MODELLING THE SPATIAL DYNAMICS OF A SEMI-ARID GRAZING SYSTEM

by

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ABSTRACT

A large proportion of the world's land surface is covered by semi-arid grasslands, and they provide an important source of income as a grazing resource. A more comprehensive understanding of these complex ecosystems is vital for the effective management of rangelands, as it will lead to an increased and more sustainable economic output.

Herbivores modify the spatial pattern of vegetation distribution and their response to spatially heterogeneous forage resources affects their performance. The spatial aspect of herbivory is often ignored although it is a necessary component of understanding grazing dynamics and the factors affecting herbivore condition.

A spatial model is developed which incorporates vegetation and animal dynamics and the interactions between these two components. The effect of different spatial foraging strategies on animal performance and vegetation was investigated. Model results were compared with the output of a non-spatial model to assess the importance of spatially explicit modelling in the context of monitoring animal performance. The relative significance of a number of aspects relating to spatial grazing and animal condition was explored.

The results from this research show that significant differences in output are obtained from spatial versus non-spatial models. While the purpose of a model will determine its nature, the results imply that in certain contexts, a spatial model is essential for accurate results and insight.

The results also indicated that foraging strategies have a large affect on herbivore condition and that spatially explicit models are necessary in the context of investigating the effect of foraging strategies on animal performance. Various aspects that significantly affected animal condition were highlighted and are useful in directing future investigations into grazing dynamics.

It is difficult to conduct field studies under spatially and temporally variable conditions where the interactions between vegetation and herbivores are so complex. In the light of this, modelling was found to be an effective tool that can be used in investigating and revealing important dynamics of semi-arid grazing systems.

PREFACE

The work described in this thesis was conducted under the supervision of Prof. J.W. Hearne of the School of Mathematics, Statistics and Information Technology, University of Natal, Pietermaritzburg and Prof. T.G. O'Connor of the School of Range and Forage Resources, University of Natal, Pietermaritzburg.

These studies present original work by the author and have not otherwise been submitted in any form to another university. Where use has been made of the work of others it is duly acknowledged in the text.

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TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER ONE
INTRODUCTION

1.1. INTRODUCTION

Rangelands are the most abundant type of land on earth and are characterized by a dominant role of herbivory (Holecheck *et al.*, 1995). The use of rangelands for grazing provides an important source of income and may have a variety of goals: commercial grazing which incorporates the efficient production of meat or fibre or other products for markets; subsistence pastoralism which has mixed goals such as milk, skins, meat, traction, fibre and other agricultural products; and wildlife grazing which includes hunting, tourism, recreation and conservation (Stafford Smith, 1996). Rangelands are among the most complex ecosystems and understanding how rangelands function is integral to the development of management interventions which will lead to increased and sustainable economic output.

1.2. COMPLEXITY OF RANGELAND ECOSYSTEMS

Complexity in an ecosystem arises through interactions or connections between the components in the system at different levels of organisation, and even relatively 'simple' systems with few entities may exhibit complex behaviour as a result of such interactions (Kolasa and Rollo, 1991). The degree of complexity depends not only on the number of entities in the system (i.e. its diversity) or on the way in which these entities differ from each other and within themselves (heterogeneity), but also on how the system is organised and the degree of interrelationship between its components (Allen and Starr, 1982). The complexity of the grazing system arises in four major areas: (1) within the food resource, (2) within the herbivore population, (3) at the plant/animal interface and (4) in the management strategy (Tainton *et al.*, 1996) and the combination of some or all of the above lead to the high degree of complexity found in rangelands.

Rangelands are particularly complex ecosystems and the characteristics of rangelands stretch the management paradigms often past their limits. Issues such as temporal and spatial heterogeneity, which may be side-stepped in many systems, become driving forces which cannot be ignored in rangelands, because of their implications at the scale of management. As a result, approaches to vegetation change, optimal animal production and even human decision-making and decision support must be reassessed and redesigned.

Rangelands tend to be critically characterised by the following continua (Stafford Smith, 1996).

1. Low productivity (water and/or nutrient limited) which has as a consequence large management units leading to units encompassing rather than segregating spatial heterogeneity.
2. Variable rainfall causes extreme interannual variability in primary production.
3. Rangelands have mainly natural vegetation with many interacting plant species which make the system ecologically complex.
4. Limited scientific attention has been paid to rangelands which means that there is less information available.

Because of the low productivity and high complexity of rangelands, research effort has been focused on more intensively used systems. There has, however, been a substantial increase in research into rangelands in the recent past with an increased emphasis on spatial and temporal diversity. This is an active area of research and much more work needs to be done on it (see for example Stafford Smith, 1996).

When considering rangelands, distribution of free-grazing herbivores is one of the major issues facing animal and rangeland managers (Bailey *et al.*, 1996). It has long been recognised that herbivores can modify spatial pattern of landscapes over several spatial scales (Hobbs, 1994) and that uneven distribution of grazing negatively impacts rangelands through over- and under- utilisation of resources (Laca, 1998).

Not only is the rangeland impacted by spatial grazing, but also the condition of the herbivores. Free-ranging large herbivores experience changes in forage quality, quantity and availability during the year and have to increase their intake as well as modify foraging behaviour both spatially and temporally to maintain a positive annual energy balance (Moen *et al.*, 1997). Consequently, herbivores respond to spatial and temporal variability in food resources by selectively foraging on the landscape (Senft *et al.*, 1987 and references therein). The degree of selectivity of the animal and the animal's foraging behaviour as it responds to the changes in vegetation spatially and temporally have a large effect on the animal condition. Animal condition is important to farm managers as it translates into economic gain, which is most often the goal of the rangeland manager. Animal condition is also an indication as to the fitness of the herd, and survival probability as well as reproductive capacity. There are two reasons why we need to understand how animals use and affect their forage resource – first, to predict the short-term economic outputs of different management strategies and, second, to predict the long-term impacts on the sustainability of production.

There have been some exciting developments in rangelands over the past decade and there continues to be active debate over management paradigms in this complex ecosystem type. Grazing systems ecology has advanced through improved mechanistic understanding of the key processes at plant, animal and systems level. Mathematical modelling based on this understanding is proving to be useful for the development of conceptual understanding of these processes. Linking the research approaches developed in natural and managed systems has resulted in progress in understanding processes in grazing systems and there is scope for initiatives in many areas of ecosystems work. The investigation of systems heterogeneity offers new insights into ecosystem behaviour, and makes new demands on data collection and analysis, and modelling. A better understanding is needed of the factors offering scope for the control of state in grazing systems (Illius and Hodgson, 1996).

There still remains much work to be done in understanding rangeland dynamics and there is increasing consensus that spatial aspects play an important part and must be considered when seeking to understand the dynamics at play in rangeland grazing systems.

1.3. AIMS AND OBJECTIVES

The primary objective of this study is to gain a better understanding of the spatial and temporal dynamics of a semi-arid grazing system, and the effect of grazing strategies on animal condition at the end of the grazing season. Of particular interest is the response of grazing herbivores to the vegetation present which changes over time and space in response to rainfall and grazing, and the effect of an animal herd's foraging behaviour on animal condition. An important objective which is linked to the primary aim, is the effective utilisation of the vegetation and natural resources. Thus, animal performance is carefully monitored in relation to stocking rate and rainfall in order to check that the animals are performing the best that they can under a given set of circumstances. Various conceptual foraging approaches adopted by other researchers are also investigated.

It is hypothesized that in order to accurately model the response of foraging animals and vegetation to herbivory, a spatial model is required. The assumed spatial foraging strategy strongly affects animal intake, animal condition and the distribution of the vegetation at the end of the grazing season. The extent of the animal herd's awareness of its surroundings and its ability to distinguish the potential returns of various locations, are crucial to the herd's performance and cannot be ignored in modelling grazing systems.

Another aspect that is of interest in managing rangelands, is the theoretical concept of stocking rate and its applicability in rangelands. Theoretically, one should stock to match the most limiting year (Dye, 1983). The hypothesis proposed in this thesis, is that models that do not incorporate any spatial dynamics do not adequately describe resource utilisation and as a result, managers are understocking or overstocking their farms and that animals armed with spatial strategies are able to perform better than if they were only able to uniformly graze an area.

Summary of Objectives

1. To develop a spatial model that would allow the investigation and greater understanding of foraging strategies of herbivores grazing in a semi-arid grassland.
2. To investigate the effect of different spatial foraging strategies on animal performance and the vegetation.
3. To compare the results of the spatial model with those of a non-spatial model in order to assess the importance of spatially explicit modelling in the context of a performance index relating to animal condition.
4. To explore the relative significance of a number of aspects relating to spatial grazing and animal condition.

1.4. METHOD

In rangelands, as elsewhere, grazing production depends on vegetation production which in turn is driven by climate, soil conditions, the feedback effects of grazing itself and management interventions, such as the use of fire. Because of the highly variable rainfall typical of rangelands which in turn causes variable forage production, and the complexity of the vegetation composition, detailed studies are difficult to carry out in rangelands and little empirical work has been done in this area. Furthermore, the study of herbivores in complex natural environments, where the scope for selection is likely to be of greatest importance to animal and vegetation alike, must inevitably be limited to a descriptive approach because controlled experimentation is infeasible. It is virtually impossible to infer the functional or mechanistic basis of foraging behaviour, especially when it is highly variable in space and time, from observations which are unsupported by controlled experimentation and detailed measurements (Illius and Hodgson, 1996). Simulation models may be the only feasible alternative when experimentation with live animals is not possible, due to problems of scale and time (Turner *et al.*, 1989).

Modelling is an effective tool for gaining a better understanding of complex real systems and this is the approach of the research presented in this thesis. Modelling can provide a basis for investigating herbivore foraging strategies and the effect of the strategies on herbivore performance and the vegetation, and provide insight into optimising system performance.

A spatial and temporal grazing model for semi-arid regions is described in the next chapter and this model was used to investigate the movement of animals in response to the vegetation present and the effect on the system in terms of animal condition and state of the vegetation. A model has been developed that simulates the dynamics of a semi-arid rangeland including the vegetation dynamics and animal behaviour. The reasonableness of the model output was checked against expected outcomes and the model was fine-tuned. Various grazing strategies are investigated and their result on animal condition is discussed. Management implications are then discussed as a result of the model output.

We begin with a discussion of some of the work done in investigating rangeland dynamics and more particularly the models that have been used. The problem of understanding grazing dynamics can be broken up into four areas. The first of these areas concerns the plant production and how to model the plant growth as it responds to various climatic conditions and grazing pressures. The next area is modelling herbivory. This has two components : where animals choose to feed and their movements, and secondly what they choose to eat. The last consideration is how to model the animal's condition in response to grazing and other activities. All four of these areas are discussed in the rest of this chapter.

1.5. PLANT PRODUCTION MODELS

Much research has gone into understanding plant production and there are many models of plant growth with varying degrees of complexity. The simplest models of plant growth are simple regressions of annual net primary production (ANPP) on rainfall-related measures (reviewed by Wisiol, 1984). This is a very basic approach which does not include factors such as season and only models the total vegetation biomass. Plant growth can also be modelled in terms of being limited by light interception as is the case in carbon budget models (e.g. Noy-Meir, 1978; Fryxell *et al.*, 1988) where growth rates are described as a function of plant biomass through its associating with light interception and respiration. Fryxell *et al.* (1988) modified Caugley's (1976) model which uses difference equations to approximate the set of differential equations. In this model, daily growth depends on an intrinsic rate of increase, a constant that shifts the productivity curve toward the origin, the vegetation biomass and the peak vegetation in the absence of grazing. Noy-Meir (1978) described a model where the rate of growth depends only on total green biomass. The growth rate is a ramp function of biomass, minus a maintenance respiration loss rate which is linearly proportional to biomass. The models of both Fryxell *et al.* and Noy-Meir neglects variations in growth parameters within the season due to variations in environmental factors and do not include the effects of variable rainfall. They describe the vegetation in terms of biomass present only and do not consider the plant components (such as leaf and stem) separately.

More complex models include both the carbon and nitrogen budget of the plants. Coughenour *et al.* (1984) modelled perennial graminoid growth in a simulation model that unites morphometric (plant form) traits with physiological processes: vegetative production (number of shoots, vegetative culms and reproductive culms), assimilation and allocation of carbon and uptake and allocation of nitrogen were all modelled in detail. Coughenour *et al.* 1984) differentiated between plant parts as well as recorded the age and height of plant tissue. The processes of shoot growth, tillering, root growth, photosynthesis, nitrogen uptake and translocation were all included. Allocation of biomass to plant parts is important when modelling foraging dynamics as the animals' response towards different plant parts differs drastically as some parts are more desirable.

Blackburn and Kothmann (1989) describe a deterministic model. The model does not simulate growth, but simulates the accumulation of live leaf and stem, the senescence of live biomass, and its transfer to dead mass using growth rates from leaf and stem for various species. This model uses age to control senescence and quality making it easy to adapt the model to different environments which have different growth patterns. The model originally included parameters for Texas.

A more detailed approach defines growth relationships based on water-use efficiency and soil-moisture budget (e.g. Hobbs *et al.*, 1994; Dye, 1983; Richardson *et al.*, 1991). The rainfall is partitioned into runoff and infiltration and incorporates evaporation from the soil and transpiration. This type of approach models plant production more realistically in rangeland systems, as water is a limiting factor and the daily rainfall as well as the pattern of rainfall have a large effect on primary production.

There exist a large number of detailed process models (Hanson *et al.*, 1988; Moore *et al.*, 1991; Richardson *et al.*, 1991) which allow for nutrient pools, litter and perhaps several plant pools on a weekly or daily time-step. Mechanistic grass-sward models (e.g. Thornley *et al.*, 1994) may incorporate complex factors such as leaf geometry, internal plant shading and the physiology of photosynthesis. Smith and Williams (1973) developed a deterministic model where the plant production was described in terms of weight of herbage ($kg.ha^{-1}$) and plant density ($plants.dm^{-2}$) for Western Australia. Historical daily rainfall data as well as pan evaporation and hours of sunlight were inputs. Equations estimate leaf area index, soil productivity and moisture. The mathematical model is a set of first order differential equations which are continuously integrated over time.

There have been large models built by various groups of researchers for the purpose of investigating the whole grazing process and all its interacting components. SAVANNA (Coughenour, 1995), SPUR (Hanson *et al.*, 1988) and GRAZPLAN (Donnelly *et al.*, 1997; Freer *et al.*, 1997; Moore *et al.*, 1997) are all examples of large grazing models incorporating detailed representations of soil moisture, plant growth, herbivory and animal dynamics. In the next few paragraphs we look at what models of plant growth they use.

SAVANNA (Coughenour, 1995) simulates net primary production in response to precipitation, water loss and water-use efficiency. It is a very detailed model using satellite images in a GIS to extract spatial, temperature and rainfall characteristics of the study area. Water loss from the system is by evaporation from the soil surface depending on soil water content. Water loss from the plant surface is by transpiration, which depends on potential evapotranspiration, stomatal conductance, vapour pressure deficit, day length, and green leaf biomass. The model also simulates light intensity and leaf area index which are then used to work out potential evapotranspiration. Coughenour includes a water budget sub-model which allocates rainfall to evaporation, runoff and infiltration into various soil stores. Water-use efficiency is a measure of plant-specific conversion of soil moisture into biomass. SAVANNA models the herbaceous, shrub and tree layers as populations which mature and change in number, size and cover.

SPUR (Simulation of Production and Utilization of Rangelands) (Hanson *et al.*, 1988) simulates the daily dynamics of given range sites. This model brings rainfall, photosynthesis and nutrients together by defining expressions for each stage of the hydrological, physiological and morphological properties of an ecosystem. This is another very detailed model that includes water, carbon and nitrogen budgets which use daily precipitation values, maximum and minimum temperatures, solar radiation levels and wind speeds. This model has been developed and tested in Texas. The hydrology component maintains daily water balance, calculates snow accumulation, snowmelt and sediment transport. The soil model tracks soil moisture by soil layer according to soil series characteristics and soil carbon and nitrogen levels. The plant module tracks carbon and nitrogen flows through various live and dead state variables, and has the potential to simulate competition between species.

GRAZPLAN (Donnelly *et al.*, 1997; Freer *et al.*, 1997; Moore *et al.*, 1997) contains a suite of complementary decision support systems for grazing systems in Australia. It was designed to be used in conjunction with local weather and farm data to test the relevance of different management procedures for individual farms. The Pasture Growth and Soil Moisture sub-models both operate at a daily time step. The pasture growth model is quite general in structure but recognises different functional groups of plants as well as different classifications of shoot tissue and the phenological development of the plants. Seed and seedling dynamics are part of the model. A mechanistic approach has been adopted here. The Soil Moisture sub-model simulates runoff, rainfall interception by plants, soil evaporation, plant transpiration and a multi-level soil storage structure.

One of the main failings of forage production models derived from high productivity pastures is that they mostly treat the pasture as an aggregated point without spatial variation. There are exceptions to this (Coughenour *et al.*, 1990; and Pickup, 1995) but none has been widely applied to management. The simplified models predict forage production adequately for most rangelands dominated by grass.

Different degrees of detail are necessary depending on the objective of the modelling, and as is clearly apparent, there exists a large spectrum of available models which have been well parameterised and tested for various sites. In rangelands, since rainfall has such a large influence on the variation in primary production, it is crucial in modelling plant growth to include rainfall as an input, and it has been argued that a detailed water-budget model is necessary to adequately capture the water dynamics. Seasonality has a large effect on grass growth and must also be included, whether in terms of temperature or radiation or day of the year. The partitioning of plant biomass into more detailed categories such as leaf and stem is important in modelling herbivory, that is, the animal's response to the vegetation, as will be discussed later. As the scope of this research does not include fieldwork, a model that has been parameterised for a suitable area and grass type is desirable, and since there exist many models already developed, an existing plant production model will be used.

1.6. FORAGING MODELS

Foraging behaviour and diet selection play a pivotal role in grazing systems, not only by linking primary and secondary production, but also because it is the selectivity of herbivores which mediates and localizes their impact on the population ecology of plant species (Brown and Stuth, 1993). For foraging ungulates the selection between patches is the main tool by which they can manipulate forage intake rate and quality (Wallis de Vries and Daleboudt, 1994). Yet, despite its importance, the mechanisms underlying diet selection remain obscure (Illius and Hodgson, 1996).

Numerous experimental studies and models have considered the basis of diet selection in grazing animals. There are theories of diet selection based on intake rate maximisation (Westoby, 1974; Owen-Smith and Novellie, 1982; Arnold, 1987; Ungar and Noy-Meir, 1988); learning through consequences (Provenza and Balph, 1990); and nutritional wisdom (Westoby, 1974). Some studies consider the effects on diet selection of previous dietary experience (Newman *et al.*, 1994; Parsons *et al.*, 1994) and of animal size and morphology (Gordon and Illius, 1988). Edwards *et al.* (1994) reveals that the diet selected is dependent on three further factors: the scale and spatial distribution of the food resource, and the physiological state of the animal. Dumont and Petit (1998) show that sheep are able to quickly learn the distribution of sites which have a preferred food, and that area-concentrated searching allows the animals to forage efficiently within the sites. Long-term spatial memory was found by Laca (1998) to be the most important factor for determining encounter rate of food locations.

Although there have been a number of approaches adopted, most foraging models have been limited to finding the strategy that optimises energy intake over short time periods (Stephens and Krebs, 1986). Free-ranging large herbivores experience changes in forage quality, quantity and availability during the year and have to increase their intake as well as modify foraging behaviour both spatially and temporally to maintain a positive annual energy balance (Moen *et al.*, 1997). Consequently, herbivores respond to spatial and temporal variability in food resources by selectively foraging on the landscape (Senft *et al.*, 1987 and references therein). Thus, the spatial component of foraging cannot be ignored when modelling herbivory of free-ranging animals.

Foraging of herbivores can be usefully categorised as a nested hierarchy of decisions (Senft *et al.*, 1987, Kotliar and Wiens, 1990) at various spatial and temporal scales. The upper levels in the hierarchy constrain processes at lower levels while lower level processes explain mechanisms producing higher ones (Allen and Starr, 1982). For example, choices of plant patches constrain the foraging behaviour of herbivores by committing them to eat plants available within the patch if they choose to remain in that patch.. However, variation in food-intake rates within the patch can explain why patches are chosen and how they are exploited. Similarly, processes operating at daily time scales set an upper limit on food intake by constraining feeding time and digestive capacity, but instantaneous intake rates explain how much food the animal is actually able to obtain within a day (Spalinger and Hobbs, 1992).

At small scales of space and time, existing models capture the essence of the feeding process and successfully predict intake rates (Gross *et al.*, 1995). Noy-Meir (1978) used a ramp function of biomass to model the consumption per animal (intake). Fryxell *et al.*

(1988) assumed that the daily rate of forage consumption by individuals is related to vegetation abundance which is a type-II functional response (Holling, 1959). The formula indicates that forage intake per herbivore rises initially with increasing vegetation biomass but levels off at high biomass because of the restricting effect of fixed handling time (feeding plus digestion). Illius and others have done much work in the area of predicting intake of herbivores (Illius and Gordon, 1998) and we parameterise the functional response they use for our purposes. The animals' intake depends on available biomass, proportions of different components in the sward such as live leaf, the selectivity of the animal, the digestive capacity of the animal, and the animals' metabolic and nutritional requirements.

The choice of where to forage and how the animals move is far less understood. Many widely varying approaches have been adopted in modelling animal movement and choice of where to forage. They vary from distributing the entire herbivore population in relationship to the spatial distribution of habitat suitability on a monthly basis (SAVANNA, Coughenour 1995), to modelling the explicit movements of the animals based on rules which may or may not be based on the theory of optimal foraging. The models differ widely in spatial scale with some incorporating migration and choice of landscapes (e.g. SAVANNA, Coughenour 1995) to hourly movements (e.g. HOOFS, Beecham and Farnsworth 1998), the latter being less researched. The next sub-section discusses the theories and models in more detail.

1.7. HERBIVORE FORAGING STRATEGIES

1.7.1. Introduction

Understanding herbivore movements emerges as an important component for understanding spatial heterogeneity in natural landscapes (Gross *et al.*, 1995). When forages are abundant, the search rule employed by a herbivore is probably unimportant, since encounter rate with food does not limit foraging efficiency (Spalinger and Hobbs, 1992, Gross *et al.*, 1993). However, as food abundance declines, an herbivore's ability to efficiently locate and move between forages can strongly affect the pattern of resource depletion and, ultimately, survival of the animal (e.g., Turner *et al.*, 1993).

The following paragraphs provide descriptions of the major theories and models relating to herbivore foraging.

1.7.2. Optimal Foraging Theory

The Concept

Optimal foraging theory (Schoener 1971, Pyke 1984) provides a functional approach for examining grazing behaviours, including diet selection, patch selection, and movements. It generally assumes that animal fitness is related to foraging behaviour, foraging behaviours are heritable, and that a currency (e.g. energy, protein) can be identified to link foraging behaviour with fitness (Pyke 1984). The theory of optimal foraging assumes that fitness will be maximised by natural selection and that the maximisation of fitness will result in the maximisation of foraging efficiency (Gray 1987). Relatively few optimal foraging theory studies have focussed on herbivores, primarily because of complications imposed by digestive constraints and the difficulty in defining discrete food items or quality (Bailey *et al.* 1996). Optimal foraging theory has been developed for predators and nectar feeders rather than large herbivores. Predators generally seek spatially scattered prey of nearly constant and high nutritional value. Large herbivores, in contrast, confront an apparent food surplus, which is of low and highly variable nutritive quality (Belovsky, 1984; Westoby, 1978). Compared with the prey consumed by predatory animals, the food of the large herbivore is much more likely to be widely dispersed over the landscape, rather than concentrated in discrete patches (Senft *et al.*, 1987).

In general, optimal foraging models are based on the assumption of independent Poisson encounters with prey (Stephens and Krebs, 1986) but search mechanisms may be more complex and such complexity may strongly modify foraging behaviour (McNair, 1979; McNamara and Houston, 1987). Spalinger and Hobbs (1992) have shown that, on a small spatial scale, the interplay between searching, handling and food density strongly influences the feeding rate of ungulates. Optimal foraging theory is useful in explaining the short-term behaviour of animals, but as the intervals of time and space are expanded, the context of feeding behaviour becomes more complex. Optimal foraging models can still be useful tools in the study of foraging behaviour of grazing animals. Most of the criticisms of the application of optimal foraging models to grazing animals can be addressed by simply refining the constraints and by including behaviours other than foraging in the model (Laca and Demment, 1996). A crucial aspect of grazing animals is the assumed search strategy, and the predictions of optimal foraging models depend critically upon this (Focardi *et al.*, 1996).

Currencies

Various currencies have been suggested that relate animal fitness to foraging behaviour. The most common currency is assumed to be the long-term average intake rate of energy (Fryxell, 1991; Murray, 1991; Thornley *et al.*, 1994; Ward and Saltz, 1994), although there have been other alternatives. Verlinden and Wiley (1989) present an alternative model of diet selection in which digestive rate is maximised as opposed to energy intake. Another alternative currency is dry matter intake rate (Illius and Gordon, 1992; Laca *et al.*, 1993). Owen-Smith and Novellie (1982) present an optimal foraging model applicable to large herbivores in which they assume that the majority of nutrients, including digestible energy as well as protein and specific minerals such as phosphorus tend to covary in their availability within plant tissues. Thus quality rankings of food types can be expressed along a single axis. A "clever ungulate", defined as a short-term maximiser for nutrient intake alone, should select a diet that maximizes the intake rate of the most limiting nutrient during foraging periods (Owen-Smith and Novellie, 1982). Murray (1991) argues that the costs of locomotion are frequently ignored in models determining the optimal diet of free-ranging ungulates. Murray hypothesises that the major constraint on diet selectivity of free ranging herbivores is not a declining rate of intake but an increasing expenditure of energy in foraging. He assumes that free-ranging ruminants usually compensate for reduced, short-term rates of intake by extending the duration of foraging periods, so maintaining daily intake on all but the shortest of pastures. Wallis de Vries and Daleboudt (1994) found that matching for digestible organic matter intake rate yielded the worst predictions of patch selection. Matching for digestibility gave the best explanation of patch selection where digestibility is an indication of the quality of food rather than quantity, and so perhaps the currency should somehow include digestibility of the available food.

