and biting rate, IIR, leaf proportion of total grazed area, and grazed proportion of total HCS area.

5.3. Within-patch intake rate and patch depletion

5.3.1. Behavioral mechanisms that determine bite rate and intake rate on HCS

Detailed descriptions of the construction and structure of experimental swards, and of the experimental procedures are in previous sections. Animals were first given access to the swards and allowed to take 6 bites (first session) after which access was blocked and bite dimensions were determined. All tillers that had been partially grazed during this first session were removed and the same animal was allowed to graze the sward a second time (second session) until *ca.* 90% of the top horizon had been grazed. All grazing sessions were recorded with a video camera. We attached a wireless

microphone on the forehead of the animals, such that grazing and chewing sounds were recorded on the sound track of the video.

Two experiments were conducted to study the effects of sward height and bulk density on instantaneous intake rate of cattle, and to explore the mechanisms involved in determining time per bite within a feeding site. For the first experiment we constructed dallisgrass (*Paspalum dilatatum* Poir.) in factorial combinations of 3 densities (378, 775, and 1550 holes m⁻²) and 2 heights (8 and 18 cm). Swards were made exclusively of leaf lamina, representing a vegetative stage with uniform foliage. For the second experiment we used alfalfa (*Medicago sativa* L.) to construct swards in combinations of 3 densities (378, 775, and 1550 holes m⁻²) and 3 heights (7, 15, and 25 cm). In both experiments we used 3 steers as blocks.

Due to difficulty in obtaining enough suitable herbage, not all treatments of the first experiment were observed in each animal, so it was not possible to perform analysis of variance. The data were used to establish the relationships between grazing behaviors and bite weight. Effects of sward structure in the experiment with alfalfa were determined by analyses of variance after correction for effects of bite weight. This approach assumes that any effects on feeding behaviors that are explained both by sward structure and bite weight, are caused via bite weight. Therefore, the ANOVA's test whether sward height and bulk density affect grazing behaviors beyond the effects via changes in bite weight. All residuals were tested for normality by a Shapiro-Wilk W-test (SAS Institute Inc., 1989).

Swards were sampled before grazing for determination of bulk density and herbage mass per unit area. Herbage intake was calculated as the difference between total dry mass offered and ungrazed residual. Total grazing time, since the first bite started until all grazed herbage was chewed and swallowed, was measured to the nearest 0.1 s by a timer displayed on each frame of the video record. Any time during which the animal was not chewing or swallowing, after access to the sward was blocked, was subtracted. Instantaneous intake rate was calculated by dividing herbage intake by total grazing time.

By watching the video records and listening to the sounds, jaw movements were counted and classified into three non-overlapping categories: (1) exclusive manipulation of the herbage to draw it into the mouth without chewing, (2) manipulation of herbage and simultaneous chewing of the forage

already in the back of the mouth with characteristic grinding sound, and (3) exclusive chewing with characteristic grinding sound, during which no manipulation of new herbage takes place. Each video record was observed 3 times, such that precision was maximized. Each time, different events and the times since the beginning of the grazing session were recorded by using a computer with timing software. First, we recorded all jaw movements. Second, we recorded exclusive chews. Finally, we recorded occurrence of simultaneous chewing and manipulation of herbage. Number of exclusively manipulating jaw movements was calculated by difference. The number of jaw movements in each uninterrupted bout of exclusive chewing (except for the bout after access to the sward was blocked) was determined for each session of the experiment with alfalfa. Bites were defined as the complete severance of the bundle of tillers previously gathered, and were associated with a characteristic head movement and tearing sound. Intake was estimated by dry matter disappearance and bite weight (BWT) was calculated as herbage intake divided by number of bites.

Three 4-year old steers averaging 750 kg live weight were used in this study. Animals were familiar with the experimental setting and protocol, and diets prior to the experiments. They were fed 1-1.5 bales (*ca.* 55 kg) of good quality alfalfa hay once daily between 6:30 and 7:00 am. Swards were offered between 12:00 and 15:00, and the steers consumed them eagerly.

5.3.2. Patch depletion by grazers

5.3.2.1. Hand-constructed-sward experiment

Experimental swards of wheat (*Triticum aestivum* L.) were constructed by hand and measurements performed as described before. The experiment was run between 13 March and 2 April 1990, while wheat phenological stages ranged from early internode elongation to early heading. We collected tillers every morning and placed them standing in water while constructing the swards. Swards were constructed exclusively of leaf lamina, by threading laminae through holes in wooden modules. Each hole contained 4 laminae, and bulk density was controlled by the number of holes filled with herbage per unit area. Height was controlled by pulling the tillers through the holes and clipping 3-5 cm of the tip, so the tapering tips were removed and all swards had a similar surface.

The experiment consisted of a factorial combination of two sward structures and six levels of number of bites removed (10, 20, 30, 40, 45, and 60). Short swards had a height of 10 cm and average bulk density equal to $1300 \pm 15 \text{ g m}^{-3}$, whereas corresponding values for the tall swards were 20 cm and $656 \pm 15 \text{ g m}^{-3}$. Both sward types had the same herbage mass per unit area (1300 ± 27 vs. $1310 \pm 27 \text{ kg ha}^{-1}$), and per patch (60 g). Each 0.46-m^2 sward represented one experimental unit and was grazed in a single occasion for a total number of bites predetermined by randomization. Treatments were replicated over two 5-yr old Hereford steers that weighed 680 (#1) and 660 kg (#2). Both animals grazed one HCS each, on each experimental day. The time sequence of treatments was randomized with the restriction that animals alternated sward structures every day. During this experiment steers were held in a pen with 3 other steers and collectively fed one bale (*ca.* 50 kg) of good quality alfalfa every morning at 09:30, *ca.* 3 h before grazing the experimental swards.

Grazing sessions were video taped. A stopwatch display on each video frame allowed timing the duration of grazing with a precision of 0.1 seconds. Number of "regrazing" bites was determined by watching the video record in slow motion and recording the number of times the mouth of the animal was located in areas previously grazed when severing a bite. These bites were considered to be in the second horizon of the sward. Intake of DM was calculated as the difference between offered herbage mass (estimated by pre-grazing measurements) and residual herbage mass. Effects of deviations of herbage mass per unit area from the mean on intake were removed by covariance analysis. The rest of the analyses were performed on the corrected data. Intake curves were derived by fitting a rectangular hyperbola model, $Y = k_1 * X * (1 + k_2 * X)^{-1}$, where k_1 is intake rate when residence time equals zero, k_1/k_2 represents the total herbage mass that can be extracted from the patch, Y is the cumulative intake and X is patch residence time. Residual height in all grazed holes was measured and average bite depth was calculated as initial height minus average residual height. Grazed area was calculated by dividing number of grazed laminae by laminae density. Apparent bite area for all bites was area grazed divided by total number of bites. Actual bite area of bites in the top horizon was calculated as grazed area divided by number of bites in the first horizon. Instantaneous intake rate was calculated as the ratio of total DM removed over time spent at the patch. Bite weight for each incremental

set of bites was calculated by dividing the difference in DM removed by the difference in number of bites.

5.3.2.2. Field Experiment

This experiment was carried out in a turf ryegrass (*Lolium perenne* cv. Manhattan II) sward, from June 6 to June 9, 1991. Most of the tillers were in vegetative stage during the experiment. Areas in which the sward was tall enough for the treatments were selected and 0.6 x 0.6 m patches were marked. Areas between patches and around them, except for areas for pre-grazing measurements adjacent to patches, were mowed to a height of 2-3 cm with a lawn mower. Patches and sample areas were trimmed to a height according to the treatment with a powered hedge trimmer. All patches were weeded by hand and presented a uniform and even surface. Pre-grazing herbage mass per unit area was estimated by clipping a 10 x 40 cm rectangle adjacent each patch, drying the herbage at 60° C for 48 h and weighing to the nearest 0.01 g. After the sample was taken, each patch was trimmed to a 0.6 x 0.6 m square.

Treatments for the measurement of intake and bite weight consisted of a factorial combination of three patch heights (7, 12.5 and 18 cm) and five numbers of bites removed from the patch (10, 20, 30, 45 and 60 bites). Three tame esophageally fistulated steers (#1, #2 and #8) of 765 kg of average live weight were used as blocks. Each combination of height and animal was replicated twice in the mornings of consecutive days, for a total of 18 patches. The experimental animal, restrained by a halter and lead rope, was allowed to take 10 bites, after which access to the patch was restricted while the harvested material was collected through the open fistula. The process was repeated for two more sets of 10 bites and two of 15 bites, until a total of 60 bites had been taken. Usually, the interruptions between sets of bites lasted 20-30 s during which the animal stood by the patch. The complete extrusa was collected in a separate ziploc bags for each set of bites, then transferred to aluminum pans, dried for 4 days at 60 C and weighted to the nearest 0.01 g. Sets of bites within the same patch were treated as repeated measures (Neter *et al.*, 1985).

A second set of 18 patches was used to measure time per bite and total time necessary to harvest 10, 20, 30, 45 and 60 bites. The same treatments as above were applied and the same three animals used as blocks. Each combination of animal and height was replicated twice as above, but in this

case one replicate was grazed for a total of 30 bites and the other for a total of 60. For the timing of bites, animals were allowed to remove the predetermined number of bites (30 or 60) without disturbance or interruption. Grazing sessions were video taped and behaviors timed as described for the HCS experiment. During grazing sessions, animals were fitted with a wireless microphone that recorded biting sounds on the sound track of the video. Tapes were viewed in the lab and the time to take 10, 20, 30, 45, and 60 bites was recorded to the nearest 0.1 s. Time measurements within patch were treated as repeated measures. Patches used to measure residence time were randomly interspersed in space and time with the patches used to measure intake and bite weight by extrusa collection.

Intakes and patch residence times from the two replicates were averaged and the averages used to fit a rectangular hyperbola of the intake curves for each animal in each height treatment. For the prediction of gain curves in patches of different herbage mass, cumulative intake was divided by patch herbage mass, data from all patches were pooled and the same rectangular hyperbola was fitted. Models were fitted and confidence intervals for the parameters calculated by the nonlinear procedure of JMP (SAS Institute, 1989).

5.4. Models of intake rate

We developed models to link sward characteristics within feeding stations with IIR at the field level. Two of these model are described in detail in reprints attached (Laca and Demment 1991, Laca and Demment in press). Additionally, a model of IIR, patch selection and utilization was developed and tested experimentally. The methods followed for this model are described in detail in section 5.5.2 of this report.

5.4.1. Graphical analysis of sward depletion by grazing.

In the present section we present a model which graphically explores the options grazers have when depleting the available forage. Grazing is discussed as a process of depletion in which the removal of herbage may be associated with a change in intake rate over a defined time period by virtue of changing options for bite selection. A non-growing, non-patchy sward of finite area is

described as a series of grazing horizons. Bite weight is constant within horizon but may differ between horizons.

Model Assumptions

- A1. The animal grazes a non-growing sward of finite area, uniform bulk density in the horizontal plane, and of initially uniform height, defined for the purpose of this model as the grazeable thickness of sward.
- A2. The size and mass of a bite are a function of the height and bulk density of the herbage where the bite is taken.
- A3. All bites taken from the same horizon have the same bite area and are equal in nutritive value.
- A4. It follows from A2 and A3 that for any initial bulk density and height, one or more potential grazing horizons can be identified.
- A5. The animal can select a potential bite from a lower horizon only after all herbage immediately above the bite area has been grazed.
- A6. A sufficient number of bites are placed contiguously so as not to impose further restrictions on the availability of lower horizons. Discontinuities in the behavior of the model (especially at very low bite number) due to the fact that bite number must be an integer, are not considered.
- A7. It follows from A5 and A6 that the ungrazed surface area of the uppermost horizon (H1) is always available for grazing. The surface area of horizon $i+1$ available for grazing is the area exposed by grazing of horizon i .

Notation

We define the following terms:

A	Total surface area of the uppermost horizon available to the animal
N	Total number of bites taken from an initially uniform sward
n_i	Number of bites taken from the i -th horizon
a_i	Surface area of a bite taken from the i -th horizon
w_i	Mass of a bite taken from the i -th horizon
p_i	Proportion of total bites taken from the i -th horizon
$N_{\max}$	Total potential number of bites provided by all horizons
I	Total intake from N bites.

In these terms, 'bite depletion' can be defined as $N/N_{\max}$. This is equivalent to 'mass depletion' only when w_i is equal in all horizons.

By definition:

$$p_i = \frac{n_i}{N} \quad (1)$$

$$\sum p_i = 1 \quad (2)$$

To facilitate graphical analysis, we consider an arbitrary maximum of three grazing horizons. Thus:

$$N = n_1 + n_2 + n_3 \quad (3)$$

$$N_{\max} = A \left(\frac{1}{a_1} + \frac{1}{a_2} + \frac{1}{a_3} \right) \quad (4)$$

Constraints

The assumptions of the model lead to the following constraints:

C1. The total area grazed on horizon H2 cannot exceed the total area grazed on horizon H1.

$$n_1 a_1 \geq n_2 a_2$$

or, dividing by N :

$$p_1 a_1 \geq p_2 a_2 \quad (5)$$

C2. The total area grazed on horizon H3 cannot exceed the total area grazed on horizon H2.

$$n_2 a_2 \geq n_3 a_3$$

or

$$p_2 a_2 \geq p_3 a_3 \quad (6)$$

C3. The maximum number of bites from H1 that can be taken for any total number of bites, N , will be N until H1 is completely grazed.

$$n_{1,\max} = \min\left[\frac{A}{a_1}, N\right] \quad (7)$$

C4. The minimum number of bites from H1 that can be taken for any N will be achieved by taking as many bites as possible from H2 and H3. Each bite from H1 exposes an area a_1 of H2. That permits a_1/a_2 bites to be taken from H2 and after these are taken, a_1/a_3 bites can be taken from H3.

$$n_{1,\min} = \frac{N}{(1 + \frac{a_1}{a_2} + \frac{a_1}{a_3})} \quad (8)$$

C5. $n_{2,\max}$ is achieved by taking a_1/a_2 bites from H2 for each bite from H1 or, equivalently, a_2/a_1 bites from H1 for each bite from H2, and no bites from H3 until H2 is completely grazed.

$$n_{2,\max} = \min[\frac{A}{a_2}, \frac{N}{1 + \frac{a_2}{a_1}}] \quad (9)$$

C6. $n_{2,\min}$ is achieved by taking no bites from H2 until H1 is completely grazed, and by taking a_2/a_3 bites from H3 for each bite from H2 thereafter.

$$n_{2,\min} = \max[0, \frac{N - \frac{A}{a_1}}{1 + \frac{a_2}{a_3}}] \quad (10)$$

C7. $n_{3,\max}$ is achieved by taking a_1/a_2 bites from H2 and a_1/a_3 bites from H3 for each bite taken from H1, or equivalently, a_3/a_1 bites from H1 and a_3/a_2 bites from H2 for each bite from H3.

$$n_{3,\max} = \frac{N}{(1 + \frac{a_3}{a_1} + \frac{a_3}{a_2})} \quad (11)$$

C8. $n_{3,\min}$ is achieved by taking no bites from H3 until horizons H1 and H2 are completely grazed.

$$n_{3,\min} = \max[0, N - \frac{A}{a_1} - \frac{A}{a_2}] \quad (12)$$

Constraints C3 to C8 can be expressed in terms of the proportion of total bites taken from each horizon (p_1, p_2, p_3) by dividing by total bite number, N . The numerical value of a constraint is then constant for combinations of total area, A , and total bite number, N , that represent the same level of depletion, i.e., that yield the same ratio $N/N_{\max}$. Taken together, the constraints define the space of possible combinations of p_1, p_2, p_3 as a function of depletion level $N/N_{\max}$.

5.5. Patch selection and intake rate in the field

5.5.1. Effects of patch height and density, and animal experience on selection and intake rate

Heterogeneity Treatments. The experiment was conducted on an irrigated pasture of "Manhattan II" perennial ryegrass located in Davis (California). Forty five days prior the start of the experiment the ryegrass was mowed (using a flail mower) to around 7-8 cm above ground level to eliminate dead residuals. The pasture was also fertilized 60 days (56 Kg N Ha⁻¹) and 15 days (37 Kg NPK Ha⁻¹) prior the start of the experiment. At the start of the experiment the ryegrass was in vegetative regrowth (fall regrowth).

Days of treatment preparation were alternated with days of measured grazing sessions. On the day preceding measured grazing sessions, 10 x 10 m² paddocks with relatively homogeneous density were selected in the pasture of ryegrass for the creation of 16 patches of 0.6 x 0.6 m² per paddock. The patches were arranged in a four by four configuration and were separated from each other and from the surrounding vegetation by 1.5 m wide strips. The strips were mowed to 3 cm above ground level, and all clippings were removed. Horizontal heterogeneity was created by manipulating height and/or density in each patch. Patch heights of 12 cm (tall) or 7.5 cm (short), were established with a rotatory lawn mower. Patch density was either the original of the pasture (original-density patches), which was 3.3 (SE = 0.14) Kg DM m⁻³ in tall patches and 4.5 (SE = 0.25) Kg DM m⁻³ in short patches, or approximately half of the original density (half-original-density patches), which was 1.5 (SE = 0.10) Kg DM m⁻³ in tall patches and 2.6 (SE = 0.11) Kg DM m⁻³ in short patches. The difference in density between tall and short

patches reflects the increase in density from top to bottom in the ryegrass sward. Reduction in density was achieved with battery operated grass shears modified to allow cutting every other 2.5 cm wide strips to ground level. Density was estimated through herbage mass measurements in 20 circular plots of 0.1 m² by cutting the ryegrass at ground level with hand clippers. Heterogeneity treatments were half of the patches tall original-density (TOD) or short original-density (SOD) (T1); half of the patches SOD or short half-original-density (SHOD) (T2); and half of the patches SOD or tall half-original-density (THOD) (T3). The two types of patches were systematically distributed within the four by four configuration of the paddocks (e.g.; short-tall-short-tall, first row; tall-short-tall-short, second row; and so on).

Grazing Sessions. Three 5-year-old, esophageally-fistulated Hereford steers of an average live weight of 737 kg were used in this study. The animals were tame, used to daily handling, and were familiar with the experimental protocol and diet prior to the experiment. Except during grazing sessions, steers remained in a corral and were maintained on alfalfa hay fed once daily between 1500 and 1600 h.

On the days of measured grazing sessions the three steers were led from their pen to the ryegrass pasture, where they were held in a previously mowed area adjacent to the 16-patch paddock areas. Electric fences were used to confine them in both areas. Only two randomly selected steers were used each day of measured grazing sessions, except the last day when only one steer was used. The selected animals were first individually offered 4 patches of each of the two patch types present in the day's treatment. Ingesta was collected from an esophageal fistula into a plastic bag. Animals were allowed to take up to 60 bites (original-density patches) or 40 bites (half-original-density patches) per patch. The extrusa from every other set of 15 bites (original-density patches) or 10 bites (half-original-density patches) was collected separately by interrupting grazing at the end of each set of bites. Extrusa samples were frozen at -20 C until their organic matter content was determined, by ashing for 4 hr at 540 C, to estimate bite weight. After extrusa collection, three ungrazed 16-patch paddocks were offered to each selected steer at intervals of 30 to 45 min. While one steer was grazing, the other two steers remained in an adjacent previously grazed area. Each grazing session was recorded with video camera and sound system via a wireless microphone mounted on the forehead of the animal, which provided bite count data. In addition,

trajectory of the animal, patch residence time, and number of bites per patch were visually recorded. Visual records were checked against video-sound records in the laboratory.

Analysis. Grazing sessions were divided in three successive 5-min grazing intervals (GI1 through GI3), which represented different degree of depletion. The time an animal started grazing a patch was used as a criterion to include the patch in a particular grazing interval.

For each grazing interval selectivity for the patches that yielded greater bite weight was calculated as the ratio of (1) number of TOD (T1) or SOD (T2 and T3) visited patches to total number of visited patches, (2) residence time in TOD or SOD patches to total residence time, and (3) number of bites in TOD or SOD patches to total number of bites. A value greater than 0.5 indicates selectivity for TOD or SOD patches, whereas a value lower than 0.5 indicates avoidance. The relationship between selectivity and potential IIR was determined through the comparison of bite ratio to IIR ratio for each treatment grazing-interval combination (Matching Law, Herrnstein 1974).

Bite weight could not be determined directly while animals were grazing the 16-patch paddocks. Extrusa collection of separate sets of bites is not possible without disturbing the animal. Therefore, intake obtained at each patch during the grazing sessions was calculated based on the number of bites actually taken in each visit, and intake curves which relate total intake from a patch to total number of bites removed. Intake curves for each patch type and each animal were derived from bite weight estimations from extrusa collection. Average bite weight was calculated for incremental sets of 15 (original-density patches) or 10 (half-original-density patches) bites, and assigned to the bite in the middle of each set. Bite weights were then determined for each bite of the sequence by linear interpolation, and intake curves calculated by summation of individual bite weights. Finally, IIR obtained each time a patch was grazed was calculated through dividing intake by residence time.

Consistency of the observed behavior with maximization of intake rate was tested by predicting number of bites and residence time in each patch type during GI1 of the three treatments. Average travel time between consecutive patches visited in GI1 was calculated for each treatment, after pooling data from the 3 animals and the 3 levels of experience. Average gain curves for each patch type were obtained by combining average intake curves

(relationship between intake obtained from a patch and number of bites taken, see above) with average time per bite for each patch type during GI1. Since steers have little opportunity to walk while chewing when bite weight is smaller than 1.5 g DM (see experiments on determinants of bite rate), it was assumed that chewing and searching between patches did not overlap. Intake rate was maximized according to the "prey and patch" model (Stephens and Krebs 1986) by numerical techniques.

The statistical design for the analysis of variance was block with restricted randomization. Treatments were offered to animals in the following order: T1, T2, and T3. Heterogeneity treatments were considered as the main effect and individual steers as blocks. Grazing intervals were analyzed separately. Each animal-treatment combination was repeated three times, which necessitated the use of a repeated measures analysis (Winer 1971, Milliken and Johnson 1984). Treatment mean differences and the differences between selectivity ratios and 0.5 were tested at $P < .05$ by using the critical range of Duncan's test.

5.5.2. Field test of the marginal value theorem with cattle

Model. To test model predictions, we constructed patches to parametrize the intake curves to be used in the model. Intake curves describe the relationship between time grazing (T_r) within a patch and intake (I_r) from the patch. For each one of the 27 experimental plots (see below) we prepared 2 additional patches representing the heights in the GE. Herbage mass prior to grazing these patches was determined in the manner specified below. All patches were weeded by hand and presented an even and uniform surface.

A rectangular hyperbola was fitted to describe the relationship between intake and residence time for each patch height. It was estimated that animals walk between feeding sites at *ca.* 0.8 m s^{-1} . Predictions for T_r in each patch type and maximum instantaneous intake rate (IIR) for the GE were obtained by applying Charnov's marginal value theorem (Charnov 1976). The theorem indicates that IIR in a patchy environment is maximized if the forager leaves patches when intake rate within each patch (slope of the intake curve) equals the average IIR for the whole environment. Important assumptions are that patches are encountered randomly and not revisited; animal has complete information of the foraging situation; searching and eating are mutually

exclusive; and that I_T is related to T_T by a negatively accelerated function. Optimal T_T for each patch height in each GE was determined by numerical iteration.

Experiment. The experiment to test model predictions consisted of 9 treatments or "grazing environments" (GE) replicated over 3 steers considered to be blocks, for a total of 27 plots. Treatments were factorial combinations of 3 sets of patch heights (all 10 cm, half 7.5 and half 12.5 cm, half 5 and half 15 cm) and 3 distances between centers of patches (1.2, 3.4, and 8.4 m). We constructed GE by mowing areas selected for homogeneity in a second-year turf ryegrass (*Lolium perenne* cv. Manhattan II) pasture. Each GE consisted of a linear arrangements of 16 0.6 x 0.6 m² patches. Areas between patches and a width of 0.6 m to each side were mowed to ca. 2 cm, and the GE were fenced with electric fence to prevent animals from turning around and revisiting patches. In the treatments with patches of two heights, the sequence of heights was randomized with the constraint that no more than 2 patches of equal height could be adjacent. Prior to grazing, 0.30-m² areas adjacent to 6 patches of each one of the 27 plots were clipped for estimation of herbage mass.

Animals were three 5-year-old, esophageally fistulated steers of 750 kg average live weight. Animals were tame and accustomed to experimental procedures, and had recent experience grazing patches of various heights in the same ryegrass pasture. While not grazing in the experiment, animals were kept in a holding pen. They were collectively fed a maintenance diet of good quality alfalfa once a day between 1400 and 1600 hours.

The experiment was performed from 10 July to 23 July 1991. Order of treatments and animals in space and time was randomized with the constraint that all 3 animals, 3 patch distances and 3 sets of heights were observed in each experimental day. Three experimental units and 6 patches for intake curves were observed each day between 0700 and 1000 hours, after which animals were taken to the holding pen and we prepared the treatments for the following day. Each grazing session started with the gazing of patches to determine the intake curves. The steer was fitted with a wireless microphone to monitor biting and chewing, and allowed to take sequential sets of 10-15 bites. Extrusa was collected via fistula in separate bags and later dried at 60°C for determination of intake. Subsequently, the animal was walked down the GE it was about to graze and released at the S end of it. All grazing was

videotaped from the distance, without disturbing the animal. We counted bites in each patch and steps between patches, and timed patch residence (T_r) and walking (T_w) between patches with a precision of 0.033 seconds.

