

MULTIPLE SCALE SPATIAL DYNAMICS
OF THE MOOSE-FOREST-SOIL ECOSYSTEM
OF ISLE ROYALE NATIONAL PARK, MI, USA

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA

BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Dr. John Pastor, Advisor

November 2008

Acknowledgements

I would like to thank my committee members for donating their time, knowledge, and experiences to the development of this thesis and to my development as a scientist. Dr. John Pastor, Dr. Lee Frelich, Dr. Claudia Neuhauser, Dr. George Host, and Dr. Ron Moen have all contributed to this thesis in one way or another. Some have provide their editorial suggestions to this and previous versions of the thesis and I thank them. Others have taught courses and published papers that had strong influences on the development of my thoughts while conducting the research for this thesis. Thank you. I am particularly grateful to my advisor, Dr. John Pastor, for his thoughtful advice throughout the entire process of creating this thesis. The chapters herein represent the work that I have done over the past four years. But they are also a culmination of weekly (sometimes daily) meetings with Dr. Pastor. These meetings were what I looked forward to as a graduate student. Thank you. I am most grateful to my wife, Alesa, not only for her companionship, but because she assisted with field work on numerous occasions and sketched figure 1 of Chapter 2.

To my mother and father

Abstract

Moose (*Alces alces*) make foraging decisions at scales that range from plant stems (centimeters) to home ranges (kilometers). These decisions determine the spatial distribution of forage consumption and the consequent impacts on plant communities and nutrient cycles. From the fine scale changes in the size and density of plant stems to the distribution of plant patches and community assemblages across landscapes, the effects of moose browsing at one spatial scale may amplify spatial heterogeneity at scales that are orders of magnitude larger than the scales at which the interactions originally took place.

In this thesis, I focused on how gradients of moose browsing in two valleys at Isle Royale National Park, MI, USA influenced plant fractal geometry and how such changes to plant geometry feedback to moose foraging across larger previously browsed landscapes. I also examined changes in larger scale patterns of forage availability, plant community composition, and soil fertility in response to recent declines in island-wide moose population density.

Increasing moose browsing influenced the geometry of deciduous and conifer species differently. The fractal dimension of bite density, bite mass, and forage biomass of aspen saplings all responded quadratically to increasing moose browsing and were greatest at $\sim 3\text{-}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ consumption. In contrast, fractal dimension of bite density, bite mass, and forage biomass of balsam fir all declined steadily with increasing moose browsing. These different responses of plant canopies to increased browsing as well as seasonal changes in bite mass altered the distribution of foraging mechanisms across larger previously browsed landscapes.

At the larger scale, recent (2005-2007) landscape patterns of available and consumed browse became decoupled from each other and distributions of available forage, plant species composition, and soil fertility were qualitatively different from patterns documented in the early 1990's. These changes are coincident with and likely driven by recent declines in the island-wide moose population of Isle Royale.

Collectively, these two studies suggest that large scale landscape patterns of browse availability, species composition, and soil fertility may emerge from finer scale impacts of browsing on plant geometry and the feedbacks to larger scale foraging decisions that moose make in addition to population density. The long-term dynamics of landscape patterns in boreal forests are therefore dependant on both fine scale foraging decisions and large scale population dynamics.

Table of contents

Acknowledgements.....	i
Dedication.....	ii
Abstract.....	iii
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	viii
Forward.....	ix
Chapter I: Introduction to the thesis.....	1-17
Introduction.....	1
Study Site.....	5
Research Questions.....	12
Chapter II: Scaling the effects of moose browsing on forage distribution, from the geometry of plant canopies to landscapes.....	18-64
Abstract.....	18
Introduction.....	20
Methods.....	26
Results.....	39
Discussion.....	51
Acknowledgements.....	64

Chapter III: Rapid changes in landscape patterns accompany recent declines in moose population density at Isle Royale National Park, MI, USA.....	65-102
Abstract.....	65
Introduction.....	67
Methods.....	73
Results.....	83
Discussion.....	95
 Chapter IV: Discussion of the thesis.....	 103-113
Synthesis and Significance.....	103
Future Directions.....	111
 Bibliography.....	 114-148

List of Tables

Chapter III

Table 1.....	86
Table 2.....	87
Table 3.....	89
Table 4.....	93
Table 5.....	94

List of Figures

Chapter 1:

Figure 1.....7
Figure 2.....8
Figure 3.....9
Figure 4.....10

Chapter 2:

Figure 1.....30
Figure 2.....31
Figure 3.....42
Figure 4.....45
Figure 5.....47
Figure 6.....49

Chapter 3:

Figure 1.....72
Figure 2.....75
Figure 3.....91
Figure 4.....92

Forward

This is a doctoral dissertation submitted as partial fulfillment of the degree of Doctor of Philosophy in Ecology, Evolution, and Behavior at the University of Minnesota. Chapter 1 is a general introduction to the questions posed and examined in Chapters 2 and 3 and provides a short historical context within which to place these questions. Chapters 2 and 3 are papers prepared for publication with coauthors. As such, these chapters use the collective "we" instead of "I". John Pastor and Angela Hodgson are coauthors of Chapter 2, which is reprinted here with kind permission from the Ecological Society of America. John Pastor and Brad Dewey are coauthors of Chapter 3, which is a work in preparation for submission to *Landscape Ecology*. Chapter 4 summarizes the main results of Chapters 2 and 3 and discusses the implications of these results for ecology, evolution, behavior and conservation.

Chapter I: Introduction to the thesis

INTRODUCTION

During the past 25 years, the ecological causes and consequences of spatial heterogeneity have emerged as fundamental problems in ecosystem science (Hobbs 2005, Turner and Chapin 2005). Ecological properties and processes are not homogeneously distributed across landscapes; instead, landscapes tend to be structured or patterned. Landscapes are also dynamic, changing because landscape patterns influence the movement and redistribution of organisms, materials, and disturbances. During the early 1980's an entire field of study, landscape ecology, developed in response to the growing interest in the complex causes of landscape patterns and the influence of landscape patterns on the movement of materials, organisms, and energy through ecosystems (Wiens 2008). But the difficulty of experimenting with large and dynamic landscapes has prevented the development of general principles of landscape dynamics. Therefore, despite nearly three decades of study, the basic questions that existed at landscape ecology's beginning remain relevant today: 1) How do we characterize spatial heterogeneity from the viewpoint of specific organisms? 2) What ecological processes are responsible for the spatial heterogeneity present in ecosystems? 3) How do organisms respond to spatial heterogeneity in terms of their ecology, evolution, and behavior? 4) How do we account for spatial heterogeneity in the management and conservation of species and ecosystems?

From its beginning, landscape ecology has focused on characterizing the patchiness of landscapes. It was pointed out very early that homogeneous patches of

ecosystem properties often occur as hierarchical mosaics of patches within patches (O’Niell 1986). In 1987, Senft et al. applied the theory of patch hierarchy to ungulate foraging and in doing so, initiated a chain of studies that would make scale a fundamentally important topic in ungulate foraging and landscape dynamics. Senft et al. (1987) pointed out that ungulate herbivores range across large areas and their foraging decisions are nested in a hierarchy, with each decision occurring at a different temporal frequency and at a different spatial scale. Relative to large herbivores, the landscape is composed of patches within patches, a patch being an area that differs from surrounding areas by a change in the animal’s nutrient intake rate (Stephens and Krebs 1986).

Coinciding with the growing interest in spatial hierarchy was an accumulation of studies revealing that the foraging decisions that herbivores make at very small scales (e.g. which plant to feed on within a patch) often change larger scale and higher level processes such as nutrient cycling, and plant community succession. Because these changes are not homogeneously distributed, they create large-scale landscape heterogeneity (Pastor et al. 1993, 1997, 1998; McInnes et al. 1992; Pastor and Naiman 1992; Pastor and Cohen 1997; Frank and Goffman 1998; Fuhlendorf and Smeins 1999; Knapp et al. 1999; Augustine and Frank 2001; Steinauer and Collins 2001). System-level models later began to demonstrate when landscape patterns become energetically unfavorable to herbivores and in turn begin to feed back on population dynamics and growth (Moen et al. 1997, 1998). Recently, efforts have been made to account for the ways that herbivores create and respond to spatial heterogeneity across multiple spatial

scales in the conservation and management of ungulate herbivores and their habitats (Bugmann and Weisberg 2003; Weisberg et al. 2006; Gordon 2006).

This progression of our understanding of herbivore-ecosystem interactions has largely depended on the integration of landscape and ecosystems ecology with the behavior and mechanics of herbivore foraging. For nearly two decades herbivore-ecosystem ecologists have been trying to identify the mechanisms that regulate nutrient intake rates for ungulate herbivores (Spalinger and Hobbs 1992, Hobbs et al. 2003). Because heterogeneity is best defined by relative rates of change in a variable of interest (Kotler and Weins 1990), this same work is beginning to provide a mechanistic basis for defining landscape heterogeneity relative to foraging herbivores. Additionally, the application of hierarchical frameworks is beginning to shape our understanding of how the decisions herbivores make at fine scales influences spatial heterogeneity at scales that are orders of magnitude larger and in turn feed back to constrain foraging processes across large landscapes. We are therefore at the cusp of understanding the role ungulate herbivores play in creating spatial heterogeneity that in turn influences the redistribution of organisms, materials, and energy through ecosystems.

In this dissertation, I build upon three decades of work which has sought to integrate landscape and ecosystems ecology with the behavior and foraging mechanics of large herbivores. In doing so, I hope to improve our general understanding of spatially dynamic ecosystems, and in particular, improve our understanding of how moose (*Alces alces*) interact with spatially dynamic boreal forests at Isle Royale National Park, MI, USA.

I chose to study the spatial dynamics of moose foraging ecology because moose respond to heterogeneity across a range of spatial scales as they forage selectively among plant assemblages, species, and parts. Moose consume large quantities of plant tissue from woody species. Moose take thousands of bites every day to obtain between 5 and 10 kg of dry mass (Saether and Anderson 1989) and focus their feeding activity on nutrient-rich photosynthetic tissue during summer and on dormant meristems in winter. By concentrating their feeding on the apical meristems of a few preferred plant species, moose browsing alters plant growth and changes the size and distribution of patches of preferred tree species across landscapes (Danell et al. 1994; Persson et al. 2005; Pastor et al. 1998; Pastor and Danell 2003; De Jager and Pastor 2008).

Moose prefer deciduous tree species that are easily digested because they have high nutrient and low lignin concentrations. These same chemical characteristics also cause the litter of these species to decompose rapidly (Melillo et al. 1982). By decreasing the height growth of deciduous species, moose convert forests to ones dominated by less preferred and relatively unbrowsed conifers. In contrast to deciduous species, conifer litter has low nutrient and high lignin concentrations, which cause it to decompose slowly (Pastor et al. 1993). This browsing-induced shift in species composition in turn depresses the rate of nutrient cycling that underpins the very productivity that moose depend on. Therefore the influence of moose on species composition and soil fertility, which are mediated by changes in plant growth, can result in landscape patterns of browse availability, species composition, and soil fertility (Pastor et al. 1998).

Changes in the patterns of browse distribution and productivity can in turn determine a moose's energy expenditure while it searches for food. Some foraging strategies could produce landscape patterns of browse distribution that cause negative energy balances and local extinction of moose (Moen et al. 1998). Therefore moose pass along environments to their offspring that can be structurally and functionally different from the ones they inherited. Since moose require 5 – 10 kg of food every day, the changes that they impose on their environment are a selective force that could determine reproductive fitness. The problem for moose, like so many other ungulates, is that each time they take a bite they aren't simply gaining a small portion of their daily energy requirement; they also generate a series of plant responses that will further alter their energy balance and that of their progeny.

STUDY SITE

I conducted the studies presented in this dissertation at Isle Royale National Park, MI (Fig. 1). Isle Royale has long been a natural laboratory for studying moose population dynamics (Allen 1979). Moose are the only ungulate at Isle Royale and their population dynamics are closely linked to the island's vegetation and wolf population. For nearly 20 years, a number of researchers from the University of Minnesota (Fig. 2) have been maintaining two sampling grids in two valleys at Isle Royale (Fig. 3). Within these grids systematic observations of available browse, consumption by moose, plant species composition, and soil nitrogen availability have been made annually since 1988. Across this same time period the island's moose population has undergone two major population

oscillations — one large oscillation with a peak of ~2200 animals in 1995 and another recent but smaller oscillation with a peak of ~1500 animals in 2002 (Fig. 4). The rise and fall of the moose population may produce large changes in plant growth and forest composition, and may generate subsequent dynamics in landscape patterns of available browse, soil fertility, and conifer abundance (Pastor et al. 1993, Pastor et al. 1998, Pastor et al. 1999). Yet we don't know how the dynamics of these patterns at scales of 10's to 100's of meters emerge from finer scale decisions the moose makes at scales of individual plants or how these medium scale patterns are embedded in larger scale patterns across the entire valley. Furthermore, how moose respond to such spatial variation in terms of their foraging rates, behavior, and population dynamics are all unknown.

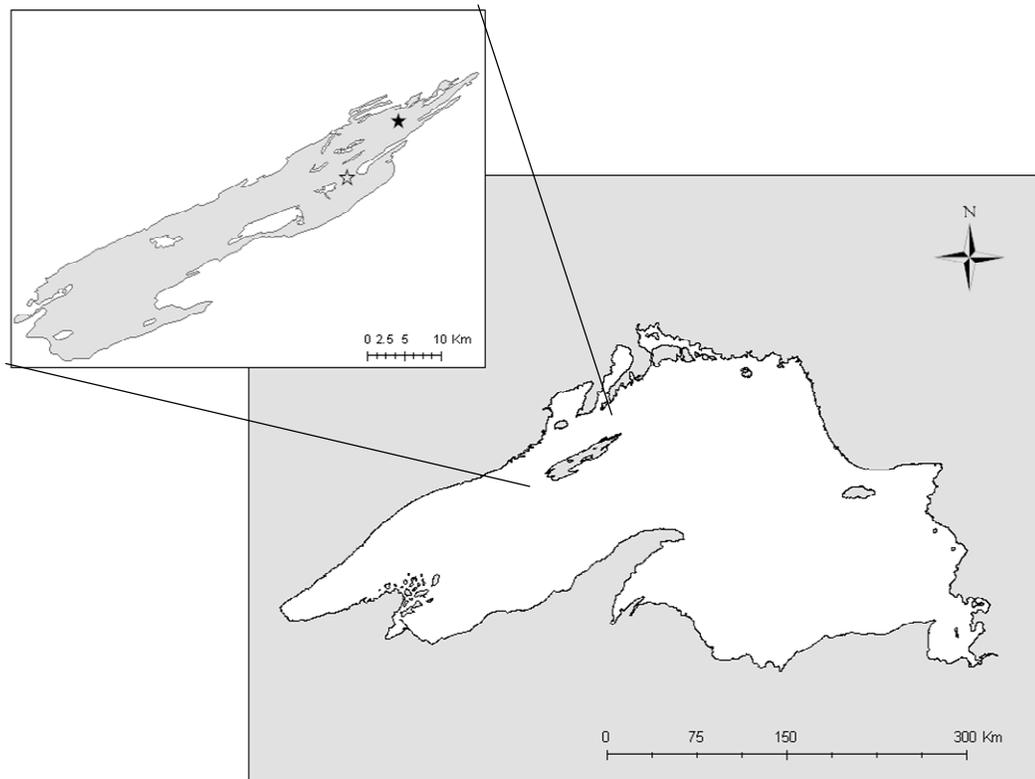


Fig. 1. Isle Royale is located approximately 20 miles off the north shore of lake Superior, USA. The studies in this dissertation were conducted in two valleys, Moskey Basin (open star) and Lane Cove (filled star) in the northeast portion of the island.



Fig. 2. The study grids at Isle Royale have been maintained by a number of researchers from the University of Minnesota. Pictured here in 1988 are from left to right: John Pastor, Ron Moen, Brad Dewey, and Pamela McInnes. Other researchers that have helped to maintain the grids but are not pictured included Angela Hodgson, Cal Harth, and Mark White.

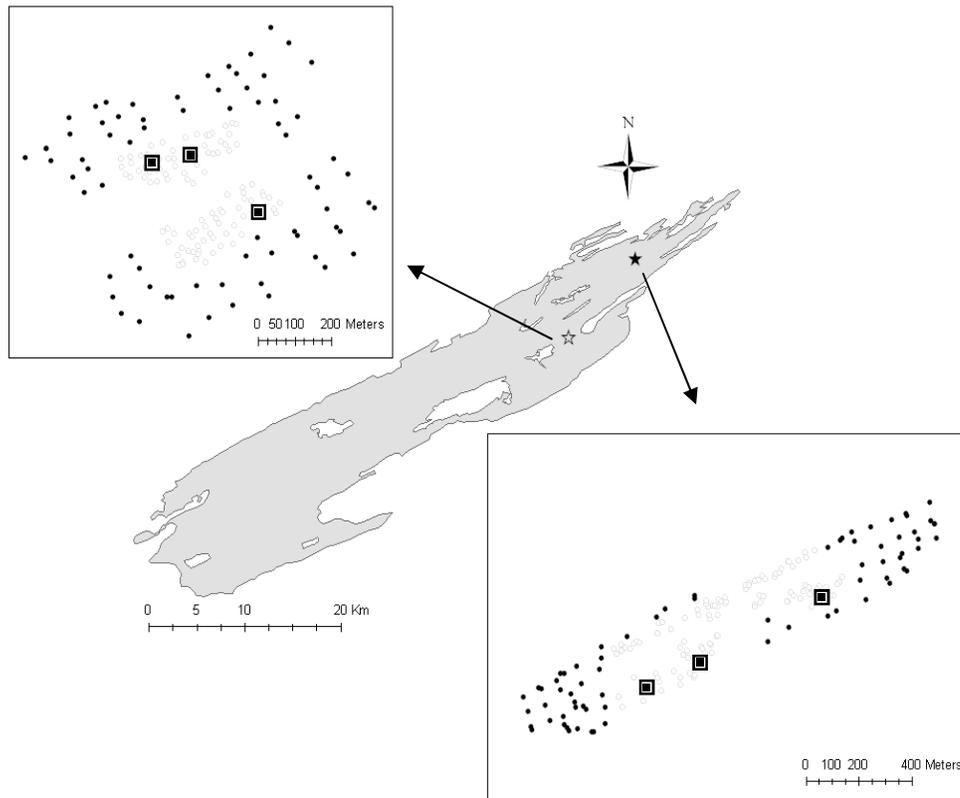


Fig.3. Three fine scale grids (14X14 m, filled boxes) are nested within one medium scale grid (open circles), which is then nested within a large scale grid (filled circles) in both valleys. Each grid has a common grain, a moose feeding station. The different resolutions allow for analysis of landscape patterns while controlling for scale dependence of such patterns.

