BARD

FINAL REPORT
PROJECT NO. IS-2331-93

**The Prediction of Daily Intake in Grazing Cattle
Using Methodologies, Models and Experiments that
Integrate Pasture Structure and Ingestive Behavior**

**E.D. Ungar, M.W. Demment, E.A. Laca, N.G. Seligman, U.M. Peiper,
M. Gutman**

1998

48735

DATE:

10 OCTOBER 1998

BARD Project Number:

IS-2331-93C

הספריה המרכזית
למדעי החקלאות
בית דגן

Project Title:

The Prediction of daily intake in grazing cattle using methodologies, models and experiments that integrate pasture structure and ingestive behavior

Investigators:
(Principal first)

Affiliated Institution:

E.D. Ungar

ARO, The Volcani Center

M.W. Demment

University of California, Davis

E.A. Laca

University of California, Davis

N.G. Seligman

ARO, The Volcani Center

U.M. Peiper

ARO, The Volcani Center

M. Gutman

ARO, The Volcani Center

Project Start Date:

11 July 1994

Type of Report:

1st Annual

2nd Annual

Final ✓

Signature:
Principal Investigator

DR. AVNER CARMİ
DEPUTY DIRECTOR FOR RESEARCH
MINISTRY OF AGRICULTURE & RURAL DEVELOPMENT
AGRICULTURAL RESEARCH ORGANIZATION

Signature:
Authorizing Official, Affiliated Institution

630.72
DAR/PRC
2nd 1997

Table of contents

1. ABSTRACT	3
2. OBJECTIVES	4
3. RELEVANT DATA, METHODOLOGY, RESULTS AND DISCUSSION	5
3.1 Introduction	5
3.2 Basic methodological issues	7
3.2.1 Creating patches in the field	7
3.2.2 Measurement error in determining bite weight	9
3.3 Patch depletion studies	23
3.3.1 Maximum depletion trials	24
3.3.2 Field-based incremental depletion trials	39
3.3.3 HCS-based incremental depletion trials	52
3.3.4 Sod-based depletion trials and testing at larger spatial scales	68
3.4 Multi-patch studies	83
3.4.1 Feeding station behaviour on single and sub-divided grazing areas	83
3.4.2 Grazing behaviour along a search path with patches at different spacings	87
3.4.3 The importance of scale of patchiness for selectivity in grazing herbivores	92
3.5 Integrating foraging mechanisms across spatial and temporal scales	112
3.5.1 Conceptual model of scales of grazing	113
3.5.2 Experimental study of scales of grazing	119
3.5.3 Conclusion	122
3.5.4 Duration of spatial memory in cattle	122
3.5.5 Integration of ingestive and digestive constraints as determinants of quantity and quality of diet consumed by ruminant livestock	131
3.6 Social interactions in grazing behaviour	144
3.6.1 On the Relative Importance of Exploitative and Interference Competition in Grazing Ungulates: an Experimental Test	144
3.6.2 Social effects of experience on finding food and social transmission of information in cattle	154
3.7 Acoustical Measurement of Intake & Behaviour of Grazing Cattle	164
3.7.1 Introduction	164
3.7.2 Acoustic study 1	165
3.7.3 Acoustic study 2	169
3.8 Acknowledgements	174
3.9 References	175
4. EVALUATION OF THE RESEARCH ACHIEVEMENTS	183
5. DESCRIPTION OF THE COOPERATION	184
6. CONCLUSIONS	185
7. LIST OF PUBLICATIONS	189

1. Abstract

This project addressed the prediction of daily intake in grazing cattle using methodologies, models and experiments that integrate pasture structure and ingestive behavior. The broad objective was to develop concepts of optimal foraging that predicted ingestive behavior and instantaneous intake rate in single and multi-patch environments and extend them to the greater scales of time and space required to predict daily intake. Specific objectives included: to determine how sward structure affects the shape of patch depletion curves, to determine if the basic components of ingestive behavior of animals in groups differs from animals alone, and to evaluate and modify our existing models of foraging behavior and heterogeneity to incorporate larger scales of time and space. Patch depletion was found to be predominantly by horizon, with a significant decline in bite weight during horizon depletion. This decline derives from bite overlap, and is more pronounced on taller swards. These results were successfully predicted by a simple bite placement simulator. At greater spatial scales, patch selection was aimed at maximizing daily digestible intake, with the between patch search pattern being non-random. The processes of selecting a feeding station and foraging at a feeding station are fundamentally different. The marginal value theorem may not be the most appropriate paradigm for predicting residence time at a feeding station. Basic components of ingestive behavior were unaffected by the presence of other animals. Our results contribute to animal production systems by improving our understanding of the foraging process, by identifying the key sward parameters that determine intake rate and by improving existing conceptual and quantitative models of foraging behavior across spatial and temporal scales.

2. Objectives

- To extend concepts of optimal foraging that predicted ingestive behavior and IIR in simple multi-patch environments to the greater scales of time and space required to predict daily intake.
- To determine how sward structure affects the shape of patch depletion curves (critical to animal behavior at a patch) and evaluate a model of depletion to explain the influence of vertical heterogeneity on depletion.
- To determine if the behavior of animals in groups differs from animals alone and if so, to incorporate the concept of competitive resource depletion into our foraging models.
- To evaluate and modify our existing models of foraging behavior and heterogeneity to incorporate larger scales of time and space and address rumen fill constraints to predict daily intake.
- To adapt and test an existing technique for continuous acoustical monitoring of grazing behavior for free-ranging animals to obtain grazing time, counts of bites, chews and rumination in a real time sequence, and explore the prediction of bite weight.

3. Relevant data, methodology, results and discussion

3.1 Introduction

Despite decades of research, there is neither a method for measuring intake rate nor a model for its prediction, at the daily time scale, that is easy to use, inexpensive and accurate. The ability to accurately and easily measure and predict daily intake rate is expected to have a major impact on grazing systems management because it is a crucial variable that has implications for many management decisions. Accuracy and timeliness in obtaining such information can enable improvements in pasture, animal and overall farm management. Furthermore, because it is a primary explanatory variable in the understanding of plant and animal dynamics over all time scales, such an ability could have a major impact on grazing systems research. The current difficulty, cost and uncertainty entailed in the measurement and prediction of daily intake rate by grazing ruminants is out of all proportion to the centrality of this variable in grazing systems. Thus our underlying hypothesis can be stated as follows:

Mechanisms that control ingestion can be combined with optimization models of behavior and methodologies that measure diurnal feeding to explain variability in daily intake rate with sufficient precision to enable managers to optimize their use of forage resources.

The prediction of intake requires the development of a conceptual model and an accurate methodology to measure intake in free-ranging animals on a daily basis. A conceptual model provides the logic for the design of efficient experiments to identify and quantify the mechanisms and grazing strategies used by the animal. The results of the experiments are combined with the concepts of the model to produce a predictive quantitative model. The new methodology provides two anticipated benefits. First, it allows results of experiments at smaller scales of time and space to be tested on a diurnal basis at the pasture and landscape level. Second, this technique may be used to monitor animals in production systems to provide information for management decisions.

The conceptual model is based on the following logic:

- Domestic animals are selected for performance in both natural and managed production systems. Production and intake are closely linked. Therefore selection should result in efficient feeding behavior and in a diet and intake near optimal, given the constraints of the animal and the landscape.
- Daily intake is a result of the integration of bites taken in time and space. An understanding of the factors that control lower level processes is important to comprehend higher level functions (Milne 1991).
- Results from our previous BARD project indicate the relationship between sward structure and bite dimensions is largely mechanistic. When bites at a patch are integrated through time, this mechanistic relationship holds and describes the depletion curve of intake through time. Depletion curves are the basis for feeding decisions at scales larger than one patch in patchy landscapes.
- A continuum exists where mechanistic relationships exert more influence on lower levels processes, such as bite dimensions and depletion curves, and the animal integrates these ingestive processes into a strategy to feed in a landscape. Our previous results indicate that grazing decisions reflect a maximization strategy. Therefore the problem is to determine the underlying mechanisms, and then identify the rules by which the animal uses the strategy to interact with the landscape.
- Just as mouth morphology and sward height are animal and sward constraints at the bite level, pasture or landscape structure, searching speed and digestive processes are constraints that impinge at larger spatial and temporal scales. To expand the scale of predictions from the patch to the landscape we need to assess these constraints and elucidate the strategies with which animals respond.
- The elucidation of mechanisms of ingestion requires the use of realistic swards where structure affects bite characteristics. The investigation of animal strategies can be approached using techniques that provide similarly shaped depletion curves but do not have sward structure. That is, feeders with hay cubes, positioned in the field serve as patches that can be manipulated, to investigate the decisions made by the feeding animal.

It is clear from the defined objectives and the above introduction that this project set out to address a wide range of questions related to daily intake, spanning different spatial and temporal scales. In order to treat these questions in a structured manner, our proposal and research program centered around a series of explicit hypotheses associated with the research objectives. This main section of the final report is structured in a similar fashion; the many experiments that were conducted and the models that were developed are reported in conjunction with the specific hypotheses of the research program. As in our previous BARD project, methodology played a crucial role in our research program. Hence we begin with the treatment of some basic methodological issues.

3.2 Basic methodological issues

3.2.1 Creating patches in the field

Our previous BARD project made considerable progress in understanding the basic mechanisms of bite formation and intake at the single patch level using an experimental protocol based on hand-constructed swards (HCS). Most of the experimentation in that project was centered around HCS work with some extension to the field level. In this continuation project, the emphasis was switched; a limited amount of work was conducted using HCS while the majority of the effort was placed on field-based techniques. While there is no question as to the utility of the HCS approach, a return to the field is unavoidable for many reasons. The use of HCS places limitations on the spatial and temporal scale of experimentation, and the number of herbage patches that can be constructed in the course of a single experiment is limited by logistic constraints. One of the methodological objectives of this project was to examine how closely one can achieve HCS-protocol conditions in a field context. The primary aim is to achieve a high degree of horizontal uniformity at the patch scale. Over the four years of the project we examined various agro-technical field methods aimed at achieving high uniformity at the patch scale in a field context that would allow the construction of hundreds of patches in the course of a season. In addition to care in the areas of cultivation, fertilization and weed control, critical agro-technical components were the method of sowing and the timing and spatial uniformity of irrigation during germination and early establishment. We examined the following methods of sowing:

- commercial drill: mono- or bi-directional, with/without seed hoses,
- precision drill: mono- or bi-directional, and at various row spacings,
- single-row manual precision planter,
- manual lawn seed/fertilizer spreader (net width 0.43 m) followed by water-filled plastic roller.

These sowing methods were tried with various plant species (barley, annual ryegrass, alfalfa and oats) and at different times of the year. The success of each technique depended on the species and the season of sowing. The two tractor-driven drills are obviously less time-consuming and also bury the seed at the correct soil depth. The primary disadvantage of the technique is the spacing between the drill rows; this could not be reduced below 15 cm with the commercial device. That is a large distance between rows in the context of determining bite dimensions and may influence bite placement on short swards. We managed to reduce row spacing to 10 and even to 8 cm with the precision drill device, though both soil tilth and machine maintenance had to be excellent in order to achieve good results at 8 cm spacing.

It was difficult to reduce row spacing below about 8 cm with the manual single-row precision planter, though an excellent stand can be obtained if soil conditions are right. Though this is the most labour intensive of all the techniques examined, it has the advantage of enabling good seed burial for large grain species, and enables small areas to be sown in a staggered fashion so that one can use plants of the same age throughout an experiment. Effective staggering of sowing is hard to organize when tractor-drawn implements are provided by the central farm services of the research station. For a small-grain species such as alfalfa, the most promising technique proved to be a manual spreader plus burial with a water-filled roller. By the end of the project we were able to obtain plots of outstanding uniformity and we plan to refine this technique further in the future. This technique is considerably faster (and easier) than the single-row precision planter and enables effective staggering of sowing. However, due to the limited seed burial provided by rolling, the technique did not yield satisfactory results with large grain species.

3.2.2 Measurement error in determining bite weight

A secondary methodological goal of this project was to move away from the use of oesophageally fistulated animals for the purposes of determining intake and bite weight. Aside from the intensive animal care required to successfully maintain fistulae, animal welfare regulations in research institutions are becoming increasingly restrictive in the use of fistulae. Furthermore, surgery may not be an option if the experimental animals are not purchased outright by the project. When using HCS or turves, one of the methods of determining intake is by weight difference (with due correction for moisture loss). When patches are constructed in the field, this option does not exist. One of the first major field experiments of the project addressed the question of measurement error in determining bite weight when the sward is established by the simplest of the sowing techniques described above - the commercial drill. Despite the relative coarseness of the technique, we were able to obtain visually good patches by sowing a relatively large area and being very selective in positioning patches in the field. This experiment examined measurement error in the estimation of intake from such patches.

One of the advantages of hand-constructed micro-swards is the ability to achieve a high degree of uniformity in the horizontal plane. As a result, the dry matter (DM) difference method can yield an accurate estimate of intake from a micro-sward. This method estimates pre-grazing DM herbage mass by clipping an area of micro-sward not offered to the animal, and measures directly the post-grazing DM herbage mass by clipping the entire micro-sward. In the hand-constructed micro-sward methodology of Laca *et al* (1992a), the DM difference method yielded a more accurate estimate of intake than did the fresh weight difference method in which the entire micro-sward assembly was weighed before and after grazing with correction for moisture loss and DM content.

The hand-constructed micro-sward methodology may be unmatched in terms of spatial uniformity, but it does have potential drawbacks and is exceedingly labour intensive. Other methodologies have used micro-swards sown in trays (Illius *et al*, 1992), turves cut from the field (Hughes *et al*, 1991; Newman *et al*, 1992; this project), and micro-swards created directly in the field (Burlison *et al*, 1991). Creating micro-swards in the field has the

advantage of providing the most natural foraging arena of all micro-sward methodologies, and may be the only feasible option when larger scales involving animal movement and multi-patch arenas are being used. (Note that in multi-patch arenas fistulation can not provide direct measurement of intake on a patch by patch basis.) Since some compromise in horizontal uniformity is inevitable at the field scale, measurement error in the estimation of herbage intake from a patch will place limits on the sensitivity of such studies.

We examined the problem of measurement error in two field-based micro-sward experiments. Sown swards under intensive management were used, within which apparently uniform areas were selected carefully for the creation of patches and the estimation of initial herbage mass. In order to test this methodology rigorously, the experiments minimized sources of variation by repeatedly grazing patches of uniform structure. Thus the analysis of variance focused on the within- and between-animal variation in bite weight.

3.2.2.1 Materials and methods

3.2.2.1.1 Field preparation

Field experiments were conducted at The Volcani Center, Bet Dagan, Israel, on an area of 2.1 ha situated near the central dairy unit. The field was sown in November 1994 to barley, alfalfa and annual ryegrass in three strips. All field preparations aimed to achieve the greatest possible uniformity.

The field was divided by electric fence across the three crops into an experiment section of 1.4 ha, and an area of 0.7 ha on which the animals grazed as a group. Patches for both experiments were constructed on a 15 x 60-m hand-weeded strip of alfalfa in the experiment section of the field. This area was cut and irrigated before each experiment. *[See Photo #1]*

3.2.2.1.2 Animals

Eight Israeli-Holstein heifers from the dairy herd of The Volcani Center, Bet Dagan, of average age 420 (± 10) d, were selected without prior inspection and housed as a group near the experimental field on 1 Feb. 1995.

The animals were trained to be approached, haltered and led by rope. From 28 February the animals grazed the electrically-fenced section of the field for 1 - 2 h daily. The animals were accustomed to being led away from the

Photo #1: Example of alfalfa patches (0.5 m²) produced in the first year of the project. The area was sown by commercial drill.

Photo #2: Heifer grazing a patch. The animal is trained to lead calmly with halter and rope. In this trial, grazing is stopped after a pre-set number of bites have been removed.

group to a separate area, where they would graze a single patch of herbage, and then returned to the group. [See Photo #2]

Grazing was usually during the period 0800 - 1000 h. On return from pasture the heifers received *ad libitum* the standard total mixed ration supplied by the dairy unit. Feed was available at the feeding gates the next morning before the animals were let out to graze. Thus hunger was not induced prior to grazing.

Mean liveweight ($\pm$ SD) of the heifers increased linearly from 379 ± 15 kg on 20 March 1995 to 482 ± 15 kg on 11 July 1995. Average date of first conception by AI for the group was 14 Feb. 1995.

3.2.2.1.3 Experimental protocol

The experiment estimated the mass of herbage removed from a patch of alfalfa in the course of 30 bites. This estimation was conducted three times per day for each of eight heifers on three non-consecutive days, giving a total of 72 patches for grazing. The experiment was conducted twice. Patches were grazed on 23, 29 May and 1 June in Expt 1, and on 4, 6 and 10 July in Expt 2. Patches were always prepared the day before they were grazed. Animals grazed the electrically-fenced section of the field for 1-2 h daily on the intermediate days of the experimental periods and during the period between the two experiments.

To create a patch, an area of c. 1 x 1.5 m was visually selected for horizontal uniformity of cover, and height slightly greater than 0.30 m. A square "central quadrat" (the patch to be grazed) of internal area 0.5 m² (0.71 x 0.71 m) was placed on the ground with minimum disturbance of the canopy, in the middle of the selected area. Two "estimation quadrats", of internal dimensions 0.71 x 0.30 m each, were used for each patch. These were placed adjacent to two opposite sides of the central quadrat, across the same drill lines as those in the central quadrat (Figure 1). The total area used for estimation was split in this way to allow for any non-apparent gradients in herbage density across the central quadrat. Quadrats were precisely welded using 12 mm construction iron.

Herbage around the central and estimation quadrats was removed to ground level. Herbage in the quadrats was clipped to a uniform height of 0.30 m. Herbage in the estimation quadrats was then clipped at ground level

Figure 1. Dimensions and spatial arrangement of quadrats used in the construction of grazed and calibration patches. Surrounding herbage was removed to ground level. For grazed patches, estimation quadrats were clipped, the central quadrat was grazed (30 bites) and its residual herbage was clipped. For calibration patches, both estimation and central quadrats were clipped.

for drying and weighing. Flat-profile high-grade shears were used throughout, with due care to minimize operator bias and soil contamination.

The following day, at about 0800 h, the eight heifers were led into the fenced section of the field. The first heifer in a randomized sequence was immediately separated from the group, led through a gate to the experimental area, and allowed to graze a patch. The target bite number was 30, though animals occasionally stopped grazing earlier. The characteristic tearing sound generated by the severance of a bite was the basis for counting bites. The actual bite number was counted and the grazing session was recorded on video. The heifer was then returned to the group to graze, and the next heifer in the cycle was separated and led to a fresh patch. Three cycles of eight heifers were completed on a grazing day, with the heifer sequence re-randomized each cycle. Average time requirement was 45 minutes per cycle of eight heifers.

The heifers were returned to the animal shed at the end of the three cycles of patch grazing. The residual herbage on each grazed patch was then clipped at ground level and bagged for drying.

An additional set of 30 "calibration" patches was prepared in the same way as the set of grazed patches, i.e. central plus two estimation quadrats. The calibration patches were interspersed randomly among the grazed patches and their preparation was spread over the same experiment days. Both the estimation quadrats and the entire central quadrat of the calibration patches were clipped at ground level and bagged separately for drying. Even though every effort was made in the methodology to ensure that the calibration and grazed patches were identical, they are nevertheless independent data sets from a statistical point of view.

All clipped herbage was dried at 60°C for at least 3 days and weighed. In Expt 2, each patch was sampled for DM content determination immediately before grazing, and residual herbage height was measured at three *grazed* points in the patch immediately after grazing.

3.2.2.1.4 Analysis of calibration patch data

Four methods of estimating the initial mass of a patch were compared. In all methods, herbage mass of the estimation quadrats was multiplied by the

ratio of central:estimation quadrat area (71/60), prior to the estimation procedure.

We define:

- C_c measured herbage mass of central quadrat of area 0.71x0.71 m of the c -th patch of the calibration set of patches, in grams DM
- $\tilde{C}_c$ predicted herbage mass of central quadrat of the c -th patch of the calibration set of patches, in grams DM
- E_c measured herbage mass of estimation quadrats of total area 0.60x0.71 m, multiplied by 71/60, of the c -th patch of the calibration set of patches, in grams DM
- n_{cal} number of patches in the calibration set for the entire experiment
- $b_{C.E}$ regression coefficient of C on E
- a Y-intercept of above regression

In estimation method 1 (EM1) $\tilde{C}_c$ was set equal to the herbage mass of the estimation quadrats matched to the same patch ("match estimate"). Thus:

$$\tilde{C}_c = E_c$$

In EM2 $\tilde{C}_c$ was set equal to the mean of all estimation quadrats in the experiment ("estimate by mean").

$$\tilde{C}_c = \sum E_c / n_{cal}$$

In EM3 $\tilde{C}_c$ was predicted by the least squares regression equation of the true mass of the central quadrat on the mass of the estimation quadrats ("regression estimate"). We did not use bivariate analysis (Model II regression) since we wish to use the resulting equation predictively (Sokal and Rohlf, 1981).

$$\tilde{C}_c = a + b_{C.E} E_c$$

In EM4 the herbage mass of the estimation quadrats of a patch was multiplied by the ratio of mean central quadrat mass to mean estimation quadrat mass ("ratio estimate").

$$\tilde{C}_c = E_c \sum C_c / \sum E_c$$

The sum of squared deviations from the true mass of the central quadrat was computed for each method, and the mean squares compared. In principle, the method with the lowest mean square is expected to introduce the

minimum measurement error. For the regression estimate (EM3), the sum of squared deviations is the residual sum of squares of the regression analysis.

3.2.2.1.5 Analysis of grazed patch data

Intake was computed as the initial minus the terminal herbage mass on a 0.5 m² patch. The predicted initial mass of each grazed patch ($\tilde{C}_g$) was estimated using the four methods described above, but based on the measured herbage mass of the estimation quadrats of the grazed patches (E_g):

$$\tilde{C}_g = E_g \quad (\text{EM1})$$

$$\tilde{C}_g = \sum E_g / n_{grz} \quad (\text{EM2})$$

$$\tilde{C}_g = a + bC.E E_g \quad (\text{EM3})$$

$$\tilde{C}_g = E_g \sum C_c / \sum E_c \quad (\text{EM4})$$

where n_{grz} is the number of patches grazed for the entire experiment. Note that EM1 and EM2 are independent of the calibration set.

In Expt 2, the herbage removed from the patch for DM determination was subtracted from initial mass estimates for intake determination. Bite weight was defined as intake divided by number of bites removed from the same patch. The video record was used to identify grazing sessions in which all 30 bites were removed in a single uninterrupted bout. Biting rate was computed for these sessions only.

Variance components were derived from the analysis of variance of intake. Categorical variables examined were animal (1-8), day of experiment (1,2,3), within-day cycle (1,2,3), and the interaction between animal and within-day cycle. Animal and day of experiment were defined as random variates. Animals did not always remove 30 bites and for this reason bite number was included as a covariate in the analyses of variance.

The experimental technique controls only the dimensions of a patch but not the bulk density of herbage in it. For the purposes of establishing variance components, it is necessary to include bulk density in the analysis of variance, since it is a primary determinant of bite weight (Laca *et al*, 1992b). Bulk density is equal to the initial estimated biomass of a patch divided by patch volume. Since patch volume is a constant, the initial estimated patch biomass was used as a covariate in the analysis, instead of bulk density. This is legitimate even though the initial estimated patch biomass is used in

the calculation of the dependent variable (intake or bite weight). The artificial covariance due to the calculations, if present, should be negative, whereas we obtained positive covariances. This indicates that the association due to bulk density derived from the mechanics of grazing. Other covariates examined were number of bites removed from the patch, time of grazing, and DM content of the herbage (Expt 2).

3.2.2.2 Results

To avoid confusion and the erroneous scaling of variances, all results are reported on a per 0.5 m² basis, the area of the central quadrat. All herbage mass values are on a DM basis.

3.2.2.2.1 Calibration patches

Mean herbage mass ($\pm$ SD) of the central and estimation quadrats of the calibration patches in Expt 1 was 114.4 ($\pm$ 15.7) and 127.0 ($\pm$ 20.3) g, respectively. Corresponding values for Expt 2 were 124.5 ($\pm$ 13.9) and 135.8 ($\pm$ 12.5) g, respectively. The mean differences between estimation and central quadrats for the two experiments were both highly significant using paired *t*-tests. Thus the match estimate (EM1) and the estimate by mean (EM2) are biased and over-estimate the initial mass of the central quadrats.

Figure 2 shows the relationship between herbage mass of the central and estimation quadrats. In both experiments, slopes of the regression lines were significantly different from zero. Mean predicted central quadrat mass must be equal to the mean of the estimation quadrats for EM1 and EM2, and to the mean of the central quadrats for EM3 and EM4. Table 1 compares the calibration mean square of error (MSE) introduced by each estimation method in the estimation of the herbage mass of the central quadrat. For EM1 and EM2 the MSE consists of the squared bias plus the calibration variance. The regression method yielded the lowest measurement error.

3.2.2.2.2 Grazed patches

Both mean herbage mass in the estimation quadrats of the grazed patches and mean residual mass in the grazed patch were remarkably similar for the two experiments (Table 2). Hence, for methods that estimate the initial mass of the grazed patch solely from the estimation quadrat mass (EM1 and EM2), the intake estimates are similar in Expt 1 and Expt 2. Methods EM1 and EM2 yield higher estimates of the initial mass of the grazed patch than do

Figure 2. Measured herbage mass (DM) of the central quadrat versus that of paired estimation quadrats in the calibration studies of Expt 1 (O=data, — = regression) and Expt 2 (Δ=data, - - - = regression). $x=y$ shown as Regression coefficients for Expt 1: 40.8 (intercept) and 0.58 (slope). Corresponding values for Expt 2: 50.9 and 0.54, respectively.

methods EM3 and EM4. Since other values in the computation of intake are the same, methods EM1 and EM2 yield higher estimates of intake as well. However, because of the relatively large residual mass that is being deducted, the effect of the estimation method on intake is amplified.

Table 1. Residual mean square (RMS) of herbage mass DM of the central quadrat of the calibration patches obtained by four methods of estimation, in Expt 1 (n=29) and Expt 2 (n=30). Units are g². RMS is based on herbage mass per 0.5 m² for central and estimation quadrats.

Estimation method	d.f.	RMS	
		Expt 1	Expt 2
EM1: match estimate	n	334	302
EM2: estimate by mean	n	398	315
EM3: regression estimate	n-2	113	152
EM4: ratio estimate	n-1	151	169

Table 2. Intake and bite weight in Expt 1 and Expt 2 using four estimation methods for initial herbage mass of the grazed patch ($\tilde{C}_g$). EM1=match estimate; EM2=estimate by mean; EM3=regression estimate; EM4=ratio estimate. Standard deviations are based on n=72 (Expt 1) and n=71 (Expt 2). All herbage mass values are grams DM. E_g is measured herbage mass of the estimation quadrats of the grazed patches. $C_{residual}$ = measured residual herbage mass after grazing. E_g , $\tilde{C}_g$ and $C_{residual}$ are on 0.5 m² basis.

Estimation method	Variable	Expt 1		Expt 2	
		Mean	SD	Mean	SD
EM1	E_g	137.7	18.3	139.9	15.5
	$C_{residual}$	106.0	16.9	108.6	15.5
	Bites	28.3	4.8	29.6	1.7
	$\tilde{C}_g$	137.7	18.3	139.9	15.5
	Intake	31.6	15.3	31.3	13.8
	Bite weight	1.16	0.59	1.07	0.49
EM2	$\tilde{C}_g$	137.7	-	139.9	-
	Intake	31.6	16.9	31.3	15.5
	Bite weight	1.16	0.62	1.07	0.53
EM3	$\tilde{C}_g$	120.6	10.6	126.7	8.4
	Intake	14.6	13.2	18.1	12.4
	Bite weight	0.52	0.46	0.62	0.43
EM4	$\tilde{C}_g$	124.0	16.5	128.2	14.2
	Intake	18.0	14.5	19.7	13.3
	Bite weight	0.65	0.51	0.67	0.46

Table 3 shows the analysis of variance model selected for both experiments, using estimation method 3. The animal x within-day cycle interaction was dropped from the model since it was not significant in Expt 1 and resulted in negative variance component estimates in Expt 2. We were unable to detect any significant between-animal variation in either experiment. Day of experiment proved highly significant in both experiments, whereas within-day cycle was not significant. Bite number was significant in Expt 1, where its variability was greater. Initial herbage mass was significant in Expt 1 only, where it was also slightly more variable.

Table 3. Analysis of variance of intake and bite weight of a heifer from a 0.5 m² patch of alfalfa in the course of c. 30 bites in Expt 1 and Expt 2. Initial herbage mass of the grazed patch estimated by regression (EM3). Each factor in the model is adjusted for all other factors ("Type III").

Source	Expt 1			Expt 2		
	Mean square	d.f.	P	Mean square	d.f.	P
<i>Intake</i>						
Animal	200	7	0.1764	153	7	0.3137
Day of Expt	1229	2	0.0003	1060	2	0.0007
Within-day cycle	285	2	0.1228	58	2	0.6346
Number of bites	680	1	0.0265	<1	1	0.9649
Initial mass	694	1	0.0250	65	1	0.4789
Error	131	58	-	127	57	-
<i>Bite Weight</i>						
Animal	0.238	7	0.2132	0.188	7	0.2752
Day of Expt	1.401	2	0.0006	1.239	2	0.0006
Within-day cycle	0.311	2	0.1640	0.076	2	0.5978
Number of bites	0.133	1	0.3763	0.241	1	0.2048
Initial mass	0.771	1	0.0358	0.079	1	0.4658
Error	0.167	58	-	0.146	57	-

Dry matter content of the grazed herbage in Expt 2 increased with day of experiment but not with time within day. Thus there was no advantage to using this variable in the model over day of experiment. Similarly, time of grazing did not improve the explanation of variance over within-day cycle.

The variance component estimates are given in Table 4 for both experiments. Using the method recommended by Sokal and Rohlf (1981), the 95% confidence interval of the residual (within-animal) variance for intake is $L_1=94$ and $L_2=196$ for Expt 1, and $L_1=91$ and $L_2=190$ for Expt 2, where L_1 and L_2 are the lower and upper bounds. For the between-animal

variance, the limits are: $L_1=0$ and $L_2=78$ for Expt 1, and $L_1=0$ and $L_2=57$ for Expt 2. Confidence limits for the estimate of the variance due to measurement error (for EM3, Table 1) are: $L_1=71$ and $L_2=209$ for Expt 1, and $L_1=96$ and $L_2=278$ for Expt 2.

Table 4. Intake and bite weight variance component estimates for animal, day of experiment and residual (within-animal), based on expected mean squares, in Expt 1 and Expt 2.

Component	Expt 1		Expt 2	
	g^2	%	g^2	%
<i>Intake</i>				
Animal	7.9	3.8	3.0	1.7
Day of Expt	68.4	33.0	41.5	24.2
Residual	131.1	63.2	127.0	74.1
<i>Bite weight</i>				
Animal	0.0081	3.2	0.0047	2.4
Day of Expt	0.0769	30.5	0.0486	24.3
Residual	0.1670	66.3	0.1464	73.3

The residual (within-animal) variance for intake consists of the calibration error introduced into the initial mass estimation and the random within-animal between-patches deviation. However, the residual (within-animal) variance component estimates for intake were of similar magnitude to the residual mean squares obtained for estimation method 3 (Table 1). This means that the noise introduced by measurement error was large relative to the variability in foraging parameters. Thus our estimates of within-animal variance are over-estimates, whereas those of between-animal variance are not necessarily changed in any one direction. Confidence limits (95%) for overall mean bite weight (by EM3) are: $L_1=0.41$ and $L_2=0.63$ for Expt 1, and $L_1=0.52$ and $L_2=0.72$ for Expt 2.

3.2.2.2.3 Biting rate

An analysis of biting rate of uninterrupted grazing sessions only, yielded a significant animal variance component in both experiments. Average biting rate was 39 bites min^{-1} in Expt 1. Percent of variation between and within animals was 26 and 74, respectively. Coefficient of variation (CV; $100 \times \sqrt{\text{variance component estimate} + \text{overall mean}}$) for between- and within-animal variation was 13% and 23%, respectively. In Expt 2, average biting rate was 45 bites min^{-1} , and percent of variation between and within animals was 46 and 54, respectively. CV for between- and within-animal

variation was 22% and 23%. Day of experiment was not significant for biting rate.

3.2.2.3 Discussion

In the two experiments reported here, heifers (c. 450 kg liveweight) grazed 30 bites from a patch of alfalfa of area 0.5 m^2 , height 0.30 m and bulk density c. 825 g DM m^{-3} . In the absence of the calibration patches, these experiments would have estimated bite weight at c. 1.1 g DM, since one could use only EM1 or EM2 to compute the initial mass of the grazed patches. When information based on a statistically independent set of patches was used, a lower estimate of c. 0.55 g DM was obtained. The results are quite similar for EM3 and EM4, suggesting that the primary factor at play here is apparent over-estimation (*i.e.*, mean estimation mass > mean central mass) and the correction for that in the form of the ratio estimate (EM4) or by regression (EM3).

Given that the regression method yielded the lowest residual mean square, the large scatter and the strong deviation from the 1:1 line seen in Figure 2 may be unexpected. However, in the context of a relatively small area of land growing a crop of uniform appearance, the degree of relatedness between adjacent spots will depend on the spatial pattern of heterogeneity over that area. If the spatial scale of change is very small, there need not be any relationship at all. This would yield an intercept equal to the mean and slope zero. The best estimate is then obtained using the mean (*i.e.*, EM2). As the degree of spatial relatedness at the 0.5 - 1.0 m scale increases, so the intercept will depart from the average, and the slope will increase so as to add a fraction of the estimate (EM3). By extension, complete relatedness between adjacent areas (with no bias) is equivalent to an intercept of zero and slope unity, which is EM1.

The statistical analyses and variance component estimates were not sensitive to estimation method. However even our lowest estimate of measurement error was high in relation to the variances being determined. Thus it is important to establish the limits to uniformity that can be attained under field conditions. In December 1995 we conducted a calibration study on an area of ryegrass sown at high seed density in the experimental field. Crop height exceeded 0.25 m 49 days after sowing, and 30 calibration patches were clipped at a height of 0.25 m over the next few days. Mean

herbage mass DM (0.5 m² basis) for the estimation quadrats was 109 g (range 92 - 130) and for the central quadrats, 105 g (range 81 - 121). Mean squares for estimation error by the four methods were: EM1, 153; EM2, 117; EM3, 98; EM4, 135. Direct estimation from the adjacent area (EM1) introduced the highest measurement error. Regression yielded the lowest error, although the slope was no longer significantly different from zero. Thus we did achieve a higher level of uniformity in the field. We nevertheless did not obtain a large reduction in the absolute error level introduced by estimation compared with the values given in Table 1.

Despite the measurement error, some effects were found to be statistically significant. In Expt 1, bulk density (represented by initial patch mass in our case) was significant in the analysis of intake and bite weight. Bite number was significant in the analysis of intake but not in that of bite weight. This is consistent with minimal feedback of patch depression on bite weight (Laca *et al*, 1994) over the first 30 bites, and with the top grazing horizon not being grazed completely. Within-day cycle was not significant in either experiment. This is in contrast to the large effect of time at pasture on bite weight reported by Dougherty *et al* (1987, 1989). In those studies, however, hunger was induced by overnight fasting prior to grazing. Hunger was not induced in the present study. It is also noted that within-day cycle was not significant in the analysis of biting rate in either experiment.

The two experiments yielded surprisingly similar variance component estimates, given the very large noise supposedly added by the estimation problem. The very wide confidence intervals given above would also seem to weigh against obtaining similar values twice in succession. If these similar estimates are indeed representative of the true values, we might estimate the variance added by measurement error to be c. 100 g². The variance components for between animals, between days and within animals are then c. 5, 50 and 30 g² (6%, 61% and 33% of the combined total), respectively. The analysis of biting rate, in which measurement error can be assumed to be negligible, revealed a larger percent of variation for the between-animal source.

3.2.2.4 Conclusions

The inclusion of calibration measurements in the experimental protocol proved important in the estimation of intake from a patch by the difference

method. The calibration set detected measurement bias and provided a coefficient for its correction. It expanded the number of alternative computational methods for estimation, and enabled their mean square error to be computed. The mean square error of the selected computational method is then an estimate of the contribution of measurement error to the total mean square error in the analysis of intake.

The mean square error introduced by the estimation of initial patch biomass from adjacent areas depends on the spatial pattern of heterogeneity in the field. It would appear difficult to reduce its value below c. 100 g² for an initial patch biomass in the range 100 - 200 g, and for a total area in the order 100 m².

The sensitivity of intake to estimation method is large at low levels of patch depletion, *i.e.*, when the residual patch biomass is high. Under such conditions, field-scale patch-oriented studies that use the difference method have insufficient resolution to provide reliable estimates of the within- and between-animal variances in bite weight. However, the methodology yielded a meaningful estimate of the average intake and bite weight, and can probably be used where treatment effects are expected to be large. It remains to be seen whether an additional non-destructive variable (*e.g.* capacitance, light penetration) can further reduce measurement error on apparently uniform swards.

On the basis of these experiments our experimental protocol for subsequent field-based patch-oriented studies did not attempt to estimate bite weight or intake on the basis of the difference method. A much greater emphasis was placed on detailed post-grazing measurements for the determination of bite dimensions coupled with bulk density and vertical profile measurements. These techniques are explained in detail later in the report.

3.3 Patch depletion studies

One of the objectives of this project was to determine how sward structure affects the shape of the depletion curve and further develop models of depletion. Our specific hypothesis was:

The patch depletion curve on horizontally uniform patches is a predictable function of the height, vertical profile of bulk density, and factors such as steminess that modify the mechanics of bite prehension.

3.3.1 Maximum depletion trials

The first set of patch depletion experiments presented a rigorous test of a simple patch depletion model developed in our previous BARD project by operating at very high levels of depletion. In addition, we added the dimension of absolute patch size. The possible interaction between patch size and within-patch grazing behaviour was not dealt with in our earlier work nor has it been examined by other research groups. Nevertheless, in natural patchy environments vegetation is presented to the foraging animal at a variety of patch sizes which can be less than the potential feeding station area.

3.3.1.1 Introduction

Bite weight is a primary determinant of intake rate in grazing ruminants (Gross, Hobbs & Wunder 1993), hence it has been the focus of much empirical and theoretical study (e.g. Spalinger, Hanley & Robbins 1988; Ungar and Noy-Meir 1988). Bite weight derives from bite volume - the effective sward volume removed in a single biting action - and the bulk density of the vegetation in that volume (Hodgson 1985). If idealized as rectangular or cylindrical, bite volume can be defined as the product of bite depth and bite area (Milne 1991; Parsons *et al.* 1994). Height and bulk density are the most important sward features that determine bite depth and bite area on green, vegetative swards (Laca *et al.* 1992b).

It follows from this simple description of bite dimensions that the profile of an initially uniform sward can be divided into grazing horizons, each with a characteristic bite depth and bite area (Hodgson 1981). By extension, we can define algebraically the maximum number of bites (N_{max}) provided by a given volume of sward (Ungar, Seligman & Demment 1992). Consider a sward of area A (m^2), and of initial sward height that provides two grazing horizons:

$$N_{max} = A (1/a_1 + 1/a_2) \quad \text{eqn 1}$$

where a_i is the bite area characteristic of the i -th grazing horizon. Equation 1 can be expressed on a per unit area basis as:

$$D_{max} = 1/a_1 + 1/a_2 \quad \text{eqn 2}$$

where D is the density of bite placement (bites per m^2).