Patch residence time was averaged for each patch height in each one of the 27 plots and the averages were analyzed as a factorial of patch height by patch distance in 3 blocks (animals). Effects of patch height and distance were tested with orthogonal polynomials. Quadratic polynomials were fitted to intake data from the additional patches (see below), to relate intake to number of bites taken from each patch (B) height. Intake per patch during the grazing of GE was estimated on the basis of B and these polynomials. Overall IIR was estimated for each of the 27 plots by dividing total intake in all patches by total time since the animal started grazing the first patch until it left the 16th one. Instantaneous intake rate was analyzed as a factorial of patch distance and height contrast in three blocks (animals). Effects of distance and contrast were tested by orthogonal polynomials. In all statistical analyses residuals were tested for deviations from normality and homoscedasticity. Transformations were used to correct significant ($P < 0.05$) deviations.

5.6. Prediction of bite weight and intake rate in the field

Bite weight, chews per bite and sward height and bulk density were measured in a series of experiments performed on hand-constructed swards. The characteristics of the swards and range of measured variables are presented in Table 1.

Experiments were performed with four fistulated steers of *ca.* 750 kg of average live weight. Data were pooled and bite weight (g) was regressed on sward height (cm), sward bulk density (kg m^{-3}) and chews per bite. Bite weight, bulk density and chews per bite were transformed logarithmically to achieve normality of errors and to stabilize variance. Initially, the model included all linear terms and interactions. Terms that exhibited non-significant ($P > 0.10$) type III sum of squares were removed, starting with higher order interactions. Residuals were plotted against observed values to detect inadequacies of the model used. Confidence intervals at the 95% level were calculated in the logarithmic scale and then transformed back to linear scale for presentation purposes.

6. RESULTS

6.1. Hand-constructed methodology

6.1.1. Sward Structure

By constructing swards by hand we successfully controlled the bulk density and height of the canopy. Sward bulk density of alfalfa was affected significantly by holes m^{-2} and was not affected by height (Tables 2 and 3). Bulk density of alfalfa HCS was linearly related to holes m^{-2} . Dallisgrass HCS of the same number of holes filled per m^2 did not differ significantly in bulk density, with one exception. Eighty-mm high dallisgrass HCS with 775 holes m^{-2} exhibited significantly lower ($P = 0.05$) bulk density than 150- and 180-mm high HCS. As intended, the natural tendency of negative covariance between total height and bulk density was effectively eliminated. The coefficient of variation of bulk density among modules within HCS was 13 and 23% for dallisgrass and alfalfa, respectively (Table 4). The coefficient of variation of bulk density between HCS of equal height and holes filled per module, but built at different times, was 22 and 25% for dallisgrass and alfalfa, respectively.

In spite of the efforts to collect homogeneous herbage over the course of the experiments, bulk density of both dallisgrass and alfalfa swards increased significantly with the number of days of regrowth. On average, bulk density of dallisgrass HCS increased $5.6 (\pm 2.7) \text{ g m}^{-3}$ per day since the field was mowed. Bulk density of alfalfa HCS increased more steeply at $46.9 (\pm 20.7) \text{ g m}^{-3}$ per day. This was attributed to an increment in the weight of individual plant parts with advancing phenology.

Bulk density of alfalfa tended to decrease down the canopy, particularly in the shorter swards (Figure 7). This response is attributed to the higher density of leaf in the upper part of alfalfa stems. Bulk density of dallisgrass swards increased with depth into the canopy, probably due to the increment in width and thickness of leaf blades.

6.1.2. Evaluation of Methods for Determining Mass of Herbage Removed

Bite weight determined by methods 2 (Y) and 3 (X) was practically the same ($Y = 0.004 + 1.075 X$, $R^2 = 0.93$). Method 1 (Y) consistently

overestimated the results of method 2 ($Y = 1.305 + 1.096 X$, $R^2 = 0.71$, Table 5). However, qualitative results and probability levels of the analysis of the effects of sward height and density on bite weight were essentially the same for both methods. There was a correlation of 0.85 between the two methods. The overestimation resulting from method 1 is attributed to an underestimation of the rate of moisture loss which was determined in a room without wind and with lower radiation flux.

Average bite weight and bite volume determined by method 1 were significantly greater and exhibited more variability than the other two methods. Averages and variability were not different between methods 2 and 3 (Table 4). Bite volume measured by the product of bite area and bite depth (method 3) is an unbiased measure of effective bite volume, because the length of each tiller severed is measured. Accordingly, we consider method 1 to be biased, since it consistently yielded significantly larger bite volumes.

Bite weights by methods 1 (X) and 2 (Y) were also compared for the grazing sessions used to determine IIR. The difference in bite weight estimated by the two methods was smaller for these longer grazing sessions than for the "6-bite" grazing sessions, likely because rate of water loss decreased with herbage and moisture depletion ($Y = 0.89 X - 0.04$, $R^2 = 0.90$). Method 1 yielded estimates approximately 12% greater than method 2.

6.1.3. Sound and Video Recordings

Bites and chews could be clearly identified and counted from the sound track of the videotapes. Visual counts of chews were not accurate, even when based on slow-motion play-back. By listening to the sounds while viewing the video recording we could distinguish clearly which jaw movements were associated with chewing and which were merely manipulative motions. The standard technique to estimate chews in grazing animals consists of subtracting number of prehending bites from total number of jaw movements (Chacon *et al.*, 1976). We calculated chews in the alfalfa experiment both by the standard technique (S), and by direct count (C) of chewing sound ($S = 40.3 (\pm 5.2) + 0.0035 (\pm 0.00033) C^2$, $R^2 = 0.83$). The ratio S/C indicates whether S over- or underestimated C. The average for this ratio varied from 0.67 (150-mm sward with 388 holes m^{-2}) to 1.47 (70-mm sward with 388 holes m^{-2}). The ratio of number of chews calculated by the standard method to actual chewing

jaw movements with an audible grinding effect was significantly affected by sward height (Table 6).

6.2. Factors and mechanisms that determine bite weight

6.2.1. Homogeneous swards

6.2.1.1. Effects of HCS height and density

Sward bulk density ranged from 571 to 2969 g m⁻³ and from 1089 to 6931 g m⁻³ for dallisgrass and alfalfa, respectively. Alfalfa swards were nearly twice as dense as dallisgrass swards with the same number of holes filled with herbage per module. Bulk density of dallisgrass was within the normal range for grass swards (Arias *et al.*, 1990). The lowest densities obtained with alfalfa were in the range of highest bulk densities measured in alfalfa fields (Dougherty *et al.*, 1988). Bulk density of dallisgrass and alfalfa swards increased linearly with holes m⁻² but was not affected significantly by sward height (Tables 7 and 8).

Bulk density increased from the top to the bottom of the dallisgrass canopy, whereas it slightly increased in alfalfa. As a result of the opposite gradients in the canopy, bulk density of the grazed horizon was lower than overall bulk density for dallisgrass, and greater than overall bulk density for alfalfa. Otherwise, bulk density of the grazed horizon followed the same trends as overall bulk density. Both percentage of stem (Figure 8) and NDF concentration in stem tissue (Y, %) increased linearly with depth in the alfalfa canopy (X, cm), and with treatment height ($Y = 41.6 + 1.27X$, $R^2 = 0.58$). Concentration of NDF in dallisgrass lamina was measured later in the season and averaged 76%.

Bulk density of swards tended to increase with days of regrowth (Tables 7 and 8) in both experiments, likely as a result of the normal increase in the weight of individual plant parts with phenology. This effect was greater in the alfalfa swards, which also exhibited a significant increase in the percentage of stem with days of regrowth.

Bite depth increased significantly with sward height in both experiments, with slope negatively affected by holes m⁻² (Figure 9 and Table 8). In short swards there was no effect of holes m⁻² on bite depth, whereas in long swards bite depth exhibited a significant negative relationship with holes

m⁻². Sward height was the most important factor that determined bite depth. On average, steers removed 55% of the dallisgrass height and 48% of the alfalfa sward height. However, the proportion of canopy height removed by a bite decreased with increasing height and density.

Bite depth differed significantly between animals. Animal #1 exhibited the greatest bite depth of all animals on alfalfa HCS, but the least on dallisgrass HCS. The relative difference between animals #3 and #8 was consistent across experiments (Table 9).

The model to predict bite depth included a significant linear effect of height and a negative interaction between height and bulk density (Figure 10). A categorical term to account for plant species effect was not significant ($P = 0.09$) when included in the above model. Sward height by itself explained 83% of the variation in bite depth ($Y = 0.59 + 0.474 X$). The effects of sward height and density on bite depth were remarkably consistent between the legume and grass species.

Measurements to infer incisor height indicated that changes in bite depth were mostly due to changes in the height at which animals positioned their heads when biting. Incisor height ranged from 17 mm for animal #3 grazing a 80-mm tall dallisgrass sward of 1300 g m⁻³, to 176 mm for the same animal grazing a 250-mm tall alfalfa sward of 6190 g m⁻³. A given increment in sward height caused a greater increment in incisor height when the sward was taller or of greater density (Figure 11), as indicated by the positive quadratic effect of height and the positive height by bulk density interaction in the predictive equation ($IH = 1.33 + 0.009 X^2 + 4.27 \cdot 10^{-5} XY$, where IH is incisor height in cm, X is sward height in cm, and Y is bulk density in g m⁻³). No significant species effect on incisor height was detected.

The average bite area of sequences of six bites ranged from 183 cm² for steer #1 on an 180-mm tall dallisgrass sward of 717 g m⁻³, to 34 cm² for steer #3 on a 250-mm tall alfalfa sward of 6190 g m⁻³. Area of individual bites showed a wider range of variation. Based on the video record, we estimated that individual bite areas by animal #1 were as great as 220 cm² when grazing an 180-mm sward of low density.

In general, bite area increased with sward height and decreased with increasing holes m⁻² (Figure 9). However, there was a significant height by density interaction on bite area (Table 8). Bite area remained relatively

constant (dallisgrass), or even showed a tendency to decrease (alfalfa), as height increased in dense swards. At the lowest density of holes filled with herbage, bite area on grass swards more than doubled from 75 to 156 cm² as sward height increased from 80 to 180 mm, and exhibited a tendency to plateau on longer swards.

Bite area differed significantly between animals in both experiments (Table 9). The absolute differences among animals were similar in both experiments, but average bite area was 33 cm² larger in the dallisgrass experiment. On average, alfalfa swards were shorter and denser than dallisgrass ones (Table 7), and yielded smaller bite areas. Such differences between experiments are consistent with the negative effect of bulk density and positive effect of height on bite area detected within each experiment. The analysis of data on bite area from both experiments pooled indicated that most of the difference between experiments was explained by height and bulk density (Figure 10). No significant species effect was detected by adding a categorical term to the model.

Bite volume ranged from 200 cm³ (steer #1 on 70-mm alfalfa sward with 16 holes m⁻²) to 3200 cm³ (steer #1 on 300-mm dallisgrass sward with 4 holes m⁻²). Sward height exhibited a positive linear effect on bite volume, whereas holes m⁻² had a negative one (Table 8). The linear by linear and linear by quadratic interactions between sward height and holes m⁻² in both experiments indicated a significant pattern. Bite volume increased linearly and steeply with height on low density swards. As density increased the initial slope was smaller and diminished with height. Varying density on short swards had no effect on the volume of bites. On tall sparse swards steers prehended canopy volumes 2 to 3 times as large as in tall dense swards (Figure 11). On tall alfalfa swards of high bulk density (>2200 g m⁻³) the increments in bite depth caused by increasing sward height were almost counteracted by reductions in bite area.

A significant effect of days of regrowth was detected on bite volume in the experiment with alfalfa. Steers exhibited a reduction in bite volume of 45 cm³ day⁻¹ (Table 8). Such an effect was caused by the increment in bulk density of alfalfa swards with days of regrowth, and agreed with the effects of bulk density treatments on bite dimensions observed in both experiments.

Contrary to bite dimensions, bite weight exhibited independent linear effects of sward height and holes m^{-2} in both experiments (Figure 12 and Table 8). Bite weight was more sensitive to sward height than to bulk density. The ratios of fractional increment in bite weight to fractional increment in height were 1.03 and 1.24 for the dallisgrass and alfalfa experiment, respectively. Corresponding values for increments in bulk density were 0.48 and 0.62. In spite of the significant differences in bite dimensions, animals did not exhibit significant differences in bite weight.

6.2.1.2. Effects of sward height, density and time within grazing bout

Bite area was influenced by sward height and grazing time, but not by sward bulk density; bite area increased with sward height (94 to 138 cm^2) and decreased with length of time animals had been grazing (139 to 113 to 97 cm^2). Bite depth was influenced only by sward height, increasing from 6 to 10 cm as sward height increased from 10 to 18 cm. Resulting bite weights were influenced by sward height, bulk density, and grazing time (Fig. 13), increasing with sward height and bulk density and decreasing with grazing time. Averaged across grazing times, bite weights observed for each combination of sward height and bulk density decreased in the order tall - high density, tall - low density, short - high density, and short - low density.

6.2.1.3. Effects of tiller density and tensile strength

At equal leaf density, bulk density of oat swards was consistently greater than that of dallisgrass (Figure 14). On average, bulk density of oats was 460 $g m^{-3}$ greater than dallisgrass. Given the greater strength of dallisgrass, the treatments included swards of equal bulk density and different strength, as well as swards of equal strength and different bulk density.

Bite area was significantly greater on oats, and the difference tended to increase with leaf density (Figure 15), but not significantly. When average bite area was related to sward bulk density there was a clear tendency of bite area to decrease more steeply in the dallisgrass swards (Figure 16). The intercepts of the lines were almost equal, but the slope was 68% steeper on dallisgrass ($P < 0.01$). The absence of a difference in intercepts indicated that there were no species differences in bite area other than those explained by the difference in strength. Since dallisgrass was 2.15 times as strong per unit weight as oats, an equivalent increment in bulk density caused a greater

reduction in bite area on dallisgrass swards. This result suggested that animals responded to sward strength.

Bite depth on oat swards was consistently greater than on dallisgrass swards of equal leaf density. Compared at equal bulk density, average bite depth was *ca.* 1.0 cm greater on oat swards. The interaction between species and bulk density was not significant, indicating that bite depth did not respond to strength but to bulk density (Figure 17). Since the difference in bite depth did not vary significantly across bulk densities, it could be explained by other differences between species as well as by the difference in strength.

6.2.1.4. Effects of sward height, density and phenological stage

Tillers were composed of a few thin leaves at the bottom and by peduncle and inflorescence at the top. Tillers in the late stage had heavy panicles, which determined a significantly greater bulk density in the top horizon ($P < 0.05$, Figure 18). No significant differences in bulk density were detected in the horizon where most tillers were severed. Doubling the number of tillers per unit area resulted in *ca.* double bulk density, but the increase was more pronounced in the "late" swards because of greater weight per tiller.

The force necessary to break two tillers (Y , newtons) by applying tension by hand was significantly affected by phenological stage ($P = 0.03$) and changed over time, but was not affected by sward height or tiller density. Strength of tillers in the "late" stage did not vary significantly with time (X days, $Y = 54 - 0.44 X$, $r^2 = 0.02$), whereas strength of tillers in the "early" stage declined significantly with time ($Y = 45 - 1.96 X$, $r^2 = 0.32$, $P < 0.001$). After correction for the effects of time, "late" tillers were significantly stronger than "early" ones (26 vs. 17 N/tiller, $P = 0.03$).

When analyzed as a function of the nominal experimental treatments, bite area was affected significantly only by phenological stage. On average, steers obtained bite areas 23 cm² greater in the swards made of tillers in early flower than in those made of more mature tillers (115 vs. 92 cm², $P = 0.014$). Since both bulk density of the swards and tiller strength varied with phenological stage, it is likely that the effect of tiller maturity on bite area was not a direct one. When bite area was analyzed as a function of phenology, tiller strength and bulk density, no single variable explained the variation beyond the other two ($P = 0.05$, Figure 19). However, sward bulk density explained the most variation by itself and was significant at the 13% level.

Bite depth was 0.7 cm smaller in swards made of tillers in the late than in the early flower stage (7.5 vs. 6.8 cm, $P = 0.01$). Additionally, bite depth increased by 3.2 cm as sward height increased from 10 to 15 cm (5.5 vs. 8.7 cm, $P < 0.001$). No other factor affected bite depth significantly.

Incisor height was significantly greater in sward made of "late" tillers (4.0 vs. 3.1 cm, $P = 0.011$), which explains the effects on bite depth. The response of incisor height to phenology was probably mediated by the greater bulk density of the upper horizons of the mature tillers (Figure 18), and by the tendency of steers to increase incisor height in response to bulk density (Laca *et al.*, 1992b). The response of bite depth to sward height is in quantitative and qualitative agreement with previous findings (Ungar *et al.*, 1991; Laca *et al.*, 1992b).

As a result of the effects on bite area and depth, bite volume increased significantly with sward height (563 vs. 925 cm³, $P < 0.001$), and decreased with advancing tiller maturity (862 vs. 626 cm³, $P = 0.006$). In spite of the smaller bite volume, steers obtained significantly heavier bites in the swards made of more mature tillers (1.71 vs. 1.1 g, $P = 0.001$) because the reduction in volume was more than counterbalanced by a greater bulk density in the more mature swards. Bite weight increased significantly with increasing sward height (1.21 vs. 1.61, $P = 0.012$), and tiller density (1.10 vs. 1.72 g, $P = 0.001$). In agreement with previous experiments with sheep (Burlison *et al.*, 1991) and cattle (Laca *et al.*, 1992b), bite weight (Y , g) was closely related to sward height (X_1 , cm) and bulk density, (X_2 , kg m⁻³):

$$Y = -0.82(\pm 0.23) + 0.102(\pm 0.016) X_1 + 0.70(\pm 0.06) X_2 \quad R^2 = 0.90$$

6.2.2. Heterogeneous swards

6.2.2.1. Vertical heterogeneity

Herbage DM mass of vegetative swards increased from 1560 to 3430 kg ha⁻¹ as sward height doubled from 8 to 16 cm, and bulk density was relatively uniform canopy horizons (Fig. 20). Reproductive swards presented a top horizon of leaf blade of low density and a bottom horizon of tough, thick, stems and sheaths with an abrupt change in bulk density at the ligule position between leaf blade and sheath. Herbage masses of 8- and 16-cm-tall reproductive swards were 1510 and 3380 kg ha⁻¹.

Bite depth was influenced by sward height in vegetative swards (Tables 10 and 11). In reproductive swards there was a significant interaction of sward height X lamina length on bite depth. On vegetative swards, steers bit deeper into the canopy when sward surface height increased. On reproductive swards steers bit deeper into canopies only when the height of swards with 8 cm of leaf was increased.

Bite area was influenced by sward height in vegetative swards and by lamina length in reproductive swards (Table 11). On vegetative swards, bite area increased when sward surface height increased. Variation in sward structure did not influence the probability of using the tongue to gather a bite or the number of tongue sweeps per prehending bite (Table 12).

As with bite area, bite DM weight was influenced by sward height in vegetative swards and by lamina length in reproductive swards (Tables 10 and 12). Bite DM weights in reproductive swards reflected bulk density characteristics of the top leaf stratum.

6.2.2.2. Horizontal heterogeneity

Experiment 1. Bite weight was greater ($P = 0.10$) on swards with heterogeneity in height than for other treatments, but was not influenced by patch size (Fig. 21). Bite area (Fig. 22) did not vary among treatments, but bite depth (Fig. 23) differences were large for patches of different height although not for patches of different density or scale of heterogeneity. The contribution of bite depth to differences in bite weight resulted from relatively constant incisor height (Fig. 24) across treatments, which was inconsistent with predictions based on homogeneous swards. Comparison of the control with predicted values indicated that animals were biting ~1 cm deeper than expected; correction of bite depth and incisor height for this difference revealed that incisor height was greater than expected on short patches and less than expected on tall patches. Consequently, bite depth responded to height at the site of the bite more steeply than expected. Although determined for a rather limited number of bites, IIR differences (Fig. 25) were explained by those in bite weight, confirming the particular importance of bite weight to rate of intake.

Animals exhibited selectivity for the patches with taller vegetation, particularly when patches were large, but not for denser patches (Fig. 26). In swards with heterogeneity in height, taller patches were encountered first as

the animal lowered its head towards the HCS. This effect was more pronounced in swards with small patches. Thus, selectivity may not have been caused by active choice by the animals. We suggest that choice of tall patches was a more active process when patches were larger.

Experiment 2. Proportion of HCS area grazed ranged from 0.30 to 0.41. Hunger satiation level had no influence on any variable measured, and did not interact with patch size (Figs. 27 through 31). Bite depth of leaf or stem (Fig. 28), bite rate, and instantaneous intake rate (Fig. 30) were not affected by experimental treatments.

Bite area on leaf patches was greater on large than on small patches, while the opposite was true on stem patches (Fig. 27). Bite weight on stem patches was larger on small (1.38 g) than on large (0.57 g) patches, since bite depth was not affected by patch size (10.2 and 9.9 cm for large and small patches, respectively) (Fig. 28). Bite weights of 0.76 and 0.59 g on large and small patches, respectively, were not different.

Area grazed on leaf patches as a proportion of total grazed area served as a selection index and was higher for large (0.83) than for small (0.71) patches (Fig. 31). Greater selection for leaf on large patches combined with greater bite area for leaf on large patches resulted in a larger total area grazed.

6.3. Within-patch intake rate and patch depletion

6.3.1. Behavioral mechanisms that determine bite rate and intake rate

Alfalfa HCS ranged in area from 0.26 to 0.44 m² (mean = 0.35). Animals removed between 33 and 94 bites (mean = 53) during grazing sessions that lasted 60 to 212 seconds. Dallisgrass HCS ranged in area from 0.26 to 0.50 m² (mean = 0.37). Animals removed between 19 and 89 bites (mean = 48). A typical grazing session consisted of an initial biting period without any chewing, a period of biting chewing and swallowing, and a final period of exclusive chewing and swallowing which took place after the animal was moved away from the HCS. Number of bites per bolus averaged 6.8 and ranged between 3.3 and 11.0, exhibiting a significant linear decline with increasing bite weight ($r^2 = 0.466$, $Y = 9.0 - 1.19 \cdot \text{BWT}$, $P < 0.001$).

Relative degree of depletion of alfalfa HCS was calculated as the ratio of total number of bites removed to maximum number of bites possible if all bites were to be placed on a previously ungrazed area. Since animals could graze each tiller more than once this ratio reached values greater than 1.0. A measure of the relative reduction in bite weight due to HCS depletion was obtained by dividing bite weight obtained in the grazing session by bite weight previously measured on the same swards when animals only removed 6 bites. As swards were depleted bite weight was reduced significantly in relative terms (Figure 32). Taller swards were significantly more depleted in relative terms ($P = 0.03$). This should tend to reduce the effects of sward structure on bite weight and IIR. However, the effects of depletion in absolute terms were negligible compared to the effects of sward structure. Therefore, depletion did not confound the effects of sward structure and was ignored in the foregoing analyses.

The effects of alfalfa height and density on bite weight during the second grazing sessions (Table 13) were consistent with what was observed in the first grazing sessions, but average bite weight was 0.25 g (12%) lower due to the greater number of bites removed. Eighty two percent of the variation in bite weight was explained by independent effects of height ($P = 0.0000$) and number of holes filled with herbage m^{-2} ($P = 0.0004$), and animal differences ($P = 0.02$).

Instantaneous intake rate increased almost linearly when BWT was below 1.50-2.00 g both in alfalfa and dallisgrass swards (Figure 33). The relationship between IIR and BWT did not differ significantly between species ($P > 0.10$). Alfalfa sward structure did not affect IIR beyond the effects explained by BWT (Table 13). Animals differed significantly in IIR. Animals that exhibited fewer chewing and manipulative jaw movements per bite achieved greater IIR (see below). After correction for the effects of bite weight, there was an inverse relationship between IIR and chews per unit intake across animals (Table 14). Animal #3, who tended to use few manipulative jaw movements per bite and few chews per unit DM intake, also tended to obtain greater IIR than expected on the basis of BWT.

There was an almost perfect linear relationship between time per bite and total number of jaw movements per bite (Figure 34) which did not differ between experiments ($P > 0.34$). The intercept was significantly greater than 0, indicating that there was a time cost per bite not related to the number of jaw

movements allocated per bite. On average animals spent 0.43 (± 0.062) seconds locating and severing each bite, and 0.68 (± 0.022) seconds per each jaw movement allocated to each bite. The slope of the line is in quantitative agreement with direct measurements of the total time involved in opening and closing the jaws.

Time per bite increased quadratically with bite weight and the relationship did not differ between experiments (Figure 35). After correction for the effects of bite weight on time per bite in the experiment with alfalfa, sward height and density had no further effect on time per bite (Table 15). Power of the tests for height and density effects was 0.11 and 0.20, respectively ($\alpha = 0.05$). Detection of a significant difference in time per bite between the observed extremes in swards of 15 and 25 cm would have required 188 experimental units or an observed difference greater than 0.32 seconds per bite. Likewise, detection of a significant difference in time per bite between swards with 388 and 1550 holes m^{-2} would have required 75 experimental units or an observed difference of 0.32 seconds per bite.

Sixty percent of the residual variation in time per bite was due to animal differences. Animal #1 exhibited the slowest biting rate, requiring an average of 0.83 seconds per bite more than animal #3, which exhibited the least time per bite (Table 14). Animal differences in time per bite were consistent with differences in the number of jaw movements per bite (see below).