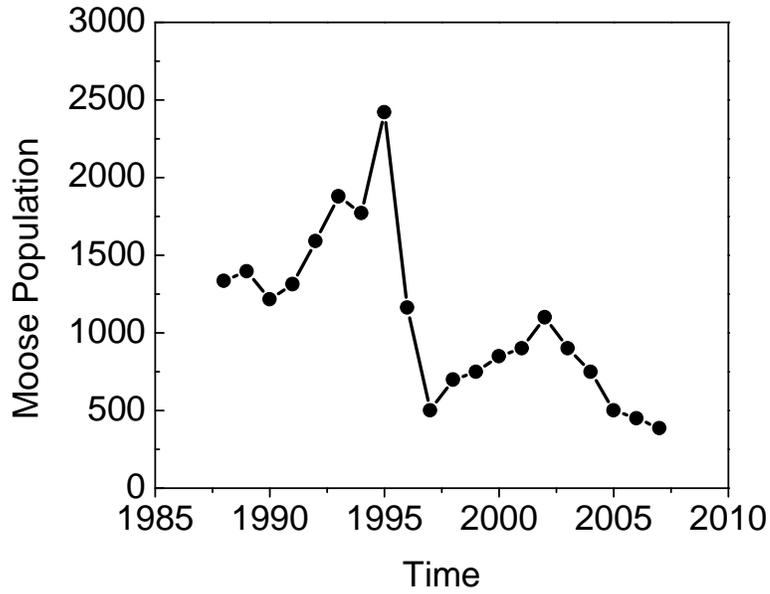


Fig. 4. Since long-term monitoring of the sampling grids at Lane Cove and Moskey Basin was initiated (1988) Isle Royale's moose population has undergone one major (mid 1990's) and one minor (early 2000's) oscillation.

To address these issues I extended the long-term sampling grids at Isle Royale temporally and spatially. Extending the spatial resolution of the grids was essential because moose make decisions at both finer and coarser scales than the 30m spacing of the current grids; fine scale patterns may emerge from and impact the foraging mechanics of moose, while coarse scale patterns may emerge from and contribute to moose population dynamics. Fig. 3 shows the sampling grids at Isle Royale. The open diagonal area devoid of grid points and which runs through the valley is occupied by streams with associated wetlands and beaver ponds. The 100 open circles in Fig. 3 make up the medium scale grids which have been maintained since 1988. Each circle is a 2m^2 feeding station, or the distance over which a moose can reach bites of plant tissue without moving its forefeet (*sensu* Senft et al. 1987). In 2003, three additional sampling grids, each encompassed within the open squares, were established in each valley by PhD candidate Angela Hodgson. Each of these grids contains 100 points spaced 1.4 meters apart and make up the fine scale grids. The purpose of these grids is to determine how the foraging activities of moose at fine scales merge into the coarse scale patterns and dynamics in the larger scale grids and to determine how changes in vegetation patterns at fine scales impact the foraging mechanics of moose. In 2005, I established 70 additional feeding stations in both valleys (the closed circles in Fig. 3) spaced on average 70 m apart. These points make up the large scale grid. The purpose of this grid is to determine how temporal changes in landscape patterns relate to Isle Royale's moose population dynamics. Collectively in both valleys, these grids contain almost 1000 points at which to

estimate available browse biomass, consumption by moose, soil nitrogen availability, and species composition.

RESEARCH QUESTIONS

Chapter 2:

Landscape heterogeneity influences individual moose by altering their feeding rates (Hobbs et al. 2003). But as moose attempt to maximize feeding rates they also create spatial heterogeneity by altering plant growth and distribution (Bergström and Danell 1987, 1995; Danell et al. 1994; Pastor et al. 1998; Persson et al. 2005; De Jager and Pastor 2008). The feeding rates of moose therefore provide a quantitative link between the causes and consequences of spatial heterogeneity across previously browsed landscapes.

It was long held that the instantaneous intake rates of ungulate herbivores increased with food biomass (Alden and Whittaker 1970, Wickstrom et al. 1984, Hudson & Watkins 1986, Renecker & Hudson 1986, Hudson & Frank 1987). But recently developed mechanistic models of herbivore intake rate and empirical tests of these models have indicated that the geometric properties of plant communities, rather than total plant biomass, controls intake by determining the rates by which herbivores encounter bites and then subsequently process bites of plant tissue (Spalinger and Hobbs 1992, Hobbs et al. 2003, Gross et al. 1993, Pastor et al. 1999, De Jager and Pastor 2008). Plant biomass only controls intake rate when it is correlated with the geometric distribution of plant forage, which is rarely the case for browsing herbivores such as

moose because they feed on woody plants with complex geometries (Spalinger and Hobbs 1992). This is because the size of bites of plant tissue available to herbivores on woody plants depends on the geometric properties of the plant crown and because the rate herbivores encounter new bites depends on the spatial arrangement of plants across the landscape.

The geometry of plant canopies regulates herbivore intake rates in food concentrated areas by limiting the available bite mass. When foraging in food concentrated patches, herbivores encounter bites of plant tissue faster than they can process them in the mouth. But the density and distribution of individual plants across the landscape regulates intake rates when food is not concentrated. This is because herbivores finish processing bites of plant tissue prior to encountering new bites. In heterogeneous environments (i.e. when the geometry of plant crowns and plant distributions vary) the feeding rates of herbivores provide a quantitative method for defining the size and distribution of food concentrated patches.

Concentrated and dispersed food distributions, and the associated controls over intake rate, are separated by a threshold distance d^* (m) that depends on the time required to process (R_{max} , g/min) and swallow a bite of plant tissue (S , g/bite), which is S/R_{max} . The distance an animal can move during that amount of time is proportional to its traveling velocity (V_{max} , m/min) and defines the threshold distance (d^*) separating concentrated from dispersed bite distributions.

$$d^* = \frac{V_{max} S}{R_{max}}$$

When d^* is greater than the actual distance between plants (d , m), intake is regulated by the rate the herbivore processes food in the mouth. But when d^* is less than d , intake is regulated by the rate the herbivore encounters new plants. Therefore d^* is a threshold distance that separates two different foraging processes and thus provides a mechanistic definition of the size of food concentrated patches.

Moose don't only respond to the size and density of plant parts in terms of their feeding rates. They also influence these same geometric properties as they attempt to maximize feeding rates. If plants alter their crown geometry in response to previous browsing, the new geometry could change the rate at which herbivores subsequently encounter and process bites of plant tissue. Consequently, by modifying d^* relative to d , herbivore-induced changes to the geometry of plant crowns may change intake rate and the distribution of the mechanisms regulating it across landscapes.

Most of what we currently know about plant responses to browsing comes from tightly controlled experiments where plant growth is manipulated by mechanically removing plant tissue. Few, if any studies have examined the response of plants to a gradient of moose browsing over large landscapes and extended time periods. Furthermore, no study has mapped the distribution of food concentrated patches as defined by d^* across real landscapes or mapped how such distributions respond to the impact of previous browsing on plant canopies. In chapter two of this dissertation I measured changes in the geometry of aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*) canopies along gradients of moose browsing from 2001-2005 at the medium scale grid points at Lane Cove and Moskey Basin (Fig. 3). I further evaluated how the

different responses of plant canopies to increased browsing as well as seasonal changes in bite mass altered d^* around plants, thereby altering which mechanisms regulated intake rate. I then mapped changes in the relationships between d^* and d using plant distributions from the three fine scale grids in both valleys (Fig. 3). These maps reveal how browsing induced changes in plant geometry at very fine scales (bites of plant tissue) influence the spatial distribution of browsing mechanics at scales that are orders of magnitude larger.

Chapter 3

Across landscapes, browsing induced changes in plant canopy geometry, plant spatial distribution, and soil fertility may develop into large scale patterns of browse availability and soil fertility as moose populations move across landscapes. The moose population of Isle Royale averages about 1000 animals, or approximately 1.8 moose/km², but is subject to frequent oscillations (Allen 1976; Peterson 1977; Vucetich and Peterson 2007). Since our long-term study grids were established in 1988, the moose population has peaked during the mid 1990's at approximately 2500 animals and again in the early 2000's at approximately 1000 animals. It has since declined to its lowest density in 50 years of recorded population censuses (Fig. 4) (Vucetich and Peterson 2007). This decline has provided the unique opportunity to examine changes in landscape patterns of ecosystem properties in response to a decline in moose population density.

The nature of the landscape patterns that herbivores create and respond to often depend on the scale of resolution (Hobbs 2003). Because ecological properties are not

uniformly distributed across landscapes, conclusions drawn from observations made at one scale can differ substantially from conclusions drawn from observations made at other scales. Consequently, decisions on scales of inquiry can determine the outcomes of observational studies (Milne et al. 1989; Duarte and Vaque 1992; Reed et al. 1993; Knopf and Sampson 1994; Martinez 1994; Palmer and White 1994; Schaefer and Messier 1995; Begg et al. 1997; Dobermann et al. 1997; Keitt et al. 1997; Stohlegren et al. 1997; Bradshaw 1998; Cooper et al. 1998; Gardner 1998; Peterson et al. 1998; Ritchie 1998; Lawes and Eeley 2000; Adler et al. 2001; Godfray and Lawton 2001; Loreau et al. 2001; Whitaker et al. 2001). Therefore, in order to accurately characterize landscape patterns and link their dynamics to herbivore populations, observations ought to be made and compared across multiple spatial scales.

In Chapter Three, I extended the spatial and temporal extent of a long-term investigation of the relationship of landscape heterogeneity to moose foraging behavior at Isle Royale. I tested three geostatistical models at two different spatial extents, the medium and large scale grids in both valleys at Isle Royale (Fig. 3), to determine if and/or how landscape patterns change with spatial scale. I also compared geostatistical models across a three year time period (2005-2007) and with models from a previous study conducted from 1988-1990 to examine temporal changes in the form of landscape patterns. The models I tested included (1) no spatial autocorrelation (random spatial distribution); (2) short-range spatial autocorrelation within a patch, but random distribution of patches at larger scales (spherical model); and (3) both short-range

autocorrelation within a patch and regular arrangement of patches at larger scales (harmonic oscillator model).

Comparing models between different spatial extents and across different time periods made it possible to investigate how fluctuations in moose population density may induce rapid changes in the distribution of ecosystem properties as reflected in the form and parameter estimates of geostatistical models and simultaneously control for scale-dependent patterns.

Chapter 4

The results from the studies presented in Chapters three and four revealed several novel research findings that will help improve our understanding of how moose and other ungulate herbivores interact with spatially dynamic landscapes. In Chapter 4 I synthesize these results and discuss significant contributions to the four general questions that I posed at the beginning of this chapter. 1) How do we characterize spatial heterogeneity from the viewpoint of specific organisms? 2) What ecological processes are responsible for the spatial heterogeneity present in ecosystems? 3) How do organisms respond to spatial heterogeneity in terms of their ecology, evolution, and behavior? 4) How do we account for spatial heterogeneity in the management and conservation of species and ecosystems? I conclude by discussing future directions for research that will continue to improve our understanding of how populations of animals interact with spatially dynamic ecosystems.

Chapter II: Scaling the effects of moose browsing on forage distribution, from the geometry of plant canopies to landscapes

ABSTRACT

Landscape heterogeneity influences large herbivores by altering their feeding rates, but as herbivores attempt to maximize feeding rates they also create spatial heterogeneity by altering plant growth and distribution. The feeding rates of herbivores therefore provide a quantitative link between the causes and consequences of spatial heterogeneity in ecosystems influenced by large herbivores.

The fractal geometry of plant canopies determines both the density and mass of twigs available to foraging herbivores. These plant properties in turn determine a threshold distance between plants (d^* , m) which distinguishes the mechanisms regulating herbivore food intake rates (*sensu* Hobbs et al. 2003). When d^* is greater than the actual distance between plants (d , m), intake is regulated by the rate the herbivore processes food in the mouth. But when d^* is less than d , intake is regulated by the rate the herbivore encounters new plants. If plants alter their crown geometry in response to previous browsing, the new geometry could change the rate at which herbivores subsequently encounter and process bites of plant tissue. Consequently, by modifying d^* relative to d , herbivore-induced changes to fractal geometry of plant crowns may change intake rate and the distribution of the mechanisms regulating it across landscapes.

We measured changes in the geometry of aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*) canopies along gradients of moose browsing from 2001-

2005 in two valleys at Isle Royale National Park. Fractal dimension of bite density, bite mass, and forage biomass of aspen saplings all responded quadratically to increasing moose browsing and were greatest at $\sim 3\text{-}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ consumption. In contrast, fractal dimension of bite density, bite mass, and forage biomass of balsam fir all declined steadily with increasing moose browsing.

These different responses of plant canopies to increased browsing as well as seasonal changes in bite mass altered d^* around plants, thereby altering which mechanisms regulated intake rate. In summer, $d^* \geq d$ for aspen saplings at all prior consumption levels. Food processing therefore regulated summer moose feeding rates across our landscapes. But in winter, changes in bite mass due to past browsing were sufficient to cause $d^* < d$ for both aspen and balsam fir. Therefore, travel velocity and food processing jointly regulated intake rate during winter. Foraging-induced changes in the small-scale geometry of plant canopies can determine intake rate at larger spatial scales by changing d^* relative to d and hence which mechanisms determine intake rate – essentially altering how herbivores sense the distribution of their food resources.

INTRODUCTION

Understanding the causes and consequences of spatial heterogeneity in ecosystems constitutes a central challenge in ecosystem and landscape ecology (Levin 1992, Pickett and Cadenasso 1995, Pascual and Levin 1999, Turner et al. 2001, Allen and Holling 2002, Chapin et al. 2002, Ettma and Wardle 2002, Perry 2002, Hobbs 2003, Turner and Chapin 2005, Hobbs 2006). Although it is well known that ecological processes are heterogeneous due to variation in abiotic conditions (i.e. climate, topography, substrate) (Jenny 1941, Turner and Chapin 2005), it is less well known how living organisms create spatial heterogeneity as well as respond to it (Hobbs 2003). Most ecosystems are composed of hierarchically nested ecological properties because processes interact with each other across a range of spatial scales (Kotliar and Weins 1990). Consequently, feedbacks between organisms may amplify spatial heterogeneity at scales that are orders of magnitude larger than the scales at which the interactions originally took place (Levin 1992).

Studying the role that large mammalian herbivores play in both responding to spatial heterogeneity and in creating it has proven useful for examining the multiple scale causes and consequences of spatial heterogeneity (Jefferies et al. 1994, Laca and Ortega 1995, Scoones 1995, Hobbs 1996, 1999; Pastor et al. 1997, 1998, 1999a; Fuhlendorf and Smeins 1999, Adler et al. 2001, Augustine and Frank 2001, Steinauer and Collins 2001). Large herbivores make foraging decisions at scales that range from plant stems (centimeters) to home ranges (kilometers). These decisions determine the spatial distribution of forage consumption and the consequent impacts on plant communities.

From small scale changes in the size and density of plant stems to the distribution of plant patches and community assemblages across landscapes, herbivory at one spatial scale may amplify spatial heterogeneity in ways that impact herbivory at other spatial scales and levels of organization. For example, the instantaneous feeding rates of herbivores are closely tied to fine scale changes in plant geometry (Spalinger and Hobbs 1992, Gross et al. 1993 a and b, Pastor et al. 1999 b, Hobbs et al. 2003). But heavy browsing or grazing can also influence the geometry of individual plant canopies (Bergström and Danell 1987 a and b, du Toit et al. 1990, Danell et al. 1991, Hjältén and Price 1996, Escós et al. 1997, Alados et al. 1999, Guillet and Bergström 2006, Stolter 2008, De Jager and Pastor 2008). The feedbacks between herbivores and the geometry of individual plant canopies can further change ecosystems at larger spatial scales as heavily browsed or grazed plants may be outcompeted by adjacent unbrowsed or ungrazed plants. Changes in the distribution and abundance of preferred forage plants across landscapes may in turn influence herbivory at higher levels of organization as populations respond to large-scale heterogeneity in food supply.

Much effort has been devoted to quantifying the functional consequences of spatial heterogeneity for herbivores (Senft et al. 1987, Kotliar and Weins 1990, Bailey et al. 1996, Searle et al. 2005). To a large herbivore, a landscape is spatially heterogeneous when discrete food patches differ from surrounding areas sufficiently to cause a change in the animal's feeding rate (Senft et al. 1987, Bailey et al. 1996, Searle et al. 2005). Differences in the rate herbivores encounter and process bites of plant tissue thus provide a useful estimation of how herbivores perceive heterogeneity in forage distribution across

multiple spatial scales. An herbivore perceives forage to be concentrated in patches when the time it takes the animal to process bites exceeds the time spent traveling between bites. When food is in a concentrated patch, competition between biting and chewing regulates intake rate within the patch because biting and chewing are mutually exclusive events for mammalian herbivores (Spalinger and Hobbs 1992). In food concentrated patches that are apparent (i.e. visible to the herbivore), intake rate increases asymptotically with bite mass (S , g/bite) to the maximum rate by which food can be processed in the mouth by chewing (R_{max} , g/min):

$$I = \frac{R_{max} S}{R_{max} h + S} \quad (1)$$

where h is the time required for cropping a bite in absence of chewing (bites/min; Spalinger and Hobbs 1992).

In contrast, dispersed food distributions are those in which distances between food items is such that the processing of a bite is completed before the next bite is reached. The animal therefore finishes processing each bite before it encounters the next bite and energy is expended between bites without any intake. When bites are dispersed and apparent, intake rate is regulated by bite mass and the time it takes to travel to the next bite, which is a function of plant density (D_p , plants/m²) as well as travel velocity (V_{max} , m/min). Under these conditions, intake rate increases asymptotically with plant density and animal travel velocity because these determine an animal's encounter rate with bites of plant tissue according to Eq. 2 (Hobbs et al. 2003)

$$I = \frac{V_{max} a \sqrt{D_p} S}{1 + ah V_{max} \sqrt{D_p}} \quad (2)$$

where a is a constant that depends on the spatial arrangement of plants and S and h are as above.

Concentrated and dispersed food distributions, and the associated controls over intake rate, are separated by a threshold distance d^* (m) that depends on the time required to process and swallow a bite of plant tissue, S/R_{max} . The distance an animal can move during that amount of time is proportional to its traveling velocity (V_{max}) and defines the threshold distance (d^*) separating concentrated from dispersed bite distributions

$$d^* = \frac{V_{max} S}{R_{max}} \quad (3)$$

Eq. 3 shows that d^* increases with bite mass. A consequence of this is that if the animal is still chewing a large bite when it arrives at the next plant, then the distribution of food appears concentrated to the animal, but if the animal is finished chewing before reaching the next plant, then the distribution of food appears dispersed. How the actual distance between plants in the landscape (d , m) compares to d^* thus defines whether and where the mechanisms regulating food intake switch from biting and chewing to biting and moving and consequently how intake rate varies across the landscape. Therefore, the relationship between d^* and d defines the boundary conditions separating food concentrated from food dispersed patches as they appear to herbivores.

