Spatial pattern and process in the fragmentation of heather moorland

by

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Declaration

I hereby declare that this thesis has been composed by myself and has not been submitted in any previous application for degree. The work of which it is a record has been carried out by myself unless stated otherwise. All sources of information have been acknowledged by means of reference to the authors.

26 March 2003

Sander Pieter Oom

Dedication

To all sheep munching away on this planet and
against all who dare to call them stupid!

The treachery of Finella

Kenneth, Malcolm's son, reigned for twenty-four years and two months. And he was killed by his own men in Fettercairn, through the treachery of Finella, the daughter of Cunthar, earl of Angus. This Finella's only son had been killed by the aforesaid Kenneth.

Translated from the Chronicle of the Kings of Scotland by A.O. Anderson (1990).

Her name was Finella; Kenneth had long before ordered her only son to be slain at Dunsinnan, I know not whether by severity of the law, or for some deed, or for any other cause. Therefore this crafty woman, eagerly aspiring after the king's death, caused to be made in a remote cottage a kind of trap never seen before. The trap had attached to it on all sides crossbows, always kept wound up, each with its cord, and fitted with the sharpest bolts and in the middle of them stood a statue like a boy, cunningly attached to the crossbows, so that if any one touched and moved it in any way he should loosen the catches of the crossbows on all sides, and immediately be pierced by the bolts discharged.

Also after completing her work for the accomplishment of this crime, the wicked woman mentioned above kept always a cheerful countenance before the king, and at last deceived him, flattering him with treacherous words. The king went hunting one day with a few followers, not far from his own dwelling, with dogs raising the beasts here and there among the woods. And he chanced to turn aside near the village of Fettercairn, where the traitress lived; and when she saw him she bent her knees, and begged him importunately to go to her house. 'Otherwise,' she said, 'I must necessarily consider that I am suspected by your Majesty's Grace. But God knows, and thou, king, shalt soon know, that although the talk of malignant men repeats many lies about me, I have always been loyal to thee, and always shall be, so long as life remains with me. For I know very well that all thou hast done recently to my most wicked son was done not undeservedly, but justly.' And she ran up to him and whispered in the king's ear. 'If but thou wilt come with me, I will expose to thee, my lord, thy betrayers, my cursed son's accomplices, and the manner of their treason; they hoped to associate me with them in their deceit, under an oath; but I refused at once to consent to their wicked treachery. They have forced me, however, to swear, touching the Gospels, that I should never betray their secrets; and although I promised them this under oath, I should nevertheless have been most false and a traitress to thee, my lord king, to whom before all others is due firm and loyal fealty, if I hid the danger of thy person. For who is unaware that no oath holds against the safety of royal majesty?'

Thus did the treacherous woman cunningly beguile the king's mind, and lead him with her, alas ! too trustful in her, to the dwelling, in spite of the opposition of all. Why dilate, why dwell upon grievous things? After the king had dismounted from his horse, she led him alone by the hand very swiftly to the house where the trap was concealed. And as if for the purpose of revealing the secrets of the traitors, as she had promised, she closed the door behind them, and showed him the statue, which was the lever of the whole trap. Upon his asking what this statue had to do with him, she answered, smiling: 'My lord king, if any one should touch and move the top of the head of this statue that thou seest, a marvellous and pleasant show will spring from it.'

Wholly ignorant of the hidden treachery, he drew easily towards him with his hand the head of the machine, and loosened the levers and catches of the crossbows; so that he was suddenly pierced from all sides by the bolts released, and died without uttering another word.

Then the traitress went out quickly by the back-door, and hid herself for the time in the shadows of the woods; but soon afterwards she came safely to her supporters. Also the king's followers waited long for his return from the house, and wondered why he delayed there. At last they beat persistently upon the door, and, hearing nothing, in rage broke it open. As soon as they knew of his death, a great outcry was raised, and they ran hither and thither searching for the wicked woman, but in vain; not finding her, and not knowing what to do, they burned the town with fire, reducing it to ashes. And they carried away with them the king's blood-stained body and shortly afterwards buried it in the royal fashion with his fathers, in Iona.

Translated from Fordun, Chronica by A.O. Anderson (1990).

Fordun's story of Finella is semi-mythical. Tradition in the Mearns says that Finella walked on the tree-tops from Finella Hill, near Fordoun, down to Finella Den, near St Cyrus: this suggests that she was a wholly mythical personage, possibly the stream-goddess of Finella Burn. Perhaps the stream's name (? *find-ela* "white swan") has influenced the form of a woman's name (*Findguala* "white shoulder").

Taken from Anderson, Alan Orr (1990).

Anderson, Alan Orr (1990). *Early sources of Scottish history: A.D. 500 to 1286.* Volume 1. Paul Watkins, Stamford, pp. 512-515.

Abstract

Grazed ecosystems, in which large mammalian herbivores interact with vegetation mosaics, account for one fifth of the earth's land surface and provide both food and economic resources. Although grazed ecosystems have provided a fruitful base for scientific study for many decades, due to the complexity of these systems and the lack of appropriate tools, analysis of the spatial aspects of plant-herbivore interactions is still in its infancy. The aim of this study was to contribute to the understanding of spatial aspects of plant-herbivore interactions within a grazed grass-shrub system, using heather moorland - an internationally important ecosystem dominating much of the Scottish uplands - as the object of investigation.

A three-year field experiment was conducted to observe plant-herbivore interactions between Scottish Blackface sheep and heather-grass mosaics. Due to the complexity of grazing systems, traditional experimentation is limited in providing insights into the complexity of interactions occurring. Therefore modelling tools were also employed to allow for virtual experimentation, thus complementing and extending the field data.

The results of the field experiment showed the importance of a spatially explicit approach to understanding the interactions. The pattern of use of the vegetation mosaics by sheep was strongly heterogeneous, with spatially limited areas of intensive use intermixed with large areas of extensive use. Foraging and ruminating behaviour showed distinctively different patterns of impact, indicating that multiple processes determine herbivore use of vegetation mosaics and their concomitant impacts on the dynamics of the vegetation.

Application of a spatial interaction model, previously used in human geography, to the field data revealed that the amount of grass in an area was a good predictor of the local heather defoliation. Heather defoliation was highest near large grass patches and lowest away from small grass patches. The virtual experiment showed further that cognitive aspects of foraging behaviour could play an important role in determining the pattern of use by herbivores. Performance of foraging strategies was strongly affected by the heterogeneity of the vegetation, suggesting that herbivores could adapt their foraging strategies depending on the pattern of vegetation.

This study provides new insights into the spatial aspects of plant-herbivore interactions in grass-shrub mosaics and offers a starting point for more detailed investigations. At the same time the results necessitate the increased use of spatially explicit approaches in the management of grazed ecosystems.

Contents

Chapter 1

Introduction

To have the ultimate even if idealistic objective of fusing the shattered fragments into the original unity is of great scientific and practical importance; practical because so many problems in nature are problems of the ecosystem rather than of soil, animals or plants, and scientific because it is our primary business to understand.

A.S. Watt (1947)

1 Introduction

1.1 Plant herbivore interactions

Rangeland ecosystems cover 20% of the earth's surface. They provide a means of existence for a large proportion of its inhabitants, while at the same time they include many of the more fragile areas of the world (Hodgson & Illius, 1996). Rangeland ecosystems are typically semi-natural ecosystems used for extensive grazing of large herbivores. They occur around the world both in temperate and semi-arid regions and frequently comprise complex mosaics of vegetation over which the grazing animals range freely. Due to their marginality and complexity, rangeland ecosystems have received relatively little attention from scientists in comparison with highly productive agricultural systems (Hodgson & Illius, 1996).

In the last decade, there has been a shift in attention in the science of plant-herbivore interactions. New insights into the functioning of ecosystems and the concomitant development of new research tools have inspired a new approach in understanding plant-herbivore interactions. In the late 1980s, scientists investigating range management realised that for a better understanding of plant-herbivore interactions, and therefore for a better support of management decisions, spatial aspects of plant-herbivore interactions had to be considered more explicitly (Bailey et al., 1996; Coughenour, 1991; Senft et al., 1987). The investigation of spatial aspects of plant-herbivore interactions was accelerated by the development of Geographical Information Systems (GIS), which allowed the handling of large spatial data sets, and the development of modelling tools. Models are increasingly used as scientific tools to investigate plant-animal interactions and to support management decisions. Improvement of these models continues to demand a better understanding of spatial aspects of plant-herbivore interactions (Bailey et al., 1998; Illius & O'Connor, 1999; Weber et al., 1998; Wiens et al., 1993).

A large body of review papers covers the many aspects of plant-herbivore interactions. An overview is given here for completeness, but more detailed literature reviews are included at the start of each individual chapter. From the animal perspective, Pyke (1984) provided the first comprehensive review of optimal foraging theory. This review was followed by a more specific review on diet selection by Allison (1985). Senft *et al.* (1987) introduced the hierarchical scales approach to plant-herbivore interactions. This paper was followed by reviews considering spatial aspects of diet selection (Stuth, 1991), foraging behaviour at feeding site and station scale (Roguet et al., 1998), and the role of cognition in foraging behaviour (Bailey et al., 1996). The spatial aspects of modelling plant-herbivore interactions were reviewed by Coughenour *et al.* (1991) and Bailey *et al.* (1996).

The plant perspective was covered in a largely separate body of reviews. Briske (1991) gave an overview of morphological and physical plant responses to herbivory, considering the tiller and genet scale, with implications for the population and community scales. At the plant community scale, aspects of herbivory were reviewed by Archer and Smeins (1991). Rosenthal and Kotanen (1994) argued that tolerance and defence can not be viewed independently, and that some plant traits affecting plant-animal interactions might have evolved as a result of herbivory. Briske (1996) linked plant ecology and entomology to come to a more functional explanation of plant resistance to grazing. Implications for grass population dynamics were discussed by Bullock (1996), while competition between grasses and woody plants was reviewed by Archer (1996).

Management implications of the spatial aspects were reviewed by Vavra and Ganskopp (1998). Rangeland management has multiple objectives, optimizing both economic returns and long term maintenance of resources (Heady & Child, 1994). Rangeland ecosystems are typically of low input, so stocking densities are optimised to maintain long-term plant production. Successful management of the balance between palatable and unpalatable vegetation requires a spatially explicit understanding of the plant-animal and plant-soil interactions (Archer, 1996).

Foraging theory has traditionally focused on the physiological aspects of diet selection (e.g. Laca & Demment, 1996; Pyke, 1984), while range management has focused on animal production (Allison, 1985). With the increased importance of multiple objectives in grazed ecosystems, such as biodiversity and soil conservation (Heady & Child, 1994), a more detailed understanding of the interactions between herbivores and the ecosystem is required. Concurrent with the realisation that the spatial pattern of defoliation should be considered explicitly (Senft et al., 1983) came the theoretical acknowledgement of the importance of spatial aspects in grazed ecosystems (Archer, 1996; Bailey et al., 1996; Coughenour, 1991; McNaughton, 1984; Senft et al., 1987).

A large body of papers considers why the world is green, or why only 10-20% of the annual net primary production in terrestrial ecosystems is consumed by herbivores (Drent & Prins, 1987; Hartley & Jones, 1997; Lawton & McNeill, 1978). Although both top-down and bottom-up arguments, i.e. herbivore control by predators or vegetation respectively, have been put forward, Hartley & Jones (1997) conclude that the lack of control of herbivores over the vegetation is mainly due to the general poor quality and high temporal and spatial heterogeneity of the resource. Processes determining vegetation quality and spatial and temporal variation, are still poorly understood (Hartley & Jones, 1997).

The importance of spatial heterogeneity in the stability of predator-prey systems has been investigated intensively (e.g. Hastings, 1977; Huffaker, 1958). Schrag & Mittler (1996) showed that, in a controlled lab experiment with a bacteria-phage system, the existence of spatial refuges was the primary factor explaining long-term stability between predator and prey. However, the role of spatial interactions in the stability and the existence of multiple stable states of plant-herbivore systems has received little attention. Woodin (1978) distinguished five types of refuge from disturbance: 1) temporal refuge outside the activity range of disturbance, 2) temporal refuge within the activity range of disturbance resulting from temporal heterogeneity, 3) spatial refuge outside the activity range of disturbance, 4) spatial refuge within the activity range of disturbance resulting from physical heterogeneity, and 5) 'biological refuges' within the activity range of disturbance resulting from biological structures that buffer the disturbance effect. An example of the refuge type resulting from physical heterogeneity has been suggested for plant-herbivore systems based on field observations (McNaughton, 1984) and model simulations (Milne et al., 1992). This spatial refuge could influence the stability of ecosystems by providing protection from herbivory for the vegetation that is not part of the plant-herbivore interface (McNaughton, 1984; Milne et al., 1992). However this suggestion has not been pursued so far in experimental studies. The role of spatial heterogeneity in the functioning of plant-herbivore systems is therefore the main focus of this study.

1.2 Carrying capacity on heather moorland

The role of spatial heterogeneity in the functioning of plant-herbivore systems is investigated in the context of heathlands. Heathlands are dominated by ericaceous dwarf-shrubs (such as *Calluna vulgaris* (L.) Hull) and have a restricted distribution in north-west Europe along the North Atlantic coast and across Britain (Gimingham, 1972; Webb, 1998). Apart from providing a forage resource for livestock, heathlands are increasingly valued as an internationally important natural resource for recreation and wildlife conservation (Gimingham, 1972; Thompson et al., 1995) and for their aesthetic and historical value (Diemont & Jansen, 1998; Kaland, 1998; Webb, 1998). However heathlands have for some time been under threat from atmospheric nitrogen deposition (Aerts & Berendse, 1988; Aerts, 1989) and changes in management practices such as 'plaggen', burning and grazing (Diemont, 1996; Thompson et al., 1995; Welch, 1984) and their range has greatly declined.

Grazing reportedly plays an important role in heathland management in Britain, whether through 'over-grazing' on upland moorlands (Thompson et al., 1995; Welch, 1984) or through 'under-grazing' in lowlands (Webb, 1990). Over- and under-grazing are subjective terms based on observations of a system from a particular objective. Thus a similar grazing pressure could be perceived as over-grazing in the context of one objective and under-grazing in the context of another objective. To successfully manage heathlands for a complex of multiple objectives, a good understanding of the herbivore carrying capacity of the vegetation is required in order to define, recognise and avoid over- or under-grazing within the context of the objectives.

However, carrying capacity, in the context of hill farming, has in the past been expressed as fixed stocking rate thresholds for the management unit or a fixed level of herbivore impact based on the proportions of heather and grass in the mosaic averaged over the heft (Grant et al., 1988; Grant & Armstrong, 1993; Hunter, 1962; Welch, 1984), thus assuming that herbivore impact is spread evenly across the vegetation mosaic. Conversely, earlier research had already suggested that herbivore impact on vegetation is strongly influenced by spatial heterogeneity of the vegetation (Grant et al., 1978) and this has since been quantified in successive experiments (Clarke et al., 1995; Hester & Baillie, 1998). HeathMod, a model simulating impact of sheep on upland heaths, successfully predicted sustainable levels of heather defoliation, but the authors concluded that an important omission of the model is the possible unevenness of defoliation patterns (Read et al., 2002). Similarly the Hill Grazing Management Model (Armstrong et al., 1997a; Armstrong et al., 1997b; Grant & Armstrong, 1993) and its successor HillPlan (Milne & Sibbald, 1998), aimed at supporting rangeland management, do not consider spatial heterogeneity. Thus, a spatially explicit understanding of herbivore carrying capacity could contribute to a more effective management of heather moorland.

1.3 Project aims and objectives

In summary, current scientific understanding is rarely spatially explicit. Although the role of spatial heterogeneity in plant-herbivore interactions is recognised, few have made an attempt to quantify the impact of spatial heterogeneity on grazed ecosystems through experimentation. Several unexplained phenomena in grazing ecology could have their justification in spatial aspects of plant-herbivore interactions. As a consequence, support for the grazing management of rangeland ecosystems in general and heather moorland in particular, also does not take into account spatial heterogeneity of herbivore impact. Furthermore, increased multiple objectivity of management requires an increased understanding of the implications of plant-herbivore interactions. To address these questions, this study has the following aims and objectives.

Aims

1. To understand the processes behind the pattern of defoliation of the less preferred vegetation type by large herbivores across rangeland vegetation mosaics.
2. To understand the herbivore foraging behaviour that creates and maintains mosaics in the vegetation resource.
3. To increase the understanding of the spatial aspects of plant-herbivore interactions to facilitate further research.
4. To provide spatially explicit understanding to support management decisions for the sustainable management of heather moorland and grass-shrub mosaics in general.

Objectives

1. To describe quantitatively the pattern of heather defoliation by sheep in a heather-grass mosaic
2. To measure the spatial pattern of vegetation change in the heather-grass mosaic.
3. To ascribe the patterns of vegetation change to interactions between the behaviour of sheep and the spatial pattern of the vegetation.
4. To construct a simulation model of the interactions between herbivores and vegetation mosaics and use this to evaluate the potential role of spatial perception in the development of defoliation patterns.

1.4 Outline of the thesis

The first three chapters of this thesis are based on the results from a three year grazing experiment within a heather dominated vegetation in north-east Scotland. The thesis starts (Chapter 2) with an investigation of the spatial pattern of heather defoliation across the heather-grass mosaic as observed during this experiment. A spatial interaction model is applied to the field observations to describe the main patterns of defoliation. The spatial interaction model predicts the probability of defoliation as a function of heather-grass mosaic characteristics. This global pattern is then refined in the next chapter (Chapter 3), in which the heather defoliation across grass-heather boundaries is investigated in more detail. The impact of defoliation and other herbivore foraging behaviour are examined (Chapter 4) through spatially explicit analysis of vegetation change over the course of the field experiment. The field experiment is then extended in the penultimate chapter (Chapter 5) with a virtual experiment, using a simulation model, to investigate the role of animal foraging strategies in the development of foraging patterns. The general discussion (Chapter 6) summarises the results of the individual chapters and discusses implications in the wider context of heathland management and the understanding of plant-herbivore interactions in grass-shrub mosaics in general.

References have been added to each chapter. Lists of figures, tables, and abbreviations have been added at the end of this thesis. Appendix A and B provide background information about the modelling environment HOOFS, which are necessary to understand the work described in Chapter 5. Note that these appendices are largely based on the work of A.J. Beecham.

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Chapter 2

Spatial interaction models: From human geography to plant-herbivore interactions

However, despite the progress in making spatial interaction models more behaviourally based, it is probably the case that many geographers still associate spatial interaction modelling with its early social physics background [...]. This is unfortunate for two reasons. The first is that, despite its very widespread application to many facets of the real world, these geopgraphers ignore or even dismiss spatial interaction modelling, not because of what it is but because of what it was 20 or 30 years ago. The second, and more important, is that spatial interaction modelling provides a very fertile area for understanding spatial behaviour and for developing theories which are explicitly spatial. It is an area that is quitessentially geographical; it is an area where geographers should be leading the way by exporting their ideas to other disciplines.

A.S. Fotheringham (2000)

2 Spatial interaction models: From human geography to plant-herbivore interactions

2.1 Introduction

This chapter considers the spatial pattern of shrub defoliation by a large mammalian herbivore across a grass-shrub mosaic. Grass-shrub mosaics are an example of a two-phased vegetation mosaic, in which a spatially localised (preferred) plant community fulfils nutritional needs, whilst a spatially extensive (less preferred) plant community meets energy requirements but is nutritionally marginal (McNaughton & Banyikwa, 1995). The less preferred plant community plays a crucial role in the stability of plant-herbivore systems, as the herbivores can switch to the less preferred plant community when the preferred plant community is unavailable (Illius & O'Connor, 2000; Wallis de Vries, 1991). This is the case for example in heather-grass mosaics, where both the quantity and the quality of the preferred vegetation type (i.e. grass) declines rapidly in autumn, forcing the animals to switch to a diet of mostly heather during the winter months (Armstrong & Milne, 1995). Relying on the less preferred plant community, allows the animals to survive long periods of poor forage availability. Thus the management of these two-phased mosaics requires different strategies for different range management objectives. Sustainable animal production requires a balance between preferred and less preferred plant communities that is favourable to the herbivore (Archer, 1996), whilst nature conservation is aimed at maintaining or increasing important flora and fauna. Limited understanding of the complexity of these ecosystems can lead to inappropriate management strategies (Bailey et al., 1998).

Spatial heterogeneity plays an important role in ecological processes (e.g. Kolasa & Pickett, 1991; Kotliar & Wiens, 1990).The study of plant-herbivore interactions in two phased vegetation mosaics requires a spatial approach (Archer, 1996; Bailey et al., 1996; Coughenour, 1991; McNaughton, 1984; Noy-Meir, 1981; Senft et al., 1987). Although the spatial pattern of defoliation is influenced by both abiotic and biotic factors (Bailey et al., 1996), here we considered only the biotic factors: forage biomass, digestibility and nutritional content. Based on these biotic factors, Senft et al. (1987) predicted spatial patterns of defoliation at community, landscape and regional scale. Focusing on the community scale, herbivores are predicted to select for the highest quality plant community, resulting in overmatching (Staddon, 1983) as the proportion of the plant community in the diet exceeds the proportion of that plant community in the vegetation mosaic.

The prediction of overmatching at the community scale has implications for the spatial pattern of defoliation of preferred and less preferred plant communities at this scale. As herbivores focus their grazing on the preferred community, their use of the mosaic will be concentrated on those areas of the mosaic where the preferred community is abundant. Further, the defoliation of the less preferred community will be strongly influenced by the pattern of use of the mosaic. Thus the spatial pattern of defoliation of the less preferred community is expected to be strongly correlated with the distribution of the preferred community.

Spatial heterogeneity in defoliation patterns has been discussed and modelled in several two-phased vegetation mosaics (Archer, 1994; Bokdam & Gleichman, 2000; Morellet & Guibert, 1999; Ring et al., 1985; Wallis de Vries, 1996; Weber et al., 2000), but the spatial pattern of defoliation has, as far as we can ascertain, only been quantified for heather moorland (Clarke et al., 1995b; Hester & Baillie, 1998).

A series of experiments in the north-east of Scotland has investigated the spatial plant-herbivore interactions within heather moorland, an internationally important natural resource for recreation and wildlife conservation (Gimingham, 1972; Thompson et al., 1995). This heather moorland consisted of grass (mainly *Agrostis capillaris* L. and *Festuca ovina* L.) dominated patches in a heather (*Calluna vulgaris* (L.) Hull) dominated matrix. Grass patches were either artificially created in the heather matrix (Clarke et al., 1995b) or part of a natural heather-grass mosaic (Hester & Baillie, 1998). The proportion of grass in the vegetation mosaics varied between 15% and 20%. For both experimental sites, Cuartas et al. (2000) found that sheep (*Ovis aries*) and red deer (*Cervus elaphus* L.) showed overmatching of grass consumption, as the proportion of grass in the diet was at least a factor of two higher than the proportion of grass in the vegetation mosaic.

Clarke et al. (1995b) found that heather defoliation by sheep is higher near the edge of grass patches than further away. This is confirmed for natural grass patches (Hester & Baillie, 1998) and for paths (Oom & Hester, 1999). Clarke et al. (1995b) also found that heather defoliation at the edge of grass patches increases with grass patch size. This effect is confirmed for red deer, but not for sheep, foraging in natural heather-grass mosaics (Hester & Baillie, 1998).

To investigate the correlation between the spatial pattern of defoliation and vegetation pattern, we employed a spatial analysis method originating from human geography. Many questions in human geography involve interactions between spatial patterns of resources and consumers. In order to study and predict spatial patterns of consumer behaviour as a function of resource patterns, a range of spatial interaction models (SIM) has been developed (see for review: Fotheringham et al., 2000; Sen & Smith, 1995). Geographers realized that many individual spatial behaviour decisions by consumers can lead to an aggregated pattern of movement. This aggregation effect has also been suggested for foraging decisions by herbivores (Staddon, 1983). SIMs attempt to describe these aggregate patterns. SIMs are regression equations, deriving an index of attraction based on characteristics of a mosaic or network from a spatial response variable. The SIM applied here could also be considered a weighted proximity analysis or a multiple regression analysis.

SIMs have been successfully used to predict road network usage, to predict optimal locations for supermarkets and petrol stations in relation to urban areas and to predict the felling probability of a patch of forest depending on the distance to wood mills. The first equations used in SIMs resembled Newton's Law of Gravity, and were thus named gravity models. The basic SIM uses this gravity analogy to calculate an index of attraction, at a given location, based on the distance between the current location and the resource, and the attractiveness of a resource (where attractiveness is the product of the resource magnitude and the attractiveness per unit resource). A quadratic distance-decay function is included, which creates an index of attraction of a resource will decrease with distance. This leads to the following index of attraction:

$$\text{index of attraction} = \frac{\text{attractiveness of resource}}{\text{distance}^2}$$ **Equation 2.1**

Using the quadratic distance-decay function assumes the resource of attraction to be a point source. Figure 1 illustrates the relationship between the index of attraction, the distance and the attractiveness of the resource as calculated using Equation 2.1. The index of attraction is then used as a predictor for a response variable. For instance, the probability that people from a suburb will be customers of a particular supermarket can be used to estimate the number of potential customers in supermarkets around a city. A regression analysis, the actual SIM, determines the relationship between the response variable and the index of attraction.

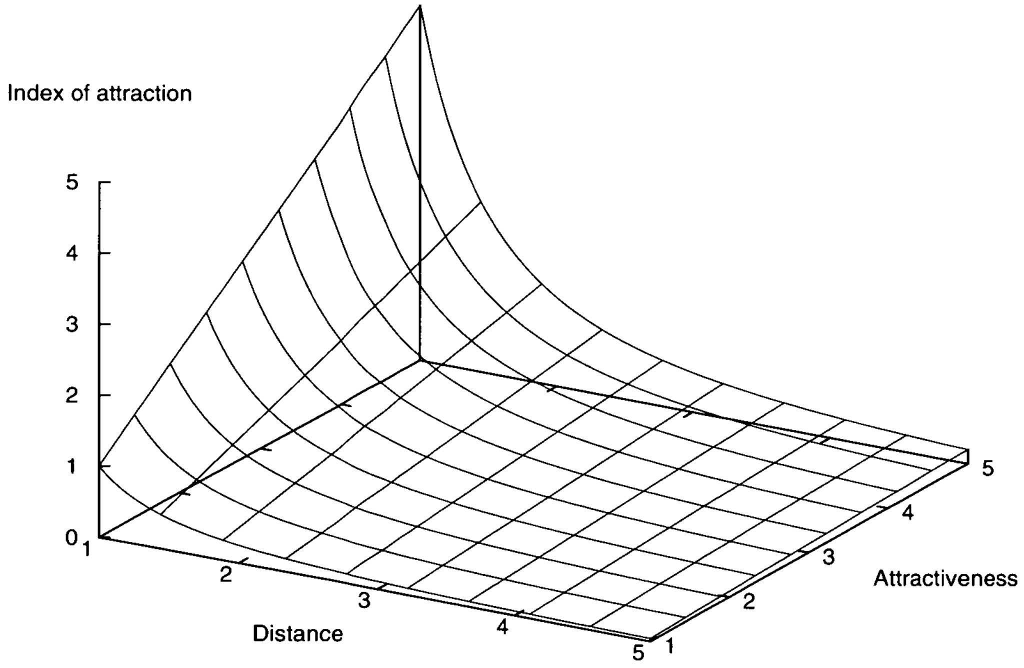

Figure 2.1. Surface plot of the index of attraction (as calculated from Equation 2.1) against the distance to and the attractiveness of a resource.

SIMs are powerful tools for describing the aggregate pattern resulting from many individual behaviour decisions. At the same time the models are poor in revealing the underlying mechanisms as individual decisions are obscured by the aggregation (Fotheringham et al., 2000). But in the quest to understand spatial foraging behaviour, the SIM can be used to investigate the spatial pattern of vegetation defoliation by herbivores.

The following section describes the process of introducing more complexity in the index of attraction only when the fit between the index of attraction and the data was improved. Several distance-decay functions were tested, but none performed better than the quadratic distance decay function used in the basic index of attraction. In the methods and results sections I only present the SIM based on the final index of attraction.

2.2 Theory

As the defoliation of a less preferred plant community is strongly correlated with the pattern of the preferred community (Clarke et al., 1995b; Hester & Baillie, 1998), we used grass as the attraction resource to calculate the index of attraction at a given location. We assumed a positive correlation between attraction and habitat use and hence defoliation of the less preferred community. We used grass patch area to represent the magnitude of the attractiveness of the resource. The attractiveness per unit resource was considered to be constant in the model. Within the heather-grass mosaics, the grass patches are connected by paths to form a network within a heather matrix. Because habitat use by sheep is strongly confined to this network (Hester et al., 1999), distances were determined as shortest path-distance to the nearest grass patches. This leads to the first index of attraction for location *j*:

$$\text{index of attraction}_j = \frac{\text{grass patch area}}{\text{distance}^2} \qquad \textbf{Equation 2.2}$$

As reviewed in the previous section, heather defoliation generally declines away from the grass-heather edge. But what is the heather defoliation at a given location on the grass-heather edge? To answer this question we investigated the correlation between the index of attraction at a given location on the network (at the edge of a patch or a path) and the heather defoliation in a 0.50 m wide zone bordering this location (heather edge zone). The index of attraction is based on the nearest patch only. Entering the basic index of attraction (Eq. 2.2) gave the following regression equation, in which *a* and *b* are the regression slope and intercept respectively, which both can be estimated by regression of observed heather defoliation on the index of attraction:

$$\text{heather defoliation}_{\mathrm{j}} = a + b \times \text{index of attraction}_{\mathrm{j}} \qquad \textbf{Equation 2.3}$$

Although it has been shown that herbivores use a mental map of grass patches (Dumont et al., 2000; Edwards et al., 1996; Roguet et al., 1998), it is unknown how they perceive clusters of patches surrounding a given location. We therefore assumed that sheep consider grass patches within a certain radius from their current location (specified in the methods section), and calculated a cumulative attraction value for all grass patches within the radius. The index of attraction is now based on the sum of the attraction of all patches within the radius. This second index of attraction (*n* is the number of patches in the cluster) for location *j* is:

$$\text{index of attraction}_{\mathrm{j}} = \sum_{i=1}^{n_j} \frac{\text{grass patch area}_{\mathrm{i}}}{\text{distance}_{\mathrm{i}}^{2}} \qquad \textbf{Equation 2.4}$$

The performance of this regression depends on the ability of herbivores to estimate patch area and distance accurately. However, animals and humans tend to mentally underestimate a stimulus when the stimulus is strong and the underestimation increases with increasing strength of the stimulus (Bateson & Kacelnik, 1998; Carlson, 1990; Stevens, 1957; 1975). This leads to a logarithmic relationship between the perceived and the objective strength of a stimulus. Therefore in this third SIM we use a logarithmic transformation on the assumption that sheep underestimate larger values of both area and distance, leading to the third index of attraction:

$$\text{index of attraction}_j = \sum_{i=1}^{n_j} \frac{\log(\text{grass patch area}_i)}{(\log(\text{distance}_i))^2}$$ **Equation 2.5**

Although the individual foraging decisions will be influenced by grass patch area and distance, the level of the aggregated heather defoliation will depend on the number of sheep present per unit grass area. We therefore introduced a measure of global grazing intensity, leading to the final index of attraction which predicts the spatial pattern of heather defoliation at the edge zone in heather-grass mosaics:

$$\text{index of attraction}_j = \frac{\text{sheep number}}{\text{total grass area}} \times \left(\sum_{i=1}^{n_j} \frac{\log(\text{grass patch area}_i)}{(\log(\text{distance}_i))^2} \right)$$

Equation 2.6

Now we consider the regression between observed heather defoliation and the index of attraction as presented in Equation 2.6. In parallel with theory and observation we expected heather defoliation at the heather edge zone to be higher at the edge of large grass patches than at the edge of small grass patches and heather defoliation, along grass paths, to be higher near grass patches as compared to further away. This would predict a positive correlation between heather defoliation and the attraction predicted by the SIM.

As for the effect of season and the grazing intensity, we would expect differences in the slope and intercept of the regression of heather defoliation and the attraction. Grass quantity and quality drop significantly during the winter (Armstrong & Milne, 1995), leading to a decrease in contrast between grass and heather. As the relative attraction of grass decreases, the sheep are expected to be less biased by the grass patch area in that season, leading to a decrease in the slope. The increased heather defoliation in the winter would lead to an increase in the intercept (Figure 2.2a). When increasing grazing intensity within a season, we would also expect an increase in heather defoliation leading to an increase in the intercept, but we would also expect sheep to remain biased towards the grass, leading to a stronger increase at high attraction values, i.e. near large grass patches, and thus an increase in the slope (Figure 2.2b). As larger grass patches become exhausted with higher grazing intensity, sheep are forced on the less attractive areas of the mosaic, leading to an increase in the intercept and thus a decrease in the slope (not shown).

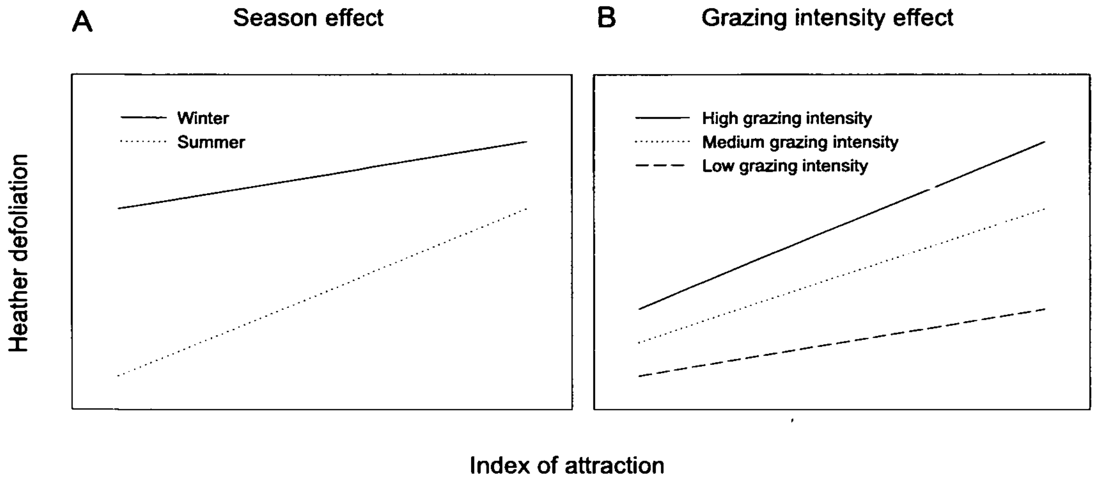

Figure 2.2. Hypothetical effects of season (A) and grazing intensity (B) on the linear regression of heather defoliation on the index of attraction.

2.3 Methods

Heather defoliation was observed during a three year experiment (1998-2001) of sheep grazing natural heather-grass mosaics. The experimental site, at the Macaulay Institute's Glensaugh Research Station, consisted of six one-hectare plots, containing natural heather-grass mosaics (described in: Hester & Baillie, 1998). The plots were located on a north north-west facing slope with a slope angle of 17°. Three grazing intensity treatments, 4, 3 and 2 sheep per hectare, were applied year round on plots 1 and 5, 2 and 6, and 3 and 4 respectively (Figure 2.3). In spring and autumn heather defoliation away from grass-heather boundaries was measured along transects laid out in the field using measuring tapes. To determine transect locations, seven 100m lines were laid out across each plot along the slope (Figure 2.3).

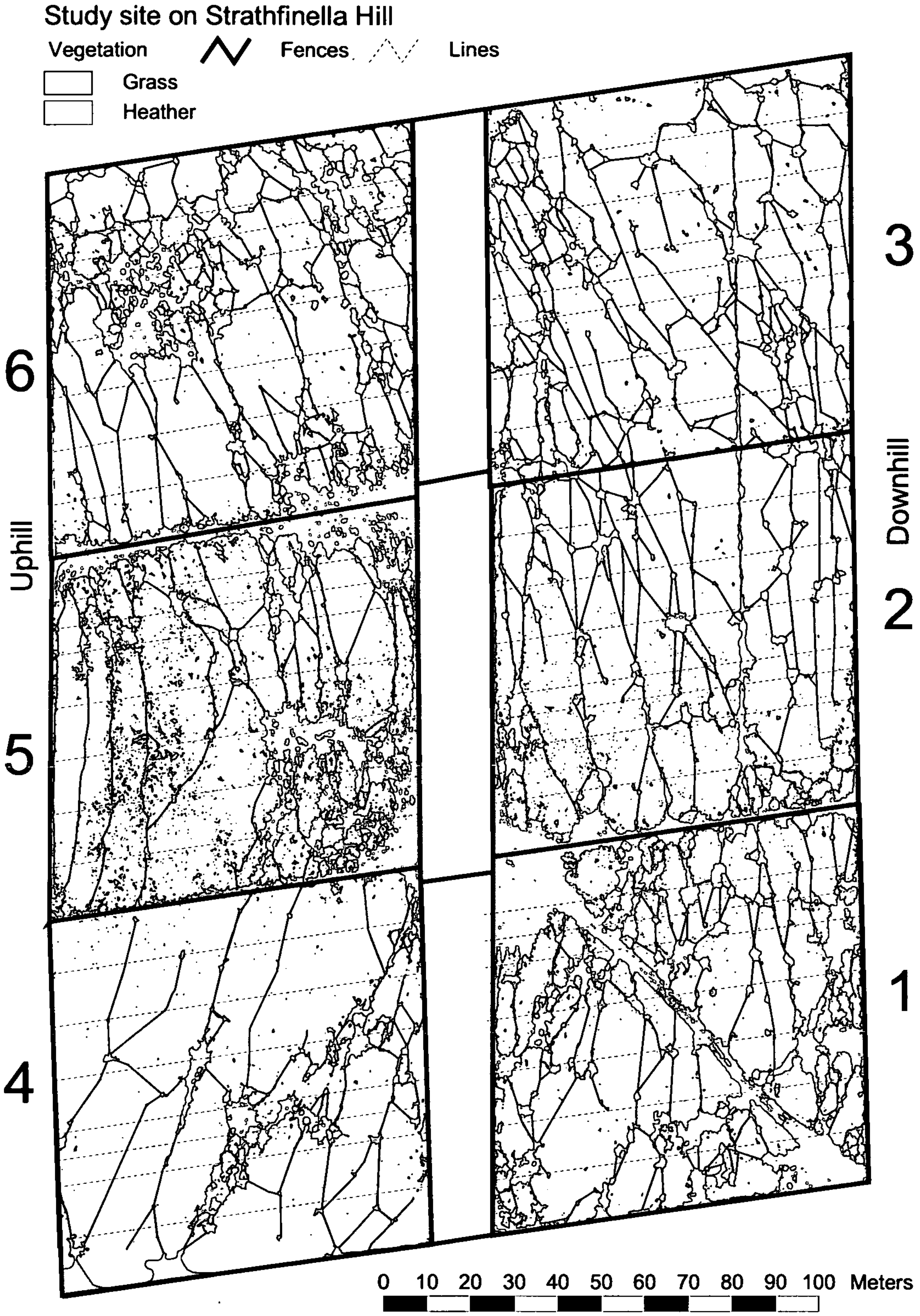

Figure 2.3. Vegetation map of the experimental site at Macaulay Institute's Glensaugh Research Station. Dotted lines indicate the lines used to determine transect locations for the measurement of heather defoliation away from grass/heather edges. Numbers indicate the respective plots.

A transect was then allocated to each grass-heather boundary, either at a path or a grass patch, crossed by a line. Transects were drawn from the edge of the grass into the heather perpendicular to the grass-heather edge. As the geometry of the paths and patches generally followed the contours, the majority of transects were up- and downhill. Transects going off the same path or grass patch, on any one line, were grouped together into a 'transect location'. This resulted in a total of 358 transect locations. Because of the different mosaics in each plot, the total number of transect locations per plot varied between 36 and 78. Heather defoliation was measured at fixed distances along each transect (0, 0.25, 0.50 m) according to the method described by Hester and Baillie (1998), providing an estimate of the percentage of current year's growth removed at each distance.

A vegetation map was created using colour aerial photographs, specially taken in October 1998 at the start of this experiment, which were digitally scanned from negatives. The resulting digital images were orthorectified, mosaiced and classified using Erdas Imagine (ERDAS Inc., USA; Version 8.3). The classification resulted in a vegetation map containing grass patches in a heather matrix. As much as possible, grass patches were defined by the classification process. Where the classification resulted in a conglomerate of individual patches (in approximately 10 cases), individual patches were manually defined according to assumed sheep perception of the mosaics, as derived from previous work on these plots (Hester and Baillie 1998; Hester *et al.* 1999). However, as the SIM model used in this study (Equation 2.6) evaluates conglomerates of patches in the same way as clusters of individually-defined patches, any division of conglomerates did not affect the results of the SIM analysis. Despite the high resolution of the image (cell size 0.05 m × 0.05 m), the lighting condition and spectral reflectance characteristics of the vegetation (generally low grass cover) prevented the classification of paths. Paths, indicated by an interruption of the heather canopy, were therefore surveyed in the field and manually digitized. The vegetation map and path elements were joined to get a map of a connected grass network in a heather matrix. The starting point of each transect, at the grass-heather boundary of the path or grass patch, was manually digitized onto the grass network. For each of these transect positions, the distance to the edge of the nearest grass patch, measured along the grass path, and the associated patch area were determined using the ‘cost-distance’ function in ArcInfo (ESRI, USA; Version 8). To accommodate the model, the distance was set to one metre for all distances less than one metre. In order to calculate the cumulative attraction of the cluster of neighbouring patches, we repeated the 'cost-distance' method for each successive larger patch connected with the transect position along the grass network. Because attraction declines rapidly with distance (i.e. distant patches contributing little to the cumulative attraction) we only considered patches within a 25 m radius from the location. All attraction values were summed to get a cumulative attractions for each transect location.

The severity of heather defoliation at the edge of grass patches and paths is known to be higher uphill than downhill (Hester & Baillie, 1998; Oom & Hester, 1999). But the data analyzed here showed no significant difference in the spatial pattern of heather defoliation up- and downhill. Therefore, a single mean was calculated for the six observations at each transect location (i.e. combining the heather defoliation measurements at 0, 0.25 and 0.50 m away from the heather for both the uphill and downhill transects). Because about 90% of the observations had a heather defoliation of less than 25%, i.e. the data were negatively skewed, the percentage heather defoliation was angular transformed before averaging. The transformation resulted in residuals not significantly different from a normal distribution. Values presented in tables and figures are based on transformed data.

The purpose of this analysis was to determine the relationship between the heather defoliation and the attraction predicted by the SIM. A regression analysis was considered most suitable for this purpose, producing slope and variation in slope, while allowing for known effects of the grazing treatment and season. The experimental design was unbalanced, due to the varying number of transects per line. Because of the hierarchical design of transects within lines within plots, correlation in the data may have arisen due to effects of plot, line and transect. To take into account the hierarchical, unbalanced design, we used the Residual Maximum Likelihood (REML) method available in Genstat (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13). REML treats factors, giving rise to different slopes and intercepts, as fixed effects and handles the correlations via the variance components associated with the random effects.

We analyzed the heather defoliation data using treatment, season and SIM as fixed effects and plot, line, and transect as the random effects. The regression analysis was based on the mean angular heather defoliation per transect location. For presentation purposes, the scatter plots are based on the average mean angular heather defoliation for ten classes (containing equal numbers of transect locations), calculated with REML, using the same random model as used for the regression analysis.

The output from REML gave a Wald statistic for each fixed effect added to the model, which provided a significance estimate equivalent to the F-test in an ANOVA (Elston, 1998). To obtain an estimate of the variance explained by the fixed effects model, an Adjusted R^2 was calculated based on the stratum variance provided by REML. The stratum variances estimate the unexplained variances of means of the different levels for each random effect and are adjusted for the degrees of freedom in the fixed effects model. Because of the hierarchical nature of the random model, a separate Adjusted R^2 had to be calculated for each random effect (plot, line, transect). The stratum specific Adjusted R^2 were calculated using the following formula: $100\% \times (1-SV_a/SV_n)$. Where SV_a and SV_n are the stratum variances for the alternative model (with fixed effects) and the null model (without fixed effects) respectively.

2.4 Results

Across all plots, values for distance ranged from 0 to 23 m, while the values for grass patch area ranged from 1 to 441 m^2. Figure 2.4 shows that the values for patch area and distance were not equally represented across the six plots. The analysis for SIM was therefore strongly unbalanced at the plot level, i.e. confounded with the grazing intensity treatment.

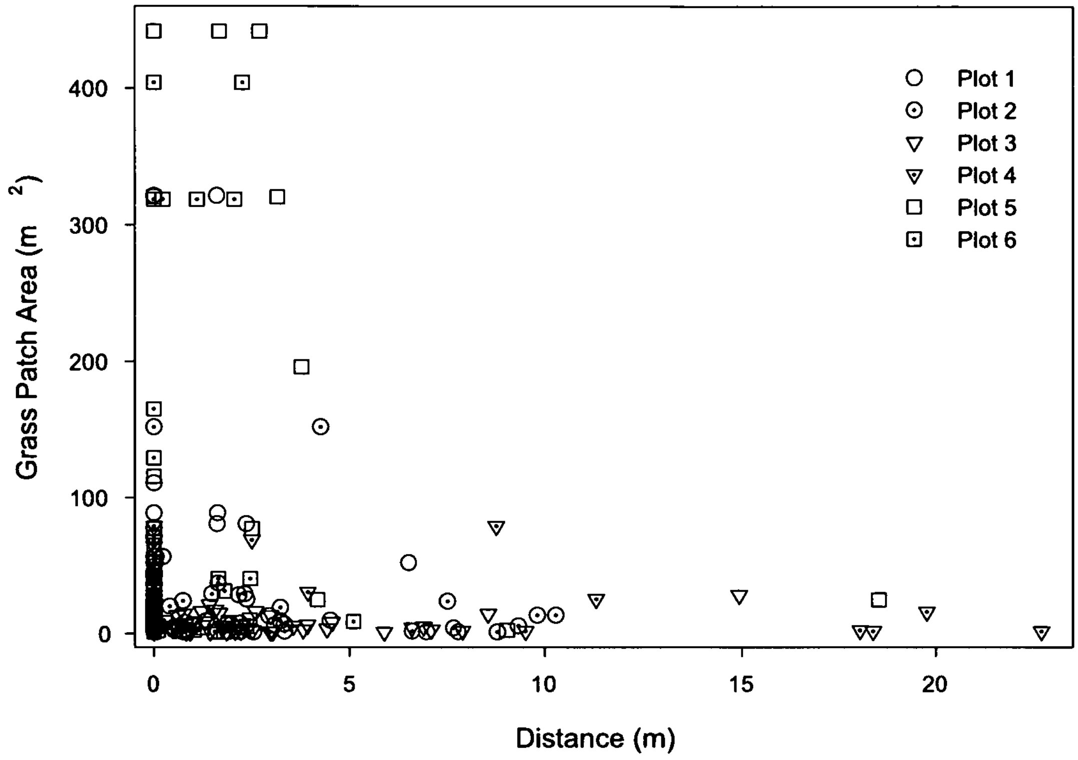

Figure 2.4. Scatter plot of grass patch area against distance (for the nearest grass patch) for each transect location (labelled by plot).

There were significant effects for season and the SIM (Table 2.1), but no significant interactions between fixed effects (not shown). As the season effect was well balanced, with all transects having all seasons, the Wald statistic came out very high. On the other hand the treatment effect (sheep per plot) was not well balanced, with only a third of the transects having any one treatment, leading to a non-significant Wald statistic.

Table 2.1. Significance of fixed effects of the REML model based on the Wald statistic as calculated by REML. P values have been calculated using the F-value, based on the Wald statistic divided by numerator degrees of freedom.