Both in alfalfa and dallisgrass swards, the number of exclusively manipulative jaw movements per bite decreased with increasing bite weight and tended to level off at a minimum for bites heavier than *ca.* 1.50 g. Conversely, the number of jaw movements that simultaneously performed manipulation and mastication increased with bite weight and tended to reach a maximum (Figure 36). Consequently, total number of manipulative jaw movements per bite (TMJWS/B) was not related to bite weight, averaging 1.87 for alfalfa and 1.54 for dallisgrass swards (Figure 37). Eighty seven percent of the variance of TMJWS/B was explained by treatment effects. Total number of manipulative jaw movements decreased with increasing sward height ($P = 0.005$), reflecting the greater difficulty animals have toprehend short tillers and how they responded in a compensatory fashion (Table 15). Animal #3 allocated significantly fewer manipulative jaw movements per bite than animals #1 and #8 ($P < 0.000$).

Number of exclusively chewing jaw movements (ECHWS/B) and total jaw movements per bite (NJWS/B) increased quadratically with bite weight (Figure 38). No species effect was detected by analysis of pooled data from alfalfa and dallisgrass swards ($P > 0.20$), nor was any relationship between NJWS/B ($P = 0.50$) or ECHWS/B ($P = 0.44$) and bite weight detected in dallisgrass swards. Because bite weight in dallisgrass ranged below 2.20 g these results are consistent with the fact that in alfalfa swards there was no change in these variables for bite weights below 2.00 g. After correction for bite weight effects, NJWS/B and ECHWS/B in alfalfa swards did not exhibit effects of sward height or density ($P > 0.35$, Table 15. Consistent with results for time per bite, animal #1 performed more jaw movements and more exclusive chews per bite than animals #3 and #8 (Table 14).

Total chews per bite increased linearly with bite weight, with a significant intercept (Figure 39). Therefore, chews per unit DM intake decreased steeply with increasing bite weights and then asymptotically approached a value of *ca.* 1 chew/g DM (Figure 40). No effects of sward structure were detected on amount of chewing per unit mass of intake ($P > 0.37$) beyond the effects via bite weight. Animal #1 also chewed significantly more per unit DM intake than the other animals.

Bouts of exclusive chewing. Overall, *ca.* 90% of the bouts consisted of 2 or fewer exclusive-chewing jaw movements (ECHWS). Fifty five percent of the ECHWS was in bouts of 2 or fewer movements. Most of the chewing was performed while manipulating new bites or in numerous bouts of very few ECHWs interspersed with manipulative movements and searching within the feeding site (Figure 41). Animals lifted their heads and stopped searching for or manipulating bites only to perform chewing bouts of more than 4 chews (Table 16).

Duration of bouts of exclusive chewing was directly related to bite weight. All of the ECHWS for bite weights below 1.50 g were performed in bouts of less than 2 chews (Figure 42). The proportion of ECHWS in bouts longer than 2 chews increased abruptly for heavier bites.

6.3.2. Patch depletion by grazers

6.3.2.1. HCS Experiment

Bite weight, the quotient of intake and number of bites, was significantly affected by sward structure and number of bites removed from the swards (Table 17). On average, the tall swards yielded bites 0.34 g (46%) heavier than the short ones ($P = 0.000$). Although the interaction between sward structure and number of bites was not significant ($P = 0.27$), there was a clear tendency of average bite weight to decrease more steeply in the tall and sparse sward. Average weight of the first 10 bites was 0.49 g (62%) greater in tall swards, whereas the difference in average weight of the first 60 bites was only 0.13 g (19%). This tendency was clearer in the estimated bite weight of incremental sets of bites (Figure 43). Bite weight in the first 3 sets of bites was greater in the tall swards ($P < 0.05$). When more than 30 bites were removed, bites were smaller in the taller swards, although not significantly.

Time per bite was not affected by animal ($P = 0.20$), sward structure ($P = 0.37$), total number of bites ($P = 0.81$), or the interaction between sward structure and number of bites ($P = 0.78$) (Table 17). An estimate of time per bite was obtained by a regression through the origin of total time at the patch on total number of bites removed. Terms for sward structure and heterogeneity of slopes due to sward structure were initially included in the model and then dropped because they were not significant ($P > 0.25$). On average, animals allocated 1.37 s per bite ($R^2 = 0.91$, $MSE = 53.4$, $n = 27$, 95% CI = [1.29, 1.45]). Time per bite was not related to bite weight between or within sward structures ($P > 0.10$).

The two sward structures exhibited different relationships between intake and patch residence time (intake curves, Figure 44). Intake rate within the patch, the slope of the intake curve, was initially greater for taller swards, but declined markedly after 40 s. The significantly greater slope of the intake curves for the tall swards is represented by the value of k_1 in the rectangular hyperbola (Table 18). In the short dense swards, within-patch intake rate declined more smoothly over the range of residence times observed. Cattle obtained greater intake in the tall swards at all residence times, but the

advantage over short swards was greatest for a residence time of *ca.* 40 seconds.

The rectangular hyperbola explained a greater proportion of the variance in intake in the short swards (Figure 44 and Table 18). Values of k_2 significantly greater than 0 in both sward types indicated that the slope of the intake curves declined significantly ($P < 0.05$) with increasing residence time. Thus, both swards exhibited depression.

Apparent bite area, calculated as total area grazed at least once divided by total number of bites, was greater and declined more steeply with number of bites in the taller swards ($P = 0.04$, Figure 45). The decline in apparent bite area was a result of the reduction of actual bite area and the increment of number of bites placed in previously grazed areas (Table 17), which did not contribute to total area grazed. Actual bite area in the first horizon was greater in the tall swards, and declined quadratically with number of bites (Figure 45) reaching a minimum at 45 bites. The interaction between sward structure and number of bites was not significant ($P = 0.79$). However, in the first set of 10 bites actual bite area was 49 cm² (44%) larger in the taller swards, whereas the difference was 35 cm² (40%) when more than 40 bites were taken. The relationship between actual bite area and number of bites taken from the top horizon (Table 19) revealed that bite area in the top horizon was significantly greater ($P = 0.000$) and declined more steeply with number of bites ($P = 0.035$) in the tall sparse swards.

Bite depth in the short swards averaged 6.0 cm and did not vary with number of bites. In the tall swards, bite depth increased from 11.8 to 14.6 cm ($P = 0.00$) as number of bites removed increased from 10 to 60. This difference between swards ($P = 0.08$) was caused by the greater number of bites in the second horizon of the tall swards.

Hand-constructed swards were grazed "by horizon" in a systematic fashion. The proportion of bites taken from the second horizon was significantly lower than expected from random grazing and independent of the total area remaining ungrazed ($P > 0.13$) until more than 95% of the patch area had been grazed at least once (Figure 46). Steers placed a significantly greater ($P = 0.02$) proportion of the bites in previously grazed areas in the short than in the tall swards, perhaps as a result of the greater contrast between grazed and ungrazed areas in the taller swards. On average, 6.5 ± 1.35 % of the bites in short swards and 3.6 ± 1.35 % of those in tall swards were placed in

previously grazed areas when the proportion of the top horizon grazed was below 0.95.

6.3.2.2. Field Experiment

Herbage mass per unit area was 340, 460, 640 g m⁻² in the 7-, 12.5-, and 18-cm patches, respectively. Herbage mass was linearly related to patch height: $Y = 135(\pm 43) + 28(\pm 3) * X$, $R^2 = 0.67$, $MSE = 8061$, $n = 39$. The significant intercept ($P = 0.004$) reflected the increase in bulk density with depth into the canopy, typical of grass swards.

Bite weight increased linearly with patch height ($P = 0.03$) and decreased significantly with number of bites removed ($P = 0.00$) (Figure 47). There was no significant interaction between sward height and number of bites. Yet, bite weight in the 7- and 12.5-cm patches did not decline in the first 2 and 3 sets of bites, respectively, whereas in the 18-cm patches there was a linear decline.

Time per bite was affected significantly by the number of bites removed from the patch ($P < 0.07$). On average, each bite within the first set required 1.60 seconds, while the rest of the bites required an average of 1.90 seconds. When cattle started grazing they had empty mouths, and the patches offered bites within the immediate reach of their heads. As a consequence, animals were able to quickly gather and harvest bites. After a certain amount of forage was in the mouth, chewing started and interfered with biting, with the consequent increase in time per bite. The lower time per bite for the first few bites can be considered an artifact of the techniques used to derive the gain curves, since in most grazing situations grazers reach acceptable patches before swallowing all herbage previously gathered.

In six out of the nine combinations of animals and sward heights, the intake curves exhibited depression (Table 20). As indicated by the significant ($P < 0.05$) values of k_2 , instantaneous intake rate within the patch declined as patches were depleted by grazing. Depression of intake rate resulted from the reduction in bite weight which was not compensated by increments in rate of biting. Intake curves also differed significantly between animals due to the differences in time per bite and bite weight among animals.

When data were pooled across animals, the tallest and shortest patches exhibited significant depression but the 12.5-cm patch did not (Figure 48). Initial intake rate (k_1) was similar in 7-cm and 12.5-cm patches, but greater in

18-cm patches. The ratio $k_1 k_2^{-1}$ is the value of the asymptote for the curves, and represents the theoretical amount of forage available to cattle at the patch (Table 21). Except for the 7-cm patches, the asymptotic value greatly overestimated the total herbage mass in the patches.

The rectangular hyperbola was appropriate to describe the curves once intake was expressed as a proportion of the initial herbage mass in the patch (Figure 49). There were no significant differences between patch heights, but curves differed significantly between animals ($P < 0.001$). Animal #1 attained an initial IIR of $0.35 \times \text{patch herbage mass min}^{-1}$, and consumed 48% of the herbage in the patch after two minutes. On the other extreme, animal #8 obtained an initial IIR of $0.56 \times \text{patch herbage mass min}^{-1}$, and consumed 59% of the patch herbage after two minutes of grazing.

6.4. Models of intake rate

Models indicated that sward heterogeneity is potentially a very important factor determining intake rate in the field (see reprints attached). When swards are heterogeneous in structure and animals graze selectively, it is not sufficient to know the relationships that link sward structure in the FS and bite weight. In order to estimate intake rate one also needs to measure or predict selectivity by the animals.

6.4.1. Graphical analysis of sward depletion by grazing

When a maximum of three grazing horizons is considered, Equation (2) conveniently permits the total space of p_1 , p_2 and p_3 , after onset of grazing, to be represented on the unit-sum triangle. Each side is the zero isogram for one of the bite proportions. The bite proportion increases with the perpendicular distance from a side to a value of unity at the opposite apex. In the figures presented here, the horizon number is indicated at the apex at which the bite proportion for that horizon is equal to unity. (A more detailed explanation of the unit-sum triangle is given in Figure 69) Figure 50 shows how the eight constraints behave in this space. Constraints C1, C2, C4 and C7 are 'stationary' constraints in that their location is dependent upon the constants a_1 , a_2 , a_3 only. Constraints C3, C5, C6 and C8 are 'dynamic' constraints in that their location changes with each bite taken.

Together, the constraint lines form a space that defines combinations of p_1, p_2, p_3 that are feasible for a given degree of depletion. Figure 51 shows how the feasible space changes and diminishes to a single point as $N/N_{\max}$ increases from a low value to unity. This point is reached when all horizons are completely grazed and there is only one possible set of bite proportions defined by the specific bite areas of each horizon. The triangular coordinate of this point is the intersection of any two of the four stationary constraints and is $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ when all a_i are equal.

The change in bite proportions with each additional bite is defined for a total of N bites as follows. If the horizon grazed by bite $N+1$ is indicated as j and the non-grazed horizons as k , then the change in p_j is

$$\frac{n_{j+1}}{N+1} - \frac{n_j}{N} = \frac{N - n_j}{N(N+1)} \quad (13)$$

and the change in p_k for the two horizons not grazed by bite $N+1$ is

$$\frac{n_k}{N+1} - \frac{n_k}{N} = \frac{-n_k}{N(N+1)} \quad (14)$$

These two expressions can equal zero only when $N = n_j$, i.e., all N bites have been taken from the same horizon as bite $N+1$. According to assumption A6, this means that the animal has grazed H1 only, represented by the lower left-hand corner of the unit-sum triangle. It follows from eqns (13) and (14) that a specific point in the feasible space for $N/N_{\max}$ connects to a maximum of three points in the feasible space for $(N+1)/N_{\max}$, assuming bite $N+1$ can still be taken from any one of the three horizons. Thus, in the process of depletion, the grazing animal charts a particular course through the feasible space. This course may exclude future proportions of bite types that can be reached only via other depletion trajectories. Grazing style can be viewed as the depletion trajectory chosen by the animal through the feasible space of possible bite proportions.

The relation between intake and the proportion of bite types is readily derived.

$$I = n_1 w_1 + n_2 w_2 + n_3 w_3 \quad (15)$$

$$I = N (p_1 w_1 + p_2 w_2 + p_3 w_3) \quad (16)$$

$$\frac{I}{N} = \overline{w} = p_1 w_1 + p_2 w_2 + p_3 w_3 \quad (17)$$

Combinations of p_1, p_2, p_3 that yield the same $\overline{w}$ define an intake isocline. When all w_i are equal, the entire feasible space represents the same intake level. When the w_i are unequal, the extrema of the intake isocline on the unit-sum triangle can be derived simply. Various rankings of the w_i can be envisaged (Figure 52). When $w_1 = w_2$, the intake isocline is parallel to the side opposite the p_3 apex, meaning that intake is insensitive to the allocation of bites between p_1 and p_2 . When $w_2 = w_3$, the intake isocline is parallel to the side opposite the p_1 apex, meaning that intake is insensitive to the allocation of bites between p_2 and p_3 . When $w_1 > w_2 > w_3$ or $w_1 < w_2 < w_3$, the intake isoclines show an intermediate slope. A major determinant of the bite weights associated with each grazing horizon in real swards is the vertical profile of bulk density. Although such detailed information is limited, it may be assumed that the wide range of sward structures encountered in natural and sown pastures includes quite different rankings of the w_i (Laca *et al.* 1992a).

Superimposition of the intake isoclines defined by a given sward structure on the diagram of the feasible space of bite proportions shows the possible levels of mean bite weight (and hence intake) for any degree of depletion (Figure 53). Maximum intake for any $N/N_{\max}$ occurs at the corner of the feasible space that lies on the highest intake isocline. If $w_1 > w_2 > w_3$, intake is maximized by removing each horizon in turn. If the a_i are equal, the corresponding depletion trajectory is to remain at (1,0,0) until the top horizon is depleted, gradually move horizontally to $(\frac{1}{2}, \frac{1}{2}, 0)$ with depletion of the second horizon, and gradually move vertically to $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ with depletion of the third horizon. If $w_1 < w_2 < w_3$, intake is maximal for any $N/N_{\max}$ by profile grazing, and implies remaining at $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ throughout, again assuming all a_i are equal. Note that if the animal adopts a grazing style closer to horizon grazing in this situation, mean bite weight can increase with depletion. Where a_i varies between horizons, the depletion trajectory will cross other areas of the feasible space.

6.5. Patch selection and intake rate in the field

6.5.1. Effects of patch height and density, and animal experience on selection and intake rate

Bite Weight and Instantaneous Intake Rate. The relationship between patch structure and bite weight for the first set of 15 (original-density) or 10 (half-original-density) bites (non-depleted condition) is in agreement with predicted values derived from artificial swards (Table 22). Bite weight was greatest in TOD and SOD patches and smallest in SHOD patches. As animals grazed the patches, bite weight declined almost linearly in all patch types (Figure 54). As a result, the relationship between intake and number of bites removed from a patch was represented by almost continuously decelerating curves (Figure 55). Although bite weight in TOD and SOD patches was similar, in GI1 of T1 IIR was higher for the former (Table 23) because of higher bite rate (bites min^{-1}) in TOD than in SOD patches (Table 24). Similarly, even though bite weight was higher in SOD than in THOD patches, in GI1 and GI2 of T3 IIR was similar in both types of patches because of higher bite rate in THOD than in SOD patches.

Selectivity. None of the variables analyzed were affected significantly by experience level or repeated exposures. Hence, all values presented are means of 3 exposures.

In general, search and movement were not directed to any patch type. Patches were encountered and entered (at least 1 bite taken) in the same proportion that they were available during all grazing intervals in all treatments, except in GI2 of T2 (Figure 56). Although in GI1 an average of 80% of available patches were visited, 87%-96% of them were previously ungrazed patches (Table 24). Grazing Interval 1 represented a non-depleted condition, whereas GI2 and GI3 represented increasingly depleted conditions. Thus, while animals did not direct their search such that a particular patch type was encountered more frequently than the other, they avoided encountering previously grazed areas in GI1. In GI1, averages times between the last bite in a patch and the first in the following one were 2.33 sec (SE = 0.11) in T1, 2.62 sec (SE = 0.12) in T2, and 2.19 sec (SE = 0.09) in T3. The results above supported the assumptions (taken in the prediction of

maximization) that encounter of patches was random and that steers experienced a non-depleting environment in GI1.

Contrary to the lack of selectivity on visits, steers did show selectivity in residence time per patch type in GI1 of T1, GI1 and GI3 of T2, and GI3 of T3 (Figure 57). In these treatments grazing-interval combinations, steers grazed longer on the patch type that yielded greater IIR. Animal responses were affected by treatment in GI1 and GI3. Steers also showed selectivity in the number of bites per patch type in GI1 of T1, GI1 of T2, and GI3 of T3 (Figure 58). They removed more bites from the patch type that yielded greater IIR. These responses were affected by treatment in GI1 only. As a result of the selective behavior steers removed more herbage mass from TOD patches in GI1 of T1 and from SOD patches in GI1-3 of T2 and GI3 of T3 (Figure 59).

The context in which a particular patch type was included affected steers responses, as clearly evident in the case of SOD patches, which were included in all treatments. Residence time and number of bites per SOD patches were relatively high when the potential IIR of the alternative patch type was lower (e.g.; 30 sec and 27 bites per SOD patch in GI1 of T2), intermediate when it was similar (e.g.; 22 sec and 21 bites per SOD patch in GI1 of T3), and relatively low when it was higher (e.g.; 17 sec and 16 bites per SOD patch in GI1 of T1).

Overmatching was the predominant pattern of selective behavior (Table 25); i.e., there was a disproportionately large increase in number of bites in response to differences in potential IIR between patch types. This pattern resulted in total intake values in GI1 of all treatments that were consistent with maximization, although observed and predicted values of residence time and number of bites per patch type differed (Table 26).

6.5.2. Field test of the marginal value theorem with cattle.

Model predictions. Intake curves, the relationship between patch residence time (T_r) and intake, patch were well described by the rectangular hyperbola (lack of fit $P > 0.10$, $R^2 = 0.87, 0.69, 0.80, 0.79$ and 0.89 for 5, 7.5, 10, 12.5, and 15-cm patches). Consistent with the fact that bite weight increases with height and decreases with T_r (Laca 1992), intake rate within the patch increased with height and decreased with increasing T_r .

If steers graze in a manner consistent with maximization of IIR, residence time in all patches should increase and IIR should decrease as distance between patches increases. As the difference in height between patches increases, IIR should increase and T_r should increase in the tall patches and decrease in the short ones.

Patch selection and utilization. In agreement with model predictions, T_r increased linearly ($P < 0.001$) with distance between patches. As difference in height between patches increased, T_r decreased in the short patch and increased in the tall one (Figure 60). No significant interaction was detected. Observed mean values of T_r (Y, s) were closely predicted by the model (X, s), although steers tended to graze for longer than predicted when predicted T_r was short [$Y = 7.65(\pm 3.61) + 0.90(\pm 0.09) X$, $R^2 = 0.89$]. In all cases except for one, predicted T_r was within the 95% CI for observed mean T_r . In 47% of the cases, predicted and observed means differed in less than one S.E.

As predicted, IIR declined linearly with increasing distance between patches ($P < 0.03$), and increased linearly with increasing difference in patch heights ($P = 0.067$, Figure 61). The interaction between patch distance and height difference was not significant ($P = 0.65$). Observed mean values of IIR (Y, g/min) were linearly related to predicted values (X, g/min) but animals achieved significantly lower IIR than predicted, particularly in the treatments with 5 and 15-cm patches [$Y = 39.3(\pm 7.0) + 0.36(\pm 0.08) X$, $R^2 = 0.73$]. Except for the treatments with 5 and 15-cm patches, predicted IIR was within the 95% CI for observed means.

6.6. Prediction of bite weight and intake rate in the field

Sward height, bulk density and chews per bite explained 72% of the total variation of bite weight in all experiments. Only the simple linear effects and the interaction of height and bulk density were significant terms in the model (Table 27).

The 95% confidence intervals for predicted bite weights are presented in Figure 62. Mean bite weight was be predicted within *ca.* $\pm 13\%$ with 95% confidence on the basis of one set of measurements. Prediction accuracy in the field can be increased by performing repeated independent measurements

on individual animals or on multiple animals and following a "double-sampling" scheme.

Animal effects were not considered in the model because for practical prediction purposes, these effects constitute variance. However, in an exploratory analysis we found that bite weight differed significantly among animals ($P = 0.002$) although the animal term accounted for only 1.7% of the total variation.

7. DISCUSSION

7.1. Hand-constructed sward methodology

The integrated methodology for studying short-term grazing behavior of cattle described in this paper has both advantages and limitations in comparison with similar studies at the field level.

Hand-constructed swards provide a degree of control over sward characteristics and a level of detail in measurements that can not be achieved by field techniques. The appearance of the herbage at the time of grazing was no different from that in the field. The willingness with which previously fed animals grazed the HCS gave no indication that the interval from cutting or our handling of the herbage modified grazing behavior. The design employing a base board and modules was well-suited for team assembly and the materials withstood intensive use over one year with the need to replace only a few modules.

The force plate provides a direct technique of measuring the force exerted in severing bites. Such information can be used to test the relation between the mechanical properties of herbage and grazing behavior. Previous studies on the effects of vegetation tensile strength on grazing behavior of ruminants used indirect indices of force per bite (Chambers *et al.*, 1981). A force platform was used by Bignall (1984) to study the grazing behavior of Barnacle geese.

The video recording of grazing sessions proved an important tool in elucidating the mechanism of bite formation and in characterizing types of jaw movements. Sound recording represents a simple and unobtrusive way of obtaining accurate counts of bites and chews, as well as a means of describing the pattern of such behaviors through time (Alkon *et al.*, 1989). The results show that the standard technique used to count chewing jaw movements in

grazing animals (Chacon *et al.*, 1976) is not adequate to measure the number of grinding jaw movements. Manipulative jaw movements and chewing overlap to a variable extent which depends on sward height and, likely, other factors of the vegetation (Table 6). The results suggest that as sward becomes taller, more jaw movements are associated with chewing. This compensatory effect tends to mask treatments effects on chewing measured by the standard method.

What is the applicability of results obtained by this integrated methodology to the field level? Some primary differences between HCS grazing and field grazing may be of concern.

1) Animals are yarded and receive conserved feeds. This may reduce grazing skills relative to animals continuously at pasture (Flores *et al.*, 1989). The physiological state determined by the stall-feeding regime and the contrast between feedstuff and HCS of fresh herbage may result in different motivational states to those of free-grazing animals. These problems are not inherent to the technique. Cut herbage of the same material used to construct the HCS can be fed in the stall, the degree of satiety when HCS are grazed can be manipulated as an experimental factor, and steers can be kept at pasture between HCS grazing sessions.

2) The short duration of grazing sessions may introduce sources of bias. Biting rate tends to be overestimated when measured over periods shorter than 2 minutes, particularly on swards that enable large bite weights (Forbes, 1988). Behaviors measured on HCS are representative of the beginning of feeding bouts. It has been demonstrated that intake rate declines as the grazing bout progresses (Dougherty *et al.*, 1989a). This effect was addressed in our experiments (see 5.2.1.2., 6.2.1.2, 7.2.1.2.). In general this effect of previous grazing time was minimal.

3) The degree of depletion of the HCS may be an important factor in determining certain aspects of grazing behavior measured in our methodology. To the extent that depletion is important on the HCS, so too is it important in the field, where depletion may vary considerably between grazing systems and animal densities. Thus the HCS experiments do not aim to simulate a particular field situation but rather aim to characterize grazing behavior for a certain degree of depletion, which can be simply controlled.

4) Walking during grazing bouts may reduce IIR in the field if less time is spent on post-bite processing of herbage in the mouth than on walking. Our

estimates of IIR from HCS will then represent maximum rates for any degree of depletion.

5) The proximity of other grazing animals may affect grazing behavior.

In our view, the above differences are least important at the lowest levels of aggregation. Thus we would assume that features of grazing behavior such as the time taken to complete one sweep of the tongue would be comparable in the field if the same sward structure in the vicinity of the mouth was being grazed. To the extent that bite dimensions result from the physical interaction of relatively fixed motor patterns with the structure of the vegetation, measured bite dimensions should be directly relevant to the field. The quantitative applicability of measurements of IIR is contingent upon the importance of the considerations listed above. The methodology permits some of these to be explicitly taken into account in experimental design. We would nevertheless expect qualitative inferences from our methodology regarding the relation between grazing behavior and sward characteristics to have more general relevance, particularly in relatively homogeneous swards.