Clearly, the density, spatial arrangement, and size of bites influence herbivore feeding rates and determine how feeding mechanisms vary across the landscape. Underlying these plant properties is the geometry of plant canopies. Woody plants generally grow via iterative self-similar (i.e. fractal) branching rules (Mandelbrot 1983, Frontier 1987). These fractal branching rules yield fractal point distributions of the twigs

which penetrate the outer hemispheric surfaces of the plant canopy (Marstrand 1954). Herbivores encounter such point distributions of twigs across the surface of a plant's canopy as they swing their head from side to side while foraging. If the density of available bites is distributed fractally across the hemispheric surface of the plant crown, then bite density will vary across the outermost hemispheric surface of plant crowns with some power, f (the fractal dimension), of the search width of the herbivore (W). The density of bites per area (D in bites/cm² outer crown surface area) is then equal to the total number of points divided by the linear dimension squared:

$$D = \frac{kW^f}{W^2} = kW^{f-2} \quad (4)$$

where k is bite density (bites/cm³) when $W=1$, and the fractal dimension of bite density is f (see Appendix A in Spalinger and Hobbs, 1992). The fractal dimension describes how the density of bites per unit surface area of the crown varies with the search width of the animal. Higher fractal dimensions correspond to a more uniform distribution of twigs across the surface of the plant canopy and, for a given k and W , increased f in turn increases the density of twigs and hence the food available to herbivores.

West et al. (1997, 1999) showed that in order to minimize energy dissipation while delivering resources throughout the volume of a fractal branching structure, various properties such as metabolic rate, growth, etc. should scale allometrically to mass with a characteristic exponent of 0.75. They derive their theory by making the assumption that each branch in the system has a fixed length and bifurcates into a fixed number of new branches. Together, these branching rules determine the fractal dimension of the branching system. But these and other studies have not accounted for changes in the

mass, length, and/or frequency of branched shoots in response to herbivory. A few studies, however, have demonstrated that herbivory indeed affects the length and mass of plant shoots (Danell 1983, Danell et al. 1985, Bergström and Danell 1987 a and b, Edenius et al. 1995, Persson et al. 2005, De Jager and Pastor 2008), the allometry of plant branching (Escós et al. 1997, Alados et al. 1999, De Jager and Pastor 2008), and that these properties may respond differently for conifer and deciduous tree species (De Jager and Pastor 2008).

The length of conifer stems usually decreases in response to moose browsing, either because large stems are removed and not replaced, or because new shoots are smaller (Brandner et al. 1990, Thompson and Curran 1993, Persson et al. 2005, De Jager and Pastor 2008). Branch frequency of Scots pine tends to decrease in response to tissue removal, resulting in lower fractal dimensions (De Jager and Pastor in press). In contrast, deciduous species display a variety of growth responses to tissue removal, including increased shoot dry mass (Danell et al. 1985, Bergström and Danell 1987) but also decreased shoot dry mass (Persson et al. 2005, De Jager and Pastor 2008). How shoot growth of deciduous species responds to browsing probably depends on growth strategy, shoot morphology, and the amount of tissue removed (Pastor and Danell 2003). Escós et al. (1997) and Alados et al. (1999) found the fractal dimension of the deciduous Mediterranean shrub *Anthyllis cytisoides* L. increased with moderate browsing by sheep and goats, and De Jager and Pastor (2008) found that the fractal dimension of Swedish birches (*Betula pubescens* and *B. pendula*) responded unimodally to increasing moose browsing rate. Thus it appears as though deciduous species have a much greater capacity

to respond positively to browsing up to moderate levels, resulting in greater fractal dimensions and in some cases larger shoots and hence larger bite mass.

Changes in the mass and fractal distribution of twigs induced by past browsing should, therefore, alter the future forage biomass differently for conifers compared to deciduous species. These changes in canopy geometry should in turn determine the magnitude of d^* (Eq. 3). These changes in d^* consequently determine whether food appears to be concentrated or dispersed across the landscape and therefore the factors that control intake rate. In this paper we examine the generality of the different responses of the fractal geometry of conifer and deciduous plant species. We also examine the feedbacks of the general responses of the geometry of deciduous and conifer species to future moose feeding rates by predicting changes in the threshold distance (d^*) which determines the mechanisms regulating herbivore feeding rates. We make our predictions spatially explicit using a Geographic Information System in order to examine changes in the controls over herbivore feeding rate across previously browsed landscapes.

METHODS

Study site

Isle Royale is located approximately 20 miles off the north shore of Lake Superior, USA. The predominant vegetation of the island is boreal forest typical of the Lake Superior region, with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and mountain ash (*Sorbus americana*) being the major deciduous species and

white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) being the major conifer species. The moose population fluctuates, but averages a density of approximately 1.8 moose/km² (Peterson 1977, Allen 1979). Although the impact of moose on forest vegetation is apparent across the island, it can differ greatly within even a single valley (Pastor et al. 1998).

In 1988 two sampling grids were established in the northeast sector of the island where aspen, birch, and mountain ash are the principal food sources of moose. Balsam fir was the only conifer in our grids that was browsed by moose. The sampling grids consist of 100 points in each of two valleys, Lane Cove and Moskey Basin. Within each valley 10 transects are spaced randomly between 0 and 100 meters apart, with points along transects also randomly spaced between 0 and 100 meters (Pastor et al. 1998).

We annually estimated consumption of plant biomass by moose by first counting the number of newly browsed twigs each spring and fall in 2m² circular plots concentric to each grid point. Spring sampling measures the amount of browse consumed over the course of the winter and fall sampling measures consumption during the summer. We then multiplied the number of newly browsed twigs by the average bite mass (g) for each plant species during winter and summer browsing periods (Miquelle 1983, Risenhoover 1987). This yields an estimate of biomass (g/m²) that moose have removed from plants within the plot. In this paper we examine the relationship between annual consumption by moose (g·m⁻²·yr⁻¹) measured during the period 2001-2005 and various geometric features of plants at grid points, such as fractal dimension of bite density, bite mass, crown width,

and sapling height (methods given below), measured during late spring 2005 after the spring browse survey was completed.

Measuring fractal dimension, bite mass, crown width, and tree height

We sampled the aspen and balsam fir saplings nearest each grid point but not more than 2 meters from grid points. Snow depths in winter on Isle Royale effectively shelter any plant 50 cm or less in height from moose browsing (Allen 1977). All trees sampled were greater than 50 cm and less than 250 cm in height. We sampled a total of 97 balsam fir and 109 aspen saplings. The fractal dimension of bite density, bite mass, tree height, crown width, and forage biomass were estimated for each tree.

To estimate the fractal dimension of the density of twigs (bites) on the surface of tree crowns, we constructed a frame that served as a template (Fig 1) for the area a moose can reach without moving its forefeet, an area that Senft et al. (1987) term a feeding station. The sampling frame was 80 cm in lateral width because moose are able to swing their head to cover at least 80 cm. All trees in the grids were less than 80 cm wide and thus the frame was able to span the crown width of all trees. The frame was 30 cm deep, the distance measured from the tip of the nose to the bell of a bull moose specimen in the collections of the Department of Biology, University of Minnesota Duluth. The frame was 60 cm in vertical width, twice the distance measured from the tip of the nose to the bell of an average adult bull moose, a reasonable minimum estimation of the diameter of vertical head movement.

In the field, the frame was placed on an adjustable tripod adjacent to each sampled tree. The frame was adjusted against a sample tree to encompass the top shoot and centered with the outermost branch just protruding through its front face (Fig. 1). We assumed that only the twigs on the current surface of the tree crown are available to a foraging animal whereas the underlying branching structure is not. However, the distribution of the twigs piercing the hemispheric surface of the tree crowns is fractal because the twigs emerge from the underlying 3 dimensional fractal branching structure (Fig. 2). Marstrand's (1954) projection theorem relates 2 and 3 dimensional fractal dimensions to each other and Nielsen et al. (1997) empirically showed that the fractal dimension of a branching structure embedded in three dimensions determines the fractal dimension of the intersection of the branches with a two dimensional surface slicing across the branching structure. Our frame therefore estimates the fractal dimension of twigs piercing the 2 dimensional surface of the tree crown.

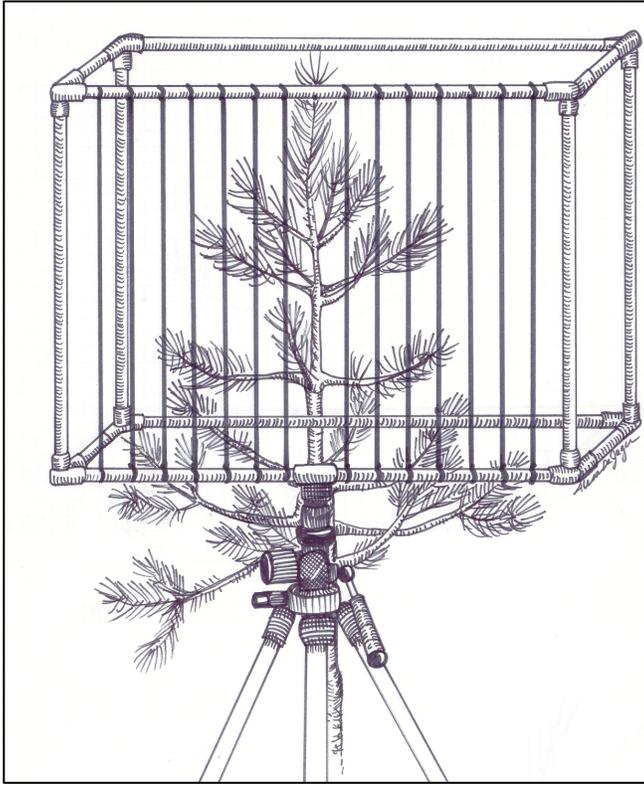


Fig 1. The frame used to measure the fractal dimension of bite density. Bites represent the intersection of the terminal end of a twig with the hemispheric surface of the tree crown. The \ln (density of bites) within distinct widths of the tree crown were regressed against \ln (crown width) in order to estimate the fractal dimension of bite density.

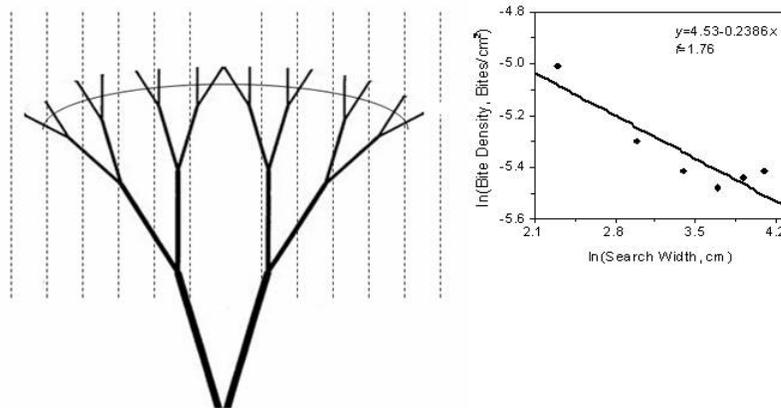


Fig. 2. When the density of twigs of a fractal branching structure is sampled at different search widths along a hemispheric cut across its outermost twigs, the plot of the \ln (density) against the \ln (search width) is linear with a slope equal to $f - 2$, where f is the fractal dimension (graph on right). Sampling twig density across the two-dimensional face of our sampling frame in Fig. 1 is a 2D analog of sampling across this 1D cut.

Once the frame was positioned on the tree, the number of twigs was counted at different lateral search widths beginning with the center 10 cm and moving outward toward the edges of the frame at 10 cm intervals. The parameters f and k in Eq. 1 were estimated for each tree by regressing the logarithm of measured bite density (D) against the logarithm of simulated search width (W). The fractal dimension of bite density (f) was estimated by adding 2 to the slope of the regression line ($d-2$), and k was estimated by taking the anti-logarithm of the y -intercept. We restricted further analyses of d and k to plants with fractal relationships of $R^2 > .9$ (Milne et al. 1992). This resulted in the removal of 22% of aspen saplings and 9 % of balsam fir saplings from analyses further considering the fractal dimension of bite density.

The average available bite mass (g/bite) of each shrub sampled was measured by selecting the first 10 twigs within the sampling frame and measuring twig length from the tip to the point at which twig diameter equals the mean diameters browsed twigs in the areas (4 mm for both aspen and balsam fir, our own unpublished observations). If the diameter of a twig was less than 4.0 mm, the length of the twig was measured from the tip to the point where it branched into a second shoot long enough to be considered a bite and both the diameter and length were recorded. We then developed regression equations to estimate the dry mass of aspen and balsam fir twigs from their basal diameters and lengths by measuring, drying, and weighing twigs of various sizes. These estimates yielded the average bite mass available to moose on these trees during winter. During summer, moose feed on the leaves of deciduous species. We established regression equations for the leaf mass of aspen shoots by measuring the length and diameter of twigs

of various sizes, stripping the leaves from those twigs, and then drying and weighing the leaves. Forage biomass per feeding station was then determined by adding together the estimated bite mass of each stem within the frame.

The height of trees (cm) was measured with a standard height pole and the width of tree crowns (cm) was estimated as the width of the entire tree crown that resided within the 80 cm sampling frame shown in Fig. 1. Estimates of height and width were rounded to the nearest 10 cm.

Statistical analysis of the effects of moose on plant crown geometry

We used least-squares regression analysis of responses of the above measurements to increasing annual consumption. We selected regression models that best described how the different plant architecture measurements related to annual consumption by using the “step” command in the statistical computing environment “R” (R Development Core Team 2006). We began with models consisting of both linear (x) and non-linear (x^2) effects of annual consumption on a measured plant trait. The step command causes all the terms in the model to be tested to see whether they are needed in the minimal adequate model. “Step” uses information theoretics (Akaike’s Information Criterion, AIC) as the model selection criterion (Burnham and Anderson, 1998). We selected models with the lowest AIC value, but only if the difference in AIC value between two candidate models was >1.0 (Ims and Yoccoz, 2000). We report the difference in the AIC value between the selected model r and the best approximating

model as Δ_r . We examined histograms of the residuals after model fitting in order to assure that the errors were normally distributed.

We also analyzed the data by grouping trees into different “bins” of annual moose consumption and then performed regression analysis of the means of different measurements within each bin against mean annual moose consumption. Data were grouped at 1 g/m² consumption increments for balsam fir and 2 g/m² consumption increments for aspen to maintain relatively consistent sample sizes within groupings and between species. Model selection was carried out as described above using AIC.

Finally, we examined the response of different quantiles of the response distribution for bite mass using quantile regression. Quantile regression is often used to assess unequal variance in response distributions (Koenker and Bassett 1978), but can be applied to any association between sets of variables (Dunham et al. 2002). We used quantile regression to define the relationship between the 50th (median) and 75th quantiles of the distribution of bite mass as it relates to increasing consumption by moose. We chose the median because it is the best approximation of the results found above using least-squares regression analysis and defines the relationship between the central tendency of bite mass and increasing past consumption by moose. We chose the 75th quantile because it defines the relationship between the bite mass we would expect moose to select in the field and past consumption by moose. We base this assumption on the findings that moose maximize intake rate by optimizing bite mass (Shipley et al. 1999). Moose typically browse ~25% of all available stems at a feeding station and maximize intake rate by selecting larger stems (Shipley et al. 1998, 1999), it is therefore likely that

the 75th quantile of bite mass most accurately quantifies the lower bounds of the bite mass we would expect moose to select. Thus, we thought that it was important to not only understand how the central tendency of available bite mass responds to past moose browsing, but also how the bite mass that we would expect moose to select while foraging responds to past moose browsing. We tested a null model consisting of a y-intercept and no slope, a linear model, and a quadratic model at both the 50th and 75th quantiles of bite mass. We compared models using Analysis of Variance and selected the least complex of the three models if there were no significant differences between the smaller and larger models ($P = 0.05$).

*Predicting the relationships between d and d^**

The procedures outlined above examine the effects of past moose browsing on a collection of geometric features of plant crowns. The most direct way in which plant geometry feeds back on future moose foraging is through changes in bite mass as outlined in Eq's 1, 2, and 3 of the *Introduction*. Thus, we inserted equations that we derived in the above analyses for the impact of moose consumption rate on bite mass into Eq. 3 for S , in order to predict how the threshold distance (d^*) around an individual plant changes because of the effect of past consumption rate, given values for R_{max} and V_{max} . We used the results from the 50th (median) and 75th quantiles of the response distribution of bite mass against annual moose consumption. This provides estimates of d^* based on the central tendency of available bite mass and the expected bite mass that moose would select in the field. We calculated d^* for a 350 kg moose and held body mass constant. We

estimated R_{max} and V_{max} in Eq. 3 from the allometric relationships found by Shipley et al. (1994, 1996), where $R_{max} = 0.70M^{0.70}$ and $V_{max} = 52.16M^{0.04}$. For a 350 kg moose, these estimates are 42.2 g/min and 65.9 m/min for R_{max} and V_{max} respectively. These estimates are similar to field estimates made for moose and similarly sized elk. Shipley et al. (1994) estimated R_{max} for a 309 kg moose to be approximately 40 g/min and Hobbs et al. (2003) estimated V_{max} for a 266 kg elk to be approximately 64.7 m/min. Given the similarity of the field measurements to estimates derived from the allometric equations for a 350 kg moose, we chose to use the estimates from the allometric equations so that we could also predict changes in d^* for moose of different body mass. By using maximum rates of foraging velocity (V_{max}) we assume no changes in acceleration or deceleration with distance between plants. Fortin (2006) showed that changes in acceleration and deceleration decrease the average foraging velocity between plants below V_{max} , which in turn decreases d^* . However we are unaware of any direct measurements of average foraging velocity for moose. We also use maximum rates of food processing (R_{max}) for moose. Here, we are assuming that food processing rates are independent of changes in plant tissue with changes in season. However, there could be rather large changes in R_{max} with seasonal changes in plant tissue structure from leaves in summer to tougher woody tissues in winter. Tougher material would essentially decrease R_{max} which would then increase d^* , however we are unaware of any study that measures R_{max} directly for moose eating different plant materials. Instead of introducing additional assumptions about how V_{max} and R_{max} change with changes in distance between plants, with changes in season, and with changes in body mass, we chose to use estimates obtained from the allometric

equations of Shipley et al. (1994, 1996) and to hold these values constant for a 350 kg moose in order to evaluate the effects of changing bite mass alone on d^* . However, we will discuss later in the paper how changes in our assumed values for V_{max} and R_{max} due to starting and stopping, the different toughness of plant tissue, and animal body mass would affect our results.

Within the two sampling grids used to collect the data on plant geometry and past moose browsing discussed above, we established six additional grids consisting of 100 contiguous 1.4 m X 1.4 m squares (approximately 2 m²); each square is the area over which a moose can reach bites of plant tissue without moving its forefeet, an area which Senft et al. (1987) have termed a feeding station. Each of these six fine-scale grids therefore represents a series of 100 contiguous feeding stations. In each valley, one of the grids was located in an area dominated by conifers, one in an area dominated by deciduous species, and one in an area of roughly equal dominance by conifers and deciduous species. Thus, the three fine-scale grids are located along a gradient of decreasing conifer and increasing deciduous density.