If horizon depletion is incomplete, equation 2 should be modified to include the fraction of each horizon grazed, f_i :

$$D = f_1 / a_1 + f_2 / a_2 \quad \text{eqn 3}$$

We assume throughout this study that sward structure is homogeneous in the horizontal plane. Thus preference in that plane is assumed not to operate, and the depletion process reduces to spatial geometry. Nevertheless, this simple geometric description of depletion has its complications, especially when applying it to a small patch of vegetation. There is empirical evidence that within-horizon bite area declines with level of patch depletion (Laca *et al.* 1994), in which case the a_i are not constant. We know from direct observation of cattle that there is a degree of overlap between the areas swept in the course of bite formation by successive bites. Micro-sward trials with cattle have shown that the area of the sward surface grazed in the course of six bites comprised one contiguous area rather than discrete areas separated by ungrazed herbage (Laca *et al.* 1992b). Furthermore, bite placement does not progress across the surface of a grazing horizon in a completely systematic way. Islands of vegetation are created that yield bites of low bite area when subsequently grazed. Such a loosely-systematic grazing style is therefore expected to reduce the effective bite area.

Bites do not have a flat base but leave in their wake a wide distribution of residual heights (Laca *et al.* 1993a). Thus grazing horizons may have quite ill-defined borders. This surface unevenness may influence the vertical positioning of bites such that a systematic horizon structure breaks down at high depletion levels.

To address these questions we conducted two patch depletion experiments at levels approaching D_{max} at which we expect the strongest effects on bite area. A primary aim of the experiments was to test if equation 3 can be applied at high depletion levels. The test is based on the observed bite numbers and frequency distributions of residual heights, from which both D and f_i in equation 3 can be derived. Thus the task is to arrive at reasonable estimates for bite area, a_i . Our expectation is that within-horizon bite area declines with depletion level. To test our hypothesis of loosely-systematic grazing style, we generated the expected relationship between bite area and depletion using a simple bite placement simulation model.

The introduction of D in equation 2 assumes implicitly that the degree of overlap between successive bites, and hence the effective bite area, is not influenced by the absolute size of the patch. We tested this assumption by using three patch sizes in the patch depletion trials. No size exceeded a single feeding station - the area reached without moving the forelegs (El Aich, Moukadem & Rittenhouse 1989; Ruyle & Dwyer 1985). In the analysis we tested for a significant influence of absolute patch surface area on D , f_r , and the amount of residual herbage per unit area.

3.3.1.2 Materials and methods

3.3.1.2.1 Field preparation

Experiments were conducted at The Volcani Center, Bet Dagan, Israel. A 2x75-m strip of oats (*Avena sativa*) was sown on 2 April 1996 for the conduct of Expt 1. A similar strip of alfalfa (*Medicago sativa*) was sown on 2 May 1996 for the conduct of Expt 2. Sowing was by drill with a row spacing of 15 cm.

3.3.1.2.2 Animals

Ten Israeli-Holstein heifers from the dairy herd of The Volcani Center, of average age 363 (± 8) d, were selected on 1 Oct. 1995. From mid-December, and throughout the experimental period, the animals grazed oats and alfalfa on an area adjoining the experimental strips from 08.00 to 10.00 h daily. On return from pasture the heifers received the standard total mixed ration supplied by the dairy unit. Feed was available at the feeding gates the next morning before the animals were let out to graze. Thus hunger was not induced prior to grazing.

Mean liveweight ($\pm$ S.D.) of the heifers increased linearly from 369 $\pm$ 20 kg on 20 Nov. 1995 to 558 $\pm$ 27 kg on 30 July 1996.

3.3.1.2.3 Experimental protocol

Expt 1 was conducted on the oat strip on 6, 7, 8, 9 and 12 May 1996. Treatments were three patch sizes (nominally 1/8, 1/4 and 1/2 m²) and two initial sward heights (H , 10 and 20 cm), replicated over 10 heifers. On each day of the experiment three sets of the six treatment combinations were prepared. One randomly-selected set of patches was clipped for an estimate of initial biomass. The second and third sets were grazed by different heifers. The sequence of the six treatment patches within heifers was randomized.

Expt 2 was conducted on the alfalfa strip on 17, 18 June and 4, 7 July 1996. Treatments were three patch sizes at $H=20$ cm. For purposes of biomass estimation, one additional medium-size patch was prepared per grazed set of patches. In all other respects the same protocol was used as in Expt 1.

Patches were prepared the same day they were grazed. To create a patch, an area of herbage was visually selected for horizontal uniformity of cover, and height of approximately 25 cm. The border of the patch was delineated with a quadrat aligned with the drill rows. Herbage around the quadrat was removed to ground level. Herbage within the quadrat was clipped to the treatment height. The effective patch width was computed as the number of drill rows included in the quadrat multiplied by the row spacing. This yielded patch sizes (A) of 0.16, 0.30 and 0.53 m² for the three size treatments. All the vegetation in the estimation patches was clipped to ground level.

The animals grazed as a group during patch preparation. At approximately 09.30 h the first heifer was led to the patch area and allowed to graze a set of patches in randomized sequence. The objective was to achieve maximal depletion. When the animal stopped removing bites from a patch, it was led away from and returned to the patch in order to induce further grazing. This process was repeated until the animal failed to remove any bites for at least 30 seconds while standing in front of the patch. The bite number was counted and the grazing session was recorded on video. The characteristic tearing sound generated by the severance of a bite was the basis for counting bites.

On each day of the experiment the residual herbage height of the grazed patches was determined immediately after the grazing sessions. An average height was recorded for every 5-cm section along each drill row of a patch (133 measurements/m²). The residual herbage was then clipped at ground level and bagged for drying.

The vertical mass profile of the vegetation was determined over the course of Expts 1 ($n=15$) and 2 ($n=6$), using herbage close to the patches and of similar initial height. The lowest four sections of 5-cm thickness were bagged separately. The vegetation was also sampled for dry matter (DM) content. Samples were clipped to 10 and 20 cm in Expt 1 ($n=15$ for each height), and to 20 cm in Expt 2 ($n=10$). All clipped herbage was dried at 60°C for at least three days and weighed.

3.3.1.2.4 Analysis

In order to test an horizon-based description of depletion, we need to establish f_i in equation 3 - the fraction depletion for each grazing horizon. This can be estimated from the frequency distribution of residual heights. The fraction depletion for the uppermost horizon is one minus the proportion of residual height measurements that are equal to the initial sward height. The calculation for the lower horizon depends on bite depth. The simplest model for mean bite depth of cattle on green vegetative patches is the 'take half' approximation found by Laca *et al.* (1992b). However, since bites are not flat-based (Laca *et al.* 1993a), a proportion of residual heights in upper-horizon grazing will be less than half the initial height. For $H=20$ cm, we ascribe residuals greater than 7 cm to upper-horizon grazing (Ravid 1997). Thus, if there are two grazing horizons, the proportion of residual heights less than or equal to 7 cm is our estimate of the fraction of the second horizon grazed.

The effect of absolute patch surface area on grazing behaviour was tested by analysis of variance. Our null hypothesis was that the relationship between the maximum number of bites the animal will remove and patch area is linear and passes through the origin. This was tested by expressing bites removed as the density of bite placement, D (bites per m^2), and testing whether patch area has a significant effect on this normalized variable. This normalization also corrects for the increase in the variance of absolute bite number with patch size. The effect of patch size on the fraction depletion of each grazing horizon, and on the amount of residual herbage per unit area, was also tested.

3.3.1.2.5 Bite placement simulator

We use the term bite placement to mean the positioning of a bite upon the surface of a patch relative to the area of the patch already grazed. The position of the first bite is assumed to be random. We know from direct observation that the placement of subsequent bites on herbage patches is not random, and that the area swept by consecutive bites tends to overlap. With this background we defined a simple bite placement algorithm to study the relationship between the number of bites taken from a single grazing horizon and mean effective bite area. The rules governing bite placement will influence the shape of this relationship.

In the simulator, bite placement is registered on a 100x100 matrix of cells, each representing 1 cm². The matrix is initialized to zero. Cell values are incremented by 1 when they fall within the area of a bite. Bites are assumed to be circular with a potential bite area defined by a parameter dependent on the height of the sward. At any moment in a grazing bout, the mean effective bite area (cm²) is the number of non-zero cells in the matrix divided by the cumulative number of bites up to that moment. Depletion of the 'sward' increases with bite number and D .

The purpose of the simulator is to generate a realistic spatial pattern of bite placement for any given D . For simplicity, the positional sequencing within the bite series is not considered, so that it is not necessary for the algorithm to interpret the state of the matrix in order to determine bite location. The algorithm generates a candidate bite location randomly, which is accepted only if its position meets two overlap criteria. The candidate bite area is divided into an inner core and an outer ring covering 40% and 60% of its total area, respectively. The algorithm computes the degree of bite overlap of the core (d_c) area as the fraction of its area already grazed. The degree of bite overlap for the outer (d_o) area is similarly computed. The overlap criteria d_c' and d_o' are threshold values for d_c and d_o ; overlap in the core must not exceed d_c' and overlap in the outer area must not be less than d_o' .

By setting d_c' to zero (*i.e.*, no overlap tolerated in the inner core of the candidate bite), and d_o' to a low constant on the order of 10%, the bite placement simulator generates a loosely systematic pattern of depletion. However, high levels of depletion can not be attained because a stage is reached at which there are no potential bite sites for which $d_c=0$. For depletion to continue, the overlap tolerated in the inner core of the candidate bite needs to be increased. The value for d_o' was set to 10%, and d_c' was defined as a function of the fraction patch area grazed, increasing linearly from 0 to 1 between 50% and 100% patch area grazed. Sensitivity to these overlap parameters was found to be low. It should be noted that model definition and parametrization were completed independently of the experimental results.

Fig. 3 shows the simulated bite placement for depletion levels of 0.25, 0.50 and 0.75 of patch area grazed. The biting sequence was not continuous from depletion level to depletion level, but rather the patch matrix was re-

Fig. 3. The simulated pattern of within-horizon bite placement for three levels of depletion, and the corresponding relationships between mean effective bite area, area grazed and bite number. The simulations were stopped when the fraction area grazed reached (a) 0.25, (b) 0.50, (c) 0.75. Areas of bite overlap are shaded darker. The curves in the graphs proceed from left to right, with the lowest depletion level terminating first.

initialized for each level. Hence there are three relationships given for the mean effective bite area and the fraction area grazed with D . The variability in the fraction area grazed showed little variation between runs of the simulator. The random differences between runs, including border inefficiencies (which we consider to be realistic), have a more marked effect on the mean effective bite area at low D . At intermediate levels of depletion, the relationship is relatively stable between runs.

3.3.1.3 Results

All herbage mass values are on a DM basis. Deviations following means are standard errors throughout.

3.3.1.3.1 Herbage

Mean herbage mass per unit area of the oat estimation patches was 105.3 ± 7.39 and 148.5 ± 6.09 g/m² ($n=15$) for $H=10$ and 20 cm, respectively. Only H was significant in an analysis of variance of mass per unit area, with the terms A , H and AXH in the model (A and H categorical). Mean herbage mass per unit area for the alfalfa estimation patches ($A=0.30$ m², $H=20$ cm) was 166.5 ± 8.50 g/m² ($n=10$).

The fraction of total herbage mass contained in the horizontal horizons of the sward profile declined with distance from ground level in both crops (Table 5). The mean DM content of the vegetation was $13.3 \pm 0.24\%$ for oats (Expt 1) and $22.5 \pm 1.27\%$ for alfalfa (Expt 2). Time of day of sampling did not have a significant effect on DM content in either experiment.

Table 5. Fraction of herbage mass contained in horizons of 5 cm thickness for a sward trimmed to 20 cm height.				
Horizon (cm)	Expt 1: oats (n = 15)		Expt 2: alfalfa (n = 6)	
	Mean	S.E.	Mean	S.E.
0* - 5	0.36	0.011	0.34	0.017
5 - 10	0.26	0.005	0.23	0.006
10 - 15	0.22	0.004	0.23	0.009
15 - 20	0.16	0.005	0.20	0.005
* ground level				

3.3.1.3.2 Density of bite placement

The mean number of bites removed by heifers is shown in Fig. 4. In the analysis of variance of bites removed per m² (*D*) for Expt 1, *H* and heifer were highly significant ($P<0.0001$), whereas patch area, *A*, and the interaction *AXH* were not significant. In the parallel analysis for Expt 2, heifer was significant ($P=0.03$), *A* was not significant. These results tell us that the maximum number of bites that an animal can be induced to remove from a patch, under our experimental conditions and stopping criteria, has a 1:1 relationship to patch area. That is, the observed density of bite placement was constant with patch area for a given plant species and initial patch height.

Mean *D* in Expt 1 was 147 ± 7.44 and 199 ± 8.17 bites per m² for *H*=10 and 20 cm, respectively. In Expt 2 mean *D* was 156 ± 8.13 bites per m². The slopes of the lines shown in Fig. 4 are equal to these values.

3.3.1.3.3 Residual height and mass

The mean residual height of grazed plant elements was 5.0 ± 0.20 cm in Expt 1. Analysis of variance of mean residual height showed that *A*, *H* and heifer had a significant effect on the mean residual height. Residual height increased with *A*, although the total range of the effect was little more than 1 cm (Table 6). The response to *H* was also small; residual height increased from 4.8 to 5.4 cm for *H*=10 and 20 cm, respectively. Residual patch biomass showed the same patterns of response as residual height (Table 6).

Table 6. Mean ($\pm$ S.E.) residual herbage height and residual mass of grazed patches in Expts 1 and 2.

Patch area (m ²)	Expt 1: oats				Expt 2: alfalfa	
	<i>H</i> =10		<i>H</i> =20		<i>H</i> =20	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Residual height (cm)						
0.159	4.6	0.461	4.7	0.532	8.5	0.885
0.300	4.6	0.391	5.3	0.518	8.8	0.753
0.530	5.2	0.335	5.8	0.564	8.9	1.043
Residual mass (g/m ²)						
0.159	37.7	3.429	46.8	5.653	85.0	11.895
0.300	43.1	3.316	51.6	3.967	79.8	9.790
0.530	51.0	6.086	55.4	6.244	80.3	10.165

Fig. 4. The relation between the number of bites removed by heifers grazing herbage patches to a high level of depletion and patch area.
 (a) Expt 1 conducted on oats at an initial sward height (H; cm) of 10 (○) and 20 (●).
 (b) Expt 2 conducted on alfalfa for H=20 (○). Values are means for 10 heifers. Vertical bars indicate standard error.
 The slope of the dashed lines is the mean density of bite placement (D; bites/m²) for each treatment height:
 (a) D=147 for H=10 (— — — — —); D=199 for H=20 (- - - - -).
 (b) D=156 for H=20 (— — — — —)

In Expt 2, the mean residual height was 8.7 ± 0.50 cm. Heifer had a significant effect on the residual height, but patch size did not (Table 6).

3.3.1.3.4 Observed horizon depletion

The frequency distribution of residual heights is shown for both experiments in Fig. 5. These distributions were used to estimate the fraction depletion attained for each grazing horizon (f_i). The simplest assumption that appears consistent with Fig. 5 is one and two grazing horizons for $H=10$ and 20, respectively. Using the method defined earlier, we estimated the fraction depletion for the upper (f_1) and lower (f_2) grazing horizons in $H=20$ treatments, and f_1 in $H=10$ treatments. In both experiments, absolute patch size had no significant effect on f_i for the upper or lower grazing horizon. Estimates of f_i averaged over patch size are given in Table 7.

Table 7. Estimated mean fraction ($\pm$ S.E.) of the lower and upper grazing horizon that was depleted in Expts 1 and 2. Values are derived from the frequency distributions of residual herbage heights, as explained in text.

Treatment	Grazing horizon			
	Lower		Upper	
	Mean	S.E.	Mean	S.E.
Expt 1				
$H=10$	0.936	0.017	-	
$H=20$	0.800	0.038	1.000	0.001
Expt 2				
$H=20$	0.385	0.060	0.981	0.009

3.3.1.3.5 Expected bite area and horizon depletion

The bite placement simulator was used to generate the expected mean effective bite area and the fraction horizon depletion as a function of D , for a single grazing horizon. We assumed potential bite areas of 100 and 150 cm² to correspond to initial sward heights of 10 and 20 cm², respectively. These estimates are based on published values for the same heights, similar bulk density, and low depletion level (Ungar, Genizi & Demment 1991). We further assumed that the relationship for $H=10$ is an adequate representation of the second grazing horizon for $H=20$. Results from repeated simulations were averaged and are shown in Fig. 6. The efficiency of a bite declines with

Fig. 5. Frequency distribution of residual herbage heights, expressed as fraction patch area, following grazing of herbage patches by heifers to a high level of depletion. (a) Expt 1 conducted on oats at an initial sward height (H ; cm) of 10 (▨) and 20 (■). (b) Expt 2 conducted on alfalfa for $H=20$ (▨). Values are means for 10 heifers and three patch sizes.

depletion level because of non-systematic bite placement, patch border effects and increasing overlap. In the Discussion we compare these expected relationships with the observed results.

3.3.1.4 Discussion

Our results indicate that patch size does not have a significant influence on the density of bite placement at high levels of patch depletion, at least in a single-patch grazing arena no larger than a feeding station. Similarly, the fraction of each grazing horizon depleted and the residual herbage mass per unit area were not influenced significantly by patch size. Ginnett and Demment (1995) used two patch sizes in their study of patch depletion by giraffes and found no significant effect of patch size on the behavioural parameters examined.

We now need to establish whether a simple geometric description of bite dimensions and grazing horizons, as outlined in the Introduction, is consistent with the observed residual herbage heights and densities of bite placement.

The expected mean residual herbage height of grazed plant units can be estimated using the 'take half' approximation (Laca *et al.* 1992b). For $H=10$ cm on oats, the heifers removed one grazing horizon of 5 cm depth, leaving a residual of 5 cm. At an initial height of 20 cm, we expect horizon depths of 10 and 5 cm. These heights need to be weighted by the fraction of patch area grazed once only and twice, by the expression

$$f_{lower} * 5 + (f_{upper} - f_{lower}) * 10.$$

Using the values in Table 7, we obtain expected residual heights of 6 and 8 cm for $H=20$ on oats and alfalfa, respectively. These expected residual heights are within 1 cm of the observed values.

We have assumed that all bites in treatment $H=10$ on oats were removed from one grazing horizon. The average effective bite area is then the reciprocal of the density of bite placement, allowing for the fraction of patch area that was not grazed (Table 7). Thus:

$$a_1 = f_1 / D = 0.936 / 147 = 64 \text{ cm}^2 \quad \text{eqn 4}$$

At 147 bites per m^2 ($H=10$) the simulator yielded the same mean effective bite area and fraction depletion as our experimental results (points A on Fig. 6).

For treatment $H=20$ on oats, we set D in equation 3 to the observed D value for that species in Expt 1, and we set f_1 and f_2 to values given in Table 7 to obtain:

$$199 = 1/a_1 + 0.800/a_2 \quad \text{eqn 5}$$

Using the observed fraction depletion of the lower grazing horizon (0.8) as a starting point, we derive the mean effective bite area ($a_2=75 \text{ cm}^2$) and bite density ($D=107$) from the relevant curves in Fig. 6. These values appear as points B in Fig. 6. The density of bites remaining for the upper horizon is then $199-107=92$ bites per m^2 . This yields $a_1=109 \text{ cm}^2$ in equation 5. If we simulate $D=92$ for the upper horizon, we obtain points C on Fig. 6, at which the expected bite area is 100 cm^2 (versus our estimate of 109 cm^2) and fraction depletion of 0.92 (versus the observed value of 1).

Similarly, for treatment $H=20$ on alfalfa we obtain:

$$156 = 0.981/a_1 + 0.385/a_2 \quad \text{eqn 6}$$

By the same process as above, and assuming potential bite area to be 100 cm^2 , when $f_1=0.385$ the expected a_2 is 84 cm^2 and the number of bites is 46 per m^2 (points D on Fig. 6). Solving equation 6 then yields $a_1 = 88 \text{ cm}^2$, with 110 bites per m^2 being removed from the upper grazing horizon. Simulating this bite number yields points E on Fig. 6, at which the expected bite area is 88 cm^2 (versus 88 cm^2) and fraction depletion of 0.96 (versus 0.98).

We expect the relationship between bite density and fraction area grazed shown in Fig. 6 to be very similar to the within-horizon gain function relating patch residence time to intake. The shape of the gain function determines in part the appropriate model at the multi-patch spatial scale. As discussed by Stephens and Krebs (1986) and Shipley and Spalinger (1995), it is appropriate to apply the marginal value theorem in a multi-patch foraging environment (to determine when to move to a new patch) only if the gain function is negatively accelerated. However, if the gain function increases linearly (indicative of consistently efficient and systematic depletion), the optimum is to exploit completely the linear section of the gain function, irrespective of inter-patch distance. Further studies employing incremental depletion levels are required to determine empirically the pattern of decline in within-horizon bite area. The present study, which used a single, maximal depletion level, provides an important end-point relative to which intermediate depletion levels can be planned.

Fig 6. Expected mean effective bite area and fraction horizon area grazed as a function of number of bites removed per m², as generated by a bite placement simulation model.

Curves given for potential bite areas of 100 (—) and 150 (---) cm², representing grazing horizons with initial heights of 10 and 20 cm, respectively. Curves are averages of 10 simulations. Labelled points indicate feasible combinations of bite number (*D*), bite area (*a*) and fraction horizon grazed (*f*) that closely fit the observed results, as explained in the text.

The 'take half' rule we assumed for the definition of grazing horizons explained the results for both oats and alfalfa well. This is not to suggest that the issue of vertical bite placement has been fully worked out. Other relationships between initial sward height and bite depth have been found in cattle (Ungar 1996), and questions remain regarding the underlying rationale to grazing depth in large and small ruminants (Illius *et al.* 1995; Parsons *et al.* 1994). Nevertheless, given the differences between the two species in morphology, bulk density and vertical biomass distribution (Table 5), it is encouraging that the same model parameters for grazing depth and bite area fit the results for both species.

In conclusion, high levels of patch depletion by grazing cattle entail a decline in within-horizon bite area, which appears to result from non-systematic bite placement, patch border effects and overlap. If this decline is accounted for, our observed results can be reconciled with a simple horizon-based model of depletion.

3.3.2 Field-based incremental depletion trials

The second set of patch depletion experiments were a logical extension of the maximal depletion trials. Once we have established the "end point" in the depletion process, we need to understand the dynamics of bite dimensions over the course of the depletion process. If we can obtain empirical data at various stages of depletion, we can also put the bite placement simulator to an effective test. The following experiments were conducted using four levels of depletion. Bite numbers for the first three levels were calibrated on the basis of the previous maximum depletion trials, and a maximal depletion level was added as a point of comparison between the trials.

3.3.2.1 Materials and methods

3.3.2.1.1 Field preparation

Experiments were conducted at The Volcani Center, Bet Dagan, Israel. Alfalfa (*Medicago sativa*) and oats (*Avena sativa*) were sown by precision drill in 75-m strips at a row spacing of 8 cm. Herbage patches for experiment 1 were prepared on three strips of alfalfa that were sown on 15 May 1996. Patches for experiment 2 were selected from six strips of oats that were sown in pairs on 9, 15 and 27 May 1996.

3.3.2.1.2 Animals

Ten Israeli-Holstein heifers of average age 363 (± 8) d were selected on 1 Oct. 1995 from the dairy unit. The animals were trained to be led with halter and rope, and were accustomed to grazing individual patches of herbage. Prior to and during the experimental period, the animals grazed alfalfa (vegetative) and oats (mature) on an area adjoining the experimental strips from 08.00 to 10.00 h daily. On return from pasture the heifers received the standard total mixed ration supplied by the dairy unit. Feed was available at the feeding gates the next morning before the animals were let out to graze. Thus hunger was not induced prior to grazing.

Mean liveweight of the heifers was approximately 500 kg during the experimental period.

3.3.2.1.3 Experimental protocol

Expt 1 was conducted on the alfalfa strips over the period 19 - 30 June 1996. Treatments were small, medium and large patch sizes (nominally 1/8, 1/4 and 1/2 m²) and four levels of depletion (defined below) replicated over six of the ten available heifers in a full factorial design. Initial sward height (H) was 20 cm. Herbage patches were prepared in sets of five of a single size. One of these was randomly selected and clipped for an estimate of initial biomass. The four levels of depletion were assigned to the remaining four patches, which were grazed by the same heifer in randomized sequence. The 18 sets of patches (6 heifers x 3 patch sizes) were constructed in random sequence with the constraint that a heifer did not graze more than one set of patches on a given day.

Expt 2 was conducted on the oats strips over the period 23 June to 3 July 1996. Patch sizes were small and medium only, at four levels of depletion, replicated over four of the six heifers used in expt 1. In all other respects the experimental protocol was identical to that of expt 1.

In both experiments, patches were prepared the day they were grazed. To create a patch, an area of herbage was selected for horizontal uniformity of cover. The border of the patch was delineated with a quadrat aligned with the drill rows. Herbage around the quadrat was removed to ground level. The natural height of the herbage within the quadrat was measured and the herbage was then clipped to the treatment height. The effective patch width

was computed as the number of drill rows included in the quadrat multiplied by the row spacing (8 cm). This yielded patch areas (A) of 0.112, 0.240 and 0.454 m² for the small, medium and large size treatments, respectively. Vegetation in the estimation patches was clipped to ground level.

Depletion levels were defined as the number of bites removed from a patch. Three of the four depletion levels were pre-set values intended to yield different degrees of depletion of the upper grazing horizon, and were based on earlier depletion trials. The fourth level of depletion determined the maximum number of bites that the animal would remove from the patch under the experimental conditions. In this treatment, when the animal stopped removing bites from a patch, it was led away from and returned to the patch in order to induce further grazing. This process was repeated until the animal failed to remove any bites for at least 30 seconds while standing in front of the patch. Table 8 shows the number of bites removed from a patch in the two experiments according to depletion level. The number of bites removed in depletion level 3 proved to be 39 and 34% of the maximum attainable under the experimental conditions (depletion level 4) for alfalfa and oats, respectively.

Table 8. The number of bites removed from a patch in experiments 1 and 2 according to patch size and depletion level					
Expt	Depletion level	Patch size			
		Small	Medium	Large	
<i>absolute bite number</i>					
1 (alfalfa)	1	4	8	16	
	2	8	16	32	
	3	12	24	48	
	4	31±2.5	60±5.1	126±8.7	
2 (oats)	1	5	11	-	
	2	11	22	-	
	3	16	33	-	
	4	54±8.9	81±3.2	-	
<i>bites/m²</i>					Average
1 (alfalfa)	1	36	33	35	35
	2	71	67	71	70
	3	107	100	106	104
	4	274	250	277	267
2 (oats)	1	45	46	-	45
	2	98	92	-	95
	3	143	138	-	140
	4	480	338	-	409

Patch grazing commenced at 10.00 h, prior to which the animals grazed as a group for approximately one hour. Patch grazing sessions were recorded on video. The video record was used to determine precisely grazing time and bite number. The characteristic tearing sound generated by the severance of a bite was the basis for counting bites.

On each day of the experiment the residual herbage height of the grazed patches was determined after the grazing sessions. An average height was recorded for every 5-cm section along each drill row of a patch (250 measurements/m²). The residual herbage was then clipped at ground level and bagged for drying.

The vertical mass profile of the vegetation was determined once per set of herbage patches. The lowest four sections of 5-cm thickness were bagged separately. The vegetation was also sampled for dry matter (DM) content immediately before each set of patches was grazed. DM samples were clipped to 20 cm height before sealing in airtight bags. Herbage close to the patches and of similar natural height was used for the profile and DM measurements. All clipped herbage was dried at 60°C for at least three days and weighed.

3.3.2.2 Results

Herbage mass is reported on a DM basis. Deviations following means are standard errors throughout.

3.3.2.2.1 Herbage

Mean herbage mass per unit area of the estimation patches in Expt 1 (alfalfa) and Expt 2 (oats) was 229.3 ± 6.67 g/m² (n=18) and 310.7 ± 23.50 g/m² (n=8), respectively. Since the treatment height of the estimation patches was 20 cm, the overall bulk density of the herbage was 1146.3 and 1553.7 g/m³ for Expt 1 and 2, respectively. Patch size was not significant in an analysis of variance of mass per unit area in either experiment. Mean natural height of the estimation patches in Expts 1 and 2 was 25 ± 0.9 and 34 ± 2 cm, respectively. This difference in natural height prior to clipping strengthened the contrast achieved in the herbage offered between the two experiments.

Table 9 shows the fraction of total herbage mass contained in the horizontal horizons of the sward profile with distance from ground level in both

experiments. The mean DM content of the vegetation was $20.6 \pm 0.55\%$ in Expt 1 (alfalfa) and $15.1 \pm 0.60\%$ in Expt 2 (oats).

Table 9. Fraction of herbage mass contained in horizons of 5 cm thickness for a sward trimmed to 20 cm height.

Horizon (cm)	Expt 1: alfalfa (n = 18)		Expt 2: oats (n = 8)	
	Mean	S.E.	Mean	S.E.
0* - 5	0.324	0.0090	0.313	0.0131
5 - 10	0.231	0.0042	0.253	0.0047
10 - 15	0.230	0.0053	0.235	0.0061
15 - 20	0.216	0.0051	0.199	0.0113

* ground level

3.3.2.2.2 Residual herbage height

The mean residual height of grazed plant elements in Expts 1 and 2 is given in Table 10 according to patch size and depletion level. For both experiments, the analysis of variance model contained the terms heifer, depletion level, patch size, natural height and the interaction between depletion level and patch size. Patch size was not significant in Expt 1 ($P=0.9915$). In Expt 2 patch size was significant ($P=0.0039$), with animals taking deeper bites on the small patches, though the average difference in biting depth between the small and medium size patches for the three pre-set depletion levels was only 1.2 cm. The natural height of the herbage patch prior to clipping was significant in Expt 1 ($P=0.0119$), there being an increase in residual height of 0.13 cm per cm increase in natural height. Heifer was highly significant in Expt 1 but not significant in Expt 2. Depletion level was highly significant in both experiments, though the decline in residual height over the first three depletion levels, averaged over patch sizes, was only 1.3 and 1.1 cm in Expts 1 and 2, respectively.

3.3.2.2.3 Bite area

Table 11 shows the mean bite area in Expts 1 and 2 according to patch size and depletion level. For both experiments, the analysis of variance model contained the terms heifer, depletion level, patch size, natural height and the interaction between depletion level and patch size. Patch size, heifer, and the interaction between patch size and depletion level were not significant in either experiment. The natural height of the herbage patch prior to clipping

was significant in Expt 2 ($P=0.0196$), there being a decrease in bite area of 2.3 cm^2 per cm increase in natural height. Depletion level was highly significant in both experiments, with a substantial decline in bite area over the first three depletion levels, followed by a precipitous drop at the maximum depletion level.

Table 10. Residual herbage height (mean $\pm$ S.E.; cm) of grazed patches in Expts 1 and 2. Patches were trimmed to a height of 20 cm prior to grazing.

Expt	Depletion level	Patch size			
		Small	Medium	Large	Average
1 (alfalfa)	1	12.1 $\pm$ 0.69	11.8 $\pm$ 0.52	11.9 $\pm$ 0.81	11.9 $\pm$ 0.37
	2	11.2 $\pm$ 0.51	11.3 $\pm$ 0.49	11.7 $\pm$ 0.56	11.4 $\pm$ 0.29
	3	10.0 $\pm$ 0.31	10.7 $\pm$ 0.66	11.1 $\pm$ 0.44	10.6 $\pm$ 0.29
	4	7.1 $\pm$ 0.89	6.8 $\pm$ 0.79	7.7 $\pm$ 1.14	7.2 $\pm$ 0.52
2 (oats)	1	11.4 $\pm$ 0.43	12.8 $\pm$ 0.70	-	12.1 $\pm$ 0.47
	2	11.4 $\pm$ 0.94	12.1 $\pm$ 0.62	-	11.8 $\pm$ 0.54
	3	10.2 $\pm$ 0.09	11.8 $\pm$ 0.74	-	11.0 $\pm$ 0.46
	4	6.9 $\pm$ 0.31	9.2 $\pm$ 0.99	-	8.1 $\pm$ 0.65

Table 11. Bite area (mean $\pm$ S.E.; cm^2) in Expts 1 and 2.

Expt	Depletion level	Patch size			
		Small	Medium	Large	Average
1 (alfalfa)	1	173 $\pm$ 22.1	154 $\pm$ 14.1	115 $\pm$ 11.6	148 $\pm$ 10.7
	2	123 $\pm$ 3.4	104 $\pm$ 6.9	101 $\pm$ 8.0	109 $\pm$ 4.2
	3	86 $\pm$ 1.4	91 $\pm$ 2.8	83 $\pm$ 2.2	87 $\pm$ 1.4
	4	38 $\pm$ 3.1	42 $\pm$ 3.8	37 $\pm$ 2.5	39 $\pm$ 1.8
2 (oats)	1	90 $\pm$ 18.0	82 $\pm$ 9.7	-	86 $\pm$ 9.6
	2	66 $\pm$ 6.8	63 $\pm$ 10.1	-	64 $\pm$ 5.6
	3	62 $\pm$ 2.6	54 $\pm$ 7.5	-	58 $\pm$ 4.0
	4	23 $\pm$ 4.9	30 $\pm$ 1.1	-	26 $\pm$ 2.6

3.3.2.2.4 Density of bite placement at the highest depletion level

The number of bites removed at the highest depletion level was not pre-set and can therefore be analyzed meaningfully. To test for an effect of patch size, the absolute number of bites removed (D) was normalized by dividing by patch size, yielding the density of bite placement. Analysis of variance of D was conducted with heifer, patch size and natural sward height in the model. Patch size was not significant in either experiment.

3.3.2.2.5 Observed horizon depletion

The frequency distribution of residual heights is shown for expt 1 in Fig. 7 and for expt 2 in Fig. 8. In order to enable comparison between patch sizes, the absolute frequencies were converted to fractions of patch area. Since initial sward height was 20 cm throughout, the fraction patch area at 20 cm represents the ungrazed area. The range of residual heights over the first three depletion levels did not change much, whereas there is a dramatic shift to the lower residual range for the maximum depletion level. Over the first three depletion levels the modal grazed residual height is 10 cm for almost every patch size. This strongly suggests horizon-oriented grazing.

These distributions were used to estimate the fraction depletion attained for each grazing horizon. Using the same method and criteria used in the maximum depletion experiment reported above, we defined the fraction upper horizon grazed as the sum of all residual categories excluding 20 cm. The fraction of the second grazing horizon grazed was defined as the sum of residuals up to and including 7 cm. The fraction of the lower horizon grazed according to depletion level and patch size in each experiment is given in Table 12. There is a small increase in fraction second horizon grazed over the first three depletion levels. This trend becomes more pronounced as patch size declines. Averaging over patch sizes, less than 5% of the second grazing horizon is grazed in the first and second depletion levels. This increases to approximately 10% at the third depletion level. Thus we can say that grazing style is predominantly, if not exclusively, horizon oriented.

Table 12. Estimated mean fraction of the lower grazing horizon that was depleted in Expts 1 and 2. Values are derived from the frequency distributions of residual herbage heights, as explained in text.

Expt	Depletion level	Patch size			
		Small	Medium	Large	Average
1 (alfalfa)	1	0.0569	0.0279	0.0355	0.0401
	2	0.0371	0.0614	0.0502	0.0496
	3	0.1922	0.1334	0.0787	0.1348
	4	0.6364	0.6359	0.6006	0.6243
2 (oats)	1	0.0541	0.0054	-	0.0298
	2	0.0313	0.0119	-	0.0216
	3	0.1164	0.0326	-	0.0745
	4	0.5695	0.2833	-	0.4264

Figure 7. Frequency distribution of residual herbage heights for alfalfa, expressed as fraction patch area, following grazing of herbage patches by heifers to four levels depletion (DL).

Patch size: =small, =medium, =large.

3.3.2.2.6 Expected bite area and horizon depletion

Having derived the mean bite area and fraction horizon grazed for each depletion level, we can now test the bite placement simulator developed earlier. Our focus in this study is on the known upper-horizon dynamics of bite area at relatively low depletion levels, i.e. the first three depletion levels. The single "unknown" in the model is the parameter for the potential bite area at zero depletion for the given initial sward height and herbage characteristics. This was the only parameter varied in the model. In all other respects, the model was identical to that used in the earlier study. Figs 9 and 10 compare the derived mean bite area and fraction upper-horizon grazed for the first three depletion levels with the predicted trajectories of the bite placement simulator. In expt 1 (alfalfa), the best fit to the data is achieved with a potential bite area of 127 cm². The fit is excellent for the large patch size at all depletion levels. The simulator under-estimates bite area for the small and medium patch sizes at depletion level 1, and for the small patch size at depletion level 2. In expt 2 (oats), the best fit is obtained with a potential bite area of 80 cm². In this expt patch sizes were small and medium only, and there is evidence here too for slight under-estimation at the lowest depletion level.

3.3.2.3 Discussion

These patch depletion trials have demonstrated clearly that cattle graze herbage patches with a predominantly horizon-oriented style. The inclusion of a maximum depletion treatment shows that our results are not due to some plant morphological "barrier" to the removal of bites from the lower reaches of the profile. It is clear from the video record of the experiments that in the maximum depletion treatment the animals continued grazing beyond completion of the upper grazing horizon with no apparent decline in motivation.

Grazing depth in both experiments was slightly less than the idealized "talk-half" value, and the difference in grazing depth between the two species used was only about 1 cm despite the strong contrast in sward characteristics. Simply on the basis of handling the patches during construction, it is clear that natural sward height prior to clipping has a strong influence on sward physical characteristics such as stiffness. Thus the very small reduction in bite depth observed in oats relative to alfalfa despite the

Figure 9. Comparison of the derived mean bite area and fraction upper-horizon grazed for the first three depletion levels on alfalfa patches (according to patch size) with the predicted trajectories of the bite placement simulator.

A potential bite area of 127 cm² was assumed.

Figure 10. Comparison of the derived mean bite area and fraction upper-horizon grazed for the first three depletion levels on oats patches (according to patch size) with the predicted trajectories of the bite placement simulator.

A potential bite area of 80 cm² was assumed.

large difference (9 cm) in natural height prior to clipping is an encouraging result.

These trials have shown that there is a significant within-horizon decline in bite area with depletion level. Since bite depth changed little over the first three depletion levels, it follows that there must be a within-horizon decline in bite weight. Our timing measurements based on the video records suggest that the animals do not fully compensate for the decline in bite weight with increasing bite rate. The bite placement simulator reproduced our experimental results well for the patch size closest to that of a feeding station. The decline in bite area in the model derives simply from increasing bite overlap with degree of horizon depletion. Thus we can conclude that patch depression is expected even when grazing is restricted to a single grazing horizon, and that the depression derived primarily from a decline in mean effective bite area due to bite overlap.