Fixed effect	Wald statistic	Numerator df	Denomerator df	P
SIM	28.1	1	1571	< 0.001
Treatment	4.6	2	3	NS
Season	296.8	1	1571	< 0.001

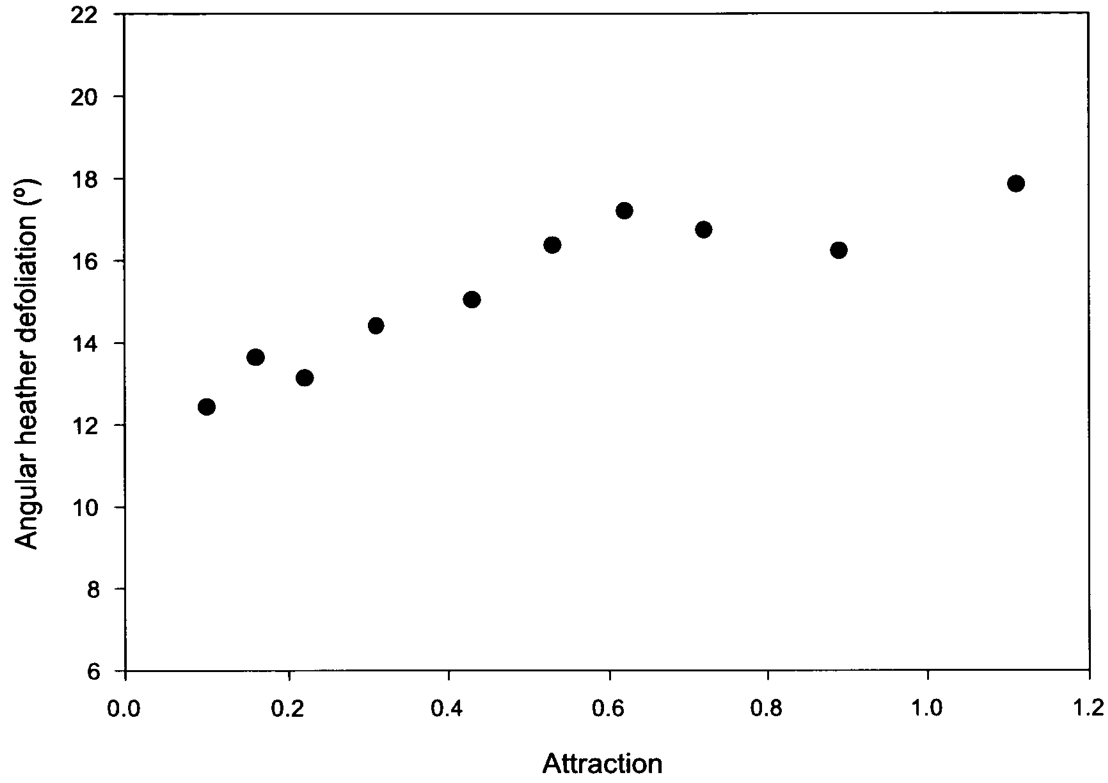

Figure 2.5. Scatter plot of mean angular heather defoliation against attraction (as predicted by the SIM). Values are average mean angular heather defoliation for ten classes calculated using REML.

The character of the significant effect of the SIM is revealed by Figure 2.5. As expected, the relationship between heather defoliation and the attraction predicted by the SIM showed a positive correlation. When the data were analyzed according to season, the same relationship is found for both summer and winter (Figure 2.6). The intercept for winter was significantly higher than that for summer, but the slopes were not significantly different (Table 2.2). The results for treatment and season × treatment interactions, although not significant, have been included for completeness (Table 2.2).

Much of the variance explained by the fixed model was explained in the plot stratum (42%), with less variance explained in the plot.line (12%) and plot.line.transect (7%) strata (Table 2.3). The low Adjusted R^2 for SIM, despite the high significance of the regression, was a result of the high variability of the heather defoliation about the regression line (see example Figure 2.7). This small-scale heterogeneity in foraging intensity could be caused by a high variability in the defoliation of individual plants. Hartley et al. (1995) showed that herbivores can use chemical cues to differentiate the quality of individual plants within a species. This was confirmed by visual observation on the experimental plots, which showed that individual heather plants may be heavily grazed whilst neighbouring plants are untouched.

Table 2-2. Slopes and intercepts for SIM and the interactions between SIM and treatment, and season, including mean standard error of differences (SED). All fixed effects contain the interactions between treatment and season; these have been averaged in the table to match the level at which the regression on SIM has been estimated.

Fixed effects		Slope		SED	Intercept		SED
SIM		5.0			12.8		
SIM.Treatment	*Low*	4.6		2.4	10.8		2.5
	Medium	3.8			13.3		
	High	6.9			14.0		
SIM.Season	*Winter*	4.6		1.1	16.0		0.7
	Summer	5.3			9.6		
		Winter	*Summer*		*Winter*	*Summer*	
SIM.Treatment. Season	*Low*	4.8	4.5	2.0^a 2.8^b	14.2	7.4	1.2^a 2.6^b
	Medium	2.6	4.6		16.7	10.0	
	High	6.7	7.0		17.0	11.0	

[a] SED within plot (i.e. Season within Treatment); [b] SED between plots (i.e. all other comparisons); Degrees of freedom for SIM and Season ≈ ∞ ; Degrees of freedom for Treatment = 3.

Table 2-3. Stratum variances and Adjusted R^2 for fixed effects based on the approximate stratum variances as calculated using REML. Adjusted R^2 are calculated for each model compared with the null model (without fixed effects) for each random stratum (plot, plot.line and plot.line.transect).

Stratum	Adj. R2 (relative to null model) %			
	Treatment	*Season*	*SIM*	*SIM*Treatment*Season*
Plot	44	1	7	42
Plot.Line	0	0	12	12
Plot.Line.Transect	0	0	7	7
Units	0	18	0	18

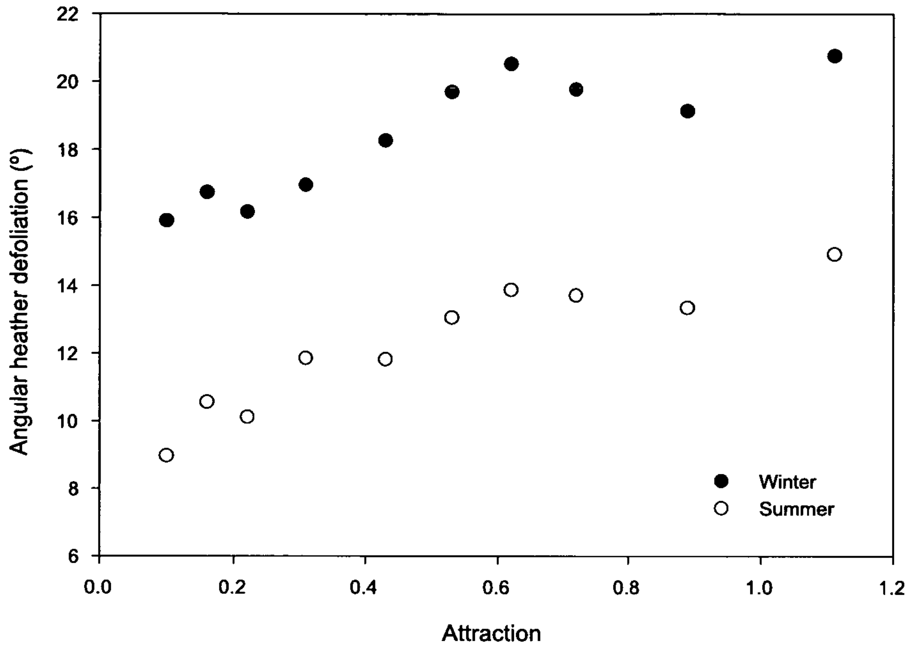

Figure 2.6. Scatter plot of mean angular heather defoliation for season against the attraction (as predicted by the SIM). Values are average mean angular heather defoliation for ten classes calculated using REML.

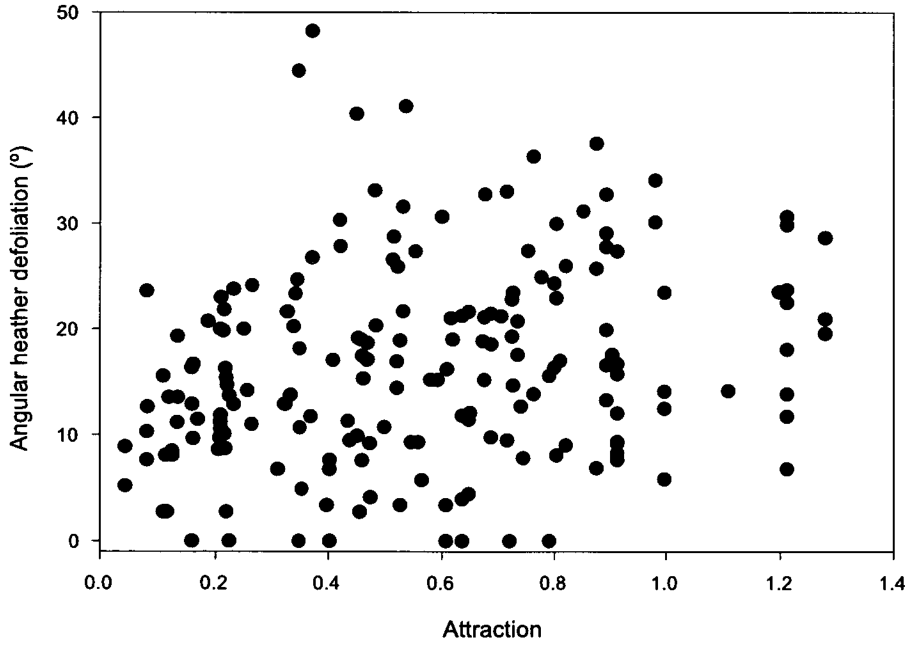

Figure 2.7. Scatter plot of angular heather defoliation against attraction (as predicted by the SIM) for a subset of observations, to illustrate variation between transects. The scatter plot is based on mean angular heather defoliation per transect (up- and downhill), averaged across three years. Observations included are for winter defoliation in plots with the high grazing intensity treatment (i.e. one value for each transect in plots 1 and 5; n=189).

2.5 Discussion

In this chapter we have shown that a simple SIM based on distance from a grass patch and grass patch area could successfully predict heather defoliation in natural heather-grass mosaics. As foreseen by theory and observations, heather defoliation and the attraction predicted by the SIM were strongly positively correlated. This implies that the heather defoliation was not spread homogeneously across the heather-grass mosaic, but that high heather defoliation locally coincided with low defoliation elsewhere. Furthermore, the positive slope of the regression showed that heather defoliation was positively associated with grass patch area, i.e. heather defoliation decreased with distance away from grass patches and increased with grass patch area.

The SIM approach worked well for sheep foraging in heather-grass mosaics, as their habitat use is strongly confined to the grass network (Hester et al., 1999). When extending the approach to other herbivores, differences in foraging characteristics, such as diet selection and body size (i.e. the ability to walk through high vegetation), might influence the correlation between the SIM and heather defoliation. For example, the correlation might be weaker for red deer, as their use of the heather-grass mosaics is less influenced by the grass network (Hester et al., 1999). On the other hand the strong decline of heather defoliation away from the grass-heather edge suggests that heather defoliation by deer is also strongly influenced by the pattern of grass (Clarke et al., 1995a; Hester et al., 1999).

When extending the approach to other grass-shrub mosaics, the correlation between shrub defoliation and attraction will depend on the contrast in preference between the preferred and less preferred plant community. A decrease in contrast is expected to lead to a decrease in the slope of the regression. The same effect would be expected when comparing two vegetation mosaics of different contrasts in preference. This effect was not shown in this study, despite the fact that the contrast between heather and grass communities decreases during the winter, with grass quality and quantity falling sharply and heather quantity and quality falling only slowly (Armstrong & Milne, 1995). We can only speculate that the grass availability was low throughout the year, or that patch geometry had an overruling influence on sheep foraging behaviour.

The SIM can be applied in three ways in addition to the application described above. Firstly the model could be used to derive a spatially explicit sampling scheme for a grazing impact study. The model from Equation 2.5 (i.e. without considering grazing intensity) could be used to calculated attraction values for a given vegetation map. Based on this map, a sampling scheme could be deployed to quantify the slope of the regression between heather defoliation and the attraction. The slope of the regression will differ with different plant communities, different herbivores and different grazing intensities. Secondly the SIM provides a tool to extrapolate heather defoliation measurements from part of a mosaic across the whole mosaic, using the regression between heather defoliation and the attraction. The result is an interpolation surface of predicted heather defoliation based on locations with known heather defoliation. Thirdly the predictions of the SIM can be used to test predictions of more mechanistic spatially explicit foraging models, such as SAVANNA (Coughenour, 1993), EASE (Moen et al., 1997) and the model developed by M.G. Turner, et al (1993). None of these models consider grass-heather mosaics, but do consider other grass/shrub combinations. The interpretation of these model outputs has focussed on the animal performance as a result of the interaction between foraging behaviour and the spatial pattern of the resources. However, these models do produce spatially explicit output which could be tested against the predictions of the SIM. Again, the strength of the SIM is in predicting the pattern of defoliation, such that the testing of model predictions should be through correlation.

The results of this study have two major implications for the management of grass-shrub mosaics. Firstly, the management of the balance between preferred (grass) and less preferred plant communities (shrub) strongly depends on the characteristics of the vegetation pattern. In highly fragmented mosaics, in which grass and shrub are intimately mixed, a large proportion of the less preferred community cover will be affected by herbivores, whilst in lightly fragmented mosaics large areas of the less preferred community will be little affected. This supports the more detailed discussions in Hester and Baillie (1998) and Clarke et al. (1995b). Secondly, as the spatial pattern of herbivore foraging is dictated by the spatial pattern of resources, it is expected that the spatial pattern of defoliation can be influenced by changing the spatial characteristics of the resources. For example, creating a grazing lawn dominated by a preferred species in one location, might relieve grazing intensity elsewhere in the mosaic, which in fact is what Clarke et al. (1995b) did in their experiment.

The results of the regression analysis show that the pattern of heather defoliation is affected by the pattern of grass in the heather-grass mosaic, such that heather around large grass patches is more likely to be grazed than heather around small grass patches. As the number of paths radiating from a patch increases with patch size (Hester & Baillie, 1998), it could be argued that the heather is more likely to be grazed because the patch is more connected, thus the observed correlation could be a causal effect of connectivity, not patch area. Thus patches are attractive because of their connectivity which leads to increased heather defoliation, subsequent heather fragmentation and thus increased patch size. However the initialisation of a network will be determined by the presence of large grass patches. For example on the scale of the Finella hill side, a network of paths was developed by sheep and cattle to connect two improved grass areas on either side of a deep gully. Patches along the new network then developed as a result of their position in the network. Results from previous experiments on Finella showed that after establishing the plot fences, sheep adapted the path network to restore cut off paths to attractive grass patches (Hester & Baillie, 1998).

In conclusion this study shows that a simple SIM can be used to describe the spatial pattern of heather defoliation in heather-grass mosaics. The method could be applied to other grass-shrub mosaics and to other habitat use indicators (e.g. dung distribution, trampling). The method could thus serve as a simple but powerful tool to describe the spatial patterns of habitat use. Insights generated by the description of spatial patterns should then be used to develop more mechanistic hypotheses, which can then be tested in experimental studies. Only with increased mechanistic understanding of spatial plant-herbivore interactions, could SIMs ultimately be dismissed as being too descriptive.

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Chapter 3

Defoliation across grass-heather boundaries: evidence for multiple stable states?

> The fundamental nature of the climax and its significance in the life-history of a vegetation are indicated by the fact that it is the mature or adult stage of the latter. As stated elsewhere, the climax formation is the fully developed community, of which all initial and medial communities are but stages of development. The general behavior of the formation as a complex organism resembles very closely that of the simple organism, the individual. The recognition of the latter is so natural and necessary a prelude to the study of its development and organization that it is taken for granted.
>
> F.E. Clements (1916)

3 Defoliation across grass-heather boundaries: evidence for multiple stable states?

3.1 Introduction

This chapter presents the results of a field experiment investigating the spatial pattern of herbivore impact on heather-grass mosaics. Herbivore impact on vegetation is an important process determining plant-herbivore interactions. Results are presented in the context of current understanding of plant-herbivore dynamics, in particular the concept of multiple stable states in grazed ecosystems.

Multiple stable states and carrying capacity

In the quest to understand plant-herbivore interactions scientists and managers alike have made use of succession and vegetation dynamics models. The traditional equilibrium-based successional model considered a linear succession with an ultimate climax state (Clements, 1916). A site would reach this climax through succession, and would return to this state after being deflected from it. The succession could be halted at any state by specific management, such as burning, mowing or grazing. The understanding of potential natural communities was based on this. Because this model poorly described observations of events in rangeland, particularly in semi-arid systems, people moved on to the model of multiple stable states or to the state-and-transition model (e.g. Holling, 1973; Westoby et al., 1989). It is argued that multiple stable states can exist as a result of positive feedbacks occurring when switching from one state to another, prohibiting or hampering the return to the original state (Holling, 1973). Stability of states is determined by their ability to return to their equilibrium state after a temporary disturbance (Holling, 1973). In contrast with such equilibrium systems, non-equilibrium systems are dominated by environmental stochasticity, such that the system is never in equilibrium (Tainton et al., 1996). It is argued that equilibrium range ecology theory is not applicable in these systems (Behnke & Scoones, 1993). The importance of herbivory might therefore be small relative to the role of rainfall in determining vegetation dynamics (Tainton et al., 1996). However in areas favourable for plant growth, herbivory is expected to be an important driver of vegetation dynamics (Tainton et al., 1996).

The role of spatial interactions in the existence of multiple stable states has received little attention, although it has been suggested that the spatial plant-herbivore interface can influence stability of ecosystems by creating a spatial refuge for part of the vegetation (McNaughton, 1984; Milne et al., 1992). Tainton et al. (1996) explores the spatial complexity of the plant-herbivore interface and the role of selective grazing, but fails to make a link with stability. Although, in general, a reduction in system heterogeneity is considered beneficial to facilitate management of the rangeland. In a review, Archer (1996) suggests that lack of spatially explicit information hampers our ability to monitor and manage grazed ecosystems appropriately.

The existence of multiple stable states has strong implications for rangeland management. The climax succession model assumes that the state of the ecosystem varies directionally with the impact of management and that the state can be changed with little effort. Thus, establishing the carrying capacity for the management of grazing systems (Roe, 1997), here considered as the maximum stocking rate which does not considerably affect the shrub cover in grass-shrub mosaics, could be a matter of trial and error. On the other hand, the multiple stable state model predicts that certain state transitions can only be made by powerful management efforts (Laycock, 1991). Thus, each alternate stable state can have its own carrying capacity. Overstocking at one stable state could lead to transition to another, possibly less preferred, stable state. Determining carrying capacity then strongly depends on the current state of the system. The understanding of multiple stable states is therefore important in relation to sustainable management of grazing systems.

Carrying capacity of heather-grass mosaics

The system under study is that of upland heather (*Calluna vulgaris* (L.) Hull) moorland in Scotland. The international importance of upland heather moorland has recently been reviewed by Thompson et al. (1995). Although overall loss of heather moorland can be ascribed to both grazing and establishment of coniferous plantations, grazing by sheep and red deer is singled out as the single factor causing shifts from heather moorland to unimproved grassland (Thompson et al., 1995). Several dramatic shifts from heather moorland to grassland, as a result of heavy grazing by sheep and cattle, were documented by Welch (1984).

Based on the observed changes resulting from grazing by herbivores at a range of different study sites, Welch (1984) provided threshold stocking rates for sheep and deer. An alternative rule of thumb often used is the '40% rule' (Grant et al., 1988). This suggested that no reduction in heather cover would occur when overall defoliation of heather did not exceed 40% of the current years growth. Thus, carrying capacity of heather moorland was expressed as a fixed stocking rate or a fixed level of herbivore impact and was based on the proportions of heather and grass in the mosaic (Armstrong et al., 1997), but assuming that herbivore impact was spread evenly across the vegetation mosaic. However, earlier research had already suggested that herbivore impact on vegetation is strongly influenced by spatial heterogeneity of the vegetation (Grant et al., 1978).

In order to improve the understanding of plant herbivore interactions and to improve the predictions of carrying capacity, a series of experiments in north-east Scotland was designed to investigate plant-herbivore interactions within heather-grass mosaics, and in particular the interaction between herbivores and the ecotone between grass and woody vegetation (heather). In order to show the contributions of the individual studies, results are reviewed chronologically. An overview of these experiments is presented in Table 3.1. All these experiments considered the impact of herbivores on heather and define heather defoliation as the proportion of current year's heather shoots grazed.

The Cairn Henney experiment studied defoliation impact on recently burned heather. Three grazing pressures (expressed as fixed levels of observed heather defoliation: 0%, 40% and 80%) were applied in two seasons (summer and autumn). At 40% overall defoliation, changes in heather cover were slight, while at 80% the reduction in cover was only significant in the case off autumn grazing. However, new shoot production in the following season was affected by the 80% defoliation treatment independent of the season. The authors concluded that young heather can withstand defoliation of at least 40% of current year's shoots (Grant et al., 1978). Despite careful formulation, the 40% figure presented was subsequently interpreted by some authors as a maximum threshold and became widely accepted as the recommended maximum grazing level for heather in general (e.g. Clarke et al., 1995a). Because it was appreciated that heather response to defoliation depends on the age of the heather stand, the levels were later adjusted to 10% and 5% for intermediate and old heather respectively (Sibbald et al., 1987). These adjusted figures were based on expert judgement for the purpose of predicting impact of grazing management strategies on heather moorland through modelling.

Table 3.1. Summary of controlled heather defoliation experiments in eastern Scotland. See text for review of experiments. Heather phases based on Watt (1947).

Location	Year	Treatment, periods and design	Heather-grass mosaic	References
Cairn Henney	1973-1977	sheep density adjusted to achieve 0, 40, 80% defoliation; summer and autumn; random 3 × 3, no replicates	natural heather-grass mosaic; pioneer heather (burned in 1971)	(Grant et al., 1978; Grant et al., 1982; Milne et al., 1979)
Birnie 1	1992	sheep, deer; 3 × 14 days: early summer; 2 replicates	artificial heather-grass mosaics; mature heather; grass patches sown in 1990	(Clarke et al., 1995a; 1995b)
Birnie 2	1992	2 sheep densities; 3 × 14 days: late summer; 2 replicates	artificial heather-grass mosaics; mature heather; grass patches sown in 1990	(Clarke et al., 1995a; 1995b)
Finella 1	1991-1995	sheep, deer, sheep + deer; 8 weeks: autumn (1991), summer (1992), split summer (1993-1995); 2 replicates	natural heather-grass mosaic; building or mature heather	(Cuartas et al., 2000; Hester et al., 1996; Hester & Baillie, 1998; Hester et al., 1999; Oom & Hester, 1999)
Finella 2	1998-2001	sheep density; year round; 2 replicates	natural heather-grass mosaic; building or mature heather	this thesis; (Oom et al., 2002)

Grant et al. (1978) noted that the distribution of grazing was not homogeneous across the experimental plots, but that heather defoliation was negatively correlated with heather cover. In two subsequent experiments (Birnie 1 and 2) the pattern of defoliation and the pattern of vegetation were more closely observed. The Birnie experiments showed that heather defoliation was strongly correlated with distance from the grass-heather boundary, with defoliation higher near grass patches than further away over a 5 m zone (Clarke et al., 1995a). In addition, the distribution of heather, either in one large patch, four medium patches or twelve small patches strongly affected the temporal use of the mosaic by sheep and to a lesser extent for red deer (Clarke et al., 1995b). The time sheep spent grazing heather increased strongly with decreasing patch size. This shows that for an area with a given heather-grass ratio, the impact of the sheep strongly depends on the distribution of patches of grass within the heather matrix. An experiment comparing stocking rates showed no difference in heather defoliation between treatments (Clarke et al., 1995a), however defoliation was low at only 3% per period. The implication of these results is that for complex heather-grass mosaics the ratio of grass to heather is a poor predictor of heather defoliation (Clarke et al., 1995b). The Birnie experiments considered three sizes of artificial grass patches in a regular pattern within a heather matrix. However, patch size and pattern of patches in natural heather-grass mosaics vary strongly. Thus, the Finella experiments were established to expand the experimental approach into natural heather-grass mosaics.

Declining heather defoliation with increasing distance from grass at Finella confirmed results from the Birnie experiments (Hester & Baillie, 1998). Although treatments considered herbivore species (either sheep, deer, or sheep and deer mixed), results across years showed strong variation in grazing intensity. Analysis showed that grazing intensities affected the width of the impact zone from 1 m at low overall intensity to 3 m at high overall intensity (Hester & Baillie, 1998). However, the background defoliation, at maximum distance from grass patches or paths, was not significantly different between years (Hester & Baillie, 1998), indicating that an increase in overall grazing intensity led to a disproportionate increase in defoliation in areas already affected by grazing. While the Birnie experiments considered different sized grass patches between treatments, the natural heather-grass mosaics of the Finella experiments provided varying grass patch size within treatments. Thus, within the herbivore species treatments, heather defoliation was observed around three classes of grass patch size. Although across treatments overall heather defoliation was higher around large and medium grass patches compared to small patches, the results varied between treatments (Hester & Baillie, 1998). Heather defoliation was highest around small patches for the sheep treatment and highest around medium patches for the sheep and red deer treatment (Hester & Baillie, 1998). The current study was initiated in order to investigate the relationship between pattern of vegetation and pattern of defoliation further.

Herbivore impact on vegetation

Grazing is generally considered synonymous with defoliation despite the fact that herbivore impact on vegetation can occur through several processes, i.e. the collateral damage associated with defoliation. In order to avoid confusion, a distinction is made here between the following types of impact of herbivores on vegetation: defoliation, trampling, uprooting and foraging. Foraging impact is defined here as the combined effects of defoliation and that part of trampling and uprooting that is directly associated with defoliation. The term grazing impact has often implicitly included both defoliation and trampling impact.

Although the experiments reviewed here focus on the defoliation impact of herbivores, all suggest that other forms of impact can be important. Uprooting was mentioned by Gimingham (1972). Later Grant et al. (1978) provided strong evidence of the increase of collateral damage caused by sheep density. In their experiment the number of uprooted or broken shoots was almost five times higher for a high sheep density treatment than for a low density treatments, with the effect most profound during autumn. The effect of trampling has more often been mentioned in the context of impact of human activity (Bayfield, 1979; Harrison, 1981). Bayfield (1979) suggested that, due to water stress on heather shoots, even partially damaged shoots can die of frost during winters following the initial impact. Clarke et al. (1995a) reported that, even at low rates of defoliation, numbers of both dead heather shoots and gaps in the heather were higher in a 5 m zone around grass patches than further away. Hester and Baillie (1998) found differing effects of trampling and defoliation as a result of prevailing slope. While heather defoliation is mainly uphill and across the hill from grass patches, trampling damage was primarily downhill from grass patches. It was also suggested that, on sloping grounds, trampling is more important than defoliation but with the relative importance of defoliation increasing with increased herbivore densities (Hester & Baillie, 1998).

3.2 Methods

Site description

The experimental site was established for a previous experiment (Hester & Baillie, 1998) on Strathfinella Hill (National Grid reference NO677782) at the Macaulay Institute's Glensaugh Research Station, Aberdeenshire, Scotland (Figure 3.1). The experimental site was located at an altitude of 200-250 m, on a north-west facing slope with a slope angle of about 17°. The soils are humus-iron podsols (Strathfinella Series) derived from Old Red Sandstone on the slopes and acid igneous rocks near the top. Bulked soil sample analysis resulted in the following measures: pH = 4.9, organic matter = 11%, lime content 2.8 mg MgO per 100 g (Gimingham, 1949).

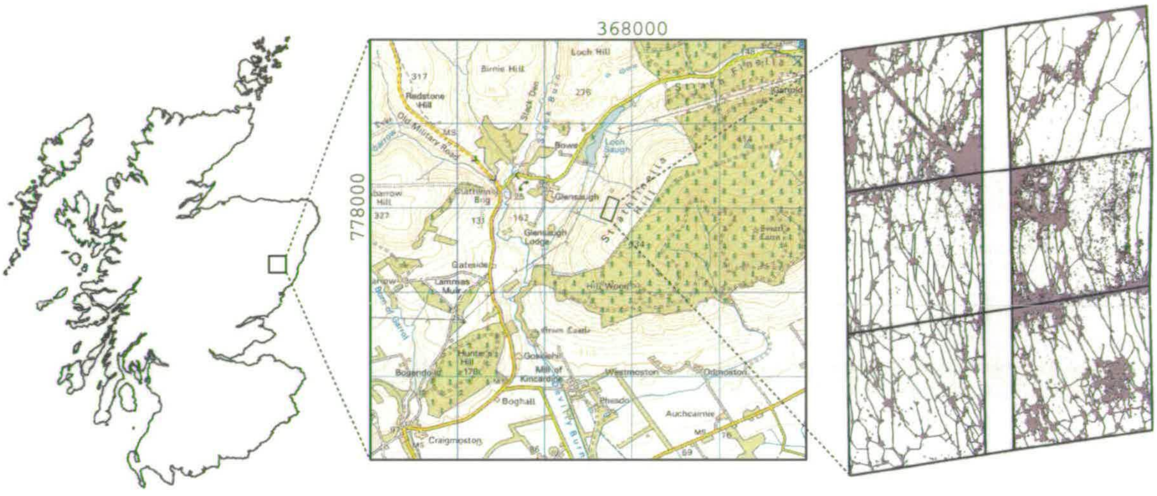

Figure 3.1. Map of the location of the experimental site in Aberdeenshire, Scotland. OS data © Crown copyright 2002. All rights reserved Macaulay Institute GD27237X 2002.

Gimingham (1949) reported that the whole hillside was burned twice in spring 1944. More localised burning occurred between 1957 and 1963 (Grant & Hunter, 1968). There is no documentation about later burning, although it is likely that the hill side was burned after the 1940s. Many years of grazing by cattle and sheep created a highly fragmented vegetation mosaic (Hester & Baillie, 1998; Nicholson & Robertson, 1958). Part of the bottom of the hillside consists of improved grassland. The experimental site consisted of six one-hectare plots (Figure 3.2). The vegetation mosaics within the experimental site was dominated by two plant communities (following Rodwell, 1991;

1992): *Calluna vulgaris - Vaccinium myrtillus* heath (H12) and *Festuca ovina - Agrostis capillaris - Galium saxatile* grassland (U4), with some patches of *Nardus stricta - Galium saxatile* (U5) and *Juncus squarrosus - Festuca ovina* grassland (U6). Plots were originally fenced with rabbit proof netting and rabbits were controlled during the first year of this experiment, leading to no further sightings of rabbit in the second and third year.

Experimental design

Replicated in two blocks (bottom and top), three stocking rate treatments (2, 3 and 4 sheep ha^{-1}), were applied year round on plots B2 and T2, B3 and T3, and B4 and T4 respectively (Figure 3.2). Sheep were removed from plots between December and February, the period with lowest temperatures and highest probability of snow cover, following common agricultural practice. Thus, true stocking rates, based on actual grazing days, were considerably lower. Because of the importance of group size in foraging behaviour (Penning et al., 1993), all treatments were applied using groups of six sheep. Therefore, in order to achieve different grazing treatments, the groups of six sheep were removed from plots at regular intervals, depending on the grazing intensity treatment required. Consequently, under high sheep density, plots were grazed for two weeks and then rested for one week, resulting in the total number of days during the summer (May-September) and the winter (October-April) presented in Table 3.2.

Table 3.2. Number of days of sheep present (in groups of six) on plots for each treatment per year, total number of days per treatment and subsequent stocking rates based on actual days. Summer and winter cover the periods May-September and October-April respectively. Stocking rate is the calculated as the number of sheep grazing days per year.

Year	**Season**	**Treatment (sheep ha^{-1})**		
		4	**3**	**2**
1998	Summer	60	50	30
	Winter	40	20	25
1999	Summer	80	60	40
	Winter	40	30	20
2000	Summer	112	60	40
	Winter	56	30	20
Average (days)		129.3	83.3	58.3
Stocking rate (days $year^{-1}$)		2.13	1.37	0.96

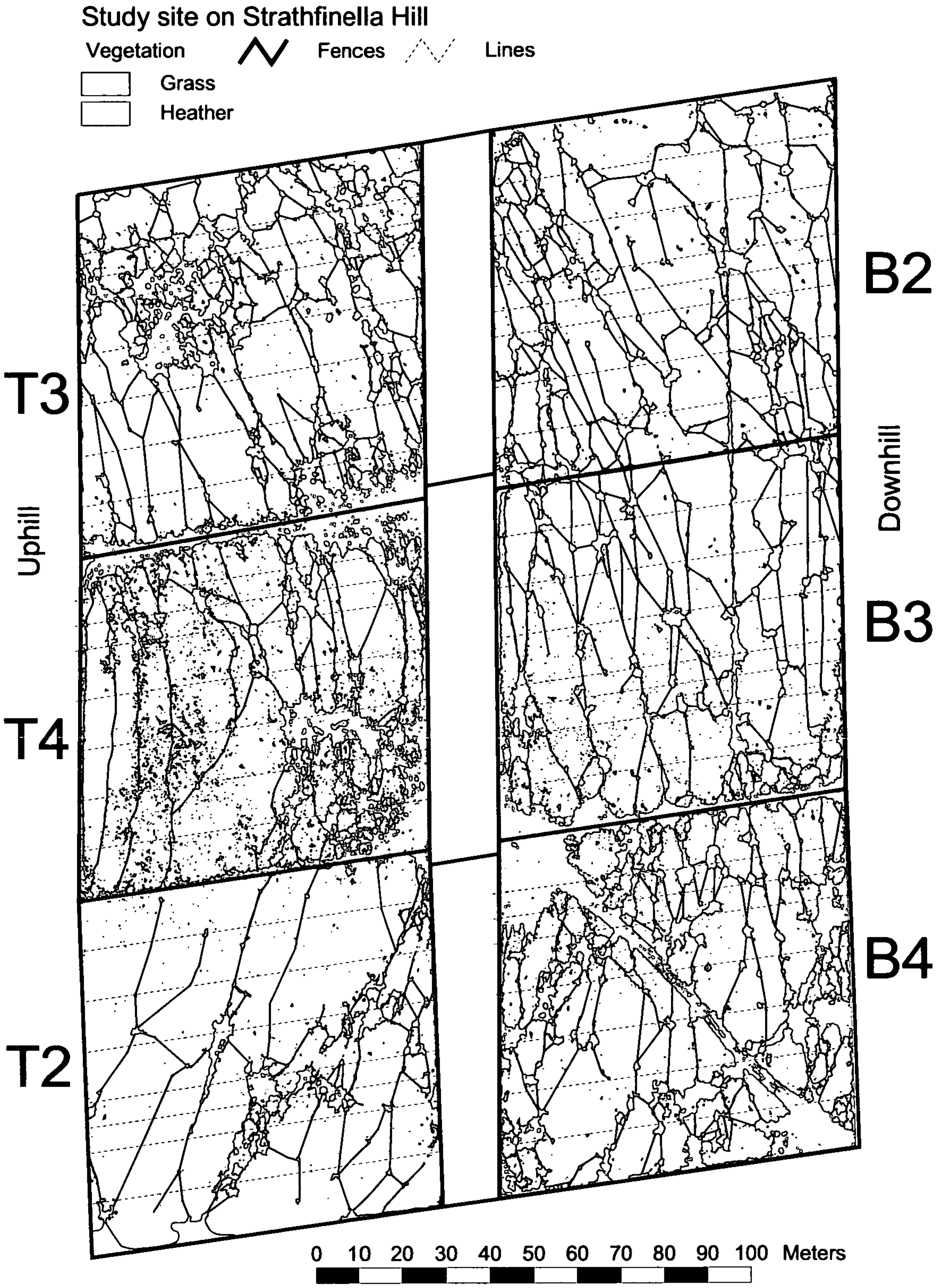

Figure 3.2. Map of Finella experimental site. Plot codes indicate block (B = bottom and T = top) and treatment (2, 3 and 4 sheep ha^{-1}).

Heather defoliation during the summer and during the whole year was measured for three subsequent years in October and May respectively, starting October 1998 and finishing May 2001. Heather defoliation was measured at fixed locations along transects away from grass-heather boundaries. To determine transect locations, seven 100 m sampling lines were laid out across each plot along the slope (Figure 3.2) at regular distances. A transect was then allocated to each grass-heather boundary, either at a path or a grass patch, crossed by one of the sampling lines. Some paths were bare, leading to a bare-heather boundary, however for clarity the term grass-heather boundary is used for all observed boundaries. Transects were laid out from the edge of the grass out into the heather perpendicular to the grass-heather boundary. The transect was ended when the next distance along the transect exceeded the distance from that point to a neighbouring grass-heather boundary or at 5 m. As the geometry of the paths and patches generally followed the contours, the majority of transects were up- and downhill. On any one sampling line, any two transects going off the same path or grass patch were grouped together into a 'transect location'.

Heather defoliation was measured at fixed distances (0, 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, 2.00, 3.00, 4.00, 5.00 m) along each transect according to the method described by Hester & Baillie (1998), providing an estimate of the percentage of current year's growth removed (i.e. percentage defoliation) at each distance. While dead shoots had previously been recorded (Hester & Baillie, 1998), here only live shoots were considered, thus the number of shoots considered in estimating the percentage defoliation was always equal to ten. Transect locations were classified in the field either as grass patches (n=698) defined as areas dominated by grasses, or paths (n=652) connecting these grass patches. Potential misclassification could have occurred where grass patches expanded in the direction of paths, or where part of an expanded path was partly covered by grasses. In these ambiguous situations a value judgement was made in the field on how to classify that transect location. Incidence of ambiguous locations was rare at approximately 5% of all 360 transect locations, therefore possible misclassification of a small number of transect locations was assumed not to affect the results.

A total of 19,046 heather defoliation observations were made on 675 transects over the course of the experiment. Based on previous experiments, it was assumed that the distinct pattern of growth of heather (Figure 3.3 and Mohamed & Gimingham, 1970) facilitates the assessment of defoliation. While this was true for autumn observations, when ungrazed current year's growth shoots provide good reference, spring observations (i.e. considering whole year defoliation) were hampered by shoot browning (Watson et al., 1966) during the winter months.

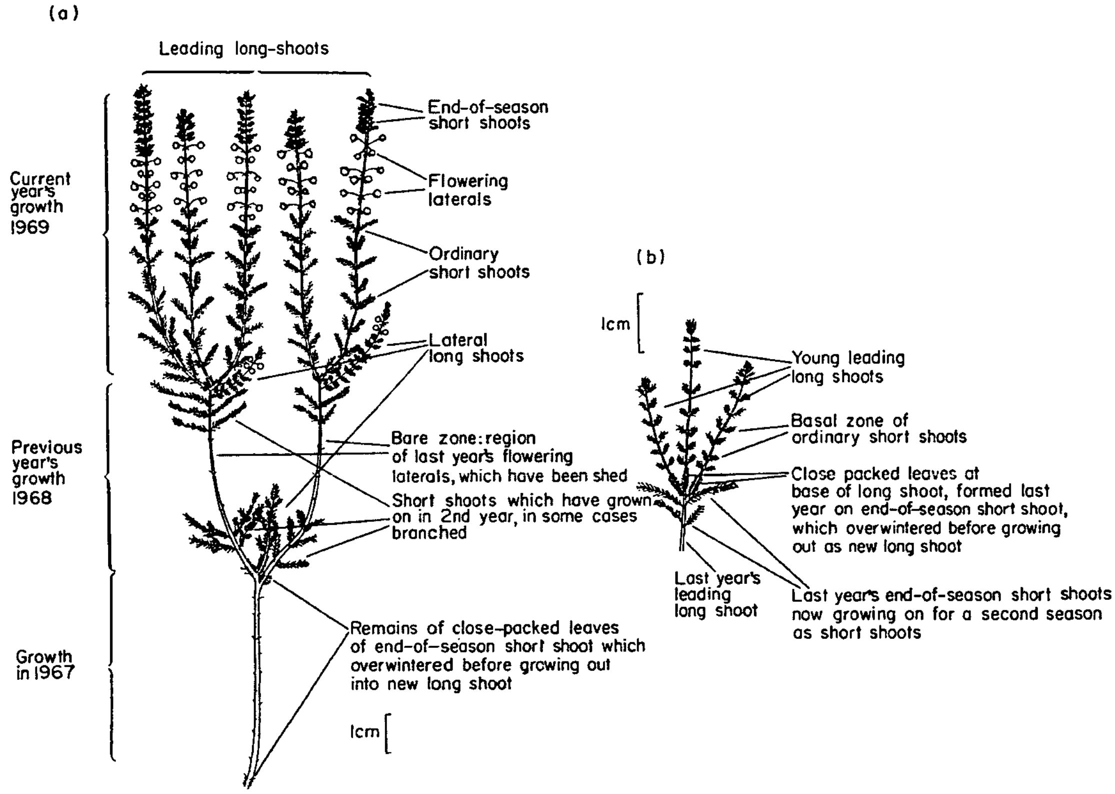

Figure 3.3. Annual growth and branching in *Calluna vulgaris*: a) condition at the end of the growing season (early October); b) shoot tip early in the growing season (June) to show new long-shoots developing from overwintered end-of-season short-shoots. From Mohamed & Gimingham, 1970. (Reproduced with permission from New Phytologist)

The spring defoliation was considered to represent the whole year grazing. However, in case of shoots grazed and subsequently browned, it was difficult to assess whether the shoots had been dead all year or died after initial grazing. This possibly led to an underestimation of the whole year defoliation, making it impossible to distinguish winter defoliation as the difference between autumn and spring measurements. Due to the number of observations it was not feasible to label shoots for controlled measurements. Throughout this thesis autumn and spring measurements are therefore used separately as summer and whole year heather defoliation respectively. Note that in Chapter 2, summer and whole year heather defoliation are referred to as summer and winter, respectively.

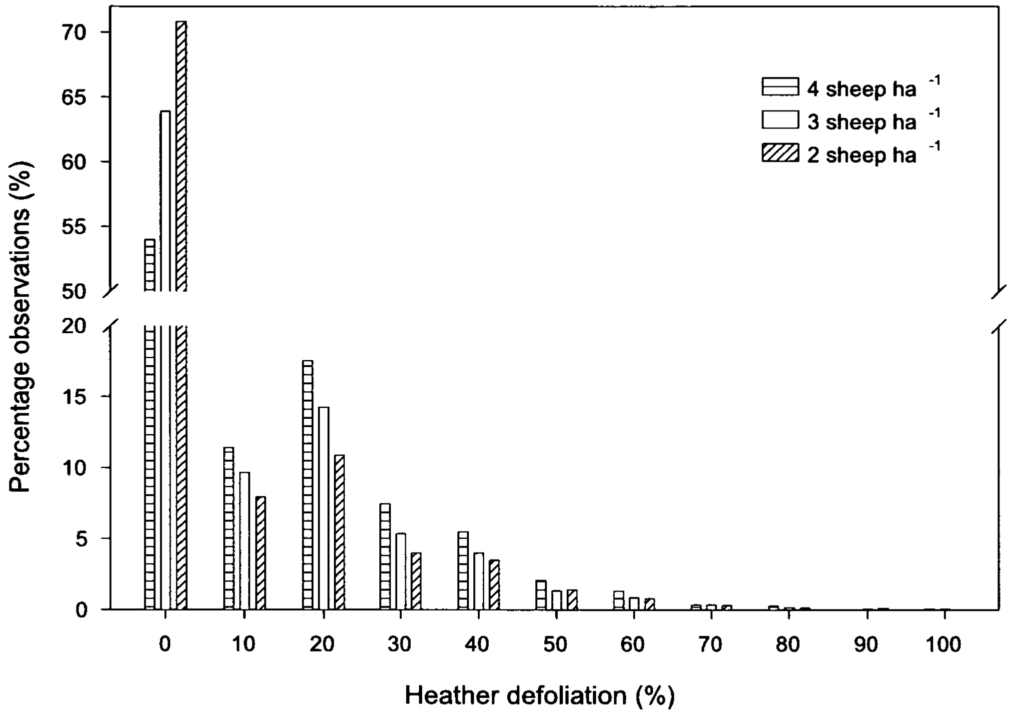

Figure 3.4. Histogram of percentage defoliation for each sheep density treatment.

Statistical analysis

Due to the design of the experiment and the characteristics of the natural mosaics under study, the data were unbalanced both in the number of transects per stocking rate treatment and the number of observations within each transect. The total number of transect locations (combination of uphill and downhill transect) per plot varied between 36 and 78. Due to the characteristics of the heather-grass mosaics, i.e. the proximity to other paths or patches, the majority of the transects were one metre or less in length with only a few transects exceeding two metres (Table 3.3). This distribution was consistent across the stocking rate treatments. For part of the analysis, individual observations of heather defoliation were averaged within distance zones (Table 3.3): edge (0.00, 0.25, 0.50 m), centre (0.75, 1.00, 1.50 m), distant (2.00, 3.00, 4.00, 5.00 m).

Table 3.3. Number of sample points per distance along the transects per plot. Plot codes indicate block (B = bottom and T = top) and treatment (2, 3 and 4 sheep ha^{-1}).

Distance	B4	T4	B3	T3	B2	T2	Overall	Distance zone	Overall
0	93	104	132	123	153	70	675	Edge	1985
25	93	104	132	123	153	70	675		
50	93	98	127	106	143	68	635		
75	85	84	113	64	124	49	519	Centre	1196
100	65	62	95	41	102	37	402		
150	45	41	69	27	65	28	275		
200	35	31	48	23	47	17	201	Distant	323
300	14	14	22	8	19	6	83		
400	2	5	9	3	4	2	25		
500	1	3	4	2	3	1	14		

Because of the unbalanced design, statistical analysis was carried out using the Residual Maximum Likelihood (REML) method in GenStat (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13). Means presented in tables and figures are means as estimated by REML, considering plot and transects within lines (Plot + Line / Transect) as the random model. All heather defoliation results presented are angular transformed (degrees) unless stated otherwise.

In order to illustrate the effect of grazing intensity on the decline of heather defoliation away from the grass-heather boundary, linear regressions were fitted. The percentage heather defoliation data was negatively skewed (Figure 3.5). Therefore percentage heather defoliation was angular transformed for analysis. The correlation between heather defoliation and distance from the edge was assumed to be negatively logarithmic (Clarke et al., 1995a) thus the regression was estimated against log-transformed distance (cm). A constant of 1 cm was added to cope with zero distances and because 1 cm represents the level of precision used in placing the quadrats, leading to: LogDistance = Log_{10}(Distance+1). Regressions were fitted using REML with the following fixed models:

- Transect defoliation + Transect defoliation × LogDistance
- Transect defoliation × Direction + Transect defoliation × Direction × LogDistance
- Transect defoliation × Season + Transect defoliation × Season × LogDistance

This analysis was at the level of transects, so no random model was specified.

Due to the design of the experiment and the characteristics of the vegetation mosaics, transect length could not be controlled for. Because areas of high herbivore impact are generally characterised by clusters of grass patches, average transect length was expected to be lower in these areas. However regressions of transect length on mean transect defoliation were only significant for minimum transect length of 0 m and 0.75 m for patches and paths respectively (Table 3.4). Due to the low coefficients and small Adjusted R^2, transect length was assumed not to affect the results presented here.

Table 3.4. Regression results for transect length (m) versus mean transect defoliation (°). Average transect length for patches and paths was 1.29 m and 1.43 m respectively.

Type	Minimum transect length	Coefficient (m/°)	Adjusted R^2 (%)	P value
Patch	all	-0.007	0.3	< 0.001
	≥ 0.50	-0.002	0.0	0.155
Path	all	-0.004	0.1	0.001
	≥ 0.50	-0.004	0.1	0.003
	≥ 0.75	-0.003	0.0	0.048

3.3 *Results and discussion*

Summary statistics showed that, even at the highest stocking rates, the percentage of shoots suffering 40% or more defoliation did not exceed 10% (Table 3.5). It should be noted that, due to the sampling design, the observations in this experiment were concentrated in the area where defoliation was expected to be most severe, such that the percentage of observations above the 40% threshold would be considerably less when averaged across the total heather area.

Table 3.5. Percentage of observations for which the percentage heather defoliation is equal to or exceeds 40%.

Defoliation (%)	Sheep density (sheep ha^{-1})		
	2	3	4
< 40%	2.8	2.8	4.1
≥ 40%	6.3	6.8	9.6

Figure 3.5 shows that both the number of shoots grazed and the severity of defoliation was highest for whole year defoliation. Due to the method of measuring cumulative defoliation over extended periods, it was not possible to know whether the defoliation

was a result of one single bite or repeated bites. Thus, it was not possible to distinguish increased bite depth from repeated defoliation or the spread of defoliation of one shoot over time. Two diagrams show the distribution of observations separated in grazed (defoliation > 0) or ungrazed (defoliation = 0) for grass patches (Figure 3.6a) and paths (Figure 3.6b) in uphill and downhill directions. Ungrazed observations were more frequent for paths and more frequent for downhill than for uphill.

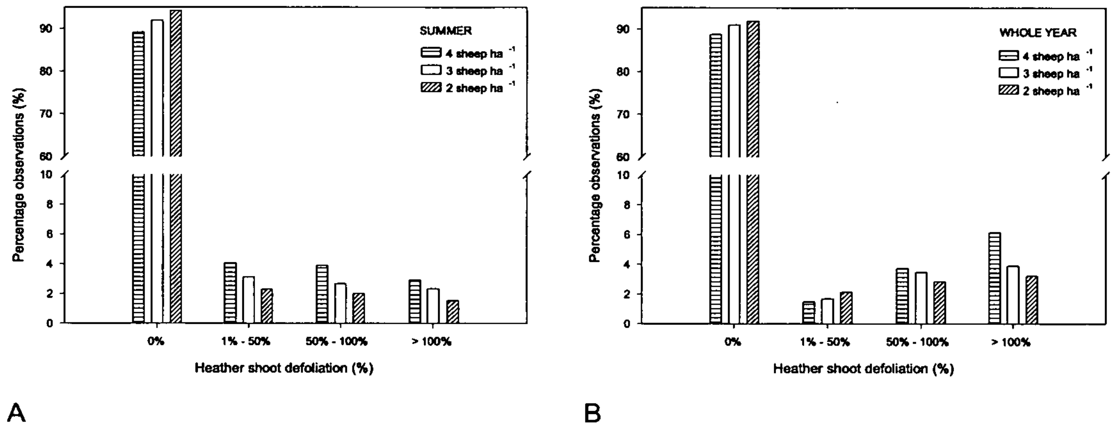

Figure 3.5. Number of observations in defoliation classes per sheep density treatment and season: A) summer, B) whole year.