7.2. Factors and mechanisms that determine bite weight

7.2.1. Homogeneous swards

7.2.1.1. Effects of HCS height and density

Besides providing an empirical assessment of the effects of sward height and density on bite dimensions, these experiments suggested the causal mechanisms by which animal behavior and sward structure interact to determine bite weight. Dallisgrass swards were made of pure lamina, and were very homogeneous in a vertical and horizontal plane. Therefore, it is unlikely that vertical or horizontal selectivity affected the results. Alfalfa swards had a gradient of increasing percentage of stem with depth into the canopy, however they were horizontally homogeneous. Vertical selectivity against stem may have been a factor determining bite depth on these swards. However, percentage of stem at the point where the forage was severed (Figures 8 and 11) increased significantly with treatment height, and animals eagerly consumed almost all forage on the experimental swards after determination of bite dimensions. These results indicated that alfalfa stem in our experiments was not a barrier to grazing, nor rejected by the animals.

Accordingly, we consider that vertical selectivity in alfalfa swards was of minor importance, compared to sward height and bulk density. Species differences did not affect bite dimensions after the basic characteristics of the swards were taken into account. Consequently, bite dimensions measured in both experiments reflect the characteristics of height and bulk density of the swards, representing the "potential" dimensions, unaffected by the presence of barriers or undesirable plant parts within the vertical profile of the sward.

The following conceptual model describes the factors controlling bite dimensions in such a sward. Effective bite area of a grazing animal is a result of the interaction of the height of the sward (in these experiments height = length of plant part) and stiffness of plant units with the harvesting behavior of the animal. Number and amplitude of tongue sweeping motions per bite seem particularly relevant in determining bite area. Observation of slow-motion playback of the video records indicated that number of tongue sweeps was negatively affected by sward density while amplitude was positively related to sward height. Animals appeared to respond to sward density (or strength) by adjusting the number and amplitude of tongue movements to gather, as effectively as possible, the largest feasible bite cross-section. The greater the sward density the less tongue movements are required, the smaller the reach and bite area. The effectiveness of the "attempted" bite area is determined by the stiffness and length of plant units. Tillers whose distance from the rooting point to the incisor edge (*ca.* center of bite) is greater than tiller length escape the bite area. Some tillers that meet this criterion spring back to place before being clamped between incisors and dental pad, and this was observed to be more frequent the stiffer the material. On tall swards of low density, animals attempted to obtain a bite area as large as possible, and bite area was limited by the maximum extension of tongue sweeps. This explains why bite area tended to reach a plateau as height increased in dallisgrass swards. Although sheep do not use the tongue as a prehension organ as do cattle, they perform gathering motions with lips and head, with similar results. This mechanism explains the overriding importance of sward height in determining bite volume and weight reported in these experiments and others (Penning 1986, Burlison 1987).

Effects detected in these experiments do not support assumptions made in earlier models of grazing behavior. With the exception of the relationship between sward height and bite area used by Arnold *et al.*, (1982), modelers

have assumed that bite area is independent of sward characteristics. Bite depth has been assumed to be a "ramp" function of sward height (Arnold *et al.*, 1982, Demment *et al.*, 1987). Our results indicate that bite area and depth by cattle are significantly and predictably affected by sward height and bulk density.

Bite depth, calculated as above, differs from depth at which animals position the incisor edge. The residual tillers remaining after a bite do not have a equal height because a shorter length is bitten from tillers rooted at greater distances from the point of severance. Bite depth is an indicator of the average length of tillers removed and thus, it is a more appropriate measure from which to calculate bite volume. Incisor height indicates the height of the point of severance and thus, it is a better measure to describe the strategy of the animal.

The ramp function used to predict bite depth is based on the assumption that there is a critical sward height below which no forage can be harvested. As height increases over the critical value, bite depth equals the difference between total height and critical height. Eventually a maximum bite depth, imposed by the animal's mouth dimensions, is reached, and bite depth remains constant for taller swards (Arnold *et al.*, 1982; Demment *et al.*, 1987, Ungar and Noy-Meir 1988). This model implies that the linear phase of bite depth has a slope of 1.0, since every increment in sward height causes an equal increment in bite depth. However, pooled data of both experiments indicate that at low sward bulk density (200 g m^{-3}), the slope of bite depth as a function of sward height is 0.52, and decreases with increasing bulk density (Figure 10). No plateau was observed in bite depth as sward height increased up to 300 mm, the maximum height used in this experiment. There may of course be a plateau beyond this range. The ramp function also predicts that incisor height remains constant in the range in which bite depth increases linearly with sward height. However, incisor height increased significantly with increasing sward height over the whole range of heights studied in these experiments (Figure 11).

These results indicate that steers appeared to remove a certain proportion of the height available, therefore increasing both incisor height and bite depth as sward height increased. Similar results were obtained by Milne *et al.*, (1982), Barthram and Grant (1984), Burlison (1987), and Wade *et al.*, (1989) under field conditions. Milne *et al.*, (1982) reported that bite depth of

sheep grazing ryegrass-white clover swards was linearly related to sward height, with an intercept of -0.8 cm and a slope of 0.33 ± 0.056 . Wade *et al.*, (1989) found that as dairy cows grazed down ryegrass paddocks, depth of grazing declined exponentially and was a constant proportion ($34\% \pm 3\%$) of ungrazed tiller height. In these two studies cited, bulk density was not controlled and increased as sward height decreased, which partly explains why the slopes were less than those in our study. Bite depth predicted on the basis of Figure 10 (X, mm) and the results (Y, mm) obtained by Wade *et al.*, (1989) exhibited a remarkable qualitative agreement indicating that the processes determining bite depth in both studies were the same, but our steers tended to bite 20 to 40 mm deeper ($Y = 6.1 + 0.68 X$, $R^2 = 0.998$). In agreement with our results, Black and Kenney (1984) detected a significant negative effect of sward density on bite depth of sheep grazing artificial ryegrass swards. However, the increase of bite depth with decreasing density reported by these authors is greater than in our study, particularly at low bulk density.

Given that sheep and cattle seem to bite only a fairly constant proportion of the height available, the question is, why do they choose to do so? It can be assumed that satiation was not moderating grazing behavior, since HCS were offered more than 7 hours after the daily meal and animals eagerly grazed the forage. The top horizon of natural swards usually has the greatest proportion of green leaf, and a high concentration of nutrients. Leaf requires less chewing than stem, and exhibits faster rates of ingestion, digestion and passage (McLeod *et al.*, 1990). Moreover, by reducing bite depth steers limit the size of particles drawn into the mouth. Consequently, there is a trade-off between bite weight and biting rate which may not favor maximization of bite weight (Dougherty *et al.*, 1989c). By removing the top half of the sward, animals may maximize nutrient intake rate by increasing biting rate rather than bite weight.

One of the mechanisms proposed to explain changes of bite area is a behavioral adaptation to limit the force necessary to sever each bite (Hodgson, 1985). In very sparse swards, bite area would be limited by the maximum area encompassed by the lips or tongue in sheep and cattle, respectively. Increments of number of leaves or stems per unit area would increase strength per unit bite area and should cause a compensating reduction in bite area, effected via a change in the behavior of the animal. Our results are in qualitative agreement with such a prediction. We detected a significant

negative effect of bulk density on bite area. Only in a few cases, on very dense swards, did we observe steers grasp bundles of forage that they could not break in the first attempt. The steers released some of the forage and then severed what remained in the reduced bite area.

Such a model explains the effects of bulk density on bite area but it ignores the significant effects of sward height on bite area demonstrated by our experiments and others (Burlison 1987). At constant bulk density, bite area increases significantly with sward height, and the slope decreases as bulk density increases (Figure 10). Burlison (1987) determined that bite area by sheep grazing grass swards exhibited negative correlations with sward density and positive correlations with sward height. Our model provides a conceptual basis to explain and predict the changes in bite area with sward height and bulk density.

Although there were significant animal effects on bite dimensions, no significant differences were detected in bite weight between animals. In the dallisgrass experiment there was compensation of bite depth and bite area among animals (Table 9). Animals with smaller bite areas also took deeper bites, which resulted in no significant differences in bite volume. In the alfalfa experiment animals differed significantly in bite volume, in spite of the negative relationship between bite depth and bite area. However, bite volume compensated for differences in the bulk density of the grazed horizons, resulting in no significant differences in bite weight.

Bite weight was affected independently by sward height and bulk density. The relationship between bite weight and herbage mass per unit area depended on whether herbage mass varies by changes of height, density, or a combination of these factors. Steers obtained heavier bites on tall sparse swards than on short dense ones with the same herbage mass per unit area (Figure 63). This result is consistent with what Black and Kenney (1984) reported for sheep, and is explained by the biting mechanism described above. In the tall sparse sward, steers not only obtained a proportionally equivalent bite depth, but also achieved larger bite areas, which resulted in heavier bites. A corollary of this is that cattle could obtain larger bites on pastures of lower herbage mass per unit area, provided that they are taller. Sward height had positive effects on both bite area and depth (Figure 9), and was more indicative of instantaneous availability than mass per unit area. However, these results strongly suggest that even in homogeneous swards, availability

cannot be described with a single value. It is necessary to know both height and density of the sward to predict bite dimensions.

7.2.1.2. Effects of sward height and density, and time within the grazing bout

Comparison of results with those from the previous study of stall-fed cattle offered similar dallisgrass HCS indicates that sward height and bulk density had the same effects on bite area, bite depth, and bite weight in both experiments. Absolute values for bite dimensions were most similar between experiments for pasture measurements obtained 4 hr after the onset of grazing. Observations under stall-fed conditions were obtained *ca.* 6-7 hr after steers had consumed their daily maintenance ration of alfalfa (*Medicago sativa* L.) hay, suggesting equivalence of hunger states among stall-fed and grazing animals at these respective times under our experimental conditions. Comparison of bite areas and bite weights to those measured in another study with stall-fed cattle offered different scales of horizontal heterogeneity among dallisgrass leaves and stems at a range of hunger (see below) levels indicates dissimilarity of hunger effects between experiments. We hypothesize that the contrast between fresh HCS tissue and the background alfalfa pellet diet in the stall environment overrode any hunger satiation effects, levels which might have applied when animals were presented with additional increments of pellets.

Agreement between ingestive behavioral responses to variations in sward structure observed under pasture and stall-fed conditions, and absence of interaction of grazing time with other treatment effects, supports the validity of extending results from HCS experimental treatments offered under stall-fed conditions to the prediction of field ingestive behavior. Disagreement between ingestive behavioral responses to variations in sward structure when hunger or fill levels were manipulated under stall-fed and pasture grazing conditions suggests the interaction of observed responses with characteristics of the background diet.

7.2.1.3. Effects of tiller density and tensile strength

Shearing and tensile strength of plant tissues have been related to acceptability and selectivity by grazing animals (Evans 1967, Hendricksen and Minson, 1980). More recently, Hogdson (1985) hypothesized that strength of

the sward can be a factor determining bite weight. According to the so-called "summit-force theory" (Burlison 1987), there is a limit to the force animals can exert to sever the tillers encompassed within bite area. As sward density or strength of the tissues increases, animals should reduce bite area to maintain force below the maximum. Experimental support for this view has been indirect and inconclusive (Chambers *et al.*, 1981) because forces exerted by grazing ruminants have not been measured. We determined that, as predicted by the theory, bite area decreases with sward bulk density (see previous sections). However, force exerted by grazing cattle did not reach a maximum or constant value. Given that strength appeared not to be an absolute limitation to bite area, and that sward strength per unit bite area is related to bulk density, the question is whether animals adjusted bite area on the basis of strength or bulk density. The answer is relevant for the prediction of bite weight and intake rate on swards that vary in strength and bulk density.

Increments in sward bulk density tend to increase bite weight. Thus, animals have the opportunity to respond by reducing bite area or bite depth without reductions in intake rate. On the other hand, the greater strength per unit bite area in denser swards may increase the rate of failure in severing bites at the first attempt. Consequently, we envision that bite area may be mechanistically related to both bulk density and strength of the plant tissues.

Separation of effects of bulk density and strength presented a challenging methodological problem. Control for the possible effects of other variables requires homogeneous swards. In homogeneous swards bulk density and sward strength are almost perfectly correlated. At equal bulk density, plant parts or species differ in strength, but they may also differ in acceptability and stiffness, both likely to affect bite area. Under the assumption that this "species" effect, if present, is constant across bulk densities it can be statistically separated from the effects of bulk density or strength.

In agreement with previous experiments, bite weight increased with diminishing returns as a function of density of the sward (Figure 64), and appeared to reach a lower asymptote in the dallisgrass swards.

In conclusion, bite area responded to sward strength and was not affected by other differences between species. Bite depth responded to bulk density and to species differences, although not conclusively to strength. A more discriminating analysis will be possible once the measurements of sward strength and force per bite are incorporated.

7.2.1.4. Effects of sward height, density and phenological stage

The observed decline in tiller strength with time in the "early" tillers is in contradiction with the significantly increase in strength with advancing phenological stage detected in this and other studies (Evans 1967). We attribute the effect of time to the way we selected tillers in the field. As the pasture matured it became more difficult to obtain abundant tillers in the early flowering stages, and we were forced to collect tillers that were thinner and smaller than earlier in the experiment. This artifact should not affect the validity of other results.

The covariance between sward bulk density, phenology and strength does not allow a discriminating test of the direct causes determining bite area. However, steers grazed swards in both stages of maturity with apparently equal eagerness, so palatability or motivational factors stemming from phenological differences did not appear to be behind the responses of bite area. Force necessary to break a bundle of leaves, as when cattle sever a bite, should increase both with bite area, tiller density and tiller strength. Tensile strength of plant tissues varies widely (Evans 1967), and grazers have no obvious way of assessing it before attempting to sever the bite. We hypothesize that animals adopt a strategy of adjusting attempted bite area on the basis of the perceived tiller density. After gaining experience with the vegetation available, animals could "fine-tune" the attempted bite area. This hypothesis is supported by the importance of bulk density in explaining bite area.

Swards made of tillers in early and late flowering stage differed in their architecture. Visual inspection of the swards clearly indicated that those in late flowering stage had more flower and stem tissues than those in early flowering stage. In spite of this qualitative differences, animals grazed both types of swards in a fashion consistent with the way they previously grazed homogeneous vegetative swards. Steers did not appear to reject stems or flowers in any way, and the responses of bite dimensions and bite weight to sward structure were qualitatively similar in both phenological stages.

Tillers in the late phenological stage were stronger than those in the early stages, but also had significantly greater bulk density. Thus, the reduction of bite area with advancing phenology was explained by both factors and none could be eliminated as a cause. However, it is a relevant result that

bulk density and height can be used to predict bite dimensions and bite weight, even across phenological stages as those described in the present work.

7.2.2. Heterogeneous swards

7.2.2.1. Vertical heterogeneity

Bite depth (Table 11) on HCS with pseudostem corresponded closely to values previously obtained on HCS vertically homogeneous in terms of plant parts (Laca *et al.*, 1992a) and swards with vertical heterogeneity in bulk density (Ungar *et al.*, 1991). Conversely, on HCS that had a horizon of stems, bite depth did differ from previous results because steers restricted their grazing to the upper leaf horizon (Fig. 4). Lamina length affected bite depth only on the 16-cm tall HCS with a bottom layer of stem. Although weight per unit length of pseudostem and lamina did not differ, weight per unit length of stem was more than three times that of the base of the lamina (Laca, unpublished data). Therefore, while in the swards with pseudostem there was no significant increase in bulk density with depth into the canopy, the HCS with a bottom layer of stem exhibited an increase in bulk density at the stem horizon (Fig. 20). Leaf and stem also differ in strength and resistance to penetration of the muzzle. The degree of differentiation in these mechanical properties is dependent on maturity (McRandal and McNulty, 1980). These results raise two questions. Was bite depth restricted by a response to bulk density, or to the presence of stem and its inherent mechanical and nutritional properties? Why did stem limit bite depth in the tall swards but not in the short ones? The combined results of the present work and previous experiments with dallisgrass (Laca *et al.*, 1992a; Ungar *et al.*, 1991) provide answers to both questions.

In reference to the first question, bite depth appeared to be limited by inherent properties of stem and not by the greater bulk density associated with the stem horizon. In other experiments (Laca *et al.*, 1992a) with the same animals, swards of similar bulk density but constructed totally of laminae did not form a barrier to bite depth. A bottom horizon of high bulk density of laminae had no effects on bite depth by steers grazing dallisgrass swards (Ungar *et al.*, 1991). At equal sward bulk density, a horizon of stem is stiffer and much tougher than one of leaf lamina. When the sward is short and dense, stems present a barrier that makes it difficult for the animal to insert its

muzzle below stem height. This effect is not limiting when stems are long and sparse, as in a tropical sward in late phenological stages, because cattle can push the stems aside and prehend the leaf (Ruyle *et al.*, 1987). This effect may also explain differences among animals in their ability to select leaf. A canopy of short stems that is a barrier to cattle because the distance between clumps of stems is much smaller than the width of the muzzle, may not represent a barrier to the much narrower muzzle of sheep, that could access the leaf interspersed with the stems. Sward characteristics of length, stiffness and density interact with animal morphology and experience, including preference (Flores *et al.*, 1989) to determine bite depth.

Given that stem horizons were not grazed, it is necessary to explain why the presence of stem did not have a significant effect on bite dimensions in the short swards. The effect of the bottom horizon of stem depended on the difference between lamina length and potential bite depth. Potential bite depth is the depth to which animals bite when the sward is 100% leaf lamina, horizontally and vertically homogeneous (Laca *et al.*, 1992a; Ungar *et al.*, 1991), and is commonly observed to be approximately one-half of sward height, averaged across a range of bulk densities for cattle (Laca *et al.*, 1992a) and sheep (Burlison *et al.*, 1991). Bite depths obtained in Exp. 1 are very close to potential bite depth, which corroborates the view that pseudostem did not constrain bite depth. Conversely, steers grazing the reproductive swards exhibited bite depth much lower than 50% of sward height. Bite depth was less than expected only when stem height was greater than the height at which animals would position the incisors in a sward without stems (Fig. 4). Potential incisor height is approximately 2.2 and 4.7 cm for 8- and 16-cm swards. Thus, on the 8-cm swards with 3 cm of stem at the bottom, incisor height only increased by about 1.3 cm. In the 16-cm swards with 8 cm of stem, incisor height increased by 3.5 cm, whereas an 11-cm horizon of stem resulted in an increase of about 6.8 cm.

The extent to which bite depth and bite area are affected by lamina length at late phenological stages is expected to increase as swards are grazed down because lamina length becomes a smaller proportion of total height. These results also suggest that assessment of the effect of vertical heterogeneity on bite depth requires comparison with a control without heterogeneity. Significant correlations between pseudostem height and grazing height can be found in the absence of a direct effect of pseudostem on

bite depth, if pseudostem height is correlated to total sward height, as found by Barthram and Grant (1984).

In apparent discrepancy with our results, Arias *et al.*, (1990) reported that cattle never grazed tall fescue (*Festuca arundinacea* Schreb.) swards below pseudostem height. While the difference may have resulted from a difference between the properties and acceptability of pseudostem between species, it may also have resulted from fescue pseudostem being below the potential bite depth in those swards. Our experiment showed that stem reduced bite depth because the pregrazing height of stem was known for all tillers. When results are based on the difference between mean bite depth for a population of bites and mean stem or pseudostem depth for a population of tillers, it is not possible to infer if stem or pseudostem was a barrier at the individual bite level.

Realized bite area is the product of the area encompassed by the mouth gape and sweep(s) of the tongue, and the probability that tillers within that area are captured and severed by the bite. Bite area can be actively adjusted by the animal by varying the area and frequency of tongue sweeps as well as mouth gape. Characteristics of individual tillers, such as position relative to the mouth, height and stiffness, affect their probability of being captured. Tillers initially encompassed by a tongue sweep that are shorter than the distance from their rooting point to the clamping point will escape capture (Laca *et al.*, 1992b). Stiffness is hypothesized to affect the probability that a tiller, initially included in the tongue sweep, will escape being grasped in the jaw by springing back to its original position. Use of the tongue in forage prehension was not significantly influenced by sward structure. Although we were unable to detect a difference in tongue sweeps between the 5- and 8- cm lamina lengths, our data indicate that animals tended to compensate for decreased lamina length by increasing the sweeps of the tongue to increase the probability of capturing tillers and enlarging bite DM weight (Table 12).

The effects observed on bite area were qualitatively similar to those on bite depth (Table 11); the longer the stem or pseudostem, the smaller the bite area. Bite area in swards with pseudostem, particularly in tall swards, was smaller than expected based on swards composed totally of laminae. Moreover, bite area was smaller in the experiment that included a bottom horizon of stems than in the experiment that included pseudostems, approaching the minimum for these animals (approximately 40 cm²).

These results can be explained on the basis of two features of the grazing mechanism (Laca *et al.*, 1992a). First, when sward height limits bite area, by inserting the incisor edge deeper into the canopy the animal should be able to grasp a greater number of plant units, because the distance between incisor edge and rooting point is reduced. Second, pseudostem and stem are stiffer than lamina and have a greater tendency to spring back to the initial position after being swept by the animal's tongue, but before being clamped between teeth and dental pad. This reduces the efficiency of the gathering motion and bite area.

Although the 8-cm swards without stem or pseudostem at the bottom were constructed totally of laminae in both experiments, bite area was smaller in the reproductive swards (Table 11). This may be explained by the difference between experiments in the stiffness and tensile strength of the laminae. In the experiment with pseudostem, laminae were thin and wide, from young leaves. In the other experiment, we used the bottom part of the oldest laminae, which were narrow and consisted mostly of a thick and fibrous midrib.

Contrary to what was observed in swards without stem, bite area was not affected by total height in HCS with stem at the bottom. Remarkably, bite area was almost equal on swards with 5 cm of lamina at the top of 3 and 11 cm of stem. Based on previous results (Laca *et al.*, 1992b), the taller sward should have yielded greater bite area (approximately 105 cm²). The difference in resistance to a bending momentum between lamina and stem (Curtis and Hendrick, 1969), and the fact that animals did not insert the incisor edge below stem height, determined that as laminae were swept by the tongue they bent at ligule height. Therefore, the effective height, relevant to the mechanism that determines bite area, was 5 cm in both the tall and short swards. In comparison, steers obtained an avg. bite area of 78 cm² on 8-cm tall dallisgrass of similar bulk density (Laca *et al.*, 1992b). The top horizon of lamina controlled both bite area and depth.

Bite DM weight increased in response to increments in sward height depending on whether pseudostem or stem comprised the bottom stratum of the sward. Bite DM weight of cattle grazing swards with stem was no longer related to sward height but to lamina length, and was severely reduced by the presence of stem (Table 12). The reduction in bite volume, combined with a reduction in leaf bulk density in the reproductive tillers led to bite sizes

considered to limit intake of grazing cattle (Chacon and Stobbs, 1976; Stobbs, 1973).

Regardless of the exact cause-and-effect relationships, our experiments address real changes of natural swards associated with maturation and regrowth of stubble. Field observations of the same animals grazing a dallisgrass sward after it had been cut evinced the "barrier" effect of the stubble of stems. Leaves growing from the bottom of the plants were protected from grazing by residual stems. Such an effect may also be important in limiting bite DM weight when cattle graze sod-seeded pastures, or range with abundant residual stems from the previous year's growth. Our results confirm that prediction of bite DM weight must take into account not only sward height and bulk density, but also the presence of stem or pseudostem horizons, and their heights relative to total sward height. That pseudostem did not act as a barrier to bite depth is a new finding from this study. Differences in physical characteristics other than bulk density are responsible for the difference in ingestive behavioral response to pseudostem and stem. This suggests that in differentiated swards, physical properties must be measured to determine bite depth. Differences in bite area can be explained by a model that conceptualizes bite formation. This conceptual model of the mechanisms governing formation of bites is useful in explaining differences in bite dimensions in response to changes in sward structure. Different functional relationships between intake and herbage mass per unit area are expected when swards differ in characteristics such as vertical heterogeneity and phenological stage.

7.2.2.2. Horizontal heterogeneity

Selection of tall patches in Expt. 1 tended to result in greater bite weights and intake rates, as expected. Bite dimensions on swards with heterogeneity in bulk density appeared to be determined by sward characteristics at the bite site. Conversely, animals appeared to adjust bite depth to the characteristics of the selected tall patches when grazing both tall and short patches within swards with heterogeneity in height.

The response of bite area and degree of selection for components of swards to scale of heterogeneity may be related to the frequency of behavioral adjustments animals must make as they graze horizontally heterogeneous swards. More frequent encounters with leaf/stem boundaries in Expt. 2

swards with small patches than in those with large patches could reduce the proportion of bites of potential bite area in a given patch. This effect could apply to stems as well as leaves, in that stem bite area could be inflated in small- relative to large-patch swards because first encounters with stem patches may be with bites adjusted to adjacent leaf conditions.

The lack of response to hunger satiation in Expt. 2 may reflect the irrelevance of internal state on bite dimensions and instantaneous selectivity. Alternatively, the contrast between fresh HCS tissue and a background diet of alfalfa pellets may override any hunger levels which might apply when animals are presented with additional increments of pellets.

7.3. Within-patch intake rate and patch depletion

7.3.1. Behavioral mechanisms that determine bite rate and intake rate

The methodology we used allowed us to classify jaw movements in a way that facilitated understanding of the grazing process. Earlier techniques for sheep (Penning *et al.*, 1984) and cattle (Chacon *et al.*, 1976) classified jaw movements as either prehending bites or chews. It was assumed that total jaw movements equaled bites plus chews. Our observations revealed a more complex and potentially more meaningful pattern of jaw movements. First, we defined a bite as the action that completely separated the prehended herbage from the plants. Bites were performed by a head movement and evinced by a characteristic tearing sound (Forbes 1988). Bites were not jaw movements but were usually preceded by 1-3 manipulative jaw movements used to gather herbage for biting. Second, we determined that cattle can use the same jaw movement for simultaneous gathering of new herbage and chewing herbage previously bitten. Chewing jaw movements produced a characteristic grinding sound.