There has been debate over rate maximisation being a valid assumption, and strictly speaking, one should not expect animals to maximise intake rate while (apparently) feeding because of other activities that are interspersed with feeding during the day (chewing, staying with the herd, etc.). Yet, rate maximisation is a useful assumption if we understand and control the context in which it is applied. Animals may maximise intake rate with respect to patch choice or diet selection within the context of grazing time restrictions (Laca and Demment 1996).

Thresholds

The predictions of optimal foraging models are often characterised by the existence of thresholds, i.e. by discontinuities in the behaviour of the animals determined by non-linear responses to resources. Thresholds arise also in the analysis of optimal patch-residence time based on the marginal value theorem (Charnov, 1976): the threshold is determined by the long-term average rate of foraging.

An essential premise of optimal patch-use models is that the forager experiences diminishing returns within a patch, and that moving to a new patch is costly in terms of time and energy. The reduction in intake rate as food is depleted within a patch has been termed as "depression" (Charnov, 1976). The decision to leave a patch and to select a new patch may be based on the rate of forage intake at the present patch, the expected rate at other patches, and the cost of moving to a new patch. Foragers should remain in a patch until forage is depleted below some threshold, until a certain amount of forage has been taken, until a certain time has passed in the patch (Charnov, 1976), until a certain time has passed since a food item has been procured (McNair, 1982), or until intake rate falls below some level (Cowie and Krebs, 1979). Thresholds are reached more quickly in poor patches than in rich ones. Thus, patch residence times will be proportional to relative food availability, resulting in a matching pattern. (Senft *et al.*, 1987)

Threshold of acceptance is presumably conditioned by recent experience. Each encounter with a high-quality item raises the threshold, while encounters with low-quality items lower the acceptance level (Senft *et al.*, 1987).

Other alternative theoretical approaches to thresholds predict a more gradual change in foraging behaviour (Focardi *et al.*, 1996) such as satisfycing (Ward, 1992) or hedyphagia (see Provenza and Balph, 1990 for a recent review). Satisfycing denotes problem solving and decision making that sets an aspiration level, searches until an alternative is found that satisfies the aspiration level criterion, and selects that alternative (Ward, 1992). The animal is satisfied after meeting some minimum requirement. The lack of complete information or an information-processing constraint limits the ability of an animal to make an optimal decision.

Momentary Maximisation

Diet selection by large herbivores requires the solution of two opposing problems: obtaining maximal quality and adequate quantity (Senft *et al.*, 1987). Herbivores may utilize momentary maximisation to solve the quality-quantity problem. Momentary maximisation dictates sequential acceptance of the most palatable items encountered at each feeding location until palatability decreases to some threshold level and describes foraging of herbivores at a small scale sufficiently. Maximisation over a longer period of time becomes far more complex as movement and awareness of the surrounding food and social factors come in to play.

Travelling salesman problem

In choosing where, when and what to eat, the animal has to move between plants and feeding stations. The time and cost of travelling between food items can be substantial, even when a forager can readily locate and move directly between foods. In this case, benefits may be maximised primarily by reducing travelling costs, rather than by careful selection for item size or quality. Thus, to maximise intake rate the foraging animal would need to solve a variant of the 'travelling salesman problem' identifying the shortest path that visits a number of discrete locations (Gross *et al.*, 1995). This implies spatial knowledge and memory of the entire area available to forage in. This is in accord with the principles of optimal foraging theory, but is not easily applied to large herbivores where the distribution of food is continuous, and there are no discrete food items separated by distances.

Ideal free distribution

Ideal free distribution refers to the theory where organisms have equilibrated their fitness by distributing their individuals proportionately as regards the resources that can be obtained from those habitats. The densities of the consumers correlate perfectly with the densities of the resources within the habitat (Rosenweig, 1991). In practise we know that most animals are social creatures and tend to stay close to the herd, and spacing of animals is not necessarily optimal with respect to forage intake.

1.7.3. Rule-based models

Herbivores frequently consume prey that can be seen from a relatively long distance, thus rules that help reduce the length of travel between plants are likely to be more important than rules used to search for cryptic prey (as in optimal foraging theory). Animals are typically confronted with a spatially complex environment containing many potential foods, and they are limited in their ability to collect, synthesize, and analyze information. Because cognitive processing abilities are limited, it is likely that foraging animals use parsimonious rules-of-thumb to navigate between foods (Gross *et al.*, 1995).

Gross *et al.* (1995) demonstrate the value of evaluating a spectrum of strategies that animals might use to solve complex problems. The use of simple rules of thumb is well-established in economic theory, based primarily on the rationale that accurate and complete information is costly to acquire and time-consuming to analyse. Foraging animals confront similar constraints.

We will discuss various approaches adopted in herbivore foraging models.

Random Walk

The simplest rule-based foraging model is the random walk model, where the animals are assumed to have no knowledge of their immediate surroundings, and leave a certain location after a period of time, or an amount of food has been consumed or a threshold has been reached. Many studies have shown that movement rules based on random walks are clearly inappropriate for many herbivores that typically consume visually apparent plants (e.g. Gross *et al.*, 1995). Ward and Saltz (1994) found that gazelles feeding on lilies followed a path that was far more systematic than a random walk. Gazelle foraging paths were characterised by a series of short moves interspersed with occasional long, straight moves to other forage 'patches'.

Nearest Neighbour

Gross *et al.* (1995) suggest the use of a nearest-neighbour rule for modelling foraging by large herbivores as a more viable rule than random walk.

Random walk – Moving Window – Travelling Salesman

Gross *et al.* (1995) modelled a spectrum of rules that could describe the movements of animals between foods. The rules were bounded at one extreme by a random walk (RW), and at the other by the shortest possible path to all available items, the travelling salesman (TS) solution (not returning to origin). Between the RW and TS rules exist a myriad of strategies that include a correlated random walk, a spiral or systematic search, and what we call a moving window rule (MW; similar to the 'L-step-look-ahead'; Anderson, 1983). The MW strategy is a variant of the TS rule, and is employed as follows. An animal looks ahead from its current location and evaluates all potential paths to n items (MW-n). It then chooses the shortest path, moves to the n plants and 'consumes' them, and continues by repeating the process. When n = 1, the animal always moves to the nearest neighbour (NN) plant and when n = total number of plants, the MW and TS solutions are the same. The value of n referred to the detection distance of the animal – how far ahead the animal considered in making its feeding decisions.

Other Rule-based Models

In the absence of data, models that incorporate foraging by large herbivores have employed several different rules to determine animal movements. For example, two recent models used directed movement at a larger scale and then assumed random searches within a smaller grid (Hyman *et al.*, 1991; Turner *et al.*, 1993). Suitability, distance from other patches, presence of other animals and time since the last visit were 4 rules used by Hyman *et al.* (1991) to direct herbivore movements in a spatially explicit foraging model. Turner *et al.* (1993) also developed a spatially explicit model in which large ungulates moved among sites based on one of three rules. Each rule assumed different cognitive abilities of the herbivore. The simplest rule was to move to the best adjacent site. The other rules were move to the nearest site with available resources and move in the best direction for the overall availability of resource sites.

Another model assumed a nearest neighbour rule for plants within a detection distance, and a correlated random walk when there were no nearby plants (Roese *et al.*, 1991).

Moen *et al.* (1997) defined a foraging strategy as a combination of a stopping rule and a movement rule in the spatially explicit model, EASE. The stopping rules are either (1) a binomial stopping rule (decide after each bite whether to move or not with the probability set at either 0.5, or 0.7, or 0.9), or (2) a fixed stopping rule (remove 33% from the feeding station and then move) or (3) a fractional stopping rule (remove 5 to 65% of the biomass uniformly and then move). The movement rules are either (1) a random neighbour movement or (2) a best neighbour movement.

Focardi *et al.*(1996) argue that the foraging behaviour of fallow deer consists of two basic components: a random search for food coupled with a threshold in the selection of foraging stations. Spatial memory has also been incorporated into several rule-based models that predict herbivore movements on a larger scale (e.g. Bailey *et al.* 1996).

An interesting adaptation of optimal foraging theory was used by Beecham and Farnsworth (1998). They developed a model system HOOFS (Hierarchical Object Oriented Foraging System) to study foraging by animals in a complex environment. They demonstrated that social interactions constrain patch choice and result in short-term reduction of intake and a greater degree of variability in the level of resources in patches. The model simulates the cyclical foraging process of evaluating discrete vegetation patches, selecting the next patch destination, deciding how long to remain on the present patch, and then moving to the next patch. The rate at which energy is obtained from a patch by an animal will depend on the energy content of the food source and the rate at which the food can be obtained. This rate is determined by the fixed time costs of searching for food and moving to a new patch and the marginal costs are either expressed as handling time per unit of energy or a marginal rate of intake. The point at which an animal gives up feeding from a patch can be calculated using the marginal value theorem of Charnov (1976). The amount of information available to an animal is assumed to be inversely proportional to its distance from the patch. The animals did not have perfect knowledge of the entire area, but were aware of their surroundings.

Many recent foraging models include rules dictating animal movements, and these are useful tools in investigating how animals move in complex environments where forage resources are not uniformly distributed and many factors (such as social interactions, memory, awareness of the surrounding locations, physiological state of the animal) interact in influencing foraging behaviour.

1.7.4. Discussion

Proponents of the optimal foraging theory have incorporated the assumption that an animal knows not only the value but also the location of all patches in patch choice and patch use models (Pyke, 1984). This is not a valid assumption over large areas, but one can assume that within a small patch, animals forage so as to maximise their fitness and that they employ other intuitive rules when making movements. Energy maximisation is a reasonable assumption in herbivore foraging strategies at a small scale, as the various dietary requirements do tend to covary (Owen-Smith and Novellie, 1982). At a larger scale, the costs of locomotion must be considered and so net energy is a more suitable currency.

Animals are confronted with two choices whilst foraging: how long to spend in a particular position, and where to move to next. There is much debate as to how intelligent grazing herbivores are, and in modelling the foraging process, it is important to evaluate a range of cognitive abilities. How social interactions constrain foraging is also not well understood. Memory effects may play a role in where an animal will move to next, but to what extent this occurs is debatable. The animal's awareness of its surroundings and its ability to evaluate the returns it will get from moving is another aspect that is not clearly defined.

Little work has been done with respect to the foraging patterns and decisions of free-ranging herds of animals. Interesting questions arise from herd movement at a smaller scale, that is not migration or seasonal movement. Bailey (1995) found that steers within a group usually followed one or two individuals as they first entered a patch. It seems probable that individual animals influence the feeding areas selected by the herd, but do they move as to maximise energy intake for themselves only, or for the herd as a whole? (herdsmen may guide the herd in which case the choice of feeding area is based on the entire herd's needs). Energy intake depends on the quality of the food in the patch, but also on the quantity, and as the animals graze, there will be diminishing returns from grazing.

In modelling foraging strategies, we will explore a number of the issues mentioned above and their effects on the herd's condition.

1.8. HERBIVORE POPULATION DYNAMICS

Most foraging models model the herbivore population dynamics explicitly in terms of births and deaths (e.g. SAVANNA, Coughenour, 1995; GRAZPLAN, Freer *et al.*, 1997; Fryxell *et al.*, 1988), and many include tracking population classes such as pregnant females, lactating new-borns as they have different requirements and metabolisms.

Population dynamics become important when one is concerned with the long-term dynamics of plant-herbivore ecosystems. Modelling the energy balance of the animals is a way of keeping track of the animal condition and many foraging models contain energy-balance sub-models (e.g. SAVANNA, Coughenour, 1995; GRAZPLAN, Freer *et al.,* 1997; HOOFS, Beecham and Farnsworth, 1998; EASE, Moen *et al.,* 1997). Sometimes other body component variables are kept track of, such as in EASE where water, protein, fat, ash and rumen contents are included.

Beecham and Farnsworth (1998) demonstrated that social interactions constrain patch choice and result in short-term reduction of intake and a greater degree of variability in the level of resources in patches. Often, patterns of space use emerge from the behavioural interactions of individual herbivores. The two general social behaviours that must be considered are grouping and repulsion (Hyman *et al.,* 1991).

A group size of 25 animals in a herd is quite standard for herbivores in African situations. A group size of 3 for cattle is still normal in rural areas but so are herds of about 200. Groups smaller than 3 are extremely rare because cattle become "unhappy" then. The essential aspect is the nearest neighbour distance. This distance depends on (a) the number of animals in the group (the larger the herd, the smaller the nearest neighbout distance), and (b) quality of the food. In some areas, the distance between individuals is about 2.5m but it can increase to about 7m. (personal communication, Prins).

Shiyomi and Tsuiki (1999) conducted a study on the spatial pattern of a small cattle herd within a fenced pasture using a mathematical model. They defined herd length to be the distance between the two most distant individuals. They found the optimum herd length for 6 cattle to be 27m during resting, 49m during feeding and 71m during moving.

A population model including births and deaths is important when modelling rangeland grazing systems over a longer time period than a year. Animal condition is important to monitor, and energy balance models are useful in this regard. Grazers must be modelled as a herd in order to capture the behaviour of the herd as a whole as well as the spatial impact of the herd's grazing on the vegetation.

1.9. CONCLUSION

In order to investigate foraging behaviour of grazing herbivores, a model shall be built based on empirical research and other grazing models. As spatial grazing strategies will be investigated, a spatially explicit model is chosen to represent the system. Since we are interested in the short-term dynamics of the system, simulations run over a single year. Animal population dynamics are not included because of the short time frame. No vegetative reproduction or seed distribution occurs over the time span of a year and so the vegetation dynamics in each cell are independent of one another. A suitable plant production model is adapted for a spatial environment, the forage intake and energy balance of herbivores are defined, and various foraging rules are included which allow us to simulate a spatial grazing system and gain an understanding of the dynamics involved.

CHAPTER TWO

FORMULATION OF THE MODEL

2.1. INTRODUCTION

The objective of building this model is to investigate how animals move around in an area and what the effect of their movements on the state of the system is. In order to achieve this, a simulation model has been constructed which is both spatially and temporally explicit. Foraging models must be spatially explicit in order to address problems with the spatial distribution of forage resources (Pyke, 1983). As the vegetation distribution and growth changes over time in response to rainfall and herbivory, the model must be temporal.

One of the fundamental questions in modelling concerns the level of detail required. A model must simulate the system's behaviour with sufficient accuracy to achieve the desired goal. The simplest type of model aims to capture the main properties of the system's behaviour with the smallest number of parameters by excluding both unnecessary detail and explicit description of the deeper causal relationships. Detailed mechanistic models aim to go much further in describing the underlying causal relationships, and are, in principle, capable of representing complexities of the system more faithfully, but risk becoming bogged down in detail and by parameters whose values are poorly defined. A balance must be struck between these two approaches, by defining the level of detail which satisfies the goals of modelling, within the constraints imposed by the quality of information about the system (Illius *et al.*, 1999).

2.2. SCALE

Timeframe and step

A vital component of the model is some indication of the fitness of the animals at the end of the year (before the new rains have fallen) as they have responded to the changes in biomass over the year. Thus, only the short-term dynamics of grazing systems are considered and a time frame of one year has been chosen which starts just before the rainy season. Primary production is driven by rainfall and the data for rainfall is usually captured on a daily basis, and so a daily time-step seems an appropriate choice for the model. Most vegetation growth data and models operate on a daily time scale as the finest level of detail and we have chosen a daily time step for the vegetation growth. Animal movement is modelled in response to the vegetation distribution, and grazing affects the spatial distribution of the vegetation, and a time step larger than a day would not capture the feedback effects of grazing adequately.

Foraging herbivores respond to the spatial pattern of resources at a variety of scales. At small scales of space and time, existing models capture the essence of the feeding process and successfully predict intake rates. Models that operate over larger scales have not exhibited a similar success, in part because we have limited understanding of the rules used by animals to make decisions in spatially complex environments, or of the consequences of departing from these rules (Gross *et al.*, 1995). Indeed, the purpose of this model is to investigate what effects various movement strategies have on the animals. The scale at which to model the feeding process in this model has been chosen so that animal movements between feeding bouts are modelled and not movements within the feeding stations (relatively well understood) which roughly translates into hourly movements depending on the density of the vegetation. A feeding station is defined as the sward volume accessible to an animal without moving its forefeet (Goddard, 1968 quoted by Roguet *et al.*, 1998). Patches consist of a continuous array of feeding stations in a grassland: Animals may visit numerous patches in a given day and a timestep simulating feeding decisions is embedded within the daily timestep. This will be discussed later.

The energy-budget component of the model is updated at the end of each feeding day.

Spatial Scale

Senft *et al.* (1987) characterised foraging by large herbivores as a nested hierarchy of responses to landscape features – plants, small patches, large patches, landscapes and regions. At the plant community scale (plants, feeding stations and small patches), herbivores are concerned with diet selection and are making approximately 20 decisions per minute hypothetically based on momentary maximisation (Senft *et al.* 1987). The landscape scale in the ecological hierarchy involves feeding area selection and a time frame of hourly decision-making with the goal of optimising foraging efficiency. At the regional level, migration and home ranges are described.

Foraging decisions at broader spatial and temporal scales can constrain choices at lower levels. The decision as to where to begin grazing at the beginning of a bout limits the potential number of smaller scale choices if the home range or pasture is large. Distant plants and patches are not available during the current bout because of geographic isolation. Distant vegetation may not be visible, and animals would incur energetic costs for travel to other feeding sites. At a smaller scale, selection of a feeding station limits the potential number of plants that an animal may select. The herbivores must search and move if plants within the chosen feeding station are rejected. However, energetic costs required to move from one feeding station to the next are usually small and the consequences of selecting a feeding station are also small (Bailey *et al.,* 1996).

As mentioned before, at small scales of space and time, existing models capture the essence of the feeding process and successfully predict intake rates rules (Gross *et al.,* 1995). We have used equations defined by Illius and Gordon. (1991, 1992, 1998), which define the functional response of the animals to available food at a patch level and are concerned only with movement between these patches or feeding areas. The model developed in this thesis looks at the large patch or landscape level only (see definition of landscape above, Senft *et al.*, 1987).

2.3. A GRID-BASED MODEL

A spatially explicit modelling approach has been adopted in order to capture heterogeneity in the landscape and vegetation cover as well as to be able to model animal movements explicitly as they move around and forage. Because the aim is to investigate spatial grazing strategies, it was necessary to have a structure that would allow us to specifically test different movement strategies and a grid-based model allows us to define exactly where the herd will feed at any given time. It also makes it possible to keep track of the changes in the spatial distribution of vegetation biomass as animals feed in the different areas. A grid-cell modelling approach also allows modelling of landscape patterns as well as distances between patches. The area to be modelled is assumed to be rectangular and is divided up into regular square grids. Each cell in the grid is defined in terms of its location or position in the grid and the area it occupies. The cells include information about the types and the amount of vegetation present in each cell as well as the proportion of live to dead and leaf to stem in each vegetation type. The area is assumed to be homogeneous in terms of soil type and rainfall distribution, but these and other factors can easily be added. The heterogeneity exists only in the distribution of vegetation biomass at this stage.

The size of the area to be modelled should be large enough to exhibit the spatial effects under investigation, and small enough so that no migration or long term movements are considered as this is beyond our scope. An area of approximately 1000ha is a suitable choice, and one can assume that water is readily available over the entire area. In order to be able to divide the area into a round number of cells, 900ha was chosen which translates into a 3km by 3km area. The cell should represent a habitat area that the organisms treat as a homogeneous unit (Hyman *et al.*, 1991). The area is divided into square cells, each one hectare in area. An area of one hectare can fit 200 animals even if the nearest neighbour distance is a maximum (7m). The distribution of vegetation is assumed to be uniform within each cell, and that grazing is uniform across the cell. Movement within the cells is negligible, as the animals in the herd are evenly distributed across the cell and are only moving between different patches.

2.4. BASIC COMPONENTS OF THE MODEL

The spatial model has 4 basic components. The first sub-model simulates the vegetation dynamics in each cell. The second sub-model simulates what the animal herd will eat in a given area. The third contains the spatial foraging rules and describes where the animals will choose to eat at any given time. The last sub-model is an energy-balance model which keeps track of the energy expended and consumed by the herd as a whole.

The plant-herbivore interactions are modelled only in terms of the plant's response to defoliation by the herbivore and the herbivore's choice of where to feed and what components of the plant it eats in response to the available vegetation. Other factors such as trampling, nutrient recycling and the effect of insects may play a role, but have not been included in this model for simplicity's sake.

2.5. PLANT DYNAMICS

Primary production is described simply as the response to rainfall, season and defoliation by herbivores for the purposes of this investigation. Vegetation succession and colonisation have not been included in the model, as we are looking at a short period of time – one year only. Since the time frame is one year, no sexual reproduction occurs and there is no spread of plants into neighbouring cells. The vegetation in a cell is independent of any other cell. Each cell determines its own vegetation dynamics based on the amount of vegetation present and the rainfall and relative humidity. In order to model animal grazing strategies, we need a model that describes animal preference in terms of which areas they would choose to forage in. This preference depends largely on the proportion of live leaf, dead leaf and dead stem, and so allocation to plant parts is an important component of the model. The different proportions of plant parts in the sward also influences the animal's intake and digestion, and so modelling the plant parts explicitly is important in terms of the animal performance.

In looking to model the vegetation in terms of the simple parameters chosen and also requiring allocation of plant growth to the various plant components, VELD, a simulation model developed by Dye (1983) was found to be suitable. VELD is a plant-growth model for a semi-arid grassland cleared of shrubs and trees. Trees and shrubs affect grass growth in many ways and are not part of the scope of this research which considers only grazers and not browsers or mixed feeders at this stage. VELD simulates primary production, given relatively simple parameters namely daily rainfall data and humidity data which are readily available. Dye's model allocates primary growth to plant parts, where many other models model only primary production, which is a vital component of what we are modelling. VELD is based on data from Matopos Research Station near Bulawayo (a semi-arid region in Zimbabwe with approximately 600mm annual rainfall) and models the growth of a grassland dominated by *Heteropogon contortus* and cleared of shrubs and trees. The model is a daily simulation model and includes a detailed water-budget sub-model and a plant growth sub-model with allocation to parts. The model is driven by rainfall and is updated on a daily basis. The plant components are described in terms of biomass present (kg.ha^{-1}) in each of live leaf, dead leaf, live stem, dead stem. The simulation starts in September, after the dry winter and it assumes that all standing biomass is burnt or mowed down before the next growth season.

VELD has two major components, the water-budget sub-model and the plant-growth sub-model. The water-budget sub-model calculates infiltration and runoff given daily rainfall, and then calculates changes in soil moisture in three stores at different levels. Evaporation from the soil, which is controlled by the atmospheric evaporative demand and aerial cover of shoot mass, and transpiration by the plants are then removed from the soil stores. VELD's plant growth sub-model assumes that net plant growth is related to transpiration rate, corrected for humidity, by a water-use coefficient and a coefficient of seasonal photosynthetic efficiency. The net growth is then allocated to plant parts, namely roots and shoots (leaf, stem and inflorescence). Death of plant tissue is also simulated. VELD has been extensively written up in Dye's (1983) Ph.D. thesis and further details are given in Appendix 1 at the end of this thesis.

The following graph in figure 1 shows results from running VELD demonstrates the change in shoot mass over time as well as the change in the proportion of stem to live leaf

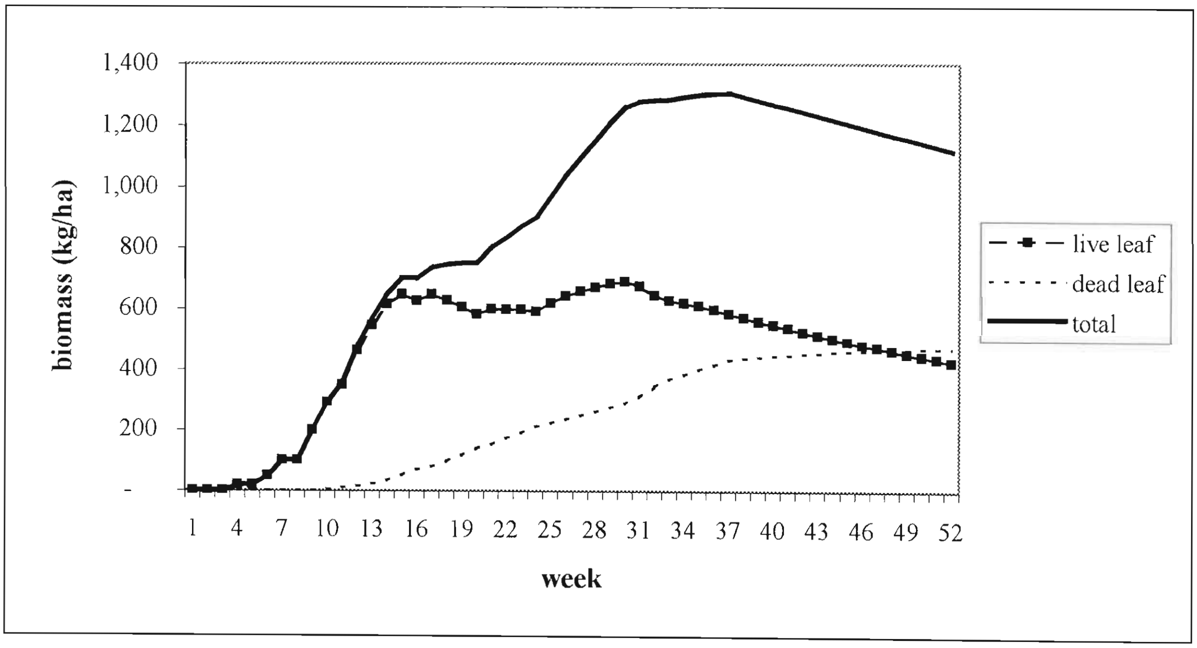

Figure 1. Growth of shoot mass as a function of time in various categories of ungrazed biomass for a semi-arid savanna dominated by *Heteropogon contortus* at Matopos, Bulawayo as given by the output of VELD.

to dead leaf with no grazing for a sward dominated by *Heteropogon contortus* at Matopos. As the animal's intake depends largely on the digestibility of the diet which in turn depends on the proportion of live to dead material, the increase of dead material towards the end of the season has a large effect on the animals' intake and condition. Figure 1 shows the change in available forage over time and the foraging animal's intake responds to this change in vegetation amount and different composition.