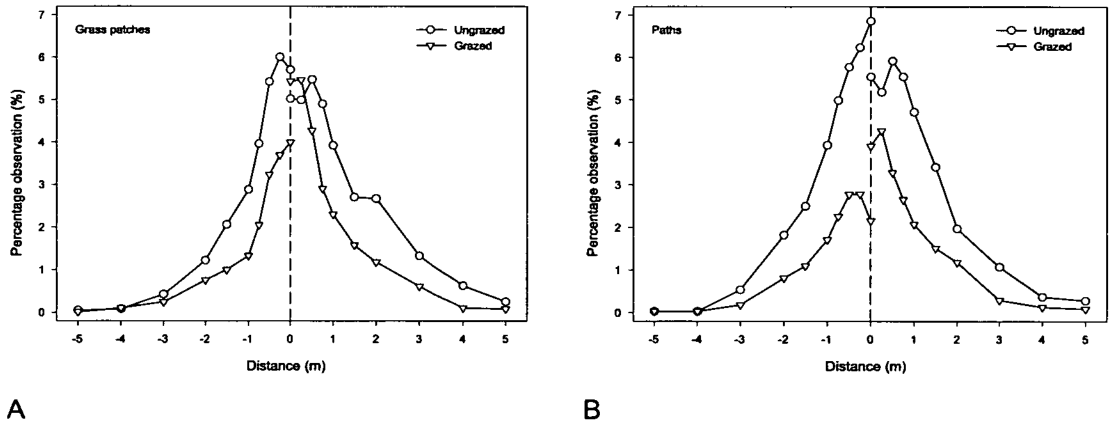

Figure 3.6. Histograms of heather defoliation (%) showing the distribution of observations divided into grazed (defoliation > 0) and ungrazed (defoliation = 0) for grass patches (n = 9922) (A) and paths (n = 9124) (B) and direction of slope either uphill (Distance > 0) or downhill (Distance < 0).

The Wald statistics of the REML analysis showed significant effects on angular heather defoliation for *sheep density* (2, 3, 4 sheep ha^{-1}), *season* (whole year or summer), *type* of transect location (grass patch or path), *direction* (up- or downhill), *distance zone* (edge, centre or distant) and the interactions (Table 3.6). Defoliation was higher around grass patches as compared to paths ($p < 0.001$). Defoliation was higher uphill of the grass patches than downhill ($p < 0.001$) and higher closer to the edge of grass patches or paths than further away ($p < 0.001$). These results confirm results from Hester & Baillie (1998) and Oom & Hester (1999) on the same site. In addition, the results show that increasing sheep density increases heather defoliation ($p = 0.003$) and that heather defoliation was higher for the whole year than in summer ($p < 0.001$).

Table 3.6. Effects of fixed terms on angular heather defoliation. Wald statistics, degrees of freedom (DF) and P values from the REML analysis when sequentially adding fixed terms and interactions. P values are Chi-squared probabilities as calculated by REML. Only significant interactions (P < 0.05) are shown.

Fixed term and interactions	Wald	DF	P values
Distance zone	65.47	2	< 0.001
Direction	77.97	1	< 0.001
Type	11.50	1	< 0.001
Sheep density	11.97	2	0.003
Season	157.74	1	< 0.001
Distance zone × Direction	36.29	2	< 0.001
Distance zone × Type	19.70	2	< 0.001
Distance zone × Sheep density	17.25	4	0.002
Distance zone × Season	6.23	2	0.044
Direction × Season	38.88	1	< 0.001
Distance zone × Direction × Season	10.11	2	0.006
Distance zone × Direction × Type × Sheep density	10.54	4	0.032

The interaction between *distance zone* and *type* ($P < 0.001$) was caused by a high defoliation at the edge zone of grass patches compared to path edges (Table 3.7), which confirmed the difference previously found between grass patches (Hester & Baillie, 1998) and paths (Oom & Hester, 1999).

Table 3.7. Mean angular defoliation for Direction and Type versus Distance zone. Means were calculated using REML. Numbers within the same Type with same superscript are not significantly different ($p < 0.05$ and average SED = 0.70).

Distance Zone	Patch		Path	
	Up	*Down*	*Up*	*Down*
Edge	12.3^{a}	9.7^{b}	10.0^{b}	7.5^{c}
Centre	9.3^{bc}	8.0^{c}	8.2^{c}	8.0^{c}
Distant	7.4^{c}	8.9^{bc}	7.9^{c}	8.0^{c}

Because previous experiments had not compared seasons, the interaction between *season* and *direction* was also a new finding. Although defoliation was higher uphill than downhill in summer, as found by Hester et al. (1998), there was no significant difference during the whole year. The interaction between *season*, *direction* and *distance zone* showed that the effect in summer was caused by a low defoliation at the edge zone in the downhill direction (Table 3.7). Contrary to other combinations, the defoliation downhill in summer was not significantly higher for the edge zone than for the middle or centre zones. The interaction between *treatment*, *type*, *direction* and *distance zone* showed another new finding. Previous experiments showed that heather defoliation declined rapidly with distance from the grass-heather boundary (Clarke et al., 1995a; Hester & Baillie, 1998; Oom & Hester, 1999). Clarke et al. (1995a) suggested that the relationship was negatively logarithmic, i.e. showing an exponential decline ($R^2 = 81.9$; $P < 0.0001$). However, the interaction between *treatment*, *type*, *direction* and *distance zone* suggests that defoliation is not always negatively correlated with distance. Figure 3.7b shows that heather defoliation even increased with increased distance downhill from the grass-heather boundary of paths at 3 and 4 sheep ha^{-1}. It should be noted that results presented here are angular transformed data and distances have been amalgamated for ease of interpretation.

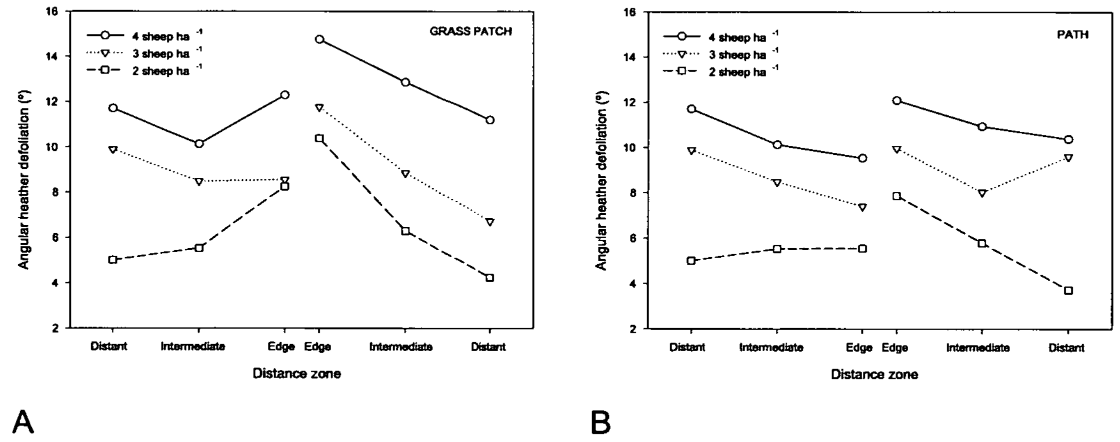

Figure 3.7. Angular heather defoliation for sheep density, type of boundary (patch (A) or path (B)), and direction of slope (left side of graph is downhill, right side is uphill) versus distance zone (edge, intermediate, distant).

So far the analysis did not reveal how and why the decline of heather defoliation with distance varies. Thus, further investigation was required. An analysis using a spatial interaction model (Chapter 2), showed that heather defoliation at the grass-heather boundary at a given location is dependent on the index of attraction, based on the size and proximity of grass patches, of that location. This demonstrates that local grazing pressure is not only determined by global grazing pressure (in this case sheep density treatments), but that it also depends on the local availability of grass, i.e. proximity and size of grass patches.

In order to investigate the decline of heather defoliation away from the grass-heather boundary as a function of actual grazing pressure at the grass-heather boundary, the sheep density per treatment (global grazing intensity) in the data set was replaced by the estimated mean grazing pressure on each individual transect (local grazing intensity). The grazing pressure at each transect was defined as the average angular heather defoliation of the whole transect (here after called *transect defoliation*). In other words a heavily grazed transect in a plot with a sheep density of 4 sheep ha^{-1} was now grouped together with a similarly grazed transect from a plot with 2 sheep ha^{-1}.

Table 3.8. Percentage of observations per bin. The total number of observations for patches and paths were 9922 and 9124 respectively.

Bin	Transect defoliation (°)		Observations (%)	
	Patch	Path	Patch	Path
0-1	0.0	0.0	20.2	26.0
1-2	1.6	1.6	1.1	3.3
2-4	2.9	3.0	8.0	9.3
4-6	5.0	4.9	8.3	10.3
6-8	6.9	7.0	10.2	8.0
8-10	9.1	9.0	8.3	9.4
10-12	11.1	10.9	8.1	5.6
12-15	13.4	13.5	10.6	7.2
15-18	16.5	16.5	7.7	6.8
18-21	19.4	19.5	5.0	4.9
21-24	22.4	22.4	4.5	3.2
24-27	25.4	25.4	3.3	2.6
27-max	32.0	30.9	4.7	3.6

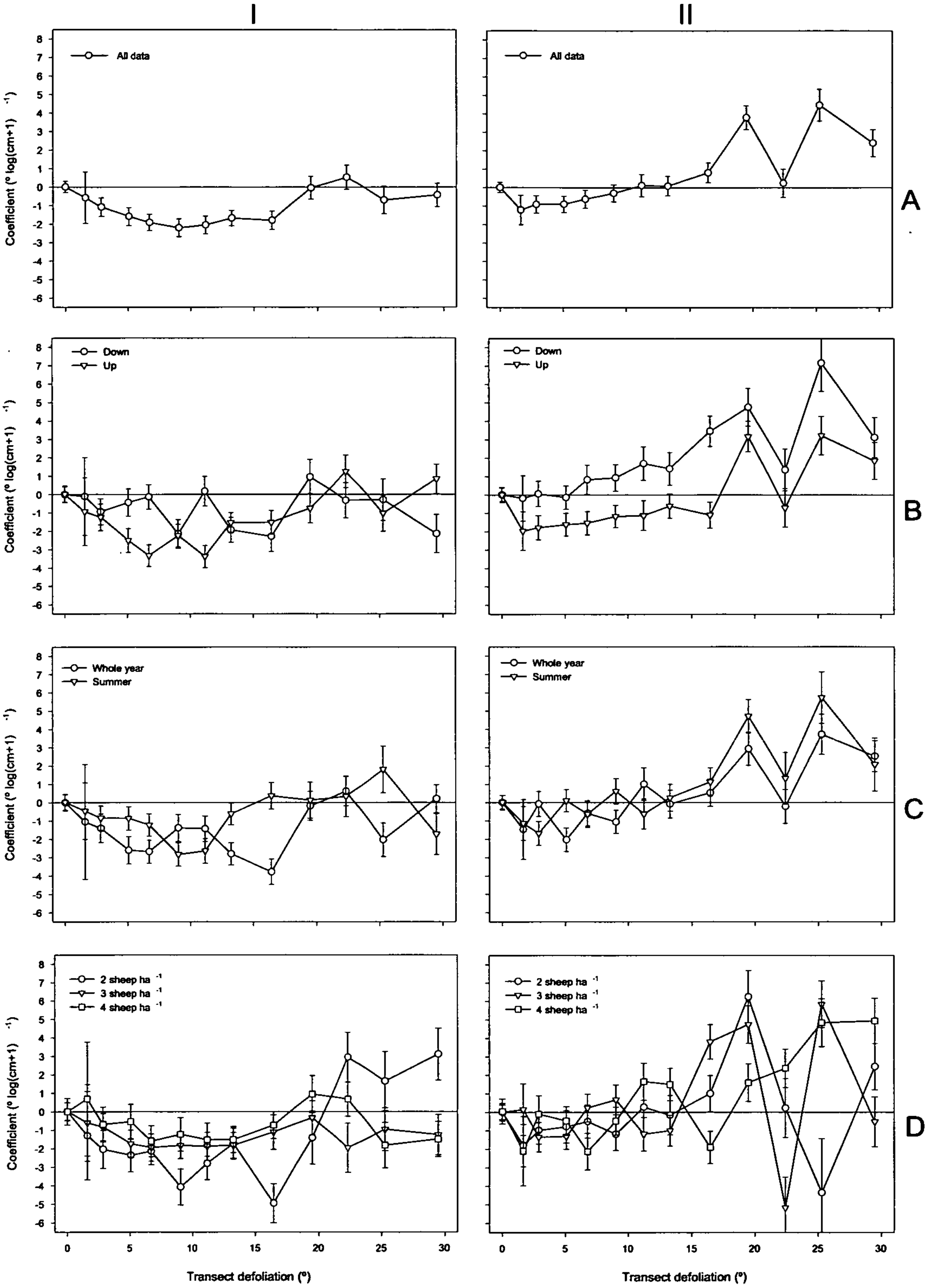

Figure 3.8. The coefficient of the angular heather defoliation and log distance for each transect defoliation bin. Figures split for grass patches (I) and paths (II), and for all data (a), direction of slope (b), season (c) and treatment (d). Error bars are based on standard errors as estimated by REML.

Assuming an exponential decline of heather defoliation with increased distance from the grass-heather boundary, following Clarke et al. (1995a), the relationship between defoliation and log transformed distance is linear. In order to fit linear equations, all transects, previously grouped per treatment, were now regrouped by transect defoliation in variable bins to accommodate the number of observations while at the same time achieving the same number of bins for both patches and paths (Table 3.8). The coefficient of the regression of angular heather defoliation on the log transformed distance (cm) ($\log_{10}$(Distance + 1)) was determined for each bin and plotted against transect defoliation. The resulting figures are shown for patches (Figure 3.8 I) and paths in (Figure 3.8 II).

At low transect defoliation the coefficient was negative, thus confirming that the heather defoliation was negatively correlated with log distance. Increased transect defoliation led to a more negative coefficient, i.e. a higher rate of decline of defoliation with distance from the grass-heather boundary. But with increasing transect defoliation, results did not fit previous findings. At moderate transect defoliation, the coefficient reached a minimum and then increased again. This indicates that increased transect defoliation led to a disproportionate increase of defoliation away from the grass-heather boundary than at the edge, thus reducing the contrast between edge and distant defoliation. At a transect defoliation of 10° (18%) and 20° (26%) for paths and patches respectively, the rate of decline was zero again, i.e. the heather defoliation remained constant with increased distance from the edge. Further increase of transect defoliation showed different responses for patches and paths, with the coefficient for paths continuing to increase and for patches to remain close to zero.

The uphill response of transect defoliation for paths was different from the downhill response (Figure 3.8 II B). Downhill from the paths the coefficient was predominantly positive. For patches the response showed no clear pattern. The results for season suggest that a negative interaction occurs between summer and whole year (Figure 3.8 C). Strong negative coefficients in one season coincided with weak negative or positive coefficients in another season. This could indicate that when a transect was mainly grazed at the edge in one season this led to more grazing further away from the edge in the next season (Figure 3.8 C) and vice versa.

There was no clear effect of the three treatments on the response of defoliation to distance from paths. However, where the global sheep density (at the plot scale) was only 2 sheep ha^{-1}, the slope of the regression was more negative than in the other treatments where the local defoliation levels (at the scale of a grass patch) were low or intermediate, but the slopes were more positive in areas of high local defoliation (Figure 3.8 D).

Where edge (0 - 0.5 m) defoliation (≤ 6°) was low, there was usually no defoliation at the distant end of the transect (4 and 5 m) (Figure 3.9). At higher levels of defoliation, however, the background defoliation increased linearly with edge defoliation with a coefficient close to 1. Thus, the background angular defoliation was roughly 6° (14%) lower than edge defoliation.

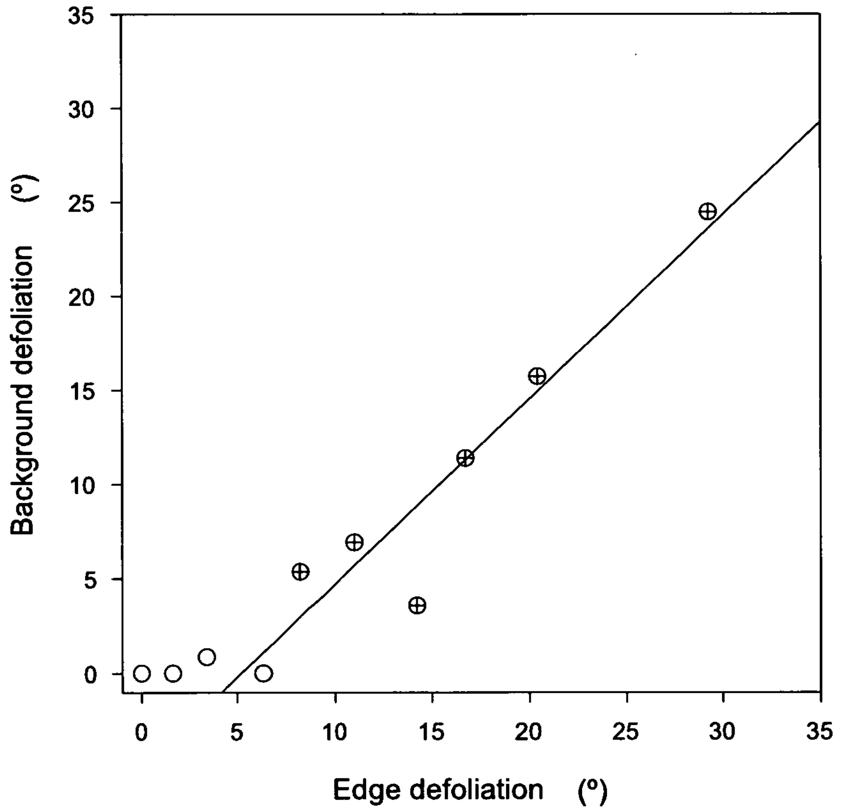

Figure 3.9. Scatter plot and regression between edge defoliation (0 + 0.25 + 0.50 m) and background defoliation (4 + 5 m) indicated by the solid circles. Solid line indicates regression line, based on points with crosshairs as discussed in the text (y = -6.6 + 0.90 × x; Adjusted R^2 = 0.88).

3.4 Hypothesis

Defoliation edge versus defoliation zone

The results presented here (Figure 3.8) suggest that heather defoliation can either decrease, increase or remain constant with distance (over a zone of 5 m) from the grass-heather boundary. A strong decrease or increase with distance means a high contrast in the level of defoliation near the edge than further away, thus causing a narrow zone of impact, while a constant level of defoliation with distance indicates a wide zone of impact.

Previous experiments concluded that heather defoliation was always negatively correlated with distance from the edge of grass (Clarke et al., 1995a; Hester & Baillie, 1998; Oom & Hester, 1999). Moreover, Clarke et al. (1995a) suggested an exponential decline away from the grass-heather boundary. This is called Hypothesis 0 (Figure 3.10-0). Hypothesis 0 predicts that increasing transect defoliation (i.e. the grazing pressure on the grass-heather boundary) will lead to an increased edge defoliation and more-or-less constant background grazing, because increasing defoliation at the edge will have little influence on distant defoliation. This will lead to increased contrast between edge and distant defoliation with increasing transect defoliation. It would also predict a skewed distribution of heather defoliation, such that at high stocking rates a large proportion of the edge heather defoliation exceeds the 40% threshold. Although an exponential decline allows for changes in the width of the impact zone as observed by Hester & Baillie (1998), it can not explain the decreasing contrast between edge and distant defoliation nor can it explain the increase in the width of the impact zone as observed in this study (Figure 3.8). Therefore three alternative hypotheses are suggested.

In order to facilitate the development of alternative hypotheses, grazing pressure is defined at three spatial scales. The first is the global grazing pressure (sheep ha^{-1}) at the scale of the plot (100 m), determined by the number of sheep in a given area of heather moorland. The global grazing pressure determines the heather defoliation for the whole plot. Next is the local background grazing pressure translating the global grazing pressure to a scale between 5 and 100 m. The pattern of local background grazing pressure shows spatial structure at scales larger than five metres, and is the result of sheep selecting feeding sites within the plot (Bailey et al., 1996). Following the results of the spatial interaction model in Chapter 2, the local background grazing pressure is expected to be higher than the global grazing pressure in areas of high grass abundance and vice versa. The local background defoliation is equivalent to the transect defoliation. Third are the local edge and distant grazing pressure at a the scale below five meters. Grazing pressure at this scale is strongly influenced by the distance of the heather from the grass-heather boundary (Clarke et al., 1995a; Hester & Baillie, 1998). The local edge grazing pressure is expected to be higher than the local background grazing pressure near the grass-heather boundary, while the distant grazing pressure is expected to be lower.

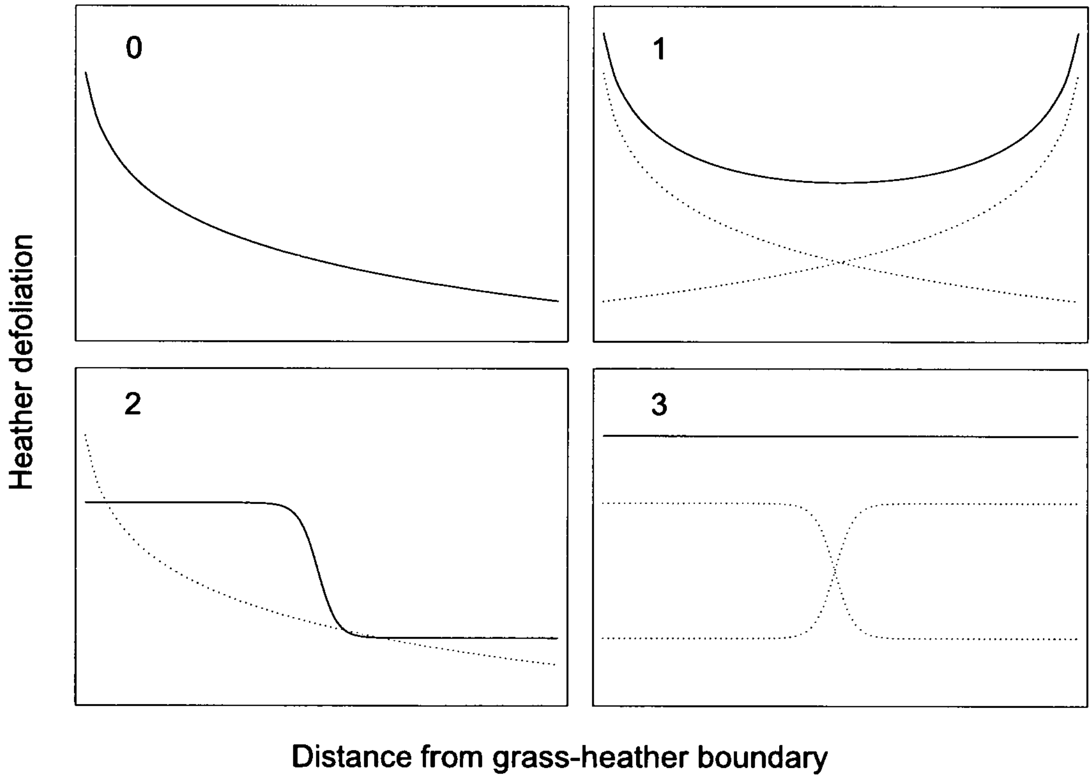

Figure 3.10. Graphs indicating the relationship between heather defoliation and distance from the grass-heather boundary for Hypothesis 0, Hypothesis 1, Hypothesis 2 and Hypothesis 3. Numbers in the graph correspond with the numbers of the hypotheses. Doted lines indicate the relationship as hypothesised in the previous hypothesis.

Hypothesis 1 (Figure 3.10-1) is a spatial extension of Hypothesis 0. It is suggested that wide impact zones occur as a result of the spatial interaction of two grass-heather boundaries at close proximity (i.e. less than 10 m apart). The observed decline away from the grass-heather boundary is thus a cumulative effect of two (or possibly more) grass-heather boundaries. This hypothesis would suggest less contrast between edge and distant heather defoliation and it could explain how defoliation can increase with distance when a transect runs away from a grass-heather boundary with low local grazing pressure (i.e. transect defoliation) to a boundary with high local grazing pressure. However, as the exponential decline still predicts high probabilities of extreme defoliation at the edge, it does not explain why so few observations are higher than 40% (or 39°) defoliation.

Hypothesis 2 (Figure 3.10-2) suggests a different response of heather defoliation to distance. Instead of the exponential decline, a sigmoidal decline is assumed. This hypothetical curve shows a wide zone of high defoliation near the grass-heather boundary, a decline over some distance and a zone of distant defoliation. Figure 3.11 shows sigmoidal response curves for increasing transect defoliation. At low levels of transect defoliation, the curve closely resembles an exponential decline. This could explain the choice of Hypothesis 0 in previous experiments, which had a considerably lower global grazing pressure than the current study had. This hypothesis is consistent with a strong correlation between local edge and distant heather defoliation. Increase in the local edge defoliation indicates increased potential herbivore impact. The distant defoliation could be a function of the local background grazing pressure, thus explaining the correlation between edge and distant heather defoliation. This hypothesis can explain the wide zone of impact independent of spatial interactions between grass-heather boundaries. As the sigmoidal curve does not rapidly increase near the grass-heather boundary, it also explains why so few heather defoliation observations are higher than 40% (Table 3.5).

The sigmoidal response curve could be explained as the result of the interaction between a spatial process and a functional response (Solomon, 1949; Spalinger & Hobbs, 1992) for sheep foraging on heather away from the grass-heather boundary. Considering a moving front, sheep would start foraging on the grass-heather boundary. How far sheep will penetrate the heather depends on the trade-off between reward and cost. A cost could be going away from the preferred vegetation type or the physical resistance of the heather, while a reward could be intake rate of heather. With increasing grazing pressure at a grass-heather boundary, herbivores could initially increase their defoliation of the edge, avoiding the cost of walking into the heather. This would lead to a decrease in the intake rate of heather as the heather is depleted, while the intake rate of the more distant heather remains constant. At some point the animals should reach a break-even point when the difference in intake rate between edge and distant heather equals the cost of entering the heather. In other words, the decreased intake rate at the edge makes it viable to overcome the cost of entering the heather. The level of the break-even point would de indicated by the observed edge defoliation. As the local background grazing pressure (transect defoliation) increases and heather is being depleted over a increasingly wide zone, the level of distant heather defoliation could approach that of the edge defoliation. At the same time the heather defoliation at the edge would still be at the threshold intake rate.

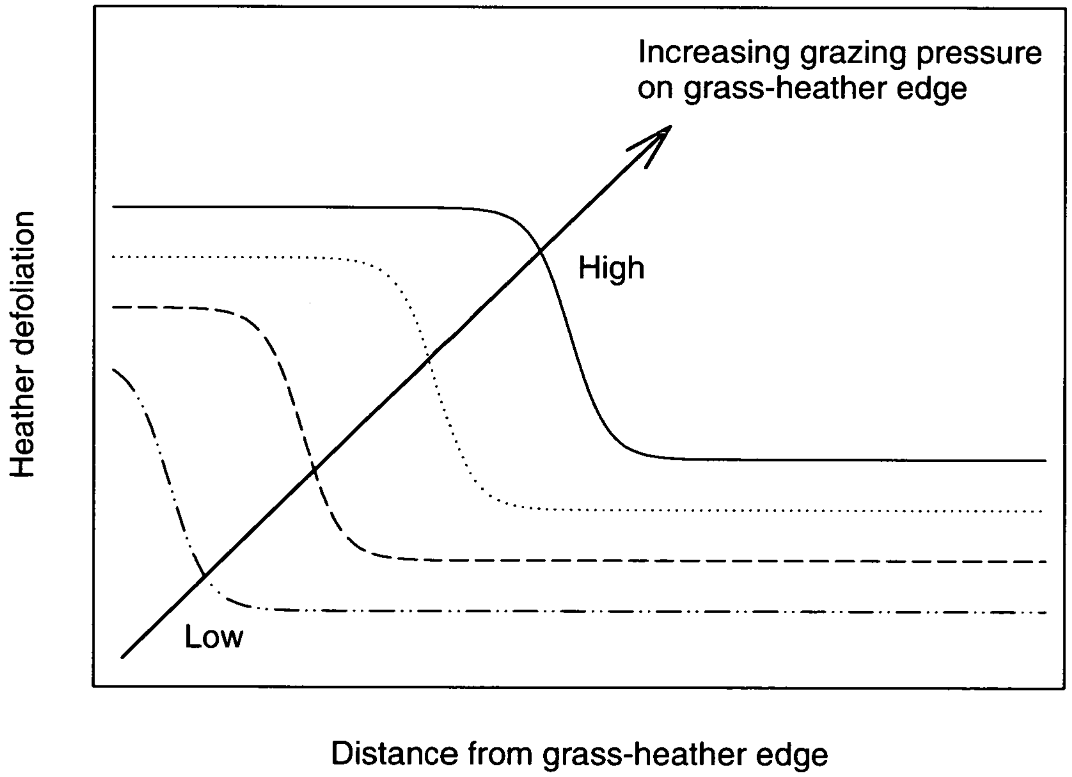

Figure 3.11. Change of sigmoidal response of heather defoliation versus distance from the grass-heather boundary as determined by transect defoliation..

The functional response between herbivore impact and plant abundance could also be explained as a plant defence mechanism against high-levels of herbivore impact (Laca et al., 2001), such that plant structure limits intake rate. In this proposition, plant structure could play a role in both physical resistance and intake rate, leading to a concentration of herbivore impact at the edge with grass but at the same time limiting high levels of impact. The result is a spatial refuge for a large proportion of the vegetation (McNaughton, 1984; Milne et al., 1992). It has however been argued that it is difficult to prove that a plant trait is induced exclusively by herbivory as many other ecological functions could possibly explain the same trait (Rosenthal & Kotanen, 1994).

Hypothesis 3 is the spatially explicit version of Hypothesis 2 (Figure 3.8 D). Similar to Hypothesis 1, heather defoliation away from the grass-heather boundary could be the result of an interaction between two grass-heather boundaries at close proximity. Due to the shape of the sigmoidal curves, the cumulative effect of defoliation in this case would be even stronger than in the case of Hypothesis 1. Thus a constant defoliation with distance would occur more frequently than in the other hypotheses.

Unfortunately, based on the current data it is not possible to conclusively distinguish between any of the alternative hypotheses. However, the existence of wide impact zones has strong implications for the plant-herbivore interactions in grass-heather mosaics and this phenomena is therefore explored in more detail.

Implications of the impact zone on the role of trampling versus defoliation

The findings of this study show that narrow zones of defoliation occur at low transect defoliation, while wide zones of defoliation occur at high levels of transect defoliation (Figure 3.8). The width of the defoliation zone has strong implications for the impact of herbivores on heather through trampling. In a narrow defoliation zone, animals can reach the heather while standing on the grass, thus limiting trampling damage on the heather. When the animals reach the break-even point of defoliation at the edge, they start moving into the heather. Increasing transect defoliation then leads to an increasing zone of heather affected by defoliation. But much more crucial, as the width of the zone increases, the trampling impact at the edge of the zone increases with the width of the zone, as a result of the sheep passing through to the distant heather. This could imply that, for the heather near the edge of grass, the impact of trampling could exceed the impact of defoliation (Figure 3.12).

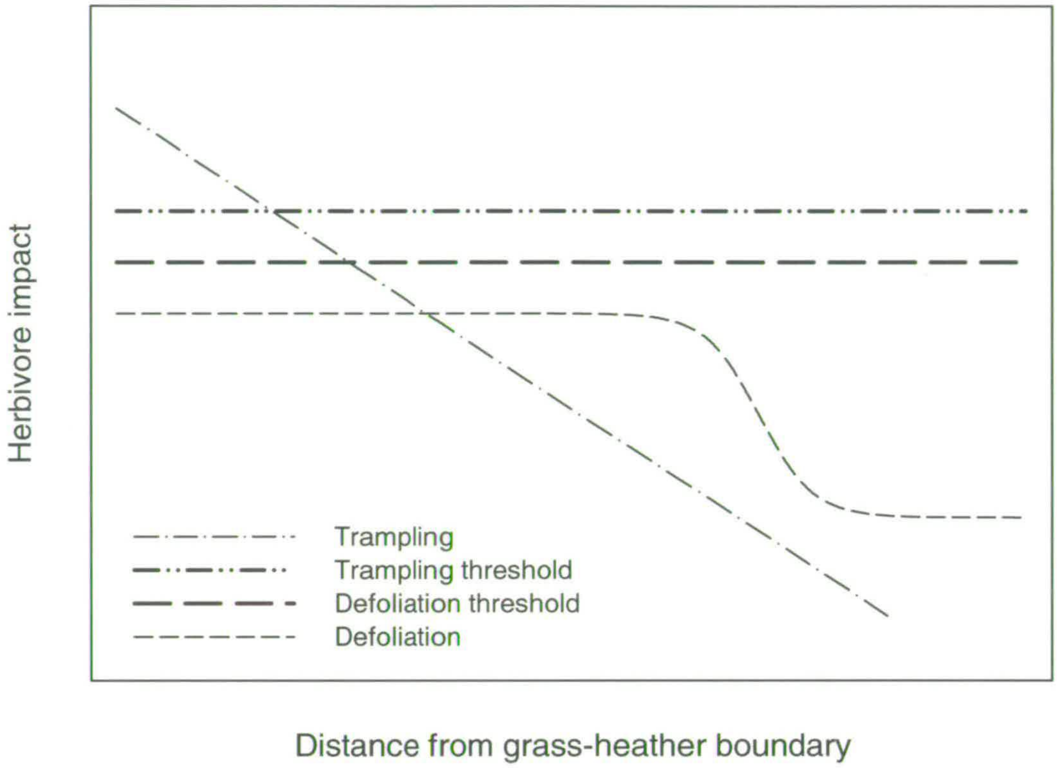

Figure 3.12. Hypothetical response of grazing and trampling impact which implies a sigmoidal response of defoliation with distance, but a linear response of trampling with distance. As animal densities increase the trampling causes a progressive increase in the amount of heather above the trampling threshold. However, an increase in the defoliation impact, following Figure 3.11, affects a wide impact zone at critical animal densities.

The balance between defoliation and trampling impact depends on the response of the width of the zone of impact and therefore differs between hypotheses. If heather defoliation declined exponentially with distance following Hypothesis 0 (causing narrow zones of defoliation) and if defoliation was the main cause of damage, one would expect heather plants at the edge to die first. The death of one plant would increase the defoliation of its neighbours, ultimately leading to their death. As heather plants at the edge of the grass die first, the resulting grass-heather boundary would be smooth. Because defoliation would always be highest on plants at or near the grass-heather boundary, isolated heather plants would not be able to survive within a grass patch.

If defoliation levels are rarely high enough to kill the heather (considering the low incidence of heather defoliation > 40% in this study), but cumulative trampling at the edge does cause fragmentation, plants would also die near the grass-heather boundary. However the death of one plant might now reduce the trampling impact on its neighbours as animals can walk through the gap left by the dead plant. Because the defoliation at the edge will not reach lethal levels, the plants can survive. This would lead to a rough grass-heather boundary with individual heather plants surviving in an edge zone of the grass.

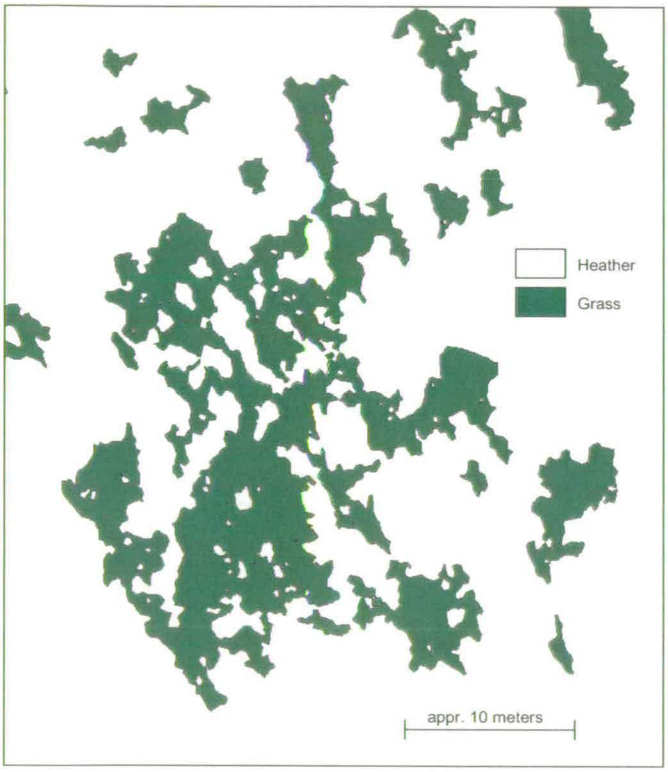

Figure 3.13. Example map of grass patch in plot T3.

Grass patches resulting from defoliation impact would therefore have a low perimeter : area ratio, while grass patches resulting from cumulative trampling would have a high perimeter : area ratio. Grass patches from the study site are characterised by rough edges, as shown by an example of a grass patch in plot T3 (Figure 3.13), and high perimeter : area ratios, as illustrated by a scatter plot of perimeter versus area for individual grass patches in the experimental plots (Figure 3.14). The difference with perfect circles is slightly exaggerated, because the grass patches are often formed from several individual grass patches converging through expansion. These observations suggest that trampling by sheep is the dominant cause of fragmentation in these heather-grass mosaics. A more detailed investigation of the interaction between herbivores and the vegetation mosaic is presented in Chapter 4.

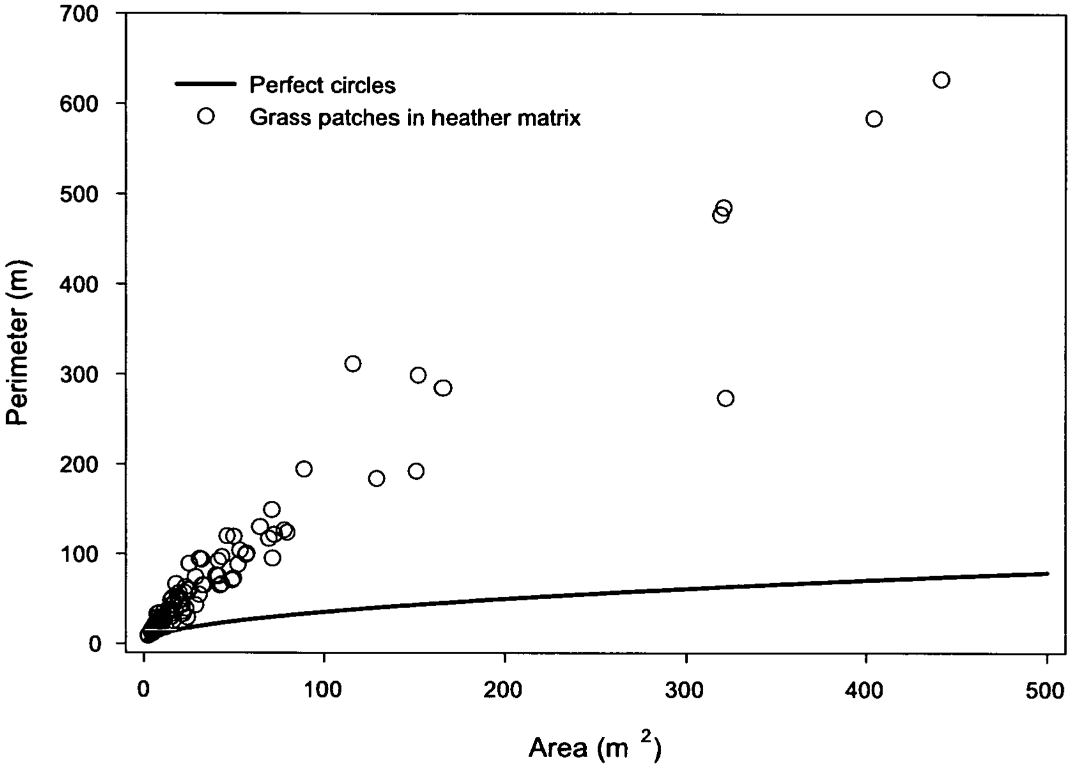

Figure 3.14. Scatter plot of perimeter versus area for all individual grass patches on the experimental site. The solid line indicates the perimeter : area response of perfect circles.

Implications of an impact zone for carrying capacity

In order to appreciate the implications of an impact zone on carrying capacity and stability, it is necessary to step up from one dimension (the transect) to two dimensions (the mosaic). How does the zone of impact as described above translate to grazing impact across a mosaic? At low grazing intensity, the impact zone will be narrow, leading to only a small proportion of the landscape suffering defoliation. Damage resulting from trampling will be limited to the formation of clearly defined paths as a result of sheep navigating through the mosaic (Hester & Baillie, 1998). Initial increase in grazing intensity will lead to higher edge defoliation, but a constant impact zone width. As grazing pressure increases, the impact zone widens, which means that a larger area of the landscape suffers defoliation. But because the increase in heather defoliation is buffered by an increase in the area of the mosaic affected, the defoliation impact remains low. Due to the width of the impact zone, some fragmentation as a result of trampling now occurs at the edge of the heather vegetation. This situation persists over a large range of grazing intensity values, as the increased grazing pressure is buffered by the increase of the zone of impact. Although the increasing impact zone initially buffers the increased grazing intensity, the defoliation in the impact zone eventually increases, following Figure 3.11. As grazing intensity is further increased, there will be a point when the level of defoliation within the impact zone exceeds the maximum defoliation tolerance of the plant. This would also occur in case of Hypothesis 0, but with a crucial difference. When, in Hypothesis 2, the heather defoliation in the impact zone exceeds the defoliation tolerance limit, suddenly the whole impact zone would be affected and thus a large area of the landscape would be damaged by grazing. This could lead to sudden and widespread loss of heather and is contrary to the effects of trampling damage which are associated with the grass-heather boundary only.

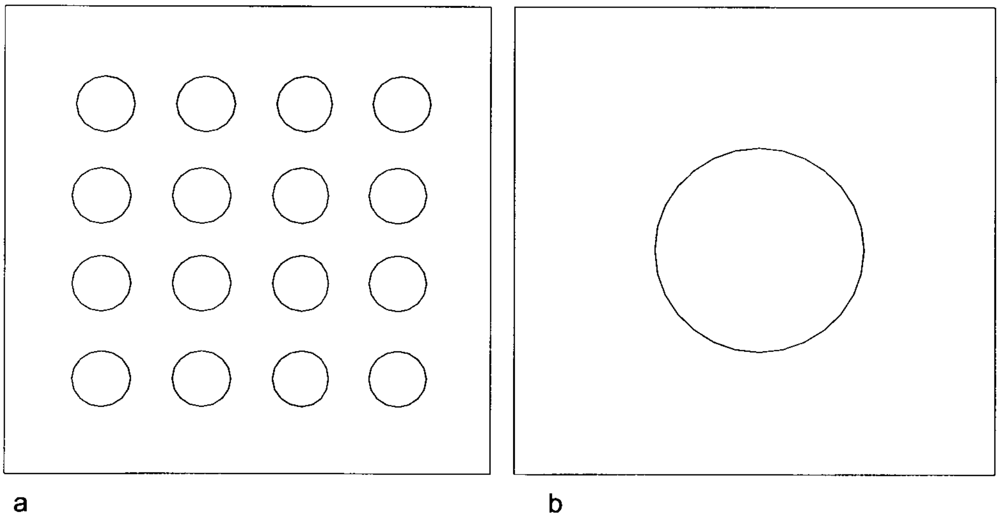

Figure 3.15. Level of mixing of grass within the heather matrix either in many small patches (a) or one large patch (b). The total area of grass is the same in (a) and (b).

The proportion of the area within a heather-grass mosaic that is potentially part of the impact zone, will depend directly upon the amount of grass-heather boundaries in the mosaic. An intimately mixed mosaic of heather with many small evenly spread grass patches will have more edge than a mosaic consisting of one big grass patch surrounded by heather (Figure 3.15). Clarke et al. (1995b) showed that fragmentation of grass into progressively smaller patches leads to an increase in the use of heather away from the edge, as a result of increased movement between grass patches, while the overall heather in the diet is not affected by the amount of fragmentation (Cuartas et al., 2000). Thus an increase in fragmentation leads to a larger area of heather being affected by grazing.

The role of the amount of grass-heather boundary within a mosaic can be illustrated effectively using a cusp catastrophe (Lockwood & Lockwood, 1993). Lockwood & Lockwood (1993) review the cusp catastrophe and its use as a theoretical framework for the study of multiple stable states in grazed ecosystems. The cusp catastrophe has been used successfully to describe catastrophic events in grazed ecosystems (Rietkerk et al., 1996). Central to the cusp catastrophe is a discontinuity of a system due to a positive feedback mechanism. In the case of semi-arid grazing systems, a positive feedback exists between herbivory and plant density. As herbivores decrease plant density, water infiltration decreases, which in turn decreases plant growth. Decreasing plant growth will increase grazing intensity on remaining plant density, leading to a catastrophic decrease of plant density. Rietkerk et al (1996) suggest that the observed discontinuity does not occur when rainfall is plentiful.

In the system under study, grass and heather are considered the multiple stable states. In case of high global grazing intensity, grass is the dominant vegetation type in the system. At very low grazing intensity heather is the dominant vegetation type. This can be explained with a cusp catastrophe diagram (Figure 3.16). The cusp model predicts a catastrophic change from heather to grass when continuously increasing the grazing intensity on the mosaic. Due to the uneven spread of the grazing intensity, local grazing thresholds are exceeded at relatively low global grazing intensities, leading to a small decrease in the proportion of heather in the mosaic. As the grazing intensity increases and the proportion of heather decreases, due to the fragmentation process, more heather is exposed to grazing by the herbivores. This leads to a positive feedback between fragmentation and increased grazing intensity, leading to a catastrophic change in the vegetation at the global grazing threshold. One could say that the system is poised across a range of grazing intensities, due to the initial small area of heather which is affected by the herbivores.

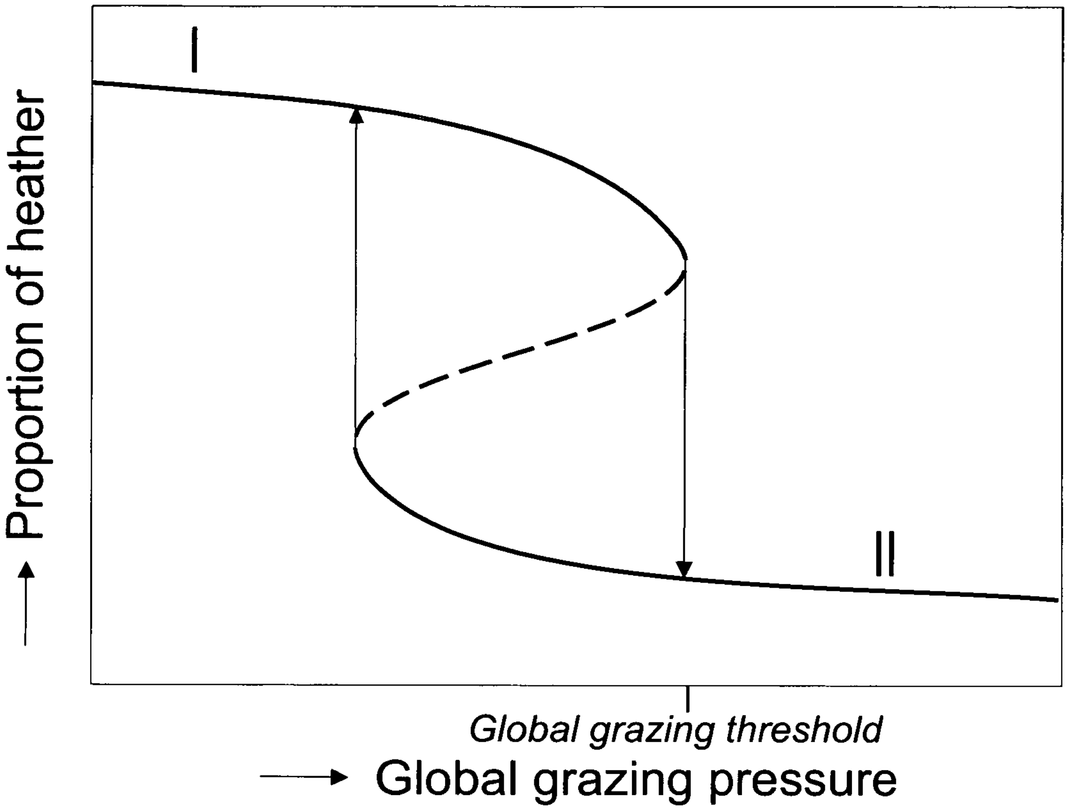

Figure 3.16. A two dimensional cusp catastrophe diagram illustrating two stable states: I) low global grazing intensity and heather dominance, II) high global grazing intensity and grass dominance.