In the field, the location of each forage plant within each 2 m² grid cell was plotted on a map after being estimated visually. Using the X-Y coordinates for aspen and balsam fir saplings, we estimated the distance to the nearest food-supplying neighbor (d) using the Nearest Features extension for Arcview 3.1 (Jenness 2004). In the summer, moose feed heavily on aspen but do not feed on balsam fir (Telfer 1984, Risenhoover 1987, Brandner et al. 1990). Thus, for summer browsing, we made nearest neighbor estimates from one aspen sapling to the nearest adjacent aspen sapling. In winter, moose

search for both aspen and balsam fir saplings and thus we made nearest neighbor estimates for when moose move from one aspen to the nearest adjacent aspen or balsam fir and from one balsam fir to the nearest adjacent aspen or balsam fir. These nearest-neighbor distances were then compared with d^* , calculated as described above.

*Mapping the distributions of d and d^**

Using Arcview 3.1 (ESRI 2000) and the mapped distributions of trees in each of the grids, we created buffers around each plant corresponding to d^* for bite mass at low, medium, and high past consumption rates and for both summer and winter. Low consumption was assumed to be 0 g/m^2 for both aspen and balsam fir, medium was assumed to be 2.5 g/m^2 for balsam fir and 4.5 g/m^2 for aspen, and high consumption rates were assumed to be 5 g/m^2 for balsam fir and 9 g/m^2 for aspen as 5 and 9 g/m^2 were the highest measured browsing rates at grid points where aspen and balsam were respectively found. For summer scenarios, we used only the mapped locations of aspens and made estimates of d^* based on the 75th regression quantile of the mass of aspen leaves. For winter scenarios we plotted the location of both aspen and balsam fir saplings and created buffers around each species in accordance with d^* based on the 75th regression quantile of bite mass of both aspen and balsam fir in winter. Although moose will select multiple bites of plant material and consume them simultaneously, 1-bite sequences occur greater than 80% of the time and also maximize intake rate (Pastor et al. 1999). For simplicity we assume that moose select single bites from plants and process them one at a time. This

assumption has also been made by Gross et al. (1993), Hobbs et al. (2003), and Fortin (2006).

To examine how d^* changes with increasing consumption rate and different plant densities, we created figures that order the grids according to measured aspen sapling density because distance between plants, d , is inversely related to density. Then, within each grid we plotted the width of d^* buffers around each plant in accordance with increased consumption rate. This provides us with mapped distributions of individual plants and predicted threshold distances (d^*) around each plant based on multiple different past consumption rates, multiple different plant densities, and for different seasons of the year.

RESULTS

Effects of moose on the geometry of plant canopies

The fractal dimension of bite density of balsam fir saplings decreased monotonically with increasing annual consumption ($R^2 = 0.3919$, $\Delta_r = 34.7$). Grouping or “binning” the data by means produced similar results (Fig. 3). In contrast, the fractal dimension of aspen saplings at first increased but then decreased with increasing annual consumption by moose ($R^2=0.2568$, $\Delta_r = 13.06$); grouping the data by means again produced similar results (Fig. 3).

Bite mass of balsam fir decreased linearly with increasing annual consumption ($R^2=0.6058$, $\Delta_r = 79.8$). As with fractal dimension, a quadratic model had the lowest AIC

for the winter bite mass of aspen saplings ($R^2=0.3035$, $\Delta_r = 21.1$) and the summer bite mass of aspen saplings ($R^2=0.3035$, $\Delta_r = 15.5$). Grouping the data by means produced similar results for both species (Fig. 3). Results using quantile regression for bite mass were linear for balsam fir and quadratic for aspen:

$$S_{A,W(\tau=.5)} = 0.377 + 0.1899x - 0.0203x^2 \quad (5)$$

$$S_{A,W(\tau=.75)} = 0.61 + 0.327x - 0.036x^2 \quad (6)$$

$$S_{B,W(\tau=.5)} = 1.107 - .111x \quad (7)$$

$$S_{B,W(\tau=.75)} = 1.26 - 0.12x \quad (8)$$

$$S_{A,S(\tau=.5)} = 1.22 + 0.29x - 0.0308x^2 \quad (9)$$

$$S_{A,S(\tau=.75)} = 1.63 + 0.53x - 0.06x^2 \quad (10)$$

where S is bite mass for either aspen (A) or balsam fir (B) during summer (S) or winter (W), for the median ($\tau = .5$) and 75th quantile ($\tau = .75$) and x is annual consumption (g). Later, we will use these equations to predict the impact of past moose browsing on d^* and the mechanistic controls over future moose feeding rates across multiple spatial scales.

Multiplying bite mass by twig density yields total forage biomass per feeding station. Total forage biomass per feeding station decreased linearly with increased consumption of balsam fir ($R^2 = 0.23$, $\Delta_r = 20.0$) but responded quadratically for aspen ($R^2 = 0.2159$, $\Delta_r = 8.6$) and results were similar when analyzed by grouping the data according to means (Fig. 3).

Tree height for both species and crown width of aspen saplings varied randomly about a constant mean for any value of consumption. But the width of balsam fir sapling crowns decreased linearly with increased consumption ($R^2 = 0.2757$, $\Delta_r = 26.4$).

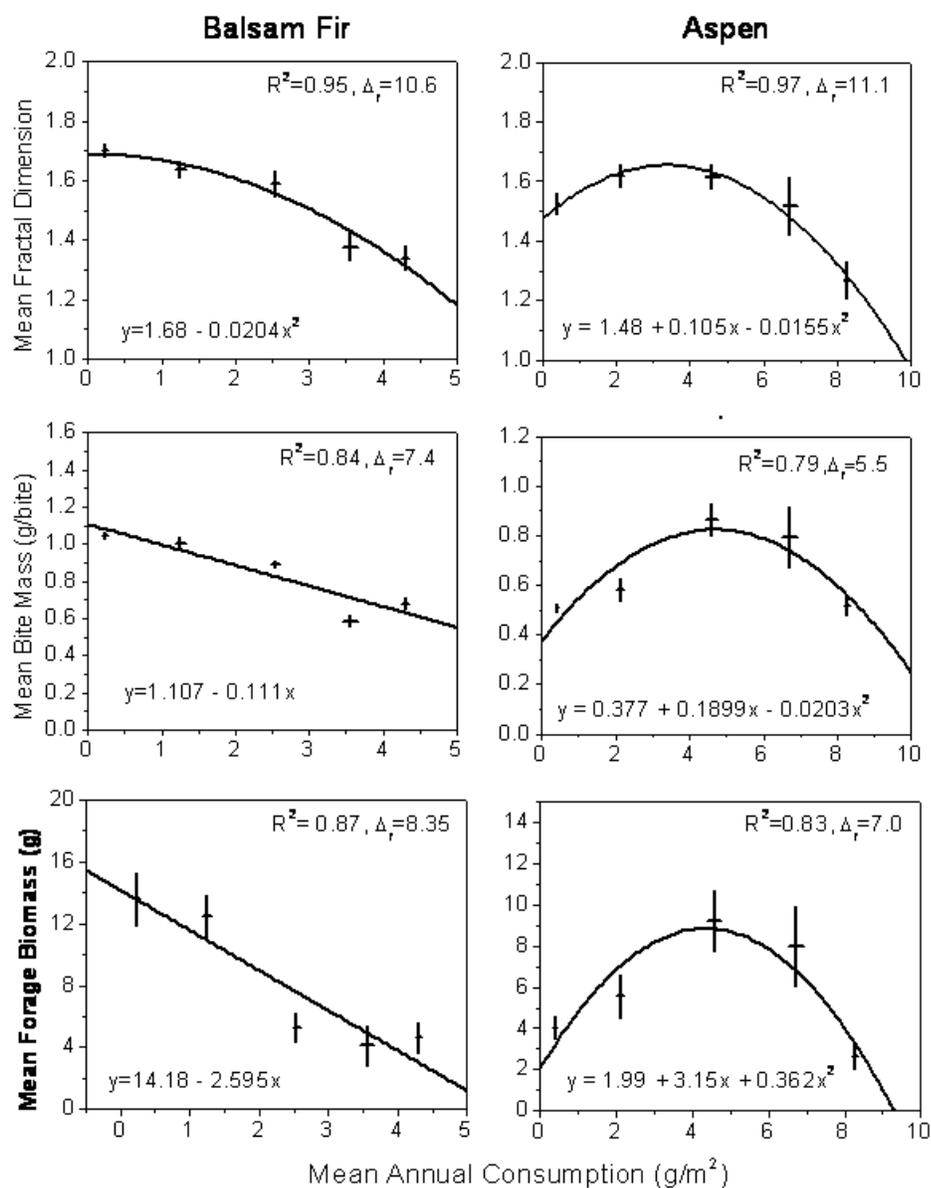


Fig 3. Mean fractal dimension of bite density, bite mass, and forage biomass per feeding station in relation to increasing mean annual moose consumption rate and associated standard errors, and least squares regression equations for aspen and balsam fir saplings. Δ_r is the difference between the models shown and the next best approximating models.

*Relationships between d and d^**

Predictions of d^* , the threshold distance between plants which separates the two intake rates (Eqs. 1 and 2), follow directly from Eqs 5-10. Larger values of d^* make it more likely that plant distributions will appear to be concentrated to the moose and intake rates therefore follow Eq. 1. For aspen, d^* responded quadratically to increasing consumption rate for both summer and winter foraging but for balsam fir, d^* decreased monotonically with increasing consumption rate (Fig. 4). The quadratic response of d^* for aspen indicates that regardless of season, plant distributions are more likely to appear concentrated when previous browsing has been moderate. For balsam fir, plant distributions are more likely to appear concentrated only when past consumption has been low. Predictions of d^* decreased from summer, when moose feed on aspen leaves, to winter when moose feed on aspen and balsam fir twigs (Fig. 4). In summer, a foraging moose is more likely to arrive at the next plant before finishing chewing a bite from the previous plant. Consequently, the plants are likely to appear to the moose to be concentrated in summer, and processing rate and bite mass control intake rate according to Eq. 1. However, plants are more likely to appear to the moose to be dispersed in winter due to smaller bite mass, and intake rate is controlled by bite mass and travel velocity according to Eq. 2.

The predictions of d^* for summer browsing were well above the mean nearest neighbor distances between aspen saplings in each of the grids (Fig. 4). Therefore, in summer, large areas may appear as one concentrated patch of food and intake rate is not limited by plant encounter rate, regardless of plant density, but instead by bite mass and

chewing rate (Eq. 1). Decreases in bite mass from summer to winter, however, sufficiently decreased d^* to the point where many grids crossed over from concentrated ($d^* > d$) to dispersed ($d^* < d$) plant distributions (Fig. 4). Because of the quadratic response of bite mass of aspen twigs and the monotonically declining response of bite mass of balsam fir twigs to increasing moose consumption, bite mass is smallest at low and high consumption rates for aspen and at high consumption rates for balsam fir. Bite mass of aspen at both low and high consumption rates is sufficiently small so that plant distributions may appear dispersed to moose during winter and intake rates are then governed by bite mass and travel velocity (Eq. 2). In the grids with lower plant density and hence longer distances between nearest neighbors, these effects become more pronounced. At moderate consumption rates, the increase in bite mass and consequently d^* is sufficient to maintain concentrated distributions in many of the grids during winter as well as summer for aspen. For balsam fir, decreases in bite mass and consequently d^* with increased consumption rate was sufficient to change plant distributions from concentrated to dispersed. These changes are more pronounced at high consumption rates and with lower plant densities and hence longer nearest neighbor distances (Fig. 4).

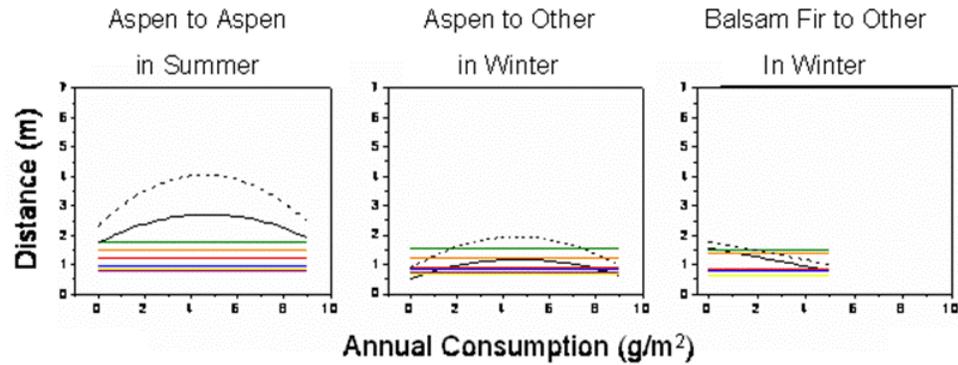


Fig. 4. Nearest neighbor distances (d) for the six fine scale grids are indicated by different colored lines and estimates of d^* calculated using the bite mass in Eq's 5-10 are indicated by the solid black line (median response) and dashed line (response of the 75th quantile). When nearest neighbor distances (d) are greater than d^* , the distribution of forage is dispersed, but when $d^* > d$ the distribution of forage is concentrated. Decreases in d^* from summer to winter are sufficient to cause switching between concentrated and dispersed plant distributions as they appear to moose. Changes in d^* due to the effects of moose browsing on plant geometry, which limit the available bite mass, further modify the seasonal changes.

*Mapped distributions of d and d^**

Distances between aspen saplings are generally closer than d^* predictions in summer, regardless of consumption rate or aspen sapling density (Fig. 4). Thus, in summer the zones of d^* around individual saplings are large enough to overlap and are thereby aggregated into a large patch, often larger than the study grids (Figs 5 a and b).

Consequently, a 350 kg moose can move directly from one plant to its nearest neighbor and still remain within d^* . It can, therefore, move directly from plant to plant and cover the entire area of the study grid without any changes in the mechanisms regulating the foraging process.

In winter, the larger d^* for balsam fir at low consumption rates has some capacity to compensate for the shorter d^* around aspen (Fig. 6 a and b). At medium consumption rates the increase in aspen d^* is sufficient to compensate for the decrease in balsam fir d^* and, with only a few minor exceptions, plant distributions throughout the study grids appear to be concentrated. But when past browse consumption is high, the bite sizes of both aspen and balsam fir saplings are small and d^* decreases according to Eq. 3. Now the grids become increasingly fragmented into smaller food concentrated patches consisting of one or a few plants. These effects are magnified with decreasing sapling density where distances between plants are longer. Therefore, the mechanisms regulating food intake rate vary across the grids, being bite mass and chewing rate in some areas and encounter rate in other areas.

Summer at Lane Cove

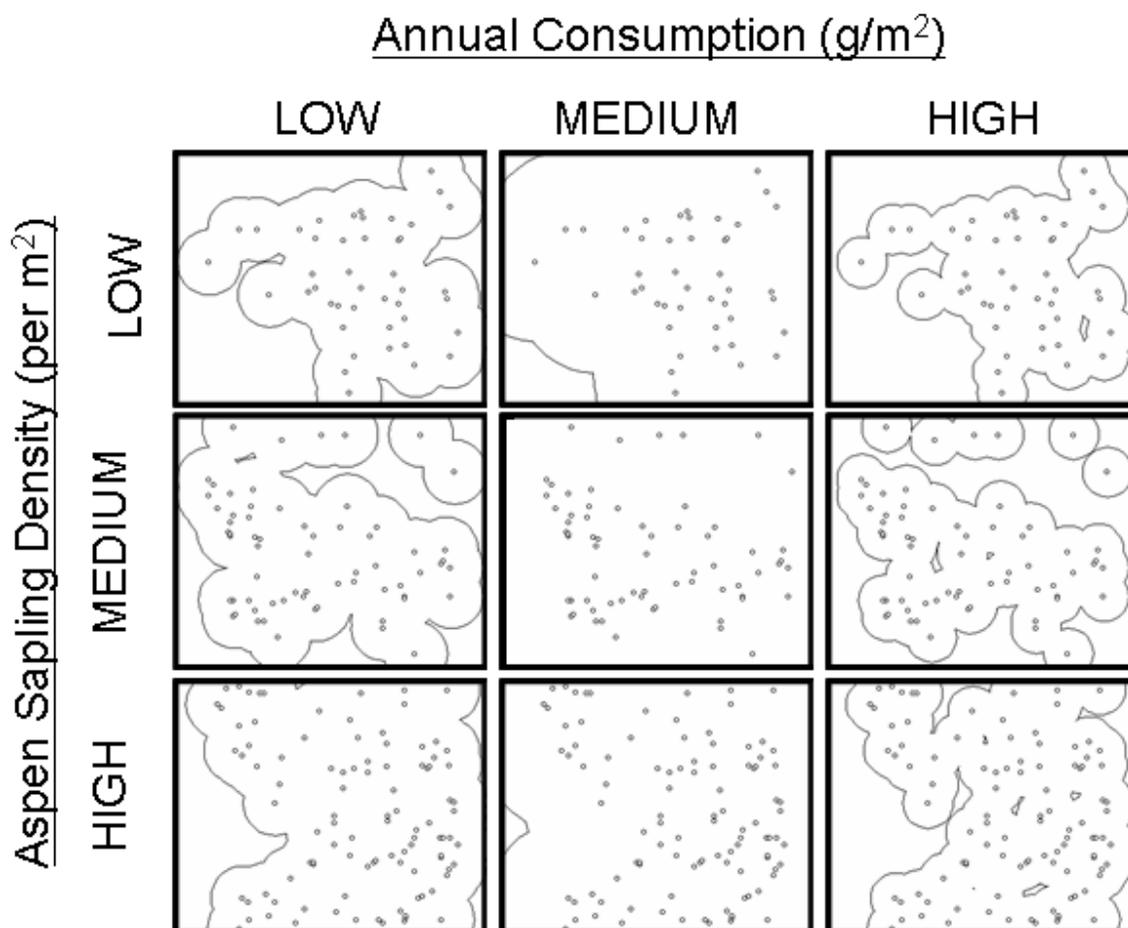


Fig. 5a.