Dye's model is incorporated into the spatial model by running VELD in each cell at the beginning of each day before any grazing has occurred. VELD only simulates the growth season – from early September for 37 weeks, until the rainy season is over. For the remaining three months, no growth is assumed and a constant specific rate of death and decomposition ($kg.kg^{-1}.day^{-1}$) is applied to the live components and dead components respectively.

2.6. HERBIVORE DYNAMICS

The herbivores are modelled as an entire unit or herd. It has been suggested that the difficulties in modelling systems with variation between individuals can be overcome by representing animals as individuals rather than as part of an indivisible population (DeAngelis and Gross, 1992). According to Beecham and Farnsworth (1998), the added complexity of the individual-based approach is not generally beneficial if the additional information needed to calibrate parts of the model, such as dispersal, is not present (Wennergren *et al.*, 1995). We therefore have modelled the herbivores as a herd of a fixed number of animals, which move together as a unit across the spatial landscape.

The herbivores are described in terms of one or more herds which move around in the grid. Each herd is defined by its position in the grid at any particular moment, the area it occupies in terms of number of grid cells, the number of animals in the herd, the average mass of the particular animal chosen, and the average fatmass of the herd. The actual position of the herd is important in terms of simulating spatial grazing, both where the animals choose to graze and the spatial patterning that results from the grazing. The number of animals in the herd allows you to model the stocking rate and investigate the effects of various stocking rates on the herbivore condition. The average mass of the animal is used in calculating intake, digestive capacity, and is also an indication of the size of the animal, which affects the feeding ability of the animal (discussed later). Average fatmass of the herd is included, as it is an indication of herbivore condition. It is a variable, which is updated on a daily basis depending on the animal's energy intake as well as expenditure. This variable translates into how healthy the animals are, what their survival will be as well as their reproductive capacity. The herd's movement is controlled by rules. Daily food intake is modelled as well as the herd's energy balance as will be discussed in the next sections.

The vegetation growth in response to rainfall and the amount of vegetation present is updated on a daily basis. In order to describe accurately the herd's movement and feeding across grid cells (which roughly translates into a time-step of one hour depending on the how dense the vegetation which affects how often the animals need to move), the animals move many times within each day. Much work has been done in the area of what an animal will select at a given feeding station or plant, and we are concerned with the movement between patches or cells and not what occurs within the patch. We assume that each grid cell is uniform in terms of the distribution of vegetation and animals in that cell.

A model defined by Illius and Gordon (1987, 1991, 1992, 1998) is used in which daily animal intake is defined in response to the vegetation and the requirements and constraints of the animal. The following section describes what a single animal will eat in a day, given a particular sward described by density and proportions of the different plant components. This model has been adapted to describe the entire herd's intake and we define the herd's intake in the section following daily animal intake.

2.6.1. Daily Animal Intake

The animal's daily intake of food is defined by a functional response, which quantifies the relationship between daily intake and food abundance. It is dependent on the size of the animal, the selectivity of the animal as well as properties of the grass it is feeding on. Daily dry matter intake of a ruminant as a function of the animal's digestive capacity, the amount of available vegetation (above a residual level below which they cannot graze) and the size of the animal given by the following equation which summarises the digestive kinetics model of Illius and Gordon (1991, 1992):

$$I = a\,(1 - e^{-b\,(B-r)}) \qquad (1)$$

where

I = daily dry matter intake (kg),

a = asymptote defined by animal's digestive capacity,

B = vegetation biomass (kg.ha^{-1})

r = residual biomass below which animals cannot graze (kg.ha^{-1}), and

b = size related constraint.

Figure 2 shows that daily intake increases as available food increases and slows down as one approaches the asymptote defined by the digestive capacity of the animal.

The digestive constraint, a, depends on the digestibility of the diet and the size of the animal and is given by the following equation as described by Illius and Gordon (1998):

$$a = 0.09 D_{diet}^{\,1.1} A^{0.81} U \qquad \text{(kg dry matter)} \qquad (2)$$

where

A = mature mass of animal (kg),

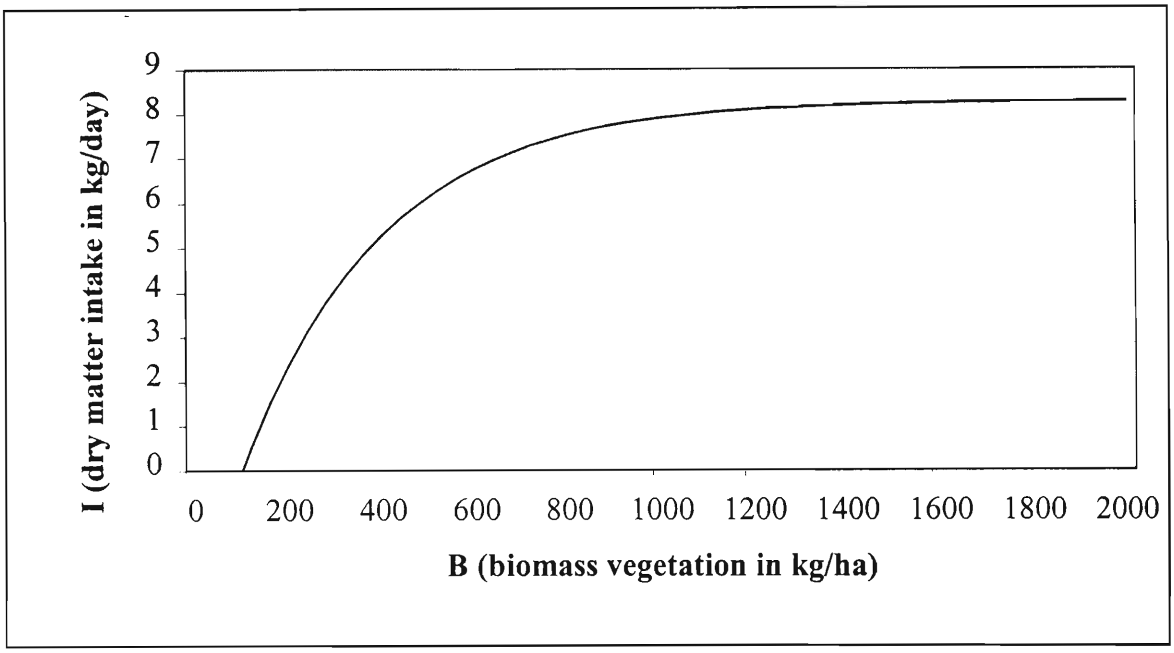

Figure 2. Dry matter intake (I) in kg per animal per day as a function of the density of vegetation present (B) for a 450 kg ruminant on mid to tall grass.

M = actual mass of animal (kg),

U = $(M/A)^{0.75}$ = mass ratio of the animal, and (3)

D_{diet} = digestibility of the diet (in vivo).

The digestibility of the animal's diet depends on the digestibility of the grass components (which is specific to the grass type) and the amount of live and dead material the animal consumes (more selective animals are able to pick out more of the live material, whereas an unselective animal's diet is very similar to the sward proportion of live to dead). The digestibility of the diet is equal to the sum of the digestibility of the live material multiplied by the proportion of live material eaten (depending on selectivity of animal) and the digestibility of the dead material times the proportion of dead material eaten :

$$D_{diet} = Lp_{diet} * D_{live} + (1 - Lp_{diet}) * D_{dead} \qquad (4)$$

where

D_{live} = digestibility of the live material,

D_{dead} = digestibility of the dead material, and

Lp_{diet} = proportion of live material in the diet.

The live proportion in the diet is related to the proportion of live material in the sward, and the selectivity of the animal (how well it is able to select the preferred green material). The live proportion in the diet is defined as the proportion of live material in the sward raised to a positive exponent which changes with the selectivity of the animal.

$$Lp_{diet} = (Lp_{sward})^n \tag{5}$$

$$n = cM^d \tag{6}$$

where

Lp_{sward} = proportion of live material in the sward,

n = an allometric function of mass with a positive exponent (lies between 0 and 1), and

c, d = parameters defining selectivity specific to the grass type.

As n approaches 1, selectivity declines and diet composition is the same as the sward composition which is the case in unselective or bulk grazers. As n approaches 0, the animal's diet becomes mainly live material (more selective or concentrate grazers). n is related to the mass of the animal – smaller animals are able to better select desirable material as they have smaller mouthparts. The larger animals have larger bites and cannot choose the green components as well as smaller animals and are mostly restricted to the sward composition.

Another constraint in the dry matter intake of an animal is body size. The variable *b* in the first equation defining daily intake models the body size of the animal which relates to the bite size as well as metabolic requirements. Comparing bite mass with animals' metabolic requirements, large animals would be predicted to be at a disadvantage to smaller ones when grazing short swards because each bite represents a smaller proportion of daily requirements. This dynamic is modelled by defining *b* as an allometric function of mass with an exponent (Illius and Gordon, 1987):

$$b = pM^q \tag{7}$$

where

b = an allometric function of mass with a negative exponent, and

p, q = parameters dependent on grass type.

Finally, the model works out the energy intake from the dry matter consumed as defined by the following equation (ARC, 1980):

$$EI = I * D_{diet} * 15.6 \tag{8}$$

where

EI = daily energy intake ($MJ.d^{-1}$) (9)

From the above equations, the following can be calculated: daily dry matter intake of the animal ($kg.d^{-1}$) and the amount of live leaf, dead leaf, live stem, dead stem eaten as well as the energy intake ($MJ.d^{-1}$) of the animal.

2.6.2. Animal Herd Intake

The above equations describe what a single animal would eat in a day on a homogeneous sward. As we wish to model an entire herd of animals moving around a non-homogeneous area with the group of animals feeding together at various locations during the day, these equations need to be scaled up numerically and implemented over the area which the herd is occupying at any given time.

The animal herd decides where to feed initially as defined by the foraging strategy implemented and begins feeding. The default "feeding unit" is equivalent to how much one animal would eat in a day, and after this time has passed, the animal herd reassesses its feeding position. As the herd is modelled as an entity and not as individuals, this translates into each animal having eaten the fraction of one divided by the total number of animals in the herd's portion of food in this "feeding unit". This parameter can be changed so that the animals reassess their position more or less frequently. The reason for discretising the day into parts is that the animals response depends on the vegetation present, and if the model only updated the vegetation's response to defoliation by grazing once a day, the model would be predicting more vegetation than was actually present.

The animal herd continues eating, assessing its current position (and moving if a better position is found, else staying where it presently is) until one of three things happen (according to Illius, personal communication):

(i) the herd's digestive capacity is reached
(ii) the herd's metabolic requirements are met
(iii) the herd has travelled a specified distance (this puts an upper bound on the amount of time the animal can travel).

2.7. FORAGING STRATEGIES MODELLED

Various foraging strategies and their effects on the herbivore condition are being investigated in this research. Thus, the only herbivore activities explicitly modelled are feeding and moving. The animals are constantly presented with the choice to carry on feeding in the present location, or to move to another location. How often they re-evaluate their situation is a parameter in the model and the default is defined as the period in which the herd has consumed one livestock equivalent's requirements for one day. One livestock equivalent(LE) is defined to be the equivalent of a 450kg steer.

One strategy for the herd deciding to move predicts that the herd will move if it will be able to increase its energy intake by a set percentage (either net energy which includes the cost of moving there, or simply the energy gained from foraging there). An important factor in whether the animal moves or not is the extent to which the herd is aware of its surroundings as it evaluates its position relative to what is available. Thus, the herd is defined to have a set "awareness horizon" which is how far away from themselves they are aware of the available vegetation.

Another strategy for moving, is defining a threshold of biomass below which the herd will move. When the biomass in the current cell falls below the threshold, the animals will move to another position.

In the choice of where to move, the herd may move to the patch with the most biomass, or to the patch which will give the best energy intake, or a random patch in the vicinity defined by the herd's awareness horizon. The animals will then feed there until they decide to move again.

2.8. - HERBIVORE ENERGY BALANCE

The model includes a simple energy balance to keep track of the herd's condition. The variable used to track these changes in condition is fat mass. Fatmass is the animal's major energy store, and reflects both the physiological maturity of the animal and its history of energy balance (Illius and Gordon, 1998). The change in fatmass depends on whether the animal herd consumed more energy than it expended, and this model keeps track of the energy expended during grazing, moving around as well as its basic metabolic needs.

Fat mass was chosen to represent the animal condition as it represents the accumulation (or loss) of energy from the beginning of the season. In trying to better understand the effect of spatial grazing strategies on animal condition, monitoring the gain or loss of fatmass during the season and the net change in fatmass at the end of the year will give an indication as to how well the animal herd performed under various scenarios. Reproduction costs are not included for simplicity's sake and as we are not modelling the population of animals as individuals, but as a whole.

There are three components to energy expended : basic requirements of the animal (fasting metabolism), energy required to graze (digestion and intake), and energy expended whilst moving (both whilst feeding and also commuting). The following equations come from
The net energy expended is given by :

$$E_{exp} = FM + E_{mov} + E_{com} + E_{graze} \tag{10}$$

where

E_{exp} = net metabolisable energy expended (MJ. d^{-1}),

FM = fasting metabolism (MJ.d^{-1}),

E_{mov} = energy expended by moving (MJ.d^{-1}),

E_{com} = energy expended by commuting (MJ.d^{-1}), and

E_{graze} = energy expended by grazing (or rut effort if not grazing) (MJ.d^{-1}).

Fasting metabolism refers to the animal's thermoneutral resting metabolism which includes maintenance and activity requirements. The following equation describes the relationship between fasting metabolism and animal mass (Illius and Gordon, 1998):

$$FM = 0.3 * A^{0.73} * M / A \tag{11}$$

The energy expended by travelling while feeding is given by equation (12) from Illius and Gordon (1998) and includes maintenance of posture (per second of grazing) and travelling (per metre travelled while foraging).

$$E_{mov} = \frac{GT * 0.748 * M^{0.735} + 15.8 * M^{0.589} * F_{dist}}{1000000} \tag{12}$$

where

F_{dist} = distance travelled while feeding (m), and

GT = grazing time (s).

In a similar way to energy expended by travelling while feeding, the model defines energy expended while commuting (and not feeding) as

$$E_{com} = \frac{CT * 0.748 * M^{0.735} + 15.8 * M^{0.589} * C_{dist}}{1000000} \tag{13}$$

$$CT = \frac{C_{dist}}{COMVEL} \tag{14}$$

$$COMVEL = 0.33 * A^{0.21} \tag{15}$$

where

CT = time spent commuting (s),

C_{dist} = distance travelled while commuting (m), and

$COMVEL$ = velocity at which animal commutes ($m.s^{-1}$).

The last component of energy expenditure is energy used while eating and is related to the time spent eating as well as the mass of the animal :

$$E_{graze} = 0.0029 * GT/(60*60) * M \tag{16}$$

Actual energy expended depends on the efficiency of use of metabolisable energy, and the model works out E_{maint} which is the actual energy expended. Equations are taken from Illius and Gordon (1991).

$$E_m = D_{diet} * 15.6 \tag{17}$$

$$K = 0.503 + 0.019 * E_m \tag{18}$$

$$E_{maint} = E_m / K \tag{19}$$

where

E_m = energy concentrate of food (metabolisable energy)

K = co-efficient of utilization which is the efficiency of utilization of metabolisable energy for maintenance

E_{maint} = actual energy expended

The daily change in fat reserves is the difference between energy intake and expenditure :

$$\frac{\delta F}{\delta t} = \frac{EI - E_{maint}}{m} \tag{20}$$

where m is a metabolic co-efficient for the conversion between energy and fat, such that $m = 54.6$ if $EI > E_{maint}$ (anabolism) and $m = 39.3$ for $EI < E_{maint}$ (catabolism) with units of MJ.kg^{-1} and F is mean body fat (in kg).

The model includes a metabolic constraint on intake such that maximum fat reserves are not exceeded.

$$F_{max} = 0.3\ \mathrm{A} \qquad (21)$$

Each time the herd feeds or moves, energy consumed and energy expended (E_{mav} , E_{com} , and E_{graze}) are recorded and at the end of the day, the net energy is calculated with fasting metabolism included, and fatmass is updated.

2.9. FLOW DIAGRAM LINKING COMPONENTS

Figure 3 shows a flow diagram of the major processes of the model. The model starts with the herd positioned in the grid, and with no vegetation biomass present. The animals only start grazing in week 9, as there is no food available in the first part of the year after burning (it is assumed that the animals will be feeding in another area or on supplementary feed until week eight). Daily rainfall is read in and the water-budgeting and plant-growth models update the water balance and plant growth in each cell. The herd then starts its daily feeding process. Constrained by the rules governing the herd movement, the herd moves to a new position if so desired. The animals graze at that position until their digestive capacity or energy requirement have been met, or until they decide to move (again dependent on the rules). As the animals graze, the plant biomass in each cell in the relevant categories is updated. If their digestive capacity or energy requirement has been met for the day or their maximum distance has been covered, the herd stops eating. The herd's energy intake and energy expended is calculated and energy balance updated, and the cycle is started again the next day. Otherwise they continue to feed until such a time.

Chapter three discusses the implementation of the model and includes parameterisation and other model specifications.

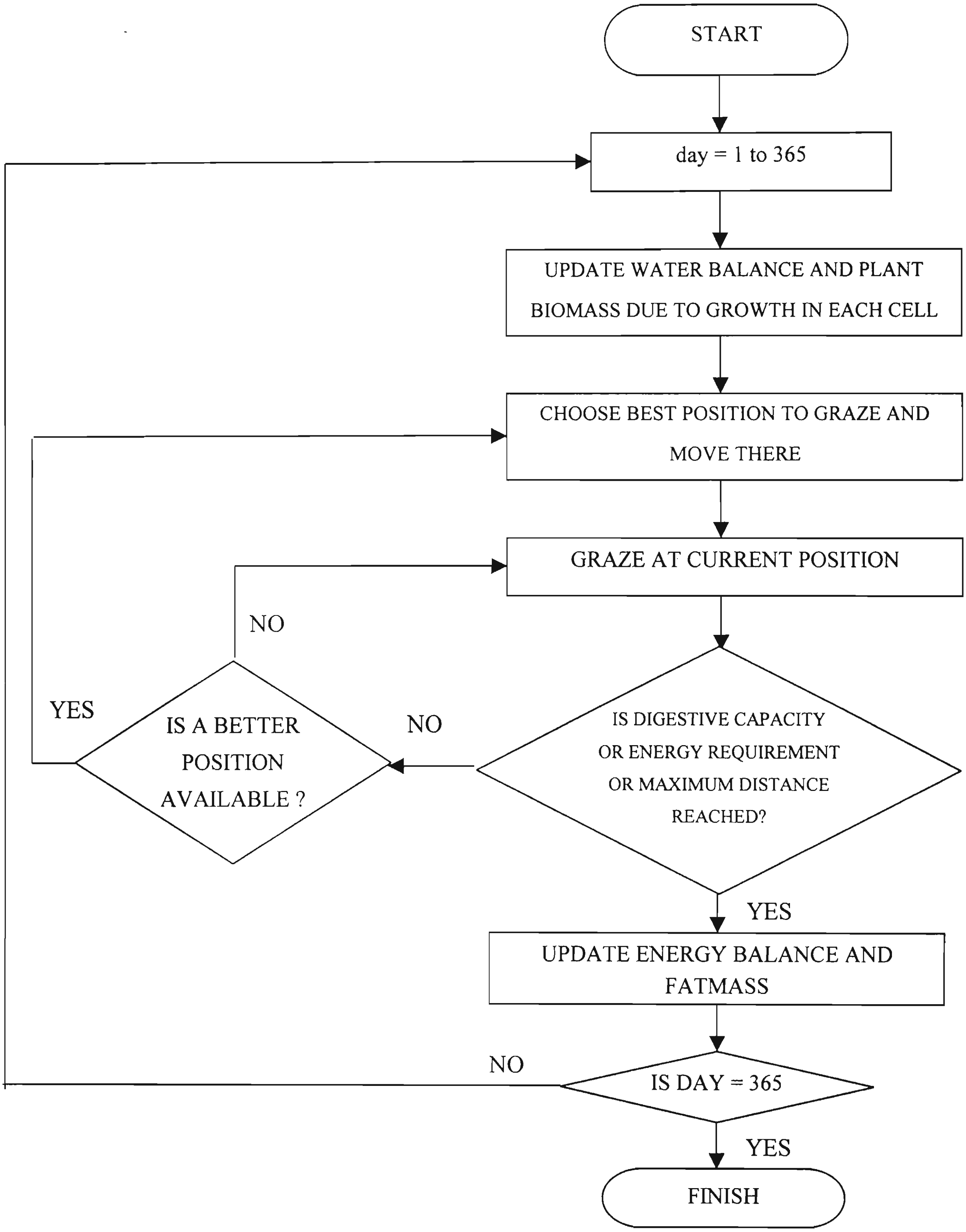

Figure 3. Flow diagram for the model.

CHAPTER THREE

IMPLEMENTATION OF THE MODEL

3.1. MODEL SPECIFICATIONS

The spatial temporal model designed to investigate grazing dynamics has been implemented in C++. The variable inputs are:

- *climate data* : daily rainfall, weekly relative humidity deficit, weekly potential evaporation
- *animal species data* : selectivity of the animal, average weight of the animal
- *herd data* : number of animals in the herd, and the desired foraging strategy.

The outputs of the model include:

- time series of fatmass, DMI (dry matter intake), energy intake per animal
- time series of biomass present including live material, dead leaf, dead stem and total above ground biomass
- final spatial distribution of the vegetation biomass
- spatial distribution of grazing impact over the entire season

As the effect of movement strategies is being considered, the model must give as output some performance index which can be used to compare strategies. The performance index chosen here is fatmass, which is the animal's major energy store, and reflects both the physiological maturity of the animal and its history of energy balance (Illius and Gordon, 1998). Since the timeframe of this investigation is only one year and reproduction is not being considered, fatmass is a suitable performance index as it indicates the cumulative net energy intake over the year. Fatmass also gives an indication of the fitness of the animal in that the animal will die when fatmass reaches zero, and an animal with a higher fatmass has a higher chance of survival. It is also useful to record what the herd eats every day (or week) in terms of biomass and energy content of the grass ingested, as well as the herd's energy expenditure every day (or week) and how often the herd moves as well as the distances travelled. This will aid in evaluating the various strategies. The amount of vegetation present is recorded as well as the spatial distribution of the vegetation and grazing impact which allows us to see how well the vegetation resources have been utilised.

It is assumed that there is no above ground biomass at the beginning of the year, either due to mowing or burning the area. The model begins on 1 September which is the beginning of the hot season preceding the rain, and continues for fifty two weeks. For the first few weeks when the grass has not started to grow yet, we assume that the animals feed elsewhere such as in another paddock or on fodder.

3.1.1. Plant Model Parameters

The grass type implemented in VELD (predominantly *Heteropogon*) is classified as a mid-grass in terms of its potential height. VELD is a model that uses very few external parameters, which is one of the reasons we choose to use the model. It requires only weekly humidity and pan evaporation, and daily rainfall. We use data from the site where the model was developed and tested (Matopos) as it is a suitable representative of a semi-arid grassland.

The climate for Matopos is divided into four seasons (Dye, 1983): a hot season (September to mid-November with low humidity and high temperatures and high evaporation rates), the main rain season (mid-November to mid-March with relatively high humidity and lower temperatures), the post rainy season (mid-March to mid-May with lower temperatures and the probability of rain steadily decreasing), and the cold season (mid-May to August with rain being very unusual and low temperatures). Year to year productivity of the veld in semi-arid grasslands depends to a large extent on the availability of soil moisture and consequently varies in response to the highly variable rainfall (Dye, 1983). The mean annual rainfall at Bulawayo is 603 mm with a median of 569 mm (Dye, 1983) with most of the rain falling between November and March (see figure 4 for the long term mean monthly rainfall figures). Actual daily rainfall data for various years is used as input into the model. Dye (1983) found a relationship between total annual rainfall and primary production, but the correlation coefficient was only 0.54 and variation in primary production cannot be explained by annual rainfall alone. The pattern of rainfall and the amount of early rain play a large role in determining the production of above ground biomass. Figure 5 shows that for higher annual rainfall years, the model predicts that there is not necessarily higher vegetation production and the condition of grazing animals is not necessarily better. The condition of grazing animals is calculated by simulating a single animal foraging homogeneously in an area of 100ha. Such a large area has been modelled to ensure that feedback effects of grazing, i.e. reduction in plant biomass, do not play a role and the condition of the animal depends entirely on the vegetation production in that year. The y-axis represents the various series (rainfall, total vegetation biomass and fatmass) scaled to the average of the three years for means of comparison. In the case with the most rainfall (1980) we find that the vegetation production is lower than in 1984, which had 212mm less rain, but the animals perform better in 1984. When looking at 1988, there was very low rainfall (figure 6) and equally low vegetation production. The animals in this case performed badly (low final fatmass). The counter-intuitive cases can be explained by looking more closely at the pattern of rainfall and not only the total annual accumulation of rainfall. 1988 was a very low rainfall year (approximately half of the average rainfall) and the vegetation biomass never exceeded 1000kg/ha. There was insufficient food (figure 7 shows the low daily dry matter intake) for the animals to gain weight and their fatmass dropped by 34kg. 1980 and 1984 were above average rainfall years. In 1980 there was very little rain in September or October (figure 6) and the animals lost fatmass initially (figure 8), but towards the middle of the season with higher rain still falling there was new growth of green leaves and the digestibility of the sward remained relatively high allowing greater intake later in the year (as shown by figure 7). In 1984, on the other hand, over

100mm rain fell during September/October and the initial vegetation growth was high. At the beginning of the growing season, the vegetation consists mostly of green leaves which are highly digestible and the dry matter intake was high and the animals quickly gained fatmass. The large amount of green leaves quickly turn to dead leaves and there is a higher rate of increase in dead stem material both of which decrease the digestibility of the available food greatly, and the animal is not able to process as much dry matter intake and energy intake is correspondingly decreased. More energy is also required to digest the food.