However, results from this study suggest that due to the uneven spread of defoliation of heather across grass heather mosaics, highly fragmented mosaics can be more sensitive to grazing as a larger proportion of the heather is exposed to the impact of herbivory. Thus, in line with the role of rainfall in semi-arid grazing systems, a discontinuity might only occur when the initial vegetation is heterogeneous. We thus apply a second axis in the cusp diagram based on the homogeneity of the system (Figure 3.17). Now the cusp catastrophe is indicated by a three dimensional folded surface (Figure 3.16). In this case, the surface is determined by the sheep stocking rate (i.e. global grazing pressure), the homogeneity of the vegetation mosaic and the proportion of heather in the mosaic. In contrast with the semi-arid application

(Rietkerk et al., 1996) in which rainfall is the second and independent explanatory variable, here we used a feature of the state variable as the second explanatory variable. The system is still considered to have the same two stable states as described before.

Consider a homogeneous mosaic, location 1 in Figure 3.17, consisting of mostly heather with the grass distributed across few patches (as in Figure 3.15 b). If the global grazing pressure is increased but homogeneity is maintained, i.e. following the green line, the few grass patches will grow as a result of trampling and defoliation, reducing the amount of heather in the mosaic. Because the small amount of grass-heather boundary in the mosaic limits the potential impact zone area, when the defoliation threshold is crossed, the transition from heather to grass goes smoothly.

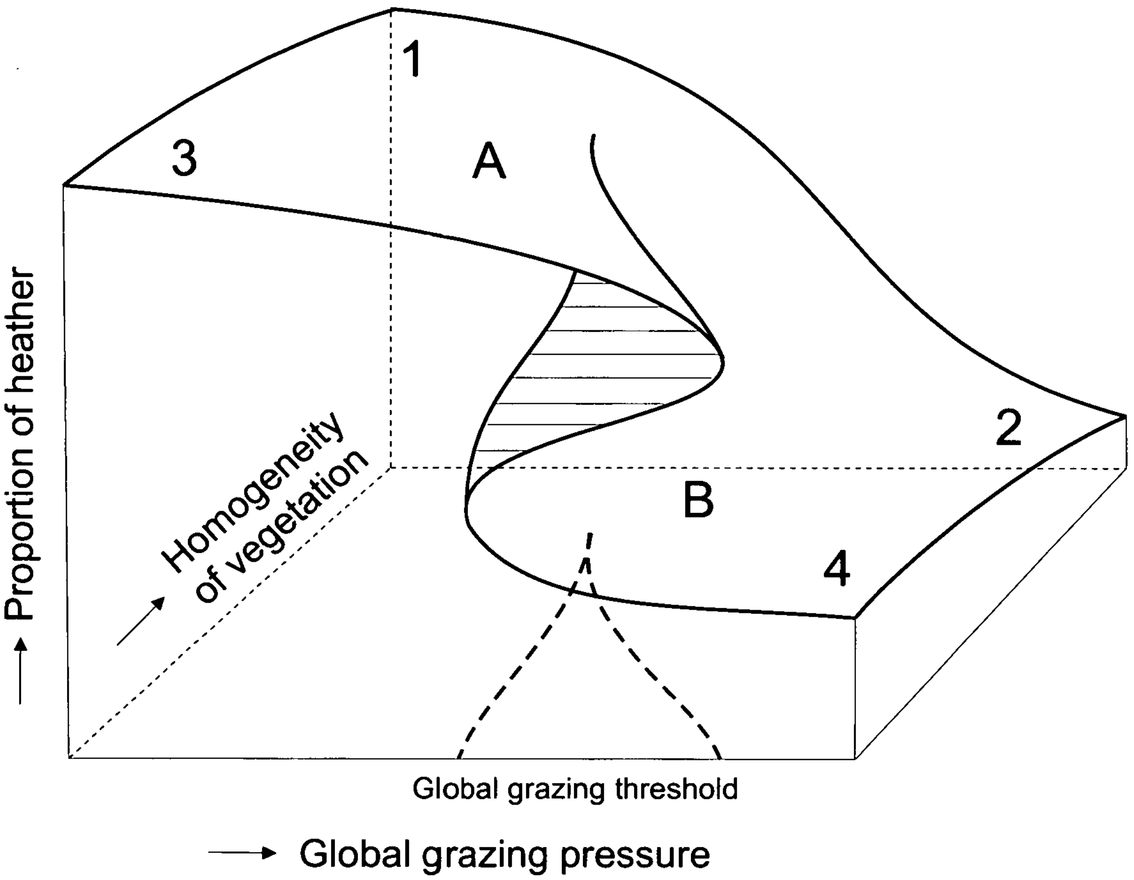

Figure 3.17. Diagram of a cusp fold surface of the state variable proportion of heather as a function of global gazing pressure and the homogeneity of the vegetation. Characters are explained in the text.

However, starting with a highly heterogeneous mosaic, location 3 in Figure 3.17, containing a large number of tiny grass patches in a heather matrix (as in Figure 3.15a), the mosaic contains a large amount of grass-heather boundary. As a result of the large amount of boundary, the increasing grazing pressure is buffered by a slowly increasing impact zone area, while trampling only has a small impact as the sheep can reach a large part of the heather while standing on the grass. Increasing global grazing pressure leads to increasing width of the impact zone and eventually to the crossing of the defoliation threshold. When the defoliation threshold is exceeded in this case, a large proportion of the heather in the mosaic is part of the impact zone. The defoliation impact thus causes a sudden widespread loss of heather, reaching location 4 through the drop illustrated by the blue line.

Through interactions between heterogeneity and global grazing pressure, alternative paths are possible. For example, starting at Location 1, but now increasing the number of grass patches (decreasing homogeneity) and at the same time slightly increasing the global grazing pressure, the vegetation smoothly transforms from a heather to a grass dominated mosaic (B in Figure 3.17). The slight increase in global grazing pressure is enough to fragment the heather before the amount of edge increased the impact zone area. In contrast, when increasing the heterogeneity faster than the global grazing pressure, the grazing pressure is buffered by the impact zone area (A in Figure 3.17). Thus the grass patches barely grow and the heather remains the dominant vegetation type.

Not only does the cusp catastrophe diagram using the second explanatory variable illustrate the discontinuity, it also illustrates that the heterogeneity of the initial vegetation mosaic could determine the timing of the catastrophe, i.e. the global grazing threshold. In highly heterogeneous vegetation, a large area of heather is exposed to the impact of herbivores. As the defoliation is spread thinly, it takes a very high global grazing pressure (at the scale of the whole mosaic) to cause the local grazing pressure (at the scale of a grass patch) to exceed the grazing threshold and subsequently for the system to collapse. When the vegetation is more homogeneous, i.e. the heather defoliation is more concentrated, the local grazing pressure could be exceeded at lower global grazing pressure. When the vegetation is highly homogeneous, heather defoliation is so concentrated that the local and global grazing pressure are synchronised. A catastrophe could therefore be avoided because fragmentation starts even at low grazing pressure. When starting from the grass dominated state, recovery of the heather follows a similar process. At high homogeneity, heather recovers continuously with decreasing global grazing pressure. At low homogeneity, the recovery of heather could be delayed as a result of the large area of heather affected by herbivory. Once the global grazing pressure threshold is passed, recovery could occur rapidly. This complex of behaviours can only be illustrated by explicitly including heterogeneity in the cusp diagram.

3.5 Conclusions

The aim of this experiment was to increase our insight into the spatial aspects of plant-herbivore interactions in grass-heather mosaics grazed by sheep which determine the distribution of heather defoliation within the heather-grass mosaic. Previous experiments showed that heather defoliation is strongly correlated with the proximity of grass. Thus, this study focussed on the distribution of heather defoliation away from the grass-heather boundary. Because the sampling scheme of this experiment was not based on pre-defined classes of factors, such as grass patch size, but instead used a random spatial grid of observations, the data provided an opportunity to consider factors as continuous variables. This resulted in new insights presented here and in Chapter 2.

The results of the spatial interaction model (Chapter 2) showed that, in an area of fixed stocking rate, heather defoliation (expressed as the mean defoliation across a 0.5 m wide zone away from the grass-heather boundary) at a given location at a grass-heather boundary is correlated with the local abundance of grass and the distance between the grass and the boundary location. The current experiment then allowed an investigation of the distribution of heather defoliation away from the grass-heather boundary.

The results (Figure 3.8) showed that the distribution of heather defoliation away from the grass-heather boundary was strongly influenced by the grazing pressure on the grass-heather boundary zone (here expressed as the mean defoliation across the observed zone). Interactions occurred with the type of grass-heather boundary (path or patch), the direction relative to the slope (uphill and downhill), the sheep density (2, 3, and 4 sheep ha^{-1}) and season (summer and whole year). Surprisingly, despite high sheep densities, only a small proportion, less than 10% in case of 4 sheep ha^{-1}, of the observations of heather defoliation was $\geq 40\%$. Results showed that increased grazing pressure on the grass-heather boundary more often led to an increase in the width of the zone of impact than an increase in the level of defoliation. This could explain the small proportion of observations of high levels of heather defoliation. The results suggest that the role of defoliation in the fragmentation of heather might be smaller than previously assumed. Through a logical argument, trampling of heather by sheep is brought forward as a potentially important factor in the fragmentation of heather. This is in addition to the importance of trampling in relation to slope (Hester & Baillie, 1998). Whether trampling could be more important than defoliation in causing loss of heather, needs to be tested through field trials.

Questioning the relative role of defoliation versus trampling and the role of vegetation heterogeneity in the fragmentation of heather, has strong implications for agri-environmental policies, scientific experimentation, or monitoring programs. Environmental schemes aiming to reduce impact of agricultural practises on semi-natural habitats, such as the Rural Stewardship Scheme (Scottish Executive Rural Affairs Department, 2000), often use recommended area based stocking rates. To ensure the effectiveness of these schemes, the recommended stocking rate should take into account the heterogeneity of the vegetation, as this study suggests that impact of a fixed area based stocking rate can vary strongly with the heterogeneity of the vegetation mosaic (Henderson et al., 1995). Monitoring methods should include a measure of both defoliation and trampling, such as the impact assessment method developed by MacDonald et al. (1998a; 1998b), while in scientific experiments defoliation can not be considered equivalent to total grazing impact.

Combining the results from the spatial interaction model (SIM) (Chapter 2) and the distribution of heather away from the grass-heather boundary (this chapter) provided strong evidence for the existence of a three-dimensional defoliation surface across a vegetation mosaic. This surface can be seen as an emergent property resulting from the interaction between sheep and the grass-heather mosaic. The surface can be characterised by peaks at locations of high grass abundance and depths in areas of high heather abundance. Global patterns of decline of defoliation from peaks to depths along the grass-heather boundary were predicted by the SIM, while results presented here predicted local patterns of decline of heather away from the grass-heather boundary as a function of transect defoliation and trampling. Results presented in Chapter 6 show that vegetation change was correlated with defoliation impact, such that low levels of impact were associated with expansion of heather while high levels of impact were associated with grass expansion.

Several factors were not considered in this experiment which could also affect the distribution of heather defoliation directly or interact with the factors observed in this experiment. Firstly, there might be an interaction between defoliation and plant production. Moderate levels of defoliation can lead to increased shoot productivity, while high levels of defoliation can lead to decreased productivity (Grant et al., 1978). Grant et al. (1978) showed that although grazing decreased standing crop, the proportion of standing crop accounted for by current year's shoots increased. However when increased shoot productivity coincides with increased shoot density but decreased mean shoot length, the availability to the herbivore might remain constant or go down depending on the effect of sward structure on intake rate (Spalinger & Hobbs, 1992).

Secondly, there might be an interaction between herbivore impact, plant morphology and age. Moderate levels of grazing (60%) of heather lead to increased compactness of structure and decreased height (Grant & Hunter, 1966). However both height and compactness of growth are likely to be negatively correlated with physical resistance of heather to penetration by sheep. Furthermore, herbivore impact on heather depends on the age, or phase (Watt, 1947), of the heather, as older heather is more sensitive to herbivore impact compared to younger heather (Grant et al., 1981).

Thirdly, there might be an interaction between defoliation and concentration of secondary compounds in heather shoots. Concentration of secondary compounds is known to affect foraging decisions (Launchbaugh et al., 2001), but no references have been found on the concentration of secondary compounds in heather and the relationship with grazing impact.

Lastly, there are many interactions between plants, herbivores and soils which could have important implications for the plant-herbivore interactions. Gradients of defoliation can affect vegetation dynamics through direct impacts on plant structure or indirectly through the creation of nutrient gradients, while vegetation dynamics can affect soil properties and vice versa, resulting in feed-back mechanisms affecting the distribution of defoliation (Pastor & Cohen, 1997; Pastor et al., 1997). Further investigation into these factors, across gradients of defoliation, vegetation and soil properties, is required to understand their role in plant-herbivore interactions with heather-grass mosaics in particular and with grass-shrub mosaics in general.

Further investigation of plant-herbivore interactions on grass-heather mosaics should be considered both through field and virtual experiments (i.e. modelling). Results from this experiment can help to design future experiments. Important processes for investigation, considered in a spatially explicit context, would be the response of the vegetation to impact by herbivores (both trampling and defoliation) and the resulting effect of plant abundance and quality on herbivore foraging. The existence of a defoliation surface as an emerging property of plant-herbivore interactions provides a challenge for virtual experiments. Both individual-based models (e.g. Beecham et al., 2002) and reaction-diffusion models (Farnsworth & Anderson, 2001; Okubo, 1980) should be applied to develop the criteria for the existence of defoliation surface and investigate their characteristics. A synthesis of spatial ecological processes and mathematical theory would be a major advance in the investigation of plant-herbivore interactions.

Results and hypotheses presented in this chapter have implications for the spatial heterogeneity of grass-heather mosaics. The importance of heterogeneity in vegetation pattern in the context of ecosystem functioning was argued by Watt (1947) and was recently reviewed by Adler et al. (2001). The findings presented here suggest that selective grazing of sheep on grass and associated heather will eventually lead to an increase in spatial heterogeneity as predicted by Adler et al. (2001) as selective grazing by sheep on the preferred vegetation type increases the contrast between grass and heather. However, the existence of rough edges around expanding grass patches indicates that the contrast at this scale is actually decreased during the fragmentation process at grass-heather boundary. Thus, short-term and small-scale herbivore impact might differ from long-term and large-scale impact. This suggests that temporal and scale aspects of herbivore impact could be important in the management of grazed ecosystems. Based on increased understanding, the need for grazing control (Grant & Hunter, 1968) can thus be specified as variation in the temporal and spatial impact of herbivores.

In conclusion, two different processes seem to determine the impact of herbivores on the boundary between grass and heather. Trampling impact on vegetation can occur across a wide range of stocking rates, but impact, at least for sheep, is possibly limited to a small area near the boundary. Considerable defoliation damage, on the other hand, is likely to occur only at higher stocking rates, but could potentially affect larger areas. The type, probability and extent of the impact has implications for monitoring and managing heather-grass mosaics and grass-shrub mosaics in general. Maintaining a system at carrying capacity by adjusting stocking rates to achieve maximum population density consistent with sustaining vegetation resources, may therefore be a risky business. In a system close to carrying capacity, a slight increases in herbivore impact, for instance in a year of low plant production, could lead to fragmentation of the shrub vegetation across a large area. This could suggest that the system has multiple stable states, depending on the spatial plant-herbivore interactions. An effective management strategy aimed at sustainable management of grass-shrub mosaics (Archer, 1996) should therefore consider the spatial aspects of the interface between plants and herbivores.

3.6 References

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Chapter 4

Remote sensing of plant-herbivore interactions at the patch scale: impact of sheep on heather-grass mosaics

> [Heathland]... a type of vegetation which has provided fascinating insights into the repercussions of man's impact upon natural systems.
>
> C.H. Gimingham (1972)

4 Remote sensing of plant-herbivore interactions at the patch scale: impact of sheep on heather-grass mosaics

4.1 Introduction

It is more than half a century since Watt (1947) successfully argued that vegetation mosaics should not be considered static; they are the result of dynamic processes that shape the current pattern of vegetation and in return the vegetation mosaics influence other processes. Processes that lead to spatial heterogeneity in vegetation mosaics are vegetation interactions with: climate, soil, vegetation dynamics, and herbivores (see review by Archer & Smeins, 1991). In this chapter attention is focussed on the interaction between vegetation and large mammalian herbivores.

An early description of a spatial plant-herbivore interaction was by Bell (1970), but quantification of links between pattern and process in plant-herbivore interactions started to emerge in the literature only recently (Adler et al., 2001; Milchunas & Lauenroth, 1993; Pastor et al., 1999). Initially, the emphasis was put on the herbivore response to heterogeneity in the vegetation (see for review: Bailey et al., 1996; Pastor et al., 1999; Senft et al., 1987). When considering the impact of the animal distribution on the vegetation, conflicting results were reported (Adler et al., 2001). Adler et al. (2001) therefore proposed a framework to classify the impact of grazing on spatial heterogeneity in vegetation mosaics.

The framework predicts whether heterogeneity in the vegetation will increase or decrease with herbivory from: the effect of the vegetation pattern on herbivore distribution; any pattern of herbivory independent of the vegetation pattern; and the effect of herbivory on the contrast between vegetation types. Spatial heterogeneity, as defined by Adler et al. (2001), is associated with high spatial dependence, non-randomness, and high contrast. Adler et al. (2001) include non-randomness, because their definition describes spatial pattern across two scales. The spatial heterogeneity applies to a mosaic consisting of several homogeneous (i.e. non-random) patches, with high contrast between the patches. The term patchiness or aggregation would have been more appropriate, but the suggested terminology is used here to avoid confusion. Spatial heterogeneity decreases either when the pattern of herbivory is independent of the pattern of vegetation but not strong enough to affect the pattern, or when the pattern of herbivory is dependent on the pattern of vegetation but the impact leads to a decrease in contrast between vegetation types. Spatial heterogeneity increases when the pattern of herbivory is independent of the pattern of vegetation and the pattern of herbivory is stronger than the pattern of vegetation, or when the pattern of herbivory is dependent on the pattern of vegetation and the impact leads to an increase in contrast between vegetation types.

In order to create a simple framework to predict the effect of herbivores on vegetation pattern, Adler et al. (2001) used the term grazing to indicate all forms of herbivore impact. Despite the existence of a strict definition, the partial removal of herbage by a herbivore (Spedding, 1971), the term grazing is generally used to describe the complex of processes associated with herbivory (Heady & Child, 1994), such as defoliation, trampling, and nutrient and seed redistribution. Moreover, herbivore impact on vegetation is considered synonymous with grazing, thus assuming a linear spatial correlation between individual processes (i.e. trampling is linearly correlated with defoliation and showing the same spatial pattern). In agricultural grazing systems, in which the vegetation consists of plant species highly tolerant of grazing (such as most grasses) and spatial heterogeneity is actively reduced (Heady & Child, 1994), impact resulting from both defoliation and other processes could be strongly spatially correlated. However in natural vegetation mosaics, spatial heterogeneity is high and grazing tolerant species are intermixed with grazing intolerant species (consider grass-shrub mosaics). In these systems, processes other than defoliation become increasingly important and their spatial interactions increasingly complex. Considering these individual processes as one single process, as Adler et al. (2001) did, hinders the progress of understanding plant-herbivore interactions in grazing systems.

Therefore, strict definitions are applied for each of these terms based on the physiological and behavioural needs of large mammalian herbivores (Stafford Smith, 1988): thirst, temperature, nutrition, night time location (orientation and predator avoidance) and rest (rumination, sleep, energy conservation). Grazing (or browsing) is the activity, motivated by hunger, leading to food intake (Briske & Heitschmidt, 1991). Side effects of grazing are trampling, and nutrient redistribution. Foraging behaviour is more loosely defined as the combination of all behaviours leading to, and including, grazing. Thus foraging includes any trampling associated with searching behaviour. Defoliation is the removal of physiologically active material through eating (Heady & Child, 1994). Aspects of defoliation are: intensity, frequency, seasonality and selectivity (Heady & Child, 1994). Trampling can effect vegetation directly and also indirectly through effects on soil and micro climate conditions (Archer & Smeins, 1991). Trampling of vegetation, as defined here, includes any physical damage to plants, including defoliation resulting from treading as opposed to eating.

While the pattern of defoliation is driven by the spatial pattern of food items, the search for water (thirst) and shelter (temperature, night-time, rest) are driven by other, non-food related, features in the landscape. Because herbivores generally forage on a low quality highly dispersed food resource, the pattern of use of non-food resources will influence the pattern of use of the food resource. For example, in semi-arid grazing systems, the distribution of defoliation will be influenced by the distribution of watering points (e.g. Weber et al., 1998). Similarly, many herbivores can be considered central place foragers (Bell, 1991), as they return to the same resting place between foraging bouts, subsequently affecting the pattern of defoliation. Thus, it is unlikely that the impacts of different processes will show the same pattern.

Considering this, it seems more appropriate to speak of the pattern of utilization, instead of grazing, when indicating the pattern resulting from the combination of several processes. Thus utilization of a vegetation mosaic is used here to describe the combination of behaviour resulting from the motivation to satisfy the different physical needs. In order to understand and correctly predict the impact of the pattern of utilization on the vegetation mosaic, analysis should be focussed on individual processes and the interactions between these processes.

Another complication overlooked by Adler et al. (2001) is the importance of temporal aspects of plant-herbivore interactions, such as plant life history traits and grazing history. Herbivore impact on plants strongly depends on the age and characteristics of the plants and whether the plant has been grazed before and to what extent. In the context of heather-grass mosaics, the growth phase of heather determines the impact of herbivory. Impact of herbivory on heather plants is strongly determined by the life history and the state of the vegetation (Grant et al., 1981; Welch, 1984), as old heather can withstand grazing less well than younger heather (Grant et al., 1981).

Three main processes emerge from the literature when considering sheep foraging behaviour: defoliation, trampling and resting behaviour. The pattern of defoliation by sheep grazing heather-grass mosaics has been intensively studied (Clarke et al., 1995; Grant et al., 1978; Hester & Baillie, 1998). Although trampling is often mentioned in these studies, quantification of the impact of trampling on heather-grass mosaics has primarily been done in the context of human impact (Bayfield, 1979; Gallet & Roze, 2001). It is well known that sheep have a voluntary limited home range (Hunter, 1962) and that they establish night-time resting areas in part of the home range (Hunter, 1962). As animals spend a large amount of time in a small area, this can lead to concentrated trampling, soil compaction and defecation (Hunter, 1962).

This study investigates the spatial pattern of impact of sheep on heather-grass mosaics. Through remote sensing the changes in vegetation during a three-year grazing experiment are quantified. A detailed description of the experiment is given in Chapter 3. The observed patterns of heather defoliation by sheep are described in Chapters 2 and 3. For this chapter, additional animal observations and the heather defoliation observations have been used to quantify herbivore impact by linking herbivore behaviour to vegetation change. These data sets enabled the investigation of the impact of ruminating behaviour as well as heather defoliation. Several other processes of plant-herbivore interactions have been investigated through qualitative examples. Maps of the vegetation have been used to explore the possible role of each process in the vegetation change.

4.2 Methods

4.2.1 Aerial Photography

In order to detect vegetation change over the course of the three-year grazing experiment, the vegetation mosaic was recorded by aerial photography at the start and end of the experiment. To minimise differences in vegetation caused by season and light conditions, a set of anniversary dates was chosen and images were recorded at the same time of day. Because the anticipated vegetation change over the three-year experiment was limited in extent and frequency, a high spatial resolution was considered crucial. Therefore the aerial photography was commissioned especially for this experiment.

The photography dates were 20th October 1998 and 28th October 2001. The aerial photographs were taken by W.H. Ekin (Engineering) Co. Ltd. Photographs were taken on Kodak Portra 400 Vivid Color using a Rolleimetric 6006 (medium format) with a Planar 2.8/80 mm lens. The target resolution was specified as 1:1.000 scale on 16" prints. This gave a flying height of approximately 500 m above ground level (AGL). As the elevation at the holding area in the middle of the study site on Strathfinella Hill is approximately 250 m above sea level, this meant a flying height of 750 m above sea level. Due to the scale of the photography it was difficult to accurately align the photography with the experimental site. As it was considered too dangerous to repeat the flying height used in 1998, the 2001 photography was done at approximately 1000 m above sea level. However, in order to compensate for this, the negatives were digitally scanned at a higher resolution than originally planned, thus maintaining the target resolution for the 2001 photography.

Weather conditions have a strong influence on the ability to classify aerial photographs successfully. Images should have a high level of brightness, but no strong shadows resulting from direct sunshine. Flying dates were thus selected for the presence of high altitude cloud cover (Figure 4.1).

The aerial photographs were digitally scanned from the original negatives by Peak Imaging Ltd. using a Flextight Precision II Scanner. The negatives were scanned for three bands (1=Red, 2=Green, 3=Blue) at a resolution of 3600 dpi (dots per inch). This scanning resolution is the maximum advised resolution for the type of film used (Kodak, pers. comm.). With a film size of 2¼ × 2¼ inch at 3600 dpi, the digital image size was approximately 7300 × 7300 pixels. Although the resulting maximum ground resolution was 0.0210 m and 0.0325 m for 1998 and 2001 respectively, the pixel size was set to 0.05 × 0.05 m. for all analyses.

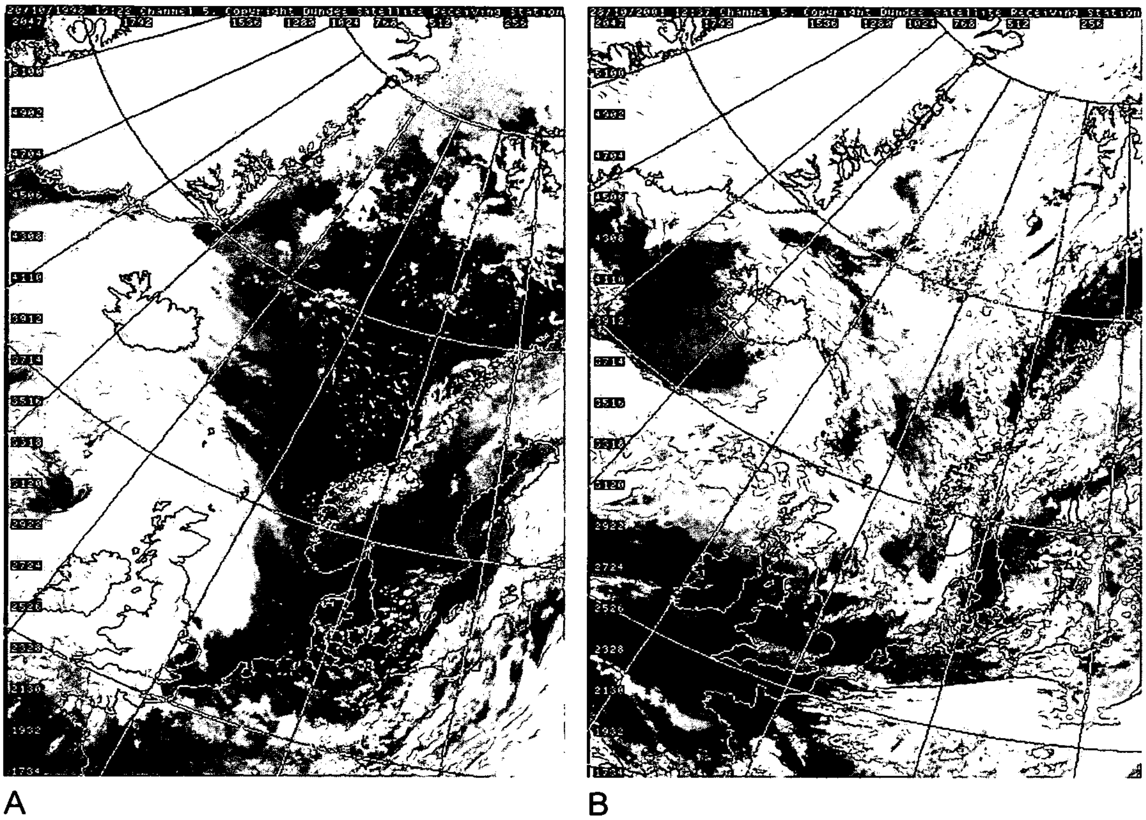


Figure 4.1. Weather satellite images (AVHRR) for photography dates on 20/10/1998 (A) and 28/10/2001 (B). Courtesy of Dundee Satellite Receiving Station, Dundee University, UK.

Due to the difference in flying height and altitude and because of the slope of the hill side (roughly 17°), to enable a comparison of the spatial pattern of the vegetation, the aerial photographs had to be ortho-rectified. Two air photos from the 1998 runs and four air photos from the 2001 runs were needed to enable this process. In order to rectify the aerial photographs to a common co-ordinate system, a set of ground control points was surveyed at the study site. Using a Wild T2a theodolite and DI4 Distomat, two orientation points and all corner fence posts were surveyed. For the purpose of this study, a local co-ordinate system was used based on the two orientation points, but using the projection of the Ordnance Survey National Grid. Using OrthoMAX (Vision International, USA; Version 8.3), a module available in Erdas Imagine (ERDAS Inc., USA; Version 8.3), these ground control points provided the reference data for the ortho-rectification of the aerial photographs. Table 4.1 shows the properties of the aerial photography resulting from the triangulation. The x, y, and z co-ordinates indicate the position of the camera relative to the co-ordinate system defined. The Omega-Phi-Kappa values indicate the roll, pitch and yaw of the camera in degrees. Comparison of these values for the two dates indicates that both the flight altitude and the yaw differ considerably. Table 4.2 shows the accuracy of the triangulation based on the ground control points for each axis both in metres and as the root mean square (RMS).

Table 4.1. Orientation of the aerial photographs relative to the co-ordinate system used (resulting from the triangulation of the ground control points). The x, y, and z co-ordinates indicate the position of the camera relative to the co-ordinate system defined. The Omega, Phi and Kappa values indicate, in degrees, the roll, pitch and yaw respectively.

Year	Photo	X	Y	Z	Omega	Phi	Kappa
1998	1	988.47	1024.78	516.74	-0.49	0.01	5.40
1998	2	994.54	1174.68	511.72	-0.90	-0.99	7.27
2001	1	953.99	759.27	735.19	-0.48	-2.38	-25.09
2001	2	975.20	907.46	741.23	-1.48	-2.74	-22.54
2001	3	997.06	1073.75	748.85	-0.72	-1.52	-18.93
2001	4	1000.88	1215.08	752.39	-0.77	0.08	-15.09

Table 4.2. Triangulation results for the ground control points. Average point residuals in metres and as the root mean square (RMS).

Axis	X	Y	Z
Average (m)	0.177	0.192	0.290
RMS	0.209	0.235	0.349

To facilitate the ortho-rectification process, a Digital Elevation Model (DEM) was created. The 2001 photography covered a larger ground area (i.e. each individual photograph covered a larger area), thus the DEM of the site was created using this set of imagery. Four air photos, i.e. three stereo pairs, provided the necessary stereo cover required for DEM collection. The DEM collection was done using OrthoMAX (see for detailed description Gooch et al., 1999; Gooch & Chandler, 2001). The DEM can be collected from any of the three colour bands (red, green, or blue). The aim of the DEM collection was to achieve the best possible match between years, through minimising the horizontal error in the ortho-photos. The DEM based on the green band showed the lowest variation in surface height, thus ensuring the minimum amount of horizontal error when ortho-rectifying the aerial photographs.

Although OrthoMAX provides several collection parameters, it is neither practical nor necessarily beneficial to vary all parameters (Gooch & Chandler, 2001). In order to improve DEM results, a conservative approach to the selection of parameter values was adopted, only varying the maximum parallax and the minimum and maximum template (Gooch et al., 1999). The resulting DEMs were then mosaiced together to form one DEM ('2001 DEM') covering the whole study site. The spatial resolution of the DEMs was one metre. A higher resolution would have been possible, but was not required for the purpose of ortho-rectifying the air photos.

The air photos of both years were ortho-rectified using the 2001 DEM, using the composite colour images of all three bands (red, green and blue). The ortho-photographs showed both systematic and variable misalignment. Because only the fence posts were suitable as control points, only the systematic misalignment was corrected. Thus, the 1998 ortho-photograph was geometrically corrected to correspond with the 2001 ortho-photograph. A first order polynomial transformation was applied using a set of control points based on the fence posts. With a minimum of three control points, a polynomial transformation produces a linear translation, scale change, and rotation for x and y co-ordinates. As a higher-order polynomial correction might overcorrect for areas away from the control points and because the variation was limited (based upon a visual evaluation), a first order polynomial correction was considered most appropriate. In addition, a two-metre wide band was clipped from the edge of each plot before further analysis to mask out the fences.

4.2.2 Classification

The aim of the classification was to derive a vegetation map of the heather-grass mosaic. The detection of vegetation change during the experiment was aimed at these two dominant vegetation types. However, it was anticipated that change in vegetation would be slow, therefore it was important to monitor the cover of mixed vegetation types considered indicative of a change-in-progress between the main vegetation types.

The ortho-photographs of 1998 and 2001 were characterised by a limited number of intimately mixed vegetation types with a large within-type variation in colour and intensity. The combination of the large within-type variation and the scale of the ortho-photographs, with each cell having an extent of 0.05 × 0.05 m, would require a very detailed ground survey. This was beyond the scope of this study. Therefore the ortho-photographs were classified using the unsupervised classification algorithm in Erdas Imagine.

The unsupervised classification within Erdas Imagine uses an isodata clustering method (Jensen, 1996). This iterative method allocates individual pixels to clusters based on their spectral characteristics, starting with arbitrary initial cluster means. After allocating all pixels to clusters, the means for the clusters are recalculated. In subsequent iterations, pixels are reallocated based on new cluster means, until a pre-set proportion (in this case 95%) of the pixels remain in their assigned cluster from one iteration to the next. Using a fully automated classification approach avoids all the errors associated with traditional manual classification of images (Green & Hartley, 2000). The classification was based on all three colour layers in the ortho-photograph and was set to distinguish 15 classes (i.e. clusters). To facilitate the classification, only the actual experimental plots were classified (also masking out the fences). Classification was done separately for 1998 and 2001.

The unsupervised classification creates classes starting with the lowest spectral values in the image (i.e. the darkest elements). Thus, the first class coincided with the black crosshairs originating from the metric camera lens. Classes 2 to 11 coincided with heather on the ortho-image. Lower classes generally covered heather away from grass patches, while higher classes were near to grass patches. The distribution of heather classes varied strongly between plots and locations within plots, both as a result of differences in photography and possibly differences in heather canopy characteristics. Two classes were associated with the zone around the grass-heather boundary: one adjacent to the heather (Class 12), the other adjacent to the grass patches (Class 13). Two classes coincided with the grass in the ortho-image (Class 14 and 15). Differences between these two classes appeared to coincide with grass sward height and was most obvious in the 1998 photography.

The results of the classification for 1998 and 2001 were visually consistent, with the same classes indicating the same vegetation type in both years. For each year, the 15 resulting classes were then grouped based upon a visual interpretation of the ortho-photographs and observations in the field. Following structural differences in vegetation composition or life history, four grouped classes were defined as: *grass*, *mixed*, *degraded heather*, and *shrub*. The *grass* class was formed from the two original classes coinciding with short and tall grass swards dominated by *Agrostis capillaris* L., *Agrostis canina* L., *Deschampsia flexuosa* L. Trin., and *Festuca ovina* L (NVC= U4; Rodwell, 1992). The *mixed* class was formed from a single class coinciding with mixed vegetation types bordering the *grass* class. The *degraded heather* class, dominated by *Calluna vulgaris* (L.) Hull (heather), was also based on a single class and was associated strongly with heather in the degenerate phase (Watt, 1947). This class was characterised by a partly dead heather canopy with low cover and little undergrowth and generally occurred at the edge of the *shrub* class. The *shrub* class was formed from 10 original classes all dominated by the shrubs *Calluna vulgaris* and/or *Vaccinium myrtillus* L. (blaeberry) (NVC= H12; Rodwell, 1991). There were indications that some of the 10 original classes were associated with either blaeberry or heather. Only an extensive ground survey would provide an accurate basis upon which to split the classes, but this was beyond the scope of this study. Although the blaeberry was much lower in total area cover compared to heather, observations in the field showed that it did occur more frequently at the edge of the *shrub* class, neighbouring the grass patches. Thus, the *mixed* class consisted predominantly of a mixture of grass and blaeberry as opposed to a mixture of grass and heather.

The classification results showed a strong 'salt and pepper effect' (Lillesand & Kiefer, 1999) for the *shrub* class. This effect, which is characterised by single pixels or small clumps of one class interspersed within large areas of another class, can result from high spectral variability in the original imagery. A possible cause of this spectral variability is the alternation of brightly lit and shadow areas in the shrub canopy (Quilter & Anderson, 2001). Because the presence of many individual pixels or small clumps is undesirable in this analysis, a post-classification image smoothing (Lillesand & Kiefer, 1999) was applied using the majority filter function in the ARC GRID module available in ArcInfo (ESRI, USA; Version 8). The majority filter scans the image with a fixed window size (in this case 3 by 3 pixels). The class of the central cell in the window is changed to the class with the majority in the window, but if there is no majority the cell stays unchanged. The smoothing reduces the number of single pixels and decreases roughness of edges. Majority filters are often applied several times, depending upon the characteristics of the classification. As the filter generally leads to a decrease of minority classes, increasing the cover of the dominating class (in this case heather), it should be applied with care. A satisfactory reduction of the 'salt and pepper effect' was achieved by applying the majority filter twice. Table 4.3 shows the changes in cover of the four classes for 1998, with changes for 2001 being of the same order.

Table 4.3. Changes in the percentages of cells in each class (for 1998) in relation to application of the majority filter: before and after the first application, after the second application and after the elimination of the crosshairs.

Name	Before	Majority 1	Majority 2	After
Grass	10.76	10.86	10.89	10.98
Mixed	3.45	3.28	3.20	3.17
Degraded heather	3.33	2.50	2.23	2.12
Shrub	80.38	81.92	82.46	83.74
Cross hairs	2.08	1.44	1.21	0.00

4.2.3 Animal observations

In the summer of 2001, a secondary experiment was carried out on the experimental site to study the social behaviour of sheep on natural heather-grass mosaics (A.M. Sibbald, personal communication, July 2001). This study made use of the existing sheep density treatments and grazing schedule and thus did not interfere with the primary experiment. I contributed to this experiment, during a four month suspension of my PhD, in the design, planning, execution and geographical analysis of the data. Although not an official part of this PhD, the data obtained from this experiment provided an excellent opportunity to gain insight into the behaviour of the sheep in relation to the vegetation mosaic.

During the experiment six sheep were present on each plot. Animal behaviour on the experimental plots was observed from a position facing the hill side, at a distance of roughly 500 m. Scan samples (Martin & Bateson, 1986) were taken over an 11 day period in June for each sheep in each plot, with 25 scan samples each day (07:30 to 21:30 hours). During a scan sample the location and orientation were marked on a vegetation map and the activity was noted. Such scan samples provide a basis for determining time budgets of behaviour and, combined with the spatial location, they enable analysis of the spatial pattern of behaviour. The locations were subsequently digitised using ArcView (ESRI, USA; Version 3.2). The following activities were distinguished: drinking, grazing, lying, standing, and walking.

4.2.4 Analysis

Four approaches have been used to provide insights into the changes in the pattern of vegetation as a result of herbivory. The first approach considers each individual cell in the 1998 classification and its successor in the 2001 classification. A pair-wise comparison gives a quantitative but non-spatial insight into the change between classifications. The second method calculates changes in the total area of each class within each plot. In the third approach a grid overlay is used to sample individual cells to allow for an analysis at a larger scale. The final approach uses the grass patches as a functional description of the spatial heterogeneity and the analysis aims to link herbivore impact to vegetation response based on the functional heterogeneity. Grass patches are an appropriate description of the vegetation mosaic as sheep tend to focus their behaviour on patches (Hester & Baillie, 1998).

The pair-wise comparison was done on the individual pixels in both classifications. The grid overlay was done using a grid with a 2 m cell size. Changes in vegetation between years were based on cell counts and not on actual area. To facilitate the analysis based on the functional heterogeneity, individual grass patches had to be derived from the classifications and because several grass patches were connected by pathways, they had to be divided manually.

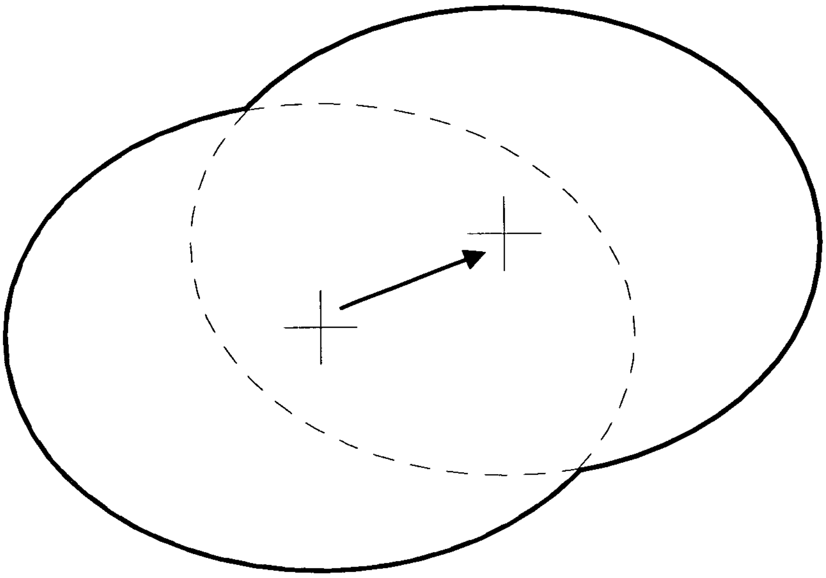


Figure 4.2. Illustration of the effect of misalignment on the extent of overlap of one patch in the two years. The arrow indicates the shift between years. The union patch used for sampling is indicated by the thick line.

As described in the previous section, a variable misalignment between the two years remained after ortho-rectification and geometric correction. To overcome the problem of misalignment of patches, a 'union patch' was created for each *grass-mixed* patch in the mosaic, covering the combined area of the patch in both years (Figure 4.2). This union patch was then used to calculate the area of each class within the patch in each year. Because the union patch was bigger than the patch in one year, the sample could also include a proportion of the *shrub* or *degenerate heather* class. The patch analysis was based on actual area of the patch (taking slope into account) instead of on cell count. This was necessary because, contrary to claims by Lillesand & Kiefer (1999), ortho-photographs do not give true area in sloping terrain.

4.3 Results

Cell-based analysis

The pair-wise cell-based analysis resulted in the transition matrix shown in Table 4.4. The transition matrix shows the total cell-by-cell changes from one class to another across all blocks and treatments. Overall changes indicate a decline of the *shrub* class (1.6%), and increases in the *mixed* (35.6%) and *degraded heather* (9.4%) classes. Large changes occurred from the *shrub* to *mixed* class, from the *shrub* to *degraded heather* and from the *mixed* to *shrub* class. The total area of the *grass* class remained unchanged during the experiment.

Table 4.4. Pair-wise cell-based changes (%) from class to class (*grass, mixed, degraded heather, shrub*) between 1998 and 2001 (1% ≅ 600 m^2).

Year		2001				
		Grass	Mixed	Degraded	Shrub	Total 1998
1998	Grass	8.61	1.17	0.16	1.04	10.98
	Mixed	0.90	0.73	0.13	1.41	3.17
	Degraded	0.44	0.44	0.14	1.10	2.12
	Shrub	1.04	1.95	1.89	78.86	83.74
	Total 2001	10.98	4.30	2.32	82.40	100.00

The transition matrix indicates net change and thus provides no insight into local increases and decreases in classes. Because the two classifications were not exactly spatially registered, a cell-by-cell comparison should be interpreted with caution. For instance the changes from *shrub* to *mixed* and *mixed* to *shrub* from 1998 to 2001 could be the result of the misalignment between ortho-images. These data are based on cell counts and not on actual area. The study site was on a convex slope, such that the plan area of cells varied with the slope of the cell. These statistics are for all plots, covering approximately six hectares, so one percent is roughly equal to 600 m^2.

Although the pair-wise comparison showed a constant area of *grass* and a decreasing area of *shrub*, when switching to the total cover of each class based on true area per plot (i.e. per treatment within each block), results show large differences between plots (Table 4.5). Due to the characteristics of the vegetation mosaics at the time of fencing and the grazing treatments of previous experiments, initial cover of classes varied strongly between plots (Table 4.5). *Grass* class cover ranged from 3% to 18% and the *degraded heather* cover ranged from 0.5% to 4.7%. Initial conditions strongly influenced the impact of the sheep density treatments. For example plot T4 was characterised by a strongly fragmented heather cover of generally visually poor quality. The combination of the initial state of the vegetation and the sheep density treatment led to a strong increase in the *mixed* class at the cost of the *shrub* class. In contrast, plot B4, characterised by a visually more vigorous heather cover, showed a slight increase of the *shrub* class. To better understand the causes of differential changes within each plot, a more spatially explicit analysis was pursued.

Table 4.5. Percentage cover of each class (*grass, mixed, degraded heather, shrub*) in 1998 and the absolute change in percentage cover of each class between 1998 and 2001. Data are presented per sheep density treatment (2, 3, 4 sheep ha^{-1}) within each block (bottom, top) indicated by codes B2, B3, B4, T2, T3, T4.

Plot	Class cover in 1998 (%)				Class change (%)			
	Grass	Mixed	Degraded	Shrub	Grass	Mixed	Degraded	Shrub
B2	7.65	1.65	0.97	89.74	-1.71	0.86	1.17	-0.32
B3	8.98	1.44	1.70	87.88	-0.92	1.42	0.44	-0.93
B4	18.50	4.30	2.77	74.44	-0.85	-0.02	-1.23	2.10
T2	3.12	2.62	0.53	93.72	-0.19	-0.65	0.07	0.78
T3	14.11	4.96	1.23	79.70	1.19	-0.63	1.02	-1.57
T4	13.16	3.53	4.71	78.61	2.12	6.12	0.88	-9.12
Total	10.92	3.08	1.98	84.01	-0.38	7.09	2.35	-9.07

Grid-based analysis

Sampling the classifications with a lower resolution grid (2 m) provided a spatially explicit insight into the local changes in the vegetation (Figure 4.3). Maps per class present the percentage change of the cover of a class within each cell between 1998 and 2001. This map does not correct for the variable misalignment, such that changes between years might result from shifts in the imagery. The maps show that herbivore impact was strongly heterogeneous, with small changes (< 10%) spread evenly around the mosaic and large changes limited to small areas. Returning to the example of plot T4, the maps show that the changes from the *shrub* class to the *mixed* class occurred mainly in two areas of the plot. To investigate the processes causing the changes and to filter out the possible effects of misalignment, the functional heterogeneity of the change between classes needed to be considered.