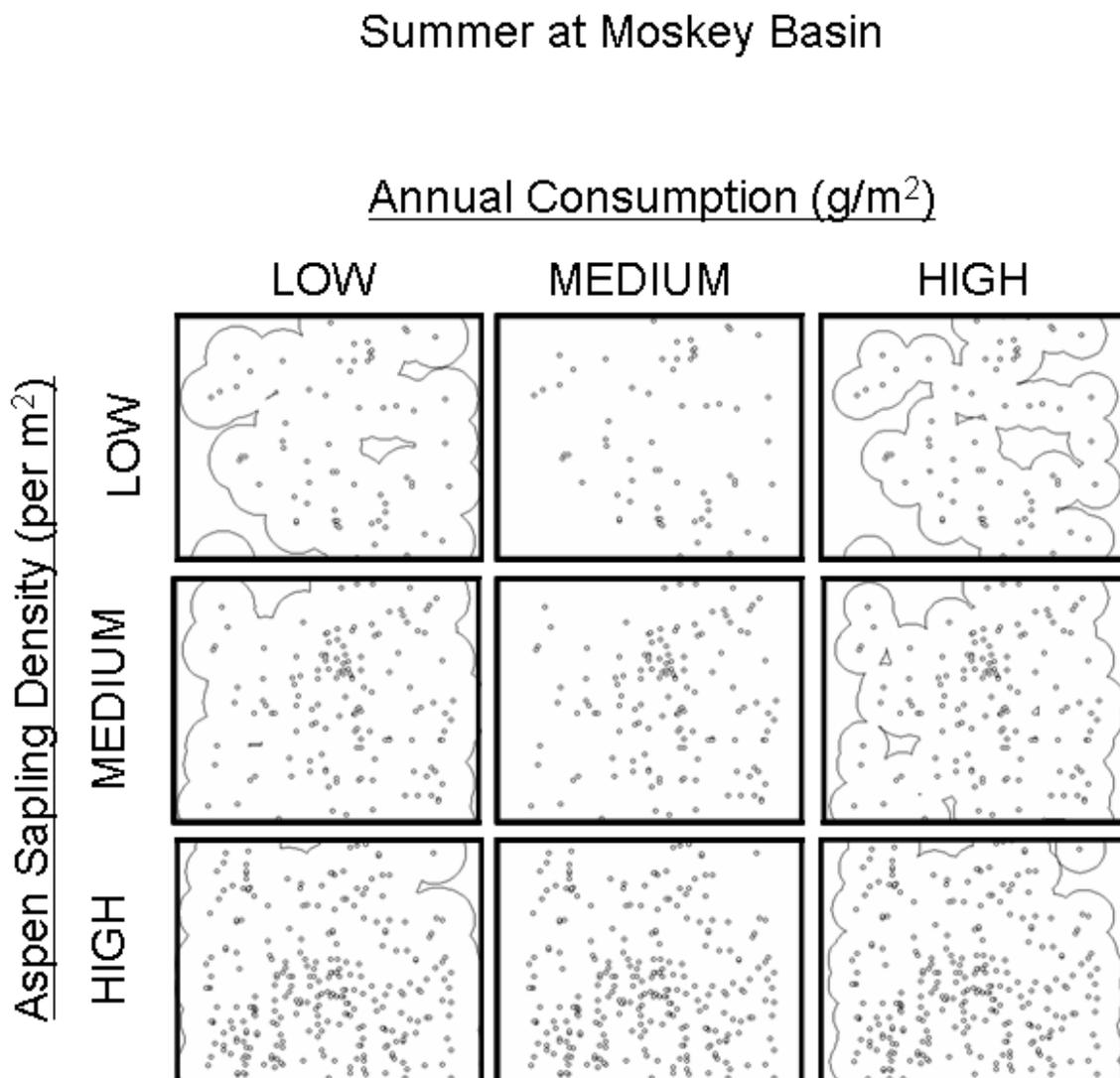


Fig. 5b

Mapped distributions of aspen in the three grids in both Lane Cove and Moskey Basin, arranged vertically as a gradient of aspen density. Each grid is 14.1X14.1 m. *d** Buffers were created around each tree in each of the six fine scale grids using Eq. 10. Inside each buffer plants appear concentrated to moose.

Winter at Lane Cove

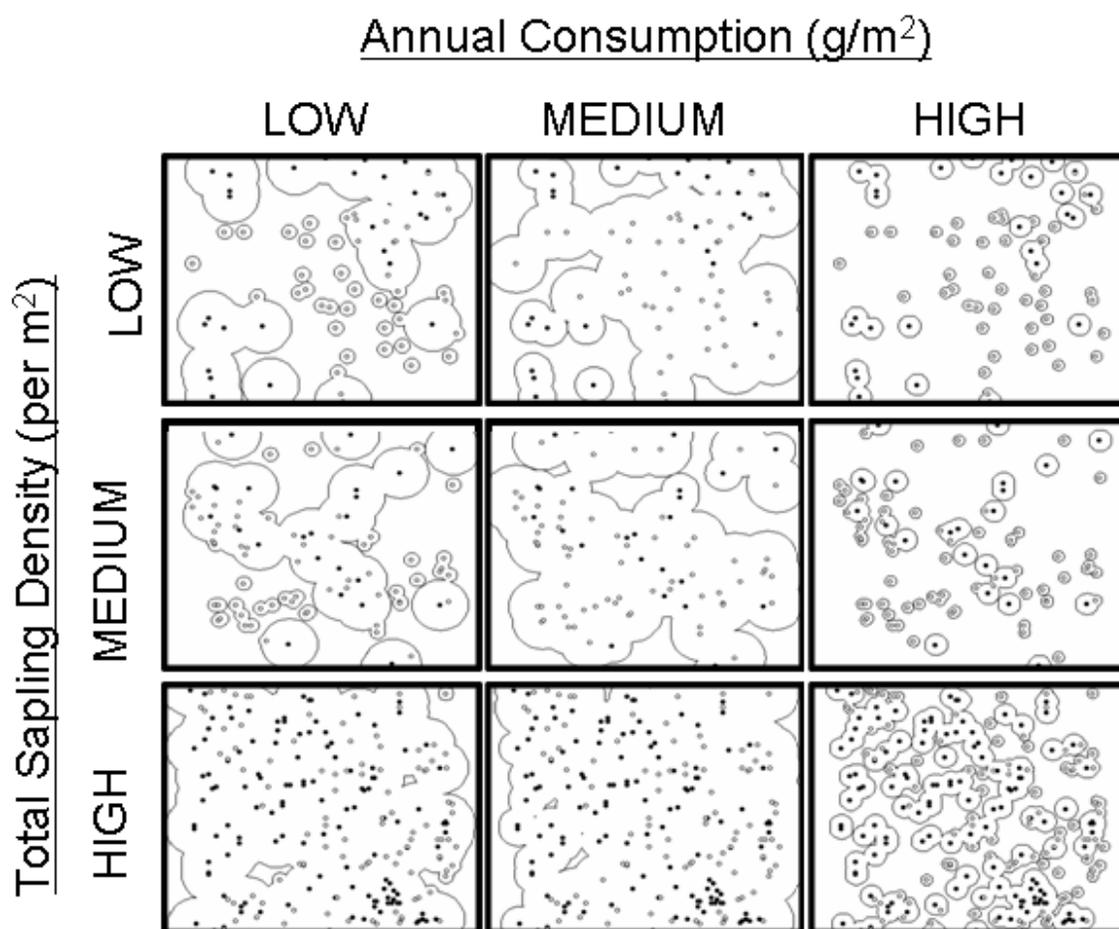


Fig. 6a

Winter at Moskey Basin

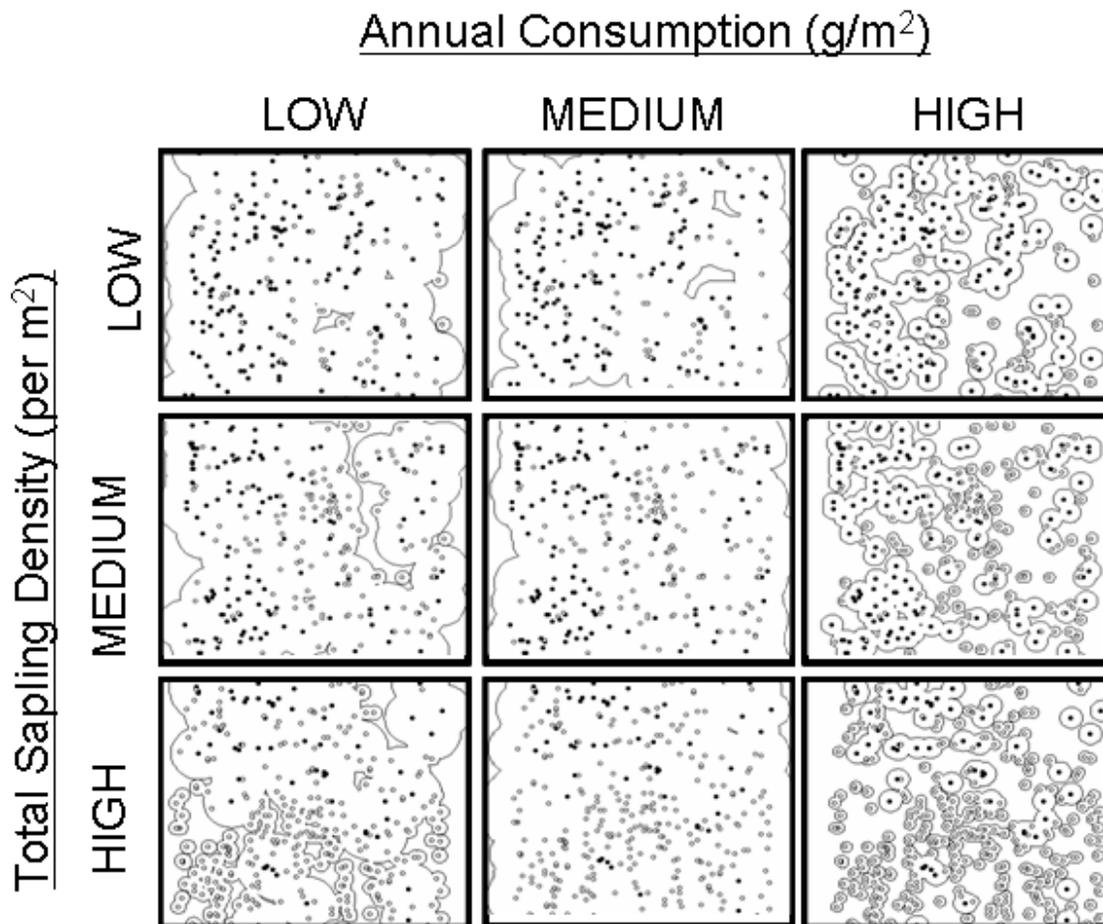


Fig. 6b

Mapped distributions of aspen (open circles) and balsam fir (closed circles) in the three grids at both Lane Cove and Moskey Basin. Each grid is 14.1X14.1 m. *d** Buffers were created around each tree in each of the six fine scale grids using Eqq. 6 and 8. Inside each buffer plants appear concentrated to moose. Plants located outside the buffers appear dispersed.

DISCUSSION

Effects of moose browsing on plant fractal geometry

Moose browsing altered the fractal dimension of bite density of balsam fir and aspen saplings differently. For the conifer species, balsam fir, the fractal dimension decreased with increased consumption by moose. In contrast, the fractal dimension of the deciduous species, aspen, responded unimodally to increased browsing and was maximal at intermediate consumption rates (~ 3 or $4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). We found similar differences between Scots pine and birch responses to increases in simulated moose browsing in northern Sweden (De Jager and Pastor, in press). As was the case for balsam fir, the fractal dimension of Scots pine decreased with increasing moose consumption. In contrast, the fractal dimension of birch saplings in Sweden responded quadratically to increasing consumption, similar to the responses of aspen reported here. Other deciduous species have displayed similar unimodal responses of their fractal dimensions to increased herbivory, with maximum fractal dimension at intermediate levels (Escós et al. 1997, Alados et al. 1999).

The degree to which conifers and deciduous species tend to exhibit apical dominance in combination with the timing of cell growth may underlie these different geometric responses. The apical meristems of woody plants suppress the outgrowth of lateral buds via local hormonal control (Cline 1994). By browsing apical meristems, herbivores reduce hormonal suppression of lateral buds (Senn and Haukioja 1994), which then elongate and develop into new side shoots. But the response of different plant species to the removal of apical dominance by herbivory also depends on the stage of the

cell cycle at the time of meristem removal (Tamas 1987). Conifers often display determinate growth, whereby cells terminate growth and development after a genetically pre-determined structure has formed. In contrast, deciduous species often display indeterminate growth. Deciduous species tend to therefore have a shorter lag period between the time when apical meristems are removed by herbivores and when lower axillary buds begin to sprout and the twigs elongate. Thus, conifers such as Scots pine and balsam fir may take over a year to replace lost tissue (Edenius et al. 1995) while the deciduous species can begin to replace lost tissue within the same growing season. The new deciduous stems can then be browsed the following year. The net result is rapidly increased “branchiness” and hence fractal dimension of the outermost branching structure. However, if browsing removes too much tissue, the plant becomes stressed and unable to replace lost stems. Thus, while moderate browsing may increase plant branchiness and fractal dimension, heavy browsing decreases it, resulting in the unimodal responses of aspen and birch to increased herbivory.

We and others (Escós et al. 1997; Alados et al. 1999) have found large changes in canopy structure due to herbivory resulting in a range of fractal dimensions within the same plant species. We might expect other environmental impacts (drought, wind, insect damage, etc.) to produce similar changes in canopy structure and result in a wide range of fractal dimensions. Thus the fractal geometry of branch networks is most likely a dynamic property of plants, rather than a static property as presented in West et al. (1997, 1999).

Effects of moose browsing on bite mass

The mass of individual twigs and leaves available to moose in the form of bites is limited by the geometry of plant canopies and by the effects of past moose browsing. Our estimates of bite mass ranged from .5 g dry mass on heavily browsed saplings up to 2.9 g dry mass on moderately browsed aspen saplings. These estimates are within the range of other studies that have estimated bite mass for moose (Renecker and Hudson 1986, Risenhoover 1987, Åström et al. 1990, Belovsky and Jordan 1978, and Shipley et al. 1999). Bite mass of balsam fir declined with any increase in moose browsing while bite mass of aspen saplings responded unimodally to increases in browsing and was maximal at intermediate consumption rates ($\sim 3\text{-}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). Other studies have found similar declines in the mass of conifer twigs to increased herbivory (Perrson et al. 2005, De Jager and Pastor in press) and others have shown that browsed conifer twigs may become weaker and eventually die (Brandner et al. 1990, Thompson and Curran 1993). Other studies have also found increases in the dry mass of deciduous shoots following moderate browsing (Danell et al. 1985, Bergström and Danell 1987, Stewart et al. 2006) with subsequent declines in bite mass with heavy browsing (Persson et al. 2005, De Jager and Pastor in press).

Scaling up from plant crowns to the landscape

Both season of the year and past consumption rate altered bite mass sufficiently to change how the distribution of food appears to moose. During summer, moose may often perceive the distribution of food as concentrated over a large range of past browsing

intensities and plant densities (Fig. 4 and 5). Thus during summer, a foraging moose can maintain high intake rates because time spent processing bites exceeds the encounter rate with new bites. So long as they encounter bites within d^* , moose could cover areas at least as large as and even much larger than the grids in Figs 5 and 6 and never move out of what appears to it to be a single, contiguous, food concentrated patch. Intake rates for moose during summer are thus most likely controlled by food processing rate (chewing) and the mass of bites (Eq. 1).

In winter, moose appear to view the same patches as being more dispersed, especially in areas with high past rates of browsing and low plant density. Food now appears as isolated fragments within what in the summer were perceived as large food concentrated patches. In winter, both encounter rate (determined by plant spacing and travel velocity) and the rate of processing a bite by chewing determine intake rate (Eq. 2). It is interesting to note that this appearance of fragmentation (to the moose) occurs without any change in the actual location of plants within the study plots. It is not the actual distributions of the plants that changes, but the appearance of the distribution of food to the foraging moose because of how previous browsing has altered the geometry of plants which in turn regulates bite mass and thus the time animals spend processing bites. Therefore, changes at one spatial scale (twig length on the order of 10's of cm and bite mass on the order of 1-2 g) can affect d^* (Eq. 3) on the order of meters around each plant. These changes to individual plant canopies in turn determine whether the moose perceives aggregated patches of concentrated food or individual fragments of dispersed food and consequently which factors determine intake rate. Larger buffers around the

plant of radius d^* on the scale of a few meters may effectively coalesce into large contiguous and concentrated patches of food on the scale of 10-50m in radius. Therefore, the small scale changes in twig length in cm, bite mass in g, and d^* in m propagate upward to the 10-50m scale of larger patches because they determine which mechanisms control intake rate and the distribution of those mechanisms across the landscape.

Throughout this paper we have assumed no change in foraging velocity (V_{max}) with changes in plant spacing (d). However, acceleration and deceleration decrease actual foraging velocity below V_{max} for browsing herbivores (Shiple et al. 1996; Fortin, 2006). In terms of our results, a slower foraging velocity due to acceleration and deceleration would decrease d^* , leading to landscapes that are even more likely to consist of dispersed forage distributions. Our finding that the effects of moose browsing on bite mass are sufficient to decrease d^* during winter thus appear to be conservative to our assumptions about a constant foraging velocity: the actual d^* may be even shorter if velocity is slower. In addition to decreases in foraging velocity due to acceleration and deceleration, we should expect slower foraging velocities in winter due to deep snow. By slowing travel velocity and thereby shortening d^* , deep snow would therefore exacerbate the dispersed forage distributions in winter. It is however, unclear whether summer forage distributions would remain concentrated given slower foraging velocities due to acceleration and deceleration and the changes in bite mass due to past moose browsing.

We also assumed that R_{max} is constant for the different plant materials that moose feed on during different seasons. We assume that because bites are larger during summer that they correspondingly take longer to chew (R_{max} is constant). Yet Illius et al. (2002)

showed that there can be rather large differences in R_{max} of roe deer depending on plant species and fiber concentration. We should expect decreases in R_{max} with seasonal changes in plant tissue consumed by moose when they shift from eating leaves in summer to tougher woody tissues in winter. By Eq. 3, a decrease in R_{max} would increase d^* and lead to landscapes that are more likely to appear concentrated to moose. Thus, our finding that d^* is shorter during winter causing some grids to appear fragmented in dispersed food patches is subject to the assumption that food processing rates do not slow sufficiently to compensate for decreases in bite mass. However, we are unaware of any study that measures R_{max} directly for moose eating different plant materials, especially woody material. Thus we are left to ponder whether hypothesized decreases in R_{max} from summer to winter can compensate for decreases in bite mass and thus whether the grids in Figs 5 and 6 remain as food concentrated patches during both summer and winter.

R_{max} , V_{max} , and the maximum bite mass obtainable by herbivores (S_{max}) scale allometrically with animal body mass (Shipley et al. 1994; Shipley et al. 1996; Hobbs et al. 2003). But we held body mass constant in order to evaluate changes in bite mass alone on d^* . It is therefore possible that our results are sensitive to the size of moose used to calculate d^* . As shown by Hobbs et al. (2003), d^* can be modeled as a function of body mass given that the maximum bite mass obtainable by herbivores (S_{max} , g) scales as $S_{max} = 0.096M^{0.72}$ (Hobbs et al. 2003), $R_{max} = 0.70M^{0.70}$ (Shipley et al. 1994), and $V_{max} = 52.16M^{0.04}$ (Shipley et al. 1996). Consequently, $d^* = SV_{max}/R_{max} = 7.1M^{0.06}$. According to these equations the 350 kg moose that we used to model d^* should be consuming bites ~6.5 g and d^* should range between ~9 and 10 m given moose ranging from 50-350 kg.