Though patch size did not have a statistically significant effect on bite area, there was a clear trend for mean effective bite area to be greater on smaller patches at the lowest depletion levels. It should be noted that the bite placement simulator yielded an excellent fit for the largest patch size at low depletion levels and the pattern of bite area decline for the small patch size can not be reproduced with the model simply by adjusting potential bite area. Though we need to re-examine the video records specifically for this purpose, our feeling at present is that the elevated bite area at low depletion on small patches is due to a border effect whereby the animal achieves a higher bite area by sweeping into the patch from the side. Our impression in the field was that the animals tended to initiate the grazing bout with such side entries more often on the small patches than they did on the large.

In the earlier maximum depletion study a potential bite area of 150 cm² was assumed in the bite placement simulator for the upper grazing horizon of a sward of initial height 20 cm. The same value was used for oats and alfalfa. In the present study, the fitted values were 127 cm² for alfalfa and 80 cm² for oats. These values are certainly qualitatively consistent with the finding of the previous project that bite area is a function of both sward height and bulk density. In the maximum depletion study, sward bulk density was similar for both species, being approximately 835 and 750 g m⁻³ for alfalfa and oats respectively. In this study, bulk densities were considerably higher (due to

changes in sowing method) and higher in oats than in alfalfa, being approximately 1150 and 1550 g m⁻³ for alfalfa and oats respectively. Hence we would expect potential bite areas to be lower in these experiments, and we would expect the potential bite area for oats to be lower than that for alfalfa. The higher natural sward height prior to clipping in the oat patches would also be expected to reduce the potential bite area.

3.3.3 HCS-based incremental depletion trials

The previous depletion experiments treated relatively uniform swards. This was certainly true in terms of the horizontal distribution of herbage mass, and the vertical distribution of mass did not deviate as strongly from a uniform distribution as is often encountered in natural swards. We therefore conducted two further depletion trials which focussed on aspects of within-patch heterogeneity by varying the spatial distribution of leaves within patches or by examining the role of reproductive stems of different lengths as potential intake rate inhibitors. These trials were conducted using the HCS methodology that was developed in the previous BARD project.

3.3.3.1 Introduction

Recent advances in our understanding of herbivore foraging mechanisms have led to two complementary approaches. These can be referred to as: 1) the functional response approach, and 2) the instantaneous dynamics approach. The functional response approach relates average dry-matter intake rates to average bite masses as animals feed from small patches of forage (e.g. Spalinger, Hanley & Robbins 1988; Spalinger & Hobbs 1992; Shipley & Spalinger 1992; Gross et al. 1993; Ginnett & Demment 1995). This approach has led to major insights into herbivore foraging behavior (Spalinger & Hobbs 1992) and techniques can be derived from it to estimate animal intake and test important hypotheses under field conditions (e.g. Ginnett & Demment 1997). However, because it is based upon average values for intake rates and bite masses, the functional response approach integrates over the moment-to-moment dynamics of bite mass and intake rate variation as animals deplete patches. There is now mounting evidence that herbivores experience patch depression (i.e. decline in instantaneous intake rate, sensu Stephens & Krebs 1986) that is concomitant with patch depletion (Bergstrom et al. 1990; Laca et al. 1994; Shipley & Spalinger 1995). This, in turn, suggests that the marginal value theorem (Charnov

1976) may have application in the understanding of short-term intake rates for grazing herbivores. In fact, published data show that herbivores can choose patch residence times that are at least qualitatively consistent with predictions based on a marginal-value theorem model (Jiang & Hudson 1993; Distel et al. 1995; Shipley & Spalinger 1995).

Short-term intake rates for ungulate herbivores are controlled in large part by bite mass (Spalinger et al. 1988; Gross et al. 1993; Ginnett & Demment 1995). Bite mass for grazers, in turn, is controlled by characteristics of the sward such as height, bulk density, and vertical heterogeneity (Black & Kenney 1984; Burlison, Hodgson & Illius 1991; Ungar, Genizi & Demment 1991; Laca et al. 1992a; Flores et al. 1993; Prache 1997). Based on these relationships, Ungar, Seligman and Demment (1992) developed a model of the patch depletion process for grazers based on a horizon grazing concept (as outlined in section 3.3.1.1 above). In this model, animals graze systematically by removing successive horizontal layers of vegetation termed horizons. Because bite mass is a function of sward height (Laca et al. 1992a), bite mass is predicted to decrease discontinuously as each horizon is removed. Laca et al. (1994) found that this model largely explains bite mass reduction and instantaneous intake rate depression in cattle, although bite weight also decreased within each horizon due to overlapping of bites with previously grazed areas. This led to a more continuous decline in bite weight than that predicted by the model.

We report two experiments designed to investigate the effects of sward characteristics on the nature of the gain functions experienced by a large mammalian grazer (*Bos taurus*). We hypothesized in experiment 1 that realistic variations in the spatial distribution of forage within a patch might lead to very different bite mass and intake rate dynamics, via the effects of sward structure on the initial bite dimensions obtained by the grazer. In experiment 2, we hypothesized that the presence of stems of different lengths would result in markedly different gain functions by physically restricting bite dimensions (principally bite depth, e.g. Flores et al. 1993) as well as through a slowing of bite rate as found by Ruyle, Hasson & Rice (1987). We discuss the implications of our results for the further development of foraging theory for herbivores, as well as for applications in herbivore production.

3.3.3.2 Materials and methods

3.3.3.2.1 Hand-constructed swards and animal trials

Both experiments were performed using the HCS technique. Fresh orchardgrass leaves (*Dactylis glomerata* L.) were collected every morning and placed in water prior to constructing the patches. Leaves were threaded through holes in wooden modules and the modules were then fastened with screws to a plywood base board such that the leaves were held firmly in place. Each module measured 10 cm by 10 cm and contained 16 holes in a symmetrical grid pattern. Tips of the leaves were then trimmed to present a uniform surface to the animals and to reduce variation in sward biomass between patches. Three modules were chosen at random prior to offering a board to an animal and the leaves clipped at the base, placed in an oven at 60 °C and dried to constant weight. These modules provided a per-module estimate of the pre-grazing biomass of forage on the board. To conduct a trial, an animal was led to the board and allowed to take either 10, 20, 30, 45, or 60 bites at which time the trial was interrupted. Each trial was recorded on videotape. After each trial, every remaining tiller was measured to the nearest millimeter to calculate bite depth, and the orts were then clipped and dried as above. Bite area was calculated as the product of the number of grazed tillers and the area per tiller (12.5 cm²/tiller). Dry-matter intake was calculated as the difference between the pre-grazing mass as estimated from the three sample modules and the post-grazing mass. Following Laca et al. (1994) we calculated instantaneous intake rate (IIR), bite mass (S), and time per bite (TPB) for each incremental set of bites (1-10, 11-20, 21-30, 31-45, 46-60 bites) by subtracting the herbage mass ingested during a trial (e.g. 20 bites) from that obtained in the next longer bite set (e.g. 30 bites). Instantaneous intake rate (IIR) was calculated as the quotient of intake and grazing time for each bite set, which was determined from analysis of the videotapes. Bite mass (S) was the quotient of intake and the number of bites taken during that bite set. Similarly, time per bite (TPB) was calculated as the quotient of grazing time and the number of bites taken.

The animals were three mixed-breed steers of ca. 600 kg live weight. The animals were maintained on good quality alfalfa hay. Trials were run in the morning prior to the animals receiving their daily ration. To avoid carryover effects only one trial was run per animal per day.

Experiment 1 Design

Our experiments utilized repeated-measures designs (e.g. von Ende 1993) in which each animal subject was exposed to each treatment. The treatments were factorial combinations of three sward structures and the five bite sets (1-10, 11-20, 21-30, 31-45, or 46-60 bites). The sward treatments (Fig. 11) were as follows: 1) Tall - 3 leaves per hole, 8 holes per module, 20 cm in height, 0.21 m² in area, 2) Short - 3 leaves per hole, 8 holes per module, 10 cm in height, 0.42 m² in area, and 3) Variable - 5 leaves per hole and each leaf trimmed to either 20, 16, 12, 8, and 4 cm in height, 8 holes per module, 0.21 m² in area. These treatments were designed such that each patch had the same pre-grazing biomass and average bulk density. The variable treatment was designed such that although the average overall bulk density was the same as in the other treatments, within the patch, bulk density increased from top to bottom as in a natural sward.

Experiment 2 Design

Experiment 2 also consisted of factorial combinations of three sward structures (Fig. 11) and the same five bite sets as in experiment 1. Each patch measured 0.24 m² in area and consisted of three orchardgrass leaves per hole, 8 holes filled per module, and 20 cm in height so that leaf biomass was constant across all treatments. The three sward structure treatments were: 1) Tall, in which 15 cm stems were placed in the 8 remaining holes in each module, 2) Short, in which 5 cm stems were used, and 3) None, in which no stems were used. Previous studies show that in homogeneous swards, cattle tend to remove 50% of the sward height in their initial bites (Ungar et al. 1991; Laca et al. 1992a). Our two stem treatments were designed to bracket this 50% value. Because our interest was in the effect of stems on intake rate of leaf, only leaf biomass is included in our intake estimates.

3.3.3.2.2 Statistical analyses

Initial bite dimensions (bite depth, bite area) were analyzed as two-way randomized block ANOVA with animals as blocks and sward treatments as the test factor. We used only the data from the 1-10 bite treatment to avoid introducing any effect of re-grazing previously grazed areas on bite dimensions. Bite mass, time per bite, and IIR for both experiments were analyzed by univariate repeated-measures ANOVA (von Ende 1993) with

Figure 11. Diagrams of the sward structure treatments for Experiments 1 and 2. Expt 1: T = tall (20 cm) swards, S = short (10 cm) swards, V = variable height swards in which individual leaves were trimmed to either 20, 16, 12, 8, or 4 cm in height. Expt 2: tall = swards with 15 cm stems, and short = swards with 5 cm stems. The no stem treatment is not depicted.

individual animals as subjects, and bite sets (5 levels) and sward treatments (3 levels) as within-subjects factors.

Gain functions were fit to cumulative intake and grazing time data for each sward structure by non-linear regression. Following Laca et al. (1994), a rectangular hyperbola ($I = k_1 T / (1 + k_2 T)$) was fitted to all sward structure treatments, where I is cumulative intake in grams dry-matter, T is the grazing time in seconds, and k_1 and k_2 are parameters estimated by the regression fitting. The parameter k_1 has units $g \text{ sec}^{-1}$ and represents the initial instantaneous intake rate; k_2 has units sec^{-1} and is the reciprocal of the time needed to ingest half of the patch contents. Note that k_1/k_2 is an estimate of the asymptotic cumulative intake (i.e. the amount of available forage in the patch). In addition, a related sigmoid function ($I = k_1 T^2 / (1 + k_2 T^2)$) was fitted to one data set. All data analyses were performed using Statistica' software. In the following text all means are given $\pm$ one standard error.

3.3.3.3 Results

3.3.3.3.1 Experiment 1

Sward structure had significant effects on the initial bite depth ($P=0.041$) and bite area ($P=0.037$) obtained by the animals. Bite depth, expressed as percent of overall sward height, was greatest in the variable bulk density treatment ($63.7 \pm 5.4\%$), and roughly equal in the tall ($52.7 \pm 3.6\%$) and short treatments ($50.3 \pm 5.2\%$). Bite area was also greatest in the variable bulk density treatment ($103.7 \pm 21.1 \text{ cm}^2$), smaller in the tall treatment ($99.7 \pm 8.4 \text{ cm}^2$), and smallest in the short treatment ($80.7 \pm 6.8 \text{ cm}^2$).

Bite mass was significantly affected by pre-grazing biomass, sward structure, and bite set (Table 13). There were no significant differences in bite mass among animals. In general, bite mass declined as the patches were depleted in the tall and variable treatments, except for a marked initial rise in bite mass in the variable bulk density treatment (Fig. 12a). In the short treatment, bite mass remained constant. These different patterns are reflected in the significant sward structure by depletion level interaction. Time per bite (Fig. 12b) was not affected by any of the treatments and averaged $1.3 \pm 0.07 \text{ sec}$. Instantaneous intake rate (IIR), exhibited a strikingly similar pattern of variation to that observed for bite mass (Fig. 12c) and was significantly affected by pre-grazing mass, sward structure, and bite set.

Figure 12. Effects of depletion level on (a) bite mass, (b) time per bite, and (c) instantaneous intake rate (IIR), of cattle foraging from hand-constructed swards.

Table 13. ANOVA results for the two experiments. Values in the table are probability values for the indicated *F*-tests. BM - bite mass, TPB - time per bite, IIR - instantaneous intake rate.

Source of Variation	df	Experiment 1			Experiment 2		
		BM	TPB	IIR	BM	TPB	IIR
Biomass	1	0.022	0.774	0.009	0.012	0.286	0.770
Subjects	2	0.878	0.107	0.056	0.304	0.559	0.021
SS*	2	0.028	0.424	0.009	0.288	0.003	0.000
Bite Set (BS)	4	0.001	0.938	0.002	0.029	0.449	0.001
SSxBS	8	0.030	0.244	0.080	0.611	0.382	0.275
Subject x SS	4	0.999	0.869	0.902	0.664	0.571	0.274
Subject x BS	8	0.575	0.035	0.033	0.694	0.571	0.370
Error	15						

*SS=sward structure

Cumulative gains by animals grazing the short treatment were essentially linear (Fig. 13). Marked negative acceleration of cumulative gains was observed in both the tall and variable patches. The initial increase in bite mass and IIR in the variable treatment suggested to us that a sigmoid gain function might be more a more appropriate description of cumulative gains in this treatment. Although the rectangular hyperbola gave a reasonable fit to the data ($R^2=0.846$), examination of the residuals revealed that the model overestimated points early in the curve and underestimated points in the middle of the curve. The sigmoid function yielded a better fit than the rectangular hyperbola ($R^2=0.885$) and a better distribution of residuals.

3.3.3.2 Experiment 2

As in experiment 1, sward structure had marginally significant effects on the initial bite area ($P=0.065$) and bite depth ($P=0.064$) of our cattle. Bite area declined from 134.2 ± 3.4 cm² in the no stem treatment to 122.5 ± 2.5 cm² on the 5 cm stem treatment to 111.7 ± 4.1 cm² in the 15 cm stem treatment. Bite depth was greatest in the no stem treatment (10.6 ± 0.7 cm), less in the 5 cm stem treatment (9.3 ± 1.9 cm), and least in the 15 cm stem treatment (7.3 ± 2.3 cm).

There was no statistically detectable influence of stem length on bite mass (Table 13) although bite mass appeared to be lower initially in the 15 cm stem treatment (Fig. 14a). Bite mass exhibited a significant decline as the

Figure 13. Cumulative gains in the three sward structure treatments for experiment 1. The solid line gives the fit for the tall treatment $I = 0.756T/(1+0.018T)$, $R^2 = 0.86$; the dashed line gives the fit for the short treatment, $I = 0.311T/(1+0.003T)$, $R^2 = 0.90$; and the dotted line gives the fit for the variable treatment, $I = 0.063T^2/(1 + 0.003T^2)$, $R^2 = 0.88$.

Figure 14. Effects of depletion level on (a) bite mass, (b) time per bite, and (c) instantaneous intake rate (IIR), of cattle foraging from hand-constructed swards.

patches were depleted. Time per bite was significantly longer in the 15 cm stem treatment relative to the no stem and 5 cm stem treatments (Fig. 14b). Patch depression is indicated by the decline in IIR in all treatments as the patches were depleted (Fig. 14c). IIR was virtually identical in the no stem and 5 cm stem treatments but was much lower in the 15 cm stem treatment.

Due to the lowered bite rate, the 15 cm stem treatment exhibits a much shallower initial slope for the gain function than the other two treatments and appears roughly linear (Fig. 15). The no stem and 5 cm stem treatments have very similar curves but the predicted asymptote is lower (33.5 g vs. 36.8 g) for the 5 cm stem treatment. Both are very close to the actual pre-grazing biomass of 35.0 ± 3.2 g (S.D.). The predicted asymptote for the 15 cm stem treatment (46.2 g) greatly overestimates the actual biomass in the patch.

3.3.3.4 Discussion

3.3.3.4.1 Mechanisms of patch depression

Some degree of patch depression was noted in all of our sward structure treatments in both experiments, except for the 10 cm leaf treatment in Experiment 1. Mechanistically, there are two possible explanations for declining IIR as patches are depleted: decreasing bite mass, and/or increasing bite handling time. In our experiments, as well as those of Laca et al. (1994), patch depression was a result of decreasing bite mass as patches were depleted but we observed no significant relationship between time per bite and depletion level. Ungar et al.'s (1992) horizon grazing model predicts a discontinuous decline in bite mass as patches are depleted. Figures 12a and 14a show clear evidence of a horizon effect occurring after 30 bites in experiment 1 (20 cm treatment) and after 20 bites in experiment 2. However, as in Laca et al.'s (1994) paper, there is some evidence for bite mass decline within horizons as well. There are two reasons for this deviation from Ungar et al.'s (1992) prediction. Because bites tend to have a circular area (Laca et al. 1994), even systematic grazing of a horizon will leave some material ungrazed that can only be ingested by taking a smaller bite. Also, some animals had a tendency to deviate from a strict horizon-based mode of depletion and took occasional smaller, second horizon bites prior to completely depleting the first horizon.

Figure 15. Cumulative gains in the three sward structure treatments for experiment 2. The solid line gives the fit for the no stem treatment $I = 1.171T/(1 + 0.032T)$, $R^2 = 0.76$; the dashed line gives the fit for the 15 cm stem treatment, $I = 0.34T/(1 + 0.007T)$, $R^2 = 0.74$; and the dotted line gives the fit for the 5 cm stem treatment, $I = 1.081T/(1 + 0.032T)$, $R^2 = 0.85$.

3.3.3.4.2 Spatial distribution of forage

Stephens & Krebs (1986) described some potential forms that gain functions might take and suggested underlying biological reasons for each. For example, they postulated that a simple asymptotic curve is probably the most reasonable description for gross gains in most patches. A linear gain function would indicate a patch that depletes but does not exhibit intake rate depression. A sigmoid curve could occur when a predator searches for mobile prey that is distributed in clumps throughout the patch. We were able to demonstrate each of these three types of gain functions for a single herbivore species simply by rearranging the same biomass of forage into different but biologically realistic spatial configurations.

Our 20 cm tall patches resulted in a "classical" gain curve which asymptotically approaches the amount of forage in the patch. In contrast, a sigmoid function appears to provide the best fit to our variable bulk density patches and is consistent with the dynamics of bite weight and IIR variation as these patches were depleted. Although a sigmoid function provided a better statistical fit for the variable height treatment than did a "classical" function, our justification for the sigmoid curve is actually mechanistic in nature. As the variable patches were depleted, bite mass and IIR increased for a time before they decreased (Fig. 12a, c). This was due to the greater bulk density in the lower parts of the sward. Eventually, as the sward height was shortened due to depletion, bite mass and IIR decreased. Now consider that IIR represents the slope (i.e. the derivative) of the gain function at any given point. Any increase in IIR with time suggests that the slope of the gain function must increase with time as well. In the "classical" gain function the slope is monotone decreasing which is in direct contrast to our empirical result that IIR increased before it eventually declined.

Gains in the short patches were not statistically differentiable from linear. There are two possible explanations for this. First, gains in this type of patch may increase in a linear fashion until the patch is entirely depleted. Second, we might have encountered patch depression if we had used a greater number of bites. In these trials, the short boards were generally almost entirely depleted after 60 bites, except for ca. 3-4 cm of stubble that remained on the board. The cattle were reluctant to continue grazing when the swards became this short because 3-4 cm appears to be a limiting sward

height for cattle and it would have been difficult or impossible to obtain longer bite sets.

The marginal value theorem (Charnov 1976) predicts that patch residence time should scale positively with inter-patch travel time. The exact solution, however, will depend on the particular shape of the gain functions experienced by the forager. Using our empirically determined gain functions, we have solved for the optimal residence time policy for habitats consisting of "monocultures" of the patch types used in experiment 1, assuming equal patch densities (Figure 16). For each habitat type, the optimal policy for the herbivore is markedly different, even though the overall biomass density of forage is the same. For habitats consisting of our tall patches, the optimal residence time would be a simple increasing function of the average inter-patch travel time. However, because the short patches did not exhibit patch depression, the optimal policy is to remain in each patch until all forage is depleted regardless of travel time. For habitats consisting of our variable bulk density patches, the optimal residence time would increase with increasing travel time except that there would exist a minimum residence time characteristic of all patches that is defined by the case where inter-patch travel time is equal to zero. These results have implications for studies that attempt to describe herbivore foraging strategies from visual observation of movement patterns. Animals foraging under the conditions of our short or variable bulk density patches could be interpreted to be foraging by a simple rule of thumb such as a constant residence time (e.g. Janetos & Cole 1981), or by a threshold rule (e.g. Focardi, Marcellini & Montanaro 1996), when in actuality they have solved a simple marginal-value theorem problem. Determining the existence of patch depression and understanding its nature is therefore necessary before making conclusions regarding patch-residency strategies for herbivores.

For herbivores that follow an optimal policy, have similar search strategies, and who eat to the same fill level, our analysis gives rise to the following qualitative predictions. Short pastures will be more intensively used on a per-feeding station basis than taller pastures but will yield lower animal performance in terms of long-term average intake rates. Taller swards will have a smaller proportion of biomass removed from each patch and grazing will be distributed over a greater number of patches. At very short and very long travel times, the taller homogeneous bulk density patches offer higher

Figure 16. Optimal patch residence times for grazing herbivores in three habitat types, each consisting of monocultures of patches that correspond to the three sward treatments in experiment 1. The solid line is the solution for a simple asymptotic gain function as obtained in the 20 cm tall treatment. The dotted line is the solution for the sigmoid function obtained in the variable bulk density treatment. The dashed line is the solution for a patch with a linear gain function as obtained in the 10 cm treatment.

performance whereas at intermediate travel times the variable bulk density patches offer slightly greater long-term intake rates.

3.3.3.4.3 Residual stems as intake rate inhibitors

Ruyle et al. (1987) found that residual stems, i.e. stems left from the previous year's growth, acted to reduce biting rate by interfering with bite formation processes. The stems in our experiment were mature reproductive stems but were still green and flexible. Flores et al. (1993) showed that mature reproductive stems can reduce bite mass by limiting the depth to which the animal can insert its incisors into the sward. In the absence of stems, in a homogeneous sward, cattle tend to remove approximately 50 percent of the sward weight when cropping their first bites (Ungar et al. 1991; Laca et al. 1992a). Because our stem treatments were designed to bracket this 50 percent value, we predicted that only the long stem treatment would have an effect on bite rate or bite depth, and that the short stems would only have an effect as the animal grazes into the second horizon. Figures 14a and 14b clearly illustrate that this is the case. Long stems affected bite weight by restricting bite depth and lengthened time per bite by interfering with bite formation. The combined effect resulted in a significant lowering of intake rate. The effect of the short stems was primarily expressed as a restriction of bite weight after approximately 30 bites had been removed from the patch. This resulted in a slight diminution of the asymptotic intake relative to the no stem treatment (Fig. 15). The predicted asymptote for the long stem treatment greatly overestimated the actual biomass in the patch. This is most likely due to the fact that after 60 bites, only about 1/2 of the biomass had been removed from the patches and so our curve is not accounting for patch depression that would have occurred later on had we allowed foraging to continue past 60 bites. If this is the case then the slope of this curve is somewhat overestimated as well which means we are slightly underestimating the effect of the long stems on cumulative intake.

If we assume the existence of habitats consisting of monocultures of each patch type, equal patch densities in each habitat, and that animals eat to the same level of fill in each habitat, we can make the following qualitative predictions concerning the pattern of grazing in stemmy vs. non-stemmy swards. Animals grazing in non-stemmy swards will have shorter residence times and remove more foliage from each patch. As a result, they should visit

fewer total patches per day, while obtaining higher intake rates than animals foraging from stemmy swards. Stemmy swards will be used less intensively on a per-patch basis, and because greater numbers of patches will be visited per animal the distribution of grazing will be more homogeneous than in a non-stemmy habitat.

3.3.3.5 Conclusions

Studies that link herbivore foraging behavior to variations in vegetation structure have the potential to generate tools for monitoring habitat quality for wild herbivores, managing production-based grazing systems, as well as to validate the patch-based approach for studying herbivore foraging in general. The present study underscores the notion that a detailed understanding of the relationship between sward structure and animal ingestive mechanisms is necessary not only for development and testing of theoretical models but also for the development of applications for grazing management (Forbes 1988; Ungar 1996). To date a number of studies have been conducted on patch use in cattle. However, because foraging mechanisms scale in important ways with body mass (Illius & Gordon 1987; Gross et al. 1993; Shipley et al. 1994) the relationships between sward structure, ingestive behavior, and patch use need to be generalized over a range of herbivore body sizes as well. Finally, for herbivores that browse on woody vegetation, models such as the horizon model (Ungar et al. 1992) are not appropriate due to the more complex architecture of woody plants. Similar research on browsers is necessary to further generalize the applicability of patch-based approaches to understanding herbivore foraging behavior.

3.3.4 Sod-based depletion trials and testing at larger spatial scales

The next series of depletion trials examined the use of cut sods as an alternative to the HCS technique for stall-based experiments. Furthermore, these trials examined the relation between grazing behaviour for the single-patch stall-based arena and a relatively large multi-patch field arena. The experiments reported above focused on sward heights of 10 to 20 cm whereas the following trials extended the height range examined to over 60 cm.

3.3.4.1 Introduction

Foraging behavior has been described as an hierarchical process in space and time (Senft et al., 1987; Stuth, 1991; Bailey et al., 1996). In the spatial dimension the following levels may be recognized ranging from the very small to the very large: the bite, the feeding station, the patch, the plant community and the landscape. The technique of using hand-constructed swards developed by Black and Kenney (1984) and Laca et al. (1992b) has enabled the quantification of bite dimensions and bite weight as a function of sward height and bulk density. This cleared the way to investigate food intake at individual feeding stations, i.e. the area available to the animals without walking. Thus, Laca et al. (1994a) succeeded in describing the feeding at a single feeding station as a process of gradual depletion. Subsequently, Distel et al. (1995) were able to investigate foraging behavior at a larger scale in an experimental pasture with discrete patches of the same size as a feeding station, separated by alleys without vegetation. It is unclear, however, whether this technique would work equally well in a continuous pasture with larger patches. Moreover, Distel et al. (1995) used oesophageally-fistulated animals, which may require costly care and maintenance. Instead, Wilmshurst et al. (1995) used cut sods that were grazed by intact animals in stall trials to estimate bite size in relation to sward standing crop. In this study we adopt the sod-grazing technique in combination with sound and video recording to examine the feasibility of using small-scale depletion curves derived from stall trials to estimate forage intake of cattle at the pasture. We hypothesize that estimations of bite weight and intake that ignore feeding station depression will be an incorrect basis to estimate intake rate at longer time scales. The sods were grazed for a variable number of bites to generate patch depletion curves (see Laca et al., 1994a) that characterize forage intake as a function of the number of bites taken at a single feeding station. Thus, the method agrees with the hierarchical approach to foraging behaviour as proposed by Stuth (1991). Two sod experiments were carried out, with the second experiment as a validation for predictions of intake. A field experiment was carried out to validate the predictions from the sod experiments with respect to both the amount and the rate of intake.

3.3.4.2 Materials and Methods

3.3.4.2.1 Pasture

The experiment was conducted in a spontaneously established, irrigated *Setaria lutescens* (Weigel) Hubb. grassland. The pasture was cut entirely and removed in mid-June 1996 and fertilized with ammonium nitrate 2 weeks later (90 kg N/ha). Tall patches were left to grow and flower. Short patches were cut again at c. 5 cm height in early August, fertilized again (180 kg N/ha) and cut for the last time 2 weeks later in a sequence so that all plots had the same 2 weeks regrowth period before the field experiment (3-11 September). The first sod experiment was conducted from 28 September till 3 October using the same pasture. The pasture was reseeded with *Lolium perenne* L. ('Bison' perennial ryegrass) using a no-till drill in early November. On 28 February 1997 ammonium nitrate was applied at 270 kg N/ha on the short patches and at 90 kg N/ha on the tall patches. Short patches were cut at regular intervals and tall patches were left to flower and mature. The second sod experiment took place from 30 June till 2 July. By then the tall patches were turning yellow and the short patches were again dominated by *Setaria lutescens* as the ryegrass had withered away.

We used 4 Hereford crossbred steers in the experiments. When not in the field, the animals were maintained on alfalfa hay, fed after experimental sessions. The steers were 30-months old and weighed 604-710 kg during the field experiment and the first sod experiment and had grown to 738-894 kg by the time of the second sod experiment, 9 months later.

3.3.4.2.2 Sod Experiments

Sods of 50x30 cm area and with a c. 8-10 cm-thick layer of soil and roots were cut from the previously irrigated pasture. They were selected to represent a certain sward height as measured with a 0.1 m² rising plate (c. 100 g) that was gently lowered onto the vegetation along a measuring rod. The principle used by the rising-plate method is described in detail by Earle and McGowan (1979). Two height measurements were made per sod. Each sod was put into a metal tray, giving an effective sward area of 0.14 m². To prevent the sod from being torn apart by the grazing animals, c. 8 thin metal rods were laid across it lengthwise. Total weight of tray plus sod typically varied between 14 and 21 kg. The tray was fastened by 4 steel rods (6 mm

diameter) placed crosswise over the thin metal rods and held down by springs to a wooden board, that itself was bolted onto an 80 kg steel plate.

The sods were offered to the animals in the morning between 9 and 12 am. The sods were placed at the narrow end of a triangular holding area of c. 6 m², next to the feedlot. They were weighed before and after grazing at 1 g accuracy. A control sod was kept under similar conditions and weighed at the same times to correct for weight loss by evapotranspiration. Total handling time for each sod was 5-15 min. Bite weight (BW, g) was calculated as:

$$BW = d [M_1 - M_2 - WL]/B$$

where d is the dry matter proportion of the fresh forage, M₁ and M₂ are the pregrazing and postgrazing fresh mass, respectively (in g), WL is the weight loss due to evapotranspiration as determined from the control sod (in g), and B is the number of bites taken.

Each grazing session was videotaped to establish a visual frame of reference. The sounds of biting and chewing were recorded on videotape by a wireless microphone taped to the animal's forehead as described in Laca et al. (1992a); the transmitter was attached to a halter. The grass of the ungrazed control sod and the residual forage of grazed sods were clipped at 2.5 cm above ground level, dried at 65°C, weighed and analyzed for nitrogen and fiber content (Goering and Van Soest, 1970). Images and sound records were later used to identify bites and chews in a time sequence using a simple event recording program. A chew was recorded every time the jaw closed in association with a grinding sound. Thus, any time a compound jaw movement took place a chew was tallied (Laca et al. 1994b).

During the first sod experiment, 24 sods of 6 different types were tested: 3 different heights of short sods and three different heights of tall sods (Table 14). One sod type was examined per day, with a random order of sod types over days and of animals within days. Each sod was grazed in three consecutive 10-bite series with sod weights recorded in between sessions.

In the second sod experiment 24 sods of 2 sod types were tested: a short *Setaria*-sod of lesser height but greater bulk density than in the first experiment and a tall sod of similar bulk density but from a different species (*Lolium perenne*) than in the first experiment (Table 14). This time only one

bite series was measured for each sod: 10, 20 or 30 bites for the short sods and 5 or 10 bites for the tall sods; longer bite series were not attempted with the tall sods as the early trials indicated that the steers were reluctant to eat senescent grass.

Table 14. Characteristics of *S. lutescens* sods (all treatments except TR) and *L. perenne* sods (TR treatment) used to determine depletion curves

	Treatment							
	Experiment 1						Experiment 2	
	SS	SM	ST	TS	TM	TT	SD	TR
Height (cm)	13.9 ±0.1	16.4 ±0.4	20.3 ±0.2	36 ±0	49 ±0	62 ±0	9.5 ±0.5	49.8 ±2.5
Standing crop (g/m ²)	328 ±34	354 ±13	422 ±29	729 ±76	959 ±46	1076 ±48	379 ±36	738 ±170
Bulk density (kg/m ³)	2.35 ±0.23	2.17 ±0.11	2.08 ±0.15	2.03 ±0.21	1.96 ±0.09	1.74 ±0.08	3.97 ±0.11	1.36 ±0.12
%NDF	63.8	64.1	64.1	70.0	66.8	69.4	60.5 ±0.6	70.1 ±1.1
%ADF	25.9	32.7	31.8	33.1	35.8	39.4	33.9 ±0.8	41.0 ±0.9

Standard error indicated where appropriate.

N=4 for height, standing crop and bulk density, and N=1 for fibre contents in Expt 1.

N=12 for height, standing crop and bulk density, and N=3 for fibre contents in Expt 2.

NDF = neutral detergent fibre, ADF = acid detergent fibre.

Sod-type acronyms: 1st letter is overall height of the swards (T=tall, S=short).

In expt 1, 2nd letter is the deviation from average overall height (S=short, M=medium, T=tall).

In expt 2, 2nd letter indicates whether the forage was desired (D) or rejected (R) in the field.

3.3.4.2.3 Field Experiment

We created 16 20x40 m plots with randomized mosaics of short/high quality and tall/low quality patches in equal proportion and at grid sizes of either 2x2 m or 5x5 m laid out in a randomized plot design (see WallisDeVries et al., in prep. for further details). The steers were brought to the pasture four days before the start of the observations. They were allowed access to a pasture with similar patch mosaics for 520 min/day on average (including time in experimental plots). During the experiment, 2 consecutive observation periods of 30 minutes per plot were recorded, starting at sunrise. The day prior to the observations, vegetation height was measured in each grid cell and standing crop was sampled in each patch type in 5 randomly chosen 0.1 m² quadrats by clipping to a height of 2.5 cm above ground level. The regression of standing crop on sward height was used to

derive a plot average following a double sampling procedure. Collected samples were dried at 60 °C. The steers were grazed together and in each plot one randomly chosen focal animal was observed for 30 minutes, giving duplicate observations per animal for each of the two patch size treatments. Sounds and images of grazing animals were recorded as in the sod experiment with a video camera operated from a 3.5 m high observation platform; in the subsequent analysis steps were recorded next to bites and chews. Idling time was excluded from the analysis.

3.3.4.2.4 Data analysis

Analysis of variance, using animals as blocks, was used to determine the effect of the number of bites on bite weight after correcting for variation in height and bulk density. The total dry matter intake (DMI, g) as a function of the number of bites taken from the sod (B), sward height (H, cm) and bulk density (BD, kg/m³) was described by fitting a rectangular hyperbola, after Laca et al. (1994a):

$$DMI = (a_1 H + a_2 BD + b) B / (1 + k B)$$

where a_1 , a_2 , b , and k_2 are constants. The factor $(a_1 H + a_2 BD + b)$ is the instantaneous intake rate (slope) when the number of bites approaches zero; bulk density was not always included in the analysis. The constant k is the reciprocal of the number of bites to remove half the available herbage mass.

Dry matter intake and bite weight in the field were estimated using the rectangular hyperbola equation with the parameters obtained in Experiment 1 and the number of bites per feeding station observed in the field; bulk density was not included as the potential improvement in the estimate was considered to be offset by the additional error introduced by the standing crop measurements. Depletion was assumed to occur over the series of bites taken at each feeding station, i.e. at each new step. The estimate of average bite size in short or tall patches over the entire observation was validated by an independent estimate based on the number of chews per bite (C/B), from data by Laca et al. (1994b):

$$BW = 0.802 \pm 0.087 C/B - 0.132 \pm 0.210 (R^2 0.715, N=36)$$

Bite weights were also estimated ignoring the effects of depletion, by assuming that all bites taken at a feeding station were of the same size as the first bite.

All statistical analyses were carried out using JMP 3.1.5 (SAS, 1995).

3.3.4.3 Results

3.3.4.3.1 Forage quantity and quality

Sward height and standing crop covaried in Expt. 1 ($r = +0.96$, $P < 0.0001$) to form a gradient in forage availability from the shortest to the tallest sods (Table 14). Bulk density was not significantly different between treatments in Expt. 1, although there was a trend of decrease in bulk density with increasing sward height ($r = -0.53$, $P = 0.007$). The bulk density of the short sods in Expt. 2 (SD) was substantially higher than for the other treatments, whereas that of the tall sods (TR) was comparable to that of the tall sods from Expt. 1. In both experiments NDF and ADF contents were lower in the short sods than in the tall ones ($P = 0.009$ and $P = 0.101$ in Exp. 1 and $P = 0.001$ and $P = 0.004$ in Exp. 2 for NDF and ADF respectively); fiber contents of residual material were not significantly different from those in the ungrazed herbage ($P > 0.05$).

3.3.4.3.2 Dry matter gain

In both experiments bite weight decreased linearly with the number of bites taken and with sward height as a determinant of initial bite size (Fig. 17). A multiple regression of bite weight (BW, g) by the number of bites (B) and initial sward height (H, cm) explained 79.6% of the variance for the data from Expt. 1 ($BW = 1.40 \pm 0.23 - 0.0610 \pm 0.00877 B + 0.0592 \pm 0.0040 H$; RMSE = 0.60). The parameters were not significantly different for Expt. 2, although the depletion effect in the TR treatment between the 5 and 10 bite levels was not significant ($P = 0.38$). Bite weight was only marginally different between individual animals ($P = 0.087$), after adjusting for treatment effects and number of bites grazed; there was no animal $\times$ treatment interaction ($P = 0.90$).

The dry matter intake in Expt. 1 was described successfully using the rectangular hyperbola as a function on the number of bites and height alone (Table 15). Including bulk density slightly increased the explained variance from 91.5 to 93.8%. Using these functions to predict dry matter intake for the sods in Expt. 2 gave a mixed result (Fig. 18). The function without bulk

Figure 17. Average bite weight (g DM) over a series of 10 bites (5 in TR) as a function of the number of bites taken by steers on 0.14 m² sods of *S. lutescens* (all treatments except TR) and *L. perenne* (TR treatment) in (a) Experiment 1 (10-bite series) and (b) Experiment 2 (5-bite series for TR and 10-bite series for SD). The data points are shown at the mid-points of the bite series. Acronyms (SS, SM, etc.) are defined in Table 14.

Figure 18. Relationship between observed dry matter intake in Experiment 2 and intake predicted on the basis of equations derived from Experiment 1; (A) predictions based on models including sward bulk density as a predictor; (B) predictions based on models without sward bulk density as a predictor. Squares represent observations from short sods (SD) and circles represent observations from tall sods (TR).

density gave an unbiased prediction of the dry matter intake in the TR sods (mean difference 0.2 ± 4.3 g, paired t-test $P = 0.97$, R^2 [obs. vs. pred.] = 0.694); including bulk density led to an overall underestimation of dry matter intake (mean difference -4.0 ± 4.1 g, paired t-test $P = 0.35$, R^2 [obs vs. pred.] = 0.721). For the SD treatment the function without bulk density consistently underestimated dry matter intake (mean difference -4.0 ± 1.7 g, paired t-test $P = 0.04$, R^2 [obs vs. pred.] = 0.438), whereas including bulk density overestimated dry matter intake (mean difference 21.0 ± 2.7 g, paired t-test $P < 0.0001$, R^2 [obs vs. pred.] = 0.609).