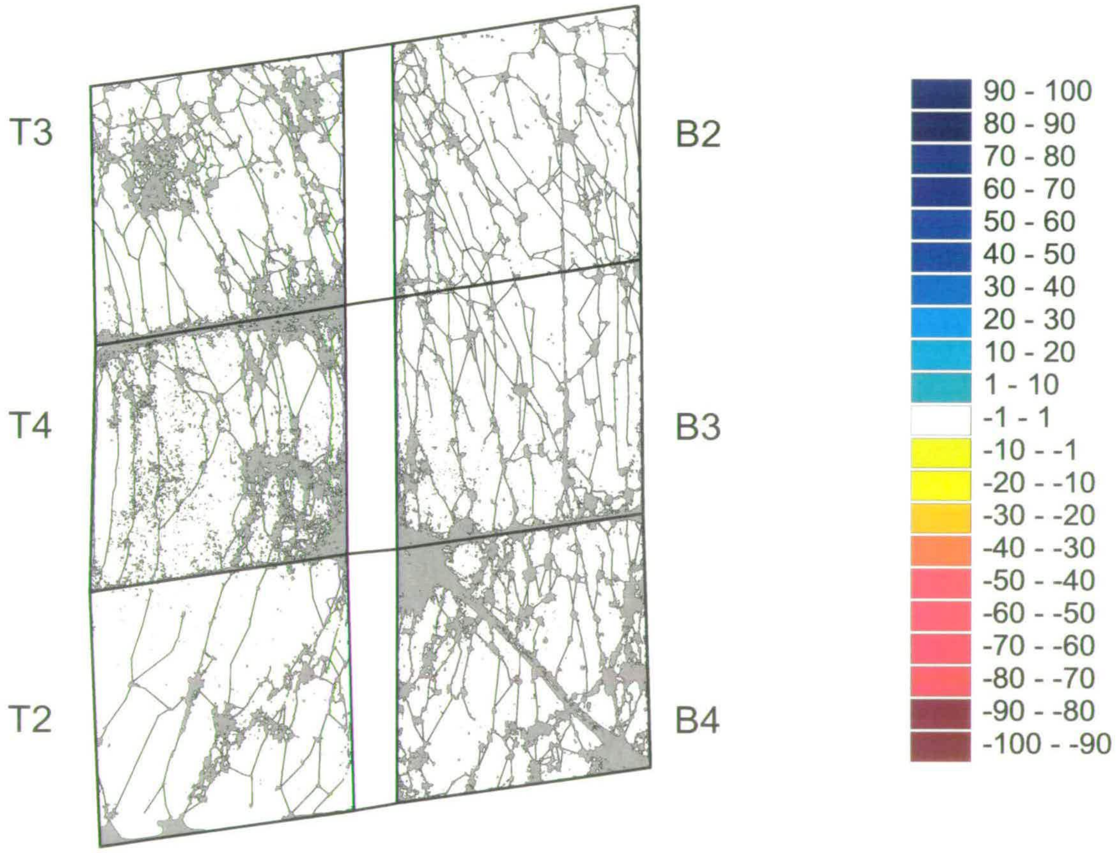
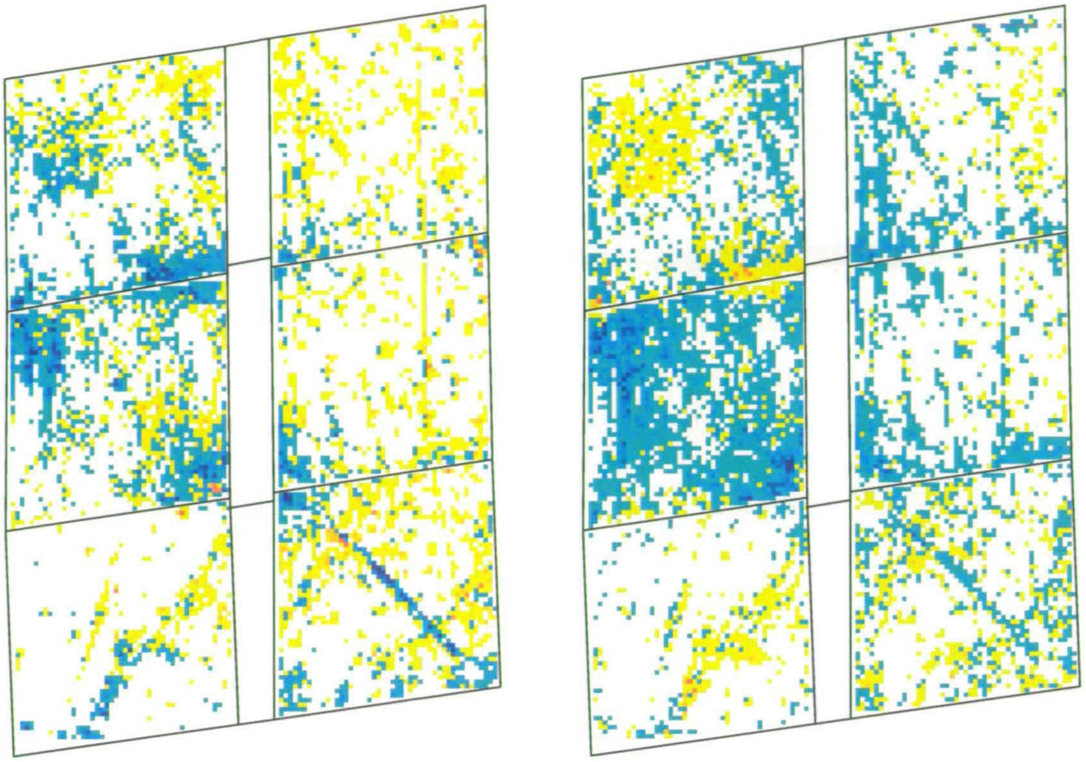
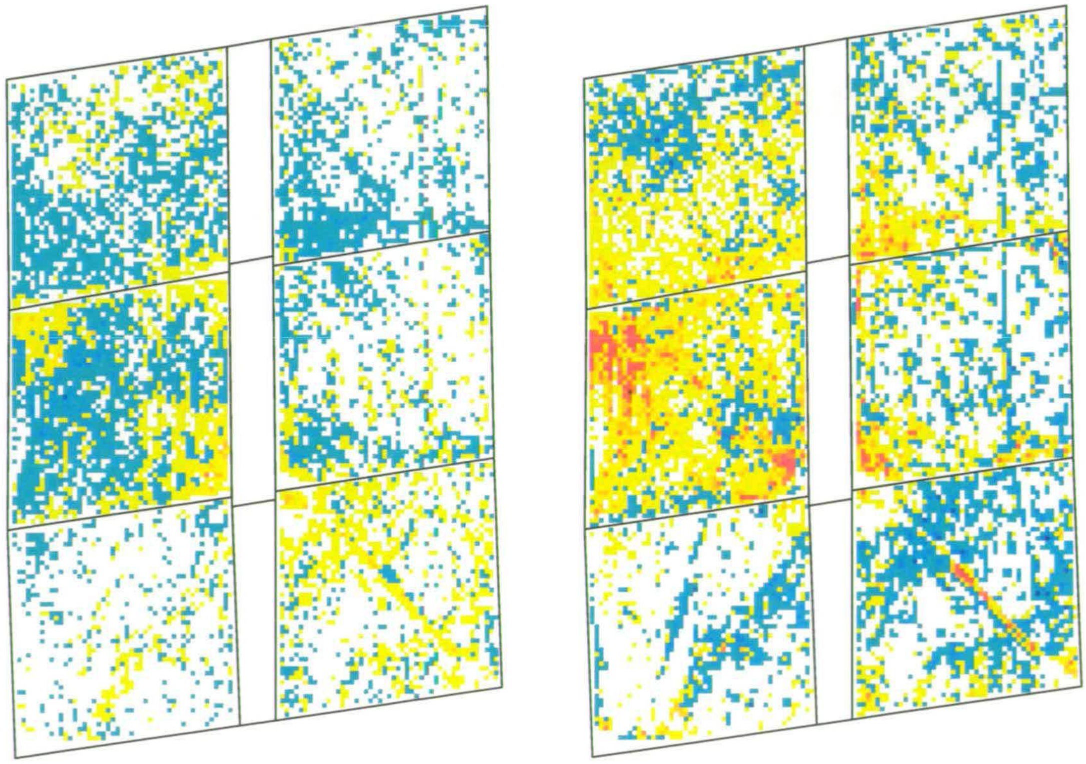


Figure 4.3 (Opposite page). Maps showing the change in the percentage of each class within 2 m grid cells between 1998 and 2001; (A) *grass*, (B) *mixed*, (C) *degraded heather*, (D) *shrub*. The underlying vegetation map is shown above for reference, together with the legend of the percentage change.



A. Grass

B. Mixed



C. Degraded heather

D. Shrub

Patch-based analysis

The functional heterogeneity was described by the grass patch structure of the vegetation mosaics. The grass patches within the mosaic provided a link between the vegetation changes of the grass patches and the observations of animal behaviour and heather defoliation on and around these patches. Patches were sampled using the union patch as described in the methods section. For each union patch, the percentage of each vegetation class in each year was determined and the change in percentage from 1998 to 2001 calculated. The data suggested that large clumped changes were associated with ruminating behaviour, while smaller wide spread changes were associated with heather defoliation.

Changes associated with ruminating behaviour

The behavioural study of the sheep foraging the plots in 2001 resulted in 8678 combined observations of location and behaviour. Data show that sheep spent the majority (95%) of their time either grazing (69%) or lying (26%). The remaining time (5%) was spent walking (2%), standing (3%) or drinking (0.06%). For the purpose of this analysis foraging was defined as the activities grazing and walking, while lying was defined as ruminating. Standing could be interpreted as either foraging or ruminating and was thus not included in the analysis. Drinking was rarely observed and thus was not expected to affect the pattern of foraging. The map of observations (Figure 4.4) shows that the distribution of ruminating behaviour was clumped.

To estimate the effect of the clumped distribution of ruminating activities on the changes in the vegetation pattern, all grass patches (*grass* class) were classified into ruminating or non-ruminating patches such that ruminating patches were defined as those patches where the percentage of observations of ruminating activity exceeded 30% (i.e. higher than the average of 26% across the plots). The areas of grass patches classified as ruminating patches were 20% and 24% of the total grass area in 1998 and 2001 respectively. The data showed that the ruminating areas were strongly associated with an increase in both the *grass* and *mixed* classes. While the total net *grass* cover across all plots decreased by 113 m^2 (with 1141 m^2 of the total area affected by change from and to *grass*), the area of *grass* in the ruminating areas increased by 211 m^2. Of the total amount of transitions from and to *grass* during the three years, 19% was associated with the ruminating areas. However, of the total amount of transitions to grass, 41% was associated with the ruminating areas.

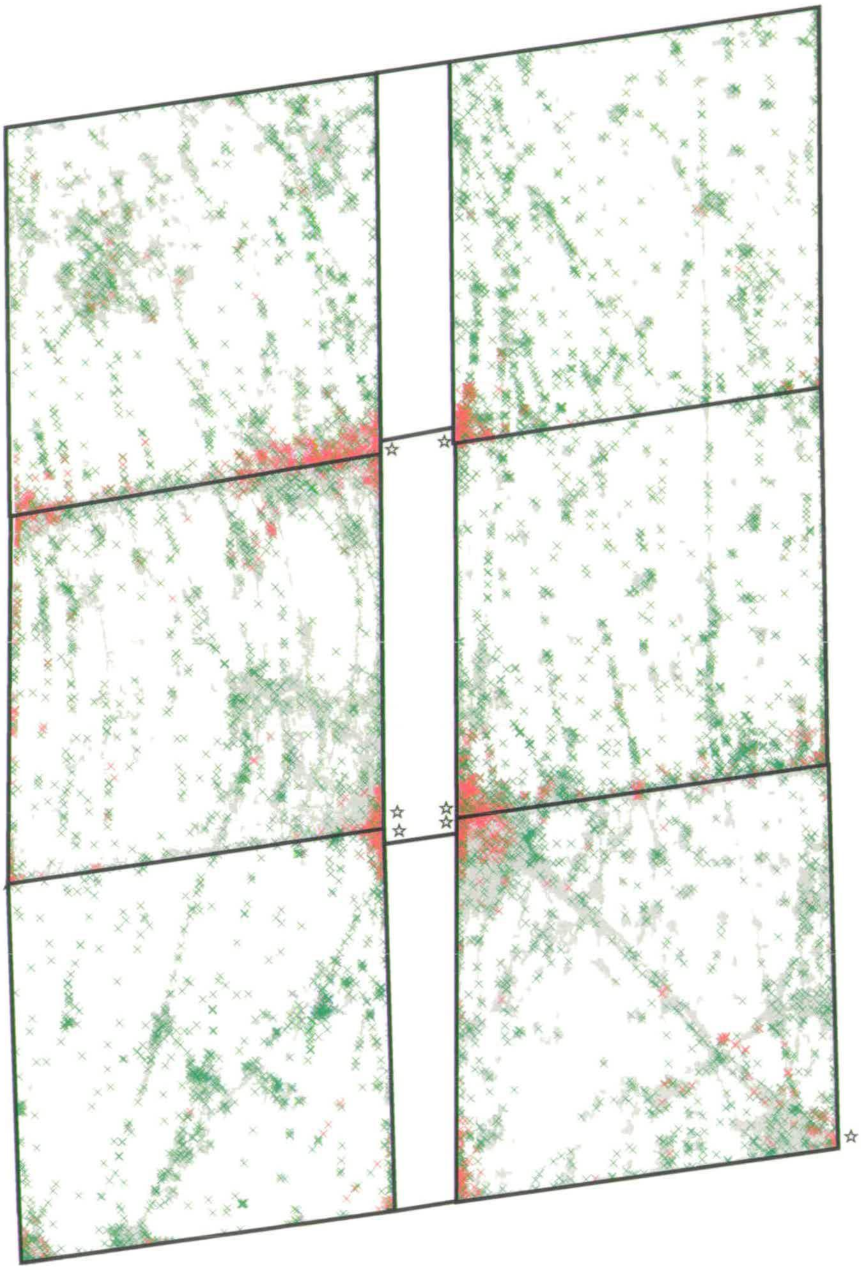


Figure 4.4. Map of observations of sheep behaviour. Each cross is an individual observation. Colours of crosses indicate the observed activity: red = lying, green = all others. Stars indicate gate entrances to the plots.

Table 4.6 shows that the changes associated with ruminating areas varied between plots. Plot T4 shows a strong increase in the *grass* and *mixed* classes. This is likely to be a result of an interaction between ruminating behaviour and the degenerate growth phase of the heather (note the percentage cover of the degraded heather class of 5% for this plot in 1998, Table 4.5). The vegetation changes in this plot were generally characterised by a sequence of changes from *shrub* to *mixed* to *grass*, thus explaining the high percentage change to *grass* and *mixed* for the plot as a whole. In contrast, Plot B4 showed an increase in *grass* for the ruminating areas, but a decrease in *grass* for the plot as a whole.

Table 4.6. Percentage change in the cover of the *grass* and *mixed* classes for ruminating areas and for the whole plot. The data only take into account patches that existed both in 1998 and in 2001.

Plot	Grass (%)		Mixed (%)	
	Ruminating	Plot	Ruminating	Plot
B2	0.07	-1.46	0.19	1.69
B3	0.20	-0.82	0.24	1.52
B4	0.32	-0.68	-0.24	-1.15
T2	0.06	-0.14	0.01	-0.50
T3	0.14	0.34	-0.06	0.66
T4	1.32	1.63	1.26	5.76
Total	2.11	-1.13	1.39	7.96

Changes associated with heather defoliation

While large vegetation changes occurred in the areas associated with ruminating behaviour, smaller changes occurred across all plots without there being any pattern apparent from the map output from the grid sampling (Figure 4.3). To investigate small changes across the plots, the change in the percentage of each vegetation class per patch were correlated with the heather defoliation measurements (as described in Chapter 3). The angular transformed heather defoliation measurements for each transect were averaged across all years and seasons, for all distances less or equal to 0.5 m from the grass-heather boundary.

Figure 4.5 shows the relationship between heather defoliation and percentage change for all four vegetation classes. All grass patches for which heather defoliation data were available are included in the figures (n = 137). Regression lines have been added when slope was significantly different from zero ($p < 0.05$), with a dashed line indicating a trend. Note that the mixed and degraded classes generally covered a smaller percentage of the region, producing smaller changes and a lower variance around the regression line. The scatter plots show the change in the percentage of each class within each patch from 1998 and 2001. Both scatter plots and regression analysis show that change in the *mixed* class was positively correlated with heather defoliation, while change in the *shrub* class was negatively correlated with heather defoliation, i.e. increasing heather defoliation generally led to an increase in the *mixed* class at the cost of a decrease in the *shrub* class. The decrease in the *shrub* class seems to be compensated also by an increase in the *grass* class. However, the slope of the regression was not significantly different from zero in the latter case.

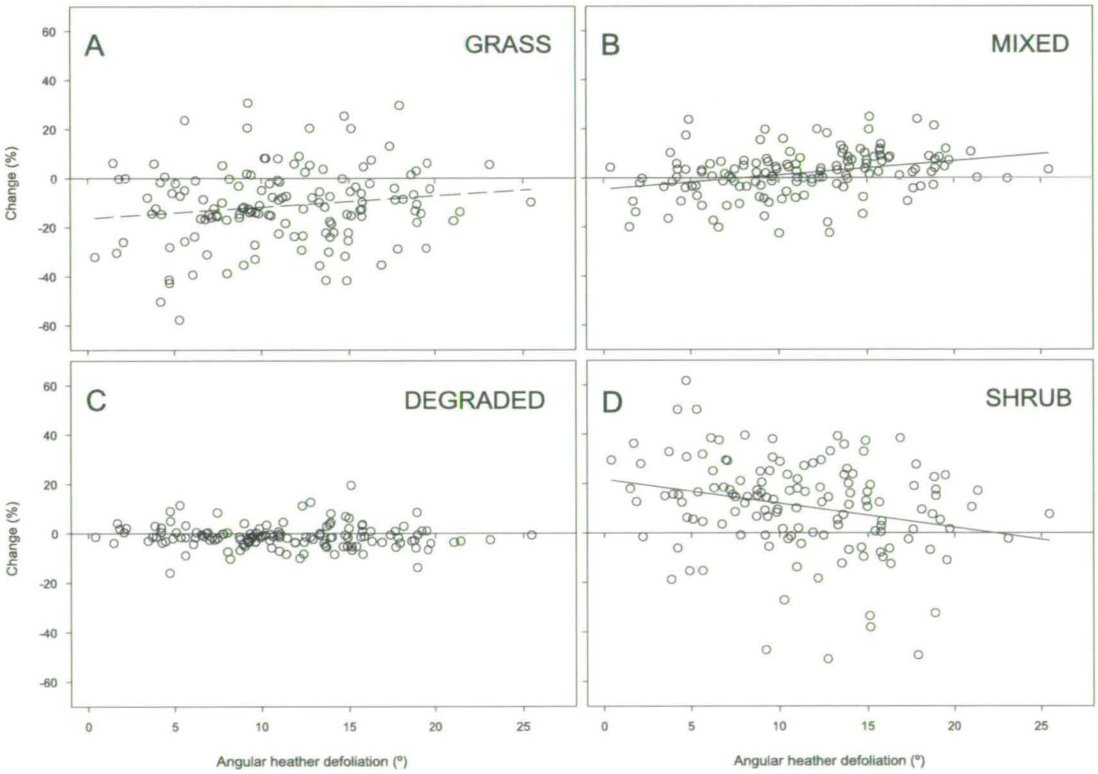


Figure 4.5. Scatter plots and corresponding regression lines (dashed if $p > 0.05$) showing change in the percentage cover of classes in the patches (n=137) between 1998 and 2001 versus mean angular heather defoliation for a 0.5 m zone away from the grass-heather boundary: (A) *grass* (R^2 = 1.1%, p = 0.115), (B) *mixed* (R^2 = 8.9%, $p < 0.001$), (C) *degraded heather* (not significant), (D) *shrub* (R^2 = 5.2%, p = 0.004).

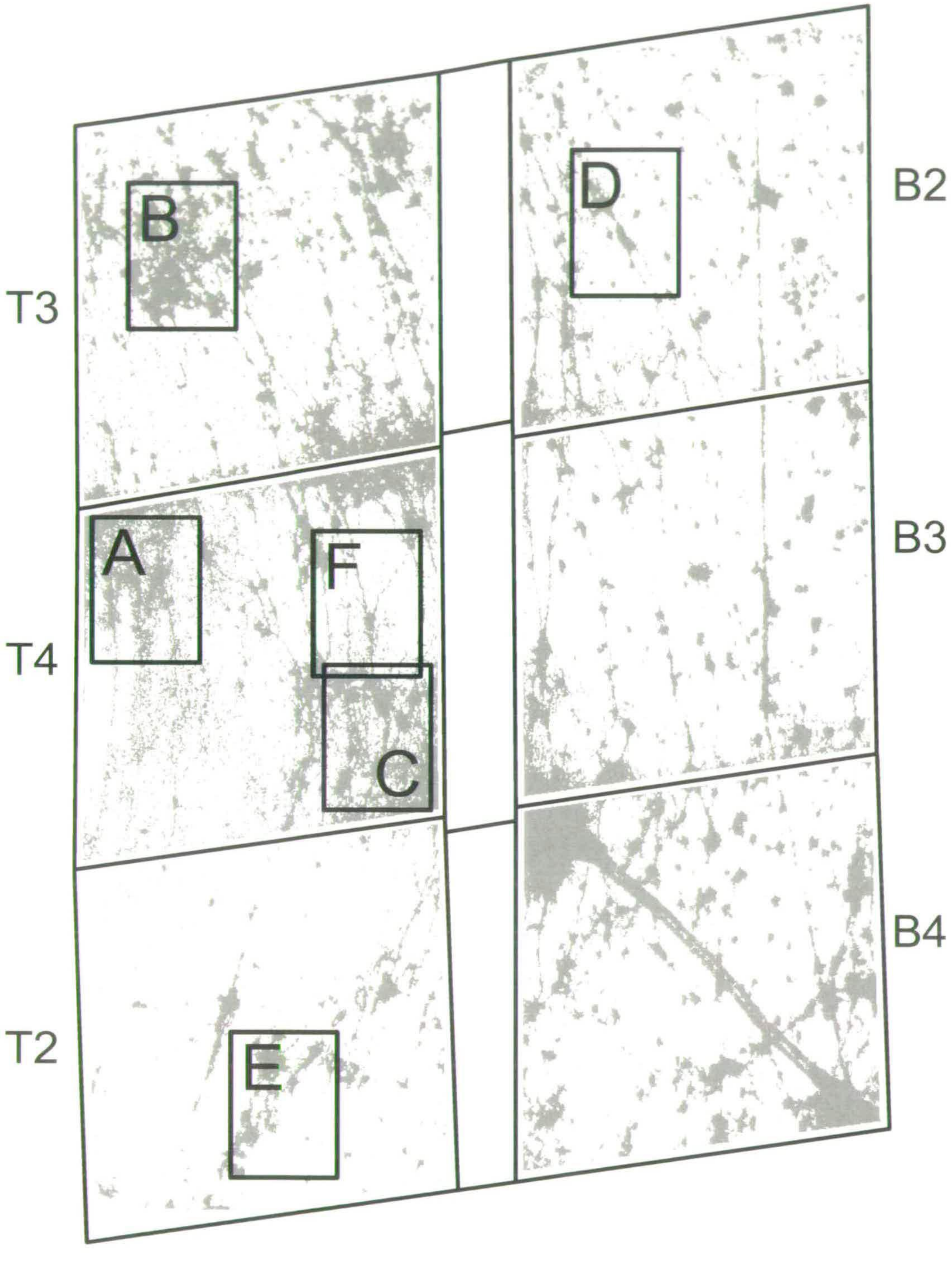


Figure 4.6. Map of the grass patch structure on the experimental plots; highlighted are the areas that are shown in the following figures: (A) Figure 4.7a, (B) Figure 4.7b, (C) Figure 4.7c, (D) Figure 4.7d, (E) Figure 4.7e, (F) Figure 4.7f.

Graphical examples of changes in pattern of vegetation

Although the experimental design did not allow further quantitative analysis, considering specific areas in the experimental site in greater detail revealed interesting changes in pattern. For several example areas (see Figure 4.6 for an overview) the changes in vegetation pattern and possible processes are hypothesised. Further experimentation would be required to test these hypotheses. Vegetation changes are illustrated for key patches in the example areas (Table 4.7).

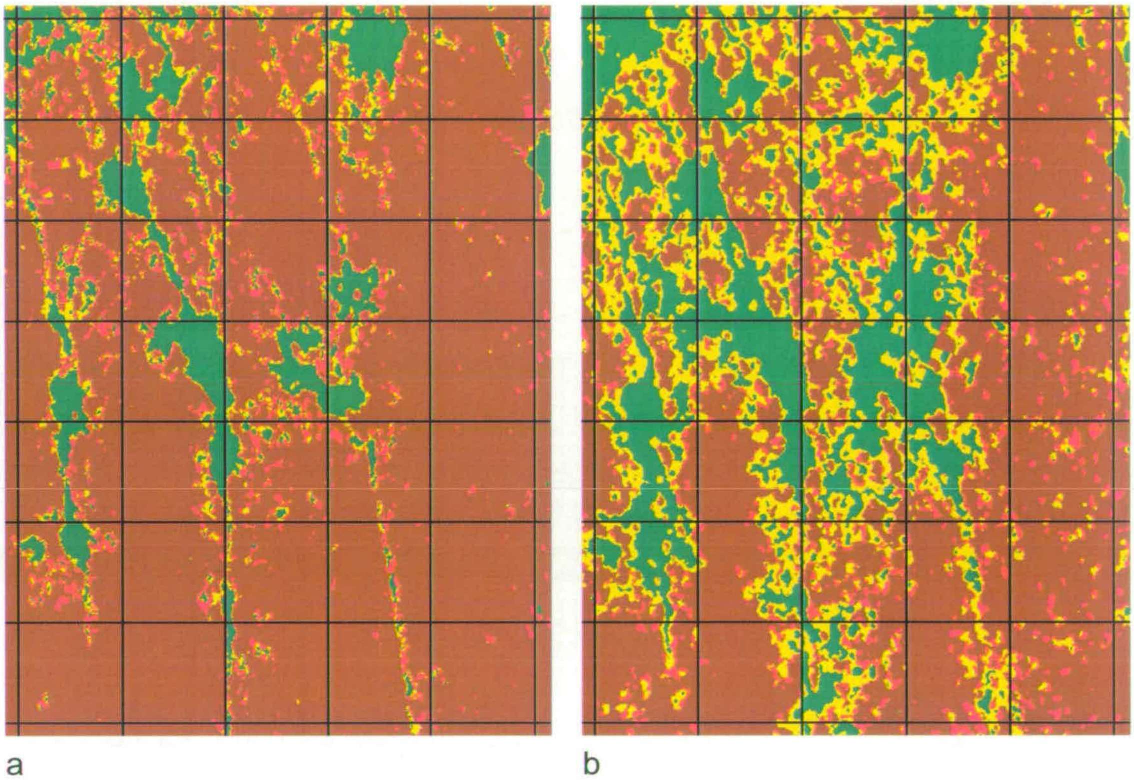


Figure 4.7a. Example area of part of the vegetation mosaic in plot T4, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*; brown = *shrub*.

The first example (Figure 4.7a) shows a strongly expanding grass patch. Expansion of the patch, as indicated by the change in percentages of classes in the union patch between 1998 and 2001, resulted from increases in the *grass* and *mixed* classes at the cost of the *degraded heather* and *shrub* classes (Table 4.7). The heather in this area was generally in the degenerate growth phase (Watt, 1947), which is indicated by the large amount of *degraded heather* (red coloured patches within the brown heather matrix) within the *shrub* class (Figure 4.7a). The heather was moderately grazed. Considering the life history (growth phase) and the proximity of a ruminating area, it is hypothesised that trampling, and not defoliation, has driven the change in this area. The increase in the *degraded heather* within the *shrub* class between 1998 and 2001 (Figure 4.7a) indicates that, under the current grazing pressure, the fragmentation of the heather will continue.

Table 4.7. Angular heather defoliation and changes in the percentage of classes in the patches in the enlargements.

Example	Plot	Defoliation (°)	Grass (%)	Mixed (%)	Degraded heather (%)	Shrub (%)
A	T4	15.13	20.25	24.85	-6.86	-38.24
B	T3	10.18	8.11	-8.80	-0.83	1.53
B	T3	10.93	-0.87	-8.26	-0.85	9.97
D	B2	9.83	-14.50	4.43	1.89	8.18
E	T2	9.19	20.54	-15.75	-3.74	-1.05
E	T2	9.16	1.75	-8.48	-2.25	8.99
F	T4	14.62	-0.27	11.66	-5.39	-6.01

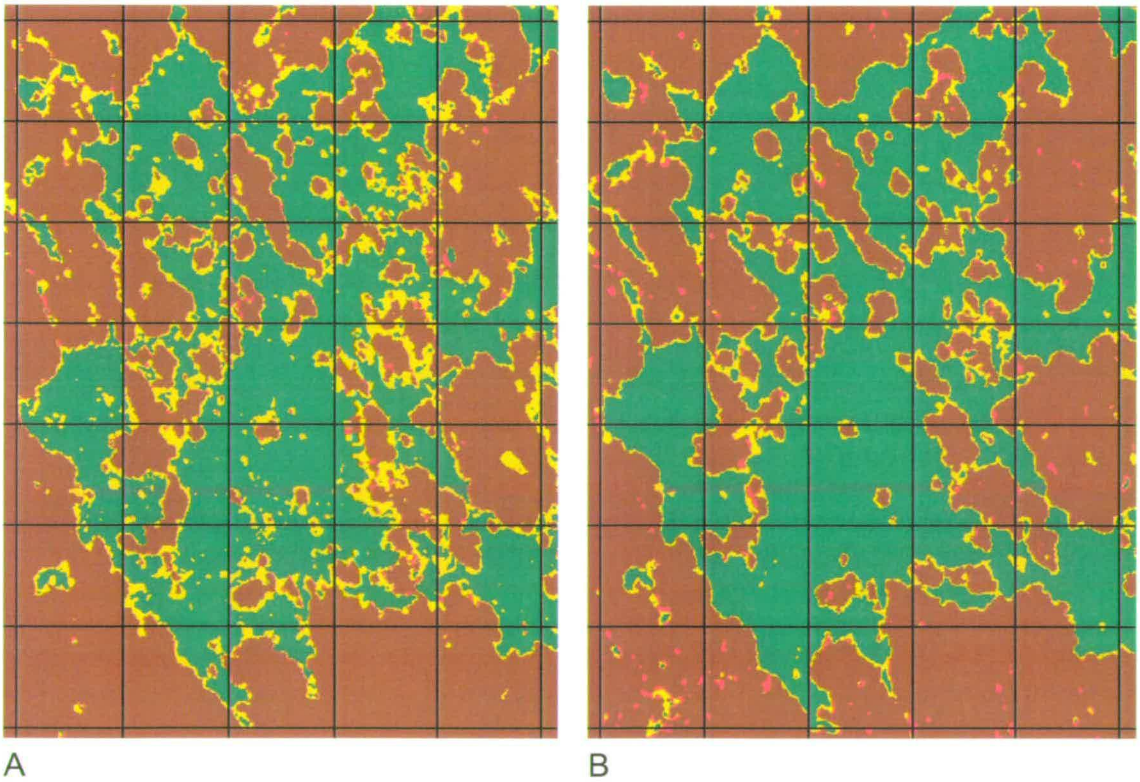


Figure 4.7b. Example area of part of the vegetation mosaic in plot T3, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*; brown = *shrub*.

The second example shows a mosaic that is stabilising (Figure 4.7b). Data for two patches have been included (Table 4.7) to illustrate that in this area both *grass* and *shrub* classes increased as a result of a decline in the *mixed* class. Both the *shrub* and *grass* became more homogeneous and, with the decrease of the extent of the *mixed* class, the contrast between the two vegetation types increased. This process presumably would lead to the disappearance of small patches (of both *grass* and *shrub*) and the consolidation of large grass patches.

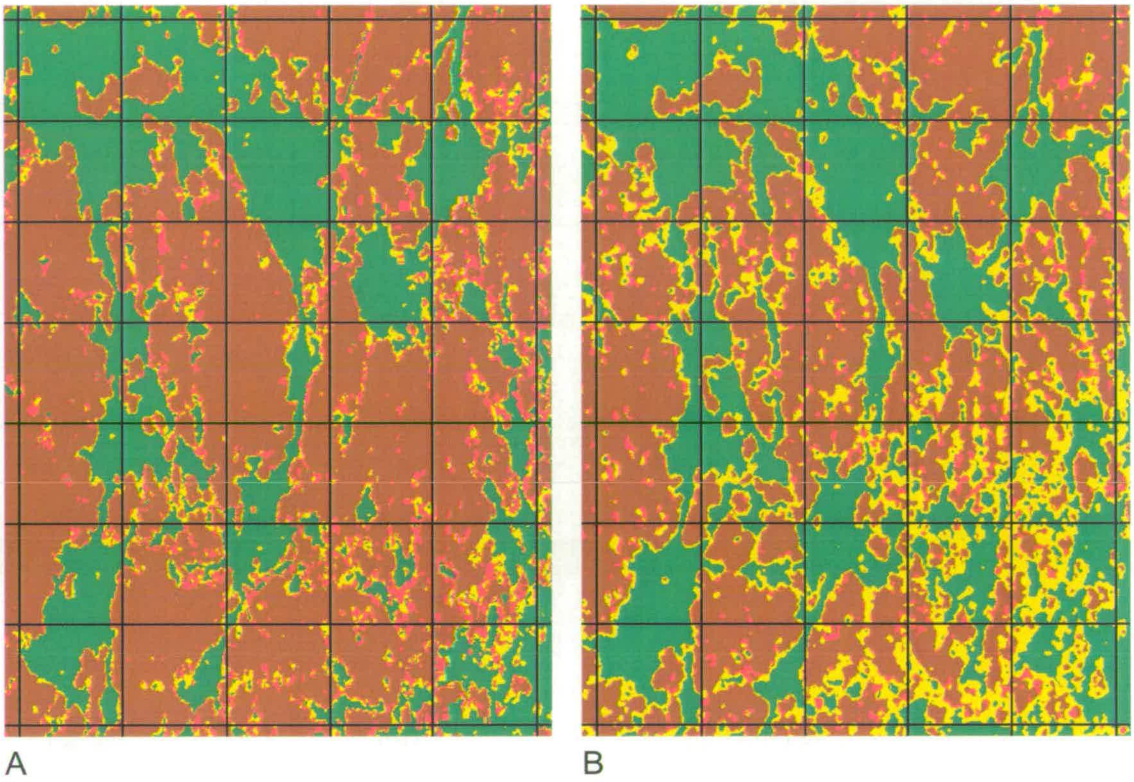


Figure 4.7c. Example area of part of the vegetation mosaic in plot T4, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*; brown = *shrub*.

The third example illustrates the effect of ruminating behaviour (Figure 4.7c). This area also has a history of ruminating impact (particularly due to red deer) as measured in previous experiments (Hester & Baillie, 1998). The sheep continued to use the area for ruminating during the current experiment. The core areas of *grass* thus expanded, but at the edges blaeberry became dominant in areas where heather had been killed. Thus, the cover of both the *grass* and *mixed* classes increased as the *shrub* class declined. Existing *degraded heather* largely disappeared as a result of the expansion of the grass patch but new patches of *degraded heather* appeared within the *shrub* class, possibly indicating continued fragmentation under the current stocking rate. The increase in the *mixed* class (with a large proportion of blaeberry), could again indicate that an interaction between the life history of the heather and trampling has driven changes in this area. If defoliation impact had been high, blaeberry would not have been expected to increase so strongly.

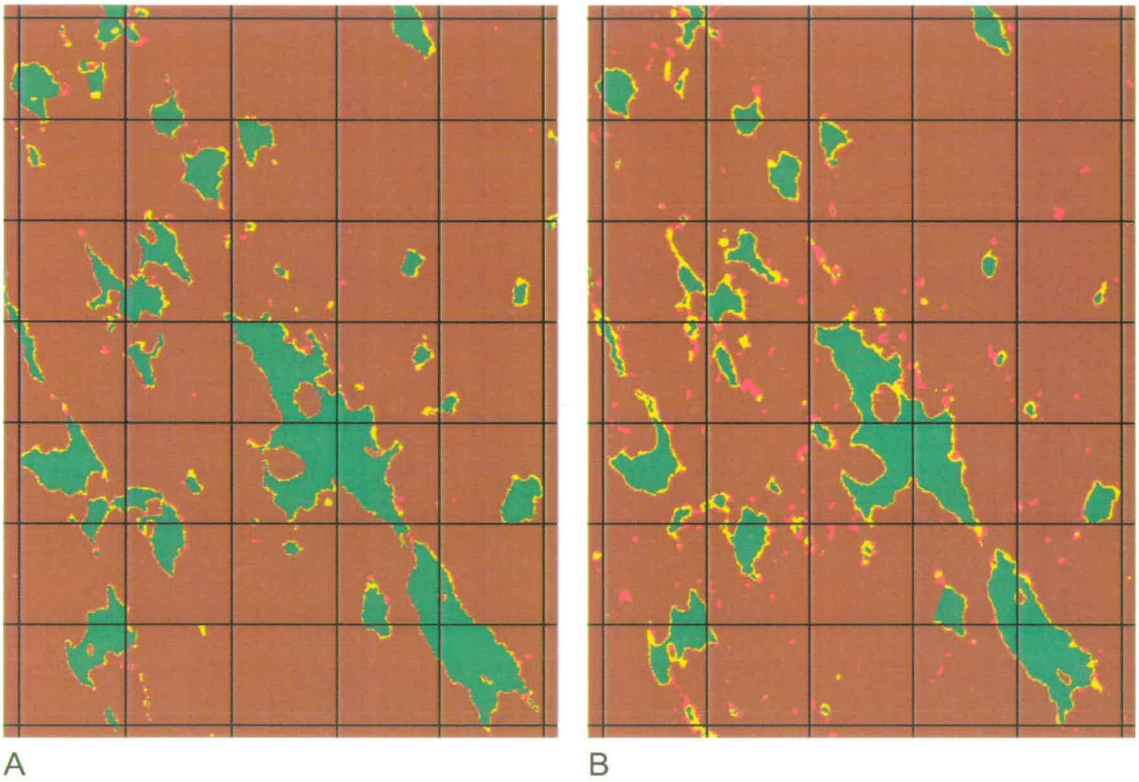


Figure 4.7d. Example area of part of the vegetation mosaic in plot B2, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*; brown = *shrub*.

The fourth example (Figure 4.7d) shows an area where the shrubs were apparently recovering from previous heavier herbivore impact as compared to the current stocking rate (2 sheep ha^{-1}). This area is characterised by the absence of blaeberry, thus the increase in the *shrub* class is only associated with heather increase. The heather is recovering at the cost of the *grass* class, generally causing large grass patches to get smaller and small grass patches to disappear. From field observations, most heather recovery seemed to be the result of increased plant size and rerooting of collapsed branches. There was little sign of new heather shoots appearing in the grass sward. The expanding heather led to smoother edges, but the increase in the *mixed* class led to lower contrast. At the current treatment, the heather in this area would presumably continue to expand at the cost of grass.

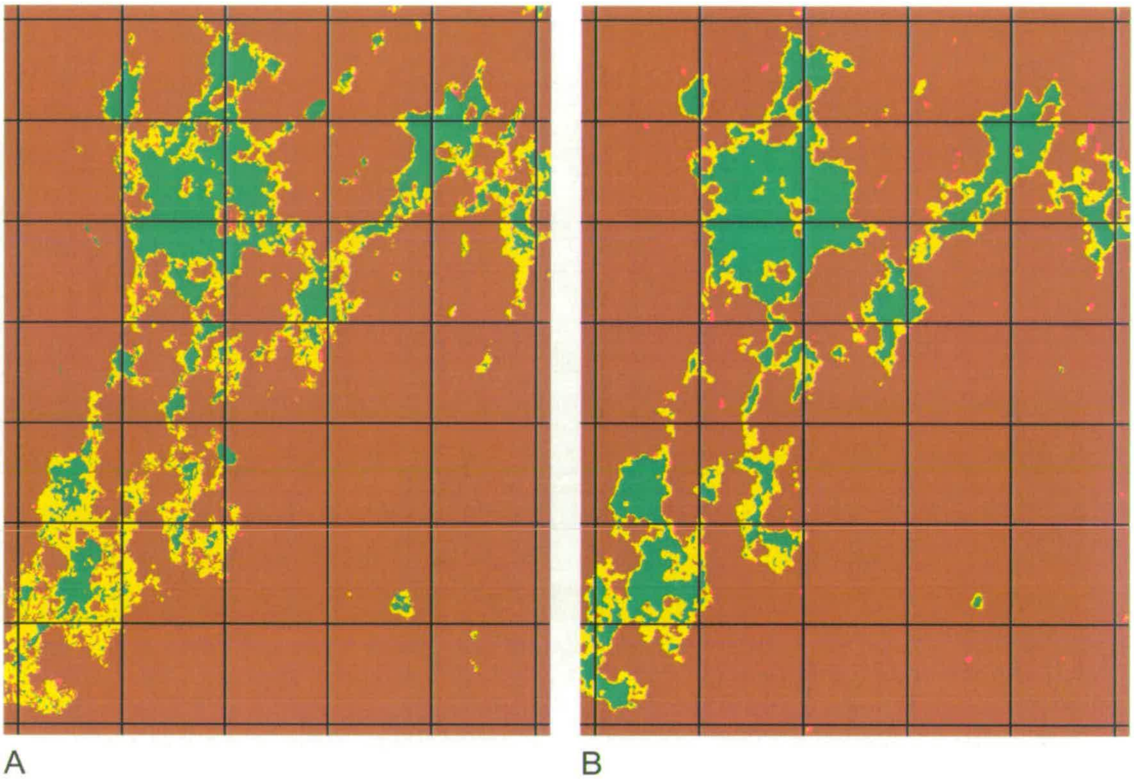


Figure 4.7e. Example area of part of the vegetation mosaic in plot T2, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*; brown = *shrub*.

The fifth example illustrates the consolidating effect of continued but decreased herbivore impact (Figure 4.7e). In 1998, the mosaic showed signs of fragmentation in progress, with a large proportion of *mixed* class, many small patches and rough edges. Following the experiment the *shrub* class had recovered, but the *grass* class had also expanded. Thus, core areas of grass remain, leading to the disappearance of small patches of *mixed* and *shrub* classes within the grass and the decrease of *mixed* class at the edge. The pattern of both *grass* and *shrub* classes is now more homogeneous and the contrast has increased. These observations agree with the concept of 'selective grazing' coinciding with increasing contrast as suggested by Adler et al. (2001).

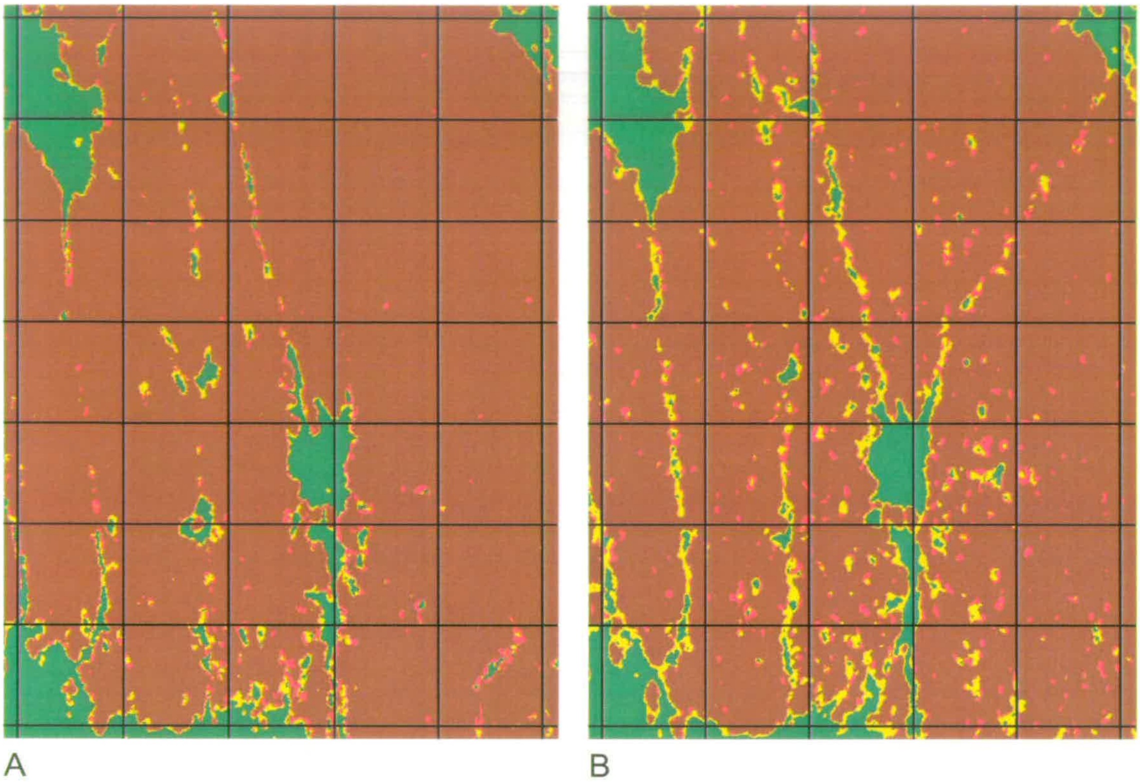


Figure 4.7f. Example area of part of the vegetation mosaic in plot T4, used to illustrate vegetation change between 1998 (A) and 2001 (B). See text for a description and discussion of changes. See Figure 4.6 for the location of the example in the experimental site. Colours indicate: green = *grass*; yellow = *mixed*; red = *degraded heather*, brown = *shrub*.

The last example shows the role of connectivity in heather-grass mosaics (Figure 4.7). This area lies between two large grass patch conglomerates and sheep regularly passed through the area. The result was a distinctive pattern of fragmentation along paths connecting both areas. Although narrow paths were not detected by the ortho-photograph classification in 1998, the effect of continued trampling along these paths was clearly visible after three years. The data for the central patch show a fragmentation of the *shrub* edge, indicated by an increase in the *mixed* class. A visual interpretation of the image suggests that along the paths both the *mixed* class and the *degraded heather* classes increased. Continued trampling would probably lead to increased width of the paths and subsequent expansion of the *grass* class.

4.4 Discussion

Results presented in this chapter provide new and interesting insights into the distribution of herbivore impact across heather-grass mosaics. Starting from the scale of the whole experimental site, analysis has zoomed in on smaller detail. At the largest scale, results indicate that the experimental sheep density treatments have led to changes in the vegetation mosaic from vegetation types dominated by heather (*shrub*) to vegetation type dominated by a mixture of grasses and blaeberry (*mixed*) and degraded heather (*degraded heather*). At the scale of individual plots, results showed large variations which could not be explained by the sheep density treatments alone. Spatial analysis showed that vegetation change was heterogeneous with large changes limited to small areas. Analysis of the drivers of vegetation change indicated that ruminating behaviour could partly explain the spatially clumped changes, while heather defoliation rates could explain more evenly spread changes in the vegetation.

Description of the characteristics of initial vegetation and subsequent changes for several examples indicated that life history of plants and the history of herbivore impact could play an important role in plant-herbivore interactions. Although they did not provide quantitative correlations, it was clear that the response of vegetation mosaics to herbivore impact depended on several processes, of which defoliation was only one.

Remote sensing methodology

The aerial photography and subsequent remote sensing analysis provided an excellent opportunity to observe changes in the vegetation at a very fine resolution. Comparison of the two sets of ortho-photographs enabled the successful detection of small scale changes between vegetation types. While cell-based analysis was affected by geometric misalignment between ortho-images, taking into account the misalignment (through the use of union patches) allowed effective analysis at the scale of individual grass patches.

The scale of photography for this study was chosen on the basis of expected changes in the vegetation. Results show that the scale of change depends on the process under study. Ruminating behaviour was associated with large changes in the vegetation concentrated in small areas (< 100 m^2). Measuring these changes would be possible at lower resolution. The changes associated with heather defoliation were spread widely across the mosaic and changes were small. Thus, a fine resolution will be crucial for the effective evaluation of heather defoliation impact. A trade-off also exists between resolution of photography and errors associated with the remote sensing analysis. The extreme resolution of this photography led to the variation in flying height and flight angle, hampering successful ortho-rectification and subsequent alignment of ortho-photographs for the two years. An increased flying height could reduce errors associated with the ortho-rectification and thus facilitate more accurate alignment albeit at the cost of reduced resolution.

Three sources can be distinguished when analysing aerial photographs in order to detect vegetation change between years: 1. change in photography (e.g. weather, light, film, processing), 2. change in vegetation characteristics (e.g. seasonality, standing biomass, water content), 3. changes in vegetation composition (i.e. the change of interest in this study). The changes in photography were successfully kept to a minimum by seeking similar suitable (cloud cover) weather and standardising film processing and scanning for both years. Changes in the characteristics of the vegetation were tried to be avoided by repeating the photography close to the original day of the year. However, changes occurred as a result of the experimental treatment and weather patterns. The autumn of 1998 was colder than the autumn of 2001. Thus, in 1998 the vegetation had partly died , while in the autumn of 2001 most of the vegetation was still green. A change in standing biomass also occurred over the three years of the experiment, such that the standing biomass was higher in 1998 as compared to 2001. However, due to the high contrast in spectral reflectance of heather and grass, these changes were expected to have little effect on the classification of grass and heather.

The colour photography, with negatives scanned at high resolution, allowed for the successful classification of vegetation types. Combined with an extensive ground survey the ortho-photographs would provide opportunities for extended image analysis for the purpose of distinguishing vegetation types such as heather and blaeberry. Seasonality of production and digestibility of the different vegetation types (Armstrong & Milne, 1995) might play an important role in herbivore nutrition. To increase the effectiveness of the classification of shrubs, the photography should occur at a time with the greatest contrast between the species. As blaeberry is deciduous, May or June might be the best period. A potentially interesting application of high resolution imagery was suggested by Quilter & Anderson (2001). They successfully correlated spectral reflectance with shrub defoliation. The use of imagery for the evaluation of herbivore impact across vegetation mosaics should be investigated further.

Plant-herbivore interactions and heterogeneity

Following the framework of Adler et al. (2001), the interactions between sheep and grass-shrub mosaics could best be classified as selective grazing. Results of the analysis here and in Chapters 2 and 3 show that the pattern of 'grazing' of sheep across heather-grass mosaics was based on the pattern of the vegetation. However, different processes had distinctively different patterns of impact. The pattern of heather defoliation and subsequent impact on the vegetation was driven by the pattern of grass, resulting in a wide spread pattern within the mosaic. In contrast, the pattern of impact resulting from ruminating behaviour showed a highly clumped distribution with areas of high impact spatially limited.