The model takes two other parameters as input: firstly the pan evaporation which is used to calculate evaporation from the soil surface, and relative humidity deficit which roughly translates into how dry the atmosphere is and is used in calculating plant transpiration. Average pan evaporation data was used (Dye, 1983) and a function estimating average humidity deficit was used (see figures 9 and 10). The humidity peaks in November at 70% making the relative humidity deficit 30%, and then drops off again as the rain stops.

VELD only runs for 37 weeks up to the beginning of the cold and dry season during which new growth rarely occurs. For the remaining weeks of the year, green leaves die and become dead leaves at a rate of 0.003 grams per gram green leaf per day and dead material, both stems and leaves, decay and are eaten by termites at a specific rate of 0.0025 $g.g^{-1}.day^{-1}$(personal communication, Illius) .

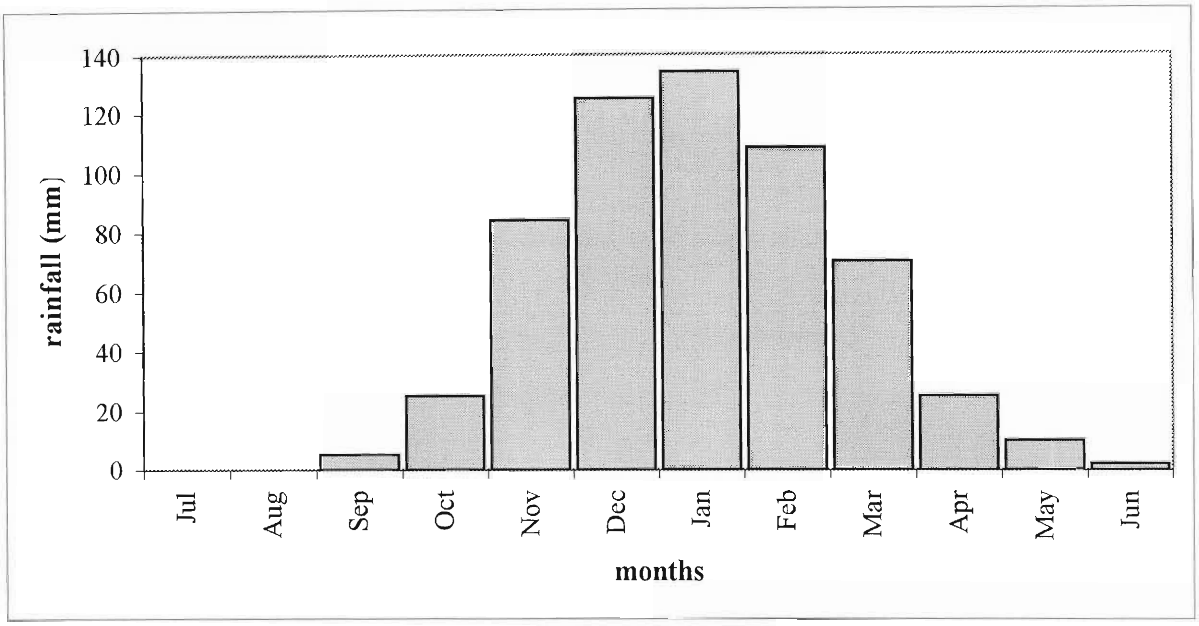

Figure 4. Long term monthly means of rainfall as recorded at Bulawayo between 1901 and 1971 (Dye, 1983).

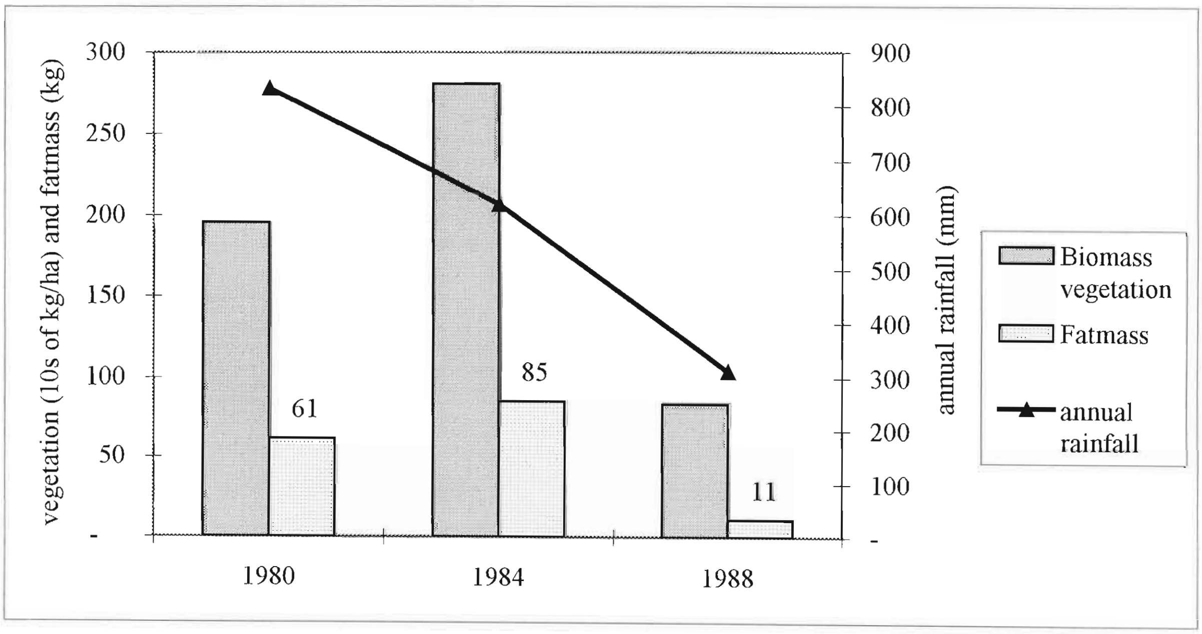

Figure 5. Annual rainfall and corresponding vegetation biomass and fatmass of one animal grazing homogeneously on a large area as given by the model for 1980, 1984 and 1988.

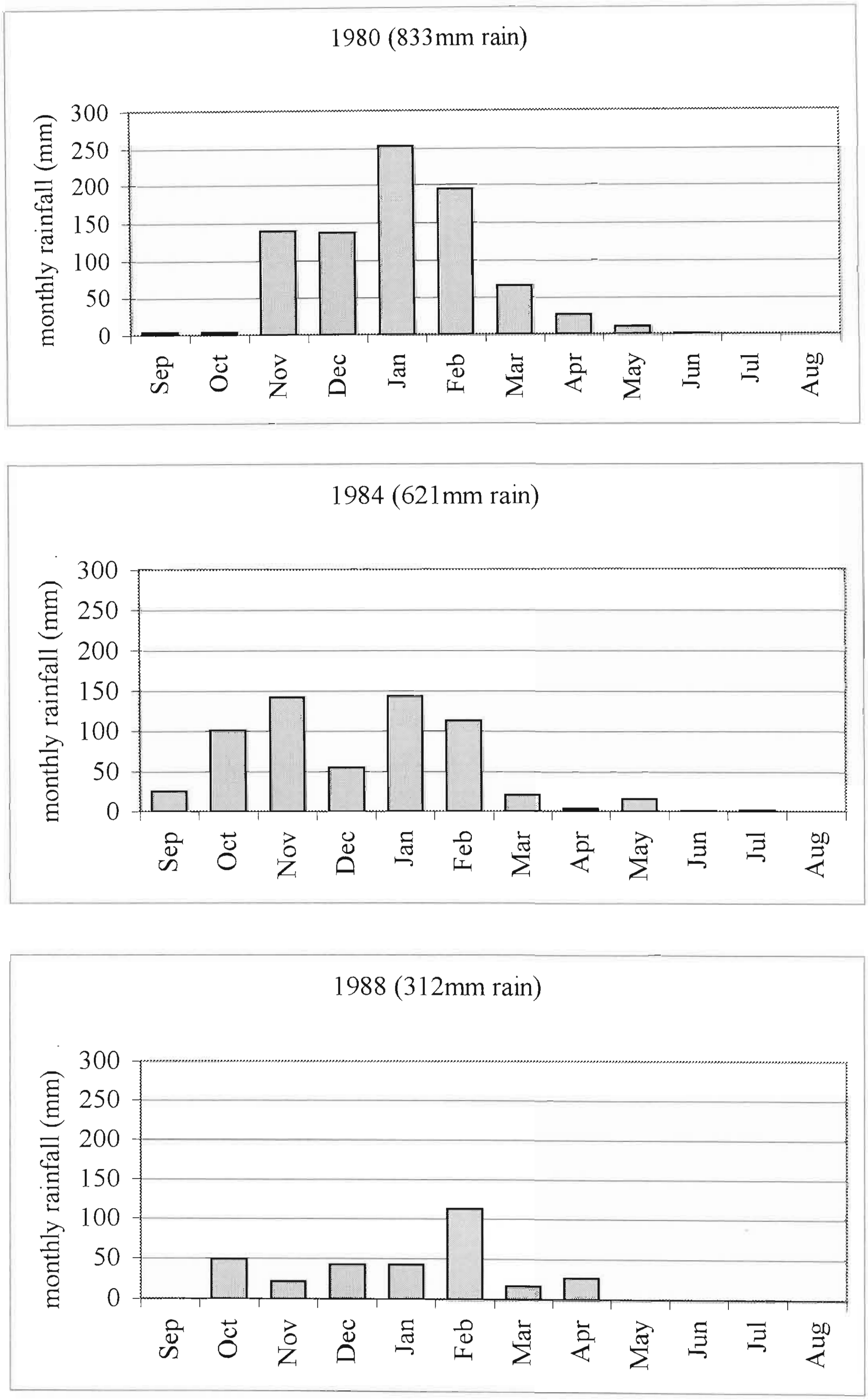

Figure 6. Monthly rainfall for 1980, 1984 and 1988 at Matopos.

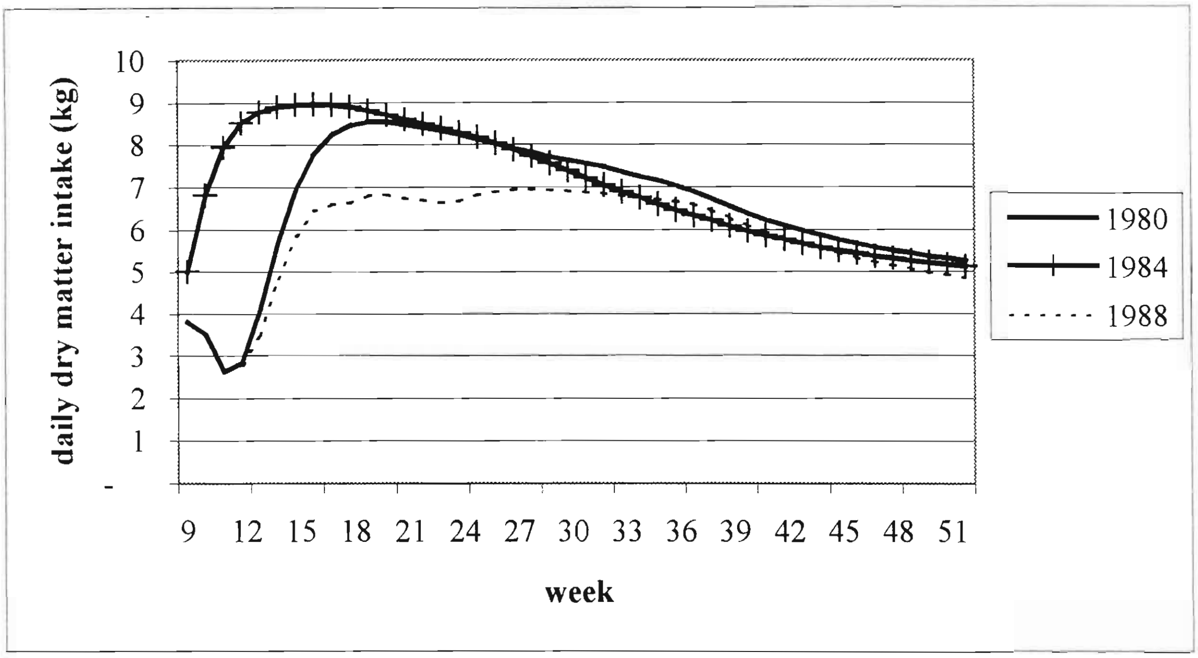

Figure 7. Average daily dry matter intake over the year for one animal grazing homogeneously on a large area as given by the model for 1980, 1984 and 1988.

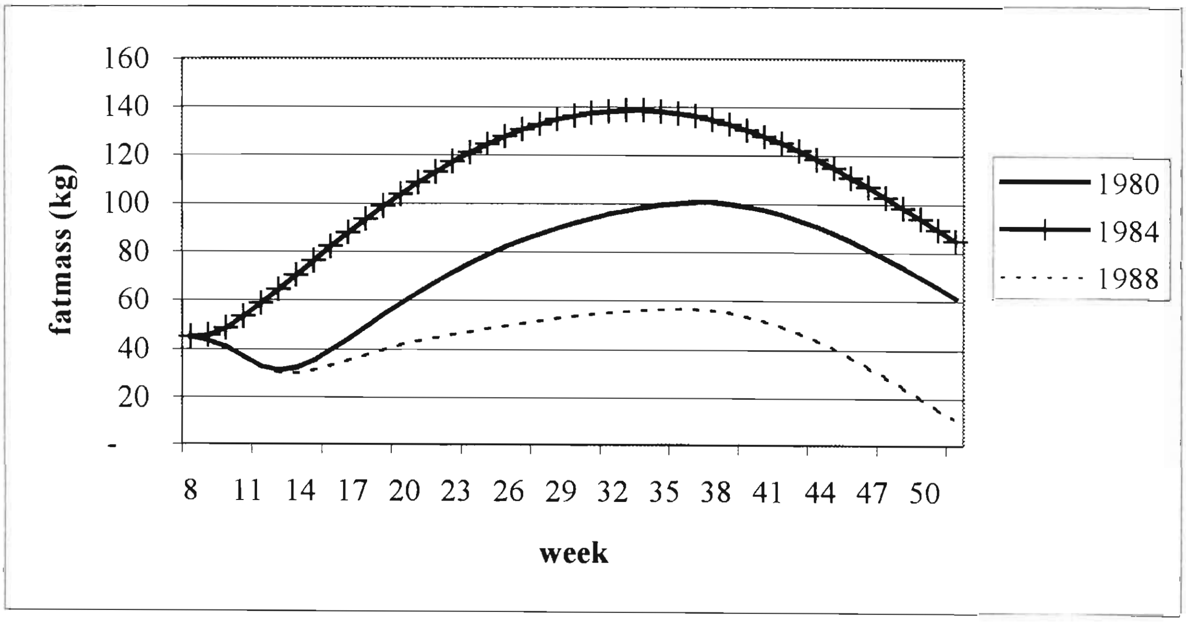

Figure 8. Fatmass over the year for one animal grazing homogeneously on a large area as given by the model for 1980, 1984 and 1988.

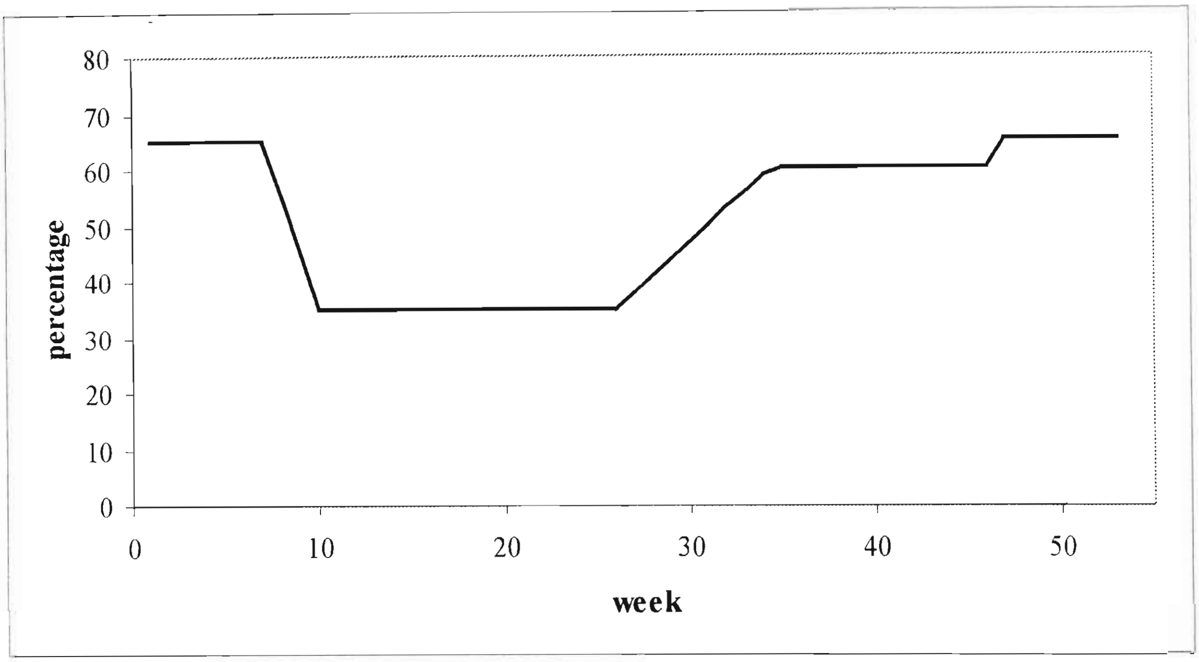

Figure 9. Function representing weekly relative humidity deficit as a percentage as used in the model.

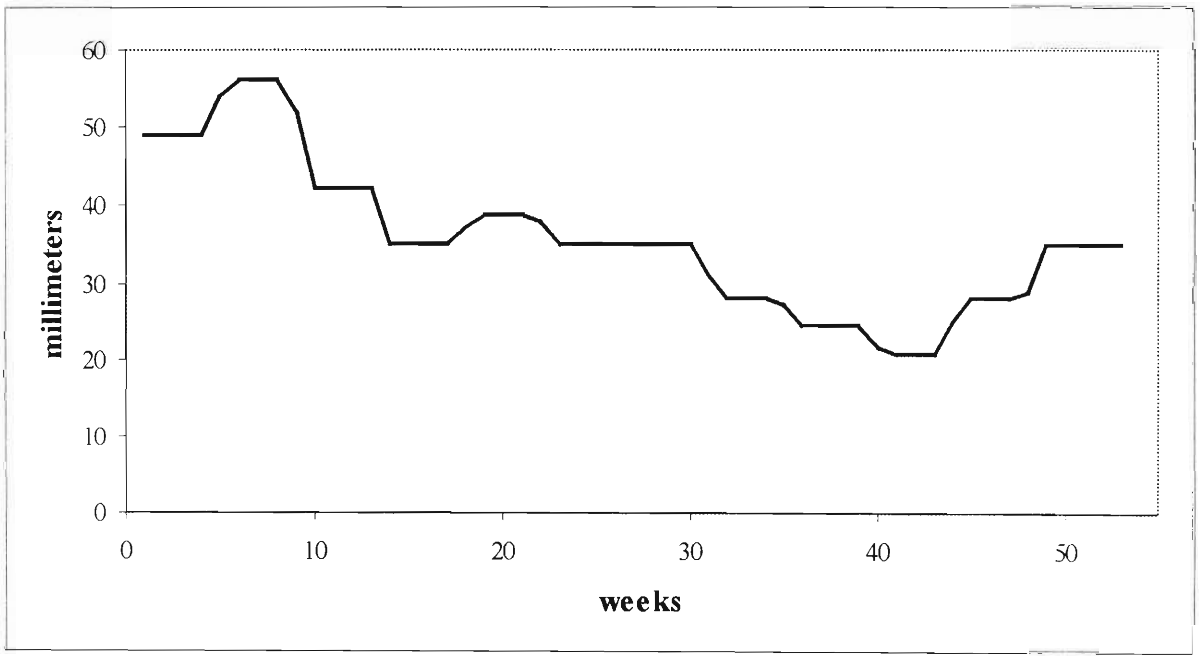

Figure 10. Average weekly pan evaporation in millimetres (average at Matopos from 1959-1979, Dye, 1983).

Animal Selectivity and Digestive Parameters

A herd of 450kg steers is chosen to be modelled where the maximum mass for each steer is 500kg.

$M = 450\text{kg}$

$A = 500\text{kg}$

The parameters used in defining the allometric functions which model the selectivity were chosen to be :

$p = 0.01 \qquad q = 0.2 \qquad c = 0.822 \qquad d = 0.021$

The parameters are unitless coefficients and exponents used in equations 7 and 8 in chapter two. These choices result in a functional response as is shown in figures 11 and 12. Because of the way larger animal's mouthparts are designed and their method of eating, they are able to do much better than smaller animals on a mid or tall grass, and also when the grass has grown taller as is shown in figure 11. The y-axis scale is energy intake ($MJ.\ d^{-1}$) as a multiple of the animal's resting metabolic rate (also $MJ.d^{-1}$) and shows that the 450 kg animal does much better relative to its metabolic requirements than the 9 kg animal. Energy intake over resting metabolic rate gives us an indication of how much more energy the animals are able to consume than they need just to survive, and allows us to make comparisons between different animals with different metabolic requirements. Free ranging animals normally consume twice their resting metabolic requirements in a day. The values chosen for p, q, c and d are suitable for a mid or tall grass (personal communication, Illius). We note for example that when the vegetation is at $500kg.ha^{-1}$ the energy intake of the small selective animal on long grass has dropped to the same as its resting metabolic rate energy requrements where the larger less selective 450kg animal takes in 1.3 times its resting metabolic rate. This means that the larger animal does much takes in 1.3 times its resting metabolic rate. This means that the larger animal does much better relative to its requirements on long grass which is true given its larger mouthparts and ability to digest more food in a day.

The crucial time for animals in semi-arid regions is the dry season, as the live material starts lignifying and dying and the digestibility of the grass decreases. This means that there is less energy in the forage, and the animals cannot eat as much forage because of digestive constraints on the amount of roughage the animal can handle . Figure 10 shows the animal's poor response to grass towards the end of the winter dry season as the live proportion of material in the sward decreases (see proportion of live material = 0.4).

The digestibility of the plant components is a measure of how much the animals can get out of eating the vegetation. Digestibility indicates what proportion of the specified plant material is digestible and is given by

$D_{live} = 0.75$

$D_{dead} = 0.35$

These parameters are valid for mid-grasses such as *Heteropogon* (personal communication, Illius).

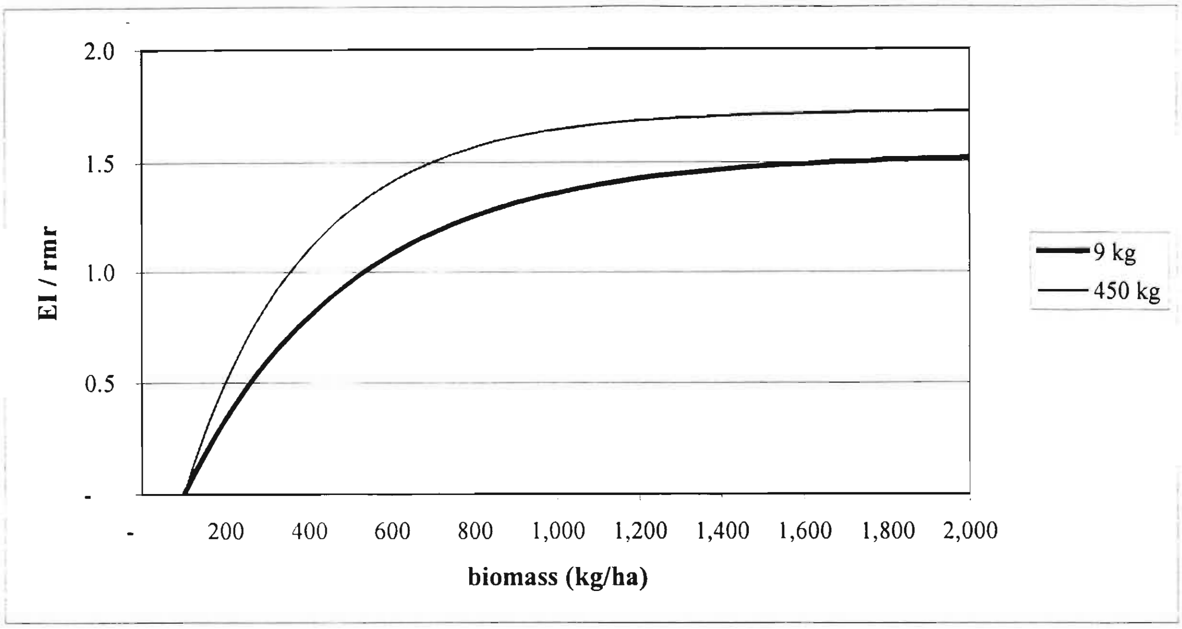

Figure 11. The functional response on long grass for a 9kg animal and a 450kg animal with a proportion of 0.8 of live material in the sward. The y-axis shows energy intake (EI) as a function of the animals resting metabolic rate (rmr), as it varies according to the density of vegetation present.