Table 15. Parameter values ($\pm$ S.E.) of the rectangular hyperbola equation describing dry matter intake (DMI, g) on the sods as a function of the number of bites (B) taken by the steers and sward height (H, cm) with or without bulk density (BD, kg/m³)

	N	a_1	a_2	b	k	R^2
Without bulk density:						
Expt 1	72	0.085 ± 0.008	-	0.34 ± 0.14	0.0153 ± 0.0042	0.915
With bulk density:						
Expt 1	72	0.095 ± 0.008	1.02 ± 0.22	-2.10 ± 0.52	0.0153 ± 0.0042	0.938
Expts 1 and 2:						
short sods	48	0.176 ± 0.022	0.56 ± 0.09	-2.19 ± 0.45	0.0244 ± 0.0060	0.886
all sods	95	0.092 ± 0.008	0.35 ± 0.11	-0.63 ± 0.34	0.0154 ± 0.0043	0.909
DMI = ($a_1 H + a_2 BD + b$) B / (1 + k B), where a_1 , a_2 , b and k are constants.						

Although steers were heavier during the second sod experiment, a comparison of bite weight on comparable swards (SD vs. SS and TM vs. TR, Table 14), from the two experiments did not reveal significant differences ($P=0.29$). Combining data from the two experiments including both height and bulk density, gave a good overall fit (Table 15), but the only function adequately describing dry matter intake in SD sods was obtained when data from the short sods were separated from the tall sods (mean difference 0.7 ± 1.4 g, paired t-test $P = 0.62$, R^2 [obs vs. pred.] = 0.598). This function was cross-validated by estimating its parameters from the data on two animals and using these to predict the dry matter intake for the two other individuals. This yielded an unbiased and accurate prediction (mean difference -0.2 ± 0.7 g, paired t-test $P = 0.80$, R^2 [obs vs. pred.] = 0.871).

3.3.4.3.3 Time budget

The time eating per feeding station, excluding idling and disturbances, could be explained to a great extent by the number of bites and chews taken (Table 16). Animal differences were apparent in both the sod experiment ($P=0.029$) and in the field ($P<0.0001$) but contributed little to explain the variation in feeding time (increase in R^2 of 0.005 and 0.015 respectively). Also, the fastest and slowest individuals were not the same in the sod experiment and in the field. Examining short and tall vegetation separately did not increase the amount of variation explained. For the same number of bites, the animals were substantially slower ($P<0.01$) when grazing the sods than in the field. Average bite rates in sod Experiment 1 are presented in Table 17. Bite rate was initially higher and declined more with number of bites grazed in short than in tall swards (interaction $P=0.02$).

Table 16. Parameter values ($\pm$ S.E.) of a linear multiple regression describing feeding time (FT, s) as a function of the number of bites (B) and the number of chews (C) taken by the steers on the sods in Experiment 1 and on individual feeding stations in the field

	N	B-coefficient	C- coefficient	Intercept	R^2
Sods	67	2.19 ± 0.26	0.80 ± 0.05	-13.80 ± 5.30	0.887
Field	2279	0.20 ± 0.02	0.80 ± 0.01	0.80 ± 0.09	0.950

Table 17. Bite rates in Experiment 1 as a function of sod type and number of bites removed

# bites	Sod type					
	SS	SM	ST	TS	TM	TT
10	45.5	50.8	38.3	18.9	15.0	15.0
20	31.9	25.1	23.3	15.8	11.9	11.7
30	27.4	23.9	23.3	15.2	12.5	12.1

Standard error was 3.15 for all cells except for SM after 20 and 30 bites, where it was 4.2 bites/min.

3.3.4.3.4 Validation of bite size estimation in the field

Based on the depletion curves and observed bites per feeding station, the average bite weight for all 16 plots in the field was estimated at 1.47 ± 0.02 g in short patches and 3.33 ± 0.08 g in tall patches. The independent estimates derived from the regression of bite weight on the number of chews per bite

were not significantly different from these values. The mean difference relative to the estimate from the rectangular hyperbola was 0.08 ± 0.05 g lower for short patches (paired t-test, $P=0.14$) and 0.00 ± 0.24 for tall patches (paired t-test, $P=1.00$). Ignoring the depletion effect significantly increased the estimate of average bite weight (0.20 ± 0.01 g in the short patches and 0.62 ± 0.06 g in the tall patches), which resulted in a significant deviation from the predictions using the chew to bite ratio ($P<0.0001$ for the short patches and $P=0.024$ in the tall patches).

3.3.4.4 Discussion

3.3.4.5 Patch depletion

Bite weight showed a linear decline with ongoing depletion (Fig. 17). In general, steers grazed the sods by horizons. However, it was apparent that bite dimensions declined within horizons due to the overlap of bites. This result is consistent with previous investigations (Laca et al., 1994a; Distel et al., 1995). The amount of explained variation in cumulative dry matter intake with depletion was high, whether using the rectangular hyperbola with sward height alone or in combination with bulk density. This result has important implications, both applied and theoretical, for the investigation of patch depletion as a function of sward characteristics and its application to grazing at larger spatial scales. Firstly, it appears that the sod grazing technique is a useful tool to investigate patch depletion of natural or sown pastures. This opens up new possibilities for research with different forage species or species mixtures and different animal species. The sod grazing technique may be especially valuable for tamed wild herbivores, for which there often is no other option than to work with intact individuals instead of oesophageal fistulates. Whereas fistulation requires intensive handling and care of very tame animals, the sod technique (with the exception of the chewing sound records) could be used without much handling of captive wild animals.

More importantly from a theoretical point of view, the findings of this study indicate that differences in sward structure can be accounted for with relative ease to generate depletion curves of a more general form. This corroborates the results from Burlison et al. (1991) and Laca et al. (1992b) on the relation between sward structure and bite dimensions. As expected, sward height was the most important sward variable explaining bite weight. Including bulk

density made only a small difference in Experiment 1. However, the results from Experiment 2 show that bulk density may matter if the high correlation between sward height and standing crop breaks down. It should be pointed out here that we measured sward height with a light pressure-plate and not with a sward stick, which will yield lower readings. In reproductive swards, however, the sward stick is less practical to use and will give more variable readings. The method we used was successfully tested by WallisDeVries (1995) and should not give fundamentally different results.

Forbes (1988) has argued that sward height is the main factor determining bite weight in vegetative swards, and that bulk density only plays a role when flowering stems appear. Our study shows that bulk density need not be an important factor for non-selective grazers, such as cattle, even when flowering stems are present. Results from WallisDeVries (1995) also revealed high correlation between sward height and standing crop for two types of temperate perennial grassland ($r=0.866$ and $r=0.921$) ranging from short vegetative to tall reproductive stages; a close relation between these two variables was also found for a sown *Lolium perenne* grassland in California ($r=0.909$, M.F. WallisDeVries unpubl. data). Thus, on the one hand, sward height may be the most important parameter of forage availability across phenological stages. On the other hand, variation in bulk density may also occur in both vegetative and reproductive stages. Increases in bulk density can be caused by frequent grazing or cutting in short swards through the stimulation of tillering (Lemaire and Chapman, 1996), whereas bulk density is relatively low in ungrazed grassland with tall flowering stems (e.g., Stobbs, 1973ab; Forbes, 1988; Flores et al., 1993). Burlison et al. (1991) even argued that bulk density was a more important determinant of bite weight than sward height within short swards. Thus, it may be that sward height is sufficient to explain bite weight in ungrazed to moderately grazed grasslands of medium height (14-60 cm in Expt. 1). For non-selective grazers bulk density may only prove a significant additional explaining variable under conditions of frequent re-grazing or in taller and less dense grasslands. For more selective grazers such as sheep, the role of bulk density should be expected to be important under a wider range of conditions (e.g., Burlison et al., 1991, Prache, 1997). Ultimately, the failure of finding a relation between bite weight and standing crop in browsing animals (Spalinger and Hobbs, 1992) is also the effect of a decrease in bulk

density of leaves and twigs in the canopy of shrubs and trees. The difference between ingestive behaviour of grazers and browsers may be reconcilable if viewed from this perspective. Experiments across animal species with a wider range of sward structures from different plant species and pasture conditions could shed more light on this matter.

3.3.4.5.1 Application to grazing of larger patches in the field

Analysis of the time budget revealed that biting occurs at a faster rate in the field than on the sods. The faster biting rate in the field was caused both by a smaller handling time per bite (B-coefficient, Table 16) and the fact that animals chewed less per bite in the field than in the sods. Time per chew (C-coefficient, Table 16) was the same in the field and sods. The number of chews per bite in the field was 1.90 ± 0.06 in the short and 4.32 ± 0.29 in the tall patches; corresponding values for the sods were 2.26 ± 0.12 and 5.12 ± 0.28 chews per bite respectively. Based on the estimated field bite weights, this translated into a relatively smaller chewing effort in the field: on average the number of chews per g DM was 1.29 ± 0.04 in the field and 1.62 ± 0.05 on the sods.

The differences between sod and field observations in chewing and handling time per bite can be explained by the fact that in the field, animals were continually moving from feeding station to feeding station, whereas only a single 'feeding station' was exploited on the sods. The incentive to process the forage rapidly in order to continue grazing is, therefore, lacking when grazing the sods. In addition, animals took an average of 7 bites per feeding station in the field, and did not exhaust the top horizon before moving on. Typically the upper horizon has forage of lower fiber content and may require less chewing. This finding should serve as a warning against relying too heavily on time budget measurements obtained for short bite series, such as in the sod experiments. Spatial and temporal heterogeneity and clumping of behaviors such as biting and chewing should also make time budgets derived from short observations inadequate for scaling up by a simple change of units (Demment et al., 1995). The inadequacy of short-term measurements of time budgets under controlled conditions should not be a major impediment to estimating intake rate in the field, because time budgets, bites, and chews can be measured directly in the field and then coupled with intake functions (intake per feeding stations as a function of

number of bites) derived from sod measurements. We want to point out that the data from Laca et al. (1994b) we used to derive the relation between bite weight and the chew to bite ratio, did not suffer from this effect as they were based on longer series of *c.* 50 bites on average.

In the field, relatively homogeneous patches are often larger than a single feeding station. Depletion then occurs locally over the foraging path followed by the animal. In this study depletion curves were applied to the grazing process at each feeding station, with the animal encountering a new supply of untouched forage only after taking a next step. Bite weight estimation using depletion curves was justified by the similarity of the predictions from Laca et al. (1994b) based on chew to bite ratios. When depletion was not taken into account, bite weights were overestimated. Therefore, patch depression effects are real and important enough to take into account. Average bite weight depends not only on sward initial conditions, but also on the degree of depletion of each feeding station before the animal decides to move on. Distel et al. (1995) and Laca et al. (1993b) found that steers depleted identical patches to different degrees depending on the context where the patches were found. Patches were depleted to a greater degree when alternative patches were poorer and when distance between patches was increased. It follows that care is needed when carrying out functional response studies in field situations (e.g., Alden and Whittaker, 1970; Trudell and White, 1981; Short, 1985; Hudson and Nietfeld, 1985; Hudson and Frank, 1987; Penning et al., 1991a; Prache, 1997). We concur with Gross et al. (1993) that bite size is the crucial variable determining intake rate. However, where they place the emphasis on the role of bite size in determining food processing rate, we have shown here that bite size in turn is significantly affected by the process of forage depletion. Local depletion causes a reduction in the measured average bite weight compared to the expectation based on initial sward conditions alone without patch depression. It should, therefore, be realized that for grazing animals the functional response at a larger spatial scale is arrived at by a repeated process of patch depression at each feeding station, and presumably, patch depression at other hierarchical levels of the feeding process.

3.3.4.6 Conclusion

We suggest that the sod grazing technique is an adequate tool to investigate food intake and forage depletion by grazing animals under experimental conditions, while using swards that represent the field situation. Nevertheless, time budgets from sods do not reflect field behavior. Measurements of depletion as a function of number of bites should be coupled with field measurements of time budgets. The quantification of the local forage depletion that can thus be obtained is a necessary step to enable the scaling up of foraging behavior and functional response analysis from the level of the feeding station to that of the patch. Scaling up by simply changing units and implicitly expanding the spatial and temporal scales of bite weight and rate measurements will yield incorrect results. As scale becomes larger, feeding encompasses processes and behaviours, such as the degree of depletion and patch selection, that are not considered in small scale measurements. These processes should be taken into account explicitly to expand the scale of the functional response. Alternatively, functional responses are strictly applicable only at the scale at which they were measured.

3.4 Multi-patch studies

The last reported experiment compared the depletion process at the single patch to what happens in a multi-patch arena. The experiments reported in the following section deal in more detail with the multi-patch situation and thereby extend the foraging concepts to greater spatial and temporal scales.

3.4.1 Feeding station behaviour on single and sub-divided grazing areas

The hypothesis:

Grazing behavior can be characterized as cycles of movement to a patch (feeding station) and removal of bites within the patch, even when sward structure is not patchy.

3.4.1.1 Introduction

A fundamental question related to the concept of the feeding station is to what extent patterns of grazing behaviour are a function of inherent animal features as opposed to being dependent on the foraging environment. This is hard to determine by direct observation on most swards since local

heterogeneity in sward structure tends to weaken the interpretation of results. In the following experiment we attempted to strengthen the empirical base by using a highly idealized grazing arena and swards of relatively high uniformity.

3.4.1.2 Material and Methods

The experiment was conducted on an area of approximately 0.3 ha, which was sown to alfalfa by precision drill on 11 and 19 June 1996 with a row spacing of 10 cm. The area was not cut prior to the experiment and the sward reached an average height of 20 cm about 30 days after sowing.

The experimental treatments were three spatial arrangements of a total sward area of 2 m²: T1: a single patch; T4: subdivision into 4 patches of 0.5 m² each with a separation of 0.7 m² between the patches; T9: subdivision into 9 patches of 0.22 m² each with corridors of 1.4 m width. Vegetation in the spaces between the patches was cut to ground level, and a similarly cut border of about 1 m width was created around each treatment. Our specially designed portable fencing system was used to enclose each treatment. [See Photo #3] A total of 12 such treatment systems was created in the course of the experiment, providing for two cycles of 6 heifers. For the purposes of animal training, each heifer grazed a T3 arrangement the day before its first experiment session.

The following protocol was followed. One set of treatments was grazed on each day of the experiment. The set was prepared the day before it was grazed. In the course of preparing the three treatment areas, additional patches were set aside for the estimation on initial biomass. For T1 a single patch of 0.5 m² was used. For T4, two patches of 0.5 m² were used. For T9, three patches of 0.22 m² each were used. Additional herbage samples were cut for determination of the vertical biomass profile and dry matter content.

Grazing always commenced with T1. Grazing was stopped on this treatment when most of the upper horizon was depleted. Bite number was counted carefully, and this number of bites was then set as the stopping criterion for the other two treatments. The order in which these two treatments was grazed was switched each day of the experiment. The heifer was always brought into the enclosure from the same corner and released. [See Photo #4] On T4 and T9 the number of bites removed from each patch and the sequence of grazing was recorded. Following grazing the residual height of

Photo #3: The grazing arena for a multi-patch experiment using a constant total herbage area of 2 m². Treatment T1 at rear; treatment T4 in the middle; part of treatment T9 in the foreground. Each treatment is enclosed with portable fencing units designed for the project. Sowing by precision drill with 10 cm row spacing.

Photo #4: Heifer grazing treatment T1 in the above experiment. Herbage is alfalfa with initial height of 20 cm.

the vegetation was measured every 5 cm along each drill row for each patch, and the residual herbage for each patch was clipped at ground level, bagged, dried and weighed.

3.4.1.3 Results and Discussion

Overall average biomass per unit area of the patches in the experiment (after clipping to an initial height of 20 cm) was 131.6 ± 5.6 g DM/m². The fraction of herbage mass in each layer of the profile was: 0-5 cm - 28%, 5-10 cm - 23%, 10-15 cm - 25%, 15-20 cm - 24%. Average dry matter content of the vegetation was $21 \pm 0.6\%$. DM content of the vegetation tended to increase over the course of the experiment.

The average number of bites removed in a treatment was 107 ± 25 (on a 2 m² basis). The frequency distribution of residual heights for the three treatments was remarkably similar (Fig 19), with a modal (grazed) residual height of 10 cm. The primary difference between the treatments was in the fraction of the available area that remained ungrazed: 27% for T9 versus 22% for T1 and 20% for T4. This difference between T9 and the other two treatments often resulted from one or more sub-patches not being reached (i.e. not grazed at all) before the maximum bite number was reached.

Mean bite depth for all treatments was 7.4 cm. Treatment did not have a significant effect on bite depth ($P=0.6875$), though natural height did. This effect of natural height is consistent with results from previous experiments. Mean effective bite area declined significantly with the degree of subdivision of the grazing area ($P=0.0028$). Bite area was 144, 133 and 123 cm² in T1, T4 and T9, respectively. Overall average bite rate was 38 bites per minute. There was very little change in average bite rate between T1 and T4, but a small yet significant decline for T9.

Though a more complete analysis of this experiment awaits more detailed examination of the video recordings of the experiment, it is clear from the analyses conducted thusfar that subdivision not only altered the time budget of intake as one might expect due to the walking/searching time introduced in treatment T9, but also the bite weight component of the intake equation. This change in mean bite weight was caused by a reduction in bite area and not by a change in bite depth. The animals grazed the upper horizon in all treatments, but the degree of bite overlap increased with patch subdivision. Intuitively, the animal should have moved to a fresh patch in treatment T9

Figure 19. Frequency distribution of residual herbage heights, expressed as fraction patch area, following grazing by heifers. Treatments comprised a total herbage area of 2 m² arranged as a single patch (T1), 4 patches of 0.5 m² (T4) and 9 patches of 0.22 m² (T9). Total bite number was equal across treatments.

sooner than it did in order to maximize instantaneous intake rate. Rather, the animal seemed to aim for more or less complete depletion of the upper horizon before leaving a patch. As illustrated earlier by the bite placement simulator, horizon completion carries a penalty in terms of inefficient bites towards the end of the depletion process. When patch size is smaller than a potential feeding station, this cost can significantly reduce the overall intake rate when compared to a continuous sward. Preliminary evidence from the video record suggests that also on the continuous patch there are cycles of local depletion before the animal steps to a new position in the patch, but the continuous nature of the sward would seem to avoid the relatively high degree of overlap observed on the most subdivided treatment.

It should also be noted that the time budget was not influenced by patch subdivision in T9 as much as might be expected on the basis of simple models of searching and intake (e.g. Ungar and Noy-Meir 1988). If we consider the total area of the grazing arena it could be said that vegetation cover decreased from 100% in T1 to 11% in T9 - a decrease of 89%. Yet our estimation of intake rate (based on bite dimensions and bite rate) declined by only 22%. Such a result would seem to support the use of different search/scan speeds for different types of environment. A relatively high search speed is appropriate in our experimental arena in which the choice is between uniform, palatable herbage and bare ground, and in which the herbage patches are highly apparent.

To the best of our knowledge, grazing trials with different spatial arrangements of a constant total grazing area have not been conducted previously and the design used here is only one of many possibilities. Our first foray into this avenue of experimentation suggests that it is a useful technique for elucidating important aspects of foraging mechanisms and we hope to develop the approach further in the future.

3.4.2 Grazing behaviour along a search path with patches at different spacings

The hypothesis:

The rate of intake from grazing small, identical patches spaced along a search path will be constant with increasing distance between the patches

when the between-patch traveling time is less than the time required to chew the herbage removed from a patch.

3.4.2.1 Introduction

In the previous experiment the total herbage area was kept constant between treatments but both patch size and distance between patches was varied. In the following experiment we again used single and subdivided grazing areas, but the subdivided treatments used the same size patch at different spacings. The main questions asked here were: when presented with vegetation in the form of a narrow row of plants of constant total length but with different spatial arrangements, how many bites will be removed in traversing the grazing course, what will the degree of depletion be for the different spatial arrangements, how will spatial arrangement influence total grazing time, and what estimates for walking speed can be derived?

3.4.2.2 Material and Methods

The experiment was conducted twice, the first time to establish feasibility of the foraging task for the animals, to accustom the animals to the foraging arena and to establish a clear experimental protocol for the field team. We report here on the second run of the experiment. The trial was conducted on a strip of vegetation of width 2 m and about 75 m length, sown to oats by precision drill on 2 May 1996. Row spacing was 15 cm. The crop reached the treatment height of about 20 cm 30 days after sowing. The experiment was conducted using all ten heifers that were trained for the season's experimentation. For experimentation of this kind, that is an unusually high degree of replication. All treatments used a single sowing row of vegetation. Treatments comprised three spatial arrangements of a total of 2 m-row: T0: a single section of 2 m-row; T50: ten units of 20 cm each separated by a gap of 50 cm; T100: ten units of 20 cm separated by a gap of 100 cm. Vegetation in the gaps was cut to ground level. Vegetation was clipped to an initial height of 20 cm throughout. In order to avoid a change in grazing behaviour towards the end of each treatment, an additional 0.5 m was prepared in treatment T0, and an additional sub-unit was added in the other two treatments. The animal was stopped after 2 m length in T0, and after the tenth sub-unit in T50 and T100. (This modification was made on the basis of results from the first run of the experiment.) The experimental strips were

Photo #5: Treatment T100 being grazed during the line-foraging pre-trial on oats. Patches are 2 sowing rows wide, 20 cm long, and spaced 100 cm apart. Herbage was relatively mature and was clipped to an initial height of 30 cm.

Photo #6: View of the arena for the main line-foraging trial. Treatment T0 in the foreground followed by the subdivided treatments T50 and T100. Herbage comprises a single row of young vegetative oats clipped to an initial height of 20 cm.

enclosed on both sides using our mobile fencing units and the animal was released from the lead rope during the trial. [See Photos #5 & #6]

In accordance with our standard protocol for all experiments, additional areas were clipped for the estimation of mass per unit area, for determination of the dry matter content of the vegetation immediately prior to grazing, and for determination of the vertical distribution of herbage mass in the sward profile. Following grazing, the residual herbage height was measured at 5 cm intervals and all residual herbage was clipped, bagged, dried and weighed.

3.4.2.3 Results and Discussion

Assuming an effective width of 15 cm, mean bulk density of vegetation in the experimental strips was $868 \pm 54 \text{ g/m}^3$. There were no significant difference in bulk density between the treatments. The fraction of mass in the sward profile declined with distance from the ground: 0-5 cm: 34.8%, 5-10 cm: 26.1%, 10-15 cm: 21.1%, 15-20 cm: 14.4%. Overall mean dry matter content was $15.8 \pm 0.5\%$ with a trend to increase over the course of the experiment.

Fig 20 shows the frequency distribution of residual heights for the three treatments. The distributions for the sub-divided treatments are quite similar, but the distribution for T0 is clearly different. The fraction patch area for 20 cm height is the ungrazed fraction. This was 19% in T0, versus 13% for T50 and 12.5% for T100. The modal residual height was 12 cm for T0 versus 9 and 10 cm in T50 and T100. In overall appearance, the distribution of grazed residuals is shifted approximately 2 cm to the right for the single, undivided strip (T0). It is stressed that in this experiment (in contrast to the previous one) the total bite number was not controlled to be equal across treatments. The stopping criterion was simply completion of the course.

Treatment was highly significant in all variables examined except derived intake rate. Thus the greater degree of depletion observed in T50 and T100 was due to a greater total bite number (Fig 21). The increase in bite number more than compensated for the increase in the overall fraction area grazed and hence mean effective bite area declined with sub-division. The length of a step was very similar for T0 and T50, but increased in T100. In addition to the overall rate of progress (m/sec) shown in Fig 21, we estimated the between-patch walking speed by deducting the grazing time in T0 from the total grazing time in T50 and T100 with due correction for bite

Figure 20. Frequency distribution of residual herbage heights, expressed as fraction patch area, following grazing by heifers. Treatments comprised a single herbage strip of 2 m length (T0), 10 sub-strips of 20 cm length with 50 cm breaks between them (T50), and 10 sub-strips of 20 cm length with 100 cm breaks (T100).

Figure 21. Grazing behaviour parameters for the herbage strip grazing experiment. Treatments comprised a single herbage strip of 2 m length (T0), 10 sub-strips of 20 cm length with 50 cm breaks between them (T50), and 10 sub-strips of 20 cm length with 100 cm breaks (T100).

number. The resulting speed of 0.46 m/sec was almost identical for treatments T50 and T100.

Sub-division of the grazing strip caused an increase in total bite number. This was accompanied by a decrease in mean effective bite area. Assuming an approximately round bite sweep area, bite diameter declined from 14 cm in T0 to 11 cm in the sub-divided treatments. Thus if the grazing style of the animal is to simply deplete the upper grazing horizon, the integer nature of bite number may result in significant inefficiencies when patch size is very small. On average, the animals invested 1.65 bites in order to remove the upper grazing horizon from a 20 cm section of treatment T0, versus 2.3 and 2.6 bites in T50 and T100. The investment of more bites per patch with increasing distance between patches has been reported elsewhere (e.g. Shipley and Spalinger 1995), and is expected according to the marginal value theorem. In our experiment, two processes appear to be at play: bite overlap in the course of horizon depletion due to the simple spatial geometry of bite dimensions - apparent in going from T0 to T50, and increased depletion due to an increase in the distance between equally sized patches - apparent in going from T50 to T100.

3.4.3 The importance of scale of patchiness for selectivity in grazing herbivores

Grazing ungulates are known to graze selectively when confronted with a patchy forage distribution. They concentrate on short, leafy swards that contain relatively high concentrations of nutrients (Jarman 1974, McNaughton 1984) but do not necessarily yield the highest intake rate (Illius et al. 1987, Langvatn and Hanley 1993, WallisDeVries and Daleboudt 1994, Wilmshurst et al. 1995). In ruminants, however, the daily intake of abundant low-quality forage will be constrained by the passage rate through the digestive tract. It has therefore been proposed that ruminant grazers trade-off forage quality and quantity so as to maximize daily instead of instantaneous nutrient intake (Fryxell 1991). Results of several grazing studies have confirmed this hypothesis (WallisDeVries and Daleboudt 1994, Wilmshurst and Fryxell 1995, Wilmshurst et al. 1995). However, in neither of these studies was selection directed exclusively at the most profitable patches. A potential explanation for partial preferences may lie in the spatial arrangement of different forage patches. Distel et al. (1995) have shown that

patch residence time in *Bos taurus*, confronted with two patch types of different profitability, can be adequately described by a marginal value rule (Charnov 1976), consisting of a trade-off of intake at the current depleting patch and travel to feed at a next, as yet undepleted patch. Partial preferences can also arise because the ability to discriminate between alternative forages becomes limited. On the one hand, selectivity may be expected to grow stronger as the differences between alternatives increase (WallisDeVries and Daleboudt 1994), because the reward of selecting becomes greater. On the other hand, selectivity should also increase with improving opportunity to select, which depends largely on the spatial arrangement of the forage types. At the extremes, it appears that selection is little affected by small-scale heterogeneity at the level of the feeding station (Griggs et al. 1991a) but is profoundly affected by large-scale heterogeneity at the landscape level (WallisDeVries and Schippers 1994). Thus, we surmise that besides the spatial arrangement of patches the scale of patchiness is another major determinant of selectivity during grazing. Our hypothesis can be stated as follows:

Due to behavioral constraints, and in response to spatial variability in the forage available, cattle feeding strategy at a patch is a function of landscape structure at an intermediate scale between a single patch and the whole landscape. Maximization is based on landscape characteristics at such intermediate scale.

3.4.3.1 Introduction

The role of scale in foraging ecology is often ignored. Thus, daily intake is often viewed as the product of instantaneous intake rate and grazing time (Hodgson 1982). Yet, this is only true in perfectly homogeneous environments. In the face of environmental heterogeneity, extrapolation from one scale level to another requires the integration of processes at various scales (Turner et al. 1989, Laca and Ortega 1995, Demment et al. 1995). For grazing herbivores the notion of scale has been incorporated in conceptual hierarchical foraging models (Senft et al. 1987, Stuth 1991, Bailey et al. 1996). Several spatial levels are recognized, each with its own corresponding behavior and time scale. At the smallest scale bite formation takes place. Local depletion and selection are the main motivations for short-term movements within a feeding bout between bite locations (head

movements), between feeding stations (a single step) and between patches (series of steps). At larger scales of time and space, decisions are made on the selection of plant communities, landscape types and seasonal ranges. Selection can occur at each scale level and may accumulate across scale levels.

Foraging behavior over multiple scales has been investigated in a number of studies (e.g., Tinbergen 1981, Ward and Saltz 1992, Jiang and Hudson 1993, WallisDeVries and Schippers 1994, Ginnett and Demment 1997). Yet, a quantitative approach to the integration of foraging mechanisms across scale levels remains to be developed. Moen et al. (1997) recently presented a spatially explicit, quantitative foraging model for moose, but scaling issues were addressed mainly by tentative foraging rules that lack sufficient support of field data. The following experiment, using *Bos taurus* as a model species, was designed to contribute to the quantification of foraging rules across spatial scales by examining foraging behavior at the level of the patch and the feeding station. We specifically tested the hypothesis that grazing selectivity is hampered when the environment is fine-grained, i.e. patches are small. Small patches should impair the ability of grazers to avoid poor areas and return or stay within preferred areas.

On this basis we hypothesized that:

- grazers should select for the patch allowing highest daily nutrient intake;
- search should be non-random, with a greater proportion of the foraging path in the most profitable patch
- selectivity for preferred patches should be stronger as more behavioral steps are integrated in the index of selectivity
- selectivity should increase with increasing the scale of patchiness
- the efficiency of search, as measured by the total number of feeding stations and bites found per unit distanced walked, should increase with the scale of patchiness
- the tortuosity of the foraging path should vary with the scale of patchiness;
- in a coarse-grained environment the residence time and number of bites per feeding station should be less than in a fine-grained environment, because the overall environment experienced by the animal would be better.

3.4.3.2 Materials and Methods

3.4.3.2.1 Pasture layout and experimental protocol

The field experiment was conducted in an irrigated *Setaria lutescens* (Weigel) Hubb. grassland. We created 16 20x40 m plots with contiguous mosaics of short/high quality and tall/low quality patches in equal proportion and at two grid sizes, randomly allocated to plots: a fine-grained of 2x2 m (200 cells per plot) and a coarse-grained of 5x5 m (32 cells per plot). The allocation of patch types to cells was randomized over blocks of 4x4 cells, so that an equal proportion of short and tall patches were obtained for each block of 16 cells. This small-scale randomization of the two patch types was imposed to avoid accidental clustering of patches of a certain type. The pasture was cut entirely in mid-June and fertilized with ammonium nitrate 2 weeks later (90 kg N/ha). Short patches were cut again in early August, fertilized anew (180 kg N/ha) and cut for the last time 2 weeks later so that all plots had the same regrowth period before the experiment (3-11 September).

Five 30-month old Hereford crossbred steers (604-710 kg) were brought to the pasture 4 days before the start of the observations. They were allowed access to a pasture with similar patch mosaics for 520 min/day on average (including time in experimental plots). The day prior to each observation, vegetation height was measured and standing crop was sampled in each patch type. Height measurements were made with a 0.1 m² square plate (c. 100 g) that was gently lowered onto the vegetation along a measuring rod. In fine-grained plots, one height measurement was made in the center of each cell (100 readings per patch type) and in coarse-grained plots one height measurement was made in every quarter of each cell (64 readings per patch type). Standing crop in each patch type was sampled in 5 randomly chosen 0.1 m² quadrats by clipping to a height of 2.5 cm above ground level. The regression of standing crop on sward height was used to derive a plot average following the procedures of double sampling (see Laca et al. 1989). The collected samples were dried at 60°C and analyzed for fiber (Goering and Van Soest 1970) and for nitrogen using the Carlo Erba technique. Dry matter digestibility (DMD, %) was estimated by the summative equation:

$$\text{DMD} = 0.98 (100\text{-NDF}) + (147.3 - 78.9 \log(100 \text{ L/ADF})) - 13$$

where NDF, L and ADF denote the percentages in the dry matter of neutral detergent fiber, lignin and acid detergent fiber respectively (Goering and Van Soest 1970).

On each day of the experiment, observations were collected in 2 plots, starting at sunrise. One observation consisted of 30 minutes with a 15 min break between the consecutive observations. The steers were grazed together and in each plot one focal animal was observed, giving duplicate observations for four animals for each of the two patch size treatments; the fifth animal was too shy to be handled. Sounds and images were recorded with a video camera from a 3.5 m high platform. These records were later used to identify bites, chews, steps and grazing location. The identification of grazing location was facilitated by the placement of coordinate markers alongside of the plots.

3.4.3.2.2 Data analysis

We examined grazing selectivity for different steps in the foraging process: selectivity during walking, selection of feeding stations, selection of bites and intake per bite. Selection was expressed in two ways. First as the percentage of events per patch type, showing an integration of events over the whole foraging process from walking to total intake; under zero selection the percentage is 50. The second approach was to consider selection at each separate step of the foraging process. To this effect we used a selectivity index consisting of the ratio of an event in short patches to that in tall patches; under zero selection the index is 1.0.

Bite frequencies were converted to intake data by calibration with a patch depletion curve determined afterwards in stall trials with sods cut from the same pasture (see WallisDeVries et al., 1998). The depletion curve had the form of a rectangular hyperbola, after Laca et al. (1994a), describing total dry matter intake (I , g) at a single feeding station as a function of the number of bites taken (B) and the height of the sward (H , cm):

$$I = (a H + b) B / (1 + k B)$$

where a , b , and k are constants. The factor $(a H + b)$ is the instantaneous intake rate (slope) when the number of bites approaches zero. The constant k is the reciprocal of the number of bites to remove half the available herbage mass. For the conditions in this experiment the measured

parameter values were $a=0.0854$, $b=0.338$, $k=0.0153$ (WallisDeVries et al. 1998).

Idling time was excluded from the analysis. Residence time per feeding station was measured as the time spent between two steps where one or more bites were taken; thus, steps where biting did not occur were not counted as feeding stations. Maximum daily intake was estimated using a fill constraint of 1.1 g NDF/kg body weight (Mertens 1987).

The tortuosity of foraging paths was determined by fractal analysis, using software by Nams (1996). The fractal dimension of the foraging path describes the movement pattern (With 1994), and indicates whether the direction of movement is linear (fractal dimension equals 1), random (fractal dimension equals 2), or patchy (intermediate values of fractal dimension). The fractal dimension of foraging paths was calculated across scales from the size of a single step and upwards, and at four separate scale levels: step size, grid cell size (2 m and 5 m), and 10 m as the largest level that allowed a reliable and meaningful estimation of fractal dimension.

In order to test whether the residence time per feeding station was consistent with the marginal value theorem (Charnov 1976), we derived gain curves of digestible dry matter intake (DI, g) as a function of time (T, s) and sward height (H, cm) using non-linear regression of calculated digestible intake per feeding station against time per feeding station and sward height. The form of the regression equation was again a rectangular hyperbola ($DI = (a H + b) T / (1 + k T)$, with a , b and k as constants). Different curves were generated for short and for tall patches. Travel time between patches was taken as the time to take a single step to the next feeding station at a speed of 0.88 m/s (walking speed from E.A. Laca, unpubl. data). The average encounter probability of a short or a tall patch type was 0.5, as determined by the plot design. Once gain curves and travel time were known, intake rate was maximized by applying the 'patch and prey' algorithm described by Stephens and Krebs (1986).

Analysis of variance was conducted to determine effects of grain size of patchiness, animal differences and their interaction. Selectivity between patch types was assessed using paired t-tests for the grazing variables with data pairs for each plot. Proportions were normalized by arcsine

transformation. All statistical analyses were carried out using JMP 3.1.5 (SAS, 1995).

3.4.3.3 Results

3.4.3.3.1 Patch characteristics

Short patches had a significantly lower standing crop and sward height, but a higher nitrogen and NDF content and a higher dry matter digestibility (Table 18). There was significant variation between plots for both forage quantity and quality ($P < 0.0001$), but differences were small or insignificant when considered across the two grain size treatments, plots allocated to individual animals and grain size x animal interactions. The differences between patch types resulted in a lower average bite weight on short patches, but a similar dry matter intake rate in short and tall patches (Table 18). Consequently, the difference between patch types in both instantaneous and daily intake rate was determined solely by the difference in quality. It was estimated that an 18 % higher daily intake rate of digestible dry matter could be achieved on the short patches compared to the tall patches (Table 18). Maximization for digestible intake on a daily basis (as well as on a short-term basis) should therefore have favored selection for the short patches.

Table 18. Characteristics of short and tall patches ($\pm$ S.E.) with significance of difference between the patch types (NDF = neutral detergent fiber, IR = dry matter intake rate, DI = digestible dry matter intake)

	Patch type		P
	Short	Tall	
Standing Crop (g/m^2)	322.5 $\pm$ 3.3	642.2 $\pm$ 5.5	<0.0001
Height (cm)	15.9 $\pm$ 0.1	42.8 $\pm$ 0.2	<0.0001
%Nitrogen	2.61 $\pm$ 0.05	1.24 $\pm$ 0.03	<0.0001
%NDF	66.7 $\pm$ 0.6	69.9 $\pm$ 0.5	<0.0001
%Dry Matter Digestibility	51.5 $\pm$ 1.2	45.7 $\pm$ 1.2	0.0008
Average Bite Weight (g)	1.47 $\pm$ 0.02	3.33 $\pm$ 0.08	<0.0001
IR (g/min)	48.9 $\pm$ 2.0	46.6 $\pm$ 2.7	NS
Max. Daily DI (kg)	5.63	4.77	not determined

3.4.3.3.2 Foraging path, patch selection and impact of grain size

Overall, the animals spent more than 50 % ($P=0.0002$) of their time grazing in the short patches (73.7(3.8 % on average), indicating significant selectivity. In both grain size treatments there was an increase in selectivity with integration level when going from the proportion of patch encounters, via the proportion of steps in short patches to the proportion of feeding station in short patches (Table 19). When considering selection along the separate steps in the foraging process, significant selectivity occurred during walking, selection of feeding stations and the formation of bites, but there was no difference in the number of bites per feeding station between short and tall patches (Table 20). This explains the leveling-off of the integrated selectivity for the proportion of bites. The percentage of digestible intake from short patches was lower than the percentage of bites, because bite size was smaller in short patches.

Table 19. Effects of grain size on accumulated foraging selectivity for different steps in the grazing process, as described by the percentage of observations in short patches ($\pm$ S.E.) (NA not applicable because fixed by the experimental design). There were no significant animal effects or interactions between patch grain size and animals.

	Patch grain size		Selectivity	Grain size effect
	Coarse	Fine	<i>P</i>	<i>P</i>
%Patch Encounters	50	50	NA	NA
%Steps	77.2 $\pm$ 1.5	67.0 $\pm$ 1.6	<0.0001	0.019
%Feeding Stations	94.5 $\pm$ 2.0	82.7 $\pm$ 3.3	<0.0001	0.027
%Bites	93.3 $\pm$ 3.9	78.4 $\pm$ 5.2	<0.0001	0.028
%Digestible Intake	88.2 $\pm$ 3.6	65.3 $\pm$ 4.0	0.0002	0.022

Grain size effects were significant for all steps in the integrative foraging process (Table 19). However, this effect was only due to the impact of grain size on selection during walking and on selection of feeding stations (Table 20). Overall tortuosity of the foraging path as expressed by the fractal dimension was not different between grain sizes (1.27 $\pm$ 0.02 and 1.25 $\pm$ 0.02 for coarse and fine grain size respectively) and neither was it affected by variation between animals or by the grain size x animal interaction. The fractal dimension (D) increased linearly with the spatial scale at which it was examined, reflecting a decreasing linearity of the foraging path at larger

spatial scales (Fig. 22; $D = 1.00 \pm 0.00 + 0.0604 \pm 0.0004$, $R^2 = 1.00$, $MSE = 0.003$). It was significantly larger than 1 at all scales ($P < 0.0001$). At the smallest scales of 0.6 m and 2 m, fractal dimension was slightly higher for the fine-grained patchiness ($P = 0.009$ and $P = 0.077$ respectively). Yet, this grain size effect did not show in the decrease in length of the foraging path between the scales of 0.6 and 5 m and between 2 and 5 m ($P > 0.65$).