But our estimates of bite mass show that plant geometry limits the available bite mass to about 1/3 or 1/4 of S_{max} and other studies report similar estimates for the bite mass observed to be selected by 350 kg moose (Renecker and Hudson 1986; Risenhoover 1987; Åström et al. 1990; Belovsky and Jordan 1978). If we divide S_{max} by 3, then d^* varies only between 2 m for a 50 kg calf and 2.5 m for a 350 kg adult. Thus, as pointed out by Hobbs et al. (2003), limitations on available bite mass (a function of plant species and their responses to prior browsing) produce much larger changes in d^* than differences in herbivore body mass. We therefore suggest that differences in moose body mass are much less influential on d^* than the effects of moose browsing on plant geometry.

Scaling up from individual moose to moose populations

The feedbacks between moose browsing and plant geometry may not only propagate upward to larger spatial scales, but may also propagate upward to higher levels of population organization. The responses of both bite mass and the fractal dimension of aspen and balsam fir saplings to browsing combined to substantially change forage biomass on individual plants. With increases in moose browsing, forage biomass of balsam fir declined from near 15 g/tree to approximately 4 g/tree. Forage biomass of aspen saplings responded unimodally to increases in moose browsing and ranged from 2 g/plant on both unbrowsed and heavily browsed plants to over 10 g/plant on moderately browsed plants.

As a consequence of these changes in forage biomass, the number of feeding stations a moose would need to visit during winter to obtain minimum daily food requirements of 5000 g dry mass (Persson et al. 2000) differs depending on the rates of past moose browsing. For example, a moose would need to visit just over 900 more heavily browsed balsam fir saplings than unbrowsed balsam fir saplings each day in order to gain 5000 g dry mass. In contrast, a moose would need to visit over 1000 more unbrowsed aspen saplings each day in order to attain the same 5000g as compared with foraging on aspens which have been moderately browsed. Thus, the responses of bite mass and fractal dimension of these species have significant effects on future energy expenditure of moose while searching for food to meet minimum daily requirements. Browsing of balsam fir causes moose to visit an increasing number of previously browsed balsam firs in order to meet daily food requirements, while moderate browsing on aspen and the consequent increase in both fractal dimension and bite mass decreases the number of trees that need to be visited to meet daily food requirements.

The different responses of aspen and balsam fir canopy geometries and forage biomass to moose browsing may cause divergent subsequent responses of moose populations. For example, in a pure balsam fir forest, no increase in moose population density appears to be sustainable because forage biomass on fir saplings decreases monotonically with increasing moose browsing. However, in a pure aspen forest, the quadratic response of aspen biomass to increasing moose browsing would enable moose population densities to increase from low to moderate levels. But if the moose population density and hence consumption increases further, aspen forage biomass would decline,

leading to declines in the moose population. This in turn would enable the aspen forage biomass to recover. Thus, the quadratic response of aspen forage biomass to moose consumption could lead to oscillations in moose populations. Mixed plant communities could give rise to additional population dynamics. The changes in plant geometry, plant biomass, and the distribution of foraging mechanisms across the landscape which we observed have not been incorporated in any previous herbivore-plant community or herbivore-ecosystem model of which we are aware. For example, models such as that developed by Moen et al. (1997,1998) simulate energy balance and foraging decisions in great detail but simplify responses of plant geometry. In order to more accurately estimate the effects of plant geometry on moose energetics, the results presented here could be linked with more detailed animal energetics and population dynamics models, such as that of Moen et al. (1997, 1998).

Implications for animal foraging behavior and effects on ecosystems

The changes in bite mass of aspen and fir strongly determine the threshold distance between plants (d^*) which regulates the mechanisms determining intake rate and the patchy appearance of the landscape to a foraging moose. Both classical foraging theory (Stephens and Krebs 1987) and landscape ecological theory (Turner et al. 2001) emphasize the patchiness of landscapes. Patches are not fixed areas, but instead vary with the life history requirements of different organisms. Nonetheless, it is difficult to quantitatively determine how specific life history requirements determine how large a homogeneous patch is. For our purposes, a patch is a discrete spatial unit that differs from

the surrounding area by a change in the animal's feeding rate (Senft et al. 1987, Bailey et al. 1996, Searle et al. 2005). Furthermore, we showed how the size of the patch as perceived by the animal can be predicted by quantitative models of intake rate and the effect of past browsing on bite mass. As they appear to foraging herbivores, food concentrated patches consist of vegetation within d^* of an individual plant. d^* is therefore a threshold distance separating two different sets of foraging processes as described by Eqn 1 and 2 (Spalinger and Hobbs 1992; Hobbs et al. 2003). In turn, d^* depends on bite mass (Eq. 3), which is influenced by prior browsing. The threshold value of d^* is a precise delineation of a patch and the factors that control its dynamics as it appears to the foraging animal. This delineation combines the density and spatial arrangement of plants across the landscape with explicit foraging mechanisms and the prior effect of browsing on plant growth.

Because we used d^* to quantify the distribution of patches, the results in Figs 5, 6, and 7 could be used as a first approximation of how herbivores can maximize intake rate as they travel through previously browsed landscapes. These figures reveal travel routes for which successive plants remain within d^* . This yields a testable prediction — not that herbivores should move to the nearest plant or feeding station, or even spend a particular amount of time within a feeding station, but that the herbivore ought to choose the next plant to browse within the buffers defined by d^* and perhaps in order of preference. If herbivores do this, they can maintain a consistently high intake rate over an entire foraging bout regardless of the number of bites removed from any single plant or feeding station. We do however caution that this prediction does not account for energy expended

while traveling. Nevertheless, examining foraging movements by consideration of the spatial distribution of food concentrated patches may lead to much better predictions of optimal foraging paths.

Classical foraging theory focuses on the question: Why do herbivores leave particular patches of food and move to new ones? But using a mechanistic definition of the size of a contiguous patch (d^*), as we have done here, reveals that during many times of the year herbivores may view their landscape as one continuous food concentrated patch but at other times the same landscape appears fragmented. In summer, herbivores can seemingly move at random by remaining within d^* and maintain a consistent intake rate. Therefore, concepts like patch residence time in relation to patch depletion may simply not apply when bite sizes are large such as during summer or with the positive effects of moderate herbivory, as on aspen saplings. But at other times of the year, such as during winter, and with changes in vegetation due to past browsing, the very same landscape could be fragmented into a series of discrete and dispersed food patches of various sizes and structures. Therefore, we suggest that some herbivore foraging decisions at the patch level depend upon season and the effects of past browsing on plant morphology. How an herbivore forages in a landscape depends not only on season and plant distribution, but also on how it and other herbivores have previously affected the geometry of plant canopies which in turn regulates bite mass.

If herbivores maximize intake rate by following the distribution of food concentrated patches, then there is great potential for further development of spatial patterns at even larger spatial scales. Because food appears to be distributed in one large

concentrated patch at low and medium consumption rates and at any consumption rate during summer, seemingly random travel routes are just as efficient as any other travel route, so long as the herbivore remains within d^* . But when past consumption rates are high, especially during winter, the size of the d^* buffers around each plant shrink and the most efficient travel routes become limited to those paths which allow an animal to continuously forage on plants separated by distances less than d^* (Fig 6 a and b). The extent to which herbivores such as moose forage on plants separated by distances within d^* is still unknown, but if herbivores consistently feed within food concentrated patches, their effects on vegetation along such travel routes could change the appearance of the patchiness of forage the following year, altering intake rates, subsequent movement patterns, and hence changing spatial patterns across the landscape. On Isle Royale, we have seen changes in the spatial pattern of preferred deciduous moose browse which are correlated with changes in moose consumption patterns (Hodgson and Pastor unpublished data). Thus, the dynamics of d^* may be a likely first step in the creation of landscape patterns by herbivores demonstrated in several studies (e.g. Ring et al. 1985, Andrew 1988, Day and Detling 1990, Hobbs et al. 1991, Ruess and Seagle 1994, Hester and Baillie 1998, Pastor et al. 1998, Person et al. 2003).

At Isle Royale, landscape patterns of many different ecosystem properties, including browse production, plant species composition, and soil fertility have been linked to the spatial distribution of browse consumption by moose (McInnes et al. 1992; Pastor et al. 1998). The linkages among moose browsing, plant geometry, forage biomass, and the dynamics of d^* may help explain the patterns of ecosystem properties.

Grid points with aspen at Isle Royale are often repeatedly browsed from one year to the next. The repeated browsing of aspen keeps saplings within the height reach of moose and, because of the unimodal responses of fractal dimension and bite mass, may increase forage biomass and create larger d^* around individual plants if browsing remains at low to moderate levels. Thus, there may be strong feeding selection for previously browsed aspen saplings. In contrast, we rarely find repeated browsing of balsam fir saplings at Isle Royale. As we have shown here, browsing results in small shoot sizes, reduced forage biomass, and shorter d^* around individual balsam fir plants. Thus while previously unbrowsed balsam fir plants may provide an energetically favorable food choice for moose, previously browsed balsam fir saplings do not. Avoidance of previously browsed balsam fir may allow it to grow out of the height reach of moose, thereby increasing dominance of balsam fir in both tree biomass and litterfall. We suggest therefore, that the different geometric changes in the canopies of these species and resulting feedbacks to future moose consumption rates can eventually restrict aspen from entering the forest canopy and change plant species and litter composition to dominance by conifers. Responses of the fractal geometry of individual trees to browsing therefore initiates a chain of events that lead eventually to changes in larger scale features of the landscape, such as species composition. We suggest that further investigations ought to account for the linkages among the mechanisms of herbivore foraging, the distribution of food resources as defined by d^* , the responses of plants to previous browsing, and the dynamics of herbivore foraging behavior at the patch and landscape level.

ACKNOWLEDGEMENTS

This research was made possible by a grant from the National Science Foundation's Long-term Research in Environmental Biology Program. The continued support of this organization is greatly appreciated. We thank Christina Bellert for assistance with field work and data collection.

Chapter III: Rapid changes in Landscape patterns accompany recent declines in moose population density at Isle Royale National Park, MI, USA

ABSTRACT

Ungulate herbivores range across large areas, making decisions at multiple spatial scales. These decisions, in turn, create and alter large scale landscape heterogeneity in forage availability, plant species composition, and soil fertility; which may, in turn feedback on the foraging success and population dynamics of herbivores. Understanding the dynamics of large-scale landscape heterogeneity is therefore central to understanding the feedbacks between ecosystems and ungulate herbivore populations. But the nature of the landscape patterns that herbivores create and respond to often depend on the scale of pattern observation. Investigations of herbivore-induced landscape heterogeneity ought to therefore consider the scale-dependence of landscape patterns.

This study extends the spatial and temporal extent of a long-term investigation of the relationship of landscape heterogeneity to moose foraging behavior at Isle Royale National Park, MI. We tested three geostatistical models at two different spatial extents in two valleys to determine if and/or how landscape patterns change with spatial scale. We also compared geostatistical models across a three year time period (2005-2007) and with models from a previous study (1988-1990) to examine temporal changes in landscape patterns. The models we tested included (1) no spatial autocorrelation (random spatial distribution); (2) short-range spatial autocorrelation within a patch, but random distribution of patches at larger scales (spherical model); and (3) both short-range

autocorrelation within a patch and regular arrangement of patches at larger scales (harmonic oscillator model).

The spatial variance of annual consumption oscillated with increasing distance in one of the valleys while the spatial variance of available browse oscillated in the other. The oscillations consistently dampened with increased spatial extent. Oscillatory patterns in 2005 and 2006 switched to random distributions in 2007. In contrast to previous results from 1988-1990 in these same valleys, patterns of available browse and consumed browse were not correlated with each other. The spherical model fit conifer basal area and soil nitrogen availability in both valleys and across both spatial extents; patterns that also differed qualitatively from patterns in the same valleys in 1988-1990.

The decoupling of landscape patterns of available and consumed browse, the short and long term changes in landscape patterns of browse availability and consumption, and the long-term changes in patterns of basal area and N availability are coincident with and likely driven by recent declines in the island-wide moose population of Isle Royale. These results suggest that landscape patterns at Isle Royale are dynamic and that fluctuations in moose population density may induce rapid changes in the distribution of ecosystem properties as reflected in the form and parameter estimates of geostatistical models.

INTRODUCTION

Ungulate herbivores influence the spatial distribution of ecosystem properties as they range across large areas and make foraging decisions across multiple spatial scales. The fine scale decisions that herbivores make when feeding on single plants and within plant patches can create complex changes in larger scale processes such as plant community composition and nutrient cycling (McNaughton 1985; Jefferies 1988, 1989; McNaughton et al. 1988; Whicker and Detling 1988; Wiens and Milne 1989; Day and Detling 1990; Coughenour 1991; Hobbs et al. 1991; McInnes et al. 1992; Pastor and Naiman 1992; Pastor et al. 1993, 1997, 1998; Jefferies et al. 1994; Steinauer and Collins 1995, 2001; Bailey et al. 1996; Hobbs 1996; Frank and Groffman 1998; Augustine and Frank 2001; Zacheis et al. 2002). These changes in plant community composition and the nutrient cycling that underpins long-term forage production can in turn change the feeding rates and energy expenditure of individuals as they sample their environment for food and shelter (Loza et al. 1992; Moen et al. 1997, 1998; Xie et al. 1999; Illius and O'Conner 2000; Kramer et al. 2001, 2003; Weisberg et al. 2002), thereby feeding back to population density and growth.

A number of herbivore-ecosystem models, such as: Roesse et al. (1991); Turner et al. (1994); Uziel and Berry (1995); Moen et al. (1997, 1998); Carter and Finn (1999); Weisberg et al. (2002), link temporal changes in landscape patterns of ecosystem properties with changes in herbivore foraging behavior and fluctuations in population density. Many of these models suggest when and how different landscape distributions of forage develop and influence population growth and dynamics. But testing how large-

scale landscape patterns of ecosystem properties interact with ungulate populations is difficult because linking populations and landscape patterns requires repeated measurements of ecosystem properties across time periods long enough to capture changes in the density of animal populations and across scales large enough to accurately characterize landscape patterns. This is not an easy task, but it is made even more difficult by the fact that the same heterogeneity in plant communities that herbivores both respond to and create imposes scale-dependence upon observations of spatial patterns (Powell 1989; Wiens 1989; Kolsa and Pickett 1991; Pickett et al. 1992; Wu and Levin 1994; Godfray and Lawton 2001; Whittaker et al. 2001).

Because ecological properties are not uniformly distributed across landscapes, conclusions drawn from observations made at one scale can differ substantially from conclusions drawn from observations made at other scales. Consequently, decisions on scales of inquiry can have a tremendous impact on the outcomes of observational studies (Milne et al. 1989; Duarte and Vaque 1992; Reed et al. 1993; Knopf and Sampson 1994; Martinez 1994; Palmer and White 1994; Schaefer and Messier 1995; Begg et al. 1997; Dobermann et al. 1997; Keitt et al. 1997; Stohlegren et al. 1997; Bradshaw 1998; Cooper et al. 1998; Gardner 1998; Peterson et al. 1998; Ritchie 1998; Lawes and Eeley 2000; Adler et al. 2001; Godfray and Lawton 2001; Loreau et al. 2001; Whittaker et al. 2001). To accurately characterize landscape patterns and link their dynamics to herbivore populations, observations ought to therefore be made and compared across multiple spatial scales.

For the past 18 years we and others have been systematically studying changes in browse availability, plant species composition, and soil fertility across two valleys at Isle Royale National Park, MI in response to browsing by moose (Pastor et al. 1998; Angela Hodgson unpublished data). A moose can consume large amounts of plant tissue (~9 metric tons annually) and prefers deciduous tree species for its diet, but does not generally prefer and may even avoid conifers (Bryant and Chapin 1985; Shipley et al. 1998; Pastor and Danell 2003). Selective foraging by moose appears to be linked to the high nutrient and low lignin contents of deciduous species relative to conifers (Bryant and Kuropat 1980). These same chemical characteristics cause the litter of conifer species to decay slowly (Flanagan and Van Cleve 1983; Pastor et al. 1993). Over time, heavy browsing of deciduous species causes a shift in plant species composition toward dominance by unbrowsed or lightly browsed conifers (McInnes et al. 1992; Pastor et al. 1998) which in turn decreases soil nitrogen availability via slowly decaying and nutrient poor litter (McInnes et al. 1992; Pastor et al. 1993; Pastor et al. 1998). Studies in small exclosures (~25 m²) at Isle Royale National Park, MI first indicated that moose could have a substantial impact on their preferred forage, on litterfall, and on rates of nutrient cycling and soil fertility (McInnes et al. 1992; Pastor et al. 1993). Recent studies from similarly sized experimental exclosures in Scandinavia have confirmed many of the results from Isle Royale and, in addition, have shown that it takes relatively little time (~2-5 years) before moose browsing impacts plant growth, species composition, and litterfall (Persson et al. 2005, 2006).

Across larger landscapes, the selective feeding of moose has been shown to create landscape patterns (Pastor et al. 1998). Using data from 1988-1990 in two valleys at Isle Royale National Park, Pastor et al. (1998) found oscillations in the spatial variance of annual browse available and annual browse consumed by moose, as well as conifer basal area and N availability with increasing distance. Such oscillations represent regularly arranged patches or bands of ecosystem properties across the landscape (Sokal 1979; Legendre and Fortin 1989; Chou 1995; Pastor et al. 1998; Radeloff et al. 2000). But the wavelengths of these oscillations were between 150 and 200 m which are on the same order of magnitude as the study grids, which have maximum spatial extents of ~400-600 m. Thus, no more than two to three waves or patches could repeat themselves across the sampling grids. Radeloff (2002) showed that detecting periodicities in spatial variance requires a large enough study area to ensure a sufficiently large number of patches or waves across the landscape. Detection of an oscillatory pattern may therefore depend on the maximum sampling distance and the location of the landscape patches. For example, oscillatory patterns may be strongest when a wave or patch is centered on the sampling grid, but may be weaker if waves or patches are on the shoulders of the same sampling grid. At the later times spatial variance may be best characterized by a random distribution or asymptotically increasing spatial variance with increasing distance. In 2005 we extended the study grids previously used to estimate the patterns in Pastor et al. (1998) to larger areas and in this paper we examine patterns of spatial variance at different spatial extents in order to determine the nature of the distribution of ecosystem properties in these valleys by controlling for scale-dependence.

Simulation models have indicated that fluctuations in moose population density can arise from and influence landscape patterns of browse availability (Moen et al. 1997, 1998; Pastor et al. 1999). Some landscape patterns imposed by moose browsing can lead to local extinction of moose by causing a negative energy balance when the energy expenditure in travel is greater than the energy gain from consuming the remaining available browse (Moen et al. 1998). Hence, landscape patterns and moose populations may be dynamic properties that fluctuate over time in concert with each other. However, such dynamics have yet to be observed across large landscapes that approximate the home range of a single moose.