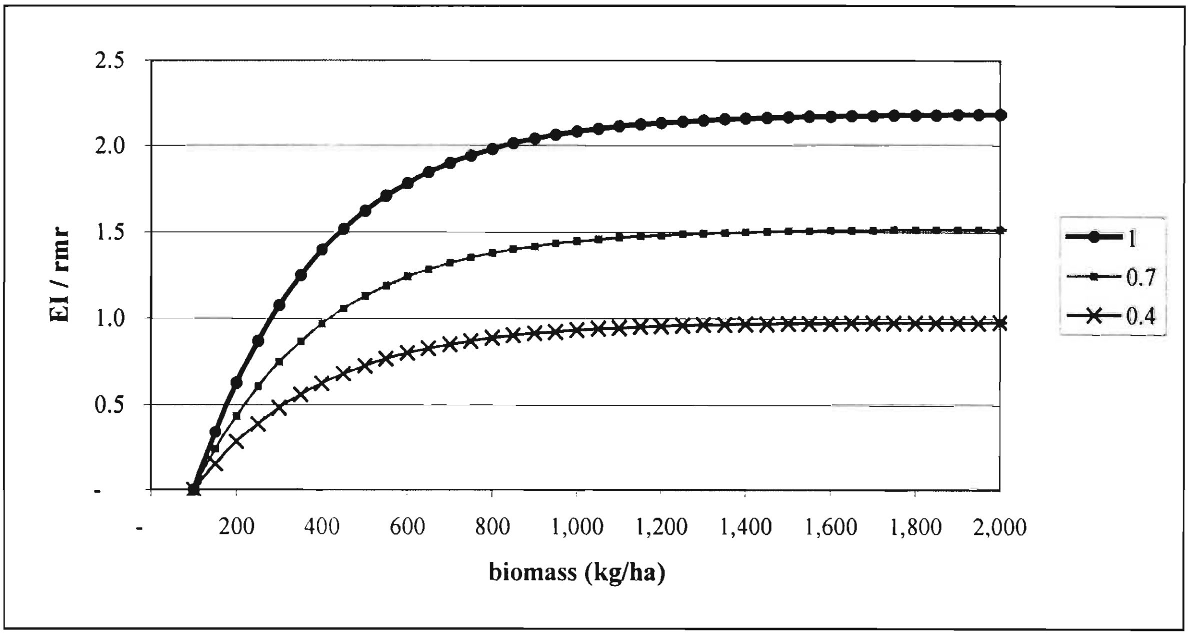

Figure 12. The functional response of a 450kg animal on swards with different proportions of live material (1.0, 0.7 and 0.4) with energy intake (EI) being expressed as a multiple of the animal's resting metabolic rate (rmr) and varying as the total vegetation density changes.

3.1.3. Homogeneous grazing

Most grazing models assume that the distribution of vegetation and the grazing impact are both homogeneous over the area. In order to show that animals armed with spatial grazing strategies do better than if they were to homogeneously graze the area they are feeding in, we first model the case of homogeneous grazing.

In the homogeneous case, we assume that each animal is enclosed in its own area. An equivalent share of the total area is allocated to each animal. The animals all graze uniformly over their area (each in an identical manner as we are assuming a herd of animals that are the same age and weight and have the same requirements). The animals certainly move around in their area, but not to the extent that a herd foraging in a spatial manner does. This is mainly because the grazing impact of one animal in a particular area is far less than that of an entire herd of say 200 animals.

Since spatial results will be compared with the homogeneous results, it is important that the distance modelled whilst feeding and that whilst commuting (and not feeding) are separate and that background movement of the animals while feeding is the same in both scenarios. If in the spatial case, the herd moves to an adjacent cell, that distance is considered to be the distance travelled while feeding (F_{dist}). If the herd moves further than an immediately adjacent cell, the distance is incorporated into commuting distance (C_{dist}).

3.2. SCENARIOS TO TEST REASONABLENESS

3.2.1. Homogeneous grazing

In order to determine whether our choice of how far a single animal in a small area travels in a day, we set up a spatial simulation with one animal in a small area. The animal moves to a neighbouring cell if the potential energy intake less the cost to move to that cell is is at least 10% better than the energy intake rate at the current position. We investigated two strategies: firstly a strategy where the animal moves to the best adjacent cell (or a random choice of equally attractive neighbours), and secondly a systematic movement along each row of the grid as in figure 13. In order to ensure that the size of the grid does not affect the results, various spatial resolutions were considered, namely, areas defined by 30 by 30 cells, 40 by 40 cells and 50 by 50 cells. The total area stays 4ha (200 m by 200 m), chosen because a stocking rate of 0.25 animals.ha^{-1} is a fairly average stocking rate. This translates into the respective cell sizes being 6.6 m by 6.6 m, 5 m by 5 m, and 4 m by 4 m.

Figure 14 shows the average daily distances a single animal moves for the movement strategy which chooses the best neighbour (the systematic movement produced a similar result). The behaviour at the beginning of the grazing season can be explained by the fact that there is a low density of biomass initially and the animals have to move more during the day to achieve their requirements. But, in the random case, the animals get stuck in areas that are all heavily grazed and as they are only aware of their immediate neighbours, they make decisions with limited knowledge and end up in areas with all cells giving low returns.

The average daily distance travelled by a single animal of all the above cases is 66 m. This seems very low, but can be explained by the fact that there is a solitary animal grazing and the grazing impact is not high, so the animal does not need to move as often as if feeding in a herd. The animal is in an area of 200 m by 200 m and a steer can easily walk far more than 200m in a day, though it need not since it is on its own and depletion of patches occurs slowly. We assume that the animal will move 200 m per day if enclosed in its own area for the purposes of this model in the homogeneous grazing scenario.

3.2.2. Various rainfall scenarios

Actual daily rain data is used as an input for the model, and in choosing which years to model we are interested in the animal dynamics during limiting years. When forage is abundant, the animals will find sufficient food all over the area, and foraging strategies are not that important. It is in the years where vegetation is not as abundant, and more importantly when live material is scarce, that the animals must forage more intelligently in order to ensure enough fat stores to last the dry season.

The condition of the animal depends on its intake. Animal intake depends on the amount of biomass present as well as the digestibility of the sward which is determined by the proportions of live to dead material in the sward. In order to find which rainfall years are important to model in terms of limiting animal intake, we simulate a single animal on an area of 100ha, which is a very low stocking rate, for the years 1975 through to 1994.

Figure 15 demonstrates that there is some correlation between annual rainfall and herbivore condition as described by the amount of fatmass at the end of the grazing season (R^2=0.46). It is clear that the herbivore condition is not adequately explained by the amount of average annual rainfall. Hence it appears that there are other influencing factors. However, one can see that it is generally true that for lower rainfall years the animals perform worse.

In choosing which rainfall years to use in simulating spatial grazing dynamics the following seem to be of interest. 1981 and 1988 have very similar total annual rainfall (313 mm and 312 mm) and yet the fatmass of the animal at the end of the year is very different (11 kg and 35 kg) as can be seen in figure 16. Figure 16 also shows that in 1985 and 1992, the final fatmass of the animals differs significantly (48 kg and 86 kg) and yet they have a difference of 66 mm rainfall. 1980 is an example of a higher rainfall year in which the animals did not perform as well as in lower rainfall years such as 1992. We will consider these years in the next chapter.

3.3. CONCLUSION

The spatial model described in this chapter simulates the animal and plant dynamics of a semi-arid system. In chapter four, various foraging strategies will be modelled using the spatial model. A herd of 450kg animals on a sward that is predominantly *Heteropogon contortus* in an area of 900ha under different rainfall scenarios will be considered. Results will be presented and discussed.

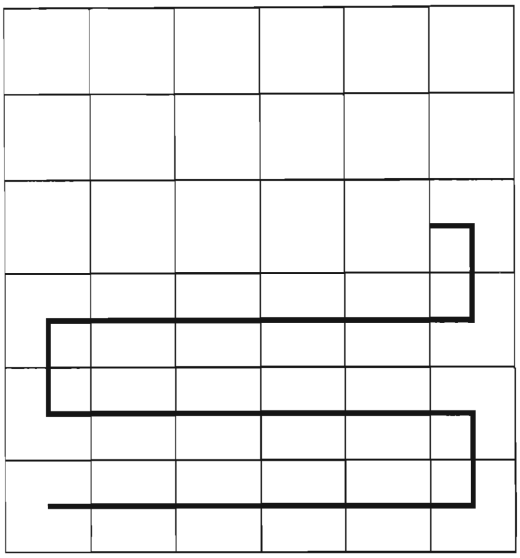

Figure 13. Diagram showing systematic movement of an animal in the spatial grid.

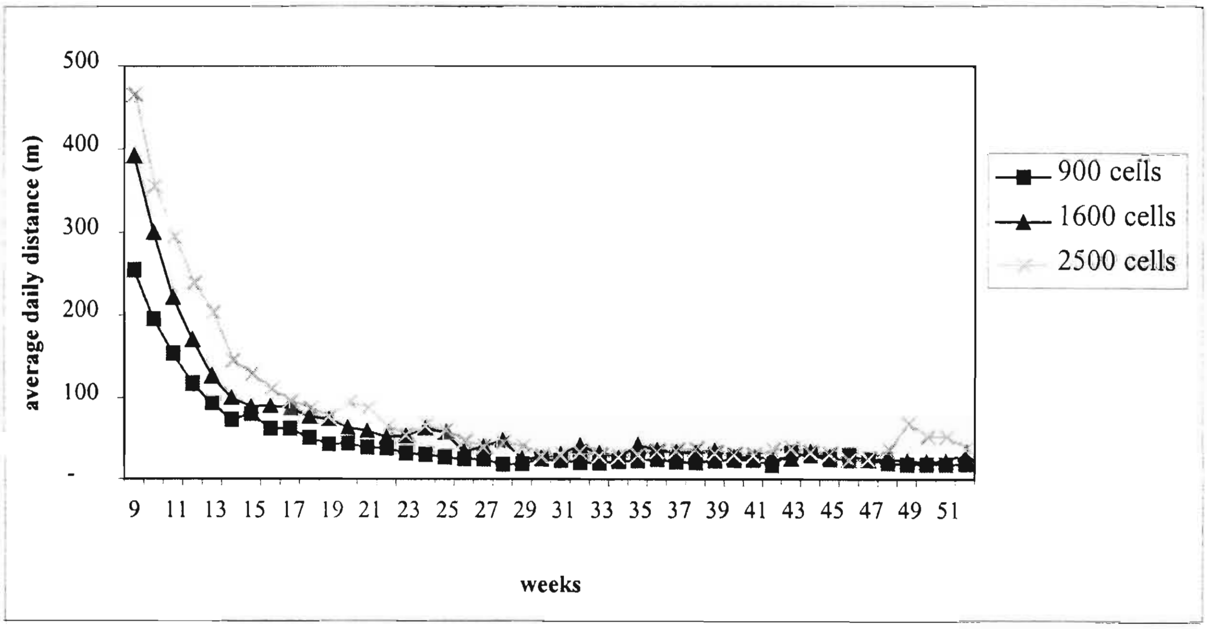

Figure 14. Average daily distance travelled by a single animal moving to the best neighbour in an area of 4 ha for 1967 rainfall and for different spatial resolutions.

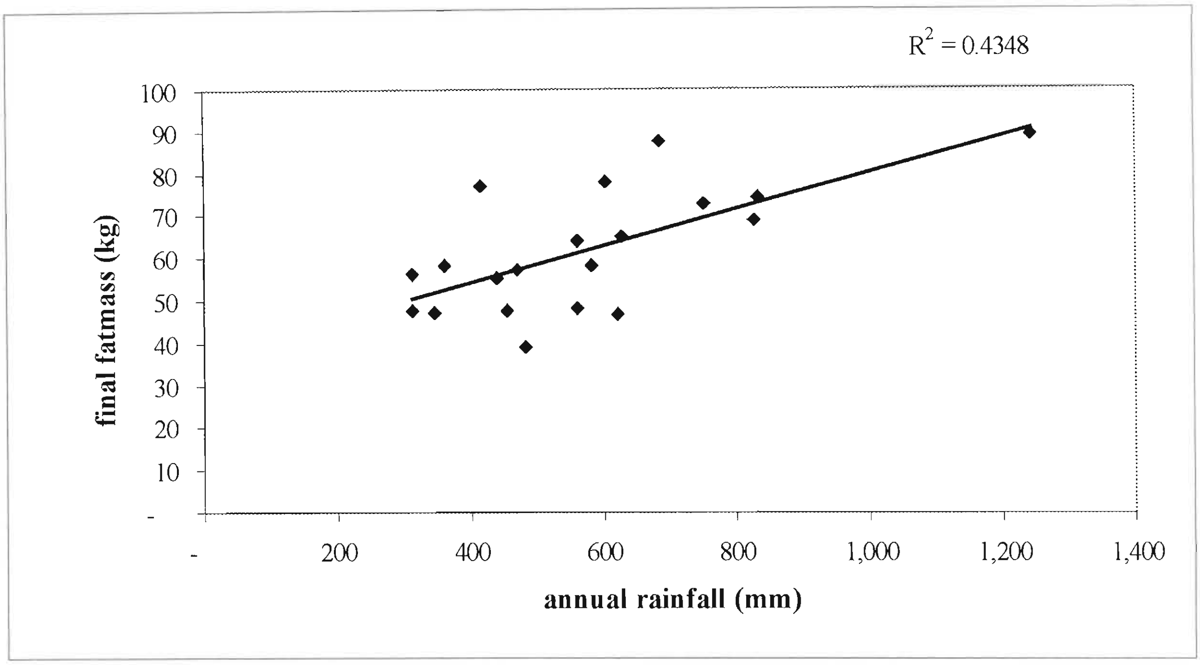

Figure 15. The relationship between annual rainfall and average daily dry matter intake for the years 1975 to 1994 for one animal grazing homogeneously on 100 ha as predicted by the model. The variation in the y-axis is due to within-year variations in rainfall.

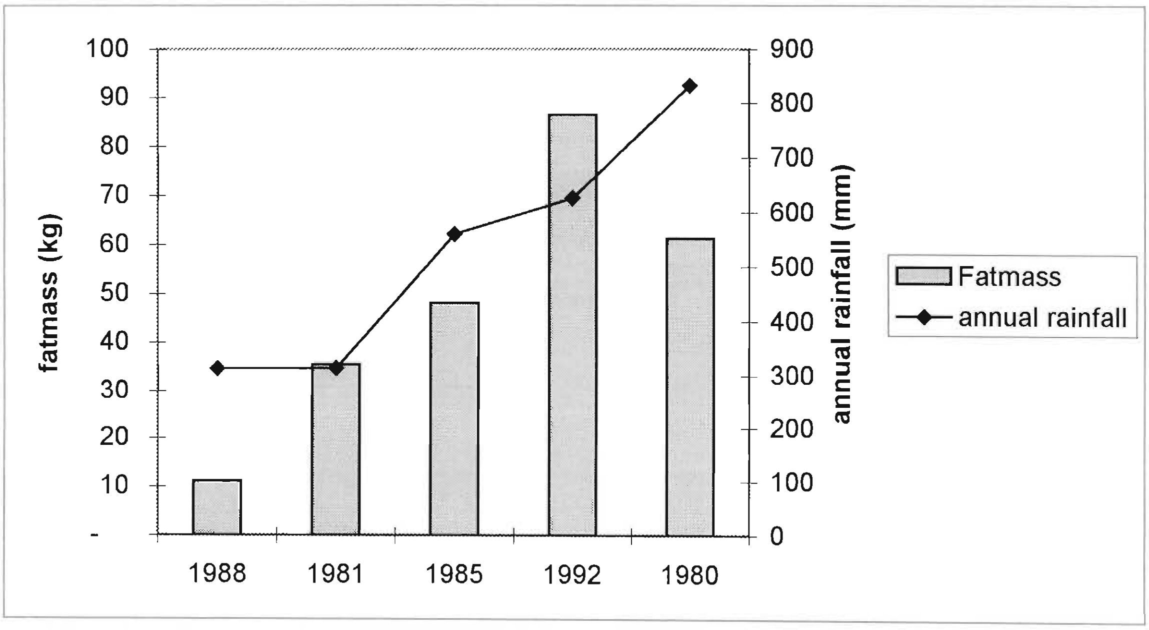

Figure 16. Annual rainfall (mm) and corresponding fatmass (kg) for various years for one animal grazing homogeneously on 100 ha as predicted by the model.

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1. INTRODUCTION

The movement of the animal herd is determined by which set of rules is applied to the herd. The various rules defined are:

(i) Move to the cell with the best rate of energy intake (Strategy 1);

(ii) Move to the cell with the most biomass (Strategy 2);

(iii) Move to the cell with the most green biomass (Strategy 3); and

(iv) Move in a systematic fashion along the rows of the grid (Strategy 4).

The animals move from a particular cell either

(i) if the biomass or energy intake falls below a specified threshold, given by the parameter *threshold*, or

(ii) if another cell is better than the present by a specified percentage, given by the parameter *moving factor* where *moving factor* = 1.2 indicates a percentage of 20% is required before moving.

900 ha translates into an area of 3 km by 3 km, which is not large in terms of animal movement. A herd of cattle can walk up to a couple of km in a day. The movement of animals in this investigation will be less than that as we assume that the animals do not need to move long distances to find water and no seasonal changes in foraging areas occur. To what extent they are aware of their surroundings is unknown and this is one of the aspects that will be investigated. The method chosen to do this, is to define an "awareness horizon" which translates into how far from its current position the herd is aware of what is available in other cells. This is specified by a parameter, *awareness horizon,* and can take on the value 1 up to the maximum number of cells of one side of the grid. In figure 17,

grid (a) shows an awareness horizon of one, which translates into the animal herd knowing what is present in the eight surrounding cells (and its own position). Grid (b) has an awareness horizon of three. In choosing the best cell within the defined awareness horizon, the herd will always move to the closer of two cells that give the same return.

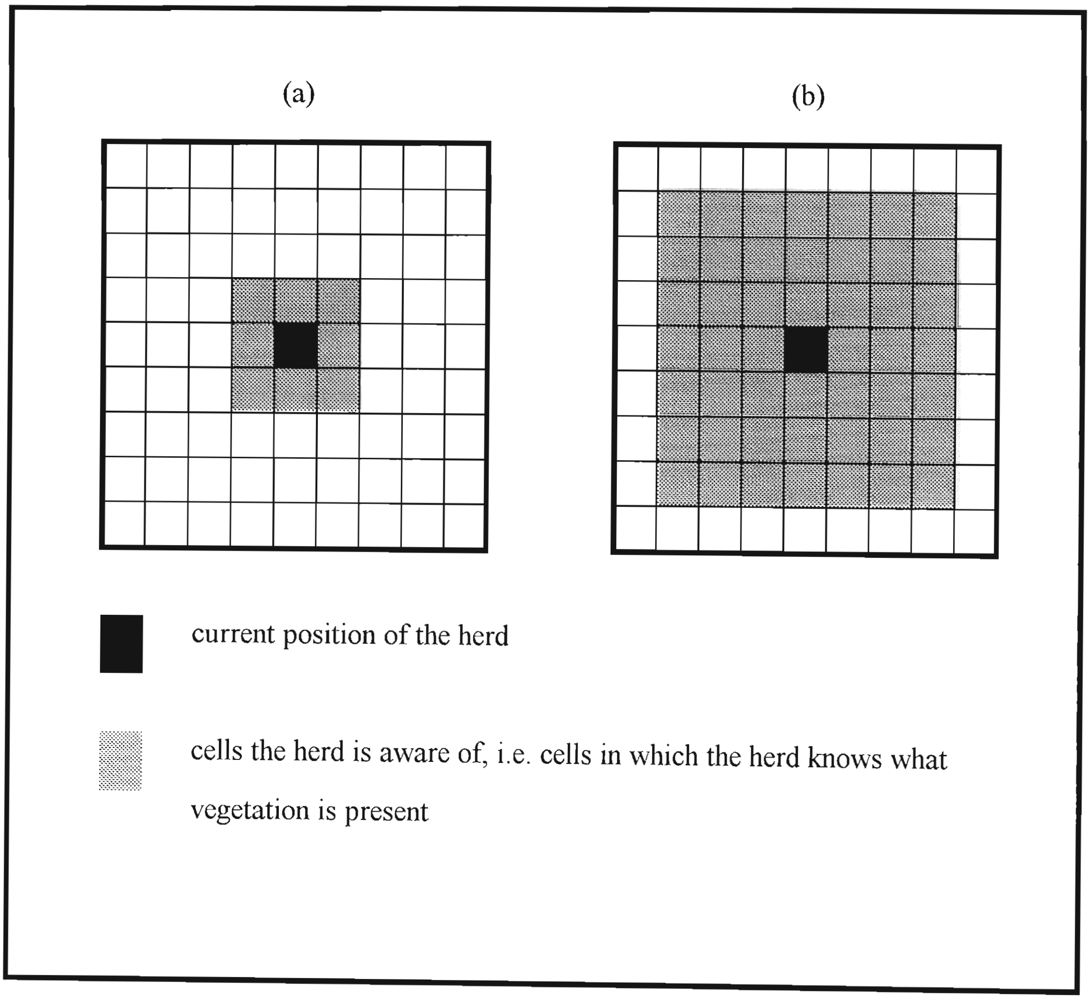

Figure 17: Drawing showing different awareness horizons. (a) shows an awareness horizon of 1, i.e. the animals can only see what is available in the immediate neighbours. (b) shows an awareness horizon of 3.

4.2. ANALYSIS OF GRAZING IMPACT

Different grazing pressures lead to different responses by the vegetation to defoliation and also to different proportions of live and dead material. If applied to a spatial grazing context, animals may move around so as to optimise the regrowth of green material. By grazing some patches and leaving others, animals are able to modify the potential intake of biomass. An investigation into how the vegetation responds to different grazing pressures was conducted. Two stocking rates were investigated: a moderate stocking rate of 1 LE to four hectares (SR = 0.25) where SR represents the stocking rate in LE per ha, and a lower stocking rate of one livestock equivalent to 100ha (SR = 0.01).

Results

Figure 18 demonstrates how in 1985 and 1992, the animals under a low stocking rate performed worse than those under a moderate stocking rate, although vegetation resources are more abundant in the former case. In 1992, the final fatmass was 6 kg higher under a moderate stocking rate (figure 18). The animals under the low stocking rate perform worse due to the high proportion of dead material in the sward. As can be seen in figure 19, there is considerably more dead material in the lower stocking rate and the difference in green plant material is not as great. In week 34, the proportion of live leaf in the sward in 51.0% under low stocking rate and is 55.6% under moderate stocking rate. This translates into an increase in dry matter intake of 0.17 kg per animal per day under the higher stocking rate.

The rapid growth of green leaves in the beginning of the growth season was quickly consumed by the larger number of animals under moderate stocking rate allowing for more green growth. In the case where the stocking rate was low, the green leaves were left standing and turned to dead leaves and the digestibility of the sward decreased causing the animals' performance to drop.

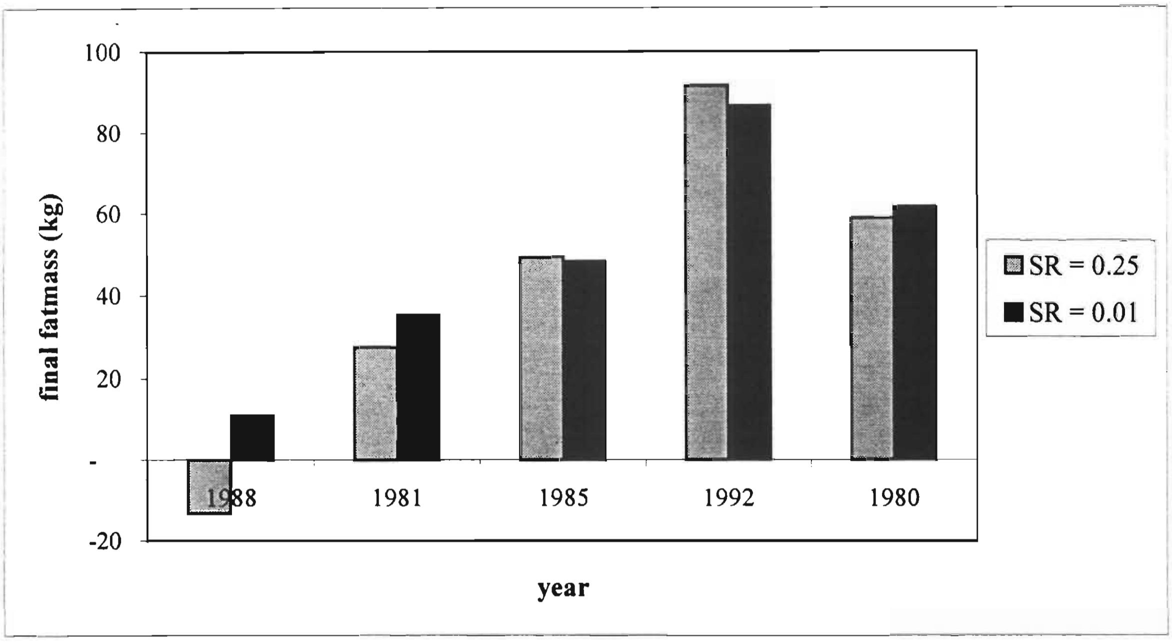

Figure 18. Performance of animals in terms of final fatmass (kg) where animals grazed homogeneously under two stocking rates (SR). SR is in LE per hectare.