In these experiments animals were stationary while grazing. The area grazed was approximately what steers were able to reach without walking (feeding station, FS) (Ruyle and Dwyer 1985). Therefore, the feeding process involved mostly head movements and searching within the FS, without any searching or walking between FS.

Instantaneous intake rate increased asymptotically with bite weight. At low bite weight, IIR was almost linearly related to BWT. The slope was

determined by the time necessary to manipulate, sever and but not strongly affected by chewing. As BWT increased IIR was progressively more affected by chewing requirements, reaching an asymptote as has been described for many ungulates (Wickstrom *et al.*, 1984, Spalinger *et al.*, 1988, Spalinger and Hobbs, in press). Usually, a phenomenological model is used. The present work elucidates the mechanisms behind the response and suggests a model in which parameters have direct biological meaning (Figure 33).

Instantaneous intake rate is the quotient of BWT and time per bite. Bite weight was a major determinant of IIR, both directly and via effects on time per bite. Time per bite had two components. The first component, the Y-intercept of Figure 34, was independent of the total number of jaw movements per bite. Such time may be associated with the location and severing of the bite by the clamping of herbage between jaws and jerk of the head (Chambers *et al.*, 1981). The second component, the time to perform all jaw movements per bite, was proportional to the total number of jaw movements per bite (Figure 34). Total number of jaw movements per bite increased with bite weight because of the greater chewing requirements per bite. The responses of time per bite (Figure 35), total jaw movements per bite, and exclusive chews per bite (Figure 38) were positive quadratic ones because of two effects. First, chewing efficiency increased with bite weight (Figure 40), and second, chewing and manipulative jaw movements exhibited greater overlap as BWT increased (Figure 36). Although a smaller range of bite weight was observed in the experiment with dallisgrass, and the data exhibited greater variability, results from alfalfa and dallisgrass swards agreed qualitatively and quantitatively.

Although time per bite showed a significant quadratic effect of BWT, a model for IIR $[BWT(a + b BWT^2)^{-1}]$ with a quadratic denominator fitted the data as well as the linear one used ($R^2 = 0.81$). A quadratic model for time per bite implies that IIR should reach a maximum and then decline with increasing BWT in the range of large bites. This does not agree with the relationship between bite weight and IIR usually reported. We preferred the model with the linear denominator because it is asymptotic with BWT, and tends to a maximum of 120 g min^{-1} which is more consistent with independent measures of the maximum IIR our animals could achieve. The relations between bite weight and jaw movements suggest that time per bite should fit a model with an increasing asymptote. As bite weight becomes very large the

slope of time per bite should tend to a constant, instead of increasing without bounds as implied by the quadratic model. We used the quadratic model because the data would not allow model discrimination, and the quadratic is more parsimonious.

Except for the tendency of total manipulative jaw movements per bite to increase in shorter swards, no other variable analyzed exhibited effects of sward height or density after the effects of bite weight were removed. Sward structure did have significant effects on bite weight itself, and therefore, we can only infer a causal relationship between bite weight and behavior, as suggested by previous research which indicates that chewing is controlled by bite weight (Hogan *et al.*, 1987, McLeod *et al.*, 1990).

The steers' ability to chew and manipulate herbage simultaneously, as depicted in Figure 65, was a compensatory mechanism for the chewing requirements per bite. A constant number of manipulative jaw movements was allocated to each bite (*ca.* 1.8), independently of BWT. At low BWT, chewing requirements per bite were met by overlapping chewing with bite manipulation, plus bouts of less than 3 exclusive chews. As BWT increased in the range below 1.5 g, the increasing chewing requirements per bite were met mostly by increasing the overlap of manipulation and chewing, and by a slight increase in the frequency of short bouts of exclusive chewing. No significant addition to the total number of jaw movements per bite was observed. As a result, time per bite remained almost constant and IIR increased linearly with BWT. Eventually, at BWT = 1.5-2.0 g the overlap reached a maximum of about 85% and increments of chewing requirements were met by a net increase of total jaw movements per bite. This was accomplished by greater frequency of much longer bouts of exclusive chewing during which animals lifted their heads and ceased searching within the patch (Table 16).

The overlap of chewing and manipulation of herbage increased intake rate by as much as 36%. We estimated IIR, assuming no overlap between chewing and manipulation, by increasing time per bite according to the relationship in Figure 34. Total number of jaw movements per bite was increased by an amount equal to the overlap of chewing and manipulative jaw movements per bite. The effect of overlapping chewing and manipulation increased in relative and absolute terms as bite weight increased, because intake rate became progressively more limited by chewing than by manipulation requirements (Figure 33). However, for bite weights as low as

0.5 g (0.66 mg/kg LW), the ability to chew and manipulate herbage simultaneously allowed an increment of 29% in IIR.

Contrary to expectations, chews per unit DM ingested was not related to proportion of stem or height of alfalfa swards. Dougherty *et al.*, (1989c) detected a significant negative effect of length of prehended alfalfa on IIR. This was attributed to the greater chewing requirements per unit DM due to particle length and stem content. Initial particle length negatively affects IIR and preference by sheep (Kenney and Black 1984, Gherardi and Black 1991). Sward height significantly affects bite depth, an indicator of length of prehended herbage (see above). However, we did not detect an effect of sward height on chewing per unit DM. This could be attributed to the smaller range of harvested particle lengths obtained in our experiments.

Chews per gram of DM declined asymptotically with increasing BWT (Figure 40). This can be explained in two ways. First, efficiency of chewing may have increased with BWT due to the discrete nature of the number of chews that can be applied to a mouthful. Chews per unit herbage mass ingested declined in an asymptotic fashion as bolus weight, a measure of the weight of a mouthful, increased (Figure 66). When bites were small, the amount of herbage held in the mouth at any given time was small, as indicated by the relationship between BWT and bolus weight ($Y = 4.5 + 3.6 X$, $R^2 = 0.69$, $MSE = 7.27$). Below a threshold BWT (ca. 1.75 g), amount of herbage in the mouth may not be enough to cover all occlusal molar area. As BWT increases, more of the available occlusal area is used and the efficiency of each chew increases. Second, as BWT decreases animals may continue to allocate a minimum number of chews per bite, occupying time that otherwise would be idle if chews per unit DM were maintained constant. These two explanations have different implications for particle size swallowed but are not incompatible. Ruminants may have a constant total (ingestive and rumination) chewing requirement per unit dry matter ingested which varies with the physical and chemical properties of the forage (Hogan *et al.*, 1987, McLeod *et al.*, 1990). However, cattle are able to reduce the amount of chewing during eating in order to increase IIR after fasting or when feeding time is restricted, and compensate by ruminating more (Greenwood and Demment 1988, Greenwood 1989). Given the importance of particle size in digestion and passage (Poppi *et al.*, 1980) and the ability of cattle to modify their chewing strategy, a complete understanding of ingestive behaviors will require more

knowledge on the role of the trade off between ingestive mastication and rumination as compensatory mechanisms in the digestion and passage of ingesta.

Bouts of exclusive chewing are relevant because they represent opportunities for the grazer to search for and reach new bites while chewing. Simultaneous chewing and searching may increase the instantaneous feeding efficiency of grazers. Underwood (1983) argued that grazing ungulates can look for nearby food items and take one or many steps while chewing previously "captured" bites. Consequently, optimal foraging models based on the trade-off between the energy and time costs of feeding behaviors would not apply to these grazers. More recently, Spalinger and Hobbs (in press) indicated that predators and herbivores differ because herbivores can continue to search for new bites while processing others. These authors pointed out that although handling of bites (cropping and chewing) does not preclude searching, it may affect it.

We agree that grazers can chew and search for new bites at the same time, but we think that these animals do face a trade-off between searching and IIR. The trade-off between IIR and searching is relevant for as long as herbivores do not perfectly match the temporal sequence of necessary bouts of exclusive chewing with that of necessary searching bouts (Owen-Smith 1988). The cost of searching in terms of reduced intake rate depends on the degree to which searching and exclusive chewing actually overlap. Our data indicates that much of the necessary exclusive chewing is performed in very short bouts of one or two jaw movements (Figure 41 and Table 16). The duration of these bouts was compatible with searching within one feeding stations. Yet, the significant intercept in the relationship between time per bite and total number of jaw movements per bite (Figure 34) suggested that, even within a feeding site, there was a time cost per bite which did not overlap with chewing or bite manipulation. This constant time per bite could be related to searching and moving the head within the FS, or to the action of clamping and severing the bite, but this study did not identify which process was most important.

Searching may interfere with IIR even when cattle chew uninterruptedly while they walk between feeding sites. Our results indicated that chewing and prehension of bites overlap. Thus, chewing performed while searching could be performed while obtaining more bites, if bites were accessible without the animal having to walk. If animals chew continuously between FS one might

assume that searching time is irrelevant for IIR, which would seem to be limited by chewing. According to the present results, such an assumption could be incorrect. We showed that by overlapping chewing and prehension, animals could transform each chew into an investment on manipulation of new bites, if forage were available at the current FS. Searching is more likely to reduce IIR when bites are small and sparsely distributed, such that most of the chewing requirements per bite are met during manipulative jaw movements (Figure 65). Additionally, small bites are associated with bouts of exclusive chewing that are short relative to the time needed to reach acceptable bites. Grazers usually face a positive correlation between bite weight and density in the vegetation. Therefore, these animals would face a decreasing availability of "free" time to search as the need for it increases.

Additionally, searching is energetically costly. Murray (1991) showed that distance traveled per unit intake by African ungulates increases exponentially as bite weight decreases, and therefore, a significant proportion of the intake of metabolizable energy is spent as heat increment due to locomotion. The inclusion of such a cost in a model of diet selection significantly changes the optimal levels of selectivity, affecting both IIR and diet quality.

In conclusion, we emphasize the implications of our observations. First, cattle can chew and manipulate new bites simultaneously. The degree of overlap depends on bite weight and sward structure, and significantly increases IIR. Second, cattle can chew and search for bites simultaneously but always face a trade-off between searching and IIR. The relationship between average chewing and searching time per bite may be an indicator of the potential overlap between these behaviors. The actual overlap depends on the coordination of temporal sequences of bouts of searching and chewing. Third, height and density of homogeneous swards did not affect time per bite and IIR beyond the effects via bite weight. The significant increase in manipulative jaw movements with decreasing sward height did not translate in greater time per bite, perhaps as a result of the overlap of chewing and manipulation.

7.3.2. Patch depletion by grazers

Tall sparse swards yielded initially larger bites and greater intake rate than short dense ones of equal herbage mass per unit area. As a result of the greater initial IIR, taller swards suffered faster depletion and exhibited

significant depression sooner than the short ones (Figures 43 and 44). Bite weight was not determined by herbage mass but by the spatial distribution of herbage mass in the volume of the canopy (Hodgson 1985, Burlison 1987, 1992aa).

Contrary to the "compensatory" relationship between bite weight and bite rate usually reported (Allden and Whittaker 1970, Chacon and Stobbs 1976, Penning 1986, Forbes 1988, but see Forbes and Coleman 1987, Dougherty *et al.*, 1989c), time per bite was not significantly affected by changes in bite weight within the patch. The lack of response of time per bite to bite weight in both experiments can be explained by two processes. First, we observed steers take as many as 20 bites before swallowing for the first time. Chewing does not start until a few bites have been gathered in the mouth, and the number of bites ingested before the onset of chewing decreases with increasing bite weight (Laca, unpublished data). This indicates that the mouth acts as an integrator or "compartment" in the flow of herbage from the sward to the rumen. Chewing responds to the characteristics of all forage that is in the mouth, not to the characteristics of the last bite ingested. Therefore, we surmise that the mouth buffers the effects of very short term changes in bite weight on time per bite. Although we were not able to detect changes in time per bite within FS, time per bite could be significantly different between homogeneous pastures that yield bite weights equal to the extremes we observed within FS. Second, time per bite does not necessarily increase with bite weight if the greater chewing requirements are met by overlapping manipulative and chewing jaw movements. We have shown that the increment in chewing requirements due to increases in bite weight from 0.5 to 1.5 g can be compensated by this overlap (Laca *et al.*, 1992b).

The effects of sward structural and physical characteristics on the dynamics of patch depletion by cattle are also illustrated by the differences between experiments (Figures 44 and 48). The 18-cm field patches contained more than 4 times as much herbage mass as the 20-cm HCS (Table 21), yet they exhibited a slower initial IIR (1.36 vs. 1.64 g s⁻¹). Patch depression, represented by k_2 , was significantly slower in the field patches (0.003 vs. 0.023 s⁻¹). Field patches exhibited a significantly greater bulk density than HCS, and bulk density increased with depth in the canopy. The bottom of the ryegrass swards was characterized by densely packed pseudostems. The high bulk density and the concentration of the herbage mass in the pseudostems at

the bottom of the sward reduced the accessibility of the forage to the steers, relative to the HCS.

In spite of the smaller area of the patches in the field experiment, the point of depletion of the top horizon was barely attained in the tallest patches. As was predicted by the quotient of patch area over bite area in the top horizon, 56 bites would have been necessary to deplete the top horizon of the 18-cm patches. In contrast, it took only 35 bites to deplete the top horizon of the tall swards in the HCS experiment. This difference between experiments is explained by the much greater bulk density of the field swards, and likely by the greater tensile strength of ryegrass vs. wheat, which determined smaller bite areas in the field than in the HCS.

The results of the present experiments provide new information to assess the validity of previous models of plant-herbivore interactions at an ecological and evolutionary level. In a model of functional response for browsers and grazers, Lundberg and Astrom (1990) assumed that the initial slope of intake curves was independent of the total biomass in the patch. Our results indicate that such assumption is plausible for large grazers like cattle, but is probably not correct in many environments. Initial slope of intake curves is determined by bite weight of the first few bites taken at the patch. The HCS experiment demonstrated that patches of equal herbage mass can yield different bite weight if they differ in canopy architecture. Previous experiments (see above) showed that swards of different herbage mass, within certain range, yield the same initial bite weight when the effects of changes in height are counterbalanced by changes in bulk density. Therefore, initial IIR can be constant across patches that differ in total biomass only if these changes are caused by differences in patch area (i.e. plant structure remains constant), or if changes in biomass per unit area are compensated by height and density, such that initial bite weight remains constant. Even for browsers, initial bite weight and IIR are not necessarily constant across levels of biomass per tree. It is likely that a tree that has reached a certain level of edible biomass by regrowing after heavy browsing will yield lower IIR than a tree that reached equal biomass undisturbed.

The relationships between sward structure and intake curves reveal an additional difference between the effects of browsers and grazers on the plant community. Lundberg and Astrom (1990) treated ramets as patches and implicitly assumed that ramet density does not affect the intake curves. These

authors concluded that at equal biomass density in the environment, an optimally foraging browser or grazer would obtain greater intake if plant biomass were in few large ramets than if it were in many small ones. From the point of view of plant strategies they concluded that a genet would suffer greater total tissue loss if it allocated all biomass to few large ramets, but each ramet would suffer a proportionally smaller loss than if biomass were allocated to many small ramets. Thus, plant architecture would experience competing selective pressures from herbivory depending on the relative importance of tissue loss per genet and per ramet on reproductive output and survival. Although such a view may be valid for large browsers for which each shrub or tree is a patch and is also a ramet, it is not valid for grazers because these herbivores typically consume more than one herbaceous ramet simultaneously. As shown in the present and previous experiments, the density and size of ramets (tillers) are central to the shape of intake curves and thus, in determining patch residence time and utilization. Our results suggest that herbaceous species do not experience the aforementioned opposite selective pressures from herbivory by large grazers similar to cattle. Cattle obtain smaller bites in swards that are composed of densely packed small ramets. Since time per bite is not significantly affected by bite weight over a wide range of values (see above), cattle that behaved as time-constrained IIR-maximizers would remove a smaller amount of biomass from swards with such a canopy architecture. Moreover, proportional damage per tiller would be lower because bite depth as a proportion of total tiller length decreases with increasing sward density (Laca *et al.*, 1992b, Ungar *et al.*, 1991). Total availability of the same herbage mass should be lower in a short dense sward than in a tall sparse one, because a greater proportion of the biomass would be in a bottom horizon that is not accessible to cattle and may constitute an "ungrazeable refuge" that increases the stability of the grazer-vegetation dynamics (Noy-Meir 1975). Individual herbaceous plants in communities that exhibit variance in plant architecture would experience an additional advantage by distributing their biomass over many shorter ramets instead of allocating it to few tall ones. Patches in which the tillers are so short and dense that initial IIR is lower than the average obtained in the whole "environment" (Stephens and Krebs 1986) by an optimally foraging grazer, would not be grazed at all. This aspect was not considered in Lundberg and

Astrom's model because they assumed that initial intake rate was the same in all patches (ramets).

The rectangular hyperbola provided a good description of the intake curves. However, it has limitations and the curves developed cannot be extrapolated beyond the range of residence times observed. In all cases, except for the 7-cm field patches, the asymptotic value of the fitted curves overestimated the total herbage mass present in the patch (Table 21). Since we determined field herbage mass by clipping to ground level, we are confident that not all herbage mass in the patch was accessible to the animals and that the asymptote for the 7-cm patches was also an overestimation. All intake curves would have exhibited a pronounced reduction in slope as happened in the 20-cm HCS (Figure 44) if animals had been allowed to graze for longer into the second horizon. Such reduction in slope is not incorporated in the Michaelis-Menten function. Development of models to correctly predict intake curves on the basis of initial sward structure will require more research on the mechanisms by which bite weight decreases within and between horizons. Meanwhile, the results of the field experiment suggest that curves can be extrapolated between FS within swards by expressing intake as a proportion of initial herbage mass (Figure 49).

The results of the HCS experiment indicated that steers grazed patches with a "horizon" grazing style (Ungar *et al.*, in press), exhibiting a highly systematic search within the patch (Figure 46). As a consequence of the systematic grazing by horizon, bite weight did not decline significantly with respect to initial values until the first horizon was depleted (Figure 67). Since tall sparse swards allowed greater bite area than short dense ones, the top horizon of these swards was depleted by *ca.* 35 bites, whereas in the short swards animals took *ca.* 50 bites from the top horizon before depleting it.

The systematic grazing suggests that intake curves can be derived on the basis of bite weight obtained from each horizon and number of bites in each horizon as the patch is depleted (Table 28). Bite weight (BWT) and dimensions were predicted on the basis of sward structure and equations previously developed (Laca *et al.*, 1992a). It was assumed that the second horizon was similar to a fresh sward of equal density and average height. Number of bites in each horizon (N_i) was calculated on the basis of proportion of area grazed and average proportion of "regrazing" bites for each sward structure (Figure 46). Time per bite was assumed to be constant at 1.37

seconds per bite. Additional, we assumed that there were only two horizons (although the model can be extended to more horizons), and that the number of bites placed in areas already grazed twice was negligible. We ignored the reduction in bite dimensions within the top horizon.

As shown in Figure 44, when bite weights were fitted statistically (Table 29), this model provided a good approximation to the intake curves in both swards. There was adequate fit to the data (20-cm swards: $Y = 1.09 \cdot X$, $R^2 = 0.72$, 10-cm swards: $Y = 0.99 \cdot X$, $R^2 = 0.98$, where Y is observed intake and X is intake predicted by the model) even when bite weights were estimated on the basis of previous experiments. The underestimation of intake in the tall swards resulted from $BWT_{1,20}$ (Table 28) being smaller than the actual values observed (Table 17). Except for $BWT_{1,20}$, bite weights fitted statistically (Table 29) did not differ significantly from values predicted on the basis of previous experiments.

In spite of the markedly systematic style of grazing, cattle exhibited patch depression both within and between sward horizons. The literature on foraging theory, developed mostly for predators hunting for discrete prey, indicates that a systematic depletion will yield intake curves without depression (Charnov *et al.*, 1976, Stephens and Krebs 1986). A systematically searching predator depletes prey locally and moves to new areas within the patch, experiencing no depression in intake rate until all the patch area has been searched and all available prey consumed. Grazing behavior of cattle differs from that of a systematically searching predator in at least two aspects that cause intake curves to have diminishing returns. These two aspects are the result of the physical mechanisms of grazing and its constraints (Laca *et al.*, 1992b) and probably apply to all grazers that exhibit a grazing style similar to cattle. First, the effectiveness of the herbage-gathering jaw and tongue motions declines as the top sward horizon is grazed, because of the curved shape of the bite volume and the consequent overlap between area attempted in new bites with areas previously bitten (Figure 45). Grazing creates "islands" of ungrazed herbage that yield a lower bite weight than the potential for the ungrazed horizon (Ungar *et al.*, in press). The overlap of bites within horizons was also detected in sheep by Burlison *et al.*, (1991). Additionally, natural swards exhibit heterogeneity in tiller length and density at scales smaller than the FS. Animals may exert selectivity for the largest potential bites first as they start grazing a horizon, which will also result in depression

within horizons. Overlap between bites and selectivity within heterogeneous horizons may explain the significant depression observed in the field experiment, since animals were not allowed to remove enough bites to deplete the top horizon of most patches.

The second cause of depression is that cattle do not totally deplete herbage mass at the site of each bite, but appear to remove a constant proportion of sward height (Wade *et al.*, 1989, Ungar *et al.*, 1991, Laca *et al.*, 1992b, Flores *et al.*, in press). Sheep exhibit similar behavior (Milne *et al.*, 1982, Black and Kenney 1984, Burlison *et al.*, 1991). Therefore, intake curves for these grazers would have decreasing slope even if bite weight did not decrease within horizons. The slope would be approximately constant within horizons, but would decrease markedly as grazing proceeded into successive horizons (Figure 44). The model of discontinuous depression was more appropriate for the tall HCS, whereas the short HCS and the field patches exhibited a smoothly declining slope.

Treatment of feeding stations (FS) as patches provides a framework to interpret and predict grazing behavior on the basis of patch depression and maximization of intake rate. The present results indicate that bite weight and intake rate depend not only on initial characteristics of the sward, but also on the time spent grazing at each feeding station. Other things being equal, the longer the grazer stays in the patch, the smaller the average bite and the lower the intake rate. Thus, prediction and understanding of intake rate requires understanding of how patch residence time is determined. Foraging theory (Stephens and Krebs 1986) provides a paradigm, the "patch" model, that can be applied for this purpose. The applicability of the "patch" model does not depend on the patches being discrete physical entities; it depends on the fundamental animal decision being patch residence time.

Study of grazing behavior has frequently focused on the FS (Ruyle and Dwyer 1985, Flores 1983, Mastel 1987, Stuth *et al.*, 1987, El Aich *et al.*, 1989). Generally, the goal has been to correlate FS behavior to animal performance, and to base management on easily observable changes of this behavior. These studies have detected diverse relationships between the forage resource or animal performance and FS behavior. Ruyle and Dwyer (1985) found that FS intervals (patch residence time) of sheep declined as forage availability decreased due to grazing. In contrast, Mastel (1987) and Stuth *et al.*, (1987) determined that cattle increase FS intervals and reduced the

proportion of grazing time devoted to searching when herbage mass decreases due to grazing. Flores (1983) found that cattle tended to reduce the number of bites per FS and FS intervals while steps between FS remained constant as herbage mass increased due to seasonal growth. In all studies, analyses and relationships were based on average FS behavior and average pasture characteristics, in spite of the spatial heterogeneity of swards.

Application of the "patch" model to FS behavior of grazers has the potential for more meaningful interpretation of the relationship between changes in the forage resource and feeding behavior, and offers a framework to predict intake rate. Optimality models indicate that FS interval depends not only on the average characteristics of the food environment, but also on the characteristics of the current patch, and frequency and spatial distribution of patches of different characteristics (Stephens and Krebs 1986, Astrom *et al.*, 1990). Therefore, no single relationship between average FS behavior and average pasture characteristics can be expected, unless the pastures are completely homogeneous or heterogeneity is controlled across changes in availability. Bazely and McCleery applied the patch model (Charnov 1976) to sheep and found that in some experiments patch residence times were in agreement with maximization of IIR. In most cases sheep tended to stay at each patch longer than predicted, but exhibited qualitative agreement with model predictions. As travel time between patches was increased, by increasing distance or hobbling the sheep, patch residence times increased significantly.

A model to predict grazing behavior and intake rate on the basis of maximization of IIR has to correctly identify the most relevant scale at which the animals make foraging decisions. The scale problem was studied by Edenius (1991) and Danell *et al.*, (1991) with moose browsing on different tree species. They concluded that moose primarily selected foods at the tree level, within larger stands or patches. Short-term measurements of the plant-animal interface are needed to understand dynamic processes of grazed ecosystems. Based on the results of the present experiments and on the literature, we conclude that the FS scale is adequate for studying foraging decisions by grazers.

7.4. Graphical analysis of sward depletion

Managed grazing systems operate over a wide range of $N/N_{\max}$. Expressed in orders of magnitude, a bite area for cattle of 10^{-2} m^2 (Illius & Gordon 1987) and a daily bite number of 10^4 (Hodgson 1982) yield a grazed surface area of 10^2 m^2 (Wade *et al.* 1989). This is comparable to the area allocated per animal in some forms of rotational grazing systems (e.g. strip-grazing), but is usually less than 2% of the area allocated per animal in set-stocking systems. In the latter, the animal is not constrained significantly in its feasible space of bite proportions on a daily basis. Intake rate can be related to initial (daily) sward structure and need not be viewed as a depletion process. A bite-driven model is more appropriate where $N/N_{\max}$ can reach values that constrain intake.