Over the past 50 years the moose population of Isle Royale has averaged 1000 animals or approximately 1.8 moose/km² but is subject to frequent oscillations (Allen 1976; Peterson 1977; Vucetich and Peterson 2007). Since our long-term study grids were established in 1988, the moose population has peaked during the mid 1990's at approximately 2422 animals and again in the early 2000's at approximately 1100 animals. It has since declined to its lowest density in 50 years of recorded population censuses (Vucetich and Peterson 2007) (Fig. 1). This decline has provided us with the unique opportunity to examine changes in landscape patterns in response to a decline in moose population density. In this paper we examine changes in landscape patterns of the moose-forest-soil ecosystem of Isle Royale National Park at different spatial extents and across time.

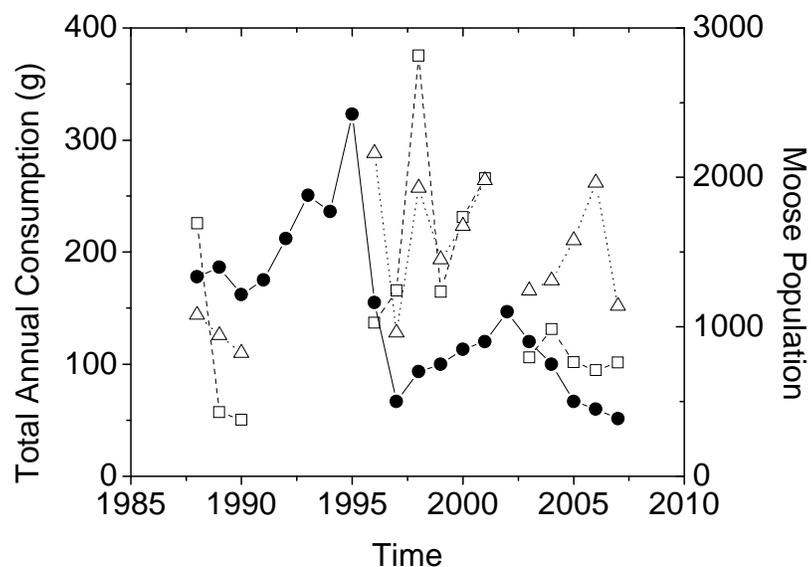


Fig. 1. Temporal changes in Isle Royale's moose population (filled circles) along with changes in total forage consumption by moose at Lane Cove (open squares) and Moskey Basin (open triangles). In 2007, the moose population reached its lowest level in 50 years while consumption estimates in both valleys have approached their lowest estimates since we and others began measuring it in 1988.

METHODS

Study sites

Isle Royale National Park, MI, (48° N, 89° W) is located approximately 20 miles off the northern shore of Lake Superior, USA (Fig. 2). The main island is approximately 554 km² and the eastern end of the island, where this study was conducted, supports boreal plant species with quaking aspen (*Populus tremuloides*), mountain ash (*Sorbus Americana*), willow (*Salix spp.*), dogwood (*Cornus stolonifera*), juneberry (*Amelanchier spp.*) and balsam fir (*Abies balsamea*) being the main food sources for moose (Krefting 1974; Snyder and Janke 1976; Risenhoover and Maas 1987; McInnes et al. 1992).

Sampling Grids

Over the past 20 years we have constructed and maintained a network of sampling grids at Lane Cove and Moskey Basin (Fig 2). At each grid point circular plots encompassing a feeding station, or the distance over which a moose can reach bites of plant tissue without moving its forefeet (*sensu* Senft et al. 1987), a radius of 80 cm or 2 m², have been established and within which annual browse availability, annual consumption, and nitrogen availability have been monitored. Three fine scale grids were established in 2003 in both valleys on sites of varying deciduous browse biomass. Each of these grids consists of 100 spatially adjacent 1.4 m² feeding stations and covers 14.1 x 14.1 m (Fig 2). These grids have been used to assess fine scale patterns of browse availability and consumption, and soil fertility (Hodgson et al. *unpublished data*). Both valleys contain a single medium scale grid (Fig 2), which dates to 1988. Differences in

topography between Lane Cove and Moskey Basin resulted in somewhat different grid shapes, but both medium scale grids cover approximately 300 x 300-500m and consist of 100 grid points spaced randomly along transects moving from the valley bottom to the valley top. Each transect is also spaced randomly with the average distance between points ~ 30 m. The valley bottoms are occupied by streams with associated beaver ponds and wetlands.

In 2005 we established additional transects that extend the medium scale grids to a large scale. The 100 grid points of the medium scale grid along with the 70 extended grid points comprise a single large scale grid of 170 points in each valley (Fig 2). The average distance between points in the large scale grids is approximately 40m. Although each sampling grid was initially established using standard survey techniques with tape and compass (Pastor et al. 1998), grid points in the medium and large scale grids have since been surveyed using handheld GPS devices with an average error of <5 m. In this study we examine data collected at the medium scale grid points and the extended grid points and compare recent landscape patterns (2005-2007) between the medium and large scale grids.

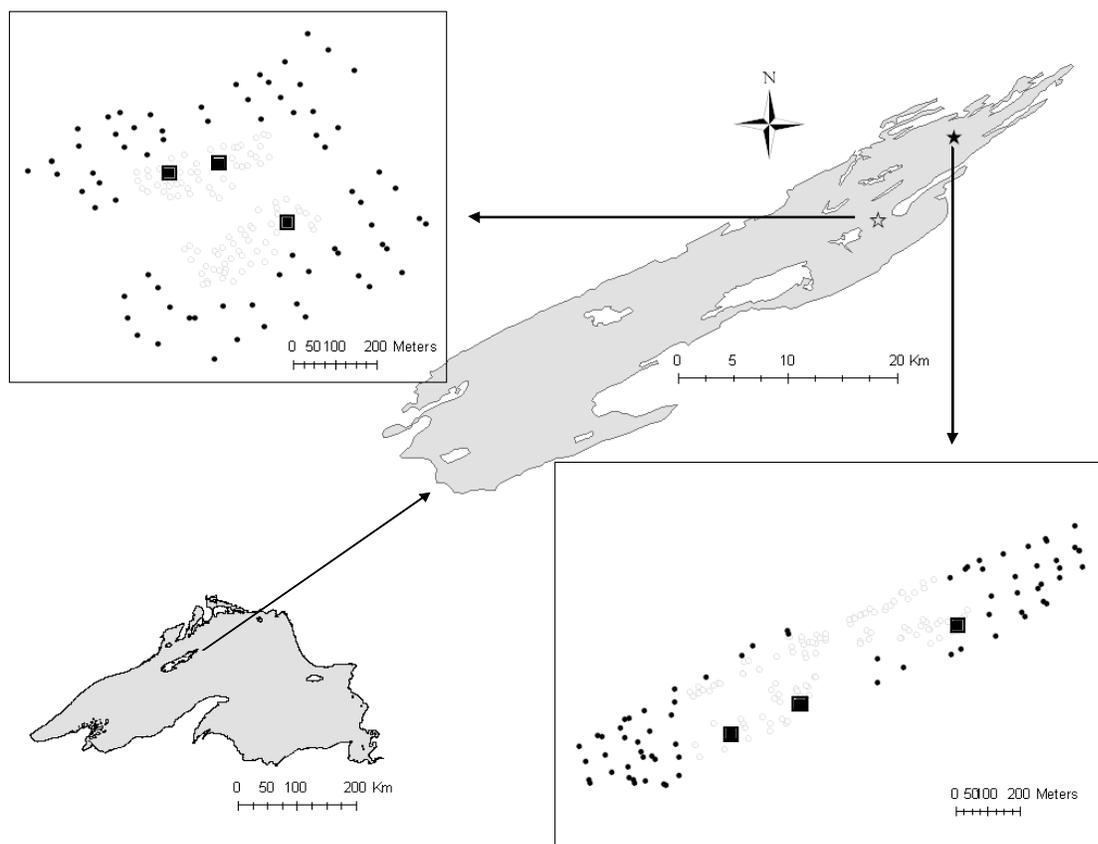


Fig. 2. Isle Royale is located approximately 20 miles off the north shore of Lake Superior, USA. In two valleys in the northeast sector, Moskey Basin (upper left) and Lane Cove (lower right), we and others have been monitoring browse available and consumed, plant species composition, and soil fertility at grid points at three spatial scales: fine (filled boxes, 100 grid points), medium (open circles, 100 grid points), and large (filled circles, 70 grid points). In this paper we compare patterns at the medium and large scale grids.

Data collection

From 2005-2007 at the medium and extended grid points, we annually estimated consumption of plant biomass by moose by counting the number of newly browsed twigs each spring and fall within the 2m² concentric circular feeding stations at each grid point. Spring sampling measured the amount of browse consumed over the course of the winter and fall sampling measured consumption during the summer. We then multiplied the number of newly browsed twigs by the average bite mass (g) for each plant species during winter and summer browsing periods (Miquelle 1983; Risenhoover 1987). This yielded an amount of biomass (g/m²) that moose removed from plants within the feeding stations. We also counted the number of unbrowsed twigs each spring and fall within the feeding stations, multiplied them by the average bite mass (g) for each plant species during winter and summer browsing periods and added this mass to that removed by moose in order to estimate the total available browse biomass.

From 2005-2006 we sampled soil nitrogen availability by installing five resin bags, each containing 10 g of Rexyn® I-300 mixed bed cation-anion exchange resin (Binkley 1984) in the Oh or A1 horizon of the soil (5 cm deep) along the perimeter of the 2m² feeding stations in late spring of 2005. These bags were left to incubate for one year, and then retrieved in late spring of 2006. After retrieving the resin bags, ammonium and nitrate were extracted from 2 g subsamples of the resin composited across all five bags per grid point by repeated washes totaling 100 mL of 1 mol/L KCl. The extracts were then analyzed by standard methods for nitrate and ammonium on a Lachat® Autoanalyzer. These methods provide an index of nitrogen availability to plants that

correlates with productivity because resin bags sample plant-available ammonium and nitrate released during decomposition of humus throughout the year (Binkley et al. 1984). In 2006 we also measured the species composition of large diameter trees around each plot by estimating the basal area (m²/ha) of different plant species using a 10x wedge prism (Avery and Burkhart 2002).

Data analysis and model selection

We used geostatistical methods to detect and describe spatial patterns of annual moose consumption, available browse biomass, plant basal area, and soil fertility by examining how the spatial variance of these properties changes with increasing distance between sampled points. We calculated standardized semivariance ($\gamma(h)$) for pairs of grid points separated by interval distance classes (h):

$$\gamma(h) = \frac{\left(\frac{1}{2N(h)} \sum [z_i - z_{i+h}]^2 \right)}{s^2} \quad (\text{Eq. 1})$$

where z_i is the measured sample value at point i , z_{i+h} is the measured sample value at point $i+h$, $N(h)$ is the total number of sample couples for the lag interval h , and s^2 is the sample variance for all z 's. Standardizing the semivariance by dividing by the sample variance allows for comparison of spatial patterns among properties with large differences in values and with differences in measurement units. Values of $\gamma(h)$ greater than one indicate uncorrelated pairs of points while values less than one indicate correlated pairs of points. We log-transformed data prior to calculations to insure that the differences between z_i and z_{i+h} were symmetrically distributed about the mean and

calculated $\gamma(h)$ for available and consumed deciduous and conifer browse biomass, conifer and deciduous basal area, and resin bag N availability using GS+ (2004). GS+ computes a number of common spatial statistics including: madograms, radograms, and correlograms. We examined the results of our analyses for a number of spatial statistics including correlograms and detected no noticeable differences in results. We chose to present our results as standardized semivariograms in order to make comparisons with results from Pastor et al. (1998) and to compare results for ecosystem properties with different measurement units. We calculated $\gamma(h)$ at 30m intervals at Moskey Basin and at 40 m intervals at Lane Cove. We carried out geostatistical analyses to one-half the distance between the farthest pairs of points (Rossi et al. 1992), which was 283 m and 500 m in the medium scale grids for Moskey Basin and Lane Cove respectively and 617 and 853 m in the large scale grids for Moskey Basin and Lane Cove respectively. These differences reflect the different configurations of the two valleys (Fig. 2). We compared directional variograms to inspect for anisotropy. We did not detect differences in experimental variograms due to direction at Moskey Basin. The configuration of Lane Cove didn't allow for dependable analysis of anisotropy due to small sample size in the NW-SE direction. We therefore present isotropic variograms.

We fit three different models to the trends in $\gamma(h)$ plotted against distance; each model representing a different type of landscape heterogeneity. Spatial heterogeneity can be random, patterned, or a combination of random and patterned (Pastor 2005). Random heterogeneity exists when the value of a property at a given point cannot be predicted given the values of properties at adjacent locations. In contrast, landscape patterns exist

when the value of a property at a given location can be better predicted by the values of properties at adjacent locations than by a random distribution of values. In other words, landscape patterns exist when values of properties are correlated with values at adjacent locations (Pastor 2005). We therefore fit a model describing *a*) random landscape heterogeneity, *b*) randomly arranged patches, and *c*) regularly arranged patches.

Model *2a* is a one parameter random model where $\gamma(h)$ is randomly distributed about a mean value that does not exhibit any trend with increasing distance:

$$\gamma(h) = \bar{\gamma} + \varepsilon(h) \quad (\text{Eq. 2a})$$

where ε is a normally distributed random number.

Model *2b* is a three parameter model, commonly referred to as the spherical model, in which there is low spatial variance between points separated by short distances, but the variance increases asymptotically with increasing distance:

$$\begin{aligned} \gamma(h) &= C[1.5h/a - (h/a)^3] + \varepsilon, & h \leq a \\ \text{and} & \\ \gamma(h) &= C, & h \geq a \end{aligned} \quad (\text{Eq. 2b})$$

The three parameters of this model include the sill (C) which is the limit of $\gamma(h)$ as $h \rightarrow a$, the range (a); and the nugget (ε , y -intercept) which is the unaccounted for spatial variance at distances shorter than the shortest distance between sample points. Model *2b* corresponds to a pattern of patches with a mean radius equal to the range (a) that are randomly distributed across the landscape at larger distances. In the case where $\gamma(h)$

appears to increase without limit, the range (a) will be larger than the maximum lag distance (h). Model b will then conform to a monotonically increasing function. If an ecosystem property exhibits continuously increasing variance, properties simply become more different with increasing distance.

Model $2c$ contains five parameters and describes periodic oscillations in $\gamma(h)$ with increasing distance.

$$\gamma(h) = \bar{\gamma} + Ae^{kh} \sin(\omega h + \beta) \quad (\text{Eq. } 2c)$$

where A is the amplitude of $\gamma(h)$ about $\bar{\gamma}$, k is the rate at which the amplitude changes with distance (h), ω is the frequency of the oscillations (radians/m), and β is the phase.

Model c describes low spatial variance between sample points separated by short distances followed by oscillations in spatial variance with increasing distance. Model $2c$ therefore accounts for patches of ecosystem properties that are themselves regularly arranged across the landscape with a wavelength $1/\omega$ (Sokal 1979; Legendre and Fortin 1989; Chou 1995; Pastor et al. 1998; Radeloff et al. 2000). For model c we occasionally fixed parameter estimates for $\bar{\gamma}$ to a value of 1 and β to a value of 0. $\bar{\gamma}$ was often very close to 1 and if $\gamma(h)$ oscillates around 1, it indicates that properties oscillate from being correlated at lag intervals ($\gamma(h) < 1$) to uncorrelated at other lag intervals ($\gamma(h) > 1$). Fixing β to a value of 0 removes the influence of changing the wavelength with increasing distance. Fixing these two parameters allowed us to reduce the number of model parameters from 5 to 3 or 4 in some cases.

We fit models $2a-c$ to trends in $\gamma(h)$ with increasing distance for deciduous and conifer consumption by moose, deciduous and conifer browse availability, deciduous and conifer basal area, and resin bag N availability using SigmaStat 3.5 (2006). Because models b and c are non-linear, we used the iterative process of nonlinear regression by the Marquardt-Levenberg algorithm (Marquardt 1963). We started by setting initial parameter estimates by visual inspection and then used the Marquardt-Levenberg algorithm in SigmaStat to repeatedly adjust the parameters by recomputing residual sums of squared errors (RSS), and continued this process until RSS no longer decreased significantly. In this manner we converged on the parameter estimates that provided the best fit between model b or c and the data. Each time we conducted non-linear regression we altered the step-size to prevent the Marquardt-Levenberg algorithm from taking too large or small initial steps when searching around suspected minima. We also altered the stopping criteria for each use of non-linear regression by changing the tolerance value. SigmaStat stops iterations when the differences between the square root of the sum of squares of the residuals from one iteration to the next is less than the tolerance value and when all parameter values stop changing in all significant places. We began with the default tolerance of 0.0001 and decreased the tolerance value to attain more precise parameter values if needed.

We tested the ability of models $2a-c$ to account for the spatial distribution of deciduous and conifer browse availability, annual consumption of deciduous and conifer browse, nitrogen availability, and deciduous and conifer basal area in the medium and large scale grids. We selected the most parsimonious models by using information

theoretics (Akaike's Information Criterion, AIC) to quantify the weight of evidence for alternative models. We began by calculating AIC with a bias adjustment for small sample sizes:

$$AIC = n \ln(RSS / n) + 2K + (2K(K + 1)) / (n - K - 1) \quad (\text{Eq. 3})$$

where n is the number of observations, RSS is the residual sums of squares, and K is the number of model parameters. As the sample size (n) increases relative to the number of parameters (K) the bias adjustment term on the far right becomes increasingly small. We quantified the plausibility of each model being the best approximating model given the data and set of candidate models by calculating and normalizing AIC weights that sum to 1:

$$w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{r=1}^R e^{(-0.5\Delta_r)}} \quad (\text{Eq. 4})$$

where Δ_i is the difference between the AIC of the best approximating model and the AIC of another candidate model (i, AIC_i). w_i is the AIC weight for model i and the denominator of Eq. 4 is the sum of the relative likelihoods for all candidate models. w_i can thus be interpreted as the relative likelihood of model i being the best model for the data given the set of candidate models. w_i can also be interpreted as the "probability" that model i is the best model given the data and set of candidate models (Burnham and Anderson 1998). We therefore selected models with the greatest w_i .

We composited the data for deciduous and conifer browse available and deciduous and conifer browse consumed from 2005-2007 by summing the browse available or consumed for spring and fall surveys and across the three-year time period in order to examine differences in semivariograms with increasing spatial extent. We also fit models to the browse data for each individual year (2005, 2006, and 2007) at the large scale to examine short-term temporal changes in the form of the semivariograms. Finally, we fit models to total browse available and total browse consumed (deciduous and conifer) for each year at the medium scale grids in order to compare results with those of Pastor et al. (1998) and thus examine long-term changes in the form of the semivariograms.

RESULTS

Patterns of browse availability and consumption

There were no differences in either the means or variances of conifer or deciduous browse available or browse consumed between the medium and large scale grid points at either location (Table 1). There were also no differences in which semivariogram model was most parsimonious with the data for the medium and large scale grids for any of the browse measurements (Tables 2 and 3).

There were, however, differences in landscape patterns between the two sites. At Lane Cove, the harmonic oscillator model applied to available deciduous browse and not consumed deciduous browse (Fig. 3). Just the opposite was true at Moskey Basin where

patterns of consumed deciduous browse conformed to the harmonic oscillator model but available deciduous browse did not (Fig. 4). Therefore, in addition to differences in landscape patterns between the two sites, patterns of available browse and consumed browse were not correlated with each other at either site.