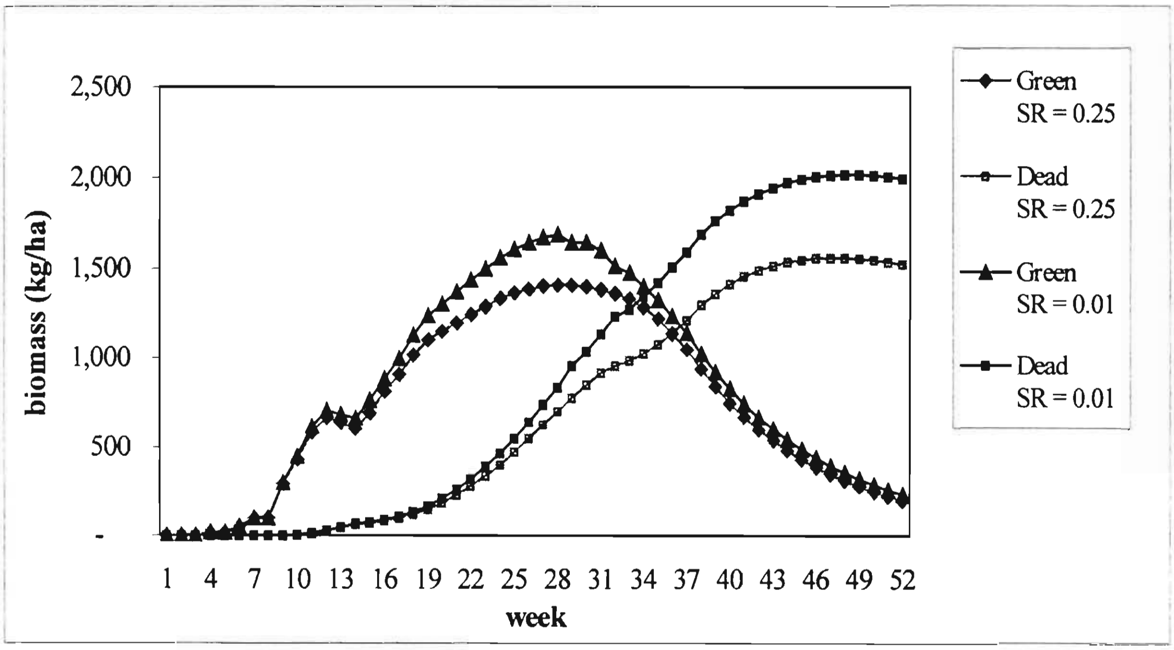

Figure 19. Different vegetation growth for 1992 rainfall under two stocking rates (0.25 and 0.01 LE.ha^{-1}) with animals grazing homogeneously.

The negative fatmass for animals grazing in 1988 with a stocking rate of 0.25 LE per hectare indicates that the animals would have died before the end of the year at that stocking rate.

The response of the vegetation to grazing can be positive, with more growth being stimulated, or negative if the vegetation is grazed too severely. Ungrazed areas will result in the sward becoming less digestible as the amount of dead material and stem increases. As animals do not forage homogeneously in relatively large areas, there will be patches of heavily grazed vegetation and patches of ungrazed vegetation.

Figure 18 highlights how animals are able to perform differently for a given rainfall pattern and stocking rate by modifying their spatial grazing distribution. This is possible as the vegetation responds differently to different grazing pressures, and animals can modify their grazing strategies to change the grazing pressure. As they are able to move around in the area, the animals can forage where the returns are highest. Thus, an initially homogeneous sward may become patchy due to grazing impact, and spatial strategies play a large role in determining the animals' intake and performance.

4.3. STRATEGY 1 : MAXIMISING INSTANTANEOUS ENERGY INTAKE RATE

The instantaneous energy intake rate for an animal in a given cell depends on the digestibility of the sward. This is determined by the proportion of live and dead plant material and the total amount of biomass in the cell. Choosing to feed where the instantaneous energy intake rate is maximised should logically result in the best animal performance. This is not always the case. The instantaneous energy intake rate does not give any indication as to how long animals will be able to feed in that cell before the rate drops significantly. Thus, animals under this strategy tend to move to the best cell and then find that after foraging a short while, the biomass may have been depleted to such an extent that the energy intake rate drops drastically and the animals must move again.

In order to investigate the effect of moving to the cell with the best energy intake rate, we run the model with the following parameters:

(i) *moving factor* = 1.1, which means animals will move to the best cell in the surrounding area if that cell will provide 10% more net energy (potential energy intake subtract energy cost of moving there) than the potential energy in the current position. Otherwise the herd remains in the current position,

(ii) *awareness horizon* = 1, 2, 3, 4, 5, 10, 30, and

(iii) 5 different rainfall years (chosen as before).

Results

The graph in figure 20 shows results for 1985. As the animals' awareness horizon increased, the total dry matter intake generally increased. The increase, however, is very small (0.2%) and is not significant at all. With an increasing awareness of the surroundings, the animal herd should forage more efficiently whereby increasing its dry matter intake. The results from the simulations show that this is not the case. The general trend of increasing dry matter intake with increasing awareness horizon was true for 1980, 1981 and 1992 but in 1988 (low rainfall year) there was a slight decrease in dry matter intake as awareness horizon increased.

Dry matter intake was less under Strategy 1 than in the case of homogeneous grazing in all five years (figure 21) indicating that the animals would be better off in the homogeneous case. The animals moving around spatially are able to get stuck foraging in areas with low digestibility causing their intake rate to drop, or in calculating whether to move or not they decide it costs too much to move to the better cells. Figure 22 shows the spatial distribution of biomass at the end of the grazing season for 1985, a year in which the animals were able to consume more dry matter intake in the case of homogeneous grazing than in the case of grazing under strategy 1. There are large patches of relatively ungrazed biomass as well as patches where the biomass is very low and was grazed to below 333 kg.ha^{-1}

In all five rainfall years, as the awareness horizon increased, so did the average daily distance travelled. With increasing costs of travelling the fatmass of the animal dropped as its awareness horizon increased. An example of this is shown in figure 23 which shows daily distance travelled and final fatmass for 1988. This increase in distance accounts for the decreasing fatmass as it results in higher travelling costs. The animals do increase their dry matter intake as the awareness horizon increases, but they also increase the distances travelled and thus more energy is expended resulting in a lower net energy.

Sensitivity of the parameter 'moving factor'

The parameter that specifies that animals must move if the next cell is 10% better than the current cell was introduced to ensure that the animals do not move around after every assessment of the area. This allows us to introduce a penalty for moving to another cell. In order to see what effect changing this parameter has on the animal performance we set *moving factor* to 1.0, 1.05, 1.1, 1.2 and 1.3 which corresponds to moving to a cell if the net energy is the same (1), 5% better (1.05), 10% better (1.1), 20% better (1.2), and 30% better (1.3). The results are shown in figures 24 and 25. In figure 24 it is clear that the animals increase their dry matter intake with *moving factor* = 1 in relation to the homogeneous case, and decrease their intake with higher values of *moving factor*. But, on the other hand, they travel substantially further in a day, which decreases their net energy intake, and so the animals perform worse when *moving factor* is 1. This can be seen in figure 25 where animals under strategy 1 with *moving factor* = 1 move more than 8 km per day on average and for higher values of *moving factor,* the animals move around less than 1 km on average per day. In all rainfall years *moving factor* = 1.05 gave the best results for animal performance in terms of final fatmass.

When comparing *moving factor* = 1.1 with *moving factor* = 1, it was found that the spatial distribution of vegetation differed considerably (figure 26). Figure 26 (a) shows the case where *moving factor* = 1.1 and it is clear that the cells were more uniformly grazed in (b) where *moving factor* = 1.0 in which the animals moved around more. In (a) there are a large number of dark cells where the biomass is less than 350 $kg.ha^{-1}$ as well as a fair amount of light cells, which represent cells with the most biomass. The animals were over-grazing some cells and undergrazing others with *moving factor* = 1.1 and the result was a diet that was less digestible and a correspondingly lower intake than the other case. Figure 27 shows the percentage of cells found in each biomass category at the end of the year. When *moving factor* = 1, there are no cells in the first two categories (< 700 $kg.ha^{-1}$) indicating that cells were not grazed down to nothing as in the other scenario. By not depleting the cells' vegetation completely, the animals were able to increase their dry matter intake (see figure 24).

When comparing *moving factor* = 1.1 with the other values of *moving factor*, one can see that the animals stayed longer in patches than when *moving factor* = 1. This decreased the frequency of moving to another cell but allowed the animals to move before the energy intake rate dropped too much. In comparison with higher values of *moving factor*, *moving factor* = 1.1 ensured that the animals did move frequently enough not to stay long in cells with low energy intake rates.

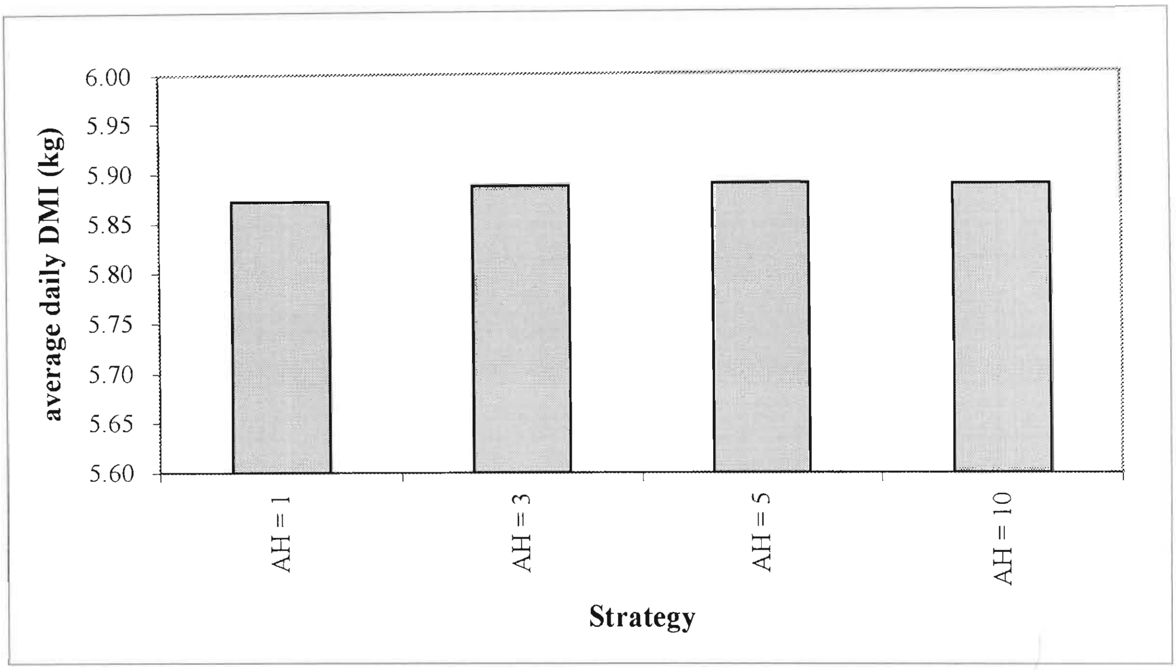

Figure 20. Average daily dry matter intake (kg) over the entire year for four different awareness horizons (AH) under Strategy 1 (moving to cell with the highest net energy intake rate) for 1985.

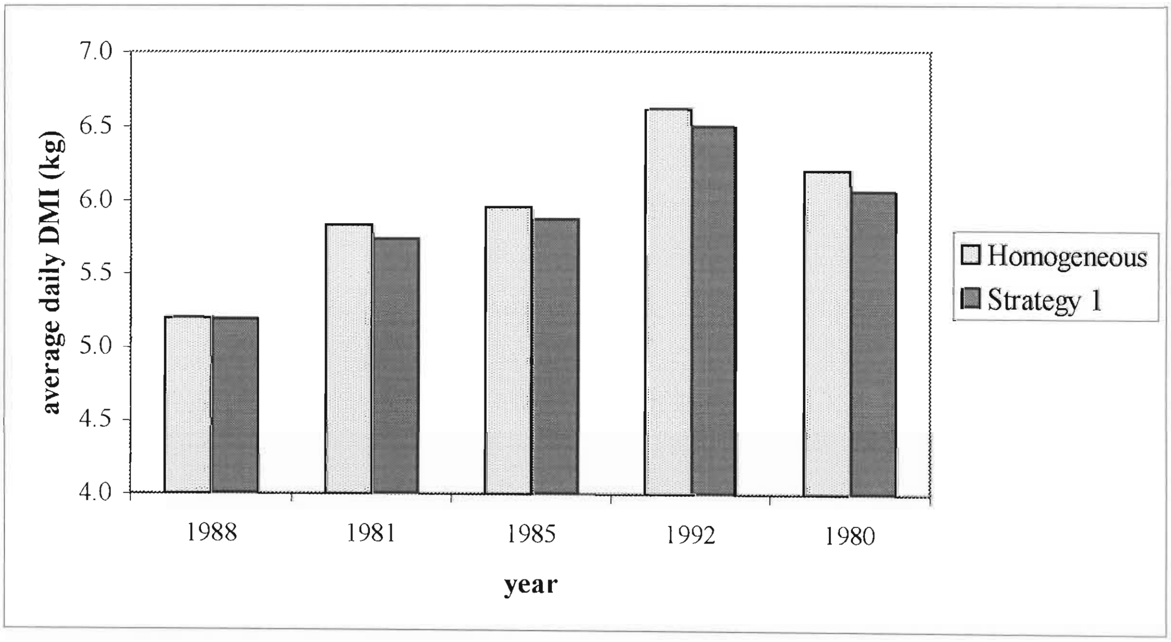

Figure 21. Average daily dry matter intake (kg) for the homogeneous grazing strategy and for spatial Strategy 1 (moving to cell with highest net energy intake rate).

Scale		
□	>=	1,300
░	>=	1,083
░	>=	867
▒	>=	650
▒	>=	433
▓	>=	217
█	>=	-

Figure 22. Diagram showing spatial density of vegetation at the end of the grazing season for strategy 1 with *moving factor* = 1.1 and *awareness horizon* = 5 in 1985. A dark cell represents a cell with very low biomass and as the shading gets lighter, more biomass is present. Scale is in kg/ha.

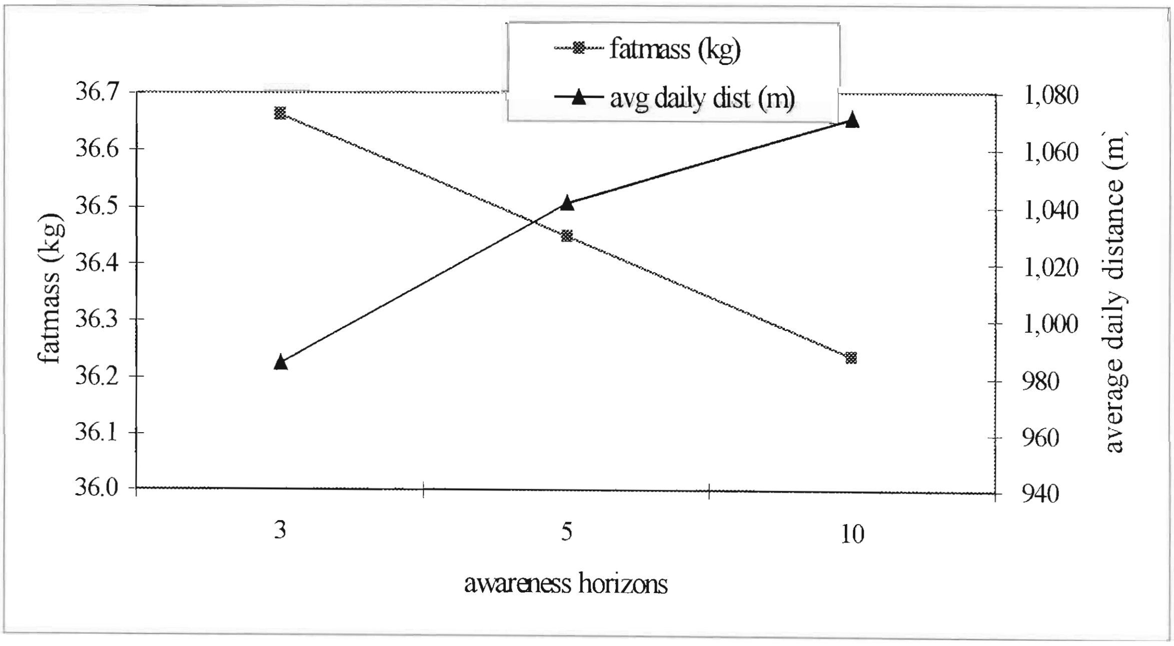

Figure 23. Changes in average daily distance and fatmass as the herd's awareness horizon changes under strategy 1 (moving to the cell with the highest instantaneous energy intake rate) with 1988 rainfall.

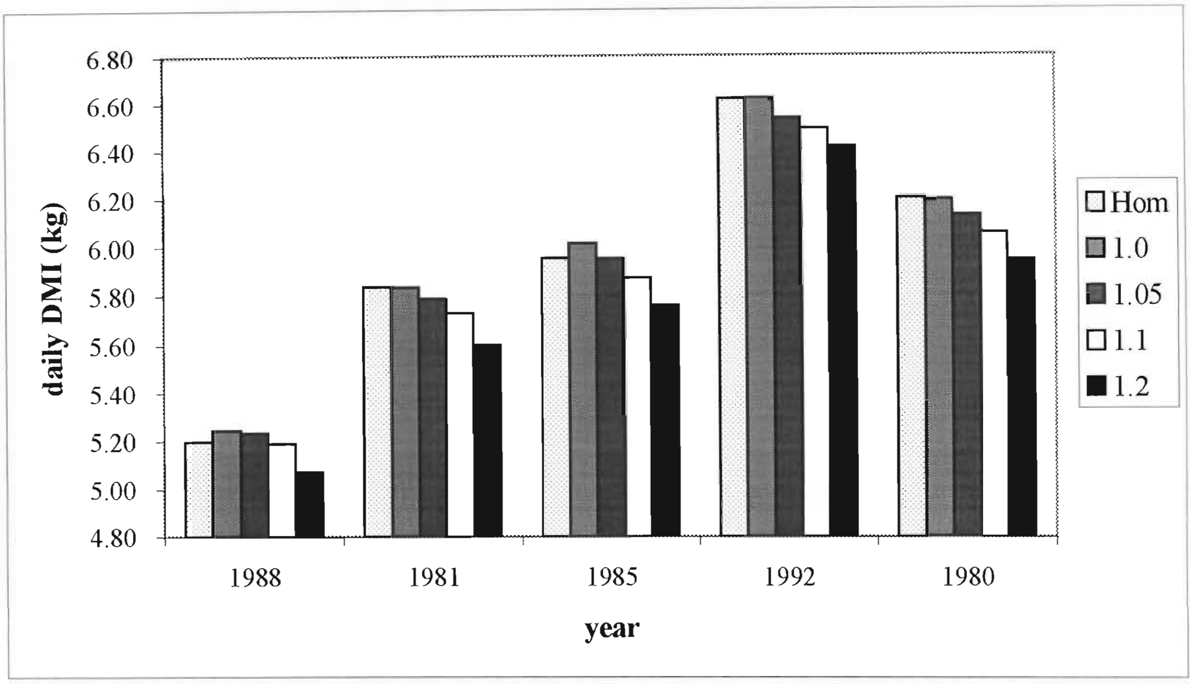

Figure 24. Average daily dry matter intake for animals moving under Strategy 1 (maximise energy intake rate) with various moving factors where 1.1 corresponds to the animals moving if the net energy is 10% better than where they are presently.

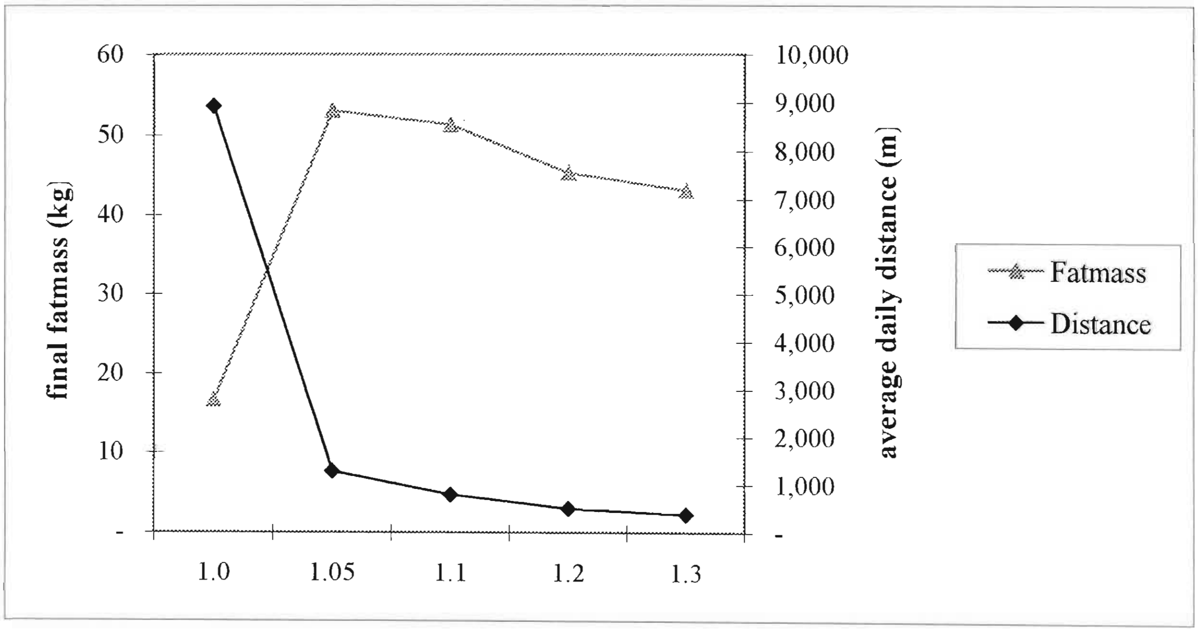

Figure 25. Final fatmass and average daily distance travelled for animals under Strategy 1 (maximise energy intake rate) in 1981 as they vary with the value of moving factor.

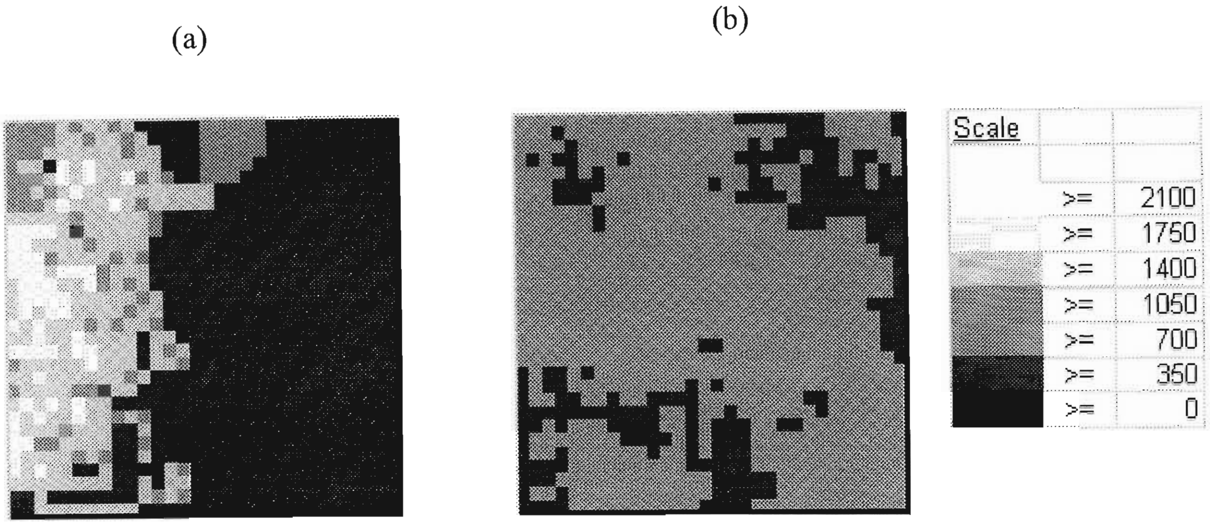

Figure 26: Final spatial distribution of the vegetation for (a) Strategy 1 with moving factor = 1.1 and (b) Strategy 1 with moving factor = 1.0 . A dark cell represents a cell with very low biomass and as the shading gets lighter, more biomass is present. The scale is in kg/ha.

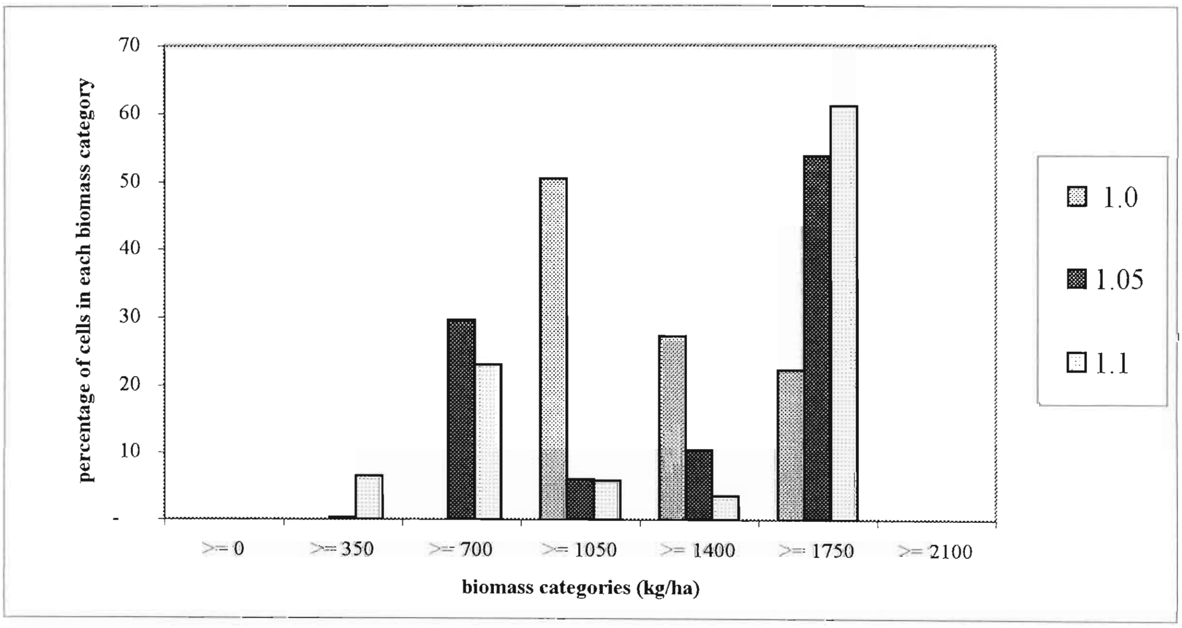

Figure 27: The distribution of biomass over all the cells for three values of *moving factor* with animals grazing under strategy 1 and 1981 rainfall.