As outlined in the introduction, Adler et al. (2001) associate spatial heterogeneity with high spatial dependence, non-randomness, and high contrast. Whether herbivore impact increased or decreased the spatial heterogeneity of the vegetation strongly depended on other aspects of the plant-herbivore interactions and the scale of perception. Areas which previously suffered high herbivore impact showed consolidation of vegetation types, increased contrast (resulting from decreased heterogeneity within patches) and thus increased spatial heterogeneity at the scale of the vegetation mosaic. On the other hand areas with increased herbivore impact or areas where the vegetation was more sensitive to herbivore impact showed fragmentation of the vegetation, leading to decreased contrast between patches and subsequently decreased spatial heterogeneity at the scale of the vegetation mosaic.

The observed complexity of possible interactions between herbivores and vegetation and the subsequent effect on spatial heterogeneity of the vegetation might suggest that the framework proposed by Adler et al. (2001) is too simplified. As pointed out by Adler et al. (2001), spatial heterogeneity is dependent on the scale of observation. Likewise functional heterogeneity, i.e. the spatial heterogeneity within the context of a process, will depend on the scale of the process. For example, insects might be affected by within-patch heterogeneity or heterogeneity of boundaries between patches, while birds might respond to heterogeneity of patches within a mosaic.

Heather defoliation methodology

In order to correlate heather defoliation with vegetation change, transects were laid out at the edge of grass patches (Chapter 3). To capture information on a large number of patches across the whole experimental area, only two transects (one uphill and one downhill from the patch) were laid out from each patch. Capturing the variability across the whole area in this way, inevitably compromised insights into local heterogeneity. Thus one set of transects was used to represent a grass patch, not taking into account that each grass patch is a complex mosaic in its own right. This led to a large variability in the observations of vegetation change versus heather defoliation and thus a low proportion of explained variance around the regression lines. Although reduction in variability would be expected when increasing the intensity of sampling of each patch, variability would be expected to remain high due to the high variation in heather defoliation at the scale of individual heather plants (as discussed in Chapter 2).

Ruminating behaviour

The clumped distribution of ruminating behaviour as observed during this experiment contrasts with patterns observed on the same site in a previous experiment (Hester et al., 1999). Hester et al. (1999) found that sheep generally ruminated in grass patches, with a preference for smaller patches, while in this experiment the sheep congregated on the large grass patches in the corners of the plots. Arnold & Dudzinski (1978) explain the different resting patterns on the basis of climatic factors. In mild weather, sheep are expected to rest at the location where a foraging bout ends, while in cold weather sheep are expected to return to a sheltered area (Arnold & Dudzinski, 1978). Another possible explanation is that herbivore impact of previous experiments, such as deer trampling of heather along fences and heather trampling at gate entrances creating large grass patches in corner, creating a suitable resting area which attracted the sheep in this experiment.

Conclusions

This chapter reports on an investigation of the changes in vegetation mosaics using high resolution aerial photography and digital air photo processing. Changes in the vegetation mosaics were related to herbivore impact during the three year experiment. It was not just the 'grazing', i.e. the actual defoliation of plant material, that caused changes in vegetation types. Ruminating behaviour was shown to be associated with strong increases in grass cover. Moreover several aspects of life history and grazing history will have affected the amount and type of vegetation change resulting from herbivore impact. Different processes affecting the mosaic are likely to have different spatial impacts. It is therefore clear that herbivory should not be considered as a single process in plant-herbivore interactions, but that individual processes should be considered when studying the impact of herbivores on vegetation mosaics.

4.5 References

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Chapter 5

Spatial pattern of defoliation by herbivores across grass-shrub mosaics: a virtual experiment

Behaviour of complex adaptive systems is not well described by trajectories around global optima. Even when a relevant global optimum can be defined, the system is typically so far from that optimum that basins of attraction, fixed points, and other apparatus used in studying optima tell little about the system behaviour. Instead competition between components of the system, aimed at 'getting and edge over neighbouring competitors', determines aggregate behaviour.

J.H. Holland (1992)

5 Spatial pattern of defoliation by herbivores across grass-shrub mosaics: a virtual experiment

5.1 Introduction

This chapter considers the role of perceptional abilities of herbivores in the patterns of defoliation resulting from plant-herbivore interactions. It has been suggested that herbivore foraging strategies could determine emergent patterns of defoliation, but so far no spatially explicit investigation has been carried out. Here, a computer based simulation model is used to carry out a virtual experiment investigating the potential impact of perceptional ability on patterns of defoliation in relation to animal performance and impact on the vegetation. The term 'animal' is used throughout the text when referring to the simulated agents in the model. To facilitate the understanding of the text, reference is made to sheep and deer as analogies to the virtual animals in the model. Similarly, the vegetation types simulated in the model are considered to have analogies with heather and grass.

Emergent properties and individual-based modelling

The importance of spatial interactions in predator-prey systems has been recognised as early as the sixties, through a classic experiment using mites and oranges (Huffaker, 1958). Theoretical explanations were developed in the seventies (Hassell & May, 1974; Hassell & Southwood, 1978), finding a wide audience in the context of plant-herbivore interactions through the review by Senft et al. (1987). The role of cognition in the foraging behaviour of herbivores has been reviewed by Bell (1991) and later by Bailey et al. (1996). Despite many theories, experimental progress has been slow due to the complexity and resource demands of hypothesis-testing experiments (Dunning et al., 1995; Kareiva, 1989). It is recognised that models enable the investigation of hypotheses at a range of spatial and temporal scales with limited resource requirements and no ethical limitations, such as animal welfare issues (Dunning et al., 1995). At the same time, models used to study spatial patterns of defoliation must be spatially explicit (Dunning et al., 1995; Pyke, 1983).

The distribution of defoliation by a population of grazing herbivores across a vegetation mosaic can be seen as an emerging property resulting from the interactions between vegetation pattern and individual foraging strategies. An emergent property arises from the interaction between higher level patterns and lower level entities (Kawata & Toquenaga, 1994). The emergent property is not apparent at the lower level, but is a direct result of the properties of the individual entities. A large number of single and local foraging decisions (entities at lower level) made by individuals in a population will accumulate to an emerging global pattern of defoliation (emergent property). This understanding has led to the development of several individual-based models. While a population-based model can be used to investigate the best possible distribution of foragers across a vegetation mosaic, an individual-based model can be used to ask what defoliation patterns result from specific individual-based foraging strategies (Grunbaum, 1998). The importance of the individual-based approach is slowly being realised by ecologists (Bolker et al., 1997; Huston et al., 1988; Judson, 1994; Uchmanski & Grimm, 1996).

Although a range of models consider spatial aspects of foraging herbivores, only two explicitly model the role of foraging behaviour and particularly the role of perception in foraging decisions (Moen et al., 1997; Turner et al., 1994). These conceptual models investigate the performance of animals using alternative foraging strategies in complex heterogeneous landscapes. The 'EASE model' (Moen et al., 1997) considers the foraging behaviour of moose (*Alces alces*). The model is spatially explicit only at the level of neighbouring cells. The foraging strategies in EASE are a combination of stopping and movement rules, determining how much animals eat in the current patch and when they leave. For example with the 'Fixed stopping rule' the animals eat 33% of the current browse in the feeding station and then move to a new feeding station. When deciding where to go the animals only consider their neighbouring feeding stations and thus do not use information about the environment at a larger scale. The model focuses on energy budgets, ignoring the spatial pattern of defoliation. Non-random foraging strategies, i.e. where movement is biased towards better browse, performed better than random foraging strategies. The differences between strategies increased with decreasing browse density. This is in line with theoretical predictions (e.g. Stephens & Krebs, 1986).

The model, developed to simulate the grazing system of northern Yellowstone Park (Turner et al., 1994), uses multiple-scale foraging rules. Apart from a random, one-step rule, the animals can either select the nearest resource site, or select the best direction based on knowledge of the environment. To get there animals can move multiple cells in one time step. The search radius of the animal is set to the maximum moving distance per day. Again strategies are most divergent in their effects at low resource density. Variability of forage intake increases with increased heterogeneity. Turner et al. (1994) also do not consider the spatial pattern of defoliation resulting from the different strategies.

Observed emergent patterns of defoliation

When considering plant-herbivore interactions in heather-grass mosaics, a clear pattern of defoliation emerges (see Chapters 2, 3 and 4 for details). Patchy distributions of animals across these heather-grass mosaics have been described as early as the 1960s (Hunter, 1962; Job & Taylor, 1978) and a series of experiments in the 1990s provided more valuable insights mosaics (Clarke et al., 1995b; Cuartas et al., 2000; Hester et al., 1999). In the latter studies, herbivores (sheep and red deer) showed a preference for grass, resulting in a large proportion of grass in the diet despite relatively low abundance of grass in the vegetation. Any heather defoliation was strongly spatially correlated with the availability of grass, such that the heather defoliation decreased rapidly with distance from the grass-heather edge (Clarke et al., 1995a; Hester & Baillie, 1998) and heather defoliation at the edge decreased with distance from grass patches and increased with the size of the nearest grass patch (taking into account clusters of grass patches) (Chapter 2; Oom et al., 2002). These results suggest that only a small area of the mosaic is intensively used and that the use concentrates around areas with high grass abundance.

Investigating emergent patterns through virtual experimentation

Possible emergent properties in grazed ecosystems include: energy intake rate of the herbivores, time spent grazing, diet composition, spatial pattern of defoliation, and severity of defoliation. The emergent properties shared by both the experimental observations and the HOOFS simulations, were the spatial pattern and severity of heather defoliation. In order to facilitate comparison between observed and simulated results, these emergent properties were quantified using the semi-variogram and the frequency distribution of the heather defoliation.

Thus this study investigates whether the observed emergent pattern of defoliation in heather-grass mosaics can be explained by the foraging strategies used by herbivores as they forage the vegetation mosaics. In order to fulfil these aims, we ran three virtual experiments considering different perceptional parameters forming foraging strategies used by herbivores grazing in an artificial vegetation mosaic. The experiments were executed using the HOOFS model (Beecham & Farnsworth, 1998). Parameterisation was based on the grazing system found in the highlands of Scotland, considering a herbivore, such as sheep *Ovis aries* or red deer *Cervus elaphus* L., foraging heather-grass mosaics.

5.2 Methods

5.2.1 Vegetation map

The foraging model used in this virtual experiment is driven by an underlying vegetation map. The spatial patterns of defoliation are the result of the interaction between the specific foraging behaviour characteristics and the characteristics of the vegetation. Although technically possible, due to computational constraints it was not feasible in this study to vary both the foraging behaviour and the vegetation pattern. Therefore we have chosen to give priority to the different foraging strategies applied to a single vegetation map.

In order to test the foraging strategies in a realistic vegetation mosaic, we have used the heather-grass mosaic (Figure 5.1) from one of the plots in the field site (see Chapter 3 for details). This vegetation pattern has developed over time as a result of foraging by sheep, deer and cattle (Hester & Baillie, 1998). The plot contained a large number of small and medium sized grass patches in a heather matrix, with local clustering of patches and isolated patches elsewhere in the mosaic. Patches were connected by an extensive network of paths. The vegetation mosaic provided a good example of a complex heather-grass mosaic, which was considered a suitable mosaic to test the foraging strategies.

The vegetation composition of the vegetation map (see Chapter 4 for detailed description of methods) contained 10.7% grass patches and 89.3% heather (Figure 5.1a). Paths were surveyed separately in the field and added to the vegetation map. The width of the paths was adjusted to get paths on the hexagonal map of at least one hexagon width. The vegetation map was sampled with the hexagonal grid such that each hexagonal cell was allocated the vegetation type present in the centre of the hexagon. As the hierarchical hexagonal grid is not square, the hexagonal grid was scaled such that most of the hexagonal grid was occupied by the vegetation map. The resulting scale of the hexagonal map gave a distance of 0.43 m between neighbouring hexagonal cells and a cell area of 0.14 m^2. The resulting vegetation map (Figure 5.1b) contained 11% grass patches, 5% grass paths and 84% heather.

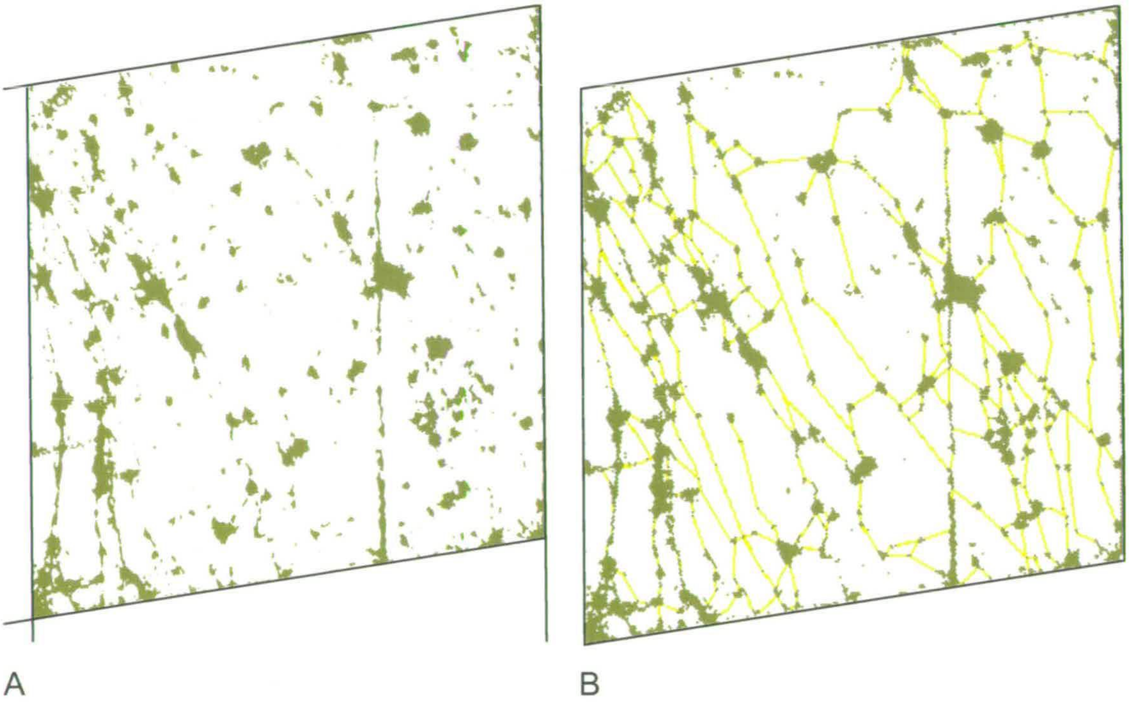

Figure 5.1. Vegetation map (A) and derived hexagonal vegetation map (B) of the experimental plot on Strathfinella Hill used as the vegetation mosaic in the virtual experiments. Colours correspond as follows: grass = green, paths = yellow, heather = white. Plot size is roughly 100 m by 100 m.

Table 5.1. Number of cells and the total biomass in the vegetation mosaic at the start of the simulation.

Vegetation	Cells	Biomass	
	%	%	10^6 g DM
Grass patches	11	2.4	0.7
Grass paths	5	1.1	0.3
Heather	84	96.5	27.7
Total	100	100	28.7

The initial total above ground biomass (g Dry Matter) of cells is set to 100 g of grass in 16% of cells (patches and paths) and 500 g (current year's growth) of heather in 84% of cells. Values were determined through an iterative process of balancing biomass availability and consumption. As a result 3.5% of the total biomass is grass and 96.5% is heather. The total dry matter of the whole vegetation mosaic at the start of the simulation is 28.7 tons in a vegetation mosaic of one hectare (Table 5.1). The biomass of the grass during the simulation increases slightly due to a faster growth rate (Appendix B). The total production of grass during the simulation depends on the foraging pattern.

5.2.2 HOOFS model

The HOOFS acronym stands for Hierarchical Object Oriented Foraging Simulator (Beecham & Farnsworth, 1998; Beecham et al., 1999). HOOFS is a spatially-explicit, individual-based model. Individuals can have different states and different responses to each other and their environment. Although HOOFS also provides an extensive social sub-model, this was switched off for the purpose of this study. Parameters for the foraging strategies were all part of the foraging sub-model. A detailed description of the foraging sub-model is given in Appendix A. The HOOFS model uses a spatial hierarchy based on the hexagonal map. Each individual cell, the lowest level in the hierarchy, is a member of a super-cell, consisting of a central cell and its six neighbours. In turn these first order super-cells are grouped in second order super-cells and so on (Figure 5.2). Several parameters in the foraging sub-model make use of this spatial hierarchy.

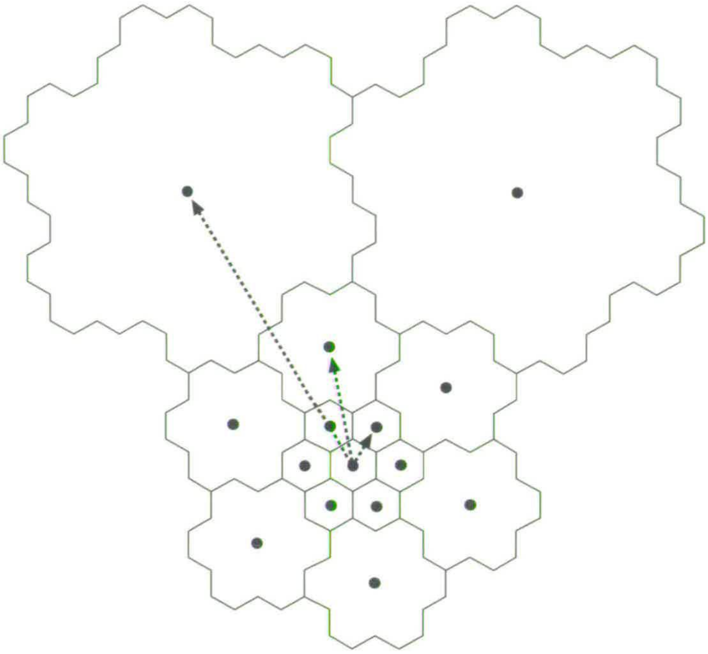

Figure 5.2. The first three levels in the hexagonal hierarchy used in HOOFS.

The initial biomass (dry matter) in heather cells was considered representative of the total amount of current year's production, but grass was allowed to grow during the simulation. The grass production was determined by the 'Birch equation' (Birch, 1999). The Birch equation does not have an integrated form, therefore in Hoofs the new biomass is estimated using the 'mid-point method' (Birch, 1999). Parameter values are given in Appendix B.

5.2.3 Input parameters and output variables

The foraging submodel is a conceptual model of animal foraging behaviour. Although it is known that animals have knowledge of their environment and that some of this knowledge is used in foraging decisions, it is largely unclear how these perceptional processes work (see reviews Bailey et al., 1996; Bell, 1991). The foraging sub-model is thus an attempt to investigate possible interactions between perceptional abilities and resource heterogeneity.

To allow the animals to scan and sample the vegetation mosaic efficiently, both a foraging and a walking mode are considered. The foraging mode can include movement and subsequent eating, while the walking mode exclusively involves walking. Depending on the foraging strategy and the quality of resources in the vicinity, animals can choose to either walk or forage. A foraging bout is defined as a continuous period spent in foraging mode. These modes are supported by data on rates of movement of sheep in heather-grass mosaics (Hester et al., 1999).

The input parameters used as treatments in the three experiments are explained below. Others, that were held constant throughout, are summarised in Appendix B.

Determinism: The foraging strategy of the animals is driven by the quality of the vegetation in the vegetation mosaic. How biased animals are towards the best quality vegetation is set by their *determinism*. When the *determinism* is zero, the animals forage at random. Animals that are fully deterministic have a theoretical *determinism* of infinity.

Distance coefficient: The *distance coefficient* determines what part of the landscape the animals take into account when taking decisions. The *distance coefficient* is similar to the reactive distance as defined by Bell (1991). The *distance coefficient* describes a relationship between the weighting of cell quality versus distance. A *distance coefficient* of zero means that all distances are weighted equal, while a *distance coefficient* between 0 and -1 leads to a lower weighting for distant cells, i.e. a bias towards cells nearby. Using a coefficient still allows very high quality cells in the distance to influence animal decisions when the cells in their vicinity are of low quality.

Discriminitive ability: The decisions of an animal foraging in HOOFS are, among others, affected by the availability of high quality food resources in their environment. The way the animal perceives its environment will strongly influence its decision making. The *distance coefficient* determines how the animal weighs resources near and further away. But when evaluating the food resources, the animal is unlikely to perceive near and distant resources with the same resolution. To accommodate for this, HOOFS summarises the resource environment by calculating mean quality of food resources at each super-cell level. The *discriminitive ability* determines how the mean resource quality is calculated at each level using the individual cells within it. Either the mean is calculated equally across all cells (*discriminitive ability* = 1), or the mean is biased towards the higher quality cells among the group of cells (*discriminitive ability* > 1). In ecological terms that means that with a high *discriminitive ability*, animals will perceive small high quality resource cells in the distance even when these cells are surrounded by poor quality cells. The *discriminitive ability* can be set for each level in the hierarchy separately.

Mode error: The *mode error* affects the choice between walking and foraging mode. When *mode error* is one, the best choice (highest *potential net energy intake rate*) is always chosen. When *mode error* is greater than one, the less than optimal choice is selected with a probability based on the value of the *mode error*.

Movement cost: Each time the animal moves from one cell to another, a *movement cost* is incurred. This is a fixed time penalty and is thus subtracted from the *foraging time*.

Relative resistance: The relative resistance determines the resistance when travelling from one cell to another and affects the *movement cost*. An indication for different perceptions of 'resistance' is shown by Hester (1999) as deer cross grass-heather boundaries more often than do sheep. The resistance encountered is calculated as the average relative resistance of the vegetation types in both cells. For example, if the relative resistance of grass and heather are one and five respectively, then going from grass to heather will give a resistance of three. Going from grass to grass or heather to heather will result in a resistance of one and five respectively.

Distance sensitivity: The *distance sensitivity* determines the willingness of animals to walk long distances when local resources are of low value compared to resources in the distance. Low *distance sensitivity* facilitates the exploration of isolated patches of high quality resource, while at high *distance sensitivity* animals tend to forage locally.

Output variables

Time (s): HOOFS does not presume any time unit. Instead the time unit is determined by the units used in rate variables, such as the intake rate. Time is expressed as simulation time. All rates are expressed per second, thus simulation time is expressed in the same units.

Standing biomass (g): The vegetation quantity is expressed as the amount of standing biomass (dry matter) per cell at the end of the simulation.

Energy intake rate (J s^{-1}): The energy intake is expressed as the average energy intake in Joule per animal per second.

Net Energy intake (J s^{-1}): The net energy intake is the difference between the *energy intake rate* and the energy cost rate of foraging.

Energy efficiency (%): The energy efficiency is the proportion of *net energy intake rate* in the total *energy intake rate.*

Movement (step): The movement is expressed as the average number of steps taken per foraging bout. Continuous grazing in one cell or its neighbour gives a movement of one. Walking several steps before grazing will give a movement value larger than one. As a result of the scaling of the vegetation map, one step is equivalent to 0.43 m in the vegetation mosaic.

Residence time (s): The average time a cell was grazed by an animal across all animals.

Grazing time (%): The *grazing time* is expressed as the proportion of simulated time spend grazing.

Biomass intake ($g \cdot s^{-1}$): The average dry matter intake per second across all animals.

Digestibility (J g^{-1}): The average digestibility of the biomass consumed by all animals during the simulation.

Heather proportion (%): The diet composition is expressed as the proportion of dry matter of heather in the diet.

Grazed area proportion (GAP) (%): The proportion of cells of a vegetation type grazed, calculated for the whole mosaic (total) and for each vegetation type (grass patch, path, heather).

Adjusted grazed area proportion (%): The proportion of cells of a vegetation type grazed relative to the proportion of the vegetation type in the mosaic. For example, the *adjusted grazed area proportion* for grass is calculated as the proportion of grazed grass cells in the total number of grazed cells in the landscape, divided by the proportion of grass in the mosaic. This gives an indication of the proportion of a vegetation type affected relative to the impact on the whole landscape. When the impact on a vegetation type is close to, or the same as, the impact on the whole landscape, the adjusted grazed area proportion will tend to 100%.

5.2.4 Experimental design

Three experiments (Table 5.2) were carried out using *determinism*, *distance coefficient*, *relative resistance* (see Table 5.3 for levels used), *discriminative ability* (see Table 5.4 for levels used), *mode error*, *movement cost* and *distance sensitivity* as treatments. The experimental design was based on expected interactions between different parameters. Experiment 1 considers the interaction between perception and motivation and the resistance of the landscape. Experiment 2 considers the role of perception across scales. Experiment 3 considers the directional choices and the trade-off between distance moving and movement cost.

Table 5.2. Overview of the three experiments. Each experiment applies three values for each of three parameters.

Exp.	**Treatment 1**			**Treatment 2**			**Treatment 3**		
1	Determinism			Distance coefficient			Relative resistance		
	1	2	3	-0.75	-0.50	-0.25	Low	Medium	High
2	Determinism			Discriminative ability			Distance coefficient		
	1	2	3	Low	Medium	High	-0.75	-0.50	-0.25
3	Mode error			Movement cost			Distance sensitivity		
	1	0.8-1.2	0.6-1.4	0.3	0.5	0.7	0.3	0.5	0.7

Table 5.3. Treatments for the *relative resistance*.

Treatment	**Vegetation type**		
	Grass	**Path**	**Heather**
Low	1	1	5
Medium	1	1	10
High	1	1	15

Table 5.4. Treatments for the *discriminative ability*.

Treatment	**Level in hierarchy**				
	2	**3**	**4**	**5**	**6**
Low	1	1	1	1	1
Medium	3	3	2	1	1
High	5	5	3	2	1

5.2.5 Spatial statistics

In order to determine the effect of foraging behaviour on the spatial pattern of defoliation, a spatial statistic was needed. The semi-variogram was chosen because it provides a good method of describing spatial continuity of complex spatial patterns (Isaaks & Srivastava, 1989). The semi-variogram, generally shortened to variogram (Isaaks & Srivastava, 1989), is a widely used spatial statistic. The variogram has its origin in mining, but is slowly being adopted by environmental scientists. This is reflected by recent publications on the application of geostatistics in environmental science (Goovaerts, 1997; Legendre & Fortin, 1989; Legendre & Legendre, 1998; Webster & Oliver, 2001).

The variogram shows the variation of a variable between two points as a function of the distance between the two points. The sample variogram (called experimental variogram in GenStat) is a scatter plot of the variance calculated for a group of point pairs in a distance class called a lag, with a fixed lag size. For spatially auto-correlated variables, the sample variogram is expected to increase with increasing distance, i.e. the variance between point pairs increases with distance, with the lowest variance at the lowest lag distance. Generally, the sample variogram reaches a maximum at the a priori variance of the variable, i.e. ignoring any spatial structure.

The model variogram is a function fitted to the sample variogram to provide estimates for the nugget, sill and range (Figure 5.3). These values are then used as descriptors of spatial structure of the variance. The nugget is the variance at minimum lag distance and suggests unexplained variance at a scale smaller than the minimum lag distance for which the variogram is calculated. The nugget is the variance that remains after accounting for the spatially structured variance (the partial sill). Either this variance is intrinsic to the data, this variance was caused by sampling or measurement error, or the sampling was done at an inappropriate spatial scale (Isaaks & Srivastava, 1989; Webster & Oliver, 2001). The sill is the maximum variance between points at any distance. The sill is the sum of the nugget (the spatially uncorrelated variance) and the spatially correlated variance (called the partial sill). The range is the distance at which the sill is reached. This is the spatial extent of the structure in the data, or points further apart than the range are not spatially autocorrelated. The sample variogram was calculated and the model variogram was fitted using the GenStat procedures Fvariogram and Mvariogram respectively (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13).

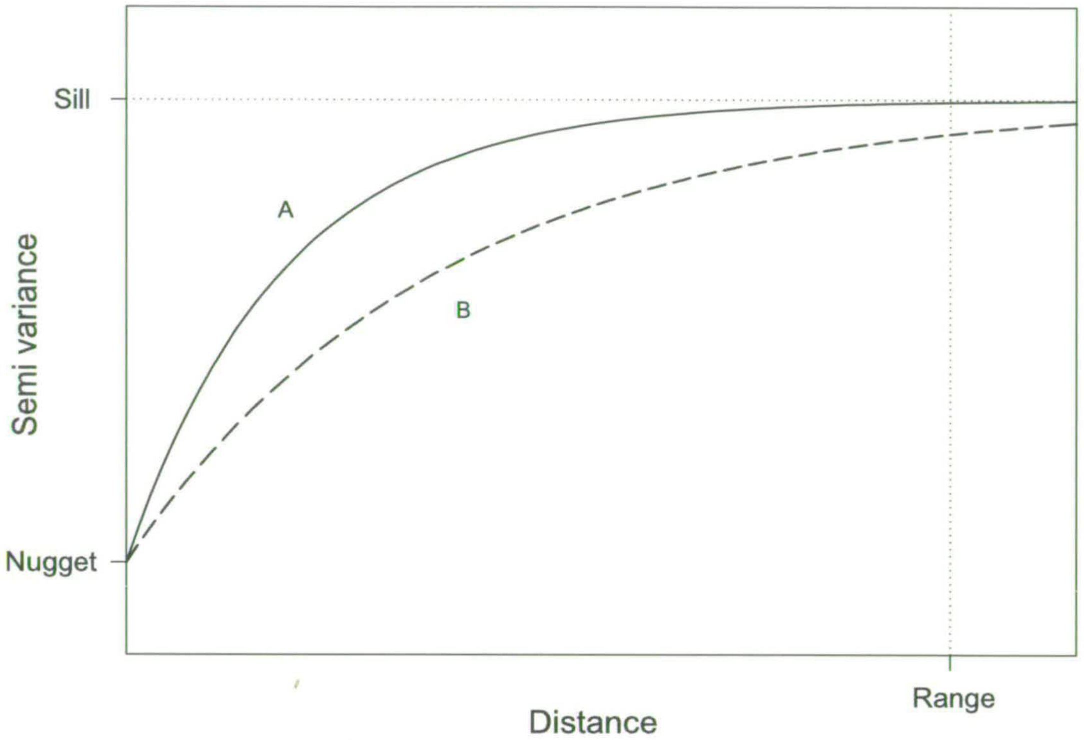

Figure 5.3. Example of model variograms indicating range, nugget and sill: A) spherical model, B) exponential model. The partial sill is the difference between the sill and the nugget.

The sample variogram was calculated using a maximum lag distance of 50 m and a lag size of 2.5 m. The effect of chosen lag size was tested, but there was no significant effect on the range, nugget or sill. Directional sample variograms were calculated for 30° sectors centred on the map's north axis: 0, 30, 60, 90, 120, 150 °.

Sample variograms across the contours showed a hole effect (Isaaks & Srivastava, 1989), as the sample variogram had a dip at intermediate distance (Figure 5.4). The hole effect is caused by the directionality and regularity in spacing of the underlying pattern of paths and patches. The directionality in the vegetation pattern was caused by the interaction between slope of the hill and the defoliation and trampling impact by sheep. As sheep prefer to follow the contours of a hill, paths generally follow the contours (Hester et al., 1999; Oom & Hester, 1999). Thus the variance between points decreases at the average distance between paths.

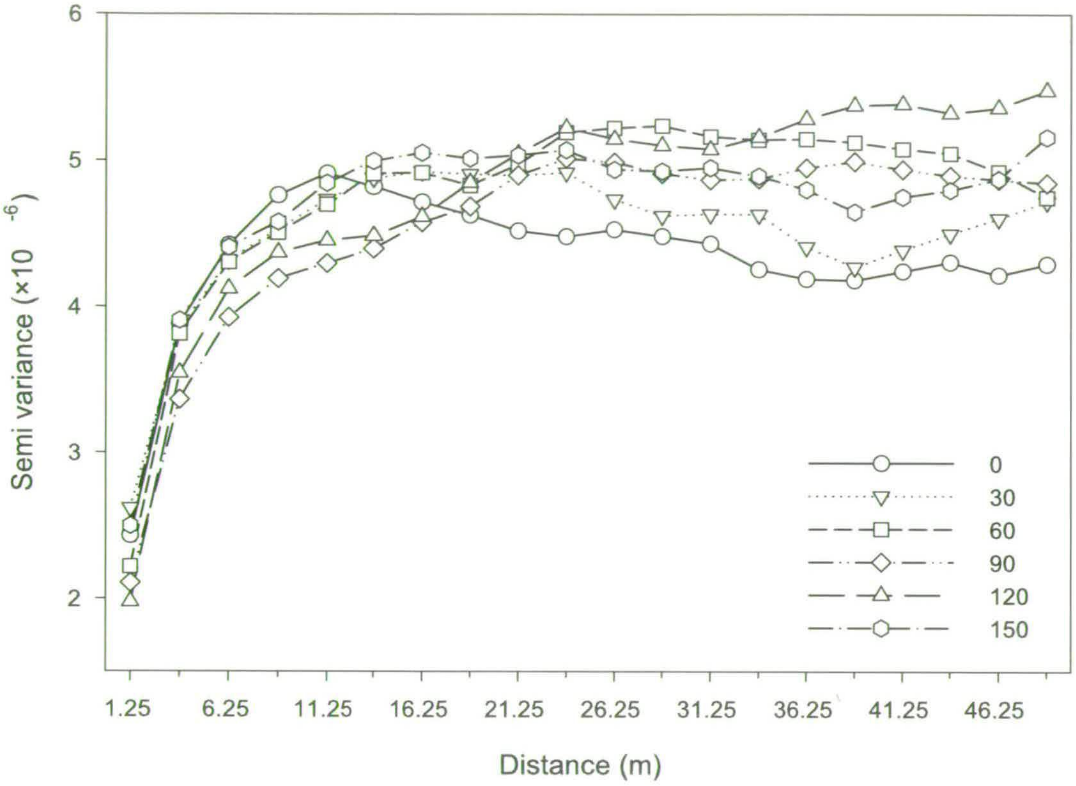

Figure 5.4. Example of six sample variograms of a vegetation defoliation pattern resulting from a model simulation run. The sample variogram was calculated for six directions: 0, 30, 60, 90, 120, 150 () with a lag size of 2.5 m and a maximum lag distance of 50 m.

The variograms also showed anisotropy (Isaaks & Srivastava, 1989) as a result of the non-stationary mean across scales, i.e. some areas of the landscape were more heavily grazed than others at the larger measured scale. As a result the variance increased or decreased with increased distance, not approaching an asymptote. This can be avoided by increasing the size of the landscape (assuming the landscape is homogeneous at larger scales), or by increasing the length of the simulation. The first option would lead to a stabilising sample variogram at a higher sill and longer range, while the latter would lead to a lower sill and range.

No attempts were made to correct for either the hole effect or the anisotropy, as all foraging strategies were applied to the same vegetation map (suffering the same anisotropy) and because the hole effect did not influence the estimates for the sill, nugget and range. In order to accommodate the directionality, sample variograms were calculated for six directions and one model variogram was then fitted to all six directional sample variograms. Several model variograms were fitted to the sample variograms, but the exponential model variogram consistently showed the best fit.

The exponential model variogram (Equation 5.1) provides estimates for the nugget (c_0), the partial sill (c_1) and theoretical range (a) of the variogram (γ), for a given lag distance (h). Because the exponential model variogram approaches the sill asymptotically, the range cannot be determined as the distance at which the sill is reached. Therefore the practical range (also referred to as effective range) is defined, by convention, as the distance at which 95% of the partial sill is reached (Isaaks & Srivastava, 1989). Note that, as the partial sill is used, the nugget does not effect the estimation of the range. The practical range is then approximately three times the theoretical range (Isaaks & Srivastava, 1989; Webster & Oliver, 2001). For exponential models, GenStat estimates the theoretical range. To avoid confusion, all range values reported in this study are theoretical ranges as calculated by GenStat.

$$\gamma(h) = c_0 + c_1\left(1 - e^{-\frac{h}{a}}\right)$$

Equation 5.1

$$RNE = \frac{c_0}{c_0 + c_1}$$

Equation 5.2

The relative nugget effect (Legendre & Legendre, 1998) was calculated (Equation 5.2) as a measure of the contribution of the nugget to the sill, the latter being the sum of the nugget and the partial sill. The relative nugget effect provides insight into the amount of variance in the data explained by spatial autocorrelation (the partial sill) relative to the spatially uncorrelated variance (the nugget).

5.2.6 Observed emergent properties

In order to compare the observed and simulated heather defoliation, two emergent properties are quantified. The first emergent property is the variogram of the spatial pattern of heather defoliation. Figure 5.5 shows the sample variogram and the fitted model variogram based on the heather defoliation pattern observed on Plot 3, i.e. the vegetation mosaic used for the virtual experiment. The model variogram is based on an exponential equation resulting in a range of 15.9 m, a nugget of 49.51 and a sill of 66.43. The relative nugget effect is 75 %. Because the variograms of the simulated heather defoliation are based on average consumption per time step, sill and nugget are not directly comparable with the variogram results of the observed heather defoliation (based on percentage defoliation per year). However the range is calculated in metres for both the simulated and observed variograms, while the relative nugget effect is dimensionless.

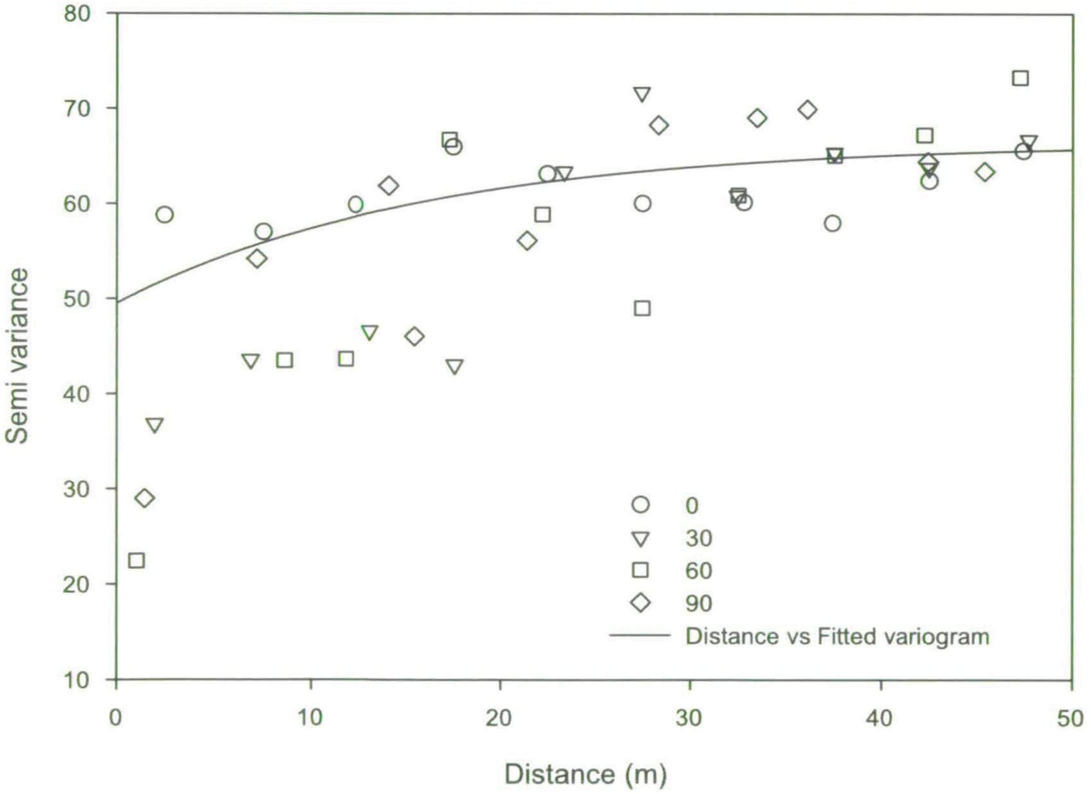

Figure 5.5. Variogram based on the observed heather defoliation pattern in Plot 3, i.e. the vegetation mosaic used for the virtual experiment.

The second emergent property is the frequency distribution of heather defoliation. Figure 5.6 shows the frequency distribution of percentage defoliation of individual observations in Plot 3 of winter observations only. As the simulation model did not include seasonality, winter observations, representing a full year of grazing, were considered most comparable to the simulated defoliation. Only grazed locations were considered and data were averaged by location or transect. In order to compare observed and simulated frequency distributions, a distribution function was fitted to the histogram. A gamma function generally provided the best fit for both the observed and simulated histograms.

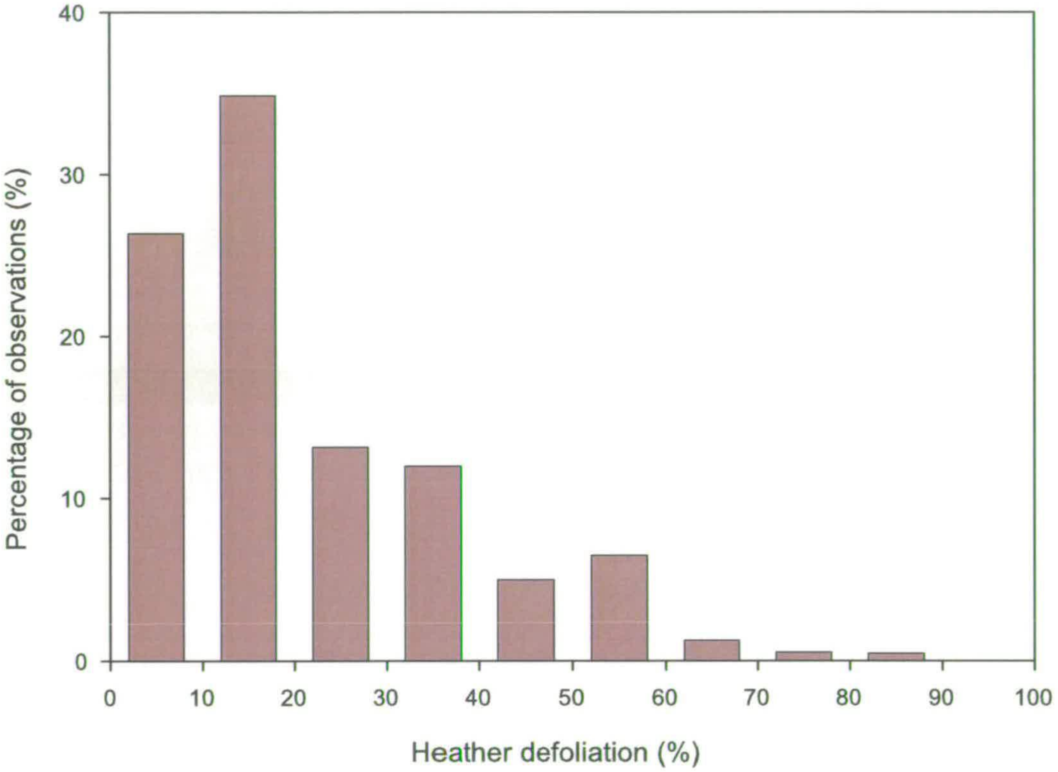

Figure 5.6. Frequency distribution of percentage defoliation for all observations in Plot 3.

The gamma function provides two variables describing the shape and the scale of the fitted curve. The scale variable *b* determines how stretched the distribution is along the x-axis. A decreasing *b* leads to a distribution increasingly skewed to the left (i.e. the peak is skewed to the left with a long tail to the right). The shape variable *k* determines the shape of the distribution. For $k = 1$, the distribution is exponential, i.e. the distribution is biased to the left. For $b = 1$ and k tending to infinity, the gamma distribution tends to a standard normal distribution. The gamma functions were fitted using the Distribution procedure in GenStat (Lawes Agricultural Trust; 5th Edition Release 4.22, Service Pack 2, GenStat Procedure Library Release PL13). The gamma function fitted to the observed frequency distribution (Figure 5.6) resulted in 0.078 and 1.69 for the b and k variables, respectively. In comparison the frequency distribution variables for heather defoliation in Plot 1 gave 0.09 and 2.22 for the b and k variables, respectively.

5.2.7 Statistical analysis

The virtual experiments were analysed as individual experiments. The random walks have been simulated to provide a comparison with the different strategies. All experiments were done using a 3×3 latin square design, with five replicates. Although an alternative statistical analysis has been proposed for virtual experiments (Parysow & Gertner, 1997), the ANOVA was used in this study. The ANOVA not only provides significance estimates for treatments, but it also provides insights into the interactions between treatments. The experimental design led to 108 degrees of freedom for all the treatment means presented in the tables. Results are marked non-significant (italic in tables) when the p-value is greater than 0.05. Generally p-values were less than 0.001, and were thus not presented in tables. Several interactions were significant and are mentioned in the text.

To bring across the main findings of these experiments, mean values of output variables are presented across the duration of the simulation. Unfortunately this averaging conceals the underlying dynamics of the output variables. However HOOFS does provide continuous information on all output variables. For example, Figure 5.7 shows the different dynamics of *energy intake rate* between different foraging strategies. Animals with low *determinism* generally have higher variability in their *energy intake rate*, as they wander through the mosaic more randomly than more determined animals. The *relative resistance* constrains animals in their movement, leading to lower energy intake rates as they stay longer in the same areas.

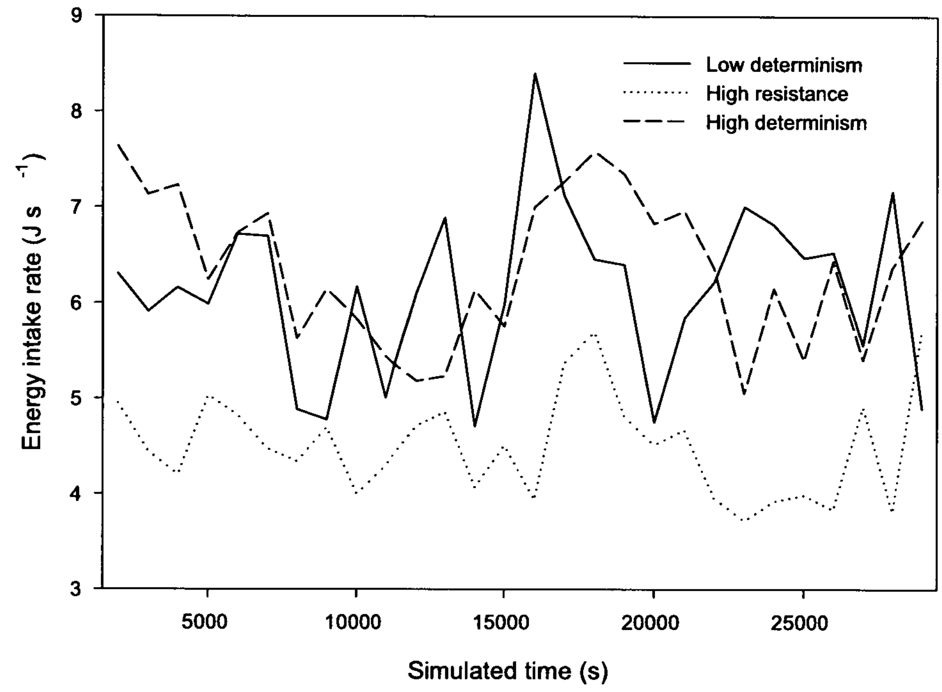

Figure 5.7. Example of energy intake versus time for different strategies.

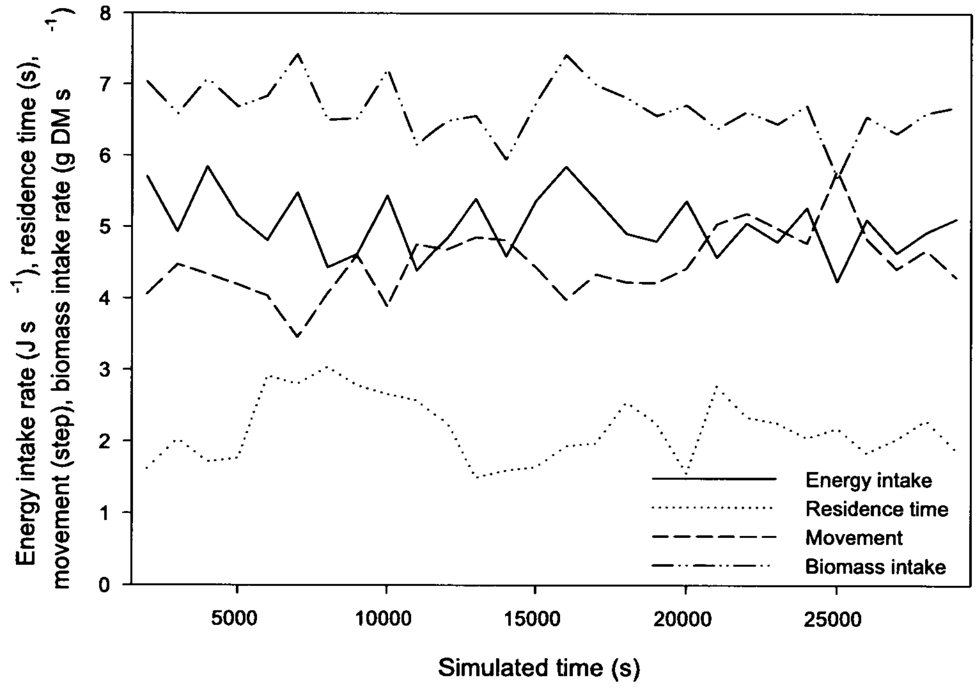

Figure 5.8. Example of predictions of several performance indicators from a single run of the model, showing the coincidence of peaks and troughs in some pairs of variables.