Table 20. Index of grazing selectivity for each individual step of the foraging process, compared between treatments of coarse-grained and fine-grained patchiness (FS = feeding station). The selectivity index is given by the ratio of short to tall patch types. Significant selectivity between patch types is apparent when the index deviates from 1.0. Also indicated is the significance of the effect of grain size treatments. No selection was possible at the level of patch encounters. There were no significant animal effects or interactions between grain size and animals.

	Patch grain size		Selectivity	Grain size effect
S/T ratio	Coarse	Fine	<i>P</i>	<i>P</i>
Steps per patch	3.39	2.03	<0.0001	0.019
FS per step	5.60	2.63	<0.0001	0.036
Bites per FS	0.85	0.83	NS	NS
Digestible intake per bite	0.49	0.49	<0.0001	NS

In the coarse-grained environment the animals selected more feeding stations per step walked than in the fine-grained environment ($P = 0.052$, Fig. 23). Selectivity increased with grain size of patchiness because the steers found a higher number of feeding stations per step in short patches ($P = 0.045$) and reduced the number of feeding stations per step in tall patches ($P = 0.051$) when grain size was coarse.

No grain size effects were observed for the number of bites per feeding station and, hence, average digestible intake per bite (Table 20). Neither the number of bites nor the residence time per feeding station were affected by grain size (Table 21). The steers took the same number of bites per feeding station in short and in tall patches, but they spent significantly more time per feeding station in tall patches.

3.4.3.3.3 Prediction of residence time per feeding station

We found the following relations between digestible intake (DI, g) as a function of residence time (T, s) and sward height (H, cm) (Fig. 24):

Figure 22. Relationship between the scale of measurement and the fractal dimension D ($\pm$ S.E.) of the grazing path of steers grazing a mosaic of tall, low quality and short, high quality grass patches. A fractal dimension of 1.0 indicates a straight path; a value of 2.0 indicates a completely random walk. Values of D between 1.0 and 2.0 reflect a patch search pattern.

Figure 23. Feeding stations selected per step walked ($\pm$ S.E.) by steers grazing mosaics of tall, low quality and short, high quality grass patches, as affected by the scale of patchiness.

Figure 24. Average gain curves for digestible dry matter intake in short and tall feeding stations.

Short patches:

$$DI = (0.0210 \pm 0.0035 H + 0.282 \pm 0.056) T / (1 + 0.0184 \pm 0.0011 T)$$

$$(R^2 = 0.811, \text{MSE} = 1.48)$$

Tall patches:

$$DI = 0.495 \pm 0.029 T / (1 + 0.00513 \pm 0.00121 T)$$

$$(R^2 = 0.756, \text{MSE} = 4.62).$$

The height coefficient was not significant for tall patches and was therefore removed.

Average step size was 0.59 ± 0.01 m and was not affected by grain size, individual animals or grain size x animal interaction. Average travel time between feeding stations was therefore taken as $0.59 \text{ m} / 0.88 \text{ m/s} = 0.67 \text{ s}$. Observed residence time per feeding station was significantly greater than predicted under the marginal value theorem, using the derived intake curves and travel time (Table 22). The discrepancy was particularly large for tall patches.

Table 21. Effects of patch grain size on average residence time and number of bites per feeding station ($\pm$ S.E.). Patch type effects were significant for residence time ($P < 0.0001$) but not for the number of bites per feeding station ($P = 0.41$).

	Patch Grain Size		<i>P</i>
	Coarse	Fine	
Residence time (s)			
Short	9.3 ± 0.7	9.9 ± 0.5	NS
Tall	25.7 ± 6.4	27.2 ± 4.5	NS
# Bites			
Short	5.9 ± 0.3	6.2 ± 0.3	NS
Tall	7.0 ± 2.8	7.5 ± 0.6	NS

Table 22. Predictions of average Feeding Station Residence Time (s) using the Marginal Value Theorem with the significance of the difference between the observed and predicted values using a paired t-test (time values ($\pm$ S.E.))

Patch type	Predicted	Observed	<i>P</i>
Short	8.1 ± 0.1	9.6 ± 0.4	0.0053
Tall	4.8 ± 0.7	26.5 ± 3.2	< 0.0001

3.4.3.4 Discussion

3.4.3.4.1 Foraging selectivity as an hierarchical process

The three hypotheses on patch selection were largely confirmed by this experiment. First, patch selection was aimed at the patch type with the highest daily digestible intake. Second, search pattern, as measured by the proportion of steps walked in the preferred patch was non-random. And third, selectivity increased when integrating the selection of feeding stations with selectivity in movement to the preferred patch. However, once a feeding station was chosen selectivity did not increase further, since the number of bites per feeding station was similar in both patch types. Selection therefore operated mainly in directing the foraging path and in selecting feeding stations. Grazing at the feeding station appeared to be governed mainly by vegetation characteristics of the patch type. Thus, bites were smaller and of higher quality in short patches than in tall patches. Dry matter intake rate was similar in both patch types, as forage quantity was not limiting in short patches and the lesser chewing effort per bite in short patches compensated for the smaller bite size (WallisDeVries et al. 1998). So, the apparent selectivity in digestible intake per feeding station reported in Table 20, should really be seen as the result of the mechanism of bite formation and processing (see Laca et al. 1994b) rather than as a true preference. Once the steers left a short feeding station after a series of bites, the disadvantage of a smaller digestible intake per bite relative to tall patches was already compensated for by the faster processing rate. The selection of feeding stations allowed the animals to capitalize on this advantage of short patches.

The hierarchical approach to describe foraging behavior followed in this study reveals that the selection of feeding stations and the feeding at feeding stations are fundamentally different processes. The largest potential for selection appears to exist in the choice of feeding stations. Selectivity at the feeding station seems mainly limited to manipulating the level of depletion before moving on, especially in large-bodied species such as cattle with a restricted ability to benefit from small-scale heterogeneity.

3.4.3.4.2 Why did the marginal value theorem fail?

We applied the marginal value theorem to predict the residence time at the feeding station, but the observations did not match the predictions.

Particularly the longer residence time at tall feeding stations compared to short feeding stations appears unexpected in view of the better quality of short patches. Altering the relative area of patch types according to the foraging path followed by the animals increases the proportion of short patches and therefore results in a reduction of predicted residence time per feeding station for both patch types. So, that alternative does not offer a solution.

It could also be argued that, once a feeding station was selected, the animals aimed to harvest a certain number of bites before leaving a feeding station, as the number of bites per feeding station was similar in both patch types. The longer residence time in tall feeding stations then would simply be the result of the longer time required to process the relatively large bites. However, both this argument and the marginal value theorem make the implicit assumption that residence time and number of bites per feeding station should follow a normal distribution with the highest probability of occurrence for values closest to the average. This assumption is clearly incorrect. In both patch types, the frequency distribution of bites per feeding station closely followed a negative exponential distribution of a survivorship curve (Fig. 25); the same result was found for the residence time per feeding station. The predicted residence time should therefore rather be compared with the median observed values: 6.3 s in short feeding stations and 18.0 s in tall feeding stations. These values are again in disagreement with the predicted residence times assuming a 50 % patch encounter rate. Yet, it may have been that the animals perceived the environment at a smaller scale once they chose to feed. If the optimal residence time per feeding station is calculated on the basis of an environment consisting of a single patch type, the predicted residence time in tall patches indeed increases to 11.6 s, as the better alternative of the short patches is left out of consideration. The same procedure reduces predicted residence time to 6.1 s in short patches. This change in emphasis from the mean to the median offers a much better agreement between observation and prediction. This supports the earlier argument that the animals operate differently when selecting a feeding station and when feeding there. Once the feeding station is chosen residence time appears better explained by the characteristics of the particular patch type grazed than by the alternatives between patch types.

Figure 25. Log-survivor curve (and 95% confidence intervals) for the number of bites per feeding station (B/FS).

a) short patches: $\ln(\text{survivorship}) = 0.157 \pm 0.043 - 0.204 \pm 0.002 \text{ B/FS}$; $R^2=0.997$, $\text{MSE}=0.128$

b) tall patches: $\ln(\text{survivorship}) = -0.322 \pm 0.060 - 0.115 \pm 0.002 \text{ B/FS}$; $R^2=0.984$, $\text{MSE}=0.203$

Slopes and intercepts of both curves are significantly different ($P < 0.01$). Data were pooled for all observations as differences in slope or intercept were not affected by individual animals, grain size or animal x grain size interaction. Confidence intervals were calculated according to Haccou and Meelis (1994).

The negative exponential distribution of residence time and number of bites per feeding station is similar to the distribution of many time-based behavioral events (Haccou and Meelis 1994). Residence time and number of bites per feeding station followed the same distribution in other studies of grazing herbivores (Underwood 1983, Jiang and Hudson 1993). Yet, the significance of this finding was not discussed by these authors. The controlled conditions under which this experiment was carried out warrant the claim that this distribution was not caused by small-scale variation in forage availability. The log-survivor curve of the number of bites per feeding station indicates that the probability of taking another bite at a certain feeding station is constant, whatever the number of bites already grazed. This means that the number of bites per feeding station is determined by a single probabilistic process. The different slopes and intercepts for the two patch types shows that the magnitude of the probability depends on the patch type, that is, the probability of taking a larger number of bites was greater in tall feeding stations than in short feeding stations. The survivorship curves show some indication of a weak break point at $N = 16$ bites in short patches and $N = 6$ bites in tall patches, as the slope of regression curves for the parts below and above those points differ ($P < 0.05$). In short patches the probability of taking more than 16 bites fell steeper, which probably points to a depletion effect. In tall patches the opposite was true, which suggests that there is a distinction in lightly and heavily exploited tall feeding stations. Yet, in both cases the confidence intervals indicate that the significance of these break points should be treated with caution.

The break point in the survivor curve, the greater probability of taking more bites at a feeding station and the longer average residence time per feeding station in tall patches may be due to preceding foraging experience in the two patch types. There was a tendency in both patch types for residence time per step in to increase with the proportion of preceding steps taken in a that patch type ($r = +0.251$, $P = 0.011$ and $r = +0.284$, $P = 0.004$ for short and tall patches respectively when considering a sequence of 20 preceding steps). The likelihood of feeding at a certain place therefore is affected by the prior foraging path. Thus, feeding in short patches was facilitated by a longer stay in short patches, because feeding efficiency increased in larger patches. Conversely, feeding in tall patches may have been promoted by a

longer stay in this less profitable patch, because this reduced the moving average of intake rate. Once a tall feeding station was chosen, the lower depletion rate may have promoted a relatively long residence time (see Ginnett et al. 1998). The data do not support the idea that variability in quantity and quality in tall patches was greater than in short patches, which could explain the long residence in tall feeding stations through the selection of exceptionally good feeding stations.

3.4.3.4.3 Effects of scale of patchiness

Two of the four hypotheses on the effect of scale of patchiness on selectivity were confirmed and two were rejected. As predicted, selectivity was greater in the coarse-grained environment and the efficiency of feeding station selection was also greater in the coarse-grained environment. However, contrary to predictions, the animals did not adjust their movement pattern to the scale of patchiness and neither was the number of bites or the residence time per feeding station.

The effect of spatial scale of patchiness on selectivity appears to be related to the discriminatory abilities by the animal and to the rewards and costs related to the effort of discriminating. Discrimination between patch types was obviously easy. This enabled a directed search for the preferred patch type and an effective selection of feeding stations in the coarse-grained environment. With an average of 93.3% of bites in short patches, selectivity was extreme when grain size was coarse. However, in the fine-grained environment selectivity was significantly impaired. Both the selectivity during walking and during the choice of feeding stations were less at the finer grain size. The steers were less successful in selecting feeding stations in the profitable short patches and were also less successful in avoiding to feed in the less profitable tall patches.

The feeding on tall vegetation could have been a deliberate choice of the animals. Although we do not see any nutritional motivation for doing so, a need for vigilance might have affected patch choice (Underwood 1983, Newman et al. 1995). As the larger bites from tall patches necessitated a larger chewing effort (WallisDeVries et al. 1998) and longer bouts of chewing were carried out with the head up, the steers had more time available to scan their surroundings in tall patches than in short patches; the fraction of grazing time spent with the head up in tall patches was twice that

in short patches ($53.5 \pm 1.8\%$ and $25.2 \pm 1.1\%$ respectively; $P < 0.0001$). But it is unlikely that vigilance played a major role in determining feeding in tall vegetation as this would not have led to the observed effects of grain size on selectivity.

We anticipated an impact of scale of patchiness on path tortuosity, and hence fractal dimension. Movement patterns of animals tend to become more tortuous in profitable patches and more linear in unprofitable patches (Bell 1992). However, in large-bodied animals the costs of movement are relatively high (Murray 1991), so their movement path is usually rather linear (Senft et al. 1987). We therefore expected a greater tortuosity at the finer scale of patchiness, assuming that the steers would try to maintain their selective foraging behavior. Although this expectation was confirmed at the two smallest scales of movement, the magnitude of the difference was small and the decrease in length of the foraging path with increasing scale was not significantly different between fine and coarse grain sizes. We therefore conclude that the animals did not adjust their movement pattern to the scale of patchiness. The inevitable result was that selectivity decreased at the finer grain size. We suggest that the animals were not willing to increase their foraging costs to obtain their preferred dietary choice, although they quite evidently were able to discriminate between patch types. Scale of patchiness thus offers an explanation for the occurrence of a dietary mix of different components. Dietary mixing should occur when the costs of discriminating outweigh the benefits.

The absence of an effect of grain size on the residence time per feeding station was contrary to expectation. However, it does fit the view presented above that selection occurs mainly at the level above the feeding station. As each distinct patch was substantially larger than a single feeding station, the scale of patchiness may have been too large to generate differences in the exploitation per feeding station.

3.4.3.4.4 Implications for Optimal Foraging Theory

The application of optimal foraging theory (reviewed by Stephens and Krebs 1986) is a potentially powerful tool to test ideas and advance our understanding of the foraging behavior of large herbivores (Laca and Demment 1996). The findings from this study have important implications for the further development of optimal foraging theory.

Firstly, we have shown that large herbivores do not follow a random movement pattern while foraging. Although it is well understood that large herbivores have the ability to develop a spatial memory of their environment (Bailey et al. 1996, Prins 1996), it is often assumed that patch encounters are random. This may be true if differences between patch types are difficult to detect from a distance, as in studies by Laca et al. (1993a), Distel et al. (1995) and Focardi et al. (1996). Our results in an environment where differences between patch types were easy to detect, suggest that a non-random movement path is followed at a scale of 1-15 m. At a smaller scale movement is essentially linear (fractal dimension $D=1$), at a larger scale movement is more or less random ($D=2$). The scale of the plots evidently limited a more comprehensive assessment of an upper scale limit where movement pattern becomes random. Still, it can be envisaged that such an upper limit exists within a certain patchy plant community. The animals are capable to follow a selective foraging path within the range that they are able to scan for information on resource availability. Beyond that range, no information will be gained on the resources ahead and, so that movement should be random at that scale. At a still larger scale, differences between plant community types should again elicit a directed search if the animals can draw on previous experience to guide them. This response to resource heterogeneity at a larger scale may modify the random search at intermediate scale to a more linear foraging path, if the animals move from one vegetation type to another while grazing. Further research at larger spatial scales is required to elucidate the integration of large-scale spatial patterns on foraging movements. Search patterns and directionality in foraging paths should be incorporated in foraging models to better reflect the actual grazing process and improve predictions on habitat utilization.

Secondly, we found that spatial scale of patchiness affected selectivity. Patch models typically are not spatially explicit and therefore ignore spatial scale. Our study indicates that selectivity is impaired at a fine grain size of patchiness. We have interpreted this as an increase in the cost of discrimination that the animals either are not willing or are not able to make. Although we think the latter explanation did not apply to the present conditions, in view of the clear difference between patch types, discriminatory ability may well be reduced when forage types are mixed at an even finer grain size or when the difference between alternative forages

is smaller. The cost of discrimination in this experiment might simply consist of an energetic cost, as incorporated in the foraging model of Thornley et al. (1994). Discrimination costs also offer an explanation for the conflicting results on grass-clover selection in sheep (see Newman et al. 1992). The cost of selection in the face of the similarity in nutritional value between the two species could well be the reason why observed selectivity varies. More consistent selection should occur when species differences are large, as pointed out by WallisDeVries and Daleboudt (1994). The present explanation is simpler than the one based on diurnal variation and predation hazard advanced in the modeling study by Newman et al. (1995), and it therefore deserves further exploration. But whatever the causal mechanism, our results demonstrate that variation in scale of patchiness should be taken into account as a factor contributing to a mixed diet.

Thirdly, our study confirmed the probabilistic nature of the utilization of individual feeding stations also found in other studies. This utilization pattern contrasts with findings from studies in which smaller patches were presented in a discontinuous arrangement (Laca et al. 1993b, Distel et al. 1995). Those studies found a good agreement between observed of patch residence time and predictions on the basis of the marginal value theorem. We suggest that the lesser performance of the marginal value theorem predictions in the present experiment is due to the size and the contiguous arrangement of the patches. Thus, the sward was a continuous one compared to the discrete patch arrangement in the above-mentioned experiments. In continuous swards of a certain patch type, large herbivores may not perceive a large patch as a collection of discrete feeding stations but rather as one continuous resource. This should promote a probabilistic distribution of residence time at the level of the feeding station. Exploitation patterns and residence time in large patches then should be expected to be constant at the scale of the patch but not at the scale of the feeding station.

3.5 Integrating foraging mechanisms across spatial and temporal scales

Rangelands are characterized by spatially and temporally variable vegetation and herbivory patterns (Coughenour 1991). Heterogeneity is essential to explain and understand real plant-animal interactions. The response of plants to herbivory is strictly dependent on the scale of the

analysis, spatial distribution of plants, and distribution of defoliation (Brown and Allen 1989; Brown and Stuth 1993). As the analysis is expanded from the micro scale, new system properties emerge, and fast, small-scale processes become embedded in slower and larger cycles. Senft et al. (1987) viewed grazing as a hierarchical process across levels of organization, from the community to the region. In this section we build upon this basis and integrate detailed information on grazing mechanisms from the scale of bites to the landscape. We propose a conceptual model of grazing patterns that integrates concepts from nutritional, behavioral and landscape ecology, and we present experimental tests of some model elements. Our general hypothesis can be stated as follows:

Instantaneous grazing behavior follows a strategy of maximization over a temporal scale of one day, and therefore, responds to changes in grazing time and digestive constraints that limit daily intake of digestible nutrients. Grazing strategy reflects maximization of daily intake of digestible nutrients.

3.5.1 Conceptual model of scales of grazing

3.5.1.1 The Importance of Scale

Scale is the resolution within the range of a measured quantity (Schneider 1994). The quantity we emphasize is plant mass removed by herbivores from each point in space. The finest level of resolution is the bite and the largest range is the area potentially available to the herbivores.

Most grazing studies have ignored scale and implicitly assumed that measurements can be extrapolated to other scales by simply changing units. For example, daily intake has been viewed as the product of instantaneous intake rate and grazing time. Yet, the leap from instantaneous to larger time scales implies a temporal and spatial rescaling of the phenomenon under study (Schneider 1994). The validity of this rescaling depends on the degree and type of spatial variability of the vegetation, and on the temporal cycles imposed by the environment and the physiological characteristics of the animal. In natural systems, the variance and range of values of vegetation variables tend to increase with the range and resolution of the observations (O'Neill et al. 1991; Wiens 1989). Thus, a greater variance and range of herbage mass per unit area and species diversity will be observed when quadrats are scattered over 10 ha than when scattered over 1 ha.

Despite the dependence of measurements on scale, the study of rangeland dynamics has focused on a single scale: the community. Likewise, grazing science emphasizes number of paddocks and scale-free stocking rates (Valentine 1990). Scaling variables such as pasture size and total number of animals are all but ignored. Yet, a multiscale approach seems to hold the key to a better understanding of rangeland dynamics (Friedel 1994).

Identification of the "domains of scale" (Wiens 1989) is crucial for devising realistic yet parsimonious models of grazing behavior, because the effects of spatial distribution of resources on herbivore behavior depend on the scales at which these interact (With 1994). We adopt six potential domains of space and time (Table 23, Bailey et al. 1996). These scales differ from previous ones (e.g., Senft et al. 1987; Stuth 1991) in that they are defined by specific behaviors and do not involve levels of organization. These new categories should be more appropriate to study grazing patterns because the degree to which spatial behaviors reflect environmental patterns is mediated by the animal's internal processing of information and resources. Moreover, selection between two options within the same level of organization does not always define the same absolute spatial scale. For example, distance between plant communities depends on their degree of interspersion.

Table 23. Domains of scale of foraging decisions by large herbivores.

Spatial level	Temporal level	Defining behavior	Motivation to move	Entity involved in movement
Home range	3-6 months	Dispersal and migration	Social; reproduction; phenology; competition; thermoregulation; water	Population
Camp	1-4 weeks	Central areas where animals drink and rest between feeding bouts	Phenology; water; cover; forage depletion and regrowth	Herd
Feeding site	2-3 hours	Feeding bout	Forage depletion; intake and digestion rate	Sub herds
Patch	15-30 min	Length and angle of sets of steps; chewing bouts (?)	Forage depletion, intake rate; species composition; olfactory and visual stimuli; social interactions	Few individuals
Feeding station	30-100 seconds	Steps and neck movements	Forage depletion; diet selection; forage abundance; mouthful	Individuals
Bite	1-2 seconds	Jaw, tongue and neck movements	Depletion; selection of diet; touch, smell and taste stimuli	Head

3.5.1.2 Hierarchical Model of Foraging Behavior

Because herbivores experience information constraints and forage in vegetation with multiscale patchiness, we hypothesize that they take a hierarchical foraging strategy. This strategy requires the ability to assess patches and effect behaviors at multiple scales, but it increases search efficiency by eliminating the need to perform costly small-scale search in patches that can be identified as poor at larger scales.

Animals receive information from their external environment and internal state (Figure 26). This information can be perceived at multiple scales, but attention to one scale constrains other scales. For example, ability to see distant patches is diminished while the animal obtains information about a bite by touch. In general, small-scale information is more accurate, but also more costly per unit of forage than large-scale information, because time costs involved in large-scale decisions are spread over a larger quantity of potential forage.

We operationally assume that the forager is continuously deciding between moving, eating or gathering information. It simultaneously decides upon the spatial scale that is emphasized for each behavior. Behaviors are not necessarily mutually exclusive (e.g., information is gathered as forage is obtained). Choice of action and location result in changes in the state of the animal. We assume that these changes are perceived as rewards (e.g., intake rate) or aversive stimuli, and are the basis for the feedback mechanisms that regulate selection of foods and foraging sites.

Foraging decisions proceed from coarse to fine, and from fine to coarse scales (Figure 27). Upon beginning to forage the animal selects a feeding site from a set of alternatives; then, it selects a patch from those available in the site, and so on. Once a bite has been selected, grazing continues at small scales for as long as short-term rewards do not fall below a certain threshold. This threshold may be based on the integration of information at the next larger temporal and spatial scale. If rewards fall below the threshold, decisions shift to the next hierarchical level where a new choice is made. Thus, when intake rate within the feeding station becomes too low, a new feeding station is selected; and when acceptable feeding stations become scarce, a new patch is selected. The consequences of foraging choices are integrated over scales of time and space by various organs and

Figure 26. Sources and scales of information perceived by the foraging animal. Information is integrated at various levels by the animal's memory, by direct perception of the environment at many scales, and by perception of the internal state as integrated by organs and tissues. Small-scale information is gathered at close range and may involve more senses, therefore, it is more accurate but also more costly per unit of potential forage assessed. Large-scale information is less accurate and averages over small scale variation, but it increases search efficiency by allowing the animal to avoid areas of generally poor profitability.

Figure 27. Spatial and temporal cascades of foraging decisions. Animal monitors reward rates (e.g., intake rate) at the scale of the feeding station, patch and feeding site. Reward rates are compared to thresholds determined by memory of rewards and perception of alternatives at larger scales. Continuous arrows represent the flow of decisions; thick discontinuous lines represent the flow of information on rewards at various scales

tissues (e.g., rumen, fat reserves, brain), and then, choices are controlled by feedback information that cascades down from large to small scales.

3.5.1.3 Short-term, Small scales: From Bites to Patches

The bite is the atom of intake and grazing pattern. Bite dimensions result from the interaction between sward height, sward density, stiffness of plant units and herbage grasping movements (Laca et al. 1993a). Bite depth is a constant proportion of sward height (Laca et al. 1992b; Ungar et al. 1991). Bite area responds to sward height, density, stiffness and tensile strength. Griggs et al. (1991b) found that hunger satiation of stabled steers had no effects on any bite dimension. However, bite area and mass declined more than 40% after 4 hours of grazing (Griggs et al. 1991b).

The second level of analysis is the feeding station. Intake rate within feeding stations is a function of bite mass, because bite rate is determined by bite mass (Laca et al. 1994b; Spalinger et al. 1988). At this level the dominant phenomenon is patch depression (Laca et al. 1994a; Spalinger et al. 1988), the reduction in intake rate determined by the depletion of forage. Feeding station depletion motivates the animal to switch from grazing at the bite level to selecting at the feeding station level, on the basis of more integrated information such as short-term memory and visual perception of alternative feeding stations. Feeding station depletion is explained by bite-level mechanisms, and in turn it explains patterns of selection at the next hierarchical level.

3.5.1.4 Long-Term, Large Scales: From Patches to Home Ranges

Intake rate at the patch level results from the integration of grazing processes over many feeding stations. When the edge of a patch is detected, or average rates fall below a certain threshold, the animal "emerges" from a low (between feeding stations within a patch) to a higher level of foraging (between patches within feeding site). For example, Jiang and Hudson (1993) determined that wapiti move to new patches when cropping rate in the last one or two feeding stations falls below the expectation for the season.

As we move from patches to feeding sites or bouts, processes that were ignored at smaller scales become relevant. Interactions between ingestion and digestion have to be considered in order to understand how digestive

constraints that operate at the level of feeding bouts affect diet selection. Ingestion and digestion are linked by the nutritional quality of the diet. Typically, forage of lower quality is easier to find (Demment and Van Soest 1985) , harder to chew, and slower to digest (McLeod et al. 1990). This negative relation between forage quantity and quality defines the fundamental trade-off faced by herbivores at the feeding site level. Intake rate during grazing bouts declines with increasing diet quality (Laca and Demment in preparation). Rate of decline depends on searching abilities of the animal and spatial autocorrelation of forage characteristics. Animals that implement a multiscale search strategy, in a landscape that exhibits multiple levels of patchiness, should suffer the least penalty in intake rate as they become more selective.

Contrary to intake rate, daily digestion increases with diet quality. Therefore, ingestive and digestive constraints cross each other. Depending on the selectivity at lower levels, intake rate over feeding bouts or days can be limited by ingestion or digestion rate. Grazing strategies that maximize instantaneous intake rate will not result in maximum daily intake of DM or nutrients, because the low quality diet obtained will quickly fill up the rumen. Hence, the interaction of digestion and ingestion integrated at scales of one or few feeding bouts should be the basis for setting degree of selectivity and thresholds for foraging decisions at the lower hierarchical levels. For example, WallisdeVries and Daleboudt (1994) found that selectivity of cattle was consistent with a principle of maximization of energy intake on a daily basis instead of short-term basis.

Distribution of water and cover take a progressively greater importance in grazing patterns at the scale of camps and home ranges. However, foraging decisions at these levels are relevant, particularly when animals can move between areas that differ in phenology, such as valleys, and north and south facing slopes of mountainous areas. At these scales, the dominant process is no longer depletion of forages, but the dynamics of forage growth and response to grazing.

3.5.2 Experimental study of scales of grazing

Our conceptual model rests on a series of assumptions about grazing behavior. Although most assumptions are supported by the literature, some required critical testing. We performed an experiment to test the ability of

cattle to exhibit multiple scales of foraging and the effect of search strategy on foraging efficiency.

Spatial characteristics and efficiency of search strategies of cattle were tested as a function of food distribution and apparency. Eight steers of ca. 450 kg of average weight were allowed to forage individually, in a 40 m x 40 m arena with a 2-m grid painted on the ground, for 20 min in each of 8 treatments. Treatments were a factorial of 4 spatial distributions (uniform, random, 2 patches and fractal, Figure 28) of 160 18-g feed pellets with or without a visual cue (1 yellow flag/pellet). The fractal distribution had patches at 5 scales ranging from 1 to ca. 23 m and a constant fractal dimension of 1.0. Pellets without flags were cryptic. Search paths were mapped on a scaled grid by direct observation. Intake was determined by difference between weight of pellets offered and pellets not consumed.

Efficiency of search (intake/distance walked) and intake rate increased ($P=0.01$) as patchiness of food increased from random and uniform to two large patches to multiple scales of patchiness (Table 24). On average, intake rate and search efficiency increased ($P<0.01$) with visual cues (flags), but the magnitude of the effect on intake rate declined with increasing food patchiness.

Table 24. Efficiency of search (g intake/m walked) and intake rate (g/min) of steers foraging in a 40 m by 40 m arena containing 160 food pellets with different spatial distributions, and with or without a visual cue (flag). Values are means of 8 steers.

	Food distribution				
Visual cue	Fractal	2 Patches	Random	Uniform	Mean
-- Efficiency of search (g/m) --					
No flags	7.8	3.9	2.5	2.3	4.1a ¹
Flags	11.8	5.9	4.6	3.9	6.6b
Mean	9.8a	4.9b	3.6bc	3.1c	5.4
-- Intake rate (g/min) --					
No flags	108ab	87c	63d	61d	80
Flags	111a	102abc	97bc	89c	100
Mean	110	94	80	75	90

¹ Numbers not followed by any common letter differ significantly according to a protected LSD test at the 2% level.

The fractal dimension (D) of the search path describes its tortuosity (With 1994) and therefore, the scale of the searching effort. A high value of D for a

Figure 28. Distribution of feed pellets (black dots) used in the study of search patterns of cattle. Continuous lines show paths followed by one steer during 20 minutes of foraging.

certain scale indicates that the path has frequent turns at that scale. Fractal dimension of paths in all treatments, except for the fractal with visual cues, was greater than 1.0, and tended to peak at a scale of 2 to 7 m. In most cases, D was not constant across scales, indicating that search paths were not self-similar, presumably because the mechanisms differed between scales. This means that animals implemented multiple scales of search. The search path in the fractal distribution with flags had a dimension between 1.0 (smooth line) and 1.1, indicating that when the perceptual range is greater, animals increase the search efficiency by walking straight to food locations and closely matching search and food patterns.

3.5.3 Conclusion

Spatial pattern of grazing impacts is a central issue for the sustainability and productivity of rangeland systems. Following developments in landscape ecology, we conclude that studies of plant-animal interactions should focus on phenomena of scale and heterogeneity. We propose a conceptual model of grazing by large ungulates as a guide for quantitative models and multiscale description of herbivory patterns.

Herbivores integrate foraging information over space and time and use it to select foods at various scales. Fractal analysis of foraging patterns identifies the domains of scale at which herbivores interact with plants. Quantitative analysis of grazing patterns across spatial scales should result in an improved ability to predict and manage grazing impacts.

3.5.4 Duration of spatial memory in cattle

3.5.4.1 Introduction

Periods of use and non-use in grazing systems are extremely important. A recovery period for forage plants is important to their survival in a plant community. Allowing a plant community to recover from grazing helps build up carbohydrate reserves and reestablishes photosynthetic material. Carbohydrates are needed for plants to initiate new growth. Regulating the length of the grazing period can limit selectivity of defoliation (Kothmann, 84). If the grazing periods are too long, tillers may be regrazed before the recovery period begins (Valentine, 1990). Valentine (1990) also stated that if the no-grazing periods are too short, the regrowth of plant tillers may be grazed too soon.

Besides manipulating the periods of grazing, an optimum goal may be to graze the available forage evenly. Even grazing results in allowing desirable forage species to compete equally for the available water and nutrients. Holechek et al. (1995) stated that uneven grazing of rangeland by livestock has always been a crucial factor affecting the productivity of rangelands. Heavily grazed areas expand when moderately grazed areas become smaller (Valentine, 1990). Valentine (1990) stated that it is important to obtain maximum use of as wide an area as possible without causing serious damage to any portion of a pasture. Selecting a range site over another may be affected by the grazing behavior of livestock.

Grazing animals use, among other mechanisms, their spatial memory to search for food. Understanding such memory may allow range managers to prevent uneven grazing. Spatial memory greatly influences the feeding behavior of animals (Olton et al., 1977). Spatial memory is the ability of organisms to orient their behavior on the basis of previous experience with a specific spatial pattern of external stimuli (Staddon and Ettinger, 1989). It is spatial memory that allows animals to orient behavior with respect to a location or object that provides no immediate stimulus whatsoever (e.g., it is out of sight). The orientation is based on a map-like representation of the position of the object in relation to other stimuli, and on the recognition of the organism's current position in relation to the same stimuli. Spatial memory can be important to increase the efficiency of locating preferred food patches. When using spatial memory, livestock can spend less time searching for feed and more time foraging.

In the present study, we tested the duration of spatial memory using an 8 row by 8 column-grid of plastic containers. In traditional mazes, animals return to the same decision area before making a choice for a particular arm. All arms have the same chance of being chosen at any given time. In real environments, animals search for food in 2 or 3 dimensions and do not need to return to any decision areas. The protocol we used, is similar to the one used by Edwards et al. (1997) and Laca (1995). It is more focused on using a more realistic testing area for long-term spatial memory. Steers would enter the paddock where the plastic containers were located and try to find a specific set of trays that contain feed.

The purpose of this experiment was to test the ability of the steers to use their spatial memory to remember the location of food. While previous studies (Bailey et al., 1989; Willson and Wilkie, 1993) focused on short-term memory, this experiment dealt with long-term or reference memory. This study emphasized the duration of spatial memory of steers. We hypothesized that steers would learn and then forget the location of food as time since last experience passes.

3.5.4.2 Materials and Methods

3.5.4.2.1 Experimental Arena and animals

The experimental arena consisted of two 55 by 55 meter-paddocks. Each paddock contained an 8 row by 8 column grid of plastic containers 5 meters apart. The area was dominated by Old-World bluestems (*Bothriochloa* spp.). This experiment was conducted from June 7 to October 19, 1994.

Six steers were used to conduct this experiment. The average weight was about 400 kilograms. The steers were grazing an Old-World-bluestem pasture when not tested. They were grazing with 4 other steers in the herd. Water was available ad libitum. The steers were fed 25 kg of feed every other day. The experimental protocol and animal handling and use were approved by the Texas Tech University Animal Care and Use Committee.

3.5.4.2.2 Treatments

Steers were trained to find trays that contained food (loaded trays) in 4 constant locations. An initial training was performed before applying treatments to each steer. Five treatments were tested. The first treatment was a control. Animals in this treatment were tested immediately after the initial training. The second treatment was a lapse of five days since last experience. In the third treatment, 10 days elapsed between the last experience and testing. The fourth treatment was 20 days since last experience. Steers in this treatment were allowed to locate the loaded food trays 20 days after their last encounter with their combination of loaded trays. The fifth treatment was 48 days since last experience. Each of the steers was used for all five combinations. First, all six possible combinations of the 5-day, 10-day, and 20-day treatments were observed. In other words, steer no. 1 was tested for the 5-day, 10-day, and then 20-day treatments, respectively. On the other hand, steer no. 2 was tested for 5-day, 20-day, and 10-day

treatments, respectively. This way, six steers were needed to observe all six combinations. The 48-day treatment was added later for all six steers.

3.5.4.2.3 Training and testing

All steers were trained initially before starting the experiment. They were trained 11 times each, over a 3-day period. Training was also done after the first testing session on each testing day. The purpose of these training sessions was to make the steers remember well the location of the four loaded trays. Each steer had a different combination of four loaded trays out of the 64 tray-grid. The combination for each steer was kept the same for the whole experiment. Steers were allowed to locate their combination of 4 loaded trays until they found them all. At that time, the training session was terminated and the animal was let out of the experimental paddock. Feed pellets were placed under each of the 64 trays to prevent the animals from finding food on the basis of odour. These feed pellets could not be seen nor eaten, they were out of reach of animals.

A calendar was established to plan the testing dates for each steer. At each testing day, a steer was allowed to locate its combination of 4 loaded trays. A testing session was stopped when the steer found all four loaded trays. At each testing day, steers were allowed to locate the loaded trays 5 times. The first time was considered testing and the other 4 times were considered training. Again, feed pellets were placed under each tray to control for smell.

3.5.4.2.4 Measured Variables

All training and testing sessions were entirely observed. At each training and testing day, a map of the paddocks was used to record data. The maps represented the location of all trays including the loaded trays. Every time a steer was tested, the path followed was drawn and trays visited were marked. At the side of the map, a table was used to record time at start of each session, time spent at each loaded tray, time spent searching and time at end of each session.

3.5.4.2.5 Calculated Variables and analysis

Number of locations visited was referred to as NL, found loaded locations visited was referred to as FL, and total visits (including revisits) was referred to as TV. Two ratios were calculated to test working and reference memory. Working memory was tested using the ratio of NL over TV (NL/TV).

Reference memory was tested using the ratio of FL over NL (FL/NL). A Z test was performed to test if searching for food by animals can be either at random or based on behavioral mechanisms (Tille et al., 1996).

A completely randomized design was used to analyze the data. A test for normality and homogeneous variances was performed to assess the validity of using an F-test to compare treatments. Dunnett's t test was used to compare the control treatment to each of the other four treatments.

3.5.4.3 Results and Discussion

The experiment allows two means of assessing the duration of spatial memory. First, the performance of steers was compared to their maximum performance achieved immediately before they started the treatment period of no exposure to the food distribution. This comparison uses each animal as its own control and removes potential differences due to prior experience of individual animals. The test is whether any decline in performance can be detected as the decay period between training and testing increases. Second, the average performance of each steer was compared to the performance expected if steers visited food trays in a random order, ignoring trays already visited within each session (no replacement). This test aims at detecting the time necessary for memory to decay until performance cannot be distinguished from random chance. By using animals as replicate and ignoring the sequence of treatments to which animals were exposed, effects of sequence of total number of exposure (Table 25) appear as error and prevent inflation of the power of the test. In any case, the average (across steers) number of exposures was the same for the 3 intermediate treatments (Table 25) and very similar to that for the 48-day treatment.

Table 25: Number of times steers were exposed to feed trays for each treatment: right after training (treatment 0), 5, 10, 20, and 48 days since last encounter.

Treatment	Steer ID						Avg.
	2R	25R	53R	61W	61R	74R	
0 (Control)	11	11	11	11	11	11	11
5	21	16	16	26	26	21	21
10	26	21	26	16	21	16	21
20	16	26	21	21	16	26	21
48	28	28	28	28	28	28	28
Total	102	102	102	102	102	102	102

Steers remembered the location of food trays for up to 48 days post training (Table 26). The analysis will be discussed for each variable separately.

Total visits or TV was transformed to its logarithm base 10 (LTV). Treatments did not affect L of TV $P>0.05$ (Table 26). The 48-day treatment had the highest value of 0.80. However, the control treatment was not significantly different when compared to each of the other four treatments $P>0.05$. The number of days since last experience did not alter the number of visits made to locate the loaded trays.