This is consistent with the different definition of functional response used in empirical studies at high and low area per animal. Set-stocking studies relate daily intake to biomass concentration, termed 'availability', or herbage mass (Hodgson 1979), with units of mass per unit area or simply height (Willoughby 1959; Arnold & Dudzinski 1967; Allden & Whittaker 1970; Arnold 1975; Jamieson & Hodgson 1979b; Baker, Le Du & Alvarez 1981; Le Du, Baker & Newberry 1981). Strip-grazing studies relate daily intake to the quantity of herbage allocated, termed 'allowance', with units of mass per day (Gibb & Treacher 1976, 1978; Marsh 1977; Reardon 1977; Combellas & Hodgson 1979; Jamieson & Hodgson 1979a; Le Du *et al.* 1979; Baker, Alvarez & Le Du 1981). The problem in both types of study is the considerable variation obtained in functional response and hence the difficulty in arriving at generally applicable management rules (Hodgson 1984). In the set-stocking situation, Ungar and Noy-Meir (1988) showed that intake rate at a given herbage mass per unit area depends strongly upon the spatial organization of the herbage. The present study suggests that sward structure is no less important in situations characterized by high levels of depletion. Since animals harvest the food in bite-size units, and the size of these varies with sward structure at the site where the bite is taken, there is reason to define the depletion process in terms of proportion of potential bites taken rather than proportion of available mass taken. The same allowance of herbage can be organized variously in space, both in terms of mass concentration per unit

area (and hence area allocation) and vertical structure. Both these can affect the number of grazing horizons and the bite weight characteristic of each. Thus an approach based upon available bite types and number over a specified time period may be of greater generality than empirical relationships between intake rate and allowance.

Support for the assumptions of the model can be found from experiments in which cattle grazed hand-constructed swards, of approximately 0.5 m² (Laca *et al.* 1992a; Ungar, Genizi & Demment 1991). In various trials, sward structure was homogeneous in the horizontal plane and of initially uniform height (assumption A1). Bite dimensions were defined in terms of mean depth of severance ('bite depth') and area covered by all plant units grazed to any depth ('bite area'). Bite dimensions were well predicted by sward height and bulk density of the herbage (A2). However, the curved and somewhat irregular shape of the effective bite volume can create ungrazed islands of herbage that yield a lower bite weight than the potential for the horizon, and assumption A3 does not hold strictly. (The horizon is nevertheless not a 'patch', since the time budget of selecting bites within and between horizons is similar.)

The heterogeneous height of residual plant units that remains after the removal of a bite, and the way it interacts with the placement of subsequent bites, will tend to result in less distinct grazing horizons than assumed here (A4). Nevertheless, groupings are discernible in the frequency distribution of residual heights after grazing, and these presumably correspond to the grazing horizons (Figure 68). Describing the sward in layers has proved useful in other empirical studies (Hodgson 1981; Milne *et al.* 1982). Observations on hand-constructed swards indicate that most bites are taken from the first two horizons at low to medium depletion. A third grazing horizon tends to appear on taller, severely depleted swards. In the two-horizon case, $p_3 = 0$ and the feasible space collapses to a single line (p_1, p_2), represented by the base of the unit-sum triangle. If $w_1 \neq w_2$, all feasible combinations of bite proportions (when $p_2 \neq 0$) yield different levels of intake for any given $N/N_{\max}$.

Dense swards of relatively uniform quality in the vertical plane are subject to little selectivity and the constraint of sequential access is met (A5). If preference declines with depth of horizon, as observed on various swards (Blaser *et al.* 1960; Chacon & Stobbs 1976; Arias *et al.* 1990), the animal is unlikely to select a bite on a lower horizon before bites immediately above it

have been selected. This too is effectively sequential access. Highly differentiated swards may approach 'direct access', whereby the animal can insert its mouth into the canopy in order to select specific plant parts (Milne *et al.* 1982; L'Huillier, Poppi & Fraser 1984). Bites placed randomly within one horizon will not usually expose as many potential bites on the next horizon as contiguous bite placement. Ignoring bite placement within horizons (A6) may be unrealistic when very few bites have been taken.

This study suggests that it is useful to differentiate a sward into components which are relevant to the grazing process in situations characterized by high levels of depletion. These components relate directly to the basic unit of intake - the individual bite. A distinction has been made between the logical constraints associated with a given number of bites, the feasible space of behavioral options (i.e., combinations of bite types) generated by these constraints, and the consequences of different grazing styles on intake. The limiting factor to the application of such a conceptual framework to real grazing systems would seem to be methodological. The bite-oriented approach requires quantitative definition of horizon depth, bite dimensions and bite weights for any given sward type. This involves great detail in the monitoring of foraging behavior. The development of new methodologies such as those of Black and Kenney (1984), Spalinger, Hanley and Robbins (1988), Forwood and Hulse (1989) and others (Burlison, Hodgson & Illius 1991; Laca *et al.* 1992a; Ungar, Genizi & Demment 1991) may represent an important step towards that goal.

The Unit-Sum Triangle. The unit-sum triangle is an equilateral triangle of unit height generated by a linear scale and clockwise rotations of the scale through 120° and 240° , as shown below in Figure 69:

Each side of the triangle is the zero isogram for one of the scales (e.g. here, the side YZ represents $p_1 = 0$); each vertex of the triangle represents the value, unity, for one of the scales (e.g. here, the vertex X represents $p_1 = 1$); each point within the triangle may be represented by three triangular coordinates (e.g. here, the point Q has coordinates (0.5, 0.3, 0.2) for p_1 , p_2 and p_3).

It can easily be shown that the sum of these three coordinates, for any point within or on the triangle, is unity. Proof: Let h_1 , h_2 , h_3 , be the three perpendicular distances from Q to the sides YZ, ZX, XY, respectively; let L be the length of each side of the triangle; let h be the height of the triangle.

Then area DQYZ = $h_1 L/2$; area DQZX = $h_2 L/2$; and area DQXY = $h_3 L/2$. But sum of areas DQYZ + DQZX + DQXY = area DXYZ. Hence $(h_1+h_2+h_3) L/2 = h L/2$, which gives $h_1+h_2+h_3 = h$, which is unity for the unit-sum triangle. Thus the sum of the coordinates of any point is unity. (By increasing the height of the equilateral triangle appropriately, the sum of the coordinates of points inside or on the triangle will increase similarly to give any arbitrary constant.)

7.5. Patch selection and intake rate in the field

7.5.1. Effects of patch height and density, and animal experience on selection and intake rate

Experimental work (Allden and Whittaker 1970; Black and Kenney 1984) suggest that IIR of grazing animals may be higher in swards with horizontal heterogeneity in height and density than in homogeneous swards of equal average characteristics. Models of grazing behavior (Demment *et al.* 1987; Ungar and Noy-Meir 1988; Laca and Demment, 1991) predict similar effects based upon the assumption that grazers respond to horizontal heterogeneity in sward structure by selectively grazing on areas that yield greater IIR. The selective responses showed by steers in this study support the idea of a beneficial effect of horizontal heterogeneity in sward structure on the rate of food acquisition. Selective behavior of steers is first discussed in relation to Matching Law (Herrnstein 1970) and Optimal Foraging Theory ("prey and patch" model, Stephens and Krebs 1986), and then discussed in terms of possible underlying mechanisms.

Steers visited different patch types with the same frequency in all treatments (Figure 56). However, they showed selectivity in the allocation of time (Figure 57) and bites (Figure 58) in all treatments but not in all grazing intervals, which resulted in a greater removal of herbage mass from patches that yielded greater IIR (Figure 59). Assuming IIR is a reward to grazing responses, these patterns of selective behavior were not in agreement with matching behavior (ratio of responses equal ratio of rewards). Steers allocated either a disproportionately large (overmatching) or small (undermatching) number of bites to the patch type with higher potential IIR in each treatment grazing-interval combination (Table 25). The degree of overmatching was

higher in T1 than in T2 and T3, evidencing an increased bias of steers to graze tall herbage (assuming no differences in quality). Moreover, the cases of undermatching involved treatments (T2 and T3) in which short patches (SOD) represented the higher potential IIR patch type.

Lack of selectivity of steers in number of visits per patch type is in agreement with maximization. In no case did maximization predict that lower potential IIR patch types should not be entered. This prediction is robust with respect to distance between patches or simultaneity in searching and chewing. For example, in T2 distance between patches can be reduced at least to 50% (or 50% of the time used by chewing during searching) before the patch of lower potential IIR is dropped. On the other hand, the allocation of time and bites in GI1 of all treatments, although not in complete agreement with predicted values, resulted in total intake values consistent with maximization. The slowly decelerated slopes of intake curves (Figure 55) contribute to explain this result. For a given intake function there is a range of residence time that approximate maximization in the rate of food acquisition (see graphical representation of marginal value theorem, Charnov 1976).

In patchy environments grazers need to decide (1) which patches to visit and (2) how much time to spend or how many bites to take per entered patch. The decision of which patches to visit may be made simply and efficiently on the basis of visual cues and previous experience (associative learning, Garcia and Holder 1985), although it has been argued that herbivores may rely on consumption-sampling to discriminate between potential IIRs of vegetation patches (Illius and Gordon 1990). However, in this study steers rarely grazed on alleys between patches. The exceptions were small areas with green and relatively longer tillers growing in depressions of the soil surface. This can be interpreted as circumstantial evidence of visual discrimination between patches. Since the alleys were not only shorter than the patches but also differed in color (except in the aforementioned soil depressions), it cannot be speculated whether animals were discriminating on the basis of color or other characteristics such as height and/or density. The ability of cattle to distinguish colors and shapes and to associate them with food rewards has been demonstrated (Entsu 1989a,b).

Steers were more selective in the allocation of time and bites (decision 2) in GI1, which represented a non-depleted condition. The way steers grazed SOD patches in T1 and T2 clearly indicates that they decided where to

concentrate grazing activities based upon information gathered from the two patch types involved in a treatment. When SOD patches represented the higher of the two potential IIRs (T2), residence time and number of bites in SOD patches were higher (almost twice as much as) than when they represented the lower of the two potential IIRs (T1) (see in Table 26 observed residence time and number of bites for SOD patches in GI1 of T1 and T2). The significant difference in the behavior on SOD patches due to context rules out a simple "rule-of-thumb" based on an instantaneous interaction between the animal and the vegetation. The effect of context indicates that decisions about the use of the current patch were based on more information than provided by the current patch; i.e., they were based on learning. The decisions of "how much time" and/or "how many bites" per patch type may have relied upon either complex cognitive processes such as evaluation and comparison or just upon simple behavioral rules-of-thumb such as "if tall and or dense spend more time and/or take more bites". Whatever the case, steers learned quickly because they grazed selectively since the first 5 min (GI1) of the first exposure. However, a more detailed examination reveals that selectivity in the allocation of time and bites tended to increase with repeated exposures in T1, but not in T2. The difference in potential IIR between patch type was larger in T2 than in T1, which may have facilitated learning in T2. Also, the kind of structural difference between patch type appears to have affected learning. Steers were more responsive to differences in height than to differences in density, as indicated by the differential response in the number of bites to differences in potential IIR in T1 relative to T2 (Table 25). A similar result was observed in artificial swards (see above).

In GI2 and GI3 steers became less selective in the allocation of time and bites per patch type. As patch depletion progressed in GI2 and GI3, patch structures became more alike, and possible cues used by animals to selectively graze high potential IIR patches in GI1 may have become less evident in GI2 and GI3. However, other factors may have influenced grazing behavior in GI2 and GI3. Steers may have become less motivated to graze previously grazed patches. Also, remaining number of potential bites may have constrained selectivity. After being grazed in GI1 and GI2, half-original-density patches were almost completely depleted in GI3.

Grazers such as cattle respond to horizontal heterogeneity in patch height and/or density by concentrating grazing activities on patches that yield

greater IIR. Thus, patchy environments appears to be beneficial to grazers relative to homogeneous conditions of equal average characteristics. Further research should address how patch contrast (degree of structural differences between patches), patch aggregation (spatial distribution of patches), patch density, patch size, animal hunger level, and animal density influence grazer responses to horizontal heterogeneity in patch structure; and how horizontal variability in structural factors in combination with horizontal variability in quality factors (e.g., live/dead ratio or leaf/stem ratio) affects grazer selective responses.

7.5.2. Field test of the marginal value theorem with cattle

The model depicts a forager that trades off searching and residence time. If patches are left too soon, much time is spent walking and IIR declines. If patches are grazed for too long, IIR declines because of the reduced intake rate within patches due to patch depletion.

The increase of IIR with increasing difference in patch heights underlines the importance of patchiness as determinant of intake (Laca and Demment 1991). In all grazing environments tested, average patch height was constant (10 cm). Because of the natural negative relationship between depth in the canopy and bulk density, average herbage mass per patch was 26% lower in the treatments with 5 and 15-cm patches than in the other treatments (100 vs. 130 g, $P < 0.000$). In spite of the lower herbage mass, animals achieved greater IIR by selectively grazing the taller patches.

In spite of the close agreement between mean observed and predicted T_r , IIR was consistently overestimated by the model. This is partially attributed to the nonlinear nature of intake curves and the deviations of T_r at each individual patch from the optimum. When T_r varies, average intake per patch is smaller than that obtained by grazing a patch for the average time.

The agreement between field results and predictions indicates that optimal foraging is a valuable paradigm to understand and predict grazing behavior by cattle. Steers seemed to quickly assess, probably visually (Bazely 1990), the grazing environment and the current patch, and adjusted their patch-residence times in a manner consistent with maximization of IIR.

7.6. Prediction of bite weight and intake rate in the field

The use of this model to predict bite weight and IIR may be complicated by two aspects. First, in swards that are extremely heterogeneous, cattle may be extremely selective in terms of which patches are grazed. In such a situation, a prediction of bite weight on the basis of average sward characteristics is not correct. Measurements of sward characteristics and chews per bite should be stratified by patch types. Bite weight within each patch type should be predicted on the basis of sward height, bulk density and chewing within the patch. Then, average bite weight should be calculated by weighting each bite weight by the proportion of total bites taken from each patch. Intake rate can thus be calculated as the product of average bite weight and average bite rate.

Second, the measurements of chews per bite used to parametrize the model were obtained by listening to the sound of chewing recorded through a microphone installed on the animal. The electronic equipment necessary for obtaining the sound is relatively cheap (\$60-200). However, attaching the microphone on animals and retrieving it may be feasible only on tame animals such as dairy cows, or it may be logistically difficult. An alternative is to develop models based on behaviors that can be observed directly, such as total number of jaw movements per bite.

The coefficients and the model developed in this paper are strictly applicable to large steers (*ca.* 750 kg). There is evidence that sward structure and body size interact in determining bite weight (Illius and Gordon 1987). For a valid extension of this model to cattle of different sizes, it is necessary to experimentally investigate these interactions. As a temporary tool, bite weight can be scaled by body size using allometric relationships between bite weight and body weight (Illius 1989).

8. REFERENCES

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9. TABLES

Table 1. Description of the swards pooled to derive a model for prediction of bite weight.

Experiment (n)	Species	Plant part	Height†	Bulk density	Chews per bite	Bite weight
A1 (52)	alfalfa	shoots	7, 15, 25	3.5±0.16§	3.0±0.17	1.99±0.11
B1 (19)	brome	tillers	10, 15	1.4±0.26	3.9±0.28	1.54±0.19
P1 (10)	dallisgrass	laminae	8, 15, 30	1.9±0.35	1.4±0.38	1.01±0.26
P2 (36)	dallisgrass	laminae	15	1.4±0.19	3.4±0.20	1.51±0.14
P6 (16)	dallisgrass	stems and laminae	15	1.3±0.28	2.9±0.30	0.85±0.21
P7 (28)	dallisgrass	laminae	10, 18	2.0±0.21	4.1±0.23	1.95±0.16
W1 (18)	wheat	laminae	10, 20	1.0±0.26	2.0±0.29	1.00±0.20

† Height is in cm, bulk density in kg m⁻³ and bite weight in g.

§ Numbers indicate mean±standard error.

Table 2. Analysis of variance of sward bulk density according to experimental design. Averages of all modules sampled within each HCS were used as individual observations

Dallisgrass				
Source	df	Mean Square	F-value	P(F>F)
Height	3	162806	3.42	0.033
Holes m ⁻²	2	12505152	262.31	0.000
Height x Holes m ⁻²	6	165834	3.48	0.012
Grodays [†]	1	210143	4.41	0.046
Error	25	47673		

Alfalfa				
Source	df	Mean Square	F-value	P(F>F)
Height	2	230852	1.28	0.305
Holes m ⁻²	2	45068850	249.19	0.000
Height x Holes m ⁻²	4	225468	1.25	0.329
Grodays [†]	1	930846	5.15	0.037
Error	17	180859		

[†] Days of regrowth, since the field was mowed.

Table 3. Least-square means for sward bulk density†

Dallisgrass		Holes m⁻²			
Height cm	388	775	1550	Mean	
8	634	1176	2682		1497
15	672	1842	2567		1694
18	731	1594	2693		1673
30	825	1360	2903		1696
Mean	715	1493	2711		

Alfalfa		Holes m⁻²			
Height cm	388	775	1550	Mean	
7	1813	3237	5836		3629
15	1612	2272	6250		3378
25	1189	2996	5637		3274
Mean	1538	2835	5908		

†Sward bulk density is expressed in g DM m⁻³.

Table 4. Partition of the variance in sward bulk density.

Dallisgrass			
Source of variation	df	Mean Square	Mean (g m ⁻³)
Treatments	11	6476526	
Between HCS within treatments	26	137282	
Between modules within HCS	69	48387	
Total	106		1670

Alfalfa			
Source of variation	df	Mean Square	Mean (g m ⁻³)
Treatments	8	36360898	
Between HCS within treatments	18	752206	
Between modules within HCS	60	646854	
Total	86		3510

Table 5. Comparison of means of bite weights and volumes estimated by the three methods described in the text

Method	Dallisgrass		Alfalfa	
	Bite weight (g)	Bite volume [†] (cm ³)	Bite weight (g)	Bite volume [†] (cm ³)
1	3.37±0.72 [§]	2544±606	3.59±0.31	1243±178
2	1.88±0.20	1422±164	2.08±0.24	690±101
3	1.70±0.17	1266±135	1.93±0.22	656±105

[†] Bite volume was calculated as bite weight divided by bulk density of the grazed horizon.

[§] Numbers are mean±S.E. of the mean.

Table 6. Treatments effects on the ratio of chews determined by the standard method over chews counted by listening to the sound

Alfalfa	Holes m ⁻²			Mean
	Height cm	388	775	
7	1.47	1.00	1.01	1.16
15	0.67	0.74	0.74	0.71
25	0.73	0.72	0.83	0.76
Mean	0.96	0.82	0.86	

S.E. = 0.078, Error df = 24. Probability values are 0.000, 0.147 and 0.010 for height, density and interaction, respectively.

Table 7. Canopy bulk density, bulk density of the grazed horizon, and percentage of stem in the grazed horizon of hand-constructed swards as affected by sward height, number of holes filled with herbage per m², and days of regrowth (covariate).

Dallisgrass swards (100% leaf lamina)													
Holes m ⁻²	388				775				1550				Days of regrowth mean = 67 (slope ± s.e.)
Height mm	80	150	180	300	80	150	180	300	80	150	180	300	
Canopy bulk density g m ⁻³	634	672	731	825	1176	1842	1594	1360	2682	2567	2693	2903	
S.E. Lsmean	140	127	130	149	128	134	126	111	140	112	130	148	
Grazed bulk density g m ⁻³	626	637	687	714	1171	1737	1488	1140	2648	2407	2504	2432	5.7 ± 2.6
S.E. Lsmean	136	123	126	145	124	130	122	108	136	110	126	143	

Alfalfa swards													
Holes m ⁻²	388			775			1550			Days of regrowth mean = 20 (slope ± s.e.)			
Height mm	70	150	250	70	150	250	70	150	250				
Canopy bulk density g m ⁻³	1813	1612	1189	3237	2272	2996	5836	6250	5637				
S.E. Lsmean	257	249	250	250	288	269	249	246	246				
Grazed bulk density g m ⁻³	1938	1701	1364	3380	2386	3222	6116	6911	6174				41.6 ± 22.0
S.E. Lsmean	274	265	266	266	307	287	265	262	262				
Grazed %	24	33	37	32	37	42	30	31	33				1.29 ± 0.15
Stem													
S.E. Lsmean	2	2	2	2	2	2	2	2	2				

Table 8. Summary of P(F>F) for effects of treatments and days of regrowth (covariate).

Variable	Source									
	Height		Holes m ⁻²		Height * Holes m ⁻²				Days of regrowth	
	L†	Q	L	Q	L*L	L*Q	Q*L	Q*Q	Slope	P(F>F)
<i>Dallisgrass</i>										
Bite area	0.000	0.002	0.000	0.874	0.020	0.913	0.122	0.096	0.290	0.227
Bite depth	0.000	0.018	0.103	0.001	0.054	0.000	0.436	0.007	0.014	0.197
Bite volume	0.000	0.077	0.000	0.044	0.000	0.005	0.614	0.791	5.043	0.103
Bite weight	0.000	0.083	0.000	0.201	0.188	0.568	0.683	0.157	0.010	0.239
Incisor height	0.000	0.094	0.062	0.001	0.232	0.000	0.268	0.108	-0.014	0.394
Bulk density	0.204	0.162	0.000	0.168	0.675	0.525	0.200	0.006	5.645	0.046
Grazed bulk density	0.524	0.123	0.000	0.175	0.334	0.535	0.246	0.008	5.663	0.042
<i>Alfalfa</i>										
Bite area	0.011	0.287	0.000	0.243	0.008	0.237	0.714	0.840	-2.588	0.011
Bite depth	0.000	0.004	0.001	0.542	0.000	0.395	0.929	0.936	-0.134	0.003
Bite volume	0.000	0.106	0.000	0.211	0.000	0.063	0.925	0.383	-44.764	0.001
Bite weight	0.000	0.204	0.004	0.448	0.824	0.514	0.526	0.493	-0.062	0.093
Incisor height	0.000	0.003	0.000	0.649	0.000	0.301	0.940	0.460	0.221	0.038
Bulk density	0.105	0.653	0.000	0.378	0.510	0.503	0.140	0.019	46.853	0.037
Grazed bulk density	0.322	0.836	0.000	0.205	0.332	0.564	0.042	0.017	41.628	0.078
% Stem	0.000	0.627	0.760	0.000	0.076	0.265	0.513	0.632	0.969	0.000
Grazed % Stem	0.001	0.495	0.449	0.001	0.017	0.900	0.279	0.741	1.292	0.000

[†] L = Linear effects; Q = quadratic effects.

Table 9. Least-square means of bite dimensions and bulk density of the grazed horizon by animal, and animal live weights.

Variable	Units	Animal #			S.E.	P-value		
		1	3	8		1 vs 3	1 vs 8	3 vs 8
Live weight	kg	680	761	817				
<i>Dallisgrass</i>								
Bite depth	mm	91	102	97	2.4	0.003	0.051	0.238
Incisor height	mm	61	51	58	3.8	0.095	0.593	0.253
Bite area	cm ²	128	107	118	5.4	0.011	0.207	0.160
Bite volume	cm ³	1242	1124	1262	69	0.231	0.834	0.174
Grazed bulk density	g m ⁻³	1444	1612	1492	61	0.059	0.575	0.180
Bite weight	g	1.56	1.87	1.83	0.19	0.257	0.327	0.870
<i>Alfalfa</i>								
Bite depth	mm	79	69	67	2.5	0.017	0.005	0.564
Incisor height	mm	56	72	69	3.2	0.034	0.015	0.473
Bite area	cm ²	93	73	87	6.1	0.035	0.503	0.124
Bite volume	cm ³	820	516	633	73	0.010	0.090	0.275
Grazed bulk density	g m ⁻³	3425	3922	3718	151	0.035	0.190	0.355
Bite weight	g	2.04	1.84	2.37	0.24	0.562	0.333	0.132

Table 10. Probability levels for the effects and interactions of hand-constructed sward height and density.

Variable	Effects		
	Height	Lamina length	Interaction
<i>Exp. 1</i>			
Bite depth	0.000	0.629	0.896
Bite area	0.004	0.433	0.861
Bite weight	0.000	0.306	0.491
Tongue sweeps per bite	0.551	0.411	0.718
Incisor height	0.000	0.977	0.435
<i>Exp. 2</i>			
Bite depth	0.004	0.000	0.005
Bite area	0.313	0.045	0.286
Bite weight	0.267	0.003	0.365
Tongue sweeps per bite	0.779	0.297	0.718
Incisor height	0.000	0.000	0.011

Table 11. Comparison of observed bite dimensions on hand-constructed dallisgrass swards with values previously observed on dallisgrass swards made of leaf lamina with similar height and bulk density.

	Sward height (cm)				
	8		16		
Pseudostem or stem height (cm)	3	0	11	8	
	Lamina length (cm)				
Sward type	5	8	5	8	SE
	Bite depth (cm)				
Vegetative	5.2	5.1	9.8	9.5	0.3
Reproductive	4.1	5.1	4.1	6.8	0.2
Laca <i>et al.</i> [†]	4.7			8.9	0.5
Ungar <i>et al.</i> [§]	4.9			--	0.1
	Bite area (cm ²)				
Vegetative	70	73	90	95	5
Reproductive	40	47	40	57	5
Laca <i>et al.</i>	80			124	11
Ungar <i>et al.</i>	91			--	4

[†] Laca *et al.*, 1992a; values for 16-cm swards were interpolated from measurements on 15- and 18-cm swards.