4.4. STRATEGY 2 : MOVING TO POSITION WITH MOST BIOMASS

Since moving to the cell with the best intake rate does not appear to be a good foraging strategy as the herd may choose a cell with high energy intake rate but low biomass which is quickly depleted by grazing, the next scenario investigated is moving to the cell with the most biomass. Biomass density affects animal intake, but the cell with the most biomass is not necessarily best in terms of energy intake because the proportion of live and dead components also affects intake rate.

In this scenario, a threshold is used in deciding when to move from the current cell. The animals continue to feed in the current position until the biomass drops below a specified density, defined as *threshold*, and they then evaluate their surroundings and choose the cell with the most biomass. In choosing what value of *threshold* to use we consider the functional response curve defining intake in terms of biomass density. The curve asymptotes towards the digestive capacity of the animal for a given sward, and the shape of the function is given by $(1\text{-}e^{-b\,(B-r)})$ (see equation 1 in chapter 2). Figure 2 in chapter 2 shows what this curve looks like. As the curve approaches its maximum, an animal's intake approaches its maximum value. At 300 $\mathrm{kg.ha^{-1}}$ an animal will be able to eat at 50% of its maximum intake rate on that sward; at 600 $\mathrm{kg.ha^{-1}}$ an animal will be able to eat at over 80% of its maximum intake rate and at 900 $\mathrm{kg.ha^{-1}}$ an animal will be able to eat at over 90% of its maximum intake rate. Values of 300, 600, and 900 $\mathrm{kg.ha^{-1}}$ were chosen as initial thresholds to investigate under this strategy.

Results

The animals performed extremely poorly under this strategy and did not survive the year (fatmass dropped below zero in all cases). A fixed threshold of 300 $\mathrm{kg.ha^{-1}}$ was too high for the first few weeks as the biomass production is below that level. Thereafter, the biomass production increases to above 1000 $\mathrm{kg.ha^{-1}}$ and the animals stay in a cell until it is grazed to below 300 $\mathrm{kg.ha^{-1}}$ despite neighbouring cells being more attractive. For the higher values of *threshold* the animals performed even worse initially because of the high threshold. Setting a fixed value of vegetation density below which the animals will not graze does not allow for any variation in the animal's response to increasing vegetation as the season progresses. The value of *threshold* was made a function of the total amount of biomass available over the entire area.

In all five years, the animals increased their dry matter intake under strategy 2 (biomass) than under strategy 1 (energy) as can be seen in figure 28 where *threshold* = 0.9 times the average biomass over the whole area. The dry matter intake was still less than that of the homogeneous grazing. The final fatmass was also higher in all years except for 1988 (in which both strategies resulted in the animals dying) as is apparent in figure 29. This indicates that using the amount of biomass present to choose the next cell to forage in is better that choosing the cell with the highest instantaneous net energy intake rate.

Sensitivity of parameter 'threshold'

In order to see what an effect changing the threshold has on the performance of the animals, we investigate threshold being equal to 0.9 of the average biomass as well as equal to the average, and 0.6 times the average. The animals did not survive with the threshold being equal to the average biomass (figure 30 shows a negative fatmass for 1985 rainfall). When the threshold is dropped from 0.9 times the average biomass to 0.6 times the average, the animals perform worse with a final fatmass of 16kg as opposed to 39kg (figure 30). Figure 31 shows that the highest dry matter intake occurs when *threshold* = average biomass and that the dry matter intake decreases as the co-efficient of the average biomass in *threshold* decreases. Although *threshold* = average biomass gives the highest dry matter intake, it also has the highest daily distance travelled: the animals move as soon as the current cell's total biomass is less than the average. The frequent moves from cell to cell result in the animals expending more energy on moving and this results in the low (in fact negative) final fatmass. Similarly figure 32 shows that the strategy with the higher threshold (0.9 * average biomass) results in more movement but the animals perform better because of the higher dry matter intake (figure 30 shows their performance as measured by final fatmass).

In terms of how well the animals utilise the spatial distribution of resources, in the case where *threshold* is set to be equal to 90% of the average biomass over the entire area, there are no cells with a density below 767 $kg.ha^{-1}$ by the end of the season (figure 33). With a lower level of threshold = 0.6 * average biomass, there is more of an uneven distribution of biomass as the animals stayed longer in cells and grazed more heavily in particular cells and regions.

Animals grazing homogeneously performed better than those grazing under strategy 2 which indicates that moving to the cell with the highest total biomass does not adequately model the returns an animal will get from a particular cell. In strategy 1, the amount of biomass was not considered in choosing a cell to feed in, and in strategy 2, the digestibility of the sward was not considered. It is likely that in order to perform well, animals need to consider both aspects.

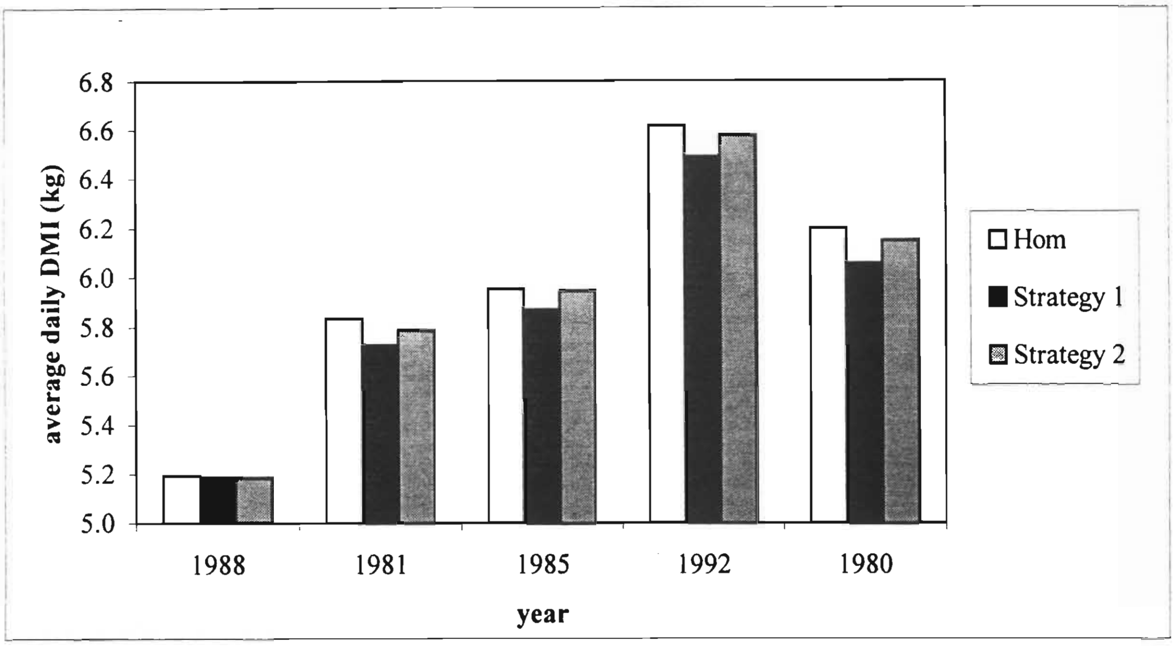

Figure 28. Average daily dry matter intake (DMI) in kg over the whole year for three scenarios: (i) Homogeneous grazing (Hom), (ii) Moving to the cell which gives the highest energy intake rate, (Strategy 1) and (iii) Moving to the cell which has the most biomass using *threshold* = 0.9 average (Strategy 2).

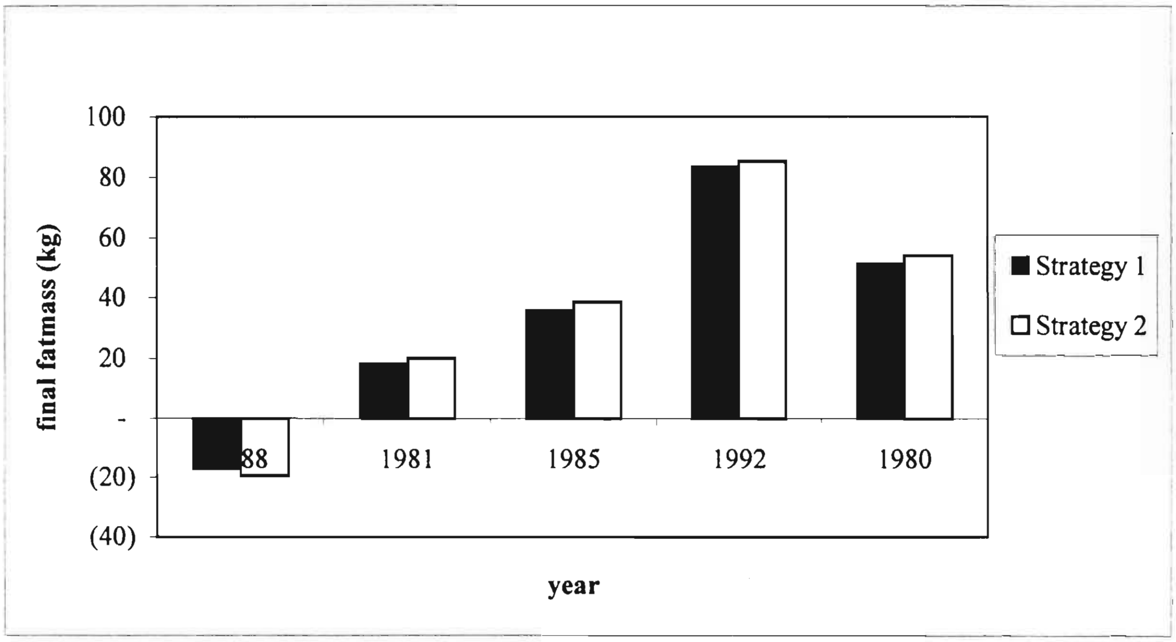

Figure 29: Final fatmass for Strategy 1 and Strategy 2 with awareness horizon 1 for various years.

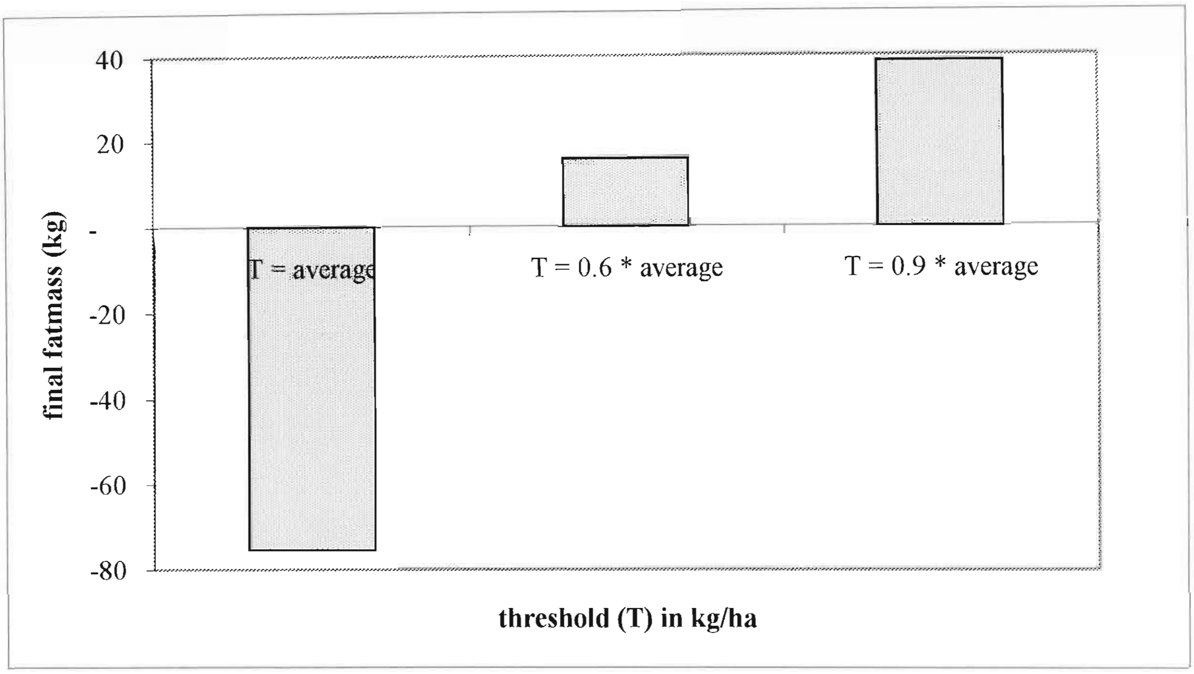

Figure 30: Final fatmass of animals under Strategy 2 (Biomass) for three different values of *threshold* with 1985 rainfall.

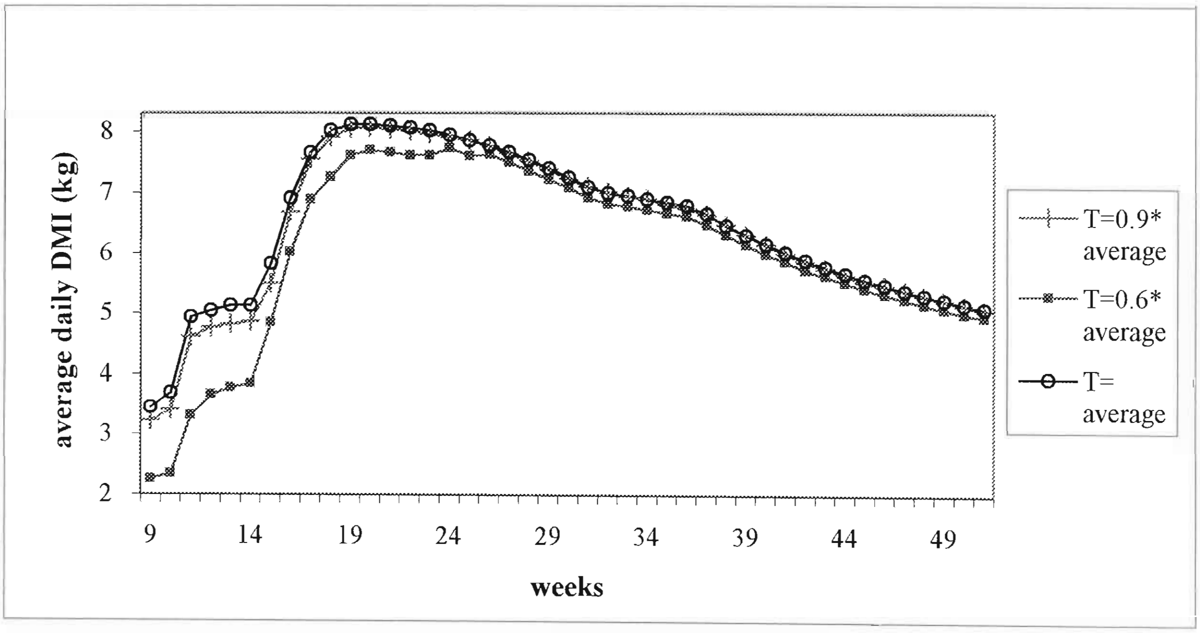

Figure 31: Average daily dry matter intake as the year progresses for three different threshold levels under Strategy 2 (Biomass) with 1985 rainfall.

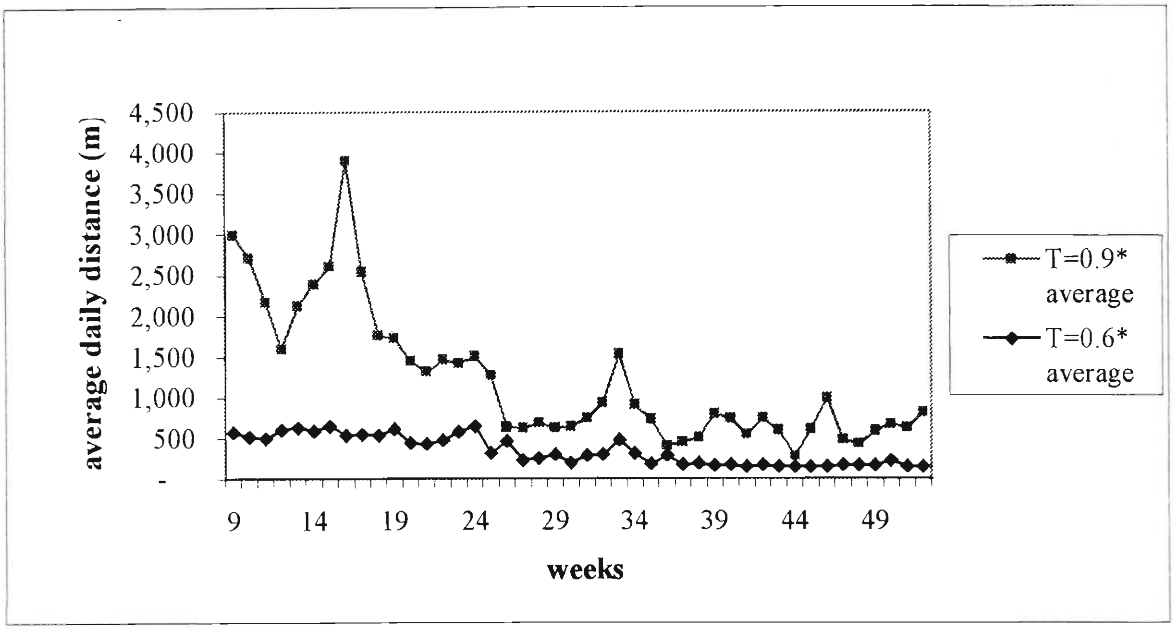

Figure 32: Average daily distance travelled by animals as the year progresses under different threshold levels with 1985 rainfall.

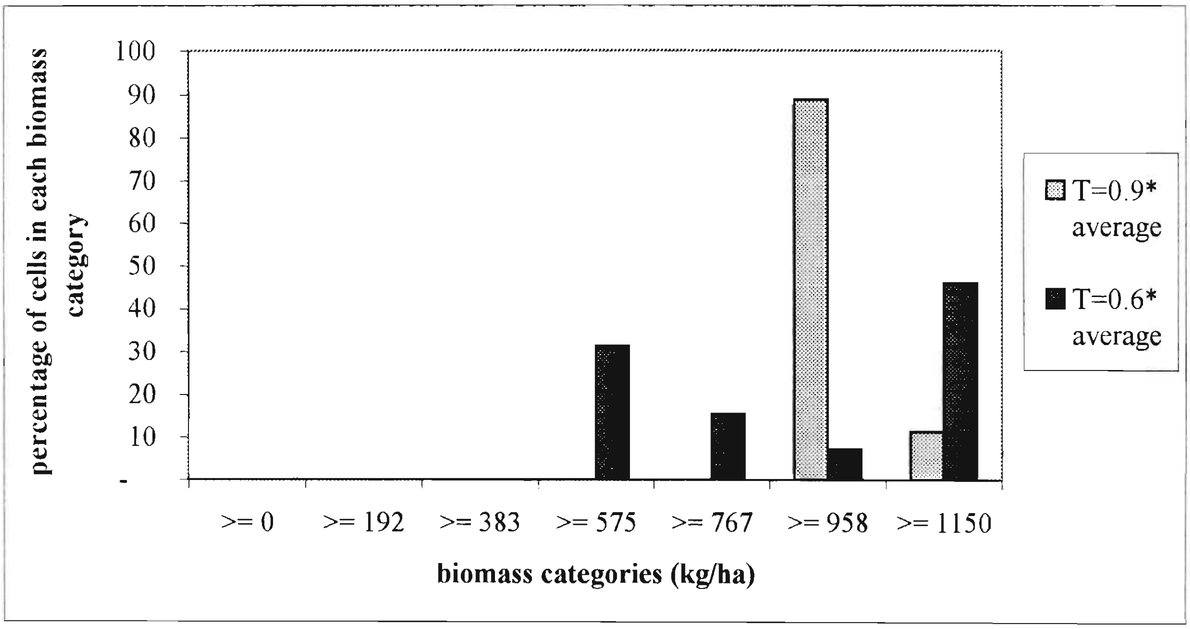

Figure 33: The distribution of biomass over all the cells for two values of *threshold* with animals grazing under strategy 2 and 1985 rainfall.

4.5. STRATEGY 3 : MOVING TO THE POSITION WITH THE MOST GREEN BIOMASS

In seeking to find ways to improve on the foraging strategies above, modelling the case where animals move to the cell with the most green biomass will capture the energy intake as well as amount of biomass to an extent. The energy intake depends on the proportion of live material in the sward, so by choosing the cell with the most green biomass animals should perform better than if just choosing the most biomass. This does not however ensure that animals move to the cell with the best proportion of live and dead material (as in Strategy 1 where energy intake rate is maximised).

Results

A threshold is chosen as in Strategy 2 and initially *threshold* is set to 0.9 times the average green biomass over the whole area as well as 0.6 times the average green biomass. Figure 34 shows the average daily dry matter intake for various strategies. Dry matter intake is the same as that under the homogenous grazing strategy with *threshold* equalling 0.9 times the average green biomass. With the threshold dropping to 0.6 times the average green biomass, the dry matter intake decreased as in strategy 2. The higher threshold results in a higher fatmass (figure 35) even though the animals move more with the higher threshold.

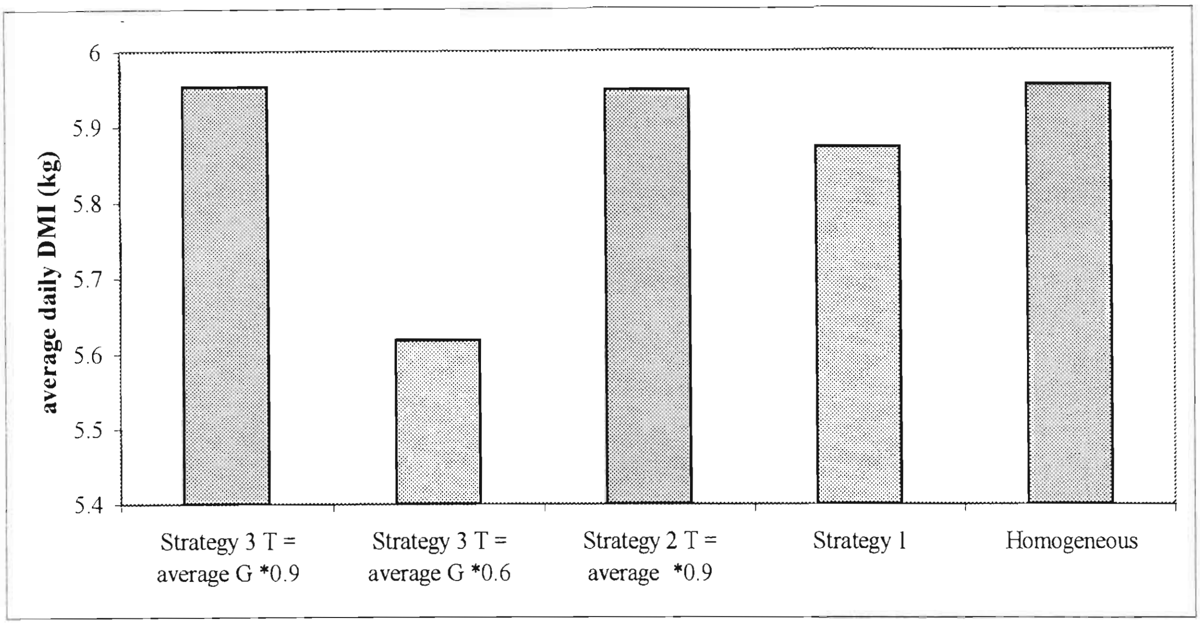

Figure 34: Average daily dry matter intake for various feeding strategies where the first two strategies are moving to the cell with the most green biomass with threshold T of green biomass in kg/ha. 1985 rainfall was used.

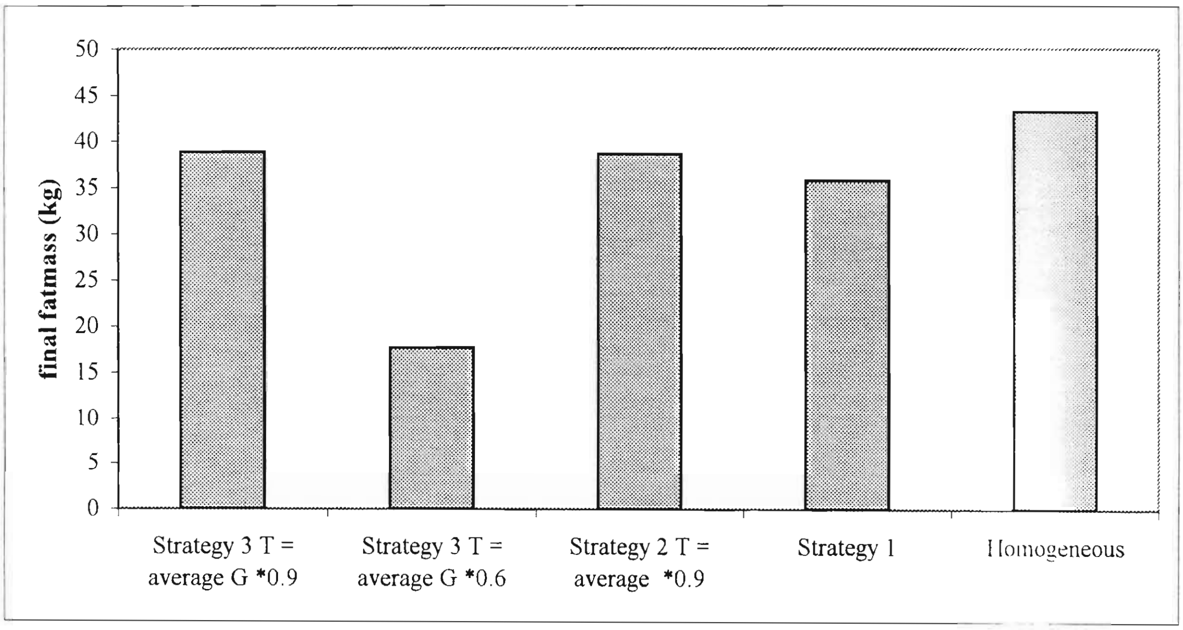

Figure 35: Final fatmass of animals for various feeding strategies where the first two strategies are moving to the cell with the most green biomass with threshold T of green biomass in kg/ha. 1985 rainfall was used.