Table 26: The performance of steers (N=6) right after training (treatment 0), 5, 10, 20, and 48 days since last encounter.						
Treatment	LTV	LNL	Z Value	SNLTV	SFLNL	LTD
0 (Control)	0.74	0.70	7.09	0.96	0.90	1.60
5	0.78	0.73	6.85	0.94	0.87	1.72
10	0.63	0.63	7.64	1.00	0.96	1.55
20	0.66	0.63	7.64	0.97	0.96	1.49
48	0.80	0.80	6.42	1.00	0.83	1.60
LTV: Logarithm base of Total Visits; LNL: Logarithm base 10 of New Locations; Z value: a Z test for randomness of ratio of New Locations per Total Visits; LFL: Logarithm base 10 of Fond Locations; SNLTV: Square Root of ratio New Locations per Total Visits; FLNL: Ratio of Found Locations per New Locations						

The variable NL was transformed to its logarithm base 10 because it did not have homogeneous variances. Treatment did not affect the log of NL (LNL; $P>0.05$; Table 26). The lowest values were observed at the 10-day and the 20-day treatments (Figure 29). Each of these two treatments had an average LNL of 0.63. The highest was 0.80 at the 48-day treatment. No significant differences were found between the control and each of the other four treatments. Steers in all treatments visited the same number of trays as the control.

The ratio NL/TV did not have homogeneous variances. For that reason, it was transformed to its square root (SNLTV). There was no treatment effect on the SNLTV $P>0.05$ (Table 26). A perfect score was observed for the 10-day and 48-day treatments (1.0 for each of the treatments). Steers in these two treatments did not revisit any of the previously located trays. The ratio gives us an idea about their working memory. Because of the absence of treatment effect, all treatments did well in avoiding previously visited locations. This is a mechanism that can be used by grazing animals in

rangelands. Grazers can use their working memory to save the energy of visiting recently depleted areas. Avoiding the depleted areas increase their chances of encountering non-depleted food patches, and therefore increases their foraging efficiency.

To test if NL/TV was better than by chance, a Z test was performed. The Z test was not different between the control and each of the other treatments $P > 0.05$ (Table 26). However, animals in all treatments did better than expected by chance (Tille et al., 1996). The average Z value for each treatment was compared to a Z table of 1.64 (Figure 30). The value of 1.64 is the limit under which a performance can be expected by chance assuming a random search without replacement. The lowest Z value was observed for the 48-day treatment (6.42), and the highest was observed for both the 10 and the 20-day treatments (7.64 for each treatment).

The ratio FL/NL did not have homogeneous variances and therefore was transformed to its square root (SFLNL). Again, treatments did not affect SFLNL $P > 0.05$ (Table 26). The highest value was observed in the 10-day and 20-day treatments with an average of 0.96. Each of the treatments when compared to the control had similar SFLNL. All treatments were similar to the control in their efficiency of finding the loaded food trays. Their success of encountering loaded trays per tray visited was the same. Length of delay since last experience did not affect their success rate.

The distance walked was transformed to its base 10 logarithm (LTD) because the original data did not meet the analysis of variance assumption of homogeneous variance. To locate the loaded trays, steers traveled the most in the 5-day treatment (Table 26). The LTD was highest in the 5-day treatment with an average of 1.72. However, the control was not significantly different from any of the other four treatments $P > 0.05$. Steers walked the same distance to locate the food trays despite the length of period since last experience. In other words, grazing animals would walk similar distances to locate preferred food patches.

This study showed that cattle can remember the location of preferred food for long periods (up to 48 days). This agrees with a study done by Kovalcick and Kovalcick (1986), where 77% of cows and 46% of heifers performed well, after six weeks of interruption. However, these results are different from the findings by Bailey et al. (1989). The authors studied the length of periods

Figure 29: The effect of days since last experience with a particular food distribution on the logarithm base 10 of new locations (LNL) visited by steers. Vertical lines indicate standard error.

Figure 30: The effect of days since last experience in randomness of finding food using a Z test. A z value below 1.64 (solid line) indicates a random search. Vertical lines indicate standard error.

that cattle remembered food locations. They found that cattle remembered the location of food for 8 hours. It is important to note that here we studied long-term spatial memory while Bailey et al. (1989) studied short-term spatial memory. Memory decay has also been studied for rats by Beatty and Shavalia (1980). Their findings agree with ours in the sense that animals have efficient spatial memory. Marsh Tits were studied by Shettleworth and Krebs (1982). They stated that Marsh Tits efficiently recovered seeds from most recently visited locations. Short-term spatial memory was tested in their protocol.

3.5.4.4 Conclusion

Days since last experience did not alter the number of visits made to locate the loaded trays. Animals did not locate food at random. They used some mechanism to be efficient. Spatial memory was assumed to have played a prominent role.

Animals learn preferred food locations based on past experience, among other factors (Valentine, 1990). Limiting the ability of the animal to learn spatial characteristics of areas grazed may be efficient in improving the distribution pattern. Laca (1995) suggests to frequently move the animals among grazing units. A grazing method that includes shorter utilization periods may be a practical scheme. However, an increase in cost may result because of the increase in fencing material. We may have to create more grazing units resulting in higher fencing charges. This scheme may be hard to accomplish considering the results we report in this experiment. Cattle remembered food locations for at least 48 days post training. Long non-use periods cannot be incorporated into most grazing methods. Nevertheless, the duration of spatial memory may be much longer than the 48 day-period tested. Our field observations suggest that cattle may remember the location of food for months and maybe for up to a year. Besides limiting the learning process of herbivores, we suggest using rewards as a tool to promote uniform grazing.

We believe that the reward of visiting a food location may affect the learning abilities of animals. Hosoi and Swift (1992) reported that it may be more important for cattle to remember how they failed than to remember how they succeeded. Training livestock to expect high rewards can be used to promote grazing distribution (Laca, 1995). Laca (1995) suggests placing

supplemental feed in different locations. This would increase the evenness of the distribution of the animals and help in increasing their reward expectations. Moreover, associating the reward such as supplementation with an artificial sound (honking) can be performed. As days pass, animals would learn to associate between the sound and the food. We can use this tool to change the area where to supplement and therefore promote spatial distribution of grazing animals. Not having a definite period for cattle to remember food locations is an important result that may shift our research attention to other fields of grazing behavior in order to promote uniform grazing in rangelands.

3.5.5 Integration of ingestive and digestive constraints as determinants of quantity and quality of diet consumed by ruminant livestock

At the daily time scale, our conceptual model of intake can be summarized as follows. The intake of grazing ruminants can be constrained by two processes: digestion (fill) and ingestion. The two constraints have opposite effects on intake (Fig. 31). Maximum intake increases curvilinearly as the NDF concentration of the diet decreases (diet quality increases) because of the fill and passage characteristics linked to cell wall (Mertens 1987, 1992). On the other hand, our foraging model generates declining curves of intake with increasing diet quality. Most grazing landscapes are heterogeneous and exhibit an inverse relationship between quality and quantity of forage. Therefore the more the animal selects for quality the lower the rate of intake (Laca and Demment 1996). The position and shape of the curves is a function of the ingestion, locomotion, grazing time and feeding strategy of the animal, as well as of the structure of the landscape in terms of abundance and distribution of forages of different quality. Our experiments address the mechanisms and curves that describe this tradeoff between quality and quantity of intake. The ingestive constraint can be predicted on the basis of ingestive models.

To optimize feeding the animal must maximize some currency. Although our results indicate that dry matter IIR was maximized, our experiment could not differentiate between this currency and digestible DM intake. This distinction is important for prediction of daily intake and is addressed in our experiments.

Figure 31. Conceptual model for experiment on temporal scale of cattle grazing strategy. Thin curves represent ingestive constraints on daily intake; $GT\ 1 < GT\ 2$ indicate the potential eating time that is available. The thick curve represents digestive constraints on daily intake, and will be determined by measurement of voluntary consumption of different mixtures of alfalfa and grass hay. The dark shaded area is the set of feasible intakes when $GT\ 1$ time is available for grazing. The light shaded area indicates the additional feasible intakes when grazing time increases from $GT\ 1$ to $GT\ 2$. Points a and b represent the expected intake and diet qualities if animals maximize instantaneous intake rate or digestible dry matter intake rate, respectively. Because these two rates do not depend on grazing time, an increase from $GT\ 1$ to $GT\ 2$ will not affect points a and b. In both cases animals reach satiation before available grazing time has elapsed. Points c and d represent the behavior of an animal that maximizes daily intake of digestible dry matter. The animal feeds selectively during all available grazing time, and responds to an increase in grazing time by increasing selectivity and reducing intake rate, such that total amount of digestible dry matter ingested is greater.

The two constraints define a domain of possible daily intakes lying below both curves (Figure 31). The maximum dry matter intakes (DMI) possible for any given diet quality lies on the lower constraint line. There is an intermediate diet quality for which a maximum daily intake is achieved. However, if the slope of the ingestive constraint curve is not too negative, maximum daily intake of digestible dry matter (DDMI) is achieved at greater diet quality than which allows maximum DM intake. If grazing strategy is to maximize DDMI, the model suggest an interesting point: in most grazing situations intake would be constrained more by ingestion than digestion.

We chose the model of Mertens (1987, 1992) over others (e.g., Groom 1987) because the model's performance on forage diets is quite good, and NDF, used as a currency in the model, is easily measured in our experiments. The model is also similar to the digestive component used by Demment and Greenwood (1988) to investigate the link between ingestion and digestion processes.

3.5.5.1 Theoretical basis for experiment

We have previously based predictions of intake and selectivity of grazing ruminants on the assumption that they maximize intake rate of forage dry matter. Other currencies, besides DM intake rate, can be proposed as equally suitable or even better alternatives. For example, grazing animals may adjust selectivity to maximize daily intake of forage DM or daily intake of digestible nutrients. The different currencies should lead to different behaviors, intakes and diet qualities. Therefore, it is important to determine which currency best explains selectivity of grazing animals. The goal of this experiment was to simultaneously select the best currency and validate a model that integrates ingestive and digestive constraints of grazing ruminants. Two aspects of this experiment differ from the experiment originally planned. First, it was done with sheep instead of cattle. Second, animals were kept in metabolic crates during the experiment.

The experiment is based on the model presented above. We hypothesized that grazing animals are subject to constraints that act on the ingestion of food. In simple terms, for any diet quality and available grazing time there is a maximum feasible intake rate (and daily intake) that animals can achieve. This maximum is assumed to decline with increasing selectivity and diet quality. Daily intake is also constrained by the animal's capacity to digest

and process forage in the gut. We hypothesize that as diet quality increases the animal is able to digest more forage per day. In the model, actual intake depends on both constraints and on what currency the animal uses. The currency that best explains selectivity and intake can be identified because the relationships between intake and diet quality that result from increases in available grazing time differ among currencies. Maximization of instantaneous intake rate implies no response of either intake or diet quality to available grazing time. Maximization of daily DM intake implies that as grazing time is increased, both intake and diet quality will increase following the path of the digestive constraint. Maximization of daily intake of N (or other nutrient or digestible DM) also implies positive responses of diet quality and intake to increases in grazing time, but DM at any diet quality is below that prescribed by the digestive constraint.

In the experiment we created conditions such that the assumed negative relation between intake rate and diet quality was true. Then, we tested the assumption that *ad libitum* intake increases with increasing diet quality. Finally animals were allowed to eat for different lengths of time and we measured the response of diet quality and intake.

3.5.5.2 Materials and methods

Twenty Merino Rambouillet ewes of 48 kg average weight were used in the experiment. Animals were kept in individual metabolic cages for the complete duration of the experiment. Water and a mineral supplement was available at all times, with the exception that the mineral supplement was not available during meals. Sheep were fed twice a day every day of the experiment. Morning meals started around 7:30 and afternoon meals at 15:00.

We used two chopped hays as the experimental feeds, good quality alfalfa (*Medicago sativa*) and timothy (*Phleum pratense*). Commercially available hays from a single batch and field each were used. Nutritional and fiber analyses of the hays are pending.

The experiment had four major phases. The first phase took place after animals had been accustomed to the metabolic cages and diets for a week. In this phase there were 5 treatments and 4 ewes were randomly allocated to each treatment. The treatments were different alfalfa:timothy percentages in the diets offered: 100:0, 25:75, 50:50, 75:25 and 0:100. Alfalfa and timothy

were finely mixed. We assess that animals were not able to select hays to any relevant extent. We measured intake of hay and feces production.

The second phase of the experiment consisted of four treatments of total time during which hay was available for consumption: 1, 2, 3 and 4 hours per day. Meal length was half of the total eating time per day. One animal from each treatment in phase 1 was randomly assigned to each treatment in phase 2. In this phase hays were offered simultaneously but in two separate sides of the feed box, so the animal always had a choice between eating alfalfa or timothy. Timothy, the low quality hay, was offered without physical restrictions. The side of the box that contained alfalfa (randomly determined) was fitted with fifteen 15-cm long, 0.9-cm thick, vertical wooden dowels. The dowels were permanently fixed in an evenly-spaced 6.3-cm square grid. The purpose of the dowels was to reduce intake rate of alfalfa below that of timothy. Animals were given 4 days of acclimation to the experimental treatments, after which we measured intake of each hay per meal during 8 days. Intake rate of timothy and depletion curves of alfalfa were measured at the end of this phase.

In phase three of the experiment meal lengths were cut in half and the physical restriction on alfalfa intake rate was increased by adding eight 15-cm vertical pieces of flexible plastic tubing of 0.6-cm diameter, and fifteen 9-cm horizontal pieces of the same tubing on top of the wooden dowels. These "T" tops could be rotated around by a gentle push. Animals were acclimated to the new time restriction, but not to the new physical restriction, during three days. We did not allow sheep to become familiar with the new physical restriction in an attempt to maximize its impact. We measured consumption of each hay in each meal during the following 5 days.

During the last phase of the experiment, three animals from each treatment were randomly reassigned to the other three treatments. We measured consumption of each hay in each meal during 5 days. Depletion curves of alfalfa and timothy were determined at the end of the experiment.

3.5.5.3 Results

- Phase 1: Digestibility increased linearly as a function of alfalfa content in the diet (Figure 32). Digestibility of alfalfa and timothy were 57.5 and 50.4.

- Phase 1: Total daily intake increased linearly as a function of alfalfa content in the diet (Figure 33). Voluntary intake, as determined by digestive constraints increased linearly from 1474 g/day for timothy to 1756 g/day for alfalfa.
- Phase 2: Daily intake (Figure 34) and proportion of alfalfa in the diet (Figure 35) decreased as a result of imposed ingestive constraints (limited feeding time and limited intake rate of alfalfa).
- Phase 3: The more extreme treatment regime resulted in clear effects of available eating time (Figure 36) and a subsequent effect on the fraction alfalfa in the diet (Figure 37).
- Phase 4: Daily intake increased as diet quality increased when animals had a choice to select their diets (Figure 38). This line describing the relationship between daily intake and diet quality was below the digestive constraint line (Figure 34). This pattern of response is most consistent with a foraging strategy that maximizes daily intake of nutrients. However, there was a large variability among animals so the data are not conclusive. The low power of the experiment may be related to the small difference in digestibility and voluntary intake between the two forages used, relative to the variability among animals.

Linear Fit				
Summary of Fit				
RSquare		0.596937		
RSquare Adj		0.571745		
Root Mean Square Error		2.196203		
Mean of Response		54.19004		
Observations (or Sum Wgts)		18		
Analysis of Variance				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	114.29312	114.293	23.6960
Error	16	77.17293	4.823	Prob>F
C Total	17	191.46605		0.0002
Parameter Estimates				
Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	50.416801	0.932092	54.09	0.0000
% alfalfa	0.0714930	0.014687	4.87	0.0002

Figure 32. Relationship between proportion of alfalfa in the diet and in vivo apparent digestibility. Phase 1 of experiment. On average, digestibility was 50% for timothy and 57% for alfalfa.

Linear Fit					
Summary of Fit					
RSquare		0.265877			
RSquare Adj		0.21344			
Root Mean Square Error		86.83331			
Mean of Response		809.7234			
Observations (or Sum Wgts)		16			
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Ratio	
Model	1	38230.80	38230.8	5.0704	
Error	14	105560.33	7540.0		Prob>F
C Total	15	143791.13			0.0409
Parameter Estimates					
Term	Estimate	Std Error	t Ratio	Prob> t	
Intercept	737.22005	38.83304	18.98	0.0000	
%aa diet	1.4061255	0.624459	2.25	0.0409	

Figure 33. Average intake of hay (weight as offered, 92% DM) per meal. Ad libitum daily DM intake of hay varied from 1356 g for pure timothy, to 1615 g for pure alfalfa.

Oneway Anova

Summary of Fit

RSquare0.263539

RSquare Adj0.240525

Root Mean Square Error210.4895

Mean of Response1067.881

Observations (or Sum Wgts)100

Analysis of Variance

Source

DF

Sum of Squares

Mean Square

F Ratio

Prob>F

Model

3

1522047.4

507349

11.4511

Error

96

4253360.6

44306

C Total

99

5775408.1

0.0000

Means for Oneway Anova

Level

Number

Mean

Std Error

1

25

859.54

42.098

2

25

1102.71

42.098

3

25

1130.05

42.098

4

25

1179.22

42.098

Std Error uses a pooled estimate of error variance

Figure 34. Daily DM intake of hay during phase 2 of the experiment as a function of time allowed per each of the 2 daily meals.

Oneway Anova				
Summary of Fit				
RSquare		0.075964		
RSquare Adj		0.047088		
Root Mean Square Error		11.83216		
Mean of Response		38.19218		
Observations (or Sum Wgts)		100		
Analysis of Variance				
Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	1104.890	368.297	2.6307
Error	96	13440.004	140.000	Prob>F
C Total	99	14544.895		0.0545
Means for Oneway Anova				
Level	Number	Mean	Std Error	
1	25	38.1186	2.3664	
2	25	36.4631	2.3664	
3	25	43.5419	2.3664	
4	25	34.6452	2.3664	
Std Error uses a pooled estimate of error variance				

Figure 35. Percentage of alfalfa selected by ewes in phase 2 of the experiment as a function of time allowed per each of the 2 daily meals.

Oneway Anova

Summary of Fit

RSquare	0.795501
RSquare Adj	0.788759
Root Mean Square Error	125.6526
Mean of Response	1090.587
Observations (or Sum Wgts)	95

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	3	5588996.7	1862999	117.9966
Error	91	1436760.7	15789	Prob>F
C Total	94	7025757.5		0.0000

Means for Oneway Anova

Level	Number	Mean	Std Error
0.5	20	699.38	28.097
1	25	992.64	25.131
1.5	25	1236.41	25.131
2	25	1355.68	25.131

Std Error uses a pooled estimate of error variance

Figure 36. Average daily DM intake in phase 3 of the experiment, as a function of time allowed per each of the 2 daily meals.

Oneway Anova					
Summary of Fit					
RSquare		0.302496			
RSquare Adj		0.278164			
Root Mean Square Error		10.52124			
Mean of Response		27.38922			
Observations (or Sum Wgts)		90			
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob>F
Model	3	4128.613	1376.20	12.4322	
Error	86	9519.893	110.70		
C Total	89	13648.506			0.0000
Means for Oneway Anova					
Level	Number	Mean	Std Error		
0.5	18	18.9364	2.4799		
1	22	22.0833	2.2431		
1.5	25	36.7095	2.1042		
2	25	28.8242	2.1042		
Std Error uses a pooled estimate of error variance					

Figure 37. Percentage of alfalfa selected by ewes in phase 3 of the experiment as a function of time allowed per each of the 2 daily meals.

Figure 38. Relationship between diet quality (as indicated by % of alfalfa selected) and daily DM intake. Averages for treatments of phase 2 and 3 of the experiment were used.

3.6 Social interactions in grazing behaviour

Thusfar in this report we have viewed the grazing behaviour of the individual animal more or less in isolation, with the implicit assumption that our results apply equally in a herd context. This ignores two potentially important factors that can moderate grazing behaviour at the herd level: competition and social effects of experience. In this section we explore these factors under the following broad hypothesis:

For initially uniform and continuous swards or patchy landscapes (trays) and given proportionate depletion, grazing style does not change with group size.

3.6.1 On the Relative Importance of Exploitative and Interference Competition in Grazing Ungulates: an Experimental Test

3.6.1.1 Introduction

Large grazing ungulates are gregarious and may form large herds (Jarman, 1974). In these large foraging groups individual animals are subject to intense intraspecific competition for forage with negative impacts on their performance (Clutton-Brock et al., 1982; Jones and Sandland, 1974; Prins, 1996; Sinclair, 1977; Smoliak, 1974; Willms et al., 1986). Competitive interactions between individuals can be classified into two main types (Schoener, 1983): exploitative competition and interference competition. In exploitative competition individuals are impacted via resource depletion without directly interfering with each other. In interference competition the access to a resource is limited by agonistic interactions between individuals. These two categories are similar to scramble and contest competition, but they are not as extreme nor exactly the same (Begon and Mortimer, 1986). Interference competition is known to be important in species of mammalian carnivores (e.g., Owens and Owens, 1978; Schaller, 1972), primates (e.g., Dittus, 1977 and 1979; Janson, 1985; Whitten, 1983) and birds (Harper, 1982). Intraspecific competition between foraging herd-living ungulates, however, has usually been regarded as exploitative competition (Clutton-Brock et al., 1982; Geist, 1974; Jarman, 1974; Sinclair, 1977). The underlying arguments are twofold. Firstly, it is not efficient for grazers to try to monopolize forage resources that are typically widely dispersed and of low nutritive value per unit weight, especially when living in a herd. Secondly,

agonistic interactions between permanent herd members, the females, are relatively rare compared to those between males, that usually live in a looser association with the herd. In female ungulates (and many other species) the acquisition of nutrients has a higher priority in terms of reproductive success than access to mates (Clutton-Brock, 1989). The lower interference frequency in females is supposed to reflect a greater emphasis on exploitative competition.

Direct interference might become important, however, when food resources are scarce and clustered, and when herds are large. Dominance hierarchies in herd-living female ungulates do commonly exist (Clutton-Brock et al., 1982; Duncan, 1992; Kondo et al., 1989; Sinclair, 1977; Van Dierendonck et al., 1995). This begs the question of their significance. Could exploitative and interference competition both be important in determining foraging efficiency? There is as yet no study that satisfactorily addressed this question. Thouless (1990) studied feeding competition in red deer (*Cervus elaphus*) but did not measure food intake and his study area was intensively utilized, which reduces the potential importance of interference competition. Possible responses to the threat of competition from a nearby grazer include taking larger bites (i.e. altering bite dimensions) or biting more quickly in order to prevent the resource from being usurped by the competitor, engaging in an agonistic interaction in which the winner gains the resource, or avoiding direct competition by moving away to fresh, unthreatened resources. This necessitates the distinction between effects of close proximity on grazing behavior and the effects of dominance. Under exploitative competition food intake rate should stay the same (if animals already forage at maximum efficiency) or be increased by close proximity, and dominance should not play a significant role. Under interference competition, however, dominant animals should gain an advantage in food intake rate over subordinates, either through disturbance at close proximity or through active displacement. Moreover, agonistic interactions should be more frequent in the preferred patches and when selectivity is constrained by availability.

We tested these hypotheses using cattle (*Bos taurus* L.) as a model species. We performed two experiments on artificial swards and one field experiment to determine the importance of interference competition in grazing ungulates. In this paper we first consider the effect of the close proximity of a

conspecific on short-term ingestive behavior in all three experiments. Next, we investigate the impact of dominance status on foraging behavior in the field.

3.6.1.2 Materials and Methods

3.6.1.2.1 Experiments on artificial swards

We tested the cattle using hand-constructed swards (HCS), prepared according to methods described by Laca et al. (1992a). Each HCS consisted of alfalfa (*Medicago sativa* L.) shoots (Exp. 1) or orchardgrass (*Dactylis glomerata* L.) "tillers" (Exp. 2). Fresh forage material was clipped each morning at 07:00 hours. Orchardgrass "tillers" consisted of three leaves. Each shoot or tiller was threaded through holes in 10 x 10 cm plywood modules at a density of eight per module. Two patches of 20 modules each were constructed by fastening modules to a plywood base board. The patches were separated by a 10 cm space which was close enough that paired animals were forced to be in physical contact during the trials. The forage was trimmed to a height of 20 cm to present a uniform surface to the animals.

The animals were 9 steers of mixed breeding (ca. 18 months of age and average live weight 620 kg) trained to be led on a halter. They were maintained on alfalfa hay, fed after experimental sessions. Animals were led to the HCS either singly or paired at random with another animal and allowed to feed side-by-side. Trials were terminated when each animal had consumed 6 bites. Grazing sessions were videotaped for later analysis to verify bite counts and determine trial length to the nearest 0.1 sec.

Prior to each trial, the forage was clipped from four modules in each patch for dry-matter (DM) determination. The samples were returned to the lab and dried at 60 °C to constant weight. The herbage mass DM of the clipped modules was then used to estimate the pre-grazing biomass of each patch. Post-grazing mass was determined by clipping all remaining forage from the HCS and processing it as described for the dry-matter modules. Bite weights and IIR were determined on the basis of the difference between pre- and post-grazing HCS biomass. Bite area was calculated from the number of tillers or shoots grazed and the area per tiller or shoot (12.5 cm²). Bite depth was determined by measuring the length of all grazed tillers or shoots

immediately after the grazing session. Time per bite was determined from analysis of the videotapes.

The data were analyzed as a 9 by 2 randomized block design with animals as blocks and single or paired constituting the two levels of the social environment factor. Where appropriate, pre-grazing HCS biomass was used as a covariate.

3.6.1.2.2 Field experiment

The field experiment was conducted in an irrigated *Setaria lutescens* (Weigel) Hubb. grassland. We created 16 20x40 m plots with contiguous mosaics of short/high quality and tall/low quality patches in equal proportion and at two grid sizes: a fine-grained of 2x2 m (200 cells per plot) and a coarse-grained of 5x5 m (32 cells per plot). The allocation of patch types to cells was randomized over blocks of 4x4 cells, so that an equal proportion of short and tall patches were obtained for each block of 16 cells. This small-scale randomization of the two patch types was imposed to avoid accidental clustering of patches of a certain type. The pasture was cut entirely in mid-June and fertilized with ammonium nitrate 2 weeks later (90 kg N/ha). Short patches were cut again in early august, fertilized anew (180 kg N/ha) and cut for the last time 2 weeks later so that all plots had the same regrowth period before the experiment (3-11 September).

Five 30-month old Hereford crossbred steers (604-710 kg) were brought to the pasture 4 days before the start of the observations. They were allowed access to a pasture with similar patch mosaics for 520 min/day on average (including time in experimental plots). On each day of the experiment, observations were collected for 2 plots, starting at sunrise. One observation consisted of 30 minutes with a 15 min break between consecutive observations. The steers were grazed together and in each plot one focal animal was observed, giving duplicate observations for four animals for each of the two patch size treatments; the fifth animal, named Homer, was too shy to be handled. Sounds and images were recorded with a video camera from a 3.5 m high platform. These records were later used to identify bites, chews, steps, grazing location and inter-individual distance using an event-recording program. Idling time was excluded from the analysis.

Bite frequencies were converted to intake data by calibration with patch depletion curves determined afterwards in stall trials with sods cut from the

same pasture (see WallisDeVries et al., 1998). The residence time per feeding station was calculated as the time spent between two steps where one or more bites were taken; thus, steps where biting did not occur were not counted as feeding stations. Both the duration and frequency of inter-individual interactions were recorded. Agonistic interactions were recognized as such when one animal was threatening with the head lowered or actually butting another. The individual that took the initiative was classified as the winner, as the other animal usually retreated. Sometimes the receiving animal did not really react, but we felt that this still showed the initiating individual as the dominant. Draws occurred when the interaction was either not clearly agonistic or when the defender responded to the aggression such that no clear winner could be assigned. However, draws were relatively rare (10% of interactions). All statistical analyses were carried out using JMP 3.1.5 (SAS, 1995).

3.6.1.3 Results

3.6.1.3.1 Effects of proximity

There were no significant differences between animals grazing singly or in pairs with respect to bite area, bite depth, time per bite, or IIR in either experiment using artificial swards (Table 27). Bite weight covaried with pre-grazing biomass in experiment 1 ($P < 0.001$) but not in experiment 2. Bite weight was not significantly affected by social regime either before or after the variation due to pre-grazing mass was controlled for. Bite depth was similar in both experiments and represented approximately 50 percent of the original sward height, which is consistent with prior experiments (Laca et al., 1992b; Ungar et al., 1991). Bite area was greater on the orchardgrass swards due to the tendency of the grass leaves to reflex and intermingle in the upper horizon of the canopy. Bite weights and IIR were greater on the alfalfa HCS due to the higher average pre-grazing biomass (41.7 g DM alfalfa vs. 21.4 g DM orchardgrass) of these swards.

The findings for the artificial swards were confirmed by the field data (Table 28). Neither the residence time per feeding station (i.e. a step where one or more bites were taken), nor the dry matter intake rate, nor bite selection were affected by the close proximity of another individual.

Table 27. Mean values ($\pm$ S.E.) for bite dimensions and intake of steers grazing alone or in pairs from artificial swards. There were no significant treatment effects ($P>0.05$).

Variable	Expt 1 (alfalfa)		Expt 2 (orchardgrass)	
	single	paired	single	paired
Bite Area (cm ²)	82.9 $\pm$ 5.9	81.9 $\pm$ 6.4	99.9 $\pm$ 6.9	104.0 $\pm$ 6.1
Bite Depth (cm)	9.6 $\pm$ 0.6	9.7 $\pm$ 0.6	10.1 $\pm$ 0.5	9.8 $\pm$ 0.5
Bite Weight* (g DM)	1.19 $\pm$ 0.10	1.25 $\pm$ 0.10	0.67 $\pm$ 0.05	0.65 $\pm$ 0.05
Time per Bite (sec)	1.52 $\pm$ 0.11	1.34 $\pm$ 0.10	1.21 $\pm$ 0.05	1.28 $\pm$ 0.05
IIR (g/sec)	0.83 $\pm$ 0.14	1.05 $\pm$ 0.13	0.56 $\pm$ 0.04	0.53 $\pm$ 0.04

* least squares means and S.E. after controlling for pre-grazing biomass

Table 28. Mean values ($\pm$ S.E.) of the average feeding station residence time (FSRT, s), DM intake rate (DMIR in g/min) and bite selection for steers grazing in close proximity (<2 m apart) and further apart in mosaics of short and tall grass patches. No effects of proximity were apparent for any of the variables ($P>0.20$), nor effects of patchiness, animals or their interactions on the difference between close and far proximity ($P>0.15$).

	Proximity	
	Close	Far
FSRT-Short	9.6 $\pm$ 0.6	9.7 $\pm$ 0.5
FSRT-Tall	24.9 $\pm$ 2.8	26.0 $\pm$ 2.5
DMIR-Short	56.7 $\pm$ 2.1	56.9 $\pm$ 1.9
DMIR-Tall	57.5 $\pm$ 5.0	53.0 $\pm$ 8.1
%Bites-Short	88.2 $\pm$ 4.2	86.7 $\pm$ 4.8

3.6.1.3.2 Effects of dominance

On average there was one interaction per 5.5 minutes of grazing time. The proportion of time spent on interactions in the field was small in magnitude, but it was higher in the treatment with fine-grained patchiness (small grid size 0.84 $\pm$ 0.08% of grazing time and large grid size 0.43 $\pm$ 0.08%; $P = 0.062$). During grazing there was a clear preference for the short patches over the tall patches: 86.8 $\pm$ 4.8 % of the bites were taken in the short patches (see also WallisDeVries et al. in prep.). At the coarse-grained patchiness, more interactions were observed on the preferred short patches than expected from the percentage of steps walked there (paired t-test $P = 0.068$); no such difference was found at the fine-grained patchiness.

There was a clear dominance hierarchy among the five steers from the field group in the order Fabio > Tufa > Astro > Milo > Homer (Table 29). The dominance hierarchy tended to be correlated with body weight for 4 of the 5

individuals (Table 30). Among the 4 observed individuals there were significant animal differences for several important variables related to foraging (Table 30). Higher-ranking individuals bit faster and stayed shorter at feeding stations in short patches, had a lower variation in residence time per feeding station in short patches, and had a higher overall dry matter intake rate than lower-ranking individuals. The steers were not evenly spaced out over the plot. Three of the four observed animals spent *c.* 50% of grazing time within 2 m of a conspecific, where the average inter-individual distance was expected to be 7.1 m under an even distribution. The lowest ranking observed individual, Milo, only rarely grazed at close proximity of the others. Patch and bite selection were not subject to individual variation.

Table 29. Dominance interactions in the group of 5 steers, as expressed by the numbers of wins and losses

Losses \ Wins	Fabio	Tufa	Astro	Milo	Homer	Total Losses
Fabio	XX	1	1	0	0	2
Tufa	15	XX	0	0	0	15
Astro	15	2	XX	4	0	21
Milo	12	15	3	XX	1	31
Homer	3	5	5	4	XX	17
Total Wins	45	23	9	8	1	86
%Wins	95.7	60.5	30.0	20.5	5.6	

Table 30. Animal differences in live weight, percentage of steps walked in close proximity, bite rate (bites/min) feeding station residence time (FSRT, s) and its standard deviation (SDFSRT, s) in short grass patches, and total dry matter in take rate (DMIR, g/min) for steers grazing in mosaics of short and tall grass patches, with the significance of animal differences after accounting for effects of pasture patchiness. Also shown is the Pearson correlation coefficient of these values with the percentage of wins in dominance interactions with its significance (d.f.=2).

	Fabio	Tufa	Astro	Milo	<i>P</i>	<i>r</i> -%Wins	<i>P</i>
Weight (kg)	709.5	697.5	648.5	603.5	0.0025	+0.87	0.087
%Steps-Close	51.1	43.9	60.5	16.9	0.0003	+0.49	0.425
Bite rate	44.1	38.3	33.6	36.7	0.0091	+0.857	0.093
FSRT-Short	8.2	9.0	9.6	11.6	0.0123	-0.88	0.126
SDFSRT-Short	6.9	7.8	9.2	9.4	0.0026	-0.98	0.011
DMIR	56.1	51.6	43.6	44.8	0.0082	+0.96	0.027

3.6.1.4 Discussion

It is clear from our study in both stall trials and a field experiment that the mere proximity of potential competitors does not alter bite size or bite rate during grazing. However, even though our data are based on a few individuals only, the results suggest that the position in the dominance hierarchy does influence grazing behavior and food intake rate. These results confirm the findings of Thouless (1990). Dominance did not play a role in the stall trials because the duration of the trials was limited to six bites and did not allow for the differences in residence time between dominant and subordinates to be exhibited. During additional informal trials in which we fed cattle from a single patch, the animals generally did not engage in agonistic behavior until the patch was nearly depleted, when one animal would displace the other. In the field, the dominance hierarchy was clear. As the group consisted of castrates only, the dominance was evidently not related to the acquisition of mates. The hierarchy appeared to correlate with body weight, although the fifth animal, lowest in rank but also the heaviest (710 kg) did not fit this pattern; however, this is likely to have been caused by its shy temperament. The result of the dominance hierarchy was that higher-ranking animals achieved a higher food intake rate. They did so by biting faster and staying shorter at feeding stations, thus maintaining a higher bite size by depleting each feeding station to a lesser degree. Also, the variation in residence time per feeding station was less in higher ranking animals, which may have been due to a lesser susceptibility to disturbance. Individual variation in bite rate was apparent but unrelated to dominance rank or body mass when the animals were grazing alone in stall trials (WallisDeVries et al., 1998). Bite weight for a given level of depletion did not differ among animals immediately after the field dominance trial ($P>0.25$), when steers grazed sods alone (WallisDeVries et al., 1998). Therefore, it is likely that the individual variation in bite rate in the field was caused by the presence of higher-ranking conspecifics and not by preexisting individual differences that could be explained by differences in body mass. Four of the five animals grazed closer to each other than expected under an even spacing-out. It is interesting to note that the lowest-ranking individual observed, Milo, usually grazed further apart from the others. The resulting reduction in disturbance may have given him the opportunity to achieve a higher intake rate by biting faster than the next low-ranking animal, Astro.

As we predicted, interference was more frequent in the fine-grain environment where selection was more difficult than in the coarse-grain environment (see WallisDeVries in prep.). Also, interference occurred more often at the preferred patch type when patchiness was coarse-grained but not when patchiness was fine-grained. As the grid size in the fine-grained environment was less than individual body length, it may be that the scale of patchiness was too small to allow a clear measurement of the effect of patch type on frequency of interference. If this is true, the finding of a significant patch type effect at the coarse grain size supports the hypothesis that interference does occur more frequently at preferred feeding sites. Interference competition has also been found to be important in other studies where food resources were concentrated in space, e.g., in red deer (Appleby, 1980, Clutton-Brock et al., 1982, Hall, 1983), woodland caribou (Barrette and Vandal, 1986) feral horses (Duncan, 1992) and cattle (Morita et al., 1989). Thouless (1990) argued that exploitative competition was the predominant competitive interaction among red deer hinds, even though he did observe a significant effect of dominance on bite rate. This may be true in the intensively grazed, homogeneous, vegetation he studied if enough area was available to the animals to space out. However, his data did not allow the assessment of the average intake rate of subordinates relative to dominants. Furthermore, his results do indicate that interference competition, whether by active displacement or by passive avoidance, should be important when the vegetation is heterogeneous or when the spacing out of individuals becomes limited by shortage of space or by other (behavioral) factors. We therefore conclude that many circumstances occur where dominant animals do have an advantage over subordinate individuals in obtaining food.

Our findings seem contradictory when examining them in the light of a predominance of exploitative or interference competition. The absence of an effect of proximity on grazing behavior and food intake points to the absence of interference competition, whereas the effect of dominance on food intake points its presence. Exploitative competition is expected to occur whenever individuals encounter patches that were partially depleted by conspecific, because of the effect of patch depression on intake rate (Laca et al., 1994a, WallisDeVries et al., 1998). We argue here that both types of competition are important. The following mechanism can be surmised. Direct interference by

dominant animals leads to the displacement of subordinates from preferred patches. Subsequently, subordinates either avoid a dominant individual by keeping their distance or they are subject to repeated harassment. The time lost by interference is minimal and appears unaffected by the position in the hierarchy. However, the consequences for food intake rate appear significant. In small herds of grazing ungulates, interference competition is likely to be the most important form of intraspecific competition as resource depletion is of small magnitude. In larger herds, however, both types of intraspecific competition can be expected to occur. Subordinates will be continually displaced by dominants until they reach a position in the herd where they will be surrounded by individuals of equal rank. So, we should expect the lowest ranking animals at the rear of the herd and the highest ranking individuals in the front. The subordinate animals in the rear, once they have resigned to their position in the herd, will suffer most severely from exploitative competition. Thus, interference competition should determine herd structure and exploitative competition then determines the relative rate of food intake. This combination of interference and exploitative competition seems to occur in African buffalo, as described by Prins (1996), although he did not discuss it in these terms. In the large buffalo herd near Lake Manyara, Tanzania, a clear structure could be recognized with animals of high condition score in front and animals of low condition score in the rear. Condition score not only shows the relative performance of an individual but also reflects its dominance status (Prins, 1996). Interestingly, animals in the sub-front had the highest condition score and the highest number of bites per step, suggesting a high dominance status and a superior food intake rate. The frontmost animals had a slightly inferior condition status and less number of bites per step. These animals had to bear the continual harassment of the dominants behind them but they had the benefit from the access to fresh resources. The animals in the rear not only had the lowest condition status but also the lowest number of bites per step. It was hypothesized by Sinclair (1977) and Prins (1996) that the splitting-up of a herd, which typically involved the rear fraction, is related to changes in food availability and distribution. The fusion of a herd, then, would serve as a means of "staying in contact with the information from the successful members of the herd" Prins (1996). Reduction of predation risk has often been advanced as an additional explanation of group formation (Geist,

1974; Jarman, 1974). Thus, as hypothesized by Caraco (1979), the cohesion of animal groups indeed can be viewed as a function of the optimization of costs and benefits between feeding, aggression and predator detection.