[§] Ungar *et al.*, 1991; values interpolated from measurements on vertically heterogeneous swards of 6 and 10 cm avg. height.

Table 12. Tongue sweeps per bite and bite DM weight in hand constructed dallisgrass swards with pseudostem (vegetative swards) or stem (reproductive swards) at the base.

Sward type	Sward height (cm)				SE
	8		16		
	Lamina length (cm)				
	5	8	5	8	
	Tongue sweeps per bite				
Vegetative	0.90	0.83	0.87	0.70	0.13
Reproductive	0.91	0.68	0.90	0.78	0.15
	Bite weight (g OM)				
Vegetative	0.57	0.46	1.32	1.30	0.06
Reproductive	0.09	0.34	0.08	0.24	0.04

Table 13. Effects of height and bulk density of alfalfa swards on bite weight, bolus weight, instantaneous intake rate, and chews per g of DM ingested. Means followed by different letters are significantly different by Fisher's LSD at the 0.01 level.

LSD at the 0.01 level.

		Density [£]	Height (cm)			
			7	15	25	Mean
Bite weight (g)	388	0.454	1.579	1.692	1.242 ^a	
	775	0.909	1.425	2.717	1.684 ^a	
	1550	1.430	2.707	3.578	2.572 ^b	
	Mean	0.931 ^a	1.904 ^b	2.662 ^c	P _{HxD} =0.32	
Bolus weight (g)	388	4.31	10.65	13.28	9.41 ^a	
	775	6.93	10.11	13.96	10.33 ^a	
	1550	10.01	13.30	17.53	13.61 ^b	
	Mean	7.08 ^a	11.35 ^b	14.92 ^c	P _{HxD} = 0.51	
IIR[§] (g/min)	388	45.5	51.6	50.4	49.2 ^a	
	775	46.9	43.0	53.3	47.7 ^a	
	1550	45.8	48.9	44.0	46.2 ^a	
	Mean	46.1 ^a	47.9 ^a	49.2 ^a	P _{HxD} = 0.33	
Chews per g DM[§]	388	1.32	1.44	1.37	1.38 ^a	
	775	1.21	1.60	1.14	1.32 ^a	
	1550	1.56	1.34	1.36	1.42 ^a	
	Mean	1.36 ^a	1.46 ^a	1.29 ^a	P _{HxD} = 0.36	

[§] Effects of bite weight on IIR, and of bolus weight on chews per g DM (shown in Figures 4.2 and 4.11b) were removed prior to ANOVA.

[£] Density units are number of holes filled with herbage m⁻².

Table 14. Ingestive behavior in alfalfa swards of the three animals used as replicates.

Variable	Units	Animal #			P-value		
		1	3	8	1 vs 3	1 vs 8	3 vs 8
Live weight	kg	680	761	817			
Bite weight	g	1.767	1.446	2.285	0.223	0.057	0.002
Bolus weight	g	8.31	10.67	14.38	0.005	0.000	0.000
IIR	g/min	39.4	54.8	49.0	0.000	0.007	0.079
Chews per g DM	chews/g	1.54	1.26	1.32	0.021	0.054	0.309
Time per bite	s	2.76	1.93	2.16	0.000	0.001	0.152
Total jaw movements per bite	----	3.35	2.11	2.61	0.000	0.007	0.062
Exclusive chews per bite	----	1.25	0.81	0.69	0.010	0.002	0.249
Total chews per bite	----	3.08	2.11	2.13	0.000	0.000	0.466
Total manipulations per bite	----	2.12	1.31	1.94	0.000	0.118	0.000
Chewing-manipulative/ Total manipulative jaw movements	----	0.86	0.90	0.71	0.125	0.000	0.000

Table 15. Effects of height and density of alfalfa swards on allocation of jaw movements per bite. Effects of bite weight on all variables (shown in Figures) were removed prior to ANOVA.

	Density [£]	Height (cm)			Mean
		7	15	25	
Time per bite (s)	388	2.20	2.20	2.19	2.20 ^a
	775	2.24	2.51	2.08	2.28 ^a
	1550	2.40	2.32	2.42	2.38 ^a
	Mean	2.28 ^a	2.35 ^a	2.23 ^a	P _{HxD} =0.68
Total jaw movements per bite	388	2.63	2.65	2.40	2.56 ^a
	775	2.67	2.97	2.33	2.66 ^a
	1550	3.00	2.82	2.73	2.85 ^a
	Mean	2.77 ^a	2.81 ^a	2.49 ^a	P _{HxD} =0.88
Exclusive chews per bite	388	0.78	0.95	0.78	0.83 ^a
	775	0.72	1.18	0.71	0.87 ^a
	1550	1.02	0.78	1.32	1.04 ^a
	Mean	0.84 ^a	0.97 ^a	0.93 ^a	P _{HxD} =0.23
Total chews per bite	388	2.37	2.46	2.23	2.35 ^a
	775	2.38	2.77	1.97	2.37 ^a
	1550	2.70	2.50	2.59	2.59 ^a
	Mean	2.48 ^a	2.58 ^a	2.26 ^a	P _{HxD} =0.63
Total manip. per bite	388	1.90	1.71	1.63	1.75 ^a
	775	1.97	1.81	1.62	1.80 ^a
	1550	2.00	2.04	1.43	1.82 ^a
	Mean	1.96 ^a	1.85 ^a	1.56 ^b	P _{HxD} =0.40
<u>CHMJW</u>[§] TMJW	388	0.86	0.83	0.87	0.85 ^a
	775	0.78	0.83	0.80	0.80 ^a
	1550	0.80	0.81	0.84	0.82 ^a
	Mean	0.81 ^a	0.83 ^a	0.84 ^a	P _{HxD} =0.65

[§] Chewing-manipulative jaw movements as proportion of total manipulative jaw movements

Table 16. Relationship between length of chewing bouts and position of the head while chewing. Numbers in the body of table indicate number of bouts. All data from alfalfa swards was pooled.

Chews per bout	Head position while chewing	
	Head down	Head up
1	272	0
2	59	0
3	7	2
4 to 7	5	10
more than 7	0	23

$G^2 = 204.6$, $P = 0.0000$.

Table 17. Average bite weight, time per bite, and number of bites placed on areas previously grazed (bites in second horizon, H₂) as affected by sward structure and total number of bites removed from the patch. HCS experiment.

		Sward [†]	Total number of bites					
			10	20	30	40	45	60
Bite weight (g)	S-D	0.78 [§]	0.78	0.78	0.70	0.71	0.65	0.72 ^a
	T-S	1.27	1.22	1.20	1.03	0.91	0.78	1.06 ^b
	Mean	1.02 ^a	1.00 ^a	0.99 ^a	0.86 ^{ab}	0.81 ^b	0.72 ^b	
Time bite ⁻¹ (s)	S-D	1.27	1.48	1.39	1.24	1.49	1.49	1.40 ^a
	T-S	1.31	1.17	1.38	1.25	1.48	1.23	1.28 ^a
	Mean	1.29 ^a	1.33 ^a	1.38 ^a	1.25 ^a	1.49 ^a	1.36 ^a	
Bites in H ₂	S-D	1.0 ^a	0.7 ^a	2.0 ^{ab}	5.0 ^{bc}	3.0 ^{ab}	10.5 ^d	3.7
	T-S	0.0 ^a	0.7 ^a	0.5 ^a	2.7 ^{ab}	8.0 ^{cd}	22.0 ^e	5.6
	Mean	0.5	0.7	1.3	3.8	5.5	16.3	

[†] S-D (short dense): 10 cm, 1300±15 g m⁻³; T-S (tall sparse): 20 cm, 656±15 g m⁻³.

[§] Means followed by the same letter do not differ significantly at the 5% level by Fisher's LSD. The interaction between number of bites and sward structure was not significant for bite weight and time per bite. Thus, means were not separated.

Table 18. Parameter values of the rectangular hyperbola of intake curves fitted for steers grazing 0.46 m² patches of wheat swards constructed by hand.

Sward	Parameter	Units	Value	95% CI
Short, dense	k ₁	g s ⁻¹	0.690	0.649 , 0.734
	k ₂	s ⁻¹	0.0065	0.0005 , 0.0078
Tall, sparse	k ₁	g s ⁻¹	1.636	1.141 , 2.473
	k ₂	s ⁻¹	0.0232	0.0107 , 0.0457

Table 19. Average bite area in the top horizon as a function of sward structure and number of bites removed from the top horizon.

Parameter	DF	Estimate	SE	t Ratio	P> t
Intercept	--	137	5.1	26.94	0.000
Animal (+A ₁ =A ₂)	1	9.2	1.93	4.75	0.000
Height (+H ₁₀ =H ₂₀)	1	-31	5.1	-6.02	0.000
Number of bites (X)	1	-0.87	0.166	-5.24	0.000
X*Height (+H ₁₀ =H ₂₀)	1	0.37	0.166	2.25	0.035

Table 20. Parameter values of the rectangular hyperbola of intake curves for steers grazing 0.4-m² patches of perennial ryegrass. k_1 has units of g·s⁻¹, and k_2 has units of s⁻¹. N = 5 in all cases.

Animal	Height (cm)	k_1 (95% CI)	k_2 (95% CI)	R ²
1	7	0.670 (0.518, 0.876)	0.0038 (0.0009, 0.0080)	0.993
	12.5	0.797 (0.648, 0.992)	0.0004 (-0.0015, 0.0030)	0.990
	18	1.495 (1.258, 1.790)	0.0054 (0.0027, 0.0088)	0.995
2	7	0.896 (0.866, 0.928)	0.0037 (0.0031, 0.0043)	0.999
	12.5	1.020 (0.851, 1.229)	0.0024 (-0.0004, 0.0059)	0.997
	18	1.344 (1.172, 1.545)	0.0040 (0.0018, 0.0067)	0.999
8	7	1.025 (0.700, 1.556)	0.0032 (-0.0016, 0.0117)	0.992
	12.5	1.257 (1.182, 1.337)	0.0026 (0.0018, 0.0035)	0.999
	18	1.852 (1.581, 2.180)	0.0057 (0.0037, 0.0083)	0.997

Table 21. Average herbage mass per patch and asymptotic values of the fitted Michaelis-Menten intake curves.

Experiment	Sward structure	Herbage	
		mass/patch (g)	k ₁ /k ₂ (g)
HCS	10 cm	60	106
	1300 g m ⁻³		
	20 cm	60	71
Field	656 g m ⁻³		
	7 cm	135	133
	4800 g m ⁻³		
	12.5 cm	184	479
	3700 g m ⁻³		
	18 cm	256	504
	3600 g m ⁻³		

Table 22. Comparison of observed vs. predicted values of bite weight. Observed values are means of 12 observations.

Patch type	Height (cm)	Bulk density (kg m ⁻³)	Bite weight	
			Observed ¹ g OM	Predicted ² g DM
(TOD)	12	3.3	1.08	0.95
(SOD)	7.5	4.5	0.99	0.97
(THOD)	12	1.5	0.93	1.05
(SHOD)	7.5	2.6	0.80	0.84

¹SE = 0.04

²Laca *et al.*, 1992b

Table 23. Instantaneous intake rate. Patch types are as in Table 22. Values are means of 41-67 observations (depending on treatment grazing-interval combination), and include 3 animals and 3 repetitions per animal.

Grazing Interval (min)	Treatment								
	1			2			3		
	TOD	SOD	SE	SOD	SHOD	SE	SOD	THOD	SE
	(g OM min ⁻¹)								
0-5	63a	57b	1.02	53a	42b	1.39	56a	56a	1.43
5-10	47a	52b	1.79	44a	35b	1.99	47a	44a	2.28
10-15	41a	41a	1.60	39a	27b	1.64	40a	31b	1.62

In each row within a treatment means with the same letter are not different ($P > .05$).

Table 24. Bite rate. Patch types are as in Table 22. Values are means as in Table 22.

Grazing Interval (min)	Treatment								
	1			2			3		
	TOD	SOD	SE	SOD	SHOD	SE	SOD	THOD	SE
	bites min ⁻¹								
0-5	65a	58b	1.30	56a	59b	1.20	57a	64b	1.22
5-10	59a	58a	1.54	53a	56a	2.06	55a	62b	2.69
10-15	58a	53b	1.73	52a	55b	1.70	54a	57a	0.51

In each row within a treatment means with the same letter are not different ($P > .05$).

Table 25. Comparison of bite and instantaneous intake rate (IIR) ratios of tall original-density to short original-density patches (T1), short original-density to short half-original-density patches (T2), and short original-density to tall half-original-density patches (T3). Number of bites and IIR values are means as in Table 22.

Grazing Interval (min)	Treatment					
	1		2		3	
	IIR Ratio	Bite Ratio	IIR Ratio	Bite Ratio	IIR Ratio	Bite Ratio
0-5	1.11	1.65 ¹	1.26	1.41 ¹	1.00	1.10 ¹
5-10	0.90	1.14 ¹	1.26	1.06 ²	1.07	1.25 ¹
10-15	1.00	1.12 ¹	1.44	1.10 ²	1.29	1.27 ²

¹Disproportionately large (overmatching) response (bites) to changing dietary reward (IIR).

²Disproportionately small (undermatching) response (bites) to changing dietary reward (IIR).

Table 26. Comparison of observed vs. predicted values of residence time and number of bites per patch type and total intake in Grazing Interval 1. Patch types are as in Table 22. Observed values of time and bites are as in Table 22, whereas observed values of intake are means of 9 observations.

Treatment	Residence Time			Number of Bites			Total Intake		
	Observed		Predicted ¹	Observed		Predicted	Observed		Predicted
	sec per patch			bites per patch			g OM		
	X	SE		X	SE		X	SE	
TOD	25	1.1	25	27	1.0	271	282	13	280
SOD	17	1.4	11	16	1.2	10			
SOD	30	1.5	33	27	1.3	31	224	12	238
SHOD	20	1.3	4	19	1.2	4			
SOD	22	1.5	27	21	1.4	26	253	10	253
THOD	17	1.0	18	19	1.0	19			

¹"prey and patch" model (Stephens and Krebs 1986).

Table 27. Coefficients of the model to predict bite weight on the basis of Ln(chews per bite), sward height (cm), and Ln(bulk density, kg m⁻³).

Term	Coefficient	S.E.	α -level
Intercept	-1.335	0.1119	0.0000
Ln Chews/bite	0.466	0.0491	0.0000
Height	0.0633	0.00677	0.0000
Ln Bulk density	0.649	0.1076	0.0000
Height*Ln Bulk density	-0.0166	0.00647	0.0109

MSE = 0.079, R^2 = 0.723, n = 179.

Table 28. Model of gain curves and parameter values based on horizon grazing, HCS experiment.

$$I = \text{BWT}_{1,s} * N_{1,s} + \text{BWT}_{2,s} * N_{2,s} \quad \text{intake, g DM}$$

$$N_{1,s} = \min\left\{ \frac{T}{t_b} * (1 - \text{RG}_s), \frac{A}{\text{BA}_{1,s}} \right\} \quad \text{bites in horizon 1}$$

$$N_{2,s} = \frac{T}{t_b} - N_{1,s} \quad \text{bites in horizon 2}$$

T is patch residence time. The subscript s refers to the structure of the sward; s = 10 indicates the short dense swards, and s = 20 indicates the tall sparse swards.

Parameters	Definition	Value	Units
BWT _{1,10}	Bite weight, 10-cm swards, horizon 1	0.755	g
BWT _{2,10}	Bite weight, 10-cm swards, horizon 2	0.288	g
BWT _{1,20}	Bite weight, 20-cm swards, horizon 1	1.111	g
BWT _{2,20}	Bite weight, 20-cm swards, horizon 2	0.374	g
t _b	Total time per bite	1.37	s
RG ₁₀	Proportion of bites in horizon 2 before depletion of horizon 1; 10-cm swards	0.065	---
RG ₂₀	Proportion of bites in horizon 2 before depletion of horizon 1; 20-cm swards	0.036	---
A	Total area of the patch	0.46	m ²
BA _{1,10}	Bite area in horizon 1, 10-cm swards	153	cm ²
BA _{1,20}	Bite area in horizon 1, 20-cm swards	102	cm ²

Table 29. Fitted values for the parameters that represent bite weight in the first and second horizons of hand-constructed swards.

Sward	Horizon	Bite weight (g)	95% Confidence interval
Short, dense	Top	0.75	0.70 , 0.81
	2nd	0.25	0.07 , 0.43
Tall, sparse	Top	1.32	1.15 , 1.49
	2nd	0.14	-0.22 , 0.49

10. FIGURES

Figure 1. Hierarchical levels, processes and scales covered within the present project.

Figure 2. Detail of module for construction of swards, and HCS.

Figure 3. Graphical description of how tillers were trimmed to obtain the desired sward structures with vertical heterogeneity.

Figure 4. Estimated incisor height by cattle grazing hand-constructed swards made of vegetative (Exp. 1) or reproductive (Exp. 2) dallisgrass tillers. In Exp. 1 the difference between sward height (SH) and lamina length (LL) is pseudostem length, and in Exp. 2 the difference between sward height (SH) and lamina length (LL) is stem length; A) SH = 8 cm, LL = 5 cm; B) SH = 8 cm, LL = 8 cm; C) SH = 16 cm, LL = 5 cm; D) SH = 16 cm, LL = 8 cm. Incisor height is indicated by a thick black line. Thin horizontal lines represent the expected incisor height on the basis of previous experiments with swards made exclusively of leaf lamina (Laca *et al.*, 1992a). Vertical bars indicate SE of means within each experiment.

Figure 5. Patch sizes within hand-constructed swards with horizontal heterogeneity in plant parts. The area of the modules (10x10 cm) was similar to the area of one bite.

Figure 6. Bulk density of control sward and patches of different heights and densities by 5-cm horizons.

Figure 7. Bulk density profile of hand-constructed swards of alfalfa and dallisgrass.

Figure 8. Percentage of stem by 50-mm horizons in the alfalfa swards. Horizontal bars indicate S.E. of the means.

Figure 9. Bite area and bite depth least-square means of cattle grazing uniform hand-constructed swards of dallisgrass and alfalfa. Symbols indicate means of three animals adjusted for covariate (days of regrowth) effects. Vertical bars are the s.e. of adjusted means.

Figure 10. Fitted response surfaces for bite area (BA, cm²) and bite depth (BD, cm) as functions of sward height (X, cm) and bulk density (Y, g m⁻³). BA = 53.1 + 7.43X - 0.0729X² - 1.426 10⁻³XY, if X < 50.95 - 9.78 10⁻³Y, BA = 242.3 - 0.0726Y + 6.973 10⁻⁶Y², if X > 50.95 - 9.78 10⁻³Y, R² = 0.78; BD = 0.81 + 0.53X - 3.015 10⁻⁵XY, R² = 0.88.

Figure 11. Incisor height and bite volume least-square means of cattle grazing uniform hand-constructed swards of dallisgrass and alfalfa. Symbols indicate means of three animals adjusted for covariate (days of regrowth) effects. Vertical bars are the s.e. of adjusted means.

Figure 12. Bite weight least-square means of cattle grazing uniform hand-constructed swards of dallisgrass and alfalfa. Symbols indicate means of three animals adjusted for covariate (days of regrowth) effects. Vertical bars are the s.e. of adjusted means.

Figure 13. Bite weights on hand-constructed dallisgrass swards differing in height and bulk density when offered at different times after the initiation of grazing.

Figure 14. Relationship between sward bulk density and density of leaves for HCS of oats and dallisgrass. Vertical bars are S.E.

Figure 15. Relationship between bite area and leaf density of swards made of oats and dallisgrass. Vertical bars are S.E.

Figure 16. Relationships between bite area and bulk density of HCS made of oats and dallisgrass. Symbols represent the means of 3 animals. Slopes of the curves are significantly different ($P < 0.05$), and intercepts are not different.

Figure 17. Bite depth as affected by bulk density of swards constructed with oat or dallisgrass leaves. Slopes are not significantly different ($P > 0.05$).

Figure 18. Bulk density of *Bromus mollis* L. hand-constructed swards by 5-cm horizons. Dashed line: 10-cm swards; solid line: 15-cm swards; open symbols: 388 tillers m⁻², solid symbols: 775 tillers m⁻²; circles: tillers in early flowering stage, triangles: tillers in late flowering stage.

Figure 19. Partition of variance in bite area of cattle grazing *Bromus mollis* L. HCS according to explanatory variables.

Figure 20. Bulk density of hand-constructed dallisgrass swards by 4-cm vertical horizons. Experiments on the effects of vertical heterogeneity of the canopy on bite weight. Horizontal bars indicate SE of means.

Figure 21. Bite weight of cattle grazing HCS with horizontal heterogeneity in height and density at two scales. D and H indicate density and height heterogeneity; 1 and 4 indicate patches of 100 or 400 cm², respectively. C is the homogeneous control. Vertical bars are S.E.

Figure 22. Comparison of average bite area observed on heterogeneous swards and values predicted based on the average characteristics of the swards and previous experiments (see section on bite dimensions on homogeneous swards). D and H indicate density and height heterogeneity; 1 and 4 indicate patches of 100 or 400 cm², respectively. C is the homogeneous control.

Figures 23. Comparison of bite depth on the different patches of heterogeneous swards, with values predicted based on equations derived for homogeneous swards. The solid line represents predicted values adjusted for the deviation of the homogeneous control from its predicted value.

Figures 24. Comparison of incisor height on the different patches of heterogeneous swards, with values predicted based on equations derived for homogeneous swards. The solid line represents predicted values adjusted for the deviation of the homogeneous control from its predicted value.

Figures 25. Intake rate by cattle grazing a 15-cm homogeneous sward and heterogeneous swards. D and H indicate density and height heterogeneity; 1 and 4 indicate patches of 100 or 400 cm², respectively. C is the homogeneous control. Vertical bars are S.E.

Figure 26. Selectivity of cattle for patches of greater height or density within the feeding site. Experiment 1.

Figures 27. Bite areas for leaf and stem patches arranged at two scales of horizontal heterogeneity in experiment 2. Vertical bars represent LSD's at the 5% level for leaf (L) and stem (S) patches.

Figure 28. Bite depths for leaf and stem patches arranged at two scales of horizontal heterogeneity in experiment 2. Vertical bars represent LSD's at the 5% level for leaf (L) and stem (S) patches.

Figure 29. Bite weights for leaf and stem patches arranged at two scales of heterogeneity in experiment 2. Vertical bars represent LSD's at the 5% level for leaf (L) and stem (S) patches.

Figure 30. Instantaneous intake rate on swards with leaf and stem patches arranged at two scales of heterogeneity in experiment 2.

Figure 31. Selectivity for leaf and stem patches arranged at two scales of heterogeneity in experiment 2. Selectivity was measured as the proportion of the total grazed area on leaf patches.

Figure 32. Reduction in bite weight due to alfalfa patch depletion. The ordinate indicates the ratio of average bite weight obtained during a grazing session of more than 60 s to average bite weight when steers were allowed to remove only 6-10 bites from swards of similar structure. The abscissa represents the ratio of total number of bites taken during the grazing session and the maximum number of bites steers could obtain without regrazing tillers. $Y = 0.0109(\pm 0.0294) - 0.6368(\pm 0.0771) X$, $r^2 = 0.74$, $MSE = 0.0187$, $n = 26$).

Figure 33. Relationship between instantaneous intake rate and bite weight. Solid symbols and solid line represent observed data; $Y = X [0.02326(\pm 0.00244) + 0.008353(\pm 0.001179) X]^{-1}$, $R^2 = 0.80$, $MSE = 62.23$, $n = 41$. Open symbols and broken line represent IIR if chewing and manipulation had not overlapped; $Y = X [0.03135(\pm 0.00334) + 0.011851(\pm 0.001589) X]^{-1}$, $R^2 = 0.82$, $MSE = 30.62$, $n = 36$. Squares represent data from dallisgrass swards.

Figure 34. Relationship between time per bite and total number of jaw movements per bite. $Y = 0.430(\pm 0.0627) + 0.682(\pm 0.0222) X$, $r^2 = 0.96$, $MSE = 0.0171$, $n = 42$. Squares represent data from dallisgrass swards.

Figure 35. Total time per bite as affected by bite weight. $Y = 1.948(\pm 0.081) + 0.1037(\pm 0.0141) X^2$, $R^2 = 0.58$, $MSE = 0.1656$, $n = 41$.

Figure 36. Effect of bite weight on the number of chewing-manipulative jaw movements per bite as a proportion of the total number of manipulative jaw movements per bite. $Y = [1.028(\pm 0.097) X - 0.246(\pm 0.066)] [0.234(\pm 0.249) + X]^{-1}$, $R^2 = 0.69$, $MSE = 0.0179$, $n = 36$. Squares represent data from dallisgrass swards.

Figure 37. Relationship between total number of manipulative jaw movements per bite and bite weight. $Y = 1.812 - 0.133 X + 0.0524 X^2$, $R^2 = 0.07$, $n = 36$.

Figure 38. Effects of bite weight on number of exclusively chewing jaw movements (Y1, filled symbols) and on total number of jaw movements per bite (Y2, open symbols). $Y_1 = 0.58(\pm 0.22) - 0.062(\pm 0.235) X + 0.132(\pm 0.050) X^2$, $R^2 = 0.70$, $MSE = 0.148$, $n = 37$. $Y_2 = 2.44(\pm 0.37) - 0.265(\pm 0.399) X + 0.198(\pm 0.085) X^2$, $R^2 = 0.54$, $MSE = 0.425$, $n = 37$. Squares represent data from dallisgrass swards.