Many output variables show correlation across time. Figure 5.8 shows the coincidence of peaks and troughs in some pairs of variables during a simulation. Obviously, *biomass intake* and *energy intake rate* are highly correlated. An increase in *movement* generally leads to a decrease in *energy intake rate*. The correlation between output variables in the experiments was investigated through principal components analysis.

5.3 Results

The individual experiments are covered in separate sections, but some general points are covered first. Differences between output variables for the different treatments and different experiments are small. This is a result of the constraints of the vegetation mosaic. As the availability of high quality grass is limited, the long-term results of different strategies converge. However, instantaneous performance (performance across a small time period) of strategies differ more strongly. Here, we have focussed on the longer term performance as we are interested in the resulting cumulative defoliation pattern. In reality, as in the model, animals are also strongly limited by the availability of resources. Constraints in the availability of grass and heather in the simulated vegetation mosaic determine the diet composition, with around 60% heather in the diet, despite high determinism or perceptional abilities.

The variogram results generally show a large *relative nugget effect*. Generally the nugget is assumed to be caused by spatial variation below the smallest spatial scale considered in the analysis, or by a measurement or sampling error (Isaaks & Srivastava, 1989; Webster & Oliver, 2001). However, this is a virtual experiment using a computer simulation model, so measurement error is negligible. At the same time the spatial pattern of defoliation is not sampled in the experimental sense. The spatial pattern of defoliation based on the hexagonal grid and the sampling population are the same. This allows us to calculate the sample variogram for the smallest possible scale, i.e. that of neighbouring cells. Although we calculated the variogram with a lag distance of 2.5 m, testing of smaller lag sizes showed no significant effect on the nugget. Possible explanations are mentioned in the discussion.

5.3.1 Random walks

In order to evaluate the performance of the different foraging strategies relative to a non-cognitive or random strategy, the model was run with a foraging strategy using zero *determinism*. Because the walking mode is not directly influenced by the lack of determinism, the random foraging strategy was run both with and without the walking mode. When animals are able to walk as an alternative to foraging, they will walk longer distances and visit more cells. The walking mode is affected by the cost of alternative routes, and therefore leads to a bias towards low resistance. This results in an increased use of path and patches. Because walking animals endure travel costs while not taking in biomass, they will perform less well compared to the animals that only forage. This is reflected by the results: *movement* and the *grazed area proportions* are higher, while the *energy intake rate* is lower (Table 5.5).

Table 5.5. Treatment effects for the two random strategies either including both walking and foraging modes, or limited to foraging only. The *determinism* is set to zero for both strategies.

Variable	***Walking and foraging mode***		***Only foraging mode***	
	Mean	**SD**[a]	**Mean**	**SD**
Energy intake rate	4.93	0.07	5.20	0.05
Net energy intake rate	4.56	0.08	5.11	0.05
Energy efficiency	92.6	0.2	98.3	0.0
Movement	5.34	0.13	1.00	0.00
Foraging time	63.4	0.7	91.1	0.1
Residence Time	2.71	0.04	3.71	0.06
Range	12.7	5.48	10.2	4.57
Sill ($\times 10^{-5}$)	0.31	0.03	0.65	0.04
Partial Sill ($\times 10^{-5}$)	0.11	0.03	0.39	0.03
Nugget ($\times 10^{-5}$)	0.19	0.01	0.27	0.06
RNE	63.1	5.60	40.7	7.96
Biomass intake	6.64	0.08	8.26	0.04
Digestibility	74.2	0.21	62.9	0.32
Heather proportion	63.4	1.7	69.0	2.6
Freq. distribution *b*	0.28	0.03	0.11	0.006
Freq. distribution *k*	2.78	0.25	1.99	0.09
GAP[b] Total	35.1	1.4	29.2	0.7
GAP Patch	76.8	6.4	31.1	3.5
Adjusted GAP Patch	218.6	14.3	106.6	11.5
GAP Path	74.0	3.1	31.4	1.7
Adjusted GAP Path	210.8	2.9	107.7	7.6
GAP Heather	27.7	1.2	28.8	0.9
Adjusted GAP Heather	79.0	1.753	98.8	1.5

[a] SD = Standard deviation; [b] GAP = Grazed area proportion.

Because the animals do not consider food quality in their foraging strategy, their performance is poor. Notable is the large *relative nugget effect* (RNE). This illustrates that most of the variation in the defoliation is a result of a non spatial process, which is not surprising for a random foraging strategy. The remaining correlated variance is a result of the fact that the animals still move from cell to cell.

Table 5.6. Biomass (%), per vegetation type, available in vegetation mosaic at the start of the simulation and biomass consumed per vegetation type during random walks.

Vegetation	**Biomass at start (%)**	**Biomass consumed (%)**	
		Walking and foraging	Foraging only
Grass patches	2.4	92.8	22.5
Grass paths	1.1	27.3	10.9
Heather	96.5	4.6	8.3
Total	100	6.9	8.6

The diet, indicated by the proportion of heather in the diet, is determined by the *biomass intake rate* of grass and heather, 30 and 10 g DM s^{-1} respectively, and the encounter rate of both vegetation types. Therefore, if sheep were given equal amounts of grass and heather, the intake rates would result in a diet of 25% heather, but with a heather cover of 90% the ratio of encounter rate of heather to grass is 9 : 1. This would be expected to give a diet of 75% heather, but because the animals start off on the grass, the percentage heather in the diet is 69% (for the animals with only foraging mode). This discrepancy would decrease with increased simulation time. When animals have the choice of the foraging or walking mode, the animals are still biased (due to the relative resistance) to walk on the grass even if their foraging mode is random. This decreases the amount of heather in the diet to 63% and shifts consumption to the grass patches and grass paths (Table 5.6).

When the walking mode is added to the random foraging mode, the animals perform significantly less well. Their *energy intake rate* drops by 5%, mostly as a result of a sharp decline in *biomass intake* (20%). The animals manage to make up for part of the decrease in *biomass intake* by increasing the *digestibility* of the diet. This is because the walking mode is always biased towards grass, leading to an increase in the proportion of grass in the diet.

5.3.2 Experiment 1: determinism, foraging extent, relative resistance

Principal component analysis

The plot of the first and second axis resulting from the principal components analysis (Figure 5.9) shows clusters of: 1) *energy* and *net energy intake rate*, *biomass intake*, *grazing time* and *movement*, 2) *heather proportion*, *range* and *nugget*. The spread of variables would suggest that the first axis is related to the mobility of the animals, while the second axis could be interpreted as the selectivity of the animals. The selectivity affects the diet (*heather proportion*) and the spatial pattern of defoliation (*range* and *nugget*).

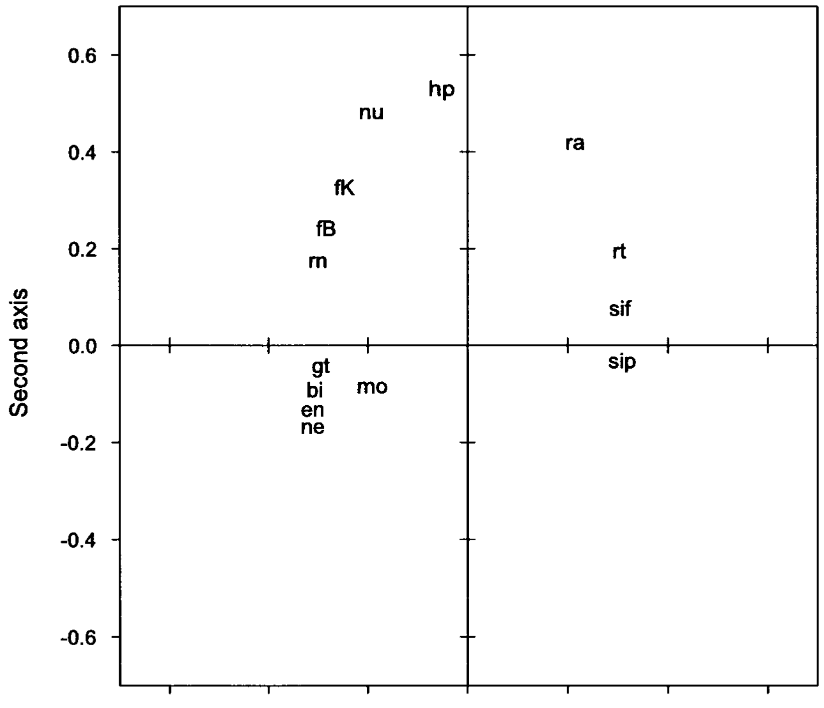

Figure 5.9. First and second axis scores resulting from the principal component analysis of Experiment 1. Labels are as follows: en = *energy intake rate*, ne = *net energy intake rate*, mo = *movement*, gt = *grazing time*, rt = *residence time*, ra = *range*, sip = *partial sill*, sif = *full sill*, nu = *nugget*, rn = *relative nugget effect*, bi = *biomass intake*, hp = *heather proportion*, fB = *frequency distribution variable B*, fK = *frequency distribution variable K*. The meaning of the axes is explained in the text.

Table 5.7. Treatment means for Experiment 1, with treatments: *determinism*, *distance coefficient*, *relative resistance*. The standard error of differences (SED) presented are averages for all treatments. Treatment means are printed in italics when treatment effect was not significant ($p > 0.05$) for that variable. See methods section for explanation and units of variables.

Variable	**Determinism**			**Distance coefficient**			**Relative resistance**			
	1	**2**	**3**	**-0.75**	**-0.5**	**-0.25**	**low**	**medium**	**high**	**SED**
Energy intake	5.12	5.65	5.95	5.58	5.66	5.48	6.45	5.37	4.90	0.03
Net energy intake	4.80	5.36	5.67	5.29	5.36	5.17	6.20	5.07	4.55	0.03
Energy efficiency	93.4	94.6	95.2	94.6	94.5	94.1	96.1	94.3	92.7	0.0
Movement	4.97	4.16	3.73	4.08	4.19	4.59	4.97	4.16	3.73	0.04
Grazing time	67.3	70.1	72.1	71.0	70.1	68.5	67.3	70.1	72.1	0.1
Residence time	2.15	1.80	1.62	1.89	1.82	1.85	1.39	2.05	2.12	0.02
Range	12.05	9.85	7.23	*10.08*	*8.75*	*10.30*	4.30	12.70	12.13	1.17
Sill (× 10^{-5})	0.51	0.57	0.60	0.50	0.55	0.63	0.60	0.55	0.53	0.02
Partial Sill (× 10^{-5})	*0.37*	*0.40*	*0.41*	0.33	0.40	0.46	*0.42*	*0.37*	*0.39*	0.02
Nugget (× 10^{-5})	0.14	0.18	0.19	*0.17*	*0.16*	*0.17*	0.18	0.18	0.14	0.01
RNE	*28.5*	*31.4*	*32.0*	35.5	29.1	27.4	31.0	32.9	28.0	1.7
Biomass intake	6.75	7.14	7.36	7.15	7.15	6.97	7.76	7.03	6.47	0.02
Digestibility	75.5	78.9	80.6	77.8	78.8	78.5	83.0	76.4	75.7	0.3
Heather proportion	61.2	59.2	59.2	60.6	60.0	58.9	60.0	60.8	58.8	0.4
Freq. variable *b*	0.20	0.22	0.23	0.22	0.23	0.20	0.24	0.21	0.20	0.005
Freq. variable *k*	2.29	2.48	2.51	2.46	2.49	2.33	2.50	2.41	2.37	0.037
GAP[a] Total	28.9	29.6	29.9	30.4	29.9	28.1	30.4	30.5	27.5	0.4
GAP Patch	68.0	75.8	81.9	77.3	76.8	71.6	91.0	71.6	63.1	1.4
Adjusted GAP Patch	231.9	255.6	274.8	*252.6*	*255.7*	*254.0*	300.5	233.7	228.2	3.3
GAP Path	66.4	74.9	80.7	74.0	75.8	72.1	90.5	70.8	60.6	1.1
Adjusted GAP Path	226.5	252.5	270.8	241.3	252.5	256.0	298.8	231.9	219.1	2.6
GAP Heather	21.9	21.3	20.5	22.1	21.4	20.2	19.4	23.1	21.1	0.3
Adjusted GAP Heather	76.4	72.0	68.6	*73.0*	*72.0*	*72.0*	63.8	75.9	77.3	0.5

[a] GAP = Grazed area proportion

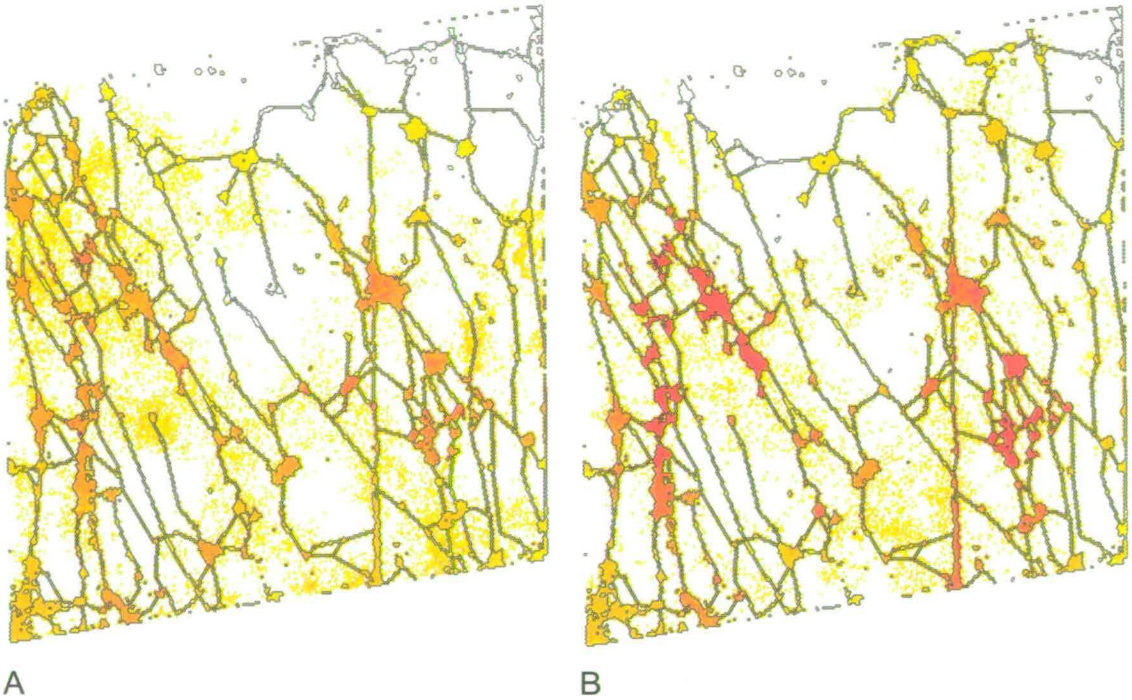

Figure 5.10. Defoliation maps resulting from animals foraging with different degrees of *determinism*: A) low *determinism*, B) high *determinism*. Values for the *distance coefficient* and the *relative resistance* are constant at -0.50 and low respectively. The grass patches and paths are indicated by their outline. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red).

Determinism

Increased *determinism* leads to a decrease in the *range* and an increase in both the *nugget* and the *partial sill* (Table 5.7). The *determinism* reflects how flexible animals are when selecting their food. Highly deterministic animals will only eat from the best quality food resource, in this case the grass, and their grazing pattern thus becomes limited to areas with lots of grass. This means that their foraging will become spatially correlated across small distances, i.e. more clustered (Figure 5.10). This means a decreasing *range* and, as the contrast between grazed and ungrazed areas increases, an increasing *sill*.

Increased *determinism* leads to an increase in both the *frequency variables b* and *k*. An increase of b indicates that the peak of the frequency distribution of the heather defoliation becomes less skewed to the left, while an increase of k indicates that the right tail has increased at the cost of the left tail. In other words, large values of heather defoliation increase in frequency with increased *determinism*. This confirms the change in pattern observed through the decreasing *range*. A decreasing *range* indicates more intensive grazing on a smaller area of heather, leading to an increased frequency of larger values of heather defoliation.

As the animals increase their determinism to eat high quality food resources, the need to move decreases. As their *foraging time* increases, the animals increase their *biomass intake*, their *digestibility*, their *energy efficiency* and subsequently their *energy intake*.

Residence time decreases with *foraging time* because the animals graze the grass patches shorter and shorter. Determined to eat high quality food, the animals manage to decrease the proportion of heather in the diet slightly.

As the *determinism* increases, both the *digestibility* and the *foraging time* increase, leading to higher *energy efficiency*. With increasing *biomass intake*, the animals increase their *net energy intake rate* by 18%. At the highest *determinism*, the animals perform 11% better than the animals using a random walk.

Distance coefficient

The *distance coefficient* has a strong effect on the mobility at the cost of the intake rates. Animals initially manage to keep *biomass intake* stable, but when the *distance coefficient* is highest *biomass intake* decreases (Table 5.7). A small *distance coefficient*, i.e. more weight given to local cells, leads to the maximum proportion of the landscape visited, coinciding with maximum *biomass intake* and maximum *grazing time*. With increasing *distance coefficient*, the animals walk more and across longer distances. As the *biomass intake* goes down, so does the *energy efficiency*. With a large *distance coefficient*, i.e. more weight given to distant cells, animals are more willing to walk, thus leading them away from poor or depleted areas.

Increased *distance coefficient* leads to an increase in the contrast between high and low defoliation areas (higher *sill*) (Table 5.7). It leads to a decrease in the contribution of small scale heterogeneity in the variance (i.e. high defoliation zones become more evenly defoliated; decreasing *relative nugget effect*). It also leads to more *movement* which leads to a higher *energy intake rate* at the intermediate *distance coefficient*, but increased *distance coefficient* results in a lower *biomass intake*. With energy cost increasing and *digestibility* stabilising, their *net energy intake* thus goes down.

The *frequency distribution variables b* and *k* both slightly increase initially and then decrease with increasing *distance coefficient* (Table 5.7). As the animals increase their walking, more heather patches are grazed at lower heather defoliation, leading to an increasingly skewed distribution.

Although the *distance coefficient* was expected to increase foraging success, the *net energy intake rate* drops by 2.3% at the high *distance coefficient* (Table 5.7). However, at the intermediate level, the *net energy intake rate* increases by 1.3%. The intermediate *distance coefficient* performs 4.9% better than the random walk (Table 5.5). Thus, while intermediate levels of perception are beneficial, responding to high perception of distant resource patches does not lead to better performance in this poor quality landscape.

Relative resistance

The animals' foraging success is strongly affected by the *relative resistance* of the vegetation (Table 5.7). Increased resistance leads to decreased *biomass intake*, decreased *digestibility* and thus a decrease in the *net energy intake rate*. Because the animals are forced to use the grass more as a result of the increasing *relative resistance* of heather, their diet contains increasingly less heather. Forced to eat the grass, the grass will get shorter and shorter.

Increased *relative resistance* of the heather constrains the animals to the grass for their foraging and walking (Figure 5.11). At low and intermediate *relative resistance* of grass and heather animals manage to visit the same number of cells, but this drops where there is high contrast in *relative resistance*. The *nugget* drops as the *grazed area proportion* decreases, i.e. increased grazing pressure on a small area, as local contrast in defoliation decreases.

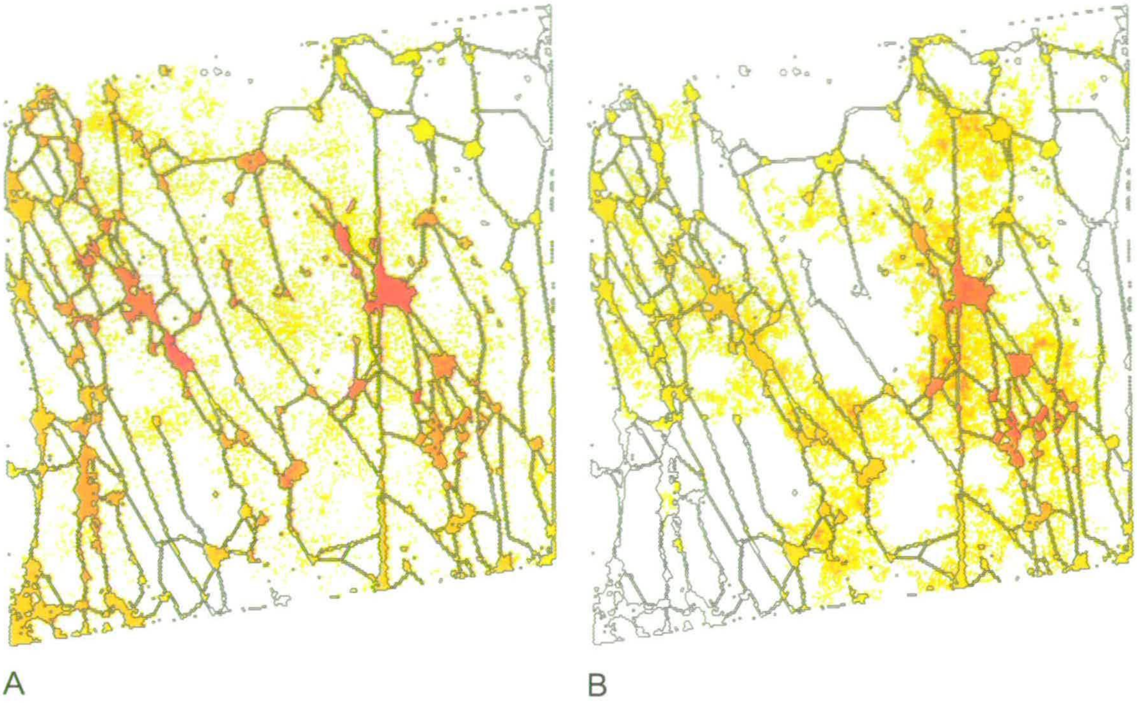

Figure 5.11. Defoliation maps resulting from animals foraging with different degrees of *relative resistance*: a) low *relative resistance*, b) high *relative resistance*. Values for the *determinism* and the *distance coefficient* are constant at 2 and -0.50 respectively. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red).

Increasing resistance makes walking through the mosaic (largely dominated by heather) too costly. Animals therefore refrain from walking long distances and spend more time grazing. Despite this, foraging costs go up and *energy efficiency* goes down. This is because animals are forced to move because they overexploit their local environment. Animals perform 21.3% better than random, but the animals endure a decrease of 24% in *net energy intake* at the highest *relative resistance* of vegetation. The relative resistance seems to overrule the effect of other perceptional abilities.

Relative resistance - distance coefficient interaction

The interaction between the *relative resistance* and the *distance coefficient* shows that the importance of the *distance coefficient* decreases with increased *relative resistance*. This suggests that in a highly resistant landscape, the performance of strategies converges.

5.3.3 Experiment 2: determinism, discriminative ability, distance coefficient

Principal component analysis

The principal component analysis (Figure 5.12) shows an interaction between the first and second axis. While the first axis again seems to be related to mobility, with movement opposite to *grazing time* and *biomass intake rate*, the second axis seems to be indicating an interaction between the mobility, local heterogeneity (*nugget*) and diet (*heather proportion* and *energy intake*). Some clusters in the previous principal components analysis are now pulled apart by the two axes.

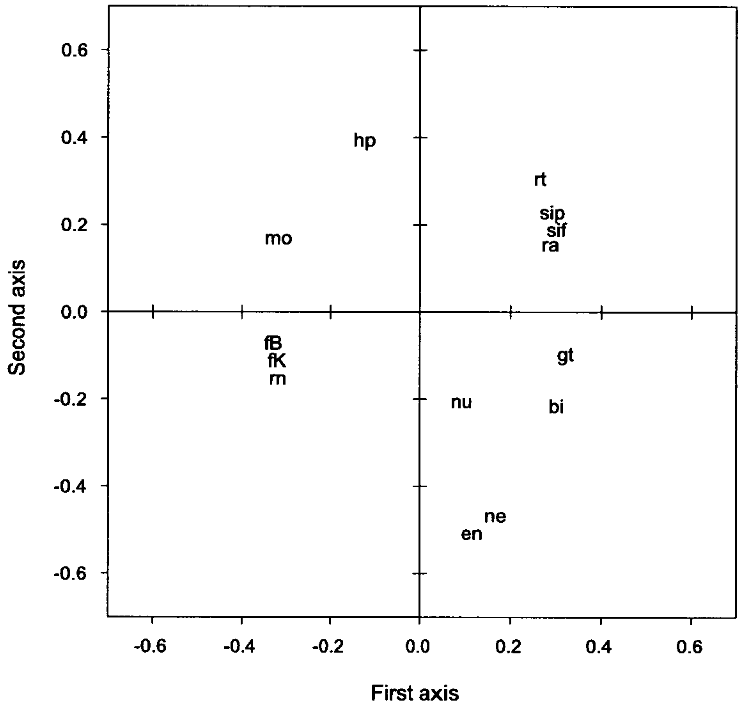

Figure 5.12. First and second axis scores resulting from the principal component analysis of Experiment 2. For explanation of labels see Figure 5.9.

Determinism

Performance, i.e. *net energy intake rate*, of the strategies is generally lower (Table 5.8) than in Experiment 1 (Table 5.7). Notable is also the higher *range*. The effects of the *discriminative ability* and/or the *resistance* are thus additive to the effect of the *determinism* and the *distance coefficient*.

Table 5.8. Treatment means for Experiment 2, with treatments: *determinism, discriminative ability,* and *distance coefficient*. The standard error of differences (SED) presented are averages for all treatments. Treatment means are printed in italics when treatment effect was not significant ($p > 0.05$) for that variable. See methods section for explanation and units of variables.

Variable	Determinism			Discriminative ability			Distance coefficient			SED
	1	2	3	low	medium	high	-0.75	-0.50	-0.25	
Energy intake	4.80	5.37	5.71	5.35	5.37	5.16	5.33	5.34	5.21	0.03
Net Energy intake	4.45	5.06	5.43	5.13	5.08	4.73	5.02	5.03	4.89	0.03
Energy efficiency	92.6	94.2	95.0	96.0	94.4	91.4	94.1	94.0	93.6	0.1
Movement	4.88	3.96	3.52	2.72	3.85	5.78	3.97	4.09	4.30	0.04
Grazing time	65.1	69.0	71.4	78.7	70.1	56.5	69.5	68.6	67.3	0.2
Residence time	2.30	2.00	1.77	2.49	2.06	1.51	*2.04*	*2.01*	*2.03*	0.03
Range	16.18	12.50	10.08	22.73	12.23	3.78	*12.95*	*12.03*	*13.78*	1.80
Sill (× 10^{-5})	*0.56*	*0.61*	*0.63*	0.82	0.54	0.44	0.54	0.57	0.69	0.03
Partial Sill (× 10^{-5})	*0.45*	*0.47*	*0.46*	0.70	0.36	0.32	0.40	0.43	0.55	0.03
Nugget (× 10^{-5})	0.12	0.14	0.17	0.13	0.18	0.12	*0.14*	*0.14*	*0.14*	0.01
RNE	*27.2*	*24.8*	*28.0*	17.4	33.8	28.8	29.4	26.5	24.1	1.4
Biomass intake	6.48	6.98	7.24	7.52	7.04	6.14	6.97	6.94	6.79	0.02
Digestibility	74.7	77.3	79.2	71.0	76.3	83.9	*76.8*	*77.3*	*77.2*	0.3
Heather proportion	62.8	60.1	58.7	*59.9*	*60.8*	*60.9*	61.3	60.9	59.5	0.5
Freq. variable *b*	*0.21*	*0.21*	*0.22*	0.14	0.21	0.29	0.22	0.21	0.20	0.005
Freq. variable *k*	*2.38*	*2.38*	*2.42*	1.99	2.44	2.75	2.45	2.38	2.35	0.036
GAP[a] Total	28.1	29.0	29.0	29.1	30.6	26.4	29.4	29.4	27.4	0.4
GAP Patch	65.6	71.9	75.0	54.4	71.1	87.0	72.5	72.7	67.4	1.3
Adjusted GAP Patch	234.5	250.9	262.5	186.2	231.5	330.2	*248.2*	*250.6*	*249.1*	3.2
GAP Path	63.8	70.8	75.0	53.4	70.9	85.3	70.1	71.7	67.9	1.2
Adjusted GAP Path	228.2	247.0	262.0	182.6	230.8	324.2	239.8	247.0	250.8	2.6
GAP Heather	21.5	21.3	20.7	24.6	23.3	15.5	21.7	21.6	20.1	0.3
Adjusted GAP Heather	76.0	72.9	70.6	84.6	76.2	58.7	*73.7*	*72.9*	*72.9*	0.5

[a] GAP = Grazed area proportion

Discriminative ability

The *discriminative ability* determines whether animals are sensitive to more distant and isolated high quality resource patches. The *discriminative ability* showed a very strong effect on the *range* of the variogram. At low *discriminative ability* the *range* is 22.7 m, while at high *discriminative ability* the *range* is 3.8 m. A low *discriminative ability* leads to a highly clumped pattern of grazing on a part of the mosaic (Figure 5.13a), as animals do not manage to distinguish good from bad. However with improved *discriminative ability,* animals successfully explore the whole complex mosaic, leading to a highly spread pattern of grazing (Figure 5.13b). High distance sensitivity enables the animals to find resource patches more effectively, leading to a better fit between defoliation and vegetation pattern. The *discriminative ability* also has an impact on the *sill.* As the *range* drops and the defoliation becomes more clumped, the correlated variance decreases. The *nugget* is high for the intermediate *discriminative ability.* The *nugget* is the unexplained variance below the minimum lag distance. As the animals find their way around the vegetation mosaic more effectively, the small scale heterogeneity initially increases, but at high *discriminative ability* the animals again zoom in on a small area, increasing grazing pressure and decreasing the small scale heterogeneity again.

Both *frequency distribution variables b* and *k* increase rapidly with increasing *discriminative ability* (Figure 5.8). This coincides with the strong decrease of the *range.* As animals find their way around the mosaic more effectively, their use of the heather becomes more associated with the grass network. The area of heather affected (*grazed area proportion*) decreases while the severity of defoliation per patch increases, leading to an increase in the frequency of high heather defoliation.

Because high quality resource patches are scattered around the environment, animals have to move more in order to visit these patches (Table 5.8). Although there is a cost associated with movement, their initial *net energy intake* remains high due to the increase in *energy intake rate.* The animals can sustain their *energy intake rate* as a result of the higher digestibility the animals achieve from the resource patches visited. This coincides with a decrease in *biomass intake,* as the animals spend more time walking. At the highest *discriminative ability,* the increased ability leads to strongly decreased *foraging time* and increased movement over longer distances. The *biomass intake* thus collapses, resulting in a very poor *energy efficiency*. The animals endure a decrease in *energy intake rate* of 8% at the highest *discriminative ability* compared with the lowest ability.

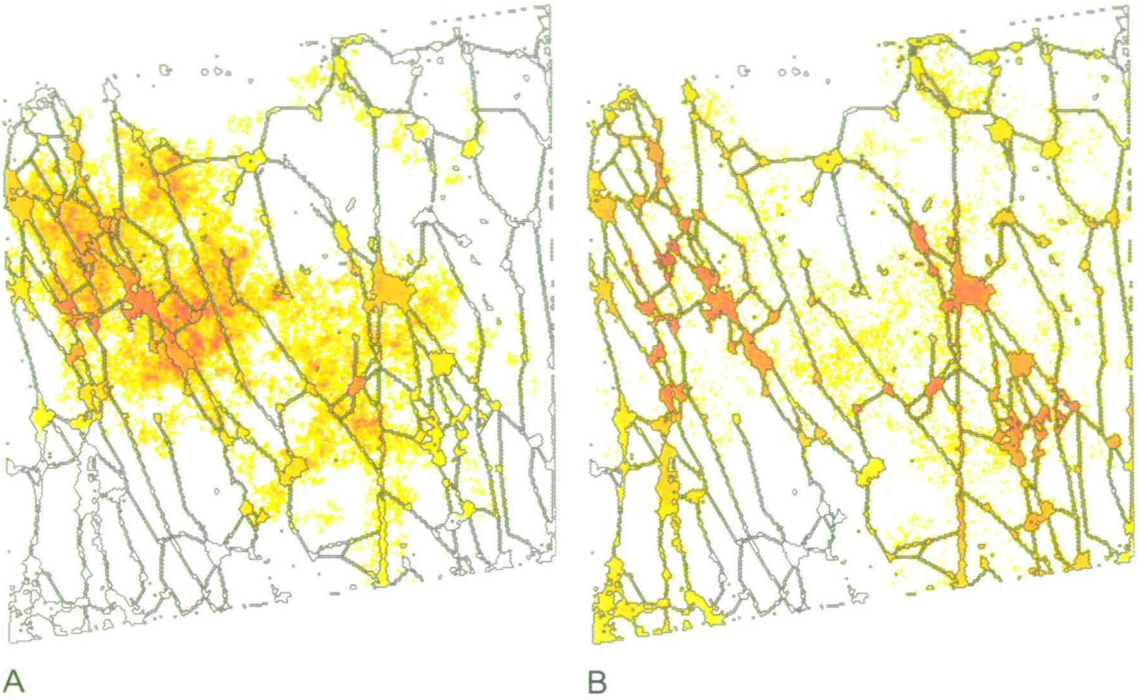

Figure 5.13. Defoliation map resulting from animals foraging with different degrees of *discriminative ability*: A) low *discriminative ability*, B) high *discriminative ability*. Values for the *determinism* and the *distance coefficient* are constant at 2 and -0.50 respectively. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red).

Distance coefficient

The results for the *distance coefficient* are similar to the results in Experiment 1. The combination of different treatments in this experiment leads to a 5.6% decrease in *energy intake rate* (for the intermediate *distance coefficient*) as compared to Experiment 1. Furthermore, several variables have no significant treatment effect. Although not surprising, it is good to be reminded that an experimental design using several treatments at the same time will influence both the significance and the strength of treatment effects. This is because the high *determinism* leads to an increased *digestibility*.

Interaction between determinism and discriminative ability

The interaction shows that high *discriminative ability* works well with high *determinism*. The decrease in *energy intake* at the highest *discriminative ability* (as described above), does not occur at high *determinism*, mainly because the biomass intake does not decline as strongly. Instead the animals manage to sustain a 2% increase in *energy intake*.

5.3.4 Experiment 3: mode error, movement cost, distance sensitivity

Principal component analysis

As in Experiment 2 the principal component plot shows interactions between the first and second axis (Figure 5.14). The first axis is defined by the cluster of *energy intake*, *net energy intake* and *heather proportion* in the diet, suggesting a selectivity factor. The second axis is defined by the clusters of the *sill* and *range* versus both frequency distribution variables *b* and *k* , indicating a spatial pattern factor.

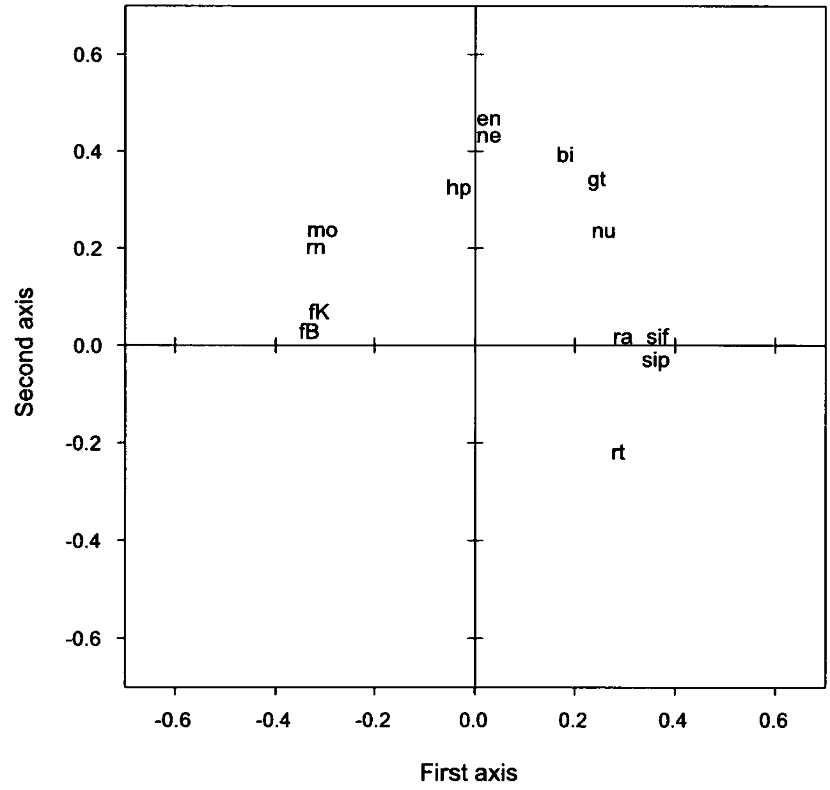

Figure 5.14. First and second axis scores resulting from the principal component analysis of Experiment 3. For explanation of labels see Figure 5.9.

Table 5.9. Treatment means for Experiment 3, with treatments: *mode error, movement cost, and distance sensitivity*. The standard error of differences (SED) presented are averages for all treatments. Treatment means are printed in italics when treatment effect was not significant ($p > 0.05$) for that variable. See methods section for explanation and units of variables.

Variable	Mode error			Movement cost			Distance sensitivity			SED
	1	0.8-1.2	0.6-1.4	0.025	0.050	0.100	0.3	0.5	0.7	
Energy	5.53	5.37	5.45	6.14	5.43	4.79	5.51	5.48	5.36	0.03
Net Energy	5.26	5.04	5.17	5.92	5.14	4.42	5.17	5.20	5.10	0.03
Energy efficiency	95.1	93.6	94.6	96.4	94.6	92.3	93.5	94.7	95.1	0.0
Movement	2.87	4.23	3.61	4.26	3.59	2.86	4.56	3.48	2.67	0.02
Grazing time	73.6	66.9	71.6	77.7	70.9	63.4	65.7	71.8	74.6	0.1
Residence time	1.94	1.88	2.09	1.74	2.00	2.16	1.59	2.02	2.29	0.02
Range	*12.53*	*11.05*	*10.80*	*10.90*	*12.48*	*11.03*	6.30	11.53	16.55	0.87
Sill (× 10^{-5})	0.74	0.63	0.59	0.72	0.66	0.58	0.58	0.63	0.74	0.02
Partial Sill (× 10^{-5})	0.56	0.46	0.43	0.52	0.49	0.44	0.42	0.45	0.58	0.02
Nugget (× 10^{-5})	0.18	0.17	0.16	0.20	0.17	0.13	0.17	0.18	0.16	0.01
RNE	*25.2*	*27.1*	*27.7*	29.1	27.3	23.7	28.9	29.0	22.1	1.2
Biomass intake	7.19	6.83	7.19	7.77	7.09	6.36	6.75	7.17	7.30	0.02
Digestibility	76.9	78.6	75.8	79.2	76.8	75.4	81.5	76.4	73.4	0.2
Heather proportion	59.5	58.0	58.9	59.5	59.4	57.5	*59.2*	*58.9*	*58.4*	0.4
Freq. variable *b*	0.16	0.22	0.21	*0.20*	*0.19*	*0.19*	0.23	0.20	0.15	0.004
Freq. variable *k*	2.09	2.42	2.39	*2.33*	*2.29*	*2.28*	2.47	2.34	2.09	0.033
GAP[a] Total	26.7	27.8	30.4	30.1	28.8	26.1	27.0	29.2	28.7	0.3
GAP Patch	68.3	70.7	67.1	78.0	69.2	58.9	78.4	67.9	59.8	1.1
Adjusted GAP Patch	258.4	255.4	220.8	265.6	243.0	226.0	294.5	231.8	208.3	2.7
GAP Path	68.0	70.3	67.4	79.0	69.2	57.5	78.9	68.0	58.7	0.9
Adjusted GAP Path	257.5	253.7	221.2	269.0	242.8	220.6	296.2	232.2	203.9	1.6
GAP Heather	19.2	20.1	23.7	21.3	21.4	20.2	17.7	22.2	23.1	0.2
Adjusted GAP Heather	71.4	72.0	78.1	69.8	74.1	77.5	64.7	76.1	80.7	0.4

[a] GAP = Grazed area proportion

Mode error

At moderate *mode error* animals walk more without improving their *energy intake rate* (Table 5.9). *Biomass intake* goes down and overhead cost goes up. At high *mode error* the extra walking leads to a recovery in intake. The *mode error* has no significant influence on the spatial pattern of defoliation (*range*), but the heterogeneity (*sill*) decreases with increasing *mode error*. Animals make more errors, i.e. more random decisions, leading to decreasing spatial structure in foraging pattern.

Movement cost

Increased *movement cost* makes the animals less willing to walk, leading to an increase in *residence time*. Although they stay longer in the same patch and travel less far, their time spent grazing goes down. This is because the *movement cost* is expressed as a time penalty and is taken off the time spent grazing. Increased *movement cost* leads to a decrease in the long distance walking, but also in the time spent grazing. Animals visit a smaller proportion of the mosaic. As a result, their *biomass intake rate* drops rapidly. As their *energy efficiency* goes down, their performance drops considerably.

Distance sensitivity

Increasing *distance sensitivity* leads to a strong decrease in the average distance walked, and an increase in *grazing* and *residence time*. The *energy intake rate* goes down, but *net energy intake rate* initially increases as a result of an strong initial increase in the *biomass intake*. Increasing *distance sensitivity* leads to an increase in the *range*, as animals make their decisions more dependent on local information. The *relative nugget effect* drops at the highest *distance sensitivity*, because increased grazing pressure on a small area decreases small scale heterogeneity. While animals manage to explore a large part of the mosaic at the low *distance sensitivity* matching the defoliation pattern to the grass pattern (Figure 5.15a), the high *distance sensitivity* hampers the perception of quality, leading to a widespread, poorly matched, pattern of grazing (Figure 5.15b). Increased *distance sensitivity* thus leads to a decrease in the correlation between the grazing and vegetation pattern. Both frequency distribution variables decrease rapidly with increased distance sensitivity, indicating that the distribution of heather defoliation becomes increasingly skewed (i.e. the peak of the distribution becomes increasingly skewed to the left). As foraging is increasingly disassociated with the vegetation pattern, more heather patches are visited with a decreasing heather defoliation per patch.

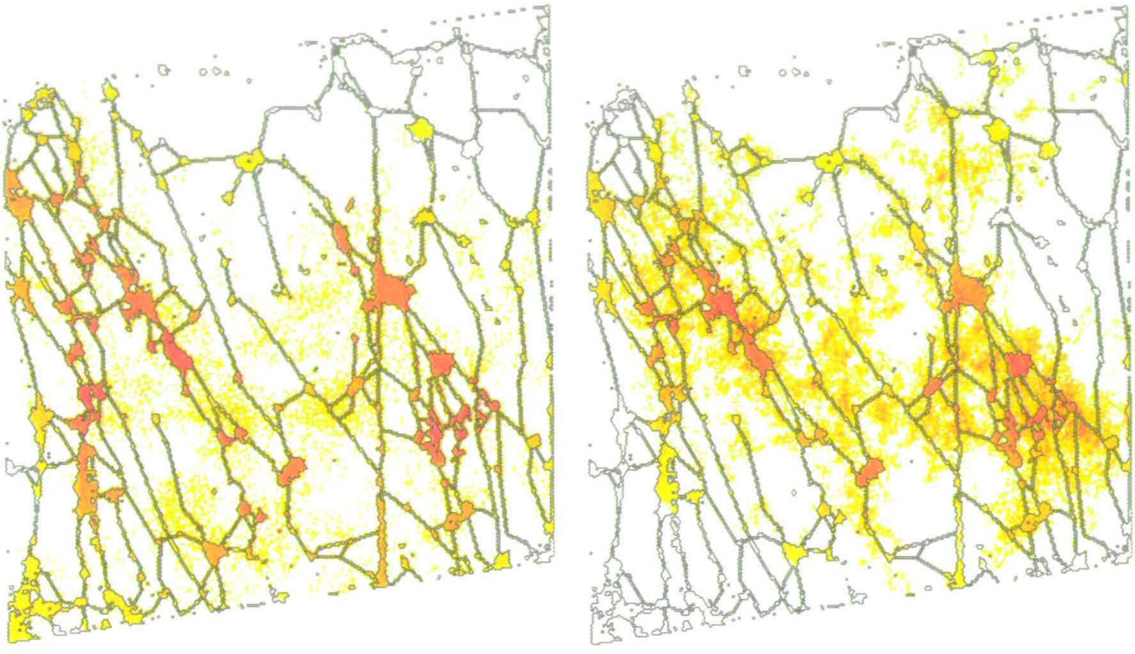

Figure 5.15. Defoliation map resulting from animals foraging with different degrees of *distance sensitivity*: A) low *distance sensitivity*, B) high *distance sensitivity*. Values for the *mode error* and the *movement cost* are constant at 0.2 and 0.05 respectively. Colours indicate amount of defoliation ranging from light (yellow) to heavy (red).

The *distance sensitivity* does not significantly influence the *heather proportion* in the diet, but *digestibility* goes down and *biomass intake rate* goes up. The *heather proportion* is constant, despite the strong decrease in the proportion of *patch cells grazed*. This implies that the grass patches that do get visited will endure a much greater defoliation. When the animals move less, their chance of finding high quality food decreases. Although this leads to a lower performance in the long run, the animals initially increase their net energy as a result of their increased *biomass intake*, resulting from increased *grazing time*.

5.4 Discussion

The results show a strong interaction between the effects of foraging strategies on the performance of the animals and the emergent pattern of vegetation defoliation.

Generally, strategies which led to a large proportion of the mosaic being visited by the animals increased their performance. However, a cost was involved in this exploration and strategies which over-stimulated mobility led to a decrease in *energy efficiency*. This suggests that high perceptional ability is not necessarily an advantage in complex, generally poor quality, vegetation mosaics.

The pattern of vegetation defoliation was strongly affected by the selectivity of the animals and their mobility. Selectivity of the animals resulting from the *determinism* to eat high quality feed resources led to an increased correlation between the vegetation and vegetation defoliation pattern. Although the overall area grazed remained constant, grazing shifted from a locally dispersed pattern to a globally converged pattern, such that at high selectivity the majority of the defoliation occurred on the grass patches and paths. Higher mobility led to an increase in the small scale, i.e. local, heterogeneity. As mobility decreases, grazing becomes increasingly spatially limited leading to increased pressure on a small area, thus decreasing the variation in defoliation between cells in the grazed area.

The aim of these experiments was to investigate foraging strategies, based on several perceptional parameters, which could explain observed foraging patterns. The frequency distribution and the range of the variogram of the spatial pattern of heather defoliation were used to relate simulated to observed patterns. In a direct qualitative comparison, the results suggest that an animal's foraging strategy would be based on low determinism, high distance coefficient, high relative resistance, low discriminative ability, low mode error, low movement cost and low distance sensitivity. This translates as a low perceptional, large scale foraging strategy. However a direct comparison was considered to be inappropriate, as the model was parameterised in order to produce varying spatial patterns, rather than to be quantitatively realistic. For example, no validation was made to ensure that observed and simulated patterns resulted from the same grazing pressure. During the simulations, grazing pressure, i.e. the number of animals, was kept constant. The difference between the frequency distributions for Plot 1 and 3 shows that grazing pressure could affect the characteristics of the heather defoliation. The frequency distribution of Plot 1 was less strongly skewed as compared to Plot 3, and more similar to the frequency distributions of the simulated patterns.

Results suggest that generally intermediate levels of selectivity and mobility lead to the best animal performance, while at the same time resulting in a strong correlation between the pattern of grass and the pattern of defoliation. Furthermore results show that perception across several scales can contribute to a better performance of the animal. This is complementary to the argument of Illius and Gordon (1993), that foraging decisions cannot be made on small scales in time and space. To achieve a high quality diet, animals have to be able to explore their environment. Although results suggest that highly perceptive strategies can lead to different diets and patterns of defoliation, differences in performance resulting from these strategies remained small. This indicates that resource heterogeneity, i.e. the complexity of the landscape, has a strong effect on strategy performance. This confirms earlier simulation studies in which performance of strategies converged with decreased abundance of the preferred feed resource (Moen et al., 1997; Turner et al., 1994).

Experiments with sheep have shown that the animals can use spatial memory to locate previously visited food patches (Edwards et al., 1996; Edwards et al., 1997). It is expected that strategies including some form of spatial memory, will do better in heterogeneous/complex mosaics when the strategy allows for a more effective exploration of the mosaic. However a trade off occurs between memory capacity and foraging success. Results from this simulation study suggest that the energy return of spatial memory could be limited due to the complexity of the landscape. Highly perceptional strategies were less successful. Animals could optimise the energy return of spatial memory by varying spatial resolution and extent of the memory. Moderate perceptional strategies might benefit from spatial memory at a low resolution and a large extent. Thus animals would be more efficient in selecting better quality resource areas at a larger scale.