In conclusion, it appears that interference competition plays a larger role in grazing ungulates than previously thought. The classic dichotomy emphasizing exploitative competition as the dominant process in the acquisition of nutrients and interference competition as the dominant process in the acquisition of mates (Clutton-Brock, 1989) may be too much of a simplification. In foraging, interference competition can be seen as the interaction that precedes the exploitative competition in herds.

3.6.2 Social effects of experience on finding food and social transmission of information in cattle

3.6.2.1 Introduction

Grazing pattern is affected by the degree of familiarity livestock have with a particular paddock. When familiarity is low, uniform grazing patterns may be expected. On the other hand, when livestock familiarity is high, uneven grazing patterns may occur. Proper grazing distribution within each grazing unit requires the scattering of grazing animals in an area to obtain even use of forages (Holechek et al., 1995). The distribution of grazing animals is affected by various complex factors. Some factors are site related; e.g. topography, location of water points; and others are animal related. Among the latter factors, grazing behavior is considered to be important. The grazing pattern may result from decisions made by animals at different spatial and temporal scales (Bailey et al., 1996). When preferred plant communities are grazed more than others, the impact can result in declining rangeland productivity at all spatial scales. Hence, unwanted and unpalatable forage species may invade the more heavily grazed areas. The impact of defoliation on palatable species can consequently be detrimental.

Past experience appears to play a prominent role in the foraging sites chosen by grazing animals (Valentine, 1990) in order to achieve even grazing distribution. Improved livestock distribution on rangelands could be accomplished if range managers succeeded in attracting them away from heavily grazed areas. In a herd of livestock, some may be more experienced

in their familiarity with a grazing site thus affecting the social learning of others in the same herd. Heyes (1994) discussed the different categories of social learning. The mixing of experienced animals with naive ones may affect the herd's grazing pattern and therefore a social interaction develops.

Social learning was defined as a behavior learned by observing conspecifics (Galef, 1988). The behavior of other individual animals can be affected by the presence and behavior of individuals of the same species (Nicol, 1995). Many large herbivores rely on their herd structure to adapt to many of their environmental conditions and to meet their day to day needs. For example, the reluctance of animals to try novel foods has been shown to be affected by social facilitation (Thorhallsdottir et al., 1990), and post-ingestive consequences (Provenza et al., 1993). In addition to novel foods, animals can learn where to forage from social interaction (Scott et al., 1995). Lynch et al. (1992) stated that social interactions affected grazing distribution. These results are in general agreement with observations of goats (Biquand and Biquand-Guyot, 1992), and sheep (Hunter and Milner, 1963).

In the present study, we tested the effects of social interaction using an 8 row by 8 column grid of plastic containers. In traditional mazes, animals return to the same decision area before making a choice for a particular arm. All arms have the same chance of being chosen at any given time. In real environments, animals search for food in 2 or 3 dimensions and do not need to return to any decision areas. The protocol we used, is similar to the one used by Edwards et al. (1997) and Laca (1995). It is more focused on using a more realistic testing area for long-term spatial memory. Steers would enter the paddock where the plastic containers were located and try to find a specific set of trays that contain feed.

In the current study, we looked into the effects of experienced animals on the distribution pattern of grazing by naive ones. We wanted to test if naive animals increase their searching efficiency when grazing with an experienced one. Naive animals may distribute themselves more evenly because their expectations of preferred areas are not as well developed as those of experienced animals (Bailey et al., 1996). In this study, we had three objectives. First, to determine if animals recently introduced to a grazing area tend to learn the grazing distribution of resident experienced

animals. Second, to determine if the grazing distribution tends to be more uniform as animals have less experience with the area. Third, to determine if the initial distribution of grazing, affects the role of social transmission.

3.6.2.2 Materials and Methods

3.6.2.2.1 Experimental Arena

The experimental arena was established in an Old-World bluestems (*Bothriochloa* spp.) pasture. Three 55 by 55 meter-paddocks were used. Each paddock consisted of an 8 row by 8 column grid of plastic containers. The total number of containers available for animal to choose from was 192. Plastic containers were equally placed at 5 meters from each other. Depending on the treatment being tested, food was placed around some of the trays. Trays with food were referred to as loaded trays. A set of four loaded trays were arranged in adjacent trays (2 by 2). The experiment was conducted from July 20 to October 29, 1996.

3.6.2.2.2 Animals

Eight steers were used to conduct the experiment. The average weight was 550 kg. When not tested, steers were grazing an Old-World bluestem dominated pasture. Water was always available, and animals were fed 12.5 kg of feed every other day. The experimental protocol and animal handling were approved by the Texas Tech University Animal Care and Use Committee.

3.6.2.2.3 Treatments

Three treatments were tested in this experiment. First, we created a clumped food distribution treatment (CDT) of 20 out of 192 trays. In this treatment an experienced animal and a naive animal were searching for loaded trays at the same time. An experienced animal is an animal that was familiar with the combination of loaded trays through training. A naive animal is an animal that did not have any prior familiarity with the location of the loaded trays. These trays were placed in sets of clumped trays. Second, a scattered distribution treatment (SDT) where an experienced animal and a naive animal were searching for loaded trays at the same time. The loaded trays were placed all over the pasture covering most of the area. Third, a control treatment (CT) where a naive animal was searching for loaded trays which were placed the same way as CDT. In order to assess the impact of

experienced animals on the searching pattern of naive animals, CDT and CT were compared. In order to test if the initial distribution of food mattered, CDT and SDT were compared. The combinations of loaded trays for all three treatments were kept the same during the whole experiment.

3.6.2.2.4 Training

Before training, twenty trays were chosen for CDT and SDT around which food pellets were placed. Pellets were distributed in a 1 meter circle around a tray. In other words, trays were used as centers for patches of pellets. This would minimize the impact of competition when more than one steer were feeding around the same tray. The experienced animals were trained to locate the combination of 20 trays (clumped for CDT and dispersed for SDT). They were trained until they established a very distinct search pattern. On average each of the experienced animals was trained for 8 days, three to four times daily. Each loaded tray contained about 100 grams of pelleted food. For CT the animals did not have any previous experience. They were introduced to the combinations of loaded trays (same combination as that of CDT) for the first time during testing.

3.6.2.2.5 Testing

The combinations of trays initially introduced during training were referred to as training trays. Additionally, 12 trays were added to each treatment during testing. For CDT and CT, we added three sets of clumped trays and for SDT we added 12 trays located all over the experimental arena. The addition of 12 trays would give the naive animals the chance to choose trays different from the ones available to the experienced animals during training. Two animals were observed until the experienced one (for both CDT and SDT) found 8 loaded trays. The loaded trays found had to be among the training trays. When the experienced animals (within each treatment) found 8 of the training trays, the session was terminated. The session for CT was terminated when a steer found 8 of the loaded trays. Animals in each treatment were tested once every day for 7 consecutive days.

3.6.2.2.6 Measured Variables

All training and testing sessions were entirely observed. A map was used to record data. The map included the locations of loaded trays and trays that did not contain food. The path followed by each steer, trays visited, time

spent eating in each loaded tray, and total time spent in each session were recorded.

3.6.2.2.7 Calculated Variables

Number of locations visited were referred to as NL, found locations that had feed were referred to as FL and total visits were referred to as TV. Two ratios were calculated to test for the presence of working and reference memory as possible searching strategies. The presence of working memory was tested using NL divided by TV (NL/TV), and the presence of reference memory was tested using FL divided by NL (FL/NL). A Z test was performed to examine if locating loaded trays was either at random or based on behavioral mechanisms (Tille et al., 1996).

3.6.2.2.8 Experimental Design and Analysis

A completely randomized design with a split plot was used to analyze the data. Treatments were used as main plot and days as sub-plots. When data were not normally distributed and/or their variances were not homogeneous, transformations were done. A Least Significant Difference procedure was used to compare treatment means.

3.6.2.3 Results and Discussion

In this experiment, we assessed the effect of social models in finding food from four different perspectives. These approaches will be discussed one by one for each variable. First, we compared the performance of steers in CT in relation to steers in CDT. This would permit evaluation of having a social model to affect the searching efficiency and pattern. Second, we compared the performance of steers in CDT to steers in SDT. This would allow examination of the initial distribution of loaded trays on the searching efficiency and pattern. Third, we compared the average performance of each steer against the performance expected by random search. Standardized values, on the basis of their means and variances, were used to compare treatments. The standardized ratio NL/TV (Z1) was calculated to test if NL/TV was better than expected by chance. The standardized ratio FL/NL (Z2) was calculated to test if FL/NL was better than expected by chance. Fourth, we used covariance analysis to investigate if rate of learning was comparable. In the following paragraphs, each variable is going to be discussed separately.

The variable TV was transformed to its base 10 logarithm (LTV). There was a treatment effect, a day effect, and an interaction day and treatment effect $P < 0.05$ (Table 31). A critical difference of 0.182 was found and used to detect any significant differences between treatments, as appropriate, within the same day or from one day to another. We observed a higher LTV for CT than for CDT on days 1, 2, 4, and 6 ($P < 0.05$). Overall, this suggested that animals in the CT visited more locations than those in CDT. Consequently, animals without the presence of social models develop a more uniform search pattern. When comparing CDT to SDT, we observed that SDT had higher LTV on the first 4 days of the experiment. This suggested that the initial distribution mattered early during the social interaction period. When preferred food is uniformly distributed, animals tend to have a more uniform grazing pattern.

The variable NL was transformed to its base 10 logarithm (LNL). There was a treatment effect ($P < 0.05$), a day effect ($P < 0.05$), and an interaction between day and treatment $P < 0.05$ (Table 31). A critical difference of 0.179 was found and used to detect any significant differences between the treatments within each testing day and from one day to another. When comparing CDT and CT, we found that the latter had higher LNL continuously starting on day 4. This suggested that social models affected the searching pattern of naive animals. However, LNL was not different between CDT and SDT the later days of the experiment. This suggested that the initial distribution did not affect the spatial pattern of searching late during the social interaction.

The variable FL was transformed to its base 10 Logarithm (LFL). There was an interaction between treatment and day $P < 0.05$ (Table 31). A critical difference of 0.156 was found and used to detect any significant differences between the treatments within the same day or from one day to another. The variable LFL was higher for CT than for CDT in the first 3 days of the experiment. The covariance analysis showed that the rate of learning was higher when comparing CDT to CT ($P < 0.05$). Steers in CDT started at a low LFL level and then increased over time. However, as days passed, finding food locations did not change for CT and SDT.

The ratio NL/TV was transformed to its square root (SNLTV). We did not detect any significant effect of treatment, day, or an interaction between day

and treatment $P>0.05$ (Table 31). The regression analysis was not significant for all three treatments ($P>0.05$). Steers did not learn to improve their working memory over time.

Table 31. Performance of steers in all treatments over the 7-day testing period.

Variable	Treatment	DAYS						
		1	2	3	4	5	6	7
LTV	CT	1.45*	1.75*	1.35	1.40*	1.42	1.39*	1.29
	CDT	1.16	1.36	1.25	1.13	1.26	1.20	1.11
	SDT	1.47*	1.61*	1.61A	1.34*	1.32	1.06	1.07
LNL	CT	1.44*	1.71*	1.34	1.39*	1.42*	1.37*	1.25*
	CDT	1.15	1.32	1.22	1.11	1.21	1.17	1.06
	SDT	1.43*	1.58*	1.59*	1.31*	1.32	1.06	1.07
LFL	CT	0.83*	0.88*	0.83*	0.83	0.86	0.88	0.83
	CDT	0.46	0.67	0.66	0.73	0.77	0.95	0.89
	SDT	0.60*	0.92*	0.84*	0.85	0.89	0.71*	0.80
SNLTV	CT	0.99	0.95	0.99	0.99	0.99*	0.97	0.96
	CDT	0.98	0.95	0.96	0.97	0.94	0.96	0.94
	SDT	0.95	0.98	0.98	0.97	0.96	0.97	0.98*
FLNL	CT	0.27	0.16	0.33	0.30*	0.29*	0.35*	0.42*
	CDT	0.25	0.25	0.30	0.45	0.40	0.66	0.77
	SDT	0.16	0.22	0.18*	0.37	0.40	0.51*	0.59*
Z1	CT	1.14	1.13	0.91	0.72	1.05	1.58	1.45
	CDT	1.14	1.07	1.05	1.07	1.63	1.40	2.01
	SDT	1.74	1.30	1.45	0.69	1.17	1.50	0.85
Z2	CT	2.76*	1.26	3.57	3.27	3.31	3.95	4.25
	CDT	1.45	2.21	2.61	4.16	3.88	6.93	7.08
	SDT	1.00	2.75	1.83	4.01	4.50*	4.38*	5.31*

* Values are significantly different from CDT within the same day at $P<0.05$.

LTV: Logarithm base of Total Visits; LNL: Logarithm base 10 of New Locations; LFL: Logarithm base 10 of Found Locations; SNLTV: Square Root of ratio New Locations per Total Visits; FLNL: Ratio of Found Locations per New Locations; Z1: a Z test for randomness of ratio of New Locations per Total Locations; Z2: a Z test for randomness of ratio Found Locations per New Locations.

CT: Control Treatment (steers did not have any prior experience as where food was located; CDT: Clumped Distribution Treatment (naive animals with the presence of an experienced, and food was in clumps of four trays); SDT: Scattered Distribution Treatment (naive animals with the presence of an experience, and food was scattered all over the paddock).

The variable FLNL had a significant interaction treatment by day $P<0.05$ (Table 31; Figure 39). A critical difference of 0.11 was found. Starting on day 4, CDT had higher FLNL than CT. This suggested that social models

affected the searching efficiency of naive animals. When comparing CDT and SDT, we found a significant difference starting on day 6 suggesting that the initial distribution of food was a decisive factor. A significant covariance analysis was detected ($P < 0.05$). Steers in CDT learned at a faster rate than those a CT. The learning rate for CDT was higher than SDT. Both, presence of model and initial distribution were substantial.

Calculated Z1 was not affected by the interaction treatment by day $P > 0.05$ (Table 31). It is important to note that Z1 was not greater than 1.64 except for SDT on day 1. This suggested that visiting recently located trays was done at random. The covariance analysis was not significant for all three treatments ($P > 0.05$). Steers in all treatments did not learn to avoid recently visited locations.

Calculated Z2 was affected by the interaction treatment by day $P < 0.05$ (Table 31; Figure 40). A critical difference of 1.23 was found. CDT had a higher Z2 starting on day 6. Social models affected the efficiency of departure from randomness in searching for food. CDT had also a higher Z2 than SDT starting on day 5 of the experiment. The initial distribution affected the efficiency of departure from randomness in searching for food. All treatments starting on day 3, had an average Z2 greater than the 1.64 limit. This showed that steers were locating loaded trays better than expected by chance. Steers in CDT learned to locate food better than by chance and improved over time ($P < 0.05$).

The presence of social models has been proven to be a major factor in feeding efficiency of animals (Provenza and Balph, 1988; Galef et al., 1984; Lynch et al., 1992; Scott et al., 1995). Galef and Whiskin (1994) reported the importance of conspecifics in learning food preferences in rats. Observational learning has been shown to play an important role in feeding behavior of animals (Chapple et al., 1987). Rats preferred food that a social model (demonstrator) ate (Galef, 1993). In this experiment, the results found showed that having a model around helped improve the efficiency of locating food. Previous work by Galef et al. (1984) proved the importance of models in feeding behavior. There was a communication of information from experienced to naive animals. Naive animals visited fewer locations when a model was present. Number of found locations visited by naive animals was lower when models were present. Drea and Wallen (1995) reported that

Figure 39: The ratio of found locations per new location visited (FLNL) over the testing period for control treatment (CT), clumped distribution treatment (CDT), and scattered distribution treatment (SDT). A star above a bar indicates difference from CDT. Vertical lines indicate standard error.

Figure 40: Z value for the ratio of found locations per new location visited (Z2) over the testing period for control treatment (CT), clumped distribution treatment (CDT), and scattered distribution treatment (SDT). Random search can be expected if Z2 drops below 1.64 (solid line). A star above a bar indicates difference from CDT. Vertical lines indicate standard error.

monkeys visited more locations to areas with reward over time. Manual searching of these monkeys was higher as experience increased. The results reported by Drea and Wallen (1995) agree with what we found. Animals with models were more efficient and therefore concentrated their search. Naive rats were shown to prefer food through observing a model (Galef, 1983; Galef and Wigmore, 1983). Steers in all 3 treatments did better than expected by random in most testing days. This supports the findings that livestock use some searching mechanisms to efficiently graze. Edwards et al. (1994) found that sheep (*Ovis aries*) performed better than expected by chance, when they tested intake rate. Galef (1980) reported the importance of social models especially when rats were young.

3.6.2.3.1 Conclusion and Management Implications

Our hypothesis was to test the importance of social models on directing search. Social models as well as food distribution affected the transmission of social information on searching pattern. The experience that a free-grazing animal develops may affect its grazing efficiency. Steers with experience established much shorter and directed search path interacting with a small proportion of the pasture (Laca, 1995). In order to limit developing familiarity with an area, animals may be supplemented at different times of the day and different places within a field. Supplementation in unpredictable locations may prevent animals from developing high expectations in specific places (Laca, 1995). Most of the available area was searched when animals did not use spatial memory (Laca, 1995). Moreover, changing the time as well as the place of supplementation may promote covering extended grazing ground. In addition to grazing methods and supplementation, mixing animals may be used to enhance grazing distribution.

Mixing experienced and naive animals in a herd may help the efficiency of grazing when vegetation is scarce and/or when drought occurs. This would result in limiting the searching pattern and increasing the grazing efficiency of the naive animals. Less energy would be used looking for food. On the other hand, we may prevent mixing experienced and inexperienced animals in a given grazing unit when forage production is good. The inexperienced animals may widen their searching areas which may lead to more even grazing. Furthermore, the level of patchiness of a plant community may play

a role in the effectiveness of social transmission of information. The distribution of food has shown to be important in shaping the search pattern even when social models are present. When preferred plants are in distinct patches, experience of one animal may be transmitted to another in a herd.

3.7 Acoustical Measurement of Intake & Behaviour of Grazing Cattle

3.7.1 Introduction

The ability to accurately and easily measure and predict bite size and intake rate of ruminants at pasture is a key to many management decisions in grazing systems. Existing methods usually rely on oesophageally fistulated animals (e.g. Forbes 1988), but these require intensive care and may not always be available. Hand-plucking is feasible but necessitates calibration between the animals and the operator (WallisDeVries 1995). Techniques monitoring behavioural characteristics using jaw and mercury switches (Stobbs & Cowper 1972), accelerometers and displacement transducers (Chambers et al. 1981), thermal conductivity cannulae (Forwood & Hulse 1987), gnathometers (Penning et al. 1991b), jaw balloons and pressure transducers (Derrick et al. 1993), and systems developed for stall-fed animals (Luginbuhl et al. 1987, Beauchemin et al. 1989, Dehareng & Godeau 1991, Beauchemin & Iwaasa 1993, Girard & Labont 1993) have proved successful in describing grazing behaviour including bite rate and grazing time. However these methods are somewhat invasive and may have unpredictable effects on ingestive behaviour. Some of these methods use equipment that is not as robust as might be desired under field conditions.

Laca et al. (1994b) found that biting and chewing actions could be identified more easily and counted more accurately by inspecting sound records than by direct observation, because of the existence of compound jaw movements that simultaneously involve biting and chewing. The sound record contains a wealth of information that can be gathered without interfering with grazing behavior, and that may lend itself to automated analysis. An important advantage of the acoustic approach is that it records true mastication jaw movements and not manipulative jaw movements. Some, if not all, of the other techniques listed above cannot make this distinction (e.g. Penning et al. 1991b). Sound records can be collected using

radio transmission to a remote recording device or direct recording to a device carried on the animal (Matsui & Okubo 1989, 1990, 1991). In this project, many grazing trials used a microphone and wireless transmitter on the animal, and a receiver attached to the video camera. The receiver is connected to the camera such that the audio signal it receives overrides the built-in microphone of the camera [See Photo #7]. Positioning of the microphone on the head of the animal is important to sound quality. Tests we conducted in the previous BARD project showed that the best position from the point of view of sound quality (and the least invasive position) is on the forehead, with the microphone head pointing inward against the skin [See Photo #8]. The quality of the sound obtained using this microphone position appears to derive from the head of the animal acting as a sound box. For basic intake studies at the bite level we regard the use of such an acoustic monitor as an indispensable component of the research protocol. Of course, the wealth of data that can be obtained from the acoustic record needs to be analyzed, and this is an extremely laborious task if conducted manually. Thus even for the purposes of basic intake studies it would be a great assistance if the acoustic analysis could be automated to some extent. Beyond the context of experimentation, acoustic analysis may have potential as a management tool - again assuming that all aspects can be automated. In acoustic study 1, we report on a preliminary examination of the acoustic signal in identifying types of jaw movement.

The problem remains, however, how to translate behavioural data into accurate estimates of intake. The HCS technique developed by Black & Kenney (1984) and Laca et al. (1992a) enables this for artificial swards but not for outdoor pastures. Wilmshurst et al. (1995) used cut sods that were grazed in stall trials to estimate bite size in relation to sward standing crop. In acoustic study 2, we adopt the sod grazing technique in combination with sound recording to examine the feasibility of using acoustics to estimate forage intake of cattle. We test the hypotheses that chews and bites can be accurately discriminated on the basis of their acoustic features, and that intake and bite weight can be predicted by the energy and intensity of the sound signal.

3.7.2 Acoustic study 1

Over the years of this project we gradually accumulated a video and sound library of grazing observations under relatively controlled conditions. In contrast to the recordings of the single- and multi-patch grazing experiments, these recordings were obtained under “free grazing” conditions in which the animal was led to a fresh and relatively uniform area of first-growth vegetation and allowed to graze freely for approximately 10 minutes. Care was taken to include the forelegs in the video image in order to analyze feeding station behaviour on continuous swards.

In order to examine the acoustic record from these grazing sessions in more detail, we extracted 5-minute sessions of uninterrupted grazing for nine different heifers. These were free grazing sessions recorded on the same day on a young vegetative sward of oats of average height between 25 and 30 cm.

The grazing sessions were “sequenced” manually. For this purpose, suitable software was used to capture the 3-minute video segments on computer file. We used Avid Videoshop v. 3.0.2 on a Power Macintosh 7600/132. From these files we generated sound files which could in turn be read by our acoustic analysis software - Canary 1.2 (Charif et al. 1995). This program enables small segments to be easily marked and repeatedly played back for sound identification purposes. In this way, we manually sequenced the audible jaw movements and classified them as pure bites, pure chews and combination chew-bites.

The first striking observation, which we confirmed by careful viewing of the video record, was the complete absence of manipulative jaw movements. These jaw movements do not generate an audio signal, but nevertheless constitute a cycle of opening and closing of the jaws, which has a time requirement in the order of 1 second. Yet the audio signal showed no such “gaps” in the record. We need to cross-check this finding with results on HCS from our previous BARD project and confirm that below a certain height and bulk density of sward the animal does not employ pure manipulative jaw movements.

The second noteworthy observation was the high degree of regularity in the rhythm of jaw movements. A sample is shown in Figure 41. Furthermore, we found that the average rate of jaw movement (all types) for the 3-minute sessions for 8 of the 9 heifers examined lay in the narrow range of 75-82 jaw

Photo #7: Components of the video and acoustic monitoring equipment used to record the grazing trials: video camera with mounted character generator; audio receiver; ear-phones; neck-strap with audio transmitter; microphone housing and straps.

Photo #8: Placement of the microphone on head of the animal during grazing trials.

Figure 41. Progressive magnification of the acoustic waveform (oscillogram showing amplitude versus time) generated by a heifer heifer. Approximate period displayed is shown at left. Magnification is from time=0 in all cases.

movements per minute. The last heifer had a slower rate of 67 jaw movements per minute.

There were large differences between heifers in the ease with which chews and chew-bites could be distinguished. For some animals, the chew-bite action is so compressed in time that it is very hard to make a definitive classification. In other animals, the closing of the jaws is slower and there is a clear separation of the two sounds. This has implications for providing a classified sound library for automatic recognition algorithms.

Despite the similarities between animals in the rate of jaw movement, there were large differences between animals in the allocation of jaw movements between bites, chews and chew-bites. Table 32 shows the results for 8 of the 9 sequences analyzed. For the excluded animal, we were unable to make a clear distinction between bites and chew-bites in 40% of jaw movements.

Table 32. Fraction allocation (%) of jaw movements between bites, chews and chew-bites for eight heifers, based on 5-minute sequences of uninterrupted grazing on an oat sward of 25-30 cm height.

Heifer	Bites	Chews	Chew-bites
1887	6	38	53
1890	36	51	12
1892*	46	37	10
1894	34	38	28
1889	33	49	18
1895	25	39	35
1899	5	25	70
1891	30	37	33
Average	27	39	32

* 7% unclassified

If we assume the effectiveness of a chew-bite to be equivalent to separate chew and bite jaw movements, then we can add the number of chew-bites to total chews and the same value to total bites to obtain the overall number of bite and chew actions. The resulting values are far less variable than those given in the above table. The overall average allocation of actions is 56% chew and 44% bite.

A number of clearly identified chew and bite sounds were subsequently subjected to a more rigorous sound analysis. The spectral profiles of these

different jaw movements proved to be less clearly distinguishable than were the auditory signals. Consequently, the pattern recognition phase of the study has not been completed and we will continue this line of investigation after formal termination of the project.

3.7.3 Acoustic study 2

3.7.3.1 Experimental procedure

Sods were cut from an irrigated *Setaria lutescens*-grassland, offered to 4 Hereford crossbred steers, and bite weight was determined, as described in detail in section 3.3.4.2 above.

Each grazing session was videotaped. The sounds of biting and chewing were recorded on videotape by a wireless microphone taped to the animal's forehead; the transmitter was attached to a halter. Images and sound records were later used to identify bites and chews in a time sequence using a simple event recording program.

Twenty four sods of 6 different types were tested: 3 different heights of short sods and three different heights of tall sods (see Experiment 1 in Table 14). One sod type was examined per day, with a random order of sod types over days and of animals within days.

3.7.3.2 Data analysis

In order to characterize the acoustics of bites and chews, the sound tracks from the video recorder were digitized for the first 10-bite series and analyzed using Canary 1.2 software (Charif et al. 1995) on a Macintosh PowerBook 1400c. All analyses were based on the original sound records without any filtering. For each bite and each chew the following measurements were obtained on the original signal: time and duration (s), energy flux density (J/m^2), average intensity (W/m^2), peak pressure (Pascal). A spectrum was obtained for each bite and chew and subdivided into 8 bands of 1 kHz each between 0 and 8 kHz. For each frequency band we determined peak frequency (Hz), peak intensity (dB) and average intensity (dB). Discriminant analysis was used to distinguish between bites and chews, and sod types. A quadratic discriminant function was used because of the lack of homogeneity of covariance matrices. A stepwise regression procedure was used to determine the best set of variable to predict intake.

For each variable an ANOVA was used to determine effects of bite weight, sod type and animals.

3.7.3.3 Results

A total of 220 bites and 734 chews were characterized acoustically. When the peak pressure and average intensity in each frequency band, signal duration, energy flux density, average intensity and peak pressure of the signal were used, a cross-validation analysis resulted in 25 bites and 35 chews being wrongly classified. Total error rate was 6.3%, assuming that prior probabilities are equal to the proportions of bites and chews in the sample. The most evident difference between bites and chews was the greater output between 4 and 8 kHz for bites. When we only used the peak pressures and average intensities for each of the 8 bands, the cross-validation error rate increased to 7.0%. When only the average intensities for each of the 8 bands were used as predictor variables, 37 bites and 37 chews were wrongly classified, for a total error rate of 7.8%.

Significant interactions between sod type (tall vs. short) and behavior (chew vs. bite) on sound characteristics indicate that the effects of sward type on sound differ between bites and chews. The energy flux density (EFD) of bite sounds increased from short to tall swards ($P=0.03$) but it did not change in chews ($P=0.10$). The average sound intensity in the 3-4 and 4-5 kHz was greater in bites from short swards than those from tall ones, whereas the converse was true for chews ($P<0.05$).

Intake obtained in 10 bites was predicted well ($R^2=0.87$) by a linear combination of energy flux density in the chewing sounds and average intensity of biting sounds in the 1-2 kHz frequency band. An outlier was eliminated from the analysis of intake because its Mahalanobis distance exceeded the critical value of 2.6 due to an error in setting the recording volume. Although a large proportion of the variation in bite weight was associated with sod type, the interaction between sod type and acoustical predictors was not significant ($P>0.12$), indicating that a single plane was adequate to predict intake in both sward types. Intake was also explained by the total energy flux density of biting and chewing sounds ($R^2=0.81$) and by sward structure ($R^2=0.81$). Bite weight (W , g) was a function of sward height and bulk density, without an interaction between these two sward characteristics ($R^2=0.84$):

$$W = -1.137(\pm 0.796) + 0.072(\pm 0.007) H + 0.739(\pm 0.345) D$$

where H is sward height (cm) and D is sward bulk density (kg/m³).

3.7.3.4 Discussion

The measurement and prediction of intake and bite weight of free grazing animals has been identified as one of the major obstacles hindering the advance of grazing sciences and management. Instantaneous, short-term measurements are inaccurate and tend to ignore the role of digestive processes on grazing behaviour. Long-term methods, most based on markers, are extremely time consuming and require complicated laboratory procedures. In addition, marker techniques are not sensitive enough to detect fast changes that can take place in intensive grazing systems. None of the traditional methods allows an estimation of the spatial location where animals obtain the forage, an important parameter for the study of environmental impacts of grazing through defoliation. This study indicates that acoustical monitoring techniques have the potential to overcome at least some of the difficulties in estimating grazing intake.

This and previous studies have shown that bite weight is predictable on the basis of sward structure at the location of the bite. Whereas this may be a useful basis to estimate bite weight or intake in relatively homogeneous pastures, it does not work for heterogeneous pastures and rangelands, where there is a significant difference between the average forage characteristics and the sward characteristics of areas selected (Laca and Demment 1996). Acoustical monitoring has potential for overcoming the difficulty posed by sward heterogeneity and animal selectivity, because it provides information about each bite after it has been selected. As indicated by the regression equations, chewing sounds seem to carry more information about intake rate than the sound made by the severing of the forage during the biting action. This is counter to our initial expectations but makes sense on the basis of previous descriptions of the ingestion process (Laca et al. 1994b). The mouth seems to act as a compartment with an inflow determined by the rate at which the forager can find and sever bites of a given size, while the outflow is given by the maximum capacity to chew and swallow. When the inflow is less than the maximum outflow rate, the amount of food in the mouth and comminuted by each chew is directly proportional to bite weight and intake rate.

New GPS-based technologies allow precise determination of the location of large herbivores with high frequencies. The coupling of an acoustical record of grazing behavior with the record of spatial locations offers the potential to determine amount of forage ingested from different areas within paddocks. This information can significantly improve our understanding of the basis for habitat selection and distribution of impact by livestock, particularly in sensitive areas such as riparian zones.

Realization of the potential of acoustical monitoring of grazing intake will require further development and solutions to some technical and practical problems. First, the generality of the prediction equations will have to be tested across a wide variety of forages, sward structures, phenological states and animals. The present study indicates that sward structure changes are implicitly taken into account through changes in the energy and spectrum of chewing and biting sounds, but further testing is necessary. Coarser, more fibrous forages usually require more chewing per unit mass than more succulent ones, and probably produce sounds that differ in power and spectrum. It is likely that animals that differ in the size and structure of their teeth, as well as in size and shape of the head, will produce different sounds even when ingesting the same forages at the same rates. The shape and size of the skull and its parts are probably very important in determining ingestive sound characteristics because they act as a filter for the sound, particularly for chewing sounds. Because the power and energy of the sound are important predictors of intake and bite weight, in order to extrapolate prediction equations it will be necessary to establish a sound standard to set the input and output levels of the equipment.

Systems for the automatic processing of sound signals will have to be implemented, particularly when trying to determine intake over periods of hours or days. In the present study signals were processed interactively with the Canary software package. Decoding of each record of 10 bites and the associated chews is nevertheless a time-consuming process.

The recording system should be improved to allow precise measurements in environments where sounds are not controlled. The use of a single microphone results in a recording with a variety of sounds unrelated to the chewing and biting of forage that hinder interpretation. Use of two or three microphones can improve the quality of the data and facilitate discrimination

between chews and bites. One microphone securely attached to a shaved patch on the forehead of the animal, as in the present study, will record chews, bites and noise. A second microphone near the head but not in direct contact with the head will record mostly bites and noise, and its signal can be subtracted from the previous one to obtain a "clean" record of chews. A third microphone could be installed away from the head on the back of the animal to record mostly noise to be subtracted from either one of the previous two signals.

3.8 Acknowledgements

Numerous individuals participated actively in conducting the long series of experiments reported above. They included research scientists, post-doctorate students, Ph.D. and M.Sc. students, laboratory technicians, a large team of field assistants and the staff of the various experimental stations at which the studies were conducted. Their participation was essential to the success of this project and we thank them for the tremendous effort that was needed in the conduct of these demanding grazing trials. We specifically thank the following:

In the US:

Kevin Alvine
Ling-ru Chu
Jo A. Dankosky
Ganga Deo
Tim F. Ginnett
L. Kirby
M. Klapp
José M. Kok
Dan Komenek
Taoufik Ksiksi
M. Lizarzaburu
Dick McGraugh
Cheryl Meehan
Isaac M. Ortega
C. Parker
S. Pettigrew
Clara Quintero
Pablo Soca
C. Veith
Michiel F. WallisDeVries

In Israel:

Avner Abet
Hagit Baram
Dani Barkai
Hamutal Cohen
Tzadok Cohen
Miki Gingold
Yossef Greenspan
Yael Hadar
Amotz Hezroni
Ilana Kastanela
Ron Methorst
Yossi Moshe
Uzzi Mualem
Daniel Orenstein
Nir Ravid
A. Tzur
Nurit Yaakov-Zaks
Tomer Zada

3.9 References

- Allden, W.G. & Whittaker, I.A.McD. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Aust. J. Agric. Res.*, 21: 755-766.
- Appleby, M.C. 1980. Social rank and food access in red deer stags. *Behaviour* 74:294-309.
- Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.*, 49:386-400.
- Bailey, D.W., Rittenhouse, L.R., Hart, R.H. & Richards, R.W. 1987. Spatial memory of heifers in Radial- and Paraller-arm mazes. *Proc. West. Sec. Amer. Soc. Anim. Sci.*, 38:7-10.
- Bailey, D.W., Rittenhouse, L.R., Hart, R.H. & Richards, R.W. 1989. Characteristics of spatial memory in cattle. *Appl. Anim. Behav. Sci.*, 23:331-341.
- Barrette, C. & Vandal, D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97:118-146.
- Beatty, W.M. & Shavalia, D.A. 1980. Spatial memory in rats: time course of working memory and effects of anesthetics. *Behav. Neural Biol.*, 28:454-462.
- Beauchemin, K.A. & Iwaasa, A.D. 1993. Eating and rumination activities of cattle fed alfalfa or orchardgrass harvested at two stages of maturity. *Canadian J. Anim. Sci.* 73:79-88.
- Beauchemin, K.A., Zelin, S., Genner, D. & Buchanan-Smith, J.G. 1989. An automatic system for quantification of eating and ruminating activities of dairy cattle housed in stalls. *J. Dairy Sci.* 72:2746-2759.
- Begon, M. & Mortimer, M. 1986. *Population Ecology. A unified study of animals and plants.* Blackwell, Oxford.
- Bell, W.J. 1992. *Searching behaviour: the behavioural ecology of finding resources.* Chapman and Hall, London, UK.
- Bergstrom, M., Lundberg, P. & Danell, K. 1990. Partial prey consumption by browsers: trees as patches. *Journal of Animal Ecology* 59, 287-300.
- Biquand, S. & Biquand-Guyot V. 1992. The influence of peers, lineage and environment on food selection of the criollo goat (*Capra hircus*). *Appl. Anim. Behav. Sci.*, 34:231-245.
- Black, J.L. & Kenney, P.A. 1984. Factors affecting diet selection by sheep. II Height and density of pasture. *Aust J Agric Res* 35, 565-578
- Brown, B. J. & Allen, T. F. H. 1989. The importance of scale in evaluating herbivory impacts. *Oikos* 54:189-194.
- Brown, J. R. & Stuth, J.W. 1993. How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant responses across hierarchical levels. *Oikos* 67:291-298.
- Burlison, A.J., Hodgson, J. & Illius, A.W. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass Forage Sci* 46, 29-38
- Caraco, T. 1979. Time budgeting and group size: a theory. *Ecology* 60:611-617.
- Chambers, A.R.M., Hodgson, J. & Milne, J.A. 1981. The development and use of equipment for the automatic recording of ingestive behavior in sheep and cattle. *Grass and Forage Sci.* 36:97-105.
- Chapple, R.S., Wodzika-Tomaszewska, M. & Lynch, J.J. 1987. The learning behavior of sheep when introduced to wheat. II. Social transmission of wheat feeding and the role of the senses. *Appl. Anim. Behav. Sci.*, 18-163-172.
- Charif, R.A., Mitchell, S. & Clark, C.W. 1995. *Canary 1.2 User's Manual.* Cornell Laboratory of Ornithology, Ithaca, NY.
- Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9:129-136.
- Clutton-Brock, T.H. 1989. Mammalian mating systems. *Proc R Soc Lond B* 236:339-372.

- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. 1982. Red Deer: The behaviour and ecology of two sexes. Univ. of Chicago Press, Chicago.
- Coughenour, M. B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J. of Range Manage.* 44:530-542.
- Dehareng, D. & Godeau, J.M. 1991. The durations of masticating activities and the feed energetic utilisation of Friesian lactating cows on maize silage-based rations. *J. Anim. Phys. and Anim. Nutr.* 65:194-205.
- Demment, M.W. & Greenwood, G.B. 1988. Forage ingestion: effects of sward characteristics and body size. *J. Anim. Sci.* 66: 2380-92.
- Demment, M. W. & Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641-672.
- Demment, M.W., Peyraud, J.-L. & Laca, E.A. 1995. Herbage intake at grazing: a modelling approach. Pages 121-141 in M. Journet, E. Grenet, M-H. Farce, M. Theriez and C. Demarquilly, editors. Recent Developments in the Nutrition of Herbivores. Proceedings of the IVth International Symposium on the Nutrition of Herbivores. INRA Editions, Paris.
- Derrick, R.W., Moseley, G. & Wilman, D. 1993. Intake, by sheep, and digestibility of chickweed, dandelion, dock, ribwort and spurrey, compared with perennial ryegrass. *J. of Agric. Sci., Cambridge* 120:51-61.
- Distel, R. A., Laca, E.A., Griggs, T.C. & Demment, M.W. 1995. Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behaviour Science* 45:11-21.
- Dittus, W.P.J. 1977. The social regulation of population density and age-sex distribution in the Toque monkey. *Behaviour* 63:281-322.
- Dittus, W.P.J. 1979. The evolution of behaviours regulating density and age-specific sex ratios in a primate population. *Behaviour* 69:265-302.
- Dougherty, C.T., Bradley, N.W., Cornelius, P.L. & Lauriault, L.M. 1987. Herbage intake rates of beef cattle grazing alfalfa. *Agron J* 79, 1003-1008
- Dougherty, C.T., Cornelius, P.L., Bradley, N.W. & Lauriault, L.M. 1989. Ingestive behavior of beef heifers within grazing sessions. *Appl Anim Behav Sci* 23, 341-351
- Drea, C.H. & Wallen, K. 1995. Gradual acquisition of visual discrimination tasks in a social group of rhesus monkeys (*Macaca mulatta*). *Anim. Learn. Behav.*, 23:1-8.
- Duncan, P. 1992 Horses and Grasses: The nutritional ecology of equids and their impact on the Camargue. *Ecol Studies* 87. Springer Verlag, New York.
- Earle, D.F. & McGowan, A.A. 1979. Evaluation and calibration of an automated rising plate meter for estimating dry matter yield of pasture. *Aust. J. Agr. Anim. Husb.* 19: 337-343.
- Edwards, G.R., Newman, J.A., Parsons, A.J. & Krebs, J.R. 1994. Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. *J. Anim. Ecol.*, 63:816-826.
- Edwards, G.R., Newman, J.A., Parsons, A.J. & Krebs, J.R. 1997. Use of cues by grazing animals to locate food patches: an example with sheep. *Appl. Anim. Behav. Sci.*, 51:59-68.
- El Aich, A., Moukadem, A. & Rittenhouse, L.R. 1989. Feeding station behavior of free-grazing sheep. *Applied Animal Behaviour Science* 24, 259-265.
- Flores, E.R., Laca, E.A., Griggs, T.C. & Demment, M.W. 1993. Sward height and vertical morphological differentiation determine cattle bite dimensions. *Agron. J.* 85: 527-532.
- Focardi, S., Marcellini, P. & Montanaro, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Animal Ecology* 65:606-620.
- Forbes, T.D.A. 1988. Researching the plant-animal interface: The investigation of ingestive behavior in grazing animals. *J. Anim. Sci.* 66: 2369-2379.
- Forwood, J.R. & Hulse, M.M. 1987. Thermal conductivity instrumentation for direct forage intake measurements of grazers, p.83-84. In: M. Rose (ed.), *Herbivore nutrition research. Proc., 2nd Int. Symp. Nutr. Herbiv.* Brisbane, Australia.

- Friedel, M. H. 1994. How spatial and temporal scale affect the perception of change in rangelands. *Rangel. J.* 16:16-25.
- Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478-498.
- Galef, B.G. & Whiskin, E.E. 1994. Passage of time reduces effects of familiarity on social learning: functional implications. *Anim. Behav.*, 48:1057-1062.
- Galef, B.G. & Wigmore, S.W. 1983. Transfer of information concerning distant foods: A laboratory investigation of the "information center" hypothesis. *Anim. Behav.*, 31:748-758.
- Galef, B.G. 1980. Diving for food: Analysis of a possible case in social learning in wild rats. *J. Comp. Physiol. Psychol.*, 95:416-425.
- Galef, B.G. 1983. Utilization by Norway rats (*R. Norvegicus*) of multiple messages concerning distant diets. *J. Comp. Psychol.*, 97:364-371.
- Galef, B.G. 1988. Imitations in animals: History, definition, and interpretation of data from psychological laboratory. In: T.R. Zentall, and B.G. Galef (Editors), *Social Learning: Psychological Biological Perspectives*, Erlbaum, Hillsdale, NJ, pp. 3-28.
- Galef, B.G. 1993. Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Anim. Behav.*, 46:257-265.
- Galef, B.G., Kennett, D.J. & Stein, M. 1984. Transfer of information concerning distant foods in rats: a robust phenomenon. *Anim. Learn. Behav.*, 12:292-296.
- Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. *Am Zool* 14:205-220.
- Ginnett, T.F. & Demment, M.W. 1995. The functional response of herbivores: analysis and test of a simple mechanistic model. *Functional Ecology* 9, 376-384.
- Ginnett, T.F. & Demment, M.W. 1997. Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* 110:291-300.
- Ginnett, T.F., Dankosky, J.A., Deo, G. & Demment, M.W. 1998. Patch depression in grazers: the roles of biomass distribution and residual stems. *Ecological Applications* (submitted).
- Girard, V. & Labont, J. 1993. Continuous registering device for daily feeding behavior and study of behavior variability in the dairy cow. *Ann Zootech.* 42:49-56.
- Goering, H.K. & Van Soest, P.J. 1970. Forage fiber analysis: apparatus, reagents, procedures and some applications. *Agricultural Handbook no. 379*. USDA. Washington, DC, USA.
- Griggs, T. C., Laca, E.A. & Demment, M.W. 1991. Bite dimensions and intake of cattle within feeding stations as affected by horizontal sward heterogeneity and hunger level, p. 173. In: *Proceedings 2nd Grazing Livestock Nutrition Conference*, Oklahoma State University, Steamboat Springs, Colorado.
- Griggs, T.C., Distel, R.A. & Demment, M.W. 1991. Bite dimensions of cattle as determined by sward height, bulk density and grazing time, p. 172. In: *Proceedings 2nd Grazing Livestock Nutrition Conference*, Oklahoma State University, Steamboat Springs, Colorado.
- Gross, J.E., Hobbs, N.T. & Wunder, B.A. 1993. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? *Oikos* 68: 75-81.
- Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E. & Wunder, B. A. 1993. Functional response of herbivores in food-concentrated patches: test of a mechanistic model. *Ecology* 74, 778-791.
- Haccou, P. & Meelis, E. 1994. Statistical analysis of behavioural data: an approach based on time-structured models. Oxford University Press, Oxford, UK.
- Hall, M.J. 1983. Social organisation in an enclosed group of red deer (*Cervus elaphus* L.) on Rhum. I. The dominance hierarchy. *Z Tierpsychol* 61:250-262.
- Harper, D.G.C. 1982. Competitive foraging in mallards: 'ideal free' ducks. *Anim Behav* 30:575-584.

- Heyes, C.M. 1994. Social learning in animals: Categories and Mechanisms. *Biol. Rev.*, 69:207-231
- Hodgson, J. 1981. Variations in the surface characteristics of the sward and the short-term rate of herbage intake by calves and lambs. *Grass and Forage Science* 36, 49-57.
- Hodgson, J. 1982. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. Pages 153-166 in J.B. Hacker, editor. *Nutritional limits to animal production from pastures*. CAB International, Farnham Royal, UK.
- Hodgson, J. 1985. The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society* 44, 339-346.
- Holechek, J.L., Pieper, R.D. & Herbel, C.H. 1995. *Range management principles and practices*. Prentice Hall, Englewood Cliffs, New Jersey. p. 526.
- Hosoi, E. & Swift, D.M. 1992. Patch selection by cattle, sheep and goats - are win strategies genetically fixed? *Proc. West. Sect. Am. Soc. Anim. Sci.* 43.
- Hudson, R.J. & Frank, S. 1987. Foraging ecology of bison in aspen boreal habitats. *J. Range Manage.* 40: 71-75.
- Hudson, R.J. & Nietfeld, M.T. 1985. Effect of forage depletion on the feeding rate of wapiti. *J. Range Manage.* 38: 80-82.
- Hughes, T.P., Sykes, A.R., Poppi, D.P. & Hodgson, J. 1991. The influence of sward structure on peak bite force and bite weight in sheep. *Proc N Z Soc Anim Prod* 51, 153-158.
- Hunter, R.F. & Milner, C. 1963. The behaviour of individual, related, and groups of south country Cheviot hill sheep. *Anim. Behav.*, 4:507-514.
- Illius, A. W., Albon, S. D., Pemberton, J. M., Gordon, I. J. & Clutton-Brock, T. H. 1995. Selection for foraging efficiency during a population crash in Soay sheep. *Journal of Animal Ecology* 64, 481-492.
- Illius, A.W., Clark, D.A. & Hodgson, J. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. *J Anim Ecol* 61, 183-194
- Illius, A. W. & Gordon, I. J. 1987. The allometry of food intake in grazing mammals. *Journal of Animal Ecology* 56, 989-999.
- Illius, A.W., Gordon, I.J., Milne, J.D. & Wright, W. 1995. Costs and benefits of foraging on grasses varying in canopy structure and resistance to defoliation. *Functional Ecology* 9, 894-903.
- Illius, A.W., Wood-Gush, D.G.M. & Eddison, J.C. 1986. A study of foraging behaviour of cattle grazing patchy swards. *Biology of Behaviour* 12:33-44.
- Janetos, A. C. & Cole, B. J. 1981. Imperfectly optimal animals. *Behavioral Ecology and Sociobiology* 9, 203-210.
- Janson, C. 1985. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cobus apella*). *Behav Ecol Sociobiol* 18:125-138.
- Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.
- Jiang, Z. & Hudson, R.J. 1993. Optimal grazing of wapiti (*Cervus elaphus*) on grassland: patch and feeding station departure rules. *Evolutionary Ecology* 7:488-498.
- Jones, R.M. & Sandland, R.L. 1974. The relation between animal gain and stocking rate: derivation of the relation from the results of grazing trials. *J Agric Sci Camb* 83:335-342.
- Kondo, S., Sekine, J., Okubo, M. & Asahida, Y. 1989. The effect of group size and space allowance on the agonistic and spacing behavior of cattle. *Appl Anim Behav Sci* 24:127-135.
- Kothmann, M.M. 1984. Concepts and Principles Underlying Grazing Systems: A Discussant Paper. In: *Natl. Res. Concil/Netl. Acad. Sci. "Developing Strategies for Rangeland Management"* Westview Pres, Boulder CO, pp. 903-916.
- Kovalcick, K. & Kovalcick, M. 1986. Learning ability and memory testing in cattle of different ages. *Appl. Anim. Behav. Sci.*, 15:27-29.
- Laca, E.A. 1995. Spatial memory and foraging efficiency of cattle. *Abstr., 48th Annual meeting. Soc. Range Manage., 1995, Phoenix, AZ.*

- Laca, E.A. & Demment, M.W. 1996. Foraging strategies of grazing animals. Pages 137-158. in J. Hodgson and A.W. Illius, editors. *The Ecology and Management of Grazing Systems*. CAB International, Wallingford, Oxon, UK.
- Laca, E.A., Demment, M.W., Distel, R.A. & Griggs, T.C. 1993. A conceptual model to explain variation in ingestive behaviour within a feeding patch, p. 710-712. In: *Proceedings of the XVII International Grassland Congress*, New Zealand.
- Laca, E.A., Demment, M.W., Winckel, J. & Kie, J.G. 1989. Comparison of weight estimate and rising-plate meter methods to measure herbage mass of a mountain meadow. *Journal of Range Management* 42:71-75.
- Laca, E.A., Distel, R.A., Griggs, T.C. & Demment, M.W. 1994a. Effects of canopy structure on patch depression by grazers. *Ecology* 75:706-716.
- Laca, E.A., Distel, R.A., Griggs, T.C., Deo, G.P. & Demment, M.W. 1993. Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilization. *Proceedings of the XVIth International Grassland Congress*, New Zealand, pp. 709-710.
- Laca, E.A. & Ortega, I.M. 1995. Integrating foraging mechanisms across spatial and temporal scales. *Proceedings of the Fifth International Rangeland Congress*, Salt Lake City, Utah, USA: 129-132.
- Laca, E.A., Ungar, E.D. & Demment, M.W. 1994b. Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science*, 39:3-19.
- Laca, E.A., Ungar, E.D., Seligman, N.G. & Demment, M.W. 1992b. 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., Ungar, E.D., Seligman, N.G., M.R. Ramey & Demment, M.W. 1992a. An integrated methodology to study short-term grazing behaviour of cattle. *Grass and Forage Science* 47:81-90.
- Langvatn, R. & Hanley, T.A. 1993. Feeding patch choice by red deer in relation to foraging efficiency: an experiment. *Oecologia* 95:164-170.
- Lemaire, G. & Chapman, D. 1996. Tissue flows in grazed plant communities. In: J. Hodgson and A.W. Illius (Editors), *The Ecology and Management of Grazing Systems*. CAB International, Wallingford, Oxon, UK, pp. 3-36.
- Luginbuhl, J.M., Pond, K.R., Russ, J.C. & Burns, J.C. 1987. A simple electronic device and computer interface system for monitoring chewing behavior of stall-fed ruminant animals. *J. Dairy Sci.* 70:1307-1312.
- Lynch, J.J., Hinch, G.N. & Adams, D.B. 1992. *The behavior of sheep: biological principles and implications for production*. SCIRO Publications, Australia.
- Matsui, K. & Okubo, T. 1989. A 24-hour automatic recording of grazing and rumination behaviour in cattle on pasture by a data logger method. *Jap. J. Zootech. Sci.*, 60:940-45.
- Matsui, K. & Okubo, T. 1990. Automatic recording over a 24-hour period for biting rate during grazing, and chewing rate and number of boluses during rumination of cow on pasture. *Jap. J. Zootech. Sci.*, 61: 493-500.
- Matsui, K. & Okubo, T. 1991. A method for quantification of jaw movements suitable for use on free-ranging cattle. *Appl. Anim. Behav. Sci.* 32:107-16.
- McLeod, M. N., Kennedy, P.M. & Minson, D.J. 1990. Resistance of leaf and stem fractions of tropical forage to chewing and passage in cattle. *Brit. J. of Nut.* 63:105-119.
- McNaughton, S.J. 1984. Grazing lawns: animals in herds, plant form and co-evolution. *American Naturalist* 124:863-886.
- Mertens, D.R. 1987. Predicting intake and digestibility using mathematical models of ruminal function. *Journal of Animal Science* 64: 1548-1558.
- Milne, J.A. 1991. Diet selection by grazing animals. *Proceedings of the Nutrition Society* 50, 77-85.
- Moen, R.A., Pastor, J. & Cohen, Y. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78:505-521.
- Morita, S., Amemiya, M. & Nishino, S. 1989. Changes of eating behavior with group size and social rank order in steers. *J Rakuno Gakuen Univ* 14:63-70.

- Murray, M.G. 1991. Maximising energy retention in grazing ruminants. *Journal of Animal Ecology* 60:1029-1045.
- Nams, V.O. 1996. The Vfractal: a new estimator for fractal dimension of animal movement paths. *Landscape Ecology* 11:289-297.
- Newman, J.A., Parsons, A.J. & Harvey, A. 1992. Not all sheep prefer clover: diet selection revisited. *Journal of Agricultural Science, Cambridge* 119, 275-283
- Newman, J.A., Parsons, A.J., Thornley, J.H.M. & Penning, P.D. 1995. Optimal diet selection by a generalist grazing herbivore. *Functional Ecology* 9:255-268.
- Nicol, C.J. 1995. The social transmission of information and behaviour. *Appl. Anim. Behav. Sci.*, 44:79-98.
- O'Neill, R.V., Gardner, R.H., Milne, B.T., Turner, M.G. & Jackson, B. 1991. Heterogeneity and spatial hierarchies, p. 85-96. In: J. Kolasa and S. T. A. Pickett (eds.), *Ecological heterogeneity*. Springer-Verlag, New York, NY.
- Olton, D.S., Collison, C. & Werz, M.A. 1977. Spatial memory and radial arm maze performance of rats. *Learn. Motiv.*, 8:289-314.
- Owens, M. & Owens, D.D. 1978. Feeding ecology and its influence on social organization in brown hyaenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *E Afr Wildl J* 16:113-135.
- Parsons, A.J., Thornley, J.H.M., Newman, J.A. & Penning, P.D. 1994. A mechanistic model of some physical determinants of intake rate and diet selection in a two-species temperate grassland sward. *Functional Ecology* 8, 187-204.
- Penning, P.D., Rook, A.J. & Orr, R.J. 1991. Patterns of ingestive behaviour of sheep continuously stocked on monocultures of ryegrass or white clover. *Appl. Anim. Behav. Sci.* 31:237- 250.
- Penning, P.D., Parsons, A.J., Orr, R.J. & Treacher, T.T. 1991. Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass For. Sci.* 46: 15-28.
- Prache, S. 1997. Intake rate, intake per bite and time per bite of lactating ewes on vegetative and reproductive swards. *Appl. Anim. Behav. Sci.* 52: 53-64.
- Prins, H.H.T. 1996. Ecology and behaviour of the African buffalo. Social inequality and decision making. Chapman and Hall, London.
- Provenza, F.D. & Balph, D.F. 1988. Diet learning by domestic ruminants: theory, evidence and practical implications. *Appl. Anim. Behav. Sci.*, 18:211-232.
- Provenza, F.D., Lynch, J.J. & Nolan, J.V. 1993. The relative importance of mother and toxicosis in the selection of foods by lambs. *J. Chem. Ecol.*, 19:313-323.
- Ravid, N. 1997. The relation between sward structure and grazing behaviour of cattle over small temporal and spatial scales. M.Sc. Thesis, The Hebrew University of Jerusalem, Israel. (Hebrew, with English abstract)
- Ruyle, G.B. & Dwyer, D.D. 1985. Feeding stations of sheep as an indicator of diminished forage supply. *Journal of Animal Science* 61, 349-353.
- Ruyle, G. B., Hasson, O. & Rice, R. W. 1987. The influence of residual stems on biting rates of cattle grazing *Eragrostis lehmanniana* Nees. *Applied Animal Behaviour Science* 19, 11-17.
- SAS, 1995. JMP User's Guide. Version 3. SAS Institute, Cary, North Carolina.
- Schaller, G.B. 1972. *The Serengeti Lion: A study of predator-prey relations*. Chicago Univ Press, Chicago.
- Schneider, D.C. 1994. *Quantitative ecology. Spatial and temporal scaling*. San Diego, California, Academic Press.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240-285.
- Scott, C.B., Provenza, F.D. & Banner, R.E. 1995. Dietary habits and social interactions affect choice of feeding location by sheep. *Appl. Anim. Behav. Sci.*, 45:225-237.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789-799.

- Shettleworth, S.J. & Krebs, J.R. 1982. How marsh tits find their hoards: The roles of site preference and spatial memory. *J. Exp. Psy.*, 4:354-375.
- Shipley, L. A., Gross, J. E., Spalinger, D. E., Hobbs, N. T. & Wunder, B. A. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist* 143, 1055-1082.
- Shipley, L. A. & Spalinger, D. E. 1992. Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate. *Canadian Journal of Zoology* 70, 1743-1752.
- Shipley, L.A. & Spalinger, D.E. 1995. Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia* 104, 112-121.
- Short, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *J. Appl. Ecol.* 22: 435-447.
- Sinclair, A.R.E. 1977. *The African Buffalo: A study of resource limitation of populations.* Univ. of Chicago Press, Chicago.
- Smoliak, S. 1974. Range vegetation and sheep production at three stocking rates on Stipa-Bouteloua prairie. *J Range Manage* 27:23-26.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry.* 2nd ed., W.H. Freeman and Company, New York, NY. 859 pp.
- Spalinger, D.E., Hanley, T.A. & Robbins, C.T. 1988. Analysis of the functional response in foraging in the sitka black-tailed deer. *Ecology* 69:1166-1175.
- Spalinger, D.W. & Hobbs, N.T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *Amer. Nat.* 140: 325-348.
- Staddon, J.E.R. & Ettinger, R.H. 1989. *Learning: An Introduction to the Principles of Adaptive Behavior.* Harcourt Brace Jananovich, San Diego, p.436.
- Stephens, D.W. & Krebs, J.R. 1986. *Foraging theory.* Princeton University Press, Princeton., N.J.
- Stobbs, T.H. & Cowper, L.J. 1972. Automatic measurement of the jaw movements of dairy cows during grazing and rumination. *Trop. Grassl.* 6:107-112.
- Stobbs, T.H. 1973a. The effect of plant structure on the intake of tropical pastures. I. Variation in the bite size of grazing cattle. *Aust. J. Agric. Res.*, 24: 809-819.
- Stobbs, T.H. 1973b. The effect of plant structure on the intake of tropical pastures. II. Differences in sward structure, nutritive value, and bite size of animals grazing *Setaria anceps* and *Chloris gayana* at various stages of growth. *Aust. J. Agric. Res.*, 24: 821-829.
- Stuth, J.W. 1991. Foraging behavior, p. 65-83. In: R. K. Heitschmidt and J. W. Stuth (eds.), *Grazing management. An ecological approach.* Portland, Oregon, Timber Press, Inc.
- Thorhallsdottir, A.G., Provenza, F.D. & Balph, D.F. 1990. Ability of lambs to learn about novel foods while observing or participating with social models. *Appl. Anim. Behav. Sci.*, 25:25-33.
- Thornley, J.H.M., Parsons, A.J., Newman, J.A. & Penning, P.D. 1994. A cost-benefit model of grazing intake and diet selection in a two-species temperate grassland sward. *Functional Ecology* 8:5-16.
- Thouless, C.R. 1990. Feeding competition between grazing red deer hinds. *Anim Behav* 40:105-111.
- Tille, Y., Newman, J.A. & Healy, S.D. 1996. New tests for departures from random behavior in spatial memory experiments. *Anim. Learn. Behav.*, 24:327-340.
- Tinbergen, J.M. 1981. Foraging decisions in starlings (*Sturnus vulgaris*). *Ardea* 69:1-67.
- Trudell, J. & White, R.G. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. *J. Appl. Ecol.* 18: 63-81.
- Turner, M.G., Dale, V.H. & Gardner, R.H. 1989. Predicting across scales: theory development and testing. *Landscape Ecology* 3:245-252.
- Underwood, R. 1983. The feeding behaviour of grazing African ungulates. *Behaviour* 84:195-243.

- Ungar, E.D. 1996. Ingestive behaviour. *The Ecology and Management of Grazing Systems*. (eds J. Hodgson & A.W. Illius), pp. 185-218. Wallingford: CAB International.
- Ungar, E.D., Genizi, A. & Demment, M.W. 1991. Bite dimensions and herbage intake by cattle grazing short hand-constructed swards. *Agron J* 83:973-978.
- Ungar, E.D. & Noy-Meir, I. 1988. Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *Journal of Applied Ecology* 25, 1045-1062.
- Ungar, E.D., Seligman, N.G. & Demment, M.W. 1992. Graphical analysis of sward depletion by grazing. *Journal of Applied Ecology* 29, 427-435.
- Valentine, J.F., 1990. *Grazing Management*. Academic Press, Inc. San Diego, CA, p. 533.
- Van Dierendonck, M.C., De Vries, H. & Schilder, M.B.H. 1995. An analysis of dominance, its behavioural parameters and possible determinants in a herd of Icelandic horses in captivity. *Neth J Zool* 45:362-385.
- von Ende, C. N. 1993. Repeated measures analysis: growth and other time-related measures. *Design and Analysis of Ecological Experiments*. (eds. S. M. Scheiner & J. Gurevitch), pp. 113-137. Chapman and Hall, New York.
- WallisDeVries, M.F., Laca, E.A. & Demment, M.W. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. *Appl Anim Behav Sci* (submitted).
- WallisDeVries, M.F. & Daleboudt, C. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* 100:98-106.
- WallisDeVries, M.F. & Schippers, P. 1994. Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. *Oecologia* 100:107-117.
- WallisDeVries, M.F., 1995. Estimating forage intake and quality in grazing cattle: a reconsideration of the hand-plucking method. *J. Range Manage.*, 48: 370-375.
- WallisDeVries, M.F., Laca, E.A. & Demment, M.W. 1998. From feeding station to patch: scaling up food intake measurements in grazing cattle. *Applied Animal Behaviour Science* (submitted).
- Ward, D. & Saltz, D. 1992. Foraging at different spatial scales: dorcas gazelles foraging for lilies in the Negev Desert. *Ecology* 75: 48-58.
- Whitten, P.L. 1983. Diet and dominance among female vervet monkeys. *Am J Primatol* 5:139-159.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Func. Ecol.* 3:385-397.
- Willms, W.D., Smoliak, S. & Schaalje, S. 1986. Cattle weight gains in relation to stocking rate on rough fescue grassland. *J Range Manage* 39:182-187.
- Willson, R.J. & Wilkie D.M. 1993. Pigeons remember briefly trained spatial location-food associations over extended time periods. *J. Exp. Psychol.*, 19:373-379.
- Wilmshurst, J.F., Fryxell, J.M. & Hudson, R.J. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* 6: 209-217.
- Wilmshurst, J.F. & Fryxell, J.M. 1995. Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's 1993) results. *Oecologia* 104:297-300.
- With, K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9:25-36.

4. Evaluation of the research achievements

The hypotheses set out in the original proposal were all addressed and the planned experiments were all conducted. In addition, we managed to conduct a number of additional studies that were either felt necessary as preparatory to the core experiments of the proposal, or that derived directly from their results and as part of the overall conceptual framework being developed. Significant progress was made towards all of the original objectives. 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 the ability of researchers to successfully approach management problems. 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: the evaluation of forage availability and its relation to animal performance, the monitoring of short-term intake rate, and the prediction of intake rate on the basis of sward characteristics.

5. Description of the cooperation

The research reported here is a continuation project from a previous BARD-funded project. In the previous project a strong emphasis was placed on direct collaboration in the form of visits and joint conduct of experiments. Thus Ungar made two long trips to the US and the basic methodologies were worked out jointly, and key HCS experiments were conducted jointly. Since this project continued that line of research, it was felt that the high costs of travel and foreign visits could be saved and better used to achieve more in the field. The present-day ease and speed of electronic communication meant that not only could the two teams collaborate closely in developing the research proposal, but could also maintain a steady and fruitful exchange of conceptual ideas, methodological issues and experimental data throughout the project. To the extent possible the teams ensured that their computer systems, software and methodologies were fully compatible. This is especially important in the area of methodology, and means that we will be able to conduct an integrative "meta-analysis" of a number of our experiments. The innovative research conducted in the framework of this collaboration has apparently had a strong impact in the scientific community; a recently published textbook on the ecology and management of grazing systems included invited chapters on foraging strategies and ingestive behaviour from the BARD team, and the findings from the BARD projects featured prominently in these publications. There is no question that the high degree of collaboration and information exchange that characterized both the previous and the current projects would not have taken place in the absence of the formal framework provided by BARD.

6. Conclusions

This project was a continuation from a previous BARD project and was a logical continuation of its research agenda. We continued to use the HCS methodology developed in the previous project but also developed and applied other methodologies that enabled us to extend the spatial and temporal scale of our studies.

Considerable progress was made over the four years of the project towards an agro-technical protocol that can yield swards of sufficiently high uniformity to conduct detailed patch-oriented studies in the field. We also adopted techniques based on cutting selected sods as an alternative to the construction of HCS for patch-oriented studies. At the largest spatial and temporal scales that we undertook in this project, and where the focus was on aspects of foraging not directly related to the mechanisms of biting and patch depletion, we adopted techniques based on trays and pellets in the field. One study was also conducted under stall-fed conditions. Thus a broad range of experimental methodologies was employed. One methodological feature that was common to many of the studies conducted was the use of acoustic monitoring for the counting of bites and the identification of different types of jaw movements (chews, bites and combination chew-bites). This methodological component was developed in our previous project and proved an invaluable tool in the studies reported here.

We found that even when sown swards are of insufficient horizontal uniformity to enable computation of intake from a patch by the difference method, post-grazing measurements of residual heights at a high density can yield good estimates of bite dimensions - mean effective bite area and bite depth - from which bite weight and intake can be derived. Residual height mapping and the derived frequency distribution of residual heights is an important tool in understanding the mechanics of patch depletion.

A series of incremental patch depletion studies demonstrated how grazing style tends to be predominantly by horizon, and how mean effective bite area tends to decline as the depletion of a horizon proceeds. These results suggest that the assumption of a constant within-horizon bite area used in a graphical model developed in the previous project may be an oversimplification. We were able to predict our experimental results closely using

a bite placement simulator based on semi-random placement. The model indicates that bite area declines primarily because of increasingly severe bite overlap with horizon depletion, but that the decline is far more severe on tall swards (with a greater potential bite area) than on short swards. This prediction was also consistent with our experimental data. Thus the simple graphical model may still have quantitative relevance on short swards. It is noteworthy and most encouraging that these conclusions derive from incremental depletion studies conducted in both the US and Israel, using different animals, different observers and different patch preparation methodologies.

At medium to high levels of patch depletion, results for different absolute patch sizes can be normalized by converting to a per unit area basis. Thus the density of bite placement (bites per square metre) becomes a central parameter in defining the intensity of grazing at the feeding station scale. However, there are indications that on patches much smaller than a feeding station, the animal is able to increase the mean effective bite area at low depletion levels, perhaps by sweeping the mouth into the patch from the side.

A common feature of natural swards is the co-presence of mature stem material with young leafy vegetation. Our empirical results show that stem presence in the grazed horizon modifies bite dimensions and the time budget of intake. We conclude that animals grazing in non-stemmy swards will have shorter residence times and remove more foliage from each patch. As a result, they should visit fewer total patches per day, while obtaining higher intake rates than animals foraging from stemmy swards. Stemmy swards will be used less intensively on a per-patch basis, and because greater numbers of patches will be visited per animal the distribution of grazing will be more homogeneous than in a non-stemmy habitat.

Bite size is the crucial variable determining intake rate. We have shown that bite size is significantly affected by the process of forage depletion. Local depletion causes a reduction in the measured average bite weight compared to the expectation based on initial sward conditions alone without patch depression. It should, therefore, be realized that for grazing animals the functional response at a larger spatial scale is arrived at by a repeated process of patch depression at each feeding station.

The spatial arrangement of patches does have a significant impact on grazing behaviour. The same herbage area presented in a single patch or subdivided with only narrow separations which are inconsequential from the point of view of search or travel time, will nevertheless result in a change in mean effective bite area and hence bite weight and intake rate. On the basis of two experiments using completely different grazing arenas to investigate the impact of the spatial arrangement of patches, it appears that horizon depletion may be the simplest guiding rule of thumb in grazing style. Increasing the distance between equally sized patches did not result in a significant entry to a lower grazing horizon. However, as patch size becomes smaller, the cost of almost complete horizon depletion increases due to the inefficiencies of bite overlap, border effects and the indivisibility of bites.

We tested hypotheses related to foraging behaviour in heterogeneous environments of different grain size. Our three hypotheses on patch selection were largely confirmed. Patch selection was aimed at the patch type with the highest daily digestible intake, search pattern was non-random, and selectivity increased when integrating the selection of feeding stations with selectivity in movement to the preferred patch. However, once a feeding station was chosen selectivity did not increase further, since the number of bites per feeding station was similar in both patch types. Selection operated mainly in directing the foraging path and in selecting feeding stations. Grazing at the feeding station appeared to be governed mainly by vegetation characteristics of the patch type. The hierarchical approach to foraging behavior reveals that the selection of feeding stations and the feeding at feeding stations are fundamentally different processes. The largest potential for selection appears to exist in the choice of feeding stations. Selectivity at the feeding station seems mainly limited to manipulating the level of depletion before moving on. We applied the marginal value theorem to predict the residence time at the feeding station, but the observations did not match the predictions. The frequency distribution of bites per feeding station closely followed a negative exponential distribution of a survivorship curve; the same result was found for the residence time per feeding station. This supports the argument that the animals operate differently when selecting a feeding station and when feeding there. Once the feeding station is chosen residence time appears

better explained by the characteristics of the particular patch type grazed than by the alternatives between patch types.

Two of the four hypotheses on the effect of scale of patchiness on selectivity were confirmed and two were rejected. As predicted, selectivity was greater in the coarse-grained environment and the efficiency of feeding station selection was also greater in the coarse-grained environment. However, contrary to predictions, the animals did not adjust their movement pattern to the scale of patchiness and neither was the number of bites or the residence time per feeding station. The absence of an effect of grain size on the residence time per feeding station was contrary to expectation. However, it does fit the view presented above that selection occurs mainly at the level above the feeding station. As each distinct patch was substantially larger than a single feeding station, the scale of patchiness may have been too large to generate differences in the exploitation per feeding station.

We presented a conceptual model of foraging at different spatial and temporal scales that integrated our empirical results from grazing trials on scale of heterogeneity and spatial memory. Information is integrated by the animal at various levels by the animal's memory, by direct perception of the environment at many scales, and by perception of the internal states as integrated by organs and tissues. Animals monitor reward rates at the scale of the feeding station, patch and feeding site. Reward rates are compared to thresholds determined by memory of rewards and perception of alternatives at larger scales.

Our investigation of social effects on foraging behaviour showed that the mere proximity of potential competitors does not alter bite size or bite rate during grazing. However, it appears that the position in the dominance hierarchy does influence grazing behavior and food intake. As predicted, interference was more frequent in fine-grain environments where selection was more difficult than in coarse-grain environments.

Progress was made in exploiting the acoustic signal generated in the course of grazing to distinguish between different types of jaw movements - specifically bites, chews and combination chew-bites, and use that information to improve our understanding of the time budget of grazing. With suitable calibration it is possible to predict intake on the basis of the acoustic signal.

7. List of publications

- Bailey, D. W., M. B. Coughenour, J. E. Gross, E. A. Laca, L. R. Rittenhouse & D. M. Swift. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Invited synthesis paper, Journal of Range Management. 49(5):386-400.
- Laca, E. A. & I. M. Ortega. 1996. Integrating foraging mechanisms across spatial and temporal scales. In: West, N. E. (ed.) Rangelands in a sustainable biosphere, Proceedings of the Fifth International Rangeland Congress, pp. 129-132, Volume II, Invited presentations, Salt Lake City, Utah, July 23-28, 1995, Society for Range Management, Denver, CO.
- Laca, E. A. & Demment, M.W. 1996. Foraging strategies of grazing animals. In: Illius, A. & Hodgson, J. (eds.), Ecology and Management of Grazing Systems, pp. 137-158, CAB International.
- Ungar, E.D. 1996. Ingestive behaviour. In: Illius, A. & Hodgson, J. (eds.), Ecology and Management of Grazing Systems, pp. 185-218, CAB International.
- Laca, E. A., A. Ash, M. Coughenour, J. Fryxell, W. Getz, J. Hearne, N. Owen-Smith & D. Ward. 1996. Second International Foraging Behavior Workshop. Bulletin of the Ecological Society of America, 77:36-38.
- Ungar, E.D., Ravid, N. and Genizi, A. & Methorst, R. (1997) Measurement error in the estimation of intake from herbage patches by non-fistulated heifers on apparently uniform swards. Ann. Zootech. 46:349-359.
- In progress:
- WallisDeVries, M. F., E. A. Laca & M. W. Demment. (Submitted to Applied Animal Behaviour Science). From feeding station to patch: scaling up food intake measurements in grazing cattle.
- WallisDeVries, M. F., E. A. Laca & M. W. Demment. (Submitted to Ecology). The importance of scale of patchiness for selectivity in grazing herbivores.
- Ungar, E.D. & Ravid, N. (Submitted to Functional Ecology) Bite horizons and dimensions for cattle (*Bos taurus*) grazing herbage patches at high depletion.

- WallisDeVries, M. F., T. F. Ginnett, E. A. Laca & M. W. Demment. (In preparation). On the relative importance of exploitation and interference competition in grazing ungulates: an experimental test.
- Laca, E. A. & M. F. WallisDeVries. (In preparation). Acoustical measurement of intake and behaviour of grazing cattle.
- Ungar, E.D., Ravid, N. & Brukental, I. (In preparation) Patch depression in *Bos taurus* grazing herbage patches at low depletion.
- Ungar, E.D. & Ravid, N. (In preparation) Short-term foraging behaviour of cattle in response to patch size and spacing.
- Abstracts and presentations
- WallisDeVries, M. F. & E. A. Laca. 1997. Scale of patchiness affects the relation between forage quality and patch choice by cattle. Proceedings of the XVIII International Grassland Congress, June 8-19, 1997, Winnipeg, Manitoba, Saskatoon, Saskatchewan, Canada. Volume III.
- WallisDeVries, M. F., E. A. Laca & M. W. Demment. 1997. Spatial aspects of ungulate foraging behavior in a patchy environment. Abstracts of the 1997 Annual Meeting, August 10-14, Albuquerque, New Mexico. Supplement to the Bulletin of the Ecological Society of America 78(4):203.
- WallisDeVries, M. F., E. A. Laca & M. W. Demment. 1997. Ungulate foraging movements in relation to environmental grain size. Annual Meeting of the US-International Association for Landscape Ecology.
- Ortega, I. M. & E. A. Laca. 1997. Effects of food spatial distribution, visual and olfactory cues on feeding efficiency of cattle. 50th Annual Meeting, Society for Range Management, February 16-21, 1997, Rapid City, South Dakota.
- Ksiksi, T. L. Spence and E. A. Laca. 1997. Do social interactions affect the rate of learning of food locations by cattle? 50th Annual Meeting, Society for Range Management, February 16-21, 1997, Rapid City, South Dakota.
- Laca, E. A., I. M. Ortega and P. Soca. 1997. Controlling diet selection of sheep by restricting eating time. 50th Annual Meeting, Society for Range Management, February 16-21, 1997, Rapid City, South Dakota.

- Laca, E. A. 1996. Escalas de espacio y tiempo en el comportamiento de pastoreo. Presentation at the Faculty of Agronomy, Universidad de Buenos Aires, Argentina, 13 November 1996.
- Laca, E. A., P. Soca, I. M. Ortega and P. Vandygriff. 1995. Controlling diet selection of sheep by restricting eating time. Research highlights 26:27, College of Agricultural Sciences and Natural Resources, Texas Tech University.
- Laca, E. A., I. M. Ortega and M. Lloyd. 1995. Effects of food spatial distribution and visual cues on feeding efficiency of cattle. Research highlights 26:28, College of Agricultural Sciences and Natural Resources, Texas Tech University.
- Ortega, I. M., E. A. Laca and P. Vandygriff. 1995. Brush density and distribution effects on cattle grazing efficiency. Research highlights 26:30, College of Agricultural Sciences and Natural Resources, Texas Tech University.
- Ortega, I. M. and Laca. 1995. Forage intake efficiency of cattle as affected by food and brush distribution. Annual Meeting of the Texas Section of the Society for Range Management, Amarillo, Texas, October 5-7, 1995.
- Ksiksi, T. and E. A. Laca. 1995. Duration of spatial memory in cattle. Annual Meeting of the Texas Section of the Society for Range Management, Amarillo, Texas, October 5-7, 1995.
- Laca, E. A. 1995. Grazing across multiple spatial scales: experiments and models. 1995 World Conference on Natural Resource Modelling, Symposium on Dimensions of sustainability in herbivore-vegetation interactions in variable environments. 5-10 July, 1995, Pietermaritzburg, South Africa.
- Laca, E. A. and I. M. Ortega. 1995. Spatial scales and efficiency of foraging of large herbivores in response to food distribution and apparency. 1995 Annual Meeting, Ecological Society of America, 31 July-3 August 1995, Snowbird, Utah.
- Laca, E. A. 1995. Spatial memory and foraging efficiency of cattle. 48th Annual Meeting, Society for Range Management, January 14-20, 1995, Phoenix, Arizona.