Figure 39. Relationship between total chews per bite and bite weight. $Y = 0.735(\pm 0.184) + 0.892(\pm 0.097) X$, $R^2 = 0.71$, $MSE = 0.349$, $n = 36$. Squares represent data from dallisgrass swards.

Figure 40. Relationship between chewing per unit herbage mass ingested and bite weight $Y = 0.957(\pm 0.115) + 0.653(\pm 0.100) X^{-1}$, $R^2 = 0.56$, $MSE = 0.164$, $n = 36$. Squares represent data from dallisgrass swards.

Figure 41. Cumulative distribution of chewing bouts and exclusive chews according to length of bouts. Data from 26 grazing sessions in alfalfa were pooled (data from one session was lost due to microphone malfunction).

Figure 42. Relationship between proportion of the total number of exclusively chewing jaw movements performed in bouts of different duration, and bite weight.

Figure 43. Average bite weight in each incremental set of bites removed by cattle from homogeneous patches of wheat made by hand. Vertical bars represent the standard error of the mean.

Figure 44. Intake curves, the relationship between total amount of forage removed from a patch and patch-residence time, for hand-constructed wheat swards of equal herbage mass and contrasting structure. Open circles indicate intake in the 20-cm swards and filled circles indicate intake in the 10-cm swards. Broken lines represent intake predicted by a rectangular hyperbola; 10-cm swards: $R^2 = 0.997$, 20-cm swards: $R^2 = 0.838$. Parameter values are given in Table 18. Solid lines represent intake predicted by the model based on horizon grazing shown in Table 5.6; 10-cm swards: $R^2 = 0.981$, 20-cm swards: $R^2 = 0.824$. Bite weights were fitted by non-linear regression and are shown in Table 29. The data point enclosed in a circle was considered an outlier and not included in the analyses because its jackknifed distance (SAS Institute 1989) was more than 4 times as large as any other one.

Figure 45. Effect of number of bites removed from the patch on apparent bite area (area grazed/total number of bites, circles) and actual bite area in the first horizon (area grazed/number of bites in the first horizon, triangles). Open symbols represent 20-cm, 656-g m⁻³ swards, filled symbols represent 10-cm, 1300 g m⁻³ swards.

Figure 46. Proportion of bites taken from the second horizon of hand constructed swards as a function of the proportion of the area that was grazed at least once. The solid line indicates the expected values assuming random placement of bites. Filled circles: 10-cm swards, open circles: 20-cm swards.

Figure 47. Effect of number of bites removed from field-ryegrass patches of different heights on bite weight obtained by esophageally fistulated steers.

Figure 48. Intake curves relating the total intake from 0.4 m² field patches of ryegrass to patch-residence time by steers. Circles: 7-cm patches, $Y = 1.07 \cdot X \cdot (1 + 0.008 \cdot X)^{-1}$, $R^2 = 0.82$. Squares: 12.5-cm patches, $Y = 1.05 \cdot X \cdot (1 + 0.002 \cdot X)^{-1}$, $R^2 = 0.93$. Triangles: 18-cm patches, $Y = 1.36 \cdot X \cdot (1 + 0.003 \cdot X)^{-1}$, $R^2 = 0.96$.

Figure 49. Cumulative intake as a proportion of initial herbage mass in the field patch as a function of patch residence time. Data from patches of all three heights (7, 12.5 and 18 cm) were pooled within animals. Circles: animal #1, $Y = 0.0058 \cdot X \cdot (1 + 0.0037 \cdot X)^{-1}$, $R^2 = 0.88$. Squares: animal #2, $Y = 0.0070 \cdot X \cdot (1 + 0.0038 \cdot X)^{-1}$, $R^2 = 0.95$. Triangles: animal #8, $Y = 0.0093 \cdot X \cdot (1 + 0.0073 \cdot X)^{-1}$, $R^2 = 0.91$.

Figure 50. Behavior of the eight constraints (C1-C8) on the proportions of bites taken from three grazing horizons. Striped area indicates the side of the constraint line that is eliminated from the feasible space. An arrow (where shown) indicates the direction in which the constraint line moves with increasing $N/N_{\max}$; the absence of an arrow means that the constraint line is independent of $N/N_{\max}$. $p_{1,\max}$ is stationary at 1 until $N > A/a_1$. $p_{2,\max}$ is stationary at $1/(1 + a_2/a_1)$ until $N > (A/a_1 + A/a_2)$. $p_{2,\min}$ is stationary at 0 until $N > A/a_1$. $p_{3,\min}$ is stationary at 0 until $N > (A/a_1 + A/a_2)$.

Figure 51. The feasible space of bite proportions taken from three grazing horizons (p_1, p_2, p_3) with increasing degree of depletion ($N/N_{\max}$ from 0.01 to 1.00), as defined by the combination of the eight constraints. Shaded area indicates the *feasible space*.

Figure 52. Combinations of bite proportions that yield the same mean bite weight, according to the ranking of bite weights (w_i) associated with three grazing horizons. A single isocline is shown for each opposite pair of rankings. An arrow indicates the direction of increasing mean bite weight for parallel isoclines. The isocline for rankings that include an equality between two w_i has a unique angle that is parallel to one side of the unit-sum triangle. Isoclines for other rankings can take any angle between the limits indicated by the dashed lines.

Figure 53. Combination of the feasible space (shaded) of bite proportions taken from three grazing horizons for $N/N_{\max} = 0.25$ ($a_1 > a_2 > a_3$) and isoclines for various levels of mean bite weight for $w_1 > w_2 > w_3$.

Figure 54. Relationship between bite weight and number of bites removed per patch for tall original-density (TOD), short original-density (SOD), tall half-original-density (THOD), and short half-original-density (SHOD) patches. Symbols indicate the mean of 4 patches and 3 animals. Vertical bars indicate the SE of the means.

Figure 55. Relationship between total intake and number of bites removed per patch for the same sward structures as in Figure 54. Curves are averages of 4 patches and 3 animals.

Figure 56. Selectivity in number of visits per sward structure in Treatments 1 (T1), 2 (T2), and 3 (T3). Rectangular bars are means of 3 animals and 3 repetitions per animal and were calculated as the ratio of the number of tall (T1) or short (T1 and T2) original-density visited patches to total number of visited patches (tall plus short original-density patches in T1, short original-density plus short half-original-density patches in T2, and short original-density plus tall half-original-density patches in T3). Linear bars indicate SE of the means. In each grazing interval means with the same letter are not different ($P > .05$). The horizontal line represents equal preference for sward structures (ratio = 0.50). * Denotes different ($P < .05$) from 0.5.

Figure 57. Selectivity in residence time per sward structure in Treatments 1 (T1), 2 (T2), and 3 (T3). Rectangular bars were calculated as in Figure 56, but for residence time. Horizontal line, linear bars, letters, and symbols indicate the same as in Figure 56.

Figure 58. Selectivity in number of bites per sward structure in Treatments 1 (T1), 2 (T2), and 3 (T3). Rectangular bars were calculated as in Figure 3, but for number of bites. Horizontal line, linear bars, letters, and symbols indicate the same as in Figure 56.

Figure 59. Proportional removal of herbage mass in Treatments 1 (T1), 2 (T2), and 3 (T3). Rectangular bars were calculated as in Figure 3, but for intake. Horizontal line, linear bars, letters, and symbols indicate the same as in Figure 56.

Figure 60. Patch residence time of cattle as a function of the distance between patches and patch height.

Figure 61. Instantaneous intake rate obtained by steers grazing nine patchy environments that differed in patch heights and distance between patches.

Figure 62. Relationship between observed bite weight and bite weight predicted on the basis of sward height, bulk density, and chews per bite.

Figure 63. Relationship between bite weight and herbage mass per unit area for swards of different bulk density. Bite weight was corrected for animal and covariate effect. Solid line: $Y = -0.67 + 0.015X$, $R^2 = 0.86$; long-dash line: $Y = -0.12 + 0.007X$, $R^2 = 0.85$, short-dash line: $Y = -0.11 + 0.005X$, $R^2 = 0.75$, dotted line: $Y = -0.27 + 0.004X$, $R^2 = 0.74$.

Figure 64. Bite weight of cattle grazing HCS of two species of contrasting tensile strength as a function of bulk density.

Figure 65. Effects of bite weight on the allocation of jaw movements to manipulation and chewing of bites.

Figure 66. Relationship between chewing per unit herbage mass ingested and bolus weight from alfalfa swards; $Y = 0.691(\pm 0.106) + 7.580(\pm 0.780) X^{-1}$, $R^2 = 0.80$, $MSE = 0.084$, $n = 24$.

Figure 67. Relationship between the ratio of bite weight to bite weight of the first 10 bites and the ratio of number of bites removed to maximum number of bites from the top horizon of HCS. Maximum number of bites from the top horizon was calculated by dividing total patch area by average bite area in the top horizon.

Figure 68. Frequency distribution of residual heights following grazing by a steer on a hand-constructed sward of 0.4 m² of *Paspalum dilatatum* tillers of uniform initial height of 0.30 m for approximately 2 minutes. The height of successive grazing horizons is approximately 0.17, 0.09 and 0.05 m, which suggests that the animal removes a constant fraction of 0.45 of initial height of horizon. Unpublished data based on technique of Laca *et al.* (1992a) collected at the University of California, Davis, on 2 May 1989.

Figure 69.

11. DESCRIPTION OF COOPERATION

11.1. Year 1989

1. While visiting Israel on BSF research, Dr. M.W. Demment had extensive discussions with Dr. E.D. Ungar and Dr. N.G. Seligman regarding the experiments to be performed . Techniques to be developed were planned and the first set of experiments were designed jointly.
2. Dr. E.D. Ungar visited UC Davis for five weeks during which procedures, experimental design, animal training and considerable work on force plate, video and sound recording systems, was accomplished. Dr. Ungar fully participated in planning and carrying out field activities.
3. In cooperation with the UC Davis team, Dr. Ungar developed and tested a sound transmitter system for monitoring grazing behavior of free-ranging animals. The equipment was built by Mr. David Paige, the UC Davis-Agronomy departmental engineer, and then sent to Israel where Dr. Ungar field-tested the equipment.
4. Parameters for the grazing behavior of cattle were calculated at Davis on the basis of field work performed at UC Davis. The parameters were incorporated in models of intake by grazing cattle developed by the Israeli team.
5. Manuscripts for later publication were jointly written (Laca *et al.*, 1992a&b).

11.2. Year 1990

1. Dr. E.D. Ungar from ARO The Volcani Center visited UC Davis for five weeks during the Spring of 1990. Funds to support his visit came primarily from other research funds available to Dr. Demment. During this period Dr. Ungar performed the following activities jointly with the UC Davis group.

Experiment #10 was planned, conducted and partially analyzed.

Manuscript #1 was revised and submitted.

Manuscript #2 was drafted.

Weekly group meetings were held at the Department of Agronomy and

Range Science, UC Davis, during which experimental results were discussed and future activities planned. The bases for the model in manuscript #5 were discussed during these meetings. Additionally, Dr. Ungar had extensive interaction with the UC Davis student-employees who were working in the project and who participated in the meetings.

2. All data gathered at UC Davis before May 1990 were organized in a standard format and sent to the Israeli group at ARO The Volcani Center to be used as a basis for the modeling work.
3. Manuscripts #1, 2, 5, and 6 were jointly developed.
4. Planning of the field stage of the project was carried out in multiple written communications between the Israeli and UC Davis groups. In specific, objectives and general layout for experiments #13 were outlined.

11.3. Year 1991

1. Manuscripts were submitted to Agronomy Journal and Journal of Applied Ecology. These manuscripts were accepted and are currently published or in the press.
2. The Israeli and U.S. groups had extensive phone discussions and written exchanges to evaluate the accomplishments of the project, to plan the last set of experiments and to outline the basis for a follow-up proposal. Among these discussions we decided on the modeling and experimental strategy to extend the results to the field.

12. EVALUATION OF RESEARCH ACHIEVEMENTS

ACCOMPLISHMENTS BARD Project No. US-1329-87				
Project	Title/Focus	Date conducted	O b j.	Reported in
1989 [accomplished in first year]				Publication & sections of Final Report
Methods & manuscript	An integrated methodology to study short-term grazing behaviour of cattle.	Nov 88- Nov 90	1, 2, 3	Grass & For. Sci. 47:81-90, & 5.1., 6.1. & 7.1.
Expt. 1	Effects of height and density of dallisgrass on bite dimensions and bite weight..	7 Jul - 27 July 89	1, 2, 3, 4	Grass & For. Sci. 47:91-102, & 5.2.1.1., 6.2.1.1. & 7.2.1.1.
Expt. 2	Effects of height and density of alfalfa on bite dimensions and bite weight.	24 May - 14 Aug 89	1, 2, 3, 4	Grass & For. Sci. 47:91-102, & 5.2.1.1., 6.2.1.1. & 7.2.1.1.
Expt. 3	Effects of horizontal heterogeneity in height and density of dallisgrass on selectivity and bite weight.	21 Aug - 1 Sep 89	3	5.2.2.2., 6.2.2.2. & 7.2.2.2
Expt. 4	Vertical heterogeneity in vegetative dallisgrass: effects of lamina length and pseudostem height on bite dimensions and bite weight. .	19 Sep - 28 Sep 89	1, 2, 3	Agron. J. in press, & 5.2.2.1., 6.2.2.1. & 7.2.2.1.
Expt. 5	Effects of plant part and height on bite dimensions and bite weight.	20 Oct - 1 Nov 89	1, 2, 3	In prep.
Expt. 6	Vertical heterogeneity in reproductive dallisgrass: effects of lamina length and stem height on bite dimensions and bite weight.	1 Nov - 10 Nov 89	1, 2, 3	Agron. J. in press, & 5.2.2.1., 6.2.2.1. & 7.2.2.1.

1990				
Project	Title/Focus	Date conducted	O b j.	Reported in
Expt. 7	Role of sward tensile strength and bulk density in determining bite dimensions.	15 Nov - 15 Dec 89	1, 2	5.2.1.3., 6.2.1.3. & 7.2.1.3.
Expt. 8	Patch depletion by cattle grazing swards of equal herbage mass/area and contrasting structure.	5 Mar - 2 Apr 90	3, 4	5.3.2.1, 6.3.2.1. & 7.3.2.
Presenta- tion 1	Sward structure to predict intake rate. Seminar on Ranch and Grazing Management, UC Ext., Willows, CA.	Apr 90	1, 2, 3	--
Presenta- tion 2	When cows bite more than they can chew they have to ruminate over it. Seminar, Animal Behavior Grad. Group, UCD.	May 90	1, 2, 3, 4	--
Model 1	The dilemma of foraging in a spatially heterogeneous environment.	Sept 90- Dec 90	4	pp. 29-44 in Palo & Robbins (eds.) CRC 1991
Model 2	Graphical analysis of sward depletion by grazing.	May 90- Oct 90	4	J. Appl. Ecol., in press, 5.4., 6.4. & 7.4.
Expt. 9	Effects of height, density and phenological stage of <i>Bromus mollis</i> swards on bite dimensions and bite weight.	6 Apr - 27 Apr 90	1, 2, 3	5.2.1.4., 6.2.1.4. & 7.2.1.4.
Expt. 10	Bite dimensions and herbage intake by cattle grazing short hand-constructed swards.	21 May - 20 Jun 90	1, 2, 3	Agron. J. 83:973-978
Expt. 11	Cattle grazing behavior as affected by levels of hunger and scale of horizontal heterogeneity among leaf and stem.	9 Jul - 31 Jul 90	1, 2, 3, 4	5.2.2.2., 6.2.2.2., & 7.2.2.2.
Presenta- tion 3	Modelling intake of a grazing ruminant in a heterogeneous environment. INTECOL, Japan, 1990.	Aug 90	3, 4, 5	Abstract,
Presenta- tion 4 & manuscript	Modelling intake of a grazing ruminant in a heterogeneous environment. Shiobara Seminar, Japan, 1990.	Aug 90	3, 4, 5	pp. 57-75 in Okubo et al., (in press), Academic Press
Presenta- tion 5	Ingestive behavior of cattle grazing alfalfa is determined by sward structure. ASA meetings 1990.	Oct 90	1, 2	Abstract
Expt. 12	Bite dimensions of cattle as determined by sward height, bulk density and grazing time.	26 Sept- 5 Oct 90	1, 2, 3, 4	5.2.1.2., 6.2.1.2., & 7.2.1.2.
Expt. 13	Effects of patch height and bulk density on patch selection and intake rate by cattle.	14 Nov- 27 Nov 90	1, 2, 3, 4	5.5.1., 6.5.1., & 7.5.1.
Presenta- tion 6	Vegetational spatial heterogeneity: the spice of an herbivore's menu. Departmental Seminar, Agronomy & Range Science, UCD	Nov 90	1, 2, 3, 4	--

1991-92				
Project	Title/Focus	Date conducted	O b j.	Reported in
Expt. 14	Relationship between residence time at feeding station and forage intake as a basis for patch use and selection by cattle grazing ryegrass.	Jun 91	3, 5	5.3.2.2., 6.3.2.2., & 7.3.2.
Expt. 15	Model and field test of patch selection and use by cattle grazing heterogeneous ryegrass paddocks.	Jun 91 - Aug 91	3, 5	5.5.2., 6.5.2., & 7.5.2.
Presentation 7 & manuscript	Cattle prefer patches that yield greater instantaneous intake rate in patchy ryegrass swards.	2-3 Aug 91	3, 5	p. 171 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 8 & manuscript	Bite dimensions of cattle as determined by sward height, bulk density and grazing time.	2-3 Aug 91	1, 2	p. 172 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 9 & manuscript	Bite dimensions and intake of cattle within feeding stations as affected by sward horizontal heterogeneity and hunger level.	2-3 Aug 91	1, 2, 3	p. 173 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 10 & manuscript	Concepts of grazing - Factors and mechanisms that determine bite weight and grazing behavior of cattle within a feeding station.	2-3 Aug 91	1, 2	p. 174 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 11 & manuscript	Hand constructed swards, video, sound, and biting forces reveal grazing mechanisms.	2-3 Aug 91	1, 2, 3	p. 175 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 12 & manuscript	Why herbage mass does not determine bite weight by grazing cattle: sward structure and bite dimensions.	2-3 Aug 91	1, 2, 3	p. 176 Proc. 2nd Graz. Livestock Nut. Conf.
Presentation 13 & manuscript	Selective behaviour of cattle grazing ryegrass swards with horizontal heterogeneity in patch height and bulk density.	8-21 Feb 93	3, 5	XVII Int. Grassl. Cong. (in press)
Presentation 14 & manuscript	Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation.	8-21 Feb 93	3, 5	XVII Int. Grassl. Cong. (in press)
Presentation 15 & manuscript	A conceptual model to explain variation in ingestive behaviour within a feeding patch.	8-21 Feb 93	1, 2, 3	XVII Int. Grassl. Cong. (in press)

All of the original objectives were accomplished successfully. The small departures from original objectives and procedures were fruitful and significantly enhanced the overall quality and importance of the research. Overall, the results of this research constitute a major contribution to the knowledge of ruminant-plant interactions both from practical and theoretical points of view. We envision that the methodology, models and conceptual framework developed will greatly enhance researcher's ability to successfully approach management problems. As is explained in the introduction of this report, our hierarchical view of the grazing process is quantitatively

integrated across levels of aggregation, which is a significant addition to current conceptual models.

From an applied point of view, our results are useful at least in three areas:

- a. Evaluation of forage availability and its relation with animal performance.
- b. Monitoring of short-term intake rate.
- c. Prediction of intake rate on the basis of sward characteristics.

The present research unequivocally demonstrates that measurement of forage availability in terms of mass per unit area or mass per animal overlooks essential aspects of availability that affect intake and animal performance. The availability of the same amount of forage per unit area, as measured by bite weight, significantly increases with sward height and decreases with bulk density. Furthermore, field heterogeneity in sward structure significantly increases intake rate. Steers achieved intake rates more than 60% greater in paddocks with spatial heterogeneity in sward height at the feeding station level than in paddocks with uniform sward height equal to the average. Consequently, we recommend that measurements of sward structure and heterogeneity be included in the evaluation of forage availability, particularly for the development of empirical and mechanistic relationships with animal performance.

Based on the methodology and equations developed in the context of this project, bite weight and intake rate of cattle can be predicted with adequate accuracy on the basis of simple measurements of sward height, bulk density and animal behavior. We developed a predictive equation applicable to large steers grazing relatively uniform swards which yields estimates of bite weight within *ca.* 13% of the actual values with 95% confidence. Intake rate can be directly estimated as the product of bite weight and observed bite rate. Accurate monitoring of intake rate can be very valuable for management of grazing systems. Estimates of intake rate can be used to make decisions regarding the end of the grazing season, animal rotation among pastures, and supplementation schedules.

The models developed can be used to predict intake rate of grazing cattle on the basis of sward characteristics and previously measured

parameters such as searching speed and bite weight in different patches of herbage. These predictions should provide a more robust link between forage supply and animal performance.

The project was an active and productive collaboration that resulted in 11 technical publications in journals or books, 6 more in press and 5 in preparation, 15 presentations of results of the research, 2 abstracts and 1 Ph. D. thesis.

13. LIST OF PUBLICATIONS

- DEMMENT, M.W., R.A. DISTEL, T.C. GRIGGS, E.A. LACA and G.P. DEO. (1993). Selective behaviour of cattle grazing ryegrass swards with horizontal heterogeneity in patch height and bulk density. *Proceedings of the XVII International Grassland Congress, New Zealand and Queensland*, (in press).
- DISTEL, R.A., T.C. GRIGGS, E.A. LACA and M.W. DEMMENT. (1991). Cattle prefer patches that yield greater instantaneous intake rate in patchy ryegrass swards. *Proceedings of the Second Grazing Livestock Nutrition Conference*, August 2-3, 1991, Steamboat Springs, Colorado, p. 171.
- FLORES, E.R., E.A. LACA, T.C. GRIGGS and M.W. DEMMENT. (In press). Sward height and vertical morphological differentiation determine cattle bite dimensions. *Agronomy Journal*.
- GRIGGS, T.C., E.A. LACA and M.W. DEMMENT. (1991). Bite dimensions and intake of cattle within feeding stations as affected by horizontal sward heterogeneity and hunger level. *Proceedings of the Second Grazing Livestock Nutrition Conference*, August 2-3, 1991, Steamboat Springs, Colorado, p. 173.
- GRIGGS, T.C., R.A. DISTEL and M.W. DEMMENT. (1991). Bite dimensions of cattle as determined by sward height, bulk density and grazing time. *Proceedings of the Second Grazing Livestock Nutrition Conference*, August 2-3, 1991, Steamboat Springs, Colorado, p. 172.
- LACA, E.A. (1992). The feeding ecology of grazing ruminants: experiments and models on the mechanisms and factors that determine intake rate. Ph.D. Dissertation, University of California, Davis, 258 pp.
- LACA, E.A. and M.W. DEMMENT. (1990). Modelling intake of a grazing ruminant in a heterogeneous environment. *Intecol, V International Congress of Ecology*, August 23-30, Yokohama, Japan (abstract).

- LACA, E.A. and M.W. DEMMENT. (1991). Herbivory, the dilemma of foraging in a spatially heterogeneous food environment. In: Palo, R.T. and Robbins, C.T. (eds.) *Plant defenses against mammalian herbivory*, pp. 29-44. CRC Press, Boca Raton, Florida.
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- LACA, E.A., E.D. UNGAR, N.G. SELIGMAN and M.W. DEMMENT. (1991). Why herbage mass does not determine bite weight by grazing cattle: sward structure and bite dimensions. *Proceedings of the Second Grazing Livestock Nutrition Conference*, August 2-3, 1991, Steamboat Springs, Colorado, p. 176.
- LACA, E.A., E.D. UNGAR, N.G. SELIGMAN and M.W. DEMMENT. (1992). Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science*, **47**, 91-102.
- LACA, E.A., E.D. UNGAR, N.G. SELIGMAN, M.R. RAMEY and M.W. DEMMENT. (1992). An integrated methodology to study short-term grazing behavior of cattle. *Grass and Forage Science*, **47**, 81-90.
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- LACA, E.A., T.C. GRIGGS, R.A. DISTEL and M.W. DEMMENT. (1991). Concepts of grazing - Factors and mechanisms that determine bite weight and grazing behavior of cattle within a feeding station. *Proceedings of the Second Grazing Livestock Nutrition Conference*, August 2-3, 1991, Steamboat Springs, Colorado, p. 174.
- UNGAR, E.D. (1990). An intake model of ruminants at pasture. *Israel Agresearch*, 4, 7-20.
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- UNGAR, E.D., N.G. SELIGMAN and M.W. DEMMENT. (1992). Graphical analysis of sward depletion by grazing. *Journal of Applied Ecology*, 29, (in press).

14. APPENDIX. REPRINTS.

- UNGAR, E.D. (1990). An intake model of ruminants at pasture. *Israel Agresearch*, 4, 7-20.
- LACA, E.A. and M.W. DEMMENT. (1990). Modelling intake of a grazing ruminant in a heterogeneous environment. *Intecol, V International Congress of Ecology*, August 23-30, Yokohama, Japan (abstract).
- LACA, E.A., T.C. GRIGGS and M.W. DEMMENT. (1990). Ingestive behavior of cattle grazing alfalfa is determined by sward structure. *American Society of Agronomy 1990 Annual Meetings*, San Antonio, Texas, October 21-26, 1990 (abstract).
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