The modelling approach used here provided an effective tool to investigate the role of perceptional parameters in an artificial plant-herbivore system. Contrary to field experiments, the modelling environment allowed us to vary parameters at will and investigate the output in great detail. Both the animal performance and the resulting pattern of defoliation responded strongly to variation in the parameter values, allowing for a functional analysis of parameters and interactions. However, possible parallels between model and field observations can only be speculative and quantitative correlations can only be achieved through further field observation and experimentation. Emergent properties can provide the bridge between model parameters and variables measurable in the field.

The spatial statistical analysis showed two interesting phenomena in the results from the virtual experiments. Firstly, the model variograms generally showed a large *relative nugget effect*, i.e. a large part of the variation in the vegetation defoliation was not spatially correlated. This also arose from the field observations of heather defoliation, which showed high variation at small spatial scales (see discussion Chapter 4). The large *relative nugget effect* could indicate that animals using strategies similar to biased random walks take random decisions at the smallest spatial scale and biased random decisions at larger scales. On the other hand the effect could be caused by the maximum fraction of biomass that can be consumed at once in a cell, possibly linked to a fixed amount eaten by herbivores per feeding station (Wallis de Vries et al., 1999). However, the pattern of defoliation of the simulation result considers both grass and heather, thus the effect could also be the result of the contrast in defoliation across the boundary between heather and grass. Therefore, further investigation is needed to understand the cause of the large *relative nugget effect* and possible ecological relevance.

Secondly, the results showed sample variograms which increased up to the maximum lag distance. This suggests that the mean vegetation defoliation of one part of the vegetation mosaic is not equal to the mean at another part of the mosaic. This violates one of the main assumptions of the semi-variogram analysis, that of the stationary mean (Isaaks & Srivastava, 1989). A non-stationary mean suggests that the spatial pattern under study is the result of at least two processes operating at different spatial scales. To ensure a stationary mean, the appropriate scale of observation has to be selected carefully. It is however questionable whether complex ecological systems have 'appropriate spatial scales'. It is likely that any scale of observation is also affected by processes working either below or above the chosen scale.

In this study three separate, latin square designed, experiments were carried out to investigate seven parameters. Although this resulted in convenient processing jobs and file sizes, facilitating the investigation of several parameters, a latin hyper-cube sampling design (McKay et al., 1979) would have provided a wider range of results. This was however not feasible given the amount of time and computer resources available. This is effectively a single latin square design, incorporating all parameters in one experiment. This provides insight into all parameters and all possible interactions, thus extending the approach used in this study. The latin hyper-cube sampling is often used in sensitivity analysis of simulation models.

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Chapter 6

Discussion

> If we are not careful to preserve a considerable area of heath as
> a memorial, then I do not doubt that our descendants will
> censure us for our short-sightedness and lack of feeling.
>
> C. Raunkiær (1913)
>
> Translated by H. Gilbert-Carter in Raunkiær et al. (1934)

6 Discussion

6.1 Results summary and synthesis

The chapters in this thesis provide an insight into the spatial pattern of defoliation by sheep across heather-grass mosaics. Chapter 2 provides a statistical description, in the form of a spatial interaction model (SIM), of the pattern of heather defoliation. The SIM shows that the pattern of defoliation of the less preferred food resource was strongly driven by the distribution of the preferred food resource, in this case the heather and grass respectively. Heather defoliation at the grass-heather edge was predicted as a function of the availability and size of grass patches in the vicinity. The model shows that heather defoliation along the paths decreased with increasing distance from the grass patches and increased with increasing patch size. An implication of the model is that the amount of heather consumed will depend on how the preferred and less preferred species are mixed within the mosaic. As the pattern of grazing will depend on the pattern of vegetation, manipulating the pattern of vegetation could be used as a management tool to influence patterns of grazing. An example of manipulation of the pattern of vegetation is provided by Clarke et al (1995a; 1995b). The mosaics used in the experiments were artificially created through cutting and fertilising.

Chapter 3 shows that the heather defoliation away from the grass-heather edge was strongly influenced by the grazing pressure at the edge zone. Increasing grazing pressure led to an increase in the width of the zone of impact, not only an increase in defoliation at the edge as previously assumed. The findings suggest that under high stocking densities, a large area of the heather could be affected, while at low stocking densities only a small area of the heather could be affected. Combining these results with those of the previous chapter would suggest that the area of heather affected by grazing would be highest for highly intermixed heather-grass mosaics at high stocking densities and lowest for lightly intermixed mosaics at low stocking densities. From the data I propose new hypotheses which involve the existence of multiple stable states. These propositions require further research.

Chapter 4 shows that, contrary to usual assumptions, defoliation was only one of a number of processes leading to fragmentation of heather (change from heather to grass) as a result of herbivore impact. Ruminating behaviour also appeared to be an important process in the fragmentation of heather. While the impact of ruminating behaviour occurred in a few large patches associated with the resting areas, the impact of heather defoliation was spread across the mosaic in small patches. Combined with results from the previous two chapters, this suggests that fragmentation of heather is more likely to occur near large grass patches and more likely to occur when grass and heather are intimately mixed within the mosaic. Qualitative findings suggested that life history and grazing history of plants also affected herbivore impact on vegetation, but this requires further investigation. As these factors are likely to be spatially correlated with the pattern of herbivore impact, they could play an important role in plant-herbivore interactions. The role of ruminating behaviour in the distribution of herbivore impact on vegetation can easily be integrated into the SIM. Instead of a model with a single source of attraction, an extended SIM predicts the attraction of a point in the mosaic based upon the attractions of both resources. Through statistical modelling the appropriate model for predicting the attraction of the resting site needs to be determined. The total attraction would then be a function of the attractions of the two sources. This could be a simple summation, if the attractions are purely additive, or more complex equations, i.e. assuming interactions between the two sources of attraction.

Chapter 5 shows, through a virtual experiment, a strong interaction between the vegetation pattern and the performance of foraging strategies, resulting in the emergent pattern of vegetation defoliation. Although increased perceptional abilities made the animals more successful in exploring their environment, increased mobility decreased energy efficiency. Thus moderate perceptual abilities enabled the highest animal performance. The patterns of defoliation resulting from foraging strategies using moderate perceptional abilities were qualitatively similar to patterns observed in the field experiment (see earlier chapters) and other field experiments. As discussed in Chapter 2, one of the strengths of the SIM is to evaluate the spatial patterns resulting from individual-based models. This approach was considered but it was not possible to pursue further due to time limitations.

6.2 Implications for plant-herbivore interactions

The field experiment in this study used the Scottish Blackface sheep, as this is the breed most commonly used in upland hill farms. Scottish Blackface sheep are renowned for being hardy and more self-sufficient than many lowland breeds, thus being suited to survive in the extreme environment of the Scottish uplands (National Sheep Association, 1987). Apart from this physical adaptation, it is likely that the breed has adapted its foraging strategy to fit the complex heather-grass mosaics on offer. A telltale sign is that the nearest neighbour distance in Scottish Blackface sheep is one of the highest among sheep breeds (Arnold & Dudzinski, 1978). This allows the flock to spread out across a vegetation mosaic with sparse grazing (National Sheep Association, 1987). Furthermore Scottish Blackface are hefted sheep, meaning that lambs are loyal to the area or hill side at which they are weaned (Hunter, 1962b; National Sheep Association, 1987). Over time the flock could increase their knowledge of the heft, thus increasing their grazing efficiency. As sheep often use fixed resting sites (Arnold & Dudzinski, 1978), they are likely to develop a central place foraging routine (Bell, 1991). This will intensify the pattern of impact on the vegetation.

This study focussed on the impact of foraging behaviour of sheep on heather-grass mosaics. However, experiments using the same experimental site also studied the behaviour of red deer (Hester & Baillie, 1998; Hester et al., 1999). Foraging behaviour and subsequent diet composition of red deer were generally less affected by the pattern of vegetation than were sheep (Hester et al., 1999). Although this can be partly explained by the increased ability of red deer to digest heather (Milne et al., 1978) and other characteristics related to body size (Gordon et al., 1996), difference in perceptional abilities (such as perception of resistance of heather) and foraging strategy (being less deterministic in foraging the preferred vegetation type) could also explain observed differences between sheep and red deer. Thus, while sheep might become encounter-limited as grass and heather get more intimately mixed, as suggested by Hester et al. (1999), red deer might be able to compensate for increased fragmentation through perceptional abilities and foraging strategy. The results from the virtual experiment suggested that both a rigid highly deterministic foraging strategy and high resistance sensitivity (a perception ability) led to reduced performance of the animals in the highly fragmented mosaic. Willingness to eat a mixed diet and a more mobile foraging strategy led to increased net animal performance, despite reduced digestibility of the diet.

The results of the virtual experiment suggest that the vegetation plays an important role in determining herbivore performance, but that perceptional abilities used in foraging strategies can improve performance. The emergent patterns of defoliation varied strongly with foraging strategy. Surprisingly, some foraging strategies resulting in similar herbivore performance showed very different patterns of defoliation. This could imply that spatial aspects of foraging strategies could play an important role in interspecific competition and facilitation between herbivore species in herbivore assemblages. For example a herbivore foraging randomly at a particular scale could facilitate a herbivore foraging selectively at that same scale. This is further discussed in the future research sections.

The spatial pattern of herbivore impact has implications for the development of heather-grass mosaics. As sheep focus on the preferred vegetation type and herbivore impact is higher around larger patches of the preferred type, large patches of the preferred type are expected to grow faster than smaller patches. Pattern initialisation in heather-grass mosaics could be similar to pattern initialisation in physical processes, such as the formation of snow flakes or air bubbles in boiling water. Both processes need nucleation points as a starting point for the process. Nucleation points for heather fragmentation could be provided by collateral damage of the herbivores (for example trampling) or the activity of other animals. For example, rabbit burrows create an opportunity for grasses to invade the heather. Once the grass is established, this grass patch could initiate increased herbivore impact and subsequent growth of the grass patch. Another possible source of nucleation points could be degenerate heather bushes, in the sense of the cyclical process of heather stages (Watt, 1947). The role of these processes can at this point only be hypothesised, and should be tested in field experiments.

The main spatial scale considered in this study was that of grass patches within heather in plots of one hectare. The findings confirmed and extended results from previous studies (Clarke et al., 1995a; 1995b; Hester & Baillie, 1998) which showed that heather defoliation occurs predominantly in a narrow zone around the edge of grass patches. Scaling up from one hectare plots to hillsides or landscapes, i.e. at the scale of the feeding site, camp or home range (Bailey et al., 1996; Roguet et al., 1998), it is likely that selection of the preferred vegetation type remains an important driver for the distribution of habitat use (Bailey et al., 1996; Senft et al., 1987). Although aspects such as topography, shelter, water access, and seasonal movement might become more important (Bailey et al., 1996), the abundance of grass within the heather-grass mosaic is hypothesised to affect the pattern of heather defoliation. Thus in parallel with the zone of defoliation around grass patches with a heather-grass mosaic, heather defoliation is hypothesised to be spatially limited to an impact zone at higher scales. Heather-grass mosaics, occurring between larger areas of homogeneous grass and homogeneous heather (homogeneous at this larger scale), could therefore form an impact zone suffering most of the heather defoliation compared with the heather area behind it. This effect can be observed on Finella Hill where, at the larger scale, sheep select for the improved grasslands on the lower part of the hill, and heather defoliation and subsequent impact occurs in a zone neighbouring the improved grassland. The homogeneous heather at the top of the hill is rarely visited. To determine whether selection of the preferred vegetation type also affects patterns of heather defoliation at larger scales, the SIM approach could be applied.

Although the insight into one ecosystem can be used to investigate other ecosystems, care should be taken to extrapolate results. Processes in one grass-shrub ecosystem can not be easily extrapolated to other systems without critical understanding of both systems and the drivers of the processes (Martinez & Fuentes, 1993).

6.3 Future research

Important extensions of the current study are required to unravel the complex of interactions between plants, herbivores, and soils. Results from this study suggested that the behaviour of herbivores could be affected by the feedback processes of vegetation responding to previous grazing impact, such as shoot density and vegetation structure. Thus characteristics of the vegetation should be observed across the grass-heather gradients following the same methods (i.e. a spatial grid of transects) deployed in this study, to quantify these responses. Some characteristics of interest are vegetation height, dry matter composition of plants (i.e. ratio of shoot to stem), shoot density, shoot length and shoot quality. Because these measurements are destructive, they can not be easily combined with animal observation studies. However the vegetation on Finella Hill provides ample opportunity to combine vegetation response data with the animal and vegetation observations presented in this study.

Across the same grass-heather gradients, the impact of defoliation and trampling should be observed and quantified separately. Due to the possible delay in trampling impact (Bayfield, 1979), observations should be carried out across multiple years. Trampling impact could be observed directly from physical signs, such as damage to the bark and broken stems, or indirectly through observing animal locations. However, controlled experiments will be required to relate either physical damage or herbivore presence to actual impact on heather. It will be a challenge to design an appropriate sheep trampling simulator!

Still considering the same grass-heather gradients, changes in soil properties, such as soil compaction, depth of litter layer and nutrient availability should be quantified and related to the other observed gradients. A pilot study to this effect has been carried out on the experimental site in 2002 (Campbell et al., unpublished).

Finally, all these aspects should be considered in the study of the vegetation dynamics occurring across the grass-heather gradient. Findings in this study suggest that selective foraging by sheep led to increased contrast between vegetation types and reduced contrast, i.e. increased homogeneity, within vegetation types. This suggests that competition between grass and heather will predominantly occur at the grass-heather edge. This has implications for the competition and possible coexistence of plant species (Murrell et al., 2001). The combination of all these different elements of the system would create a unique case-study to investigate the complex plant-herbivore-soil dynamics in grazed ecosystems (Pastor et al., 1997) and would be an empirical observation related to the theoretical advances made through reaction-diffusion theory in the context of grass-heather boundaries (Farnsworth & Anderson, 2001).

A major question in grazing ecology is how a large number of different herbivores can coexist within an ecosystem (Farnsworth et al., 2002; Murray & Illius, 1996; Olff et al., 2002; Prins & Olff, 1996; Sinclair, 2000). One of the best known examples is the Serengeti-Mara ecosystem (Sinclair & Norton-Griffiths, 1979; Sinclair & Arcese, 1995). The findings presented in this thesis suggest that the spatial pattern of habitat use by herbivores is strongly influenced by the pattern of vegetation and that the herbivore foraging strategy can affect herbivore performance. Thus spatial aspects of foraging behaviour could play an important role in the competition or facilitation of herbivores in large herbivore assemblages. In order to investigate this, either the behaviour of several herbivores can be spatially quantified simultaneously (following the method of animal observation described in Chapter 4), or the emergent pattern of herbivore impact can be observed for different subsets of the total herbivore assemblage (following the method of heather defoliation observation in Chapter 3). Different patterns of competition and facilitation should be expected at each spatial scale, such that the experimental sampling scheme should follow a nested design across several scales.

The HOOFS model provides an excellent opportunity to investigate the role of numerous aspects of foraging behaviour and vegetation dynamics on emergent spatial patterns of herbivore impact. Currently in the model, foraging decisions made by the animals are independent of the state of the animal. An important extension of the model would therefore be a state dependent diet selection module (e.g. Newman et al., 1995). The investigation of state-dependent foraging behaviour could reveal shifts in foraging strategy across spatial and temporal scales. These changes can be difficult to observe in diet composition field trials, as diet is an emergent property resulting from many single foraging decisions. The role of memory is already being investigated and early results suggest that animals with increased spatial memory forage more efficiently in complex mosaics than forgetful animals (Beecham et al., 2002).

Early results suggest that livestock breeds can have different responses to vegetation mosaics and subsequently impact on vegetation (Bullock & Oates, 1998; Newborn, 2000). With the increasing use of large herbivores as nature conservation management tools (van Wieren, 1995; Wallis de Vries et al., 1998), there is an urgent need to understand the role of breed differences in plant-herbivore interactions. An experimental facility such as present on Finella Hill, would enable the investigations of foraging behaviour of different breeds and quantify their foraging pattern and their pattern of impact.

A potentially interesting application of high resolution aerial photography (such as used in this study) was suggested by Quilter & Anderson (2001). They successfully correlated heterogeneity in spectral reflectance with levels of shrub defoliation. The ortho-photographs prepared to detect vegetation change in this study would provide a good opportunity to investigate this application. If successful, large areas of habitat could be surveyed at very high detail with little effort relative to the effort needed to achieve the same detail through field observations. It would also facilitate repeated monitoring to investigate temporal aspects of plant-herbivore interactions.

The SIM approach presented in Chapter 2 provides a new tool to investigate spatial aspects of plant-herbivore interactions in different ecosystems and at different spatial and temporal scales. As herbivores are selective across a range of scales (Roguet et al., 1998; Senft et al., 1987), the sources for selection are likely to cause a characteristic pattern of attraction at various scales, which can be very effectively investigated using the SIM approach. The SIM used in this study considered one resource at one scale (grass patches), but there are no methodological limitations preventing an application of a SIM for multiple resources across multiple scales. Moreover, the applicability could be considered of the more mechanistic spatial interaction models based on spatial information processing theory, including spatial cognition and hierarchical decision making (Fotheringham et al., 2000).

To test whether selection of the preferred vegetation type affects the spatial pattern of heather defoliation across multiple scales, the SIM approach should be applied to observations of herbivore impact across several scales. The Macaulay Institute is in possession of such data sets resulting from very extensive habitat impact assessments. With the spatial data readily available and considering the simplicity of the SIM approach, this should be an attractive project to pursue. Relating emergent patterns at the landscape scale with individual foraging behaviour of red deer would be facilitated by the insight achieved through animal tracking studies in similar habitats (Sibbald et al., 2001).

6.4 Implications for management of heather-grass mosaics

Although this PhD considered a fundamental element of grazing ecology, an attempt is made here to suggest possible management implications of the increased understanding of the spatial aspects of plant-herbivore interactions. The spatial pattern of free ranging herbivores, their impact on vegetation and subsequent vegetation change could have implications for management of heather-grass mosaics and rangelands in general. Maybe counter intuitively, their impact could be either good or bad depending on the objectives of the management. Consider the example of heather moorland mentioned in the introduction where, from a conservation objective, 'over-grazing' by sheep has often occurred in the uplands and 'under-grazing' has often occurred in the lowlands. In the uplands where fragmentation of heather is perceived as a conservation problem, the results of this study suggest that 'over-grazing' by sheep can be effectively avoided by reducing grazing pressure, i.e. stocking densities. The findings from the SIM (Chapter 2) suggest that reducing animal numbers should lead to a rapid decrease in the area of heather affected by herbivores, thus limiting the herbivore impact and potential vegetation change.

However the challenge for the lowland heathlands is very different. Here the disappearance of heather is often due to tree invasion. To halt this process successfully, herbivores would have to visit a large part of the mosaic to visit all area subject to tree invasion. However, because free ranging sheep focus their grazing on the preferred food resources, a large part of the mosaic is likely to be frequented considerably less. Only extremely high stocking densities could force sheep to graze all corners of the mosaic. However these stocking densities are not sustainable from the herbivore's performance point of view (Wallis de Vries, 1991; Wallis de Vries & Schippers, 1994) and will be likely to cause negative impact (such as severe fragmentation or erosion) on and around the, by the herbivore, preferred vegetation type (Bokdam & Gleichman, 2000; Gimingham, 1992; Hester & Baillie, 1998).

Although a system of free ranging herbivores is most natural, it might be inappropriate for the achievement of some conservation objectives as illustrated above. An increased understanding of the processes determining the spatial pattern of herbivore impact, facilitates an active manipulation of the grazing pattern for the purpose of specific objectives. Many such manipulations have been used for centuries to try to achieve optimal production from grazing systems (Gimingham, 1972; Heady & Child, 1994). Five approaches are distinguished here: 1) periodic grazing; 2) shepherding; 3) different species and breeds of herbivores; 4) manipulation of vegetation; 5) other sources of attraction.

To achieve a specific objective, grazing could be made periodical across several time scales. Limiting herbivores to daytime access only (as occurs in shepherding systems across the world), could create a gradient of herbivore impact, with herbivore impact decreasing with distance from the night time resting area (i.e. similar to central place foraging). A fixed resting area, outwith the grazing area, could also lead to a removal of nutrient from the grazed area to the night time area (Bokdam & Gleichman, 2000). Limiting grazing periods to certain seasons of the year could also affect spatial patterns of impact. As the pattern of defoliation is strongly correlated with the pattern of the preferred vegetation type, the herbivores are expected to concentrate on this vegetation type during the summer when quality is high, leading to a patchy pattern of herbivore impact, but grazing might be more evenly spread across a mosaic in winter when contrast in quality between the preferred and the less-preferred vegetation types is smaller. However, this study did not conclusively show the difference in pattern of defoliation between summer and winter periods. This was likely due to the fact that winter observations considered whole year defoliation and were thus confounded with the summer observations. Further investigations are required to support this hypothesis.

The spatial pattern of grazing could be actively managed through shepherding or through the creation of paddocks (Heady & Child, 1994). Shepherding limits the herbivore in its habitat selection at higher scales. Although animals are expected to be selective within the feeding site, animals could be forced to forage in areas of a landscape they would otherwise not select. A combination of herding and free ranging could be considered appropriate as it has been suggested that herding might force the herbivore to explore its home range (Hunter, 1962a). Temporary fencing or permanent paddocks could achieve the same result, but are unlikely to be compatible with nature conservation objectives.

As described above, the spatial pattern of herbivore impact is hypothesised to depend on the herbivore species and, in the case of livestock, the breed. Taking into account the role of behavioural characteristics of Scottish Blackface and other upland breeds, such as hefting and their increased nearest neighbour distance, it is hypothesised that lowland breeds, not having these characteristics, will cause a different pattern of defoliation and subsequent pattern of impact on vegetation. Early results suggest a role of selected livestock breeds in nature conservation (Newborn, 2000), but more research is needed. Several studies have shown that different herbivore species can have different responses to and subsequently impact on vegetation mosaics (Bokdam & Gleichman, 2000; Grant et al., 1987; Hester & Baillie, 1998). Implications for rangeland management have been extensively discussed elsewhere (van Wieren, 1995; Wallis de Vries et al., 1998).

As the spatial pattern of habitat use by herbivores is strongly correlated with the vegetation pattern, it is likely that the pattern of habitat use can be altered through altering the vegetation mosaic. For instance, creating a large high quality patch of a preferred vegetation type will attract herbivores and consequently reduce herbivore impact away from the artificial patch. Patches could be created by improving areas of less-preferred vegetation types, e.g. through burning or mowing, or herbivores could be given access to areas not currently part of the foraging area, such as neighbouring grassland (Wallis de Vries, 1991).

Other sources of attraction could influence the spatial pattern of habitat use by herbivores. Water points are obvious sources of attraction in semi-arid regions (Weber et al., 1998), but supplementary feed or mineral licks can be used to the same effect in temperate regions. Artificial shelter, either from heat or cold, can also be applied to attract free ranging herbivores to specific areas of a landscape (Arnold & Dudzinski, 1978).

Together with grazing, fire is an important tool in the management of heather moorland (Gimingham, 1972). It is generally recommended that for the purpose of grouse management, a 10 to 15 year heather burning cycle is most appropriate (Gimingham, 1972). This cycle leads to a patchwork of heather stands of varying ages providing both food and shelter for grouse (Gimingham, 1972). Government guidelines have recently taken into account plant-herbivore interactions. For newly burned heather moorland grazed by livestock, an initial burning of 40% of the area is recommended (Scottish Executive, 2001). Although heather burning is nowadays mostly used as a tool for the management of red grouse (Gimingham, 1972), the pattern of burned patches will affect the pattern of defoliation by sheep (Gimingham, 1972; Grant & Hunter, 1968). As recently-burned heather patches have a higher nutritional value, sheep will focus at least part of their grazing on these patches, thus leading to a decrease in defoliation in other parts of the mosaic (Grant & Hunter, 1968). This is consistent with prediction of the SIM, considering the young heather as the preferred and the old heather as the less-preferred vegetation type. The findings of herbivore impact presented in this thesis suggest that, as sheep focus on the burned patches, heather fragmentation would be more likely to occur around these burned patches than further away. Thus fire could initiate the development of grass patches within a heather matrix. Under grazing by sheep, this mosaic would be expected to develop a network of paths and patches connecting the originally burned patches. However, the characteristics of mosaics resulting from fire strongly depend on factors such as the timing of fire and the existing pattern of vegetation. Fire occurring in heather-grass mosaics could thus have a range of effects.

Furthermore, little is known about the long term effects of such a burning cycle. Research on nutrient dynamics during heather burning suggest that nutrient loss could be important (Evans & Allen, 1971). As fire will probably have little effect on established grass patches, the spatial pattern of grass patches in heather could affect nutrient cycling. Nutrients lost from the heather stand through fire, could partly return as ash deposits on the grass patches, leading to a flow of nutrients from the heather to the grass. This effect could be strengthened by herbivory as sheep focus their movement and thus possibly their return of nutrients on the grass network (Hester et al., 1999). A combination of grazing and intensive heather burning could thus lead to a net flow of nutrients from the heather to the grass patches, affecting the longer term vegetation dynamics. It is clear that these are important questions which need further study both to increase our fundamental understanding of plant-herbivore-fire interactions and to increase our understanding in the role of fire in the context of moorland management.

The distinction between trampling and defoliation impact and the spatial pattern of herbivore impact as observed in this study could have implications for monitoring techniques. Monitoring programmes, such as in the context of the UK 'Environmentally Sensitive Area' scheme (Henderson et al., 1995; Thompson et al., 1995), should include observations of both defoliation and trampling impact. Design of sampling schemes should take into account the spatial pattern of herbivore impact. The SIM could be used as a tool to increase the effectiveness of a spatial sampling design and to appropriately interpret the herbivore impact of a whole area based on the distribution and intensity of herbivore impact.

6.5 Heathlands: the past and the future

In addition to the naturally occurring heathlands in coastal areas and above the tree line (Gimingham, 1972), extensive areas of heathlands in the Atlantic zone of Europe were created by humans from about 4000 years ago through forest clearances and subsequent agricultural practices that prevented regeneration to forest (Diemont & Jansen, 1998; Gimingham, 1972 ; Webb, 1998). Heathlands once covered possibly between 3-5 million hectares, reaching from western Norway to Portugal, but conversion of these 'wastelands' in the nineteenth century to agricultural land and forest reduced the area of heathlands to around 300-500 thousand hectares (Diemont & Jansen, 1998 ; Webb, 1998).

Although the conservation value of heathlands has been argued (e.g. Thompson et al., 1995), due to their semi-natural character, the cultural value is emphasised more and more (Diemont & Jansen, 1998; Webb, 1998). The current revival of heathlands as the 'Atlantic Cultural Landscape of Europe' (Diemont & Jansen, 1998) coincides with a general emphasis on regional cultural and environmental values within Europe and a serious crisis in intensive farming. Continued intensification of agriculture has led to overproduction and extensive environmental damage (Hindmarch & Pienkowski, 2000). This process is no longer economically and politically sustainable (Bignal, 1998). In the case of heathlands, European sheep farmers were compensated (under the common agricultural policy - CAP) for market returns lower than target herds set by the European Community (EC) and also received a fixed premium per animal independent of stocking density (Baldock et al., 1996). The subsidy had the side effect of providing a strong incentive for overstocked farms to hold on to livestock and at the same time discouraging the reintroduction of livestock into area from where they had disappeared (Baldock et al., 1996). This subsequently created a divergence between financially attractive stocking rates and appropriate stocking rate for nature and environmental conservation objectives. Changes in the CAP and the increased attention on cultural and environmental heritage suggest new opportunities for extensive and traditional agricultural systems (Bignal, 1998; Hindmarch & Pienkowski, 2000; Thompson et al., 1995). The traditional grazing of heathlands is a prime example of an extensive agricultural system (Thompson et al., 1995).

A subsidy-driven reduction in sheep numbers might therefore suggest that knowledge of sheep impact on heather moorland becomes redundant, but to the contrary. Combining agricultural production with other objectives, such as soil conservation and biodiversity, will instead lead to a renewed demand for understanding of the complex interactions in grazed ecosystems and their implications for the management of grazed ecosystems in general and heathlands in particular.

6.6 References

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Machteld, our career partnership has been successful, now lets go and enjoy our private partnership!

Sander.

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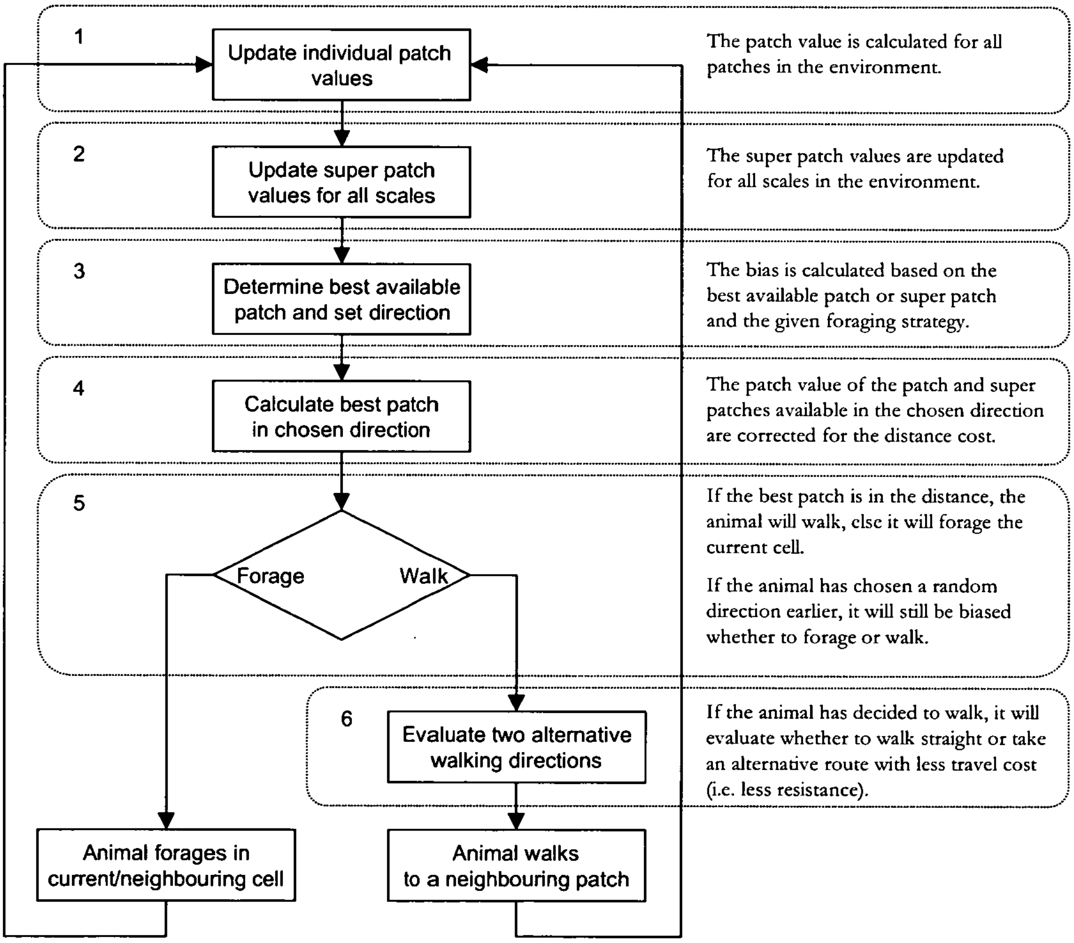
List of abbreviations

Abbreviation	*Description*
AGL	Above Ground Level
ANOVA	ANalysis Of VAriance
DEM	Digital Elevation Model
DF	Degrees of Freedom
DM	Dry Matter
GAP	Grazed Area Proportion
GPS	Global Positioning System
HOOFS	Hierarchical Object-Oriented Foraging Simulator
NVC	National Vegetation Classification
PCA	Principal Component Analysis
REML	Residual Maximum Likelihood
RMS	Root Mean Square
RNE	Relative Nugget Effect
SED	Standard Error of Differences
SIM	Spatial Interaction Model

Appendix A: Hoofs foraging sub-model

Beecham, A.J. and Oom, S.P.

The foraging sub-model contains the algorithms concerned with the animals' foraging strategy. The motivation for the strategy is maximisation of the quality of the resource cells from which they forage. Every time an animal is ready to forage it will go through a number of decisions. Through these decisions the animal will evaluate its environment, decide the best place to forage and choose how to get there. Although HOOFS has a social sub-model (Beecham & Farnsworth, 1998), this was switched off for the purpose of this study. Thus each individual in the model operated independent of the other animals in the environment. The decisions are summarised in a flow diagram (Figure A.1; numbers in figure correspond with text).



The patch value is calculated for all patches in the environment.

The super patch values are updated for all scales in the environment.

The bias is calculated based on the best available patch or super patch and the given foraging strategy.

The patch value of the patch and super patches available in the chosen direction are corrected for the distance cost.

If the best patch is in the distance, the animal will walk, else it will forage the current cell.

If the animal has chosen a random direction earlier, it will still be biased whether to forage or walk.

If the animal has decided to walk, it will evaluate whether to walk straight or take an alternative route with less travel cost (i.e. less resistance).

Figure A.1. Flow diagram of the HOOFS foraging submodel. Numbers refer to numbers explained in the text.

The measure of vegetation quality is the *potential energy intake rate*, which is determined by the *potential specific net energy* of a cell and the cost endured during a foraging bout. Firstly, the animal gathers the information on the environment for individual cells (1) and all super-cells (2). Then the animal determines a directional bias (3). After the animal has decided which direction to select, the animal determines the best patch in that direction (4), and determines whether to forage or walk (5) in the direction of that patch. If the animal decides to walk, the animal adjusts the direction in order to take the path of least resistance (6).

1. Update of individual patches

The quality of the environment is measured as the *potential energy intake rate* in each cell or super-cell. In order to evaluate the environment, the animal is provided with an update of the current environment. To save processing time, only the grazed patches are recalculated, and only every 100 time steps. The *potential energy intake rate* is determined by the digestibility of the vegetation in a patch and the travel, search and handling costs associated with the patch.

The digestibility is expressed as the *potential specific net energy* (D; Equation A.1). As herbivores graze down vegetation, the proportion of dead stem increases, leading to a decrease in the digestibility. Thus the digestibility decreases when biomass is reduced and recovers with time since defoliation (T_{def}). The recovery curve is sigmoidal set by the speed of recovery (D_{slope}) and the recovery delay (T_{delay}). The digestibility varies between the *maximum* (D_{max}) and *minimum digestibility* (D_{min}) for that vegetation type.

$$D = D_{\mathrm{max}} - \left(\frac{D_{\mathrm{max}} - D_{\mathrm{min}}}{1 + e^{-D_{\mathrm{slope}}\left(T_{\mathrm{def}} - T_{\mathrm{delay}}\right)}} \right)$$

Equation A.1

$$B_{\mathrm{eaten}} = F_{\mathrm{biomass}} \times \left(B - B_{\mathrm{inacc}}\right)$$

Equation A.2

$$T_{\mathrm{grazing}} = T_{\mathrm{handling}} + \frac{B_{\mathrm{eaten}}}{r_{\mathrm{veg}}}$$

Equation A.3

$$T_{\text{travel}} = T_{\text{step}} \times \frac{R_a + R_b}{2}$$ **Equation A.4**

$$E_{\text{maint}} = T_{\text{travel}} \times I_{\text{maint}}$$ **Equation A.5**

$$I = \frac{\left(B_{\text{eaten}} \times D \times F_{\text{energy}}\right) - E_{\text{maint}}}{T_{\text{grazing}} + T_{\text{travel}}}$$ **Equation A.6**

To determine the actual intake rate for a foraging bout, the animal evaluates costs incurred during the foraging bout. The costs are expressed as time penalties. The costs considered are: *maintenance cost* (E_{maint}), *travel cost* (T_{travel}) and *grazing cost* (T_{grazing}). The *grazing cost* (T_{grazing}; Equation A.3) is the sum of the time it takes to consume the biomass, calculated as the *biomass eaten* (B_{eaten}) divided by the *intake rate* (r_{veg}), and a *fixed handling cost* (T_{handling}; putting head down). The *biomass eaten* (B_{eaten}; Equation A.2) is calculated as the difference between the total above ground biomass in the patch (B) and the inaccessible biomass (below minimum sward height) for that vegetation type (B_{inacc}), multiplied by the *fraction of the biomass* that can be consumed in one foraging bout (F_{biomass}). Note that the biomass of heather only comprises the current years growth. The fraction of biomass available in each foraging bout was introduced to limit the time animals spent in any one cell, in particular in heather cells which have a whole current years growth as initial biomass. The *travel cost* (Equation A.4) is the product of the *step cost* (T_{step}) and the average *relative resistance* (R) of the vegetation types travelled through, going from the current cell (a) to one of its neighbours (b), R_a and R_b respectively. The maintenance cost (E_{maint}) is the product of the *travel cost* (T_{travel}) and a fixed *maintenance energy rate* (I_{maint}) (Equation A.5).

The final *potential energy intake rate* (I) is then calculated using the endured costs and the fraction of the biomass that is indigestible (Equation A.6). As animal species can differ in their energy assimilation efficiencies, an *energy fraction* (F_{energy}) is used to correct the energy return from the available biomass.

2. Update super-cell values

With the individual cell quality recalculated, the super-cell values can now be updated (Equation A.7) for all higher levels in the hierarchy (h+1). The *discriminative ability* factor (γ) determines how animals perceive aggregation of cells across different levels. A high *discriminative ability* leads to a bias towards higher quality patches within a super-cell.

$$I_{h+1} = \left(\frac{\sum_{h=1}^{7} I_h^{\gamma}}{7} \right)^{1/\gamma} \qquad \textbf{Equation A.7}$$

Note that the factor seven in the denominator is replaced by a lower value at the edges of the environment. This is to cope with the square vegetation map in a hexagonal hierarchy. Without the correction, the mean patch value would be higher at the edge of the map, leading to a bias towards the edge. The value is set to induce a slight bias towards the centre of the map.

3. Calculating the foraging bias

Now, the animal is ready to calculate its directional foraging bias, i.e. the bias part of the biased random walk. This is where the animal's foraging strategy is applied to the its environment. The animal has six directions to choose from, and the directional bias will provide a probability of selecting each direction. A loaded dice will then be thrown taking into account the calculated probabilities (p_d; Equation A.8) for each direction (d).

$$p_d = \frac{\sum_{h=0}^{5} 7^{\mu h/2} \left(A_h I_{dh} + (1 - A_h) I_{(d+1)h} \right)^{\beta}}{\sum_{h=0}^{5} 7^{\mu h/2} \sum_{d=1}^{6} \left(A_h I_{dh} + (1 - A_h) I_{(d+1)h} \right)^{\beta}} \qquad \textbf{Equation A.8}$$

$$p_{d,\text{adjusted}} = p_d \times q_f \text{ or } p_d \times q_w \qquad \textbf{Equation A.9}$$

The foraging bias is calculated using the *potential energy intake rate* (I) (Equation A.6) of the neighbouring individual cells and the super-cells at higher scales (Equation A.8)

(Beecham et al., 1999). The bias is influenced by the *determinism* (β) to select the best possible *potential energy intake rate* and the *distance coefficient* (μ). The *distance coefficient* determines the weighting of cells near and further away. When *distance coefficient* is zero, all distances are rated equal, while a negative *distance coefficient* leads to bias towards cells closer by. Although the bias is calculated in the six directions (d) of the neighbouring cells, due to the hexagonal hierarchical system, the super-cells are not all aligned with these directions. Therefore, a correction factor (A) is applied to the six directions (d) for the six levels in the hierarchy (h). For alternate levels the correction factors are 1 and 0.682 respectively. This is illustrated by the arrows in Figure A.2.

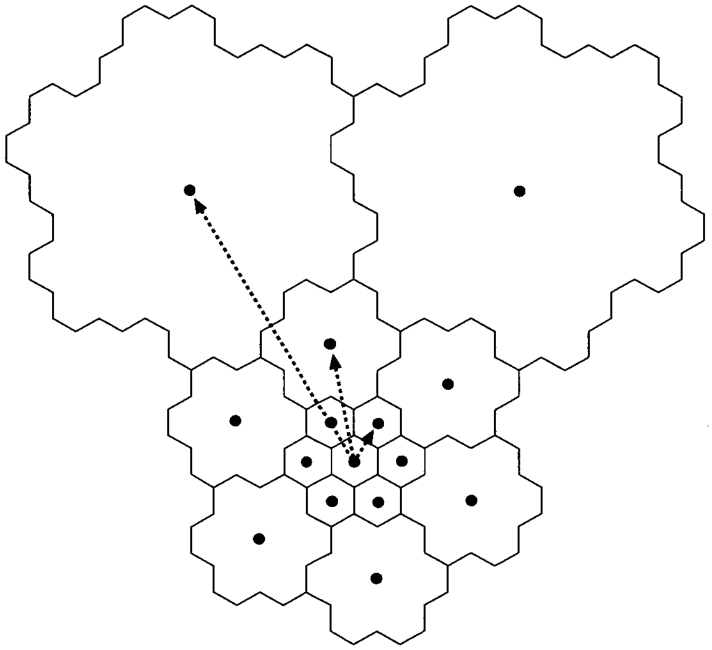


Figure A.2. The first three levels in the hexagonal hierarchy used in HOOFS.

Finally the *directional probability* (p_d) is multiplied with the *directional persistence* (q_f or q_w) (Equation A.9). The *directional persistency* controls the turning behaviour of the animal, making it more or less persistent in maintaining its current direction (compare with turn angle concentration; p 301 Bell, 1991). The *directional persistence* is set separately for the walking and foraging mode, to take into account which mode the animal selected previously.

4. Selecting the best patch in chosen direction

When the *potential energy intake rate* (I) of the animal's local environment is low compared to its global environment, it is better for the animal to walk instead of graze. Thus, the animal can avoid grazing costs in any cells that it walks through. Therefore, the animal should evaluate whether to walk or forage. Therefore, it has to decide which patch to select in the chosen direction, which depends on the way it evaluates distance and resistance. The resistance is calculated cascading through the hierarchy (Equation A.10). The resistance at scale $h+1$ is based on the resistance of cells at level h, corrected by the *resistance sensitivity* (p_r). The *mean resistance* (R_{mean}) is calculated as the average resistance for the total distance travelled. The *resistance sensitivity* determines how animals perceive the resistance across scales.

Should the animal evaluate the *step cost* (T_{step}) on the basis of one cell in the distance or should it spread the travel cost across a group of cells in the distance? If the walk results in just a single cell consumed followed by a walk back this would scale with distance. If more cells are eaten with greater distance this scaling is less, i.e. the cost of distance is spread across several cells visited (and thus less than when only a single cell is visited), down to no scaling (0^{th} power) when the whole super cell is consumed before a further walk of the same or greater magnitude is undertaken. The animal is therefore provided with a *distance sensitivity* (p_d). If the power is high the animal thinks that it is worthwhile to walk off into the distance, i.e. it assumes the grass is greener elsewhere.

For all super-cell levels the value of the *potential energy intake rate* ($I_{foraging}$) is obtained. This value is corrected with the *walking cost* ($E_{walking}$) and the fixed *handling time* ($T_{handling}$) (Equation A.12). The *walking cost* is based on *maintenance energy rate* (I_{maint}), the *step cost* (T_{step}), the *mean resistance* (R_{mean}), the distance between the current animal location and the destination cell (*Dist*) and the *distance sensitivity* (p_d) (Equation A.11). Leading to the corrected *potential energy intake rate* (I_{dist}).

5. Checking for walking or foraging mode

To simulate indecisiveness in the foraging behaviour, the *potential energy intake rate* is then adjusted by the *mode error* (ε_w) (Equation A.13). The *mode error* is taken from a uniform distribution between minimum and maximum *mode error.* A uniform distribution was chosen because this was the least computationally demanding. The animal then evaluates whether to forage or walk depending on the highest value, i.e. if the neighbouring cell is better than any distant cell it will forage and vice versa. If the animal decides to forage it will now make the necessary steps. If the animal decided a random direction, it will still be biased in the decision to walk or forage. Because it chose a random direction, it is more likely to walk, as it is likely to be directed to a less optimal direction.

$$R_{h+1} = \left(\frac{\sum_{h=1}^{7} R_h^{\,p_r}}{7} \right)^{1/p_r}$$

Equation A.10

$$E_{\text{walking}} = I_{\text{maint}} \times T_{\text{step}} \times R_{\text{mean}} \times \left(Dist^{P_d} \right)$$

Equation A.11

$$I_{\text{dist}} = I_{\text{foraging}} - \frac{E_{\text{walking}}}{T_{\text{handling}}}$$

Equation A.12

$$I_{\text{walk}} = I_{\text{dist}} \times \varepsilon_w$$

Equation A.13

$$I_{\text{path}} = I_{\text{dist}} \times \varepsilon_t$$

Equation A.14

6. *Choosing walking direction*

If the animal decides to walk, the walking direction is adjusted to facilitate the animal to follow paths. For the chosen destination cell value, three paths are evaluated. This is done by calculating the two alternative paths relative to the optimal path, taking one initial step to the left or to the right. The destination cell value is calculated as before. The two alternatives are then multiplied by *allow turn* (ε_t) (Equation A.14), thus allowing the animal to either go left or right relative to the optimal direction in order to avoid high travel costs. The animal then chooses the highest of the three values and takes one step in that direction. A possible correction for slope could also be implemented at this stage. This was, however, beyond the scope of this study.

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Appendix B: HOOFS parameters and variables description

Parameters

Description	Symbol	Unit	Dim.[a]	Range		Default value(s)
Animal parameters						
Population size	N	-	ani	1	∞	10
Initial energy	E_{init}	J	ani	0	∞	5000
Directional persistence (foraging)	q_f	-	hier	0	1	1-1-0.5-0.2-0.5-1
Directional persistence (walking)	q_w	-	hier	0	1	1-1-0.2-0.2-0.2-1
Allow turn	ε_t	-	ani	0	∞	1
Mode error	ε_w	-	ani	0	1	0.2
Determinism	ß	-	ani	0	∞	2
Distance sensitivity	p_d	-	hier	0	∞	0.5
Distance coefficient	μ	-	ani	0	-∞	-0.25
Discriminative ability	γ	-	ani	0	∞	3-3-2-1-1-1
Step cost	T_{step}	s	ani	0	∞	0.05
Relative resistance	R	-	veg	0	∞	1-1-5
Resistance sensitivity	p_r	-	ani	0	1	0.02
Inaccessible biomass	B_{inacc}	g DM [b]	veg	0	∞	50-50-50
Intake rate	r_{veg}	g DM s^{-1}	veg	0	∞	30-30-10
Handling cost	$T_{handling}$	s	veg	0	∞	0.5-0.5-0.5
Biomass fraction	$F_{biomass}$	-	veg	0	1	0.3-0.3-0.1
Maximum digestibility	D_{min}	J DM^{-1}	veg	0	1	0.7-0.7-0.5
Minimum digestibility	D_{max}	J DM^{-1}	veg	0	1	1.0-1.0-0.6
Digestibility recovery delay	T_{delay}	s	veg	0	∞	500 - 500 - 500
Speed of digestibility recovery	D_{slope}	-	veg	0	1	0.001-0.001-0.001
Energy fraction	F_{energy}	-	ani	0	1	1
Maintenance energy rate	I_{maint}	J s^{-1}	ani	0	∞	1
Runtime						
Potential energy intake rate	I	J s^{-1}	cell	0	∞	
Grazing cost	$T_{grazing}$	s	cell	0	∞	
Travel cost	T_{travel}	s	cell	0	∞	
Eating cost	T_{eating}	s	cell	0	∞	
Biomass eaten	B_{eaten}	g DM	cell	0	∞	
Mean resistance	R_{mean}	-	cell	0	∞	
Maintenance energy	E_{maint}	J	ani	0	∞	
Vegetation parameters						
Maximum above ground standing biomass	K	g DM m^{-2}	veg	0	∞	150-120-525
Maximum growth rate	a	s^{-1}	veg	0	1	0.0013-0.0001-0.0001
Standing biomass for maximum growth rate	c	-	veg	0	∞	6-6-3
Runtime						
Standing biomass	B	DM	cell	0	∞	
Time since defoliation	T_{def}	s	cell	0	∞	

[a] Dimensions of parameters: hier = six levels of hexagonal hierarchy; veg = number of vegetation types (respectively: grass patch, grass path, heather); ani = number of animal species (this case one); cell = 117.649. [b] DM = Dry matter content.

Variables

Description	Unit	Dimension[a]
Animal variables		
Energy intake rate	$J\ s^{-1}$	ani
Net energy intake rate	$J\ s^{-1}$	ani
Energy efficiency	%	ani
Movement	step	ani
Residence time	s	ani
Grazing time	s	ani
Biomass intake	$g\ DM\ s^{-1}$ [b]	ani
Digestibility	$J\ g^{-1}$	ani
Heather proportion	%	ani
Grazed area proportion (GAP)	%	veg
Adjusted grazed area proportion	%	veg
Vegetation variables		
Standing biomass	g DM	cell

[a] Dimensions of variables: veg = number of vegetation types (respectively: grass patch, grass path, heather); ani = number of animal species (this case one); cell = 117.649. [b] DM = Dry matter content.