4.6. STRATEGY 4: SYSTEMATIC MOVEMENT

Herbivores do not move in a systematic fashion along rows in the area they are feeding, but we consider this case to see how the animals would perform under those constraints. The animal herd starts in one of the corners of the 900 ha and moves systematically along the rows until it has covered the entire area. It then moves back in a similar fashion to the starting point. The animals move when the next position offers a 10% better intake rate net of movement costs.

The animal performance is worse than strategy 1 and strategy 2 as can be seen by the final fatmass of the animals in figure 36 which shows that moving systematically up and down so that the entire field is covered is not the best strategy in terms of animal performance.

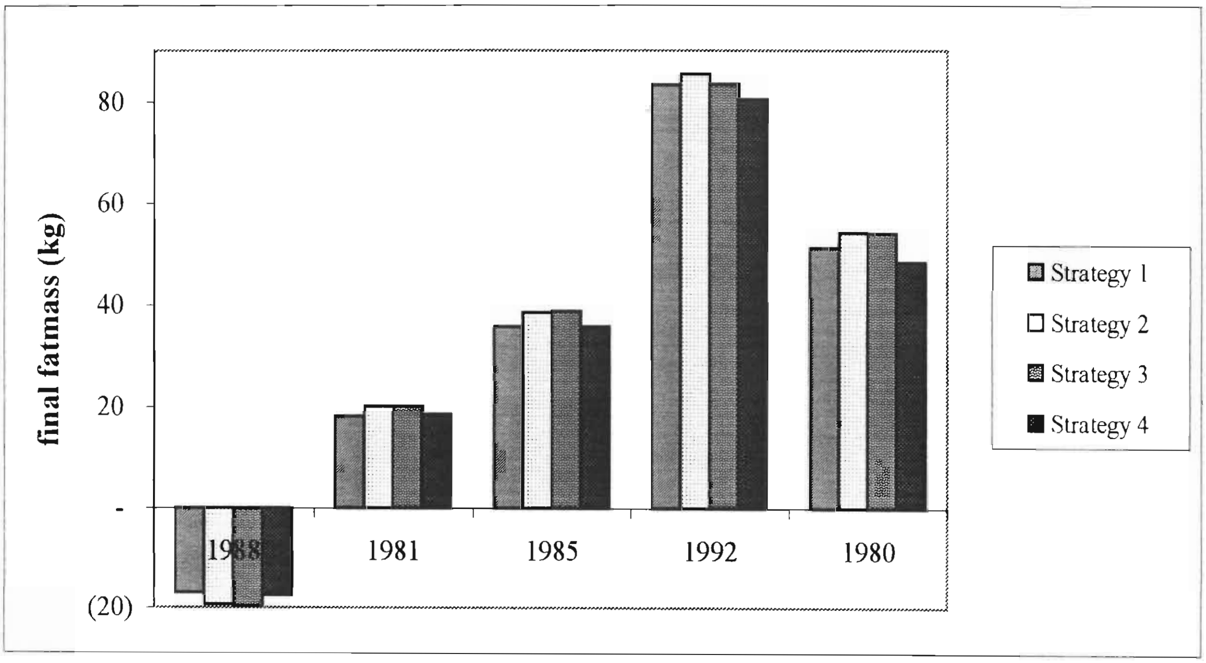

Figure 36: Performance of animals at the end of the season as given by final fatmass under different grazing strategies : (i) Strategy 1 refers to the strategy where animals move to the cell with the best energy intake rate; (ii) Strategy 2 refers to the strategy where animals move to the cell with the best biomass; (iii) Strategy 3 refers to the strategy where animals move to the cell with the best green biomass; (iv) Strategy 4 refers to animals moving up and down rows in the grid in an ordered fashion.

4.7. DISCUSSION

The objective of this study was to investigate various grazing strategies on animal condition at the end of the season. From the investigations conducted using the spatial model developed, the following observations can be made.

1. Spatial grazing strategies have a large effect on animal dry matter intake, fatmass and the vegetation.
2. Assuming that grazing impact is homogeneous does not capture the response of the vegetation to defoliation, or the animal herd movement, which affects fatmass.
3. Results indicated that moving to the cell with the highest biomass or green biomass were the strategies which resulted in the best animal performance.
4. The criteria for moving from a current location had a large affect on the performance of the animals. The state of the current location as well as the state of the surrounding cells must be considered.
5. The role of acquiring an adequate quality and quantity of forage was highlighted. Results yielded criteria to be used in choosing the next cell to move to. The criteria should include a measure of the quality of the forage material as well as the period over which they can feed at a desirable intake rate.
6. The *awareness horizon* influenced results only slightly and suggested that the animals' awareness of their surroundings is not significant in terms of their performance over a homogeneous area of 900ha.

These will now be discussed in more detail.

Spatial grazing strategies

From the model output, the change in dry matter intake for different strategies differed substantially depending on the strategy chosen. The difference in dry matter intake for 1992 rainfall was found to be 39 kg less per animal over the year for animals moving under strategy 4 than those grazing homogeneously. Furthermore, there was noteworthy variation in dry matter intake between different spatial strategies. Grazing strategies affected the final fatmass of the animals. Animals grazing under strategy 2 were able to gain 5kg more fatmass than animals grazing under strategy 2 in 1992 with the same awareness horizon

The vegetation distribution differs widely for different grazing strategies as is evident in the previous sections. Some areas are grazed heavily while others are hardly grazed over the season. The total amount of vegetation at the end of the foraging season also changes under different grazing strategies as the vegetation responds to the different spatial grazing pressures and the animals respond to the different distribution of vegetation (see for example Coughenour, 1991).

Clearly, the spatial foraging strategy employed by herbivores has a large effect on animal performance and the vegetation. More information is needed as to how animals respond spatially at this landscape scale which is larger than plant selection and smaller than region selection. As field experiments to collect such data will be difficult to conduct, modelling can certainly provide meaningful insight into how animals behave.

Homogeneous grazing

The majority of grazing models assume that grazing is homogenous over the area being modelled. The problem with assuming homogenous grazing, even though the sward may be initially spatially homogeneous, is that the vegetation responds differently to different levels of defoliation depending on the season, rainfall, intensity of grazing and the selectivity of the grazers. In assuming homogeneous grazing, the simplification is made that animals will cover the entire area regularly and evenly, as this would be necessary to ensure that the vegetation responded uniformly over the entire area. From the results of the model developed in this thesis, this is an unreasonable assumption. In almost all the simulations, the end distribution of vegetation was very patchy with certain areas being over-utilised and others under-utilised. The response of vegetation to frequent defoliation has been found to result in grazing lawns (see Coughenour, 1991 and references therein). These grazing lawns occur in response to frequent close grazing and result in a greater forage quality in the particular patches. Another phenomenon known to occur is patch grazing (Coughenour, 1991). Regrowth on grazed patches becomes higher in quality than the surrounding ungrazed patches. The ungrazed patches are then avoided, resulting in those patches becoming even more undesirable.

Initially homogeneous swards respond to grazing pressures and become non-homogeneous, which affects where the animals choose to forage and their diet composition. In all the spatial grazing strategies, the total vegetation at the end of the season was less than that predicted under homogeneous grazing. Under 1985 rainfall, the final vegetation for homogeneous grazing was 1060 kg.ha^{-1}, and for animals grazing under strategy 1, the vegetation biomass was 1086 kg.ha^{-1}, which is 26 kg.ha^{-1} more than that of the homogeneous case. Homogeneous grazing does not adequately simulate the response of the vegetation as animals forage non-homogeneously across the area.

Another aspect highlighted by the results of the spatial model discussed in this thesis, is the effect of the distance travelled on the fatmass of the animals. The distance depends largely on the spatial strategy employed by the animals and also the abundance of resources. The increase in the average daily distance travelled by foraging animals had a significant effect on the fatmass of the animals. More energy was expended in travelling and the final fatmass of the animals decreased. Homogeneous models cannot describe animal movement accurately.

Strategy for best animal performance

Strategy 2 and 3 (choosing the cell with the most biomass or most green biomass) resulted in the best performance, as given by the highest final fatmass, in all scenarios. This is in accordance with results found by Roguet *et al.* (1998) where green leaf mass was found to be the best indicator of choice of feeding station in a study conducted on ewes and that the choice was found to be independent of sward state. The results presented in this thesis conflict with results found by Wallis de Vries and Daleboudt (1994) in which foraging steers were observed. They found that matching for digestibility (similar to strategy 1) gave the best predictions of where steers chose to feed and matching for digestible organic matter gave the worst predictions of patch selection. Digestibility is the largest determinant of intake rate and corresponds to energy intake rate except where biomass density is very low. Matching for digestible organic matter can be considered to be similar to strategy 2 or strategy 3 as it is an indication of the amount of biomass available. The performance of the animals under strategy 1 was poor as the digestibility of the grass in a cell gives no indication as to the amount of material present.

Deciding when to move

As animals feed in a cell, the biomass becomes depleted and the functional response of the animal changes with a decrease in biomass. The digestibility of the cell also decreases depending on the selectivity of the animal, as green leaves are selected and this too alters the energy intake rate of the cell, though to a lesser degree. If animals remain too long in a location, their energy intake rate as well as diet composition is compromised.

The scenarios for investigating when the herd should move clearly indicated that the decision must be based on the current state of the cells that the animal herd could move to next. Under strategy 2 and 3 when *threshold* was set to a fixed biomass density, the animals performed poorly in terms of dry matter intake and final fatmass. Setting the *threshold* i.e. relative threshold to depend on the available vegetation gave much better results.

Distel *et al.* (1995) and Laca *et al.* (1993) found that steers depleted identical patches to different degrees depending on the context where the patches were found. This supports the idea that animals move when a cell in the neighbourhood offers better returns than that of the cell that the herd presently occupies (as is modelled in strategy 1), rather than animals grazing biomass down to some level. In investigating how soon the herd moves, setting *moving factor* to 1, which translates into the animals moving as soon as the returns from another cell are better than the current returns, resulted in the highest dry matter intake for each year – even higher than the homogeneous case. But, the animals moved so frequently that their energy expended in travelling to new cells was far higher than any other strategy and the result was a low fatmass. Animals moving when cells offered a 10% better net energy offered the best overall performance as indicated by final fatmass. This meant that there was a penalty involved in moving from the current position and so the animals did not move around unnecessarily. It also ensured that the penalty was not so great that it would result in the animals staying too long in a cell and decreasing their intake rate as the cell biomass decreased.

In a model developed by Focardi *et al.* (1996), the threshold below which animals did not forage was determined by the long term average rate of foraging as given by the marginal value theorem (Charnov, 1976). Bailey *et al.* (1990) conducted a study in which they found that it was unlikely that cattle were using a “giving up” rule that would be predicted by the marginal value theorem and that a systematic and predictable patch alternation pattern should not be expected. The marginal value theorem provides the optimal solution to maximising herbivore fitness, but its appropriateness to animals foraging in practise has been debated. There have, however, been studies conducted which found evidence to support the marginal value theorem successfully predicting patch selection and utilisation (for example Laca *et al.*, 1993). Strategies 2 and 3 implement a rough approximation of the marginal value theorem when *threshold* is set to some proportion of the average biomass over all the cells.

Strategy 2, in which animals moved to the cell with the most biomass, depended largely on what the value of *threshold* was chosen to be. As the grassland has a different production capacity each year depending primarily on rainfall, and that the density of biomass varies greatly with season, choosing a cut-off point biomass below which animals will move is not a sensible choice. Defining the *threshold* (relative threshold) in terms of the average available biomass allowed the animals to perform better. They were not moving around unnecessarily at the beginning of the season when vegetation was scarce, nor were they staying too long in cells once the vegetation had had a chance to grow and the threshold was now too low. This scenario did not include any penalty for moving a longer distance and so as awareness horizon increased, the animals performed worse.

The decision to move off from a particular location must depend on the state of the current location as well as that of the surrounding cells.

Quality and quantity

Animals foraging homogeneously were found to have the highest dry matter intake when compared with the spatial strategies. Homogeneous grazing, in this case, referred to each animal feeding on its own in an area of 4 ha. Thus, grazing impact was small in comparison with the spatial strategies where the entire herd of 200 animals fed in a cell simultaneously. Animals feed in herds because of social factors, and localised grazing impact is an important consideration in grazing systems. In choosing where to feed next, maximising energy intake rate is a good choice only if there is sufficient biomass in the cell to make moving there worthwhile for the entire herd. Bailey (1995) found that steers within a group usually followed one or two individuals as they first entered a patch. An interesting question to consider, is whether the animals leading the herd are moving so as to optimise their own fitness and thus instantaneous intake rate, or whether the optimisation is more long term and that the amount of biomass present is also important.

In order to maximise fitness of the herd, net energy must be maximised. There are energy costs involved in moving to another cell, and each cell has an instantaneous rate of energy intake. But, as the animals graze in the cell, the rate of energy intake will decrease. This decrease will be rapid in cells with low biomass. A measure of how long the energy intake rate will stay at the same rate would be useful in choosing the best next cell to forage in.

The strategies modelled highlighted the two conflicting sides to foraging, namely, quality versus quantity. In the cases where quality was used to decide where to move, the quantity did not correspond in a positive way and the animals resulted in having to move more often (strategy 1). When animals chose to move to cells with higher quantity, the quality was sacrificed (strategies 2 and 3). The results from this model suggest that the animals' ability to maximise for both these variables will result in the most efficient foraging strategy.

Importance of awareness horizon

In seeking an optimal solution to maximising fitness whilst foraging, optimal foraging theory suggests that a variant of the travelling salesman problem should be solved. Observations of bighorn sheep (Gross *et al.*, 1995) provided no indication that they can accomplish such an intellectual feat. Optimal foraging theory must necessarily assume either that animals integrate formidable amounts of information about forage resource distributions, or it must assume natural selection for simple behavioural rules-of-thumb that yield approximately optimal solutions, but require far less cognitive function. Focardi *et al.* (1996) found in a study that fallow deer were not able to detect and exploit food patches.

By including the parameter *awareness horizon*, a scale of cognitive abilities was modelled. When *awareness horizon* was one, the animals were only aware of their immediate neighbours and chose the best of all neighbours. As *awareness horizon* increased, the animals had more knowledge about the vegetation present further away from them and made decisions based on the increased amount of information.

An increase in *awareness horizon* led to slightly better performance of the animals under the feeding strategies modelled which suggests that this is not as an important factor in foraging strategies.

Summary

It is clear from the simulations that the spatial pattern of foraging does influence animal performance in terms of animal intake and distances travelled. Animals grazing on a homogeneous sward modify the spatial distribution of vegetation and respond to the heterogeneity created by grazing impact. The animals' awareness of their surroundings and ability to choose the best place and time to forage in a different location affected animal performance and a greater understanding of how intelligently herbivores forage is necessary. Spatial grazing models are necessary in order to correctly capture the dynamics at play in a semi-arid ecosystem.

CHAPTER FIVE

CONCLUSION

The aim of this study was to gain a better understanding of the spatial and temporal dynamics of a semi-arid grazing system and the effect of grazing strategies on animal condition at the end of a single grazing season. A grid-based modelling approach was adopted in developing a model that simulated plant and animal dynamics and the interactions between them. Various spatial grazing strategies were investigated using the model and particular attention was paid to the condition of the herbivores at the end of the season. Total dry matter intake, which is an indication of energy gain, and the total distance travelled, which affects the animals' net energy, were also monitored. Results from the model were able to provide useful insights into the dynamics involved in a semi-arid grazing system.

It was evident from the model output that foraging strategies have a large effect on herbivore condition, influencing their intake as well as their energy expenditure. Herbivore condition varied widely for different foraging strategies, as was measured by the chosen performance index of fatmass. The distribution of vegetation and the total amount of biomass at the end of the grazing season varied depending on the foraging strategy implemented. The importance of animal foraging strategies and their effect on animal performance and state of vegetation have not been widely investigated by researchers, and from this study it has emerged as an important consideration in grazing systems.

The results from the spatial model showed that spatially explicit models are necessary in the context of investigating animal performance. The non-spatial model produced different results for dry matter intake when compared with the spatial model output. In the spatial model, the response of the vegetation to uneven grazing pressure led to heterogeneity in the sward, which affected animal intake. It was not possible to model this dynamic in a non-spatial model. How the animals utilised the spatial resources was an important factor in their performance, since where the animals foraged affected their intake rate and the amount of available energy. The distance travelled by the herd affected their energy expenditure. The heterogeneity in available energy in the sward due to uneven grazing pressure and how far the animals need to move to meet their nutritional and metabolic requirements affected the animals' condition. These factors must be spatially modelled. The research in this thesis has shown that spatial aspects of grazing cannot be ignored if animal performance is to be adequately modelled, and that spatial grazing models are useful tools in investigating the spatial grazing dynamics that affect animal condition.

A number of aspects that significantly affect animal condition were highlighted. To what extent the animals were aware of their surrounding vegetation was not found to be an important determinant of animal condition. The ability to assess both the digestibility of the vegetation in a cell as well as the amount of vegetation was found to have improved animal performance remarkably. The criteria for moving from a current location was important as it regulated how often the animals moved as well as how long they spent in a particular cell whilst foraging. Moving too soon resulted in increased movement which decreased net energy and moving too late caused the animals to remain in the cell once the vegetation had been depleted considerably and the intake rate had dropped. These factors influencing animal condition have to a large extent been neglected in the literature, and are felt to be an area for future research both in the field and using modelling techniques.

Empirical studies have been conducted for single animals as well as for small groups of animals in small enclosed areas. Migration and long-term movement has been the subject of much investigation. Data is lacking when it comes to the movements of a large herd of animals within a specified region (i.e. not migratory patterns), and how animals utilise vegetation spatially is not well understood and is an area that needs more research conducted into it.

A spatial model is a useful tool in investigating foraging strategies as it allows one to record the distances travelled and the differences in vegetation cover in response to grazing pressures. Other spatial features that have not been included in this research, but can be easily added, are the position of water holes, differences in soil types, and different vegetation types.

Many grazing systems include more than one type of herbivore, for example, cattle and sheep where cattle are less selective than sheep. In addition, grazing systems include a mix of vegetation, which may include short grass species and tall grass species. A spatial model would be particularly useful in investigating the dynamics of such a complicated system and providing insight into what ratio of different species should be kept. The model described in this thesis has been parameterised for a mid to tall grass growing at Matopos, but can be parameterised for other grass-species and a more general location. The animal intake dynamics depend on the mass of the animal, and parameters defining the animals' selectivity, and can be easily changed to model any ruminant.

Other important management questions that have arisen from these initial investigations can be investigated using this spatial model. In most of the spatial strategies, some portion of the total area was not grazed at all, and an interesting question that could be investigated, is the optimum size of an enclosed area in which animals forage. Animals in smaller herds impact the vegetation less along their foraging path, and optimum herd size could be analysed using the model.

This research shows the usefulness of a spatial grazing model in understanding grazing dynamics and providing insight to rangeland management.

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APPENDIX 1 : DESCRIPTION OF VELD

The following was taken from Dye (1983).

Water budget sub-model

1. Initial values of soil moisture in three stores at the start of the season are taken to be 10.5, 29.5 and 42.5 mm.
2. Rainfall for a particular day is read in. If it is less than 12 mm, all of it is regarded as infiltrating the soil. If it equals or exceeds 12 mm, a quadratic relation is used to partition daily rainfall into runoff and infiltrating water. The effects of rainfall intensity, plant cover and antecedent soil moisture on this partition are not simulated.
3. The quantity of rainfall infiltrating into the soil is used to sequentially fill up the three stores on the basis of field capacity data. Any infiltrating water remaining after all three stores are full is regarded as lost to the soil through deep drainage. It is assumed that moisture allocation is rapid and is not impeded at any depth. The uppermost soil store fills to field capacity before the next store begins to fill and similarly for the other two stores. It is assumed that no moisture is held above field capacity, and that no movement of unsaturated soil moisture occurs between stores.
4. Evaporation from the soil surface is assumed only to occur from the top soil store (0 – 10 cm). The daily rate of evaporation from bare soil at field capacity is controlled by atmospheric evaporative demand and is taken to equal pan evaporation. Shoot mass and consequently aerial cover, increase through the growing season and progressively impede evaporation from the soil. Consequently, evaporation from bare soil is reduced to a potential evaporation rate for a given mass of shoot material. The moisture content of the top store is then taken into account to obtain an actual evaporation rate which may be lower than potential evaporation rate if the top store is below field capacity. The drop in evaporation with declining soil moisture is rapid and reaches zero as the

top store declines to 16 mm. Actual evaporation for a particular day is then deducted from the top store.

5. Daily potential transpiration per gram of green dry matter and per mm pan evaporation is estimated as a function of the total shoot mass at the end of the previous week. This rate of transpiration is expected to apply when the soil moisture is non-limiting. The total soil moisture in all three stores is then considered in defining an index which may reduce potential transpiration rate to a lower actual transpiration rate if soil moisture is limiting transpiration.
6. The estimated daily actual transpiration is now removed from the soil

Plant growth sub-model

1. Before the first harvest of each new growing season, the shoot mass remaining from the previous season was removed either by burning or by mowing and raking. Hence, the initial mass of green leaves, dead leaves, culms and inflorescences are set at zero at the start of each new simulation.
2. New green leaves appear each year towards the end of September in response to the seasonal rise in temperature which occurs around the beginning of the month. Green mass increases slowly, even in the absence of rain and in apparently dry soil. However, should the first rains be late, growth ceases when the shoot mass reaches approximately 25 $g.m^{-2}$ and only resumes after the first rains have fallen. Pre-rain growth is thus made a function of week. If these newly formed leaves are transpiring water, it must be taken up either from within the soil profile (despite a very high water potential) or else from the sub-soil which is penetrated only by the few deepest roots.
3. The main period of growth is initiated by the advent of the first significant rains.
4. From the cumulative weekly actual transpiration an increment of net growth is derived. This is obtained by first correcting weekly actual transpiration for variation in weekly

mean relative humidity and then multiplying this quotient by a transpiration coefficient, and an index simulating the seasonal decline in photosynthetic efficiency.

5. This weekly increment of growth is then allocated to green leaves, culms, inflorescences and roots plus crown. The pattern of assimilate partition to plant components varies through the season in response to changing magnitudes of carbohydrate sources and sinks, which in turn are largely determined by phenological development.
6. The normal pattern of growth allocation is known to alter as moisture stress becomes severe in range grasses, with higher translocation rates to crowns and roots. Consequently, allocation to green leaves is reduced to 0.6 when the total available soil moisture declines below 110 mm and ceases altogether below 95 mm.
7. It is important to simulate the rate at which green leaves die since transpiration occurs only from live leaves. The death of green leaves increases with the overall age of the leaves (broadly a function of week) and with a decline in the total available soil moisture.
8. Weekly growth (and death in the case of green leaves) is then considered in updating the mass of plant components.

APPENDIX 2: SUMMARY OF VARIABLES USED

Variable	Definition	Units
I	daily dry matter intake	kg
a	asymptote defined by animals digestive capacity	kg
B	vegetation biomass	kg.ha^{-1}
r	residual biomass below which animals cannot graze	kg.ha^{-1}
b	size related constraint	
A	mature mass of animal	kg
M	actual mass of animal	kg
U	mass ratio of the animal	
D_{diet}	digestibility of the diet (in vivo)	
D_{live}	digestibility of the live material,	
D_{dead}	digestibility of the dead material, and	
Lp_{diet}	proportion of live material in the diet	
Lp_{sward}	proportion of live material in the sward	
n	allometric function of mass with a positive exponent	
c, d	parameters defining selectivity specific to the grass type	
b	allometric function of mass with a negative exponent	
p, q	parameters defining relationship between body mass and bite mass	
EI	daily energy intake	MJ.d^{-1}
E_{exp}	net metabolisable energy expended	MJ.d^{-1}
FM	fasting metabolism	MJ.d^{-1}
E_{mov}	energy expended by moving	MJ.d^{-1}
E_{com}	energy expended by commuting	MJ.d^{-1}

Variable	**Definition**	**Units**
E_{graze}	energy expended by grazing (or rut effort if not grazing)	$MJ.d^{-1}$
F_{dist}	distance travelled while feeding	m
GT	grazing time	s
CT	time spent commuting	s
C_{dist}	distance travelled while commuting (m), and	m
$COMVEL$	velocity at which animal commutes ($m.s^{-1}$)	$m.s^{-1}$
E_m	energy concentrate of food (metabolisable energy)	$MJ.d^{-1}$
K	co-efficient of utilization which is the efficiency of utilization of metabolisable energy for maintenance	
E_{maint}	actual energy expended	$MJ.d^{-1}$
m	metabolic co-efficient for the conversion between energy and fat	$MJ.kg^{-1}$
F	mean body fat	kg
F_{max}	maximum value for body fat	kg