When the harmonic oscillator model best fit the data, oscillations always dampened at increasingly large distances between pairs of points (Fig's 3 and 4). Thus, patches of browse availability or consumption may be regularly arranged across short to moderate distances (<350m) before becoming randomly arranged at longer distances (>350m). Oscillations in browse availability and consumption also dampened over time. In 2005 and 2006 the harmonic oscillator model was most parsimonious with the data for deciduous browse available at Lane Cove but in 2007 distributions were random (Table 4). At Moskey Basin, the harmonic oscillator model fit the data best for deciduous browse consumed in 2005 and 2006 but in 2007 distributions were random (Table 4). Landscape patterns of all other browse measurements remained unchanged from 2005-2007 in both valleys (Table 4).

We also examined longer-term changes in browse availability and consumption (Table 5) and found that models fit to each browse measurement eventually switched from either the harmonic oscillator or the spherical model in the early 1990's to random distributions by 2007. At Lane Cove, where browse consumption has been consistently low since 2003 (Fig. 1), the spherical models found in Pastor et al. (1998) switched to random distributions in 2005 and remained random through 2007. At Moskey Basin, where browse consumption only recently decreased in 2007 (Fig. 1), the oscillatory

patterns in consumed browse found in Pastor et al. (1998) switched to random distributions, but not until 2007.

Patterns of Basal Area and Nitrogen Availability

There were differences in conifer basal area and its variance between the medium and extended grids at both sites and differences in deciduous basal area and its variance at Lane Cove (Table 1). The changes in spatial variance of basal area with increasing distance conformed to the spherical model at both spatial extents and locations (Fig. 3 and 4, Tables 2 and 3). At Lane Cove the range was shorter than the total lag distance revealing well defined patches with radii of ~ 200 m. At Moskey Basin, the range was always longer than one-half the distance between the farthest pairs of points, indicating that basal area continues to become more different with increasing distance. These spherical patterns differ from the oscillatory patterns found from 1988-1990 (Table 5). In both valleys, regularly arranged patches from 1988-1990 were replaced with randomly arranged patches by 2006.

Resin bag N availability was similar for the medium and extended grids at Moskey Basin but not at Lane Cove (Table 1). At Lane Cove, resin bag N availability was lower in the extended grids, but its variance was similar between the two grids. Spherical models applied to each site and at each spatial extent (Fig's 3 and 4, Tables 2 and 3). But as for basal area, well defined patches with a range of ~ 200-300 m existed at Lane Cove but not at Moskey Basin. In both valleys, the oscillatory patterns found in 1988-1990 were replaced with the spherical model in 2006 (Table 5).

Table 1. Comparison of the means and variances of ecosystem properties between the medium scale grid points and the extended grid points. Data for browse are sums of surveys conducted from 2005-2007 inclusive while data for resin bag N is from resin bags incubated in the field from 2005-2006 and basal area was surveyed in 2006. Conifer basal area and nitrogen availability were the only properties differing between the grids with higher conifer basal area in the extended grids in both valleys and higher deciduous basal area and lower N availability in the large scale grid at Lane Cove.

Location	Ecosystem Property	Medium Grid	Extended Grid	<i>P</i>	Eq. Variance Test
Moskey Basin	Deciduous Browse Available	10.375 (1.529)	10.275 (1.646)	0.965	Passed
	Deciduous Browse Consumed	2.524 (0.423)	2.032 (0.462)	0.440	Passed
	Conifer Browse Available	13.972 (2.016)	16.640 (2.888)	0.435	Passed
	Conifer Browse Consumed	1.487 (0.380)	1.304 (0.319)	0.727	Passed
	Conifer Basal Area	10.950 (0.690)	15.566 (1.554)	0.003**	Failed
	Deciduous Basal Area	4.233 (0.498)	5.538 (0.989)	0.204	Passed
	Resin Bag N Availability	233.141 (11.810)	212.088 (13.311)	0.244	Passed
Lane Cove	Deciduous Browse Available	26.332 (1.866)	23.483 (2.267)	0.333	Passed
	Deciduous Browse Consumed	1.633 (0.267)	1.627 (0.333)	0.988	Passed
	Conifer Browse Available	4.545 (1.122)	7.602 (1.742)	0.124	Passed
	Conifer Browse Consumed	0.345 (0.138)	0.222 (0.0843)	0.498	Passed
	Conifer Basal Area	10.742 (0.666)	16.995 (1.257)	<0.001***	Failed
	Deciduous Basal Area	10.433 (0.894)	14.604 (1.444)	0.010*	Failed
	Resin Bag N Availability	211.511 (8.299)	156.908 (10.113)	<0.001***	Passed

Table 2. Variogram model statistics for the Medium Scale Grids. Models selected are in bold and shown in figures 2 and 3.

Site	Ecosystem Property	Model	K	RSS	AIC	Δ_i	w_i
Lane Cove	Deciduous Browse Available	Random	1	0.221	-45.51	1.28	0.186
		Spherical	3	0.137	-44.58	2.21	0.113
		Oscillator	4	0.068	-48.23	0	0.699
	Deciduous Browse Consumed	Random	1	0.080	-57.72	0	>0.999
		Spherical	3	0.241	-37.84	19.88	<0.001
		Oscillator	4	0.133	-40.24	17.47	<0.001
	Conifer Browse Available	Random	1	0.126	-52.21	6.69	0.029
		Spherical	3	0.041	-58.90	0	0.833
		Oscillator	4	0.038	-55.29	3.61	0.136
	Conifer Browse Consumed	Random	1	0.280	-42.66	0	0.963
		Spherical	3	0.281	-36.04	6.62	0.035
		Oscillator	5	0.198	-29.19	13.47	0.001
	Deciduous Basal Area	Random	1	0.243	-44.35	11.71	0.002
		Spherical	3	0.052	-56.07	0	0.953
		Oscillator	4	0.059	-49.92	6.14	0.044
Conifer Basal Area	Random	1	0.221	-45.51	4.82	0.076	
	Spherical	3	0.084	-50.33	0	0.847	
	Oscillator	4	0.086	-45.51	4.82	0.076	
Resin Bag Nitrogen	Random	1	0.103	-54.59	0.85	0.394	
	Spherical	3	0.055	-55.44	0	0.603	
	Oscillator	4	0.101	-43.61	11.83	0.001	
MoskeyBasin	Deciduous Browse Available	Random	1	0.018	-67.62	0	0.939
		Spherical	3	0.016	-61.82	5.80	0.051
		Oscillator	4	0.014	-58.22	9.40	0.008
	Deciduous Browse Consumed	Random	1	0.078	-51.90	1.62	0.260

	Spherical	3	0.045	-50.85	2.67	0.153
	Oscillator	4	0.022	-53.52	0	0.585
Conifer Browse Available	Random	1	0.026	-63.98	0	>0.999
	Spherical	3	0.055	-48.84	15.14	<0.001
	Oscillator	4	0.061	-42.30	21.68	<0.001
Conifer Browse Consumed	Random	1	0.152	-44.63	0	0.995
	Spherical	3	0.218	-33.67	10.95	0.004
	Oscillator	4	0.221	-28.29	16.33	<0.001
Deciduous Basal Area	Random	1	0.173	-43.19	15.46	<0.001
	Spherical	3	0.022	-58.66	0	>0.999
	Oscillator	4	0.087	-38.49	20.16	<0.001
Conifer Basal Area	Random	1	0.122	-47.07	1.16	0.358
	Spherical	3	0.058	-48.24	0	0.641
	Oscillator	5	0.124	-27.30	20.93	<0.001
Resin Bag Nitrogen	Random	1	0.098	-49.44	2.20	0.249
	Spherical	3	0.042	-51.65	0	0.750
	Oscillator	4	0.103	-36.61	15.03	<0.001

Table 3. Variogram model statistics for the large scale grids. Models selected are in bold and displayed in Figures 2 and 3.

Site	Ecosystem Property	Model	K	RSS	AIC	Δ_i	w_i
Lane Cove	Deciduous Browse Available	Random	1	0.198	-95.67	1.14	0.331
		Spherical	3	0.177	-92.80	4.02	0.078
		Oscillator	4	0.126	-96.82	0	0.589
	Deciduous Browse Consumed	Random	1	0.049	-124.77	0	0.978
		Spherical	3	0.056	-117.05	7.72	0.020
		Oscillator	4	0.062	-111.20	13.57	0.001
	Conifer Browse Available	Random	1	0.239	-91.76	16.44	0.000
		Spherical	3	0.085	-108.20	0	0.839
		Oscillator	4	0.083	-104.89	3.31	0.159
	Conifer Browse Consumed	Random	1	0.365	-82.87	0	0.616
		Spherical	3	0.601	-67.18	15.69	0.000
		Oscillator	4	0.257	-81.92	0.94	0.383
	Deciduous Basal Area	Random	1	0.344	-84.08	31.09	<0.001
		Spherical	3	0.061	-115.17	0	0.994
		Oscillator	4	0.083	-104.89	10.28	0.005
	Conifer Basal Area	Random	1	0.499	-76.30	18.38	<0.001
		Spherical	3	0.162	-94.69	0	0.99
		Oscillator	4	0.212	-85.33	9.35	0.009
Resin Bag Nitrogen	Random	1	0.524	-75.27	1.20	0.350	
	Spherical	3	0.386	-76.48	0	0.640	
	Oscillator	4	0.488	-67.83	8.64	0.008	
Moskey Basin	Deciduous Browse Available	Random	1	0.087	-112.82	0	>0.99
		Spherical	3	0.239	-86.54	26.28	<0.001

Deciduous Browse Consumed	Oscillator	4	0.249	-82.60	30.22	<0.001
	Random	1	0.063	-119.66	1.07	0.298
	Spherical	3	0.051	-118.76	1.97	0.190
	Oscillator	4	0.040	-120.74	0	0.510
Conifer Browse Available	Random	1	0.117	-106.70	0	0.919
	Spherical	3	0.116	-101.70	5.00	0.075
	Oscillator	4	0.129	-96.29	10.41	0.005
Conifer Browse Consumed	Random	1	0.170	-98.86	0	0.959
	Spherical	3	0.180	-92.42	6.44	0.038
	Oscillator	4	0.208	-86.37	12.48	0.001
Deciduous Basal Area	Random	1	0.341	-84.27	40.32	<0.001
	Spherical	3	0.039	-124.60	0	>0.99
	Oscillator	4	0.278	-80.28	44.32	<0.001
Conifer Basal Area	Random	1	0.430	-79.41	26.00	<0.001
	Spherical	3	0.097	-105.42	0	>0.99
	Oscillator	5	1.088	-51.64	53.77	<0.001
Resin Bag Nitrogen	Random	1	2.247	-44.71	37.98	<0.001
	Spherical	3	0.287	-82.70	0	>0.99
	Oscillator	4	2.094	-37.91	44.79	<0.001

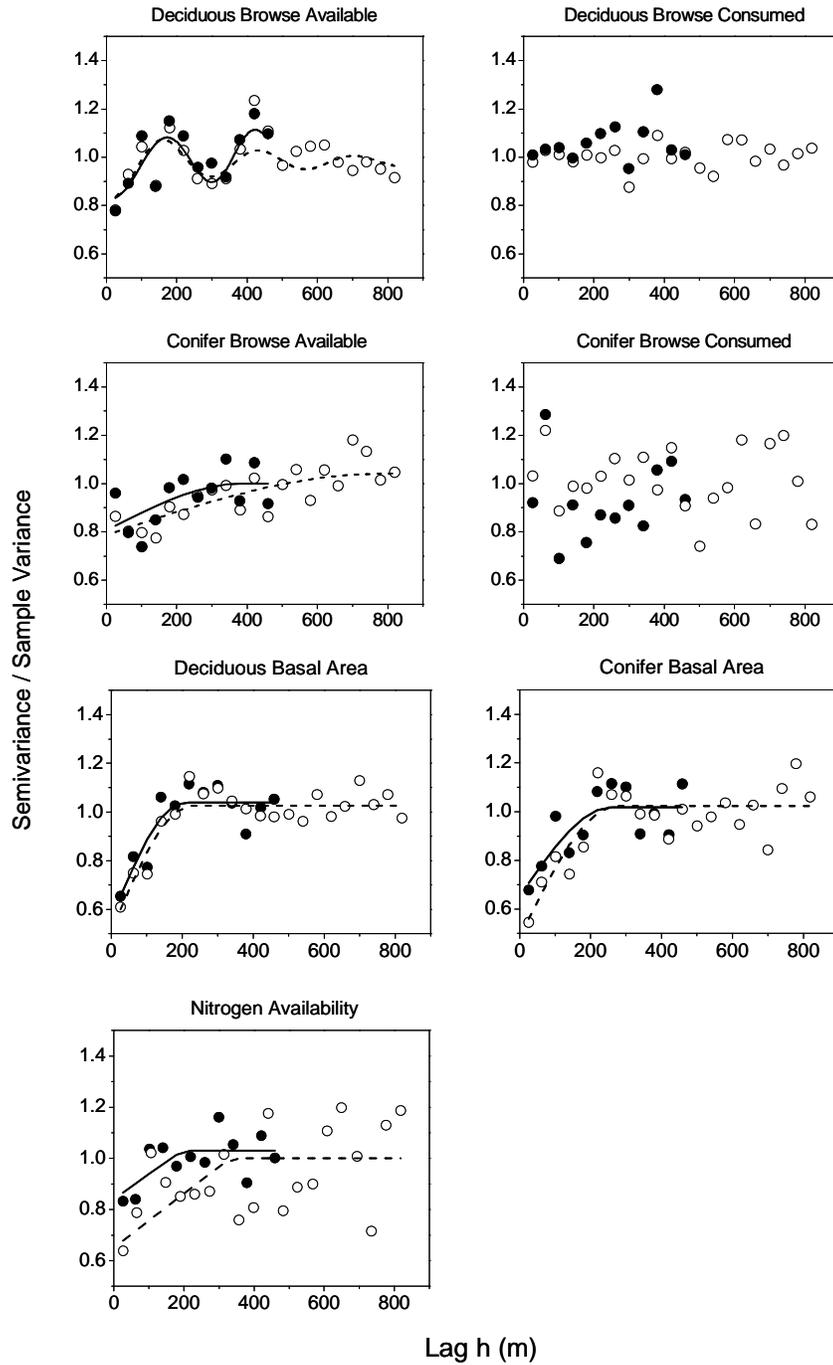


Fig. 3. Landscape pattern at the medium scale (filled circles and dark lines) and large scale grids (open circles and dashed lines) at Lane Cove. Model statistics are given in tables 2 and 3.

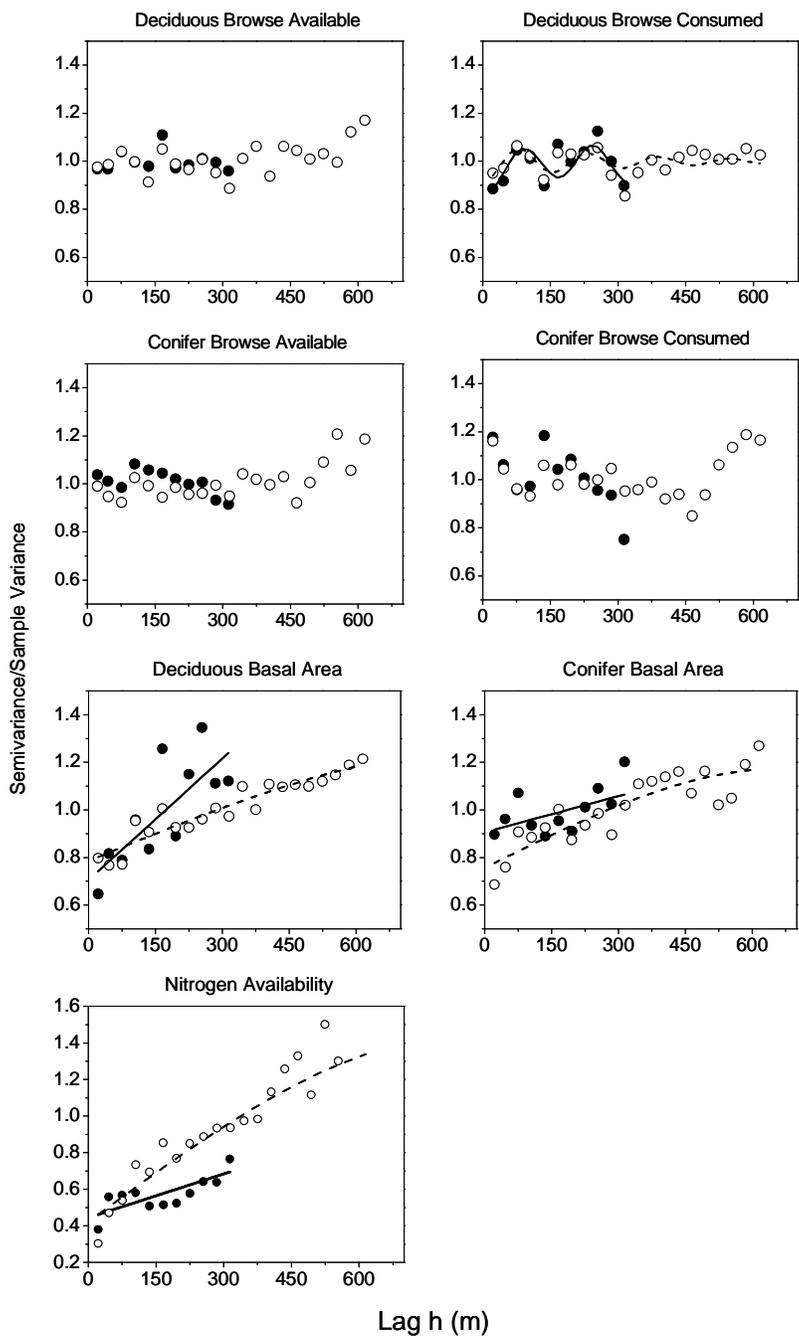


Fig. 4. Landscape patterns at the medium scale (filled circles and dark lines) and large scale grids (open circles and dashed lines) at Moskey Basin. Model statistics are given in tables 2 and 3.

Table 4. Temporal changes of landscape patterns of browse available and consumed in the large scale grids. Deciduous browse available at Lane Cove and deciduous browse consumed at Moskey Basin switched from correspondence with the harmonic oscillator model to a random distribution from 2005-2007.

Site	Browse Measurement	Year	Model	w_i
Lane Cove	Deciduous Browse Available	2005	Oscillator	0.99
		2006	Oscillator	0.62
		2007	Random	0.99
	Deciduous Browse Consumed	2005	Random	0.99
		2006	Random	0.99
		2007	Random	0.98
	Conifer Browse Available	2005	Spherical	0.99
		2006	Spherical	0.96
		2007	Spherical	0.92
	Conifer Browse Consumed	2005	Random	0.99
		2006	Random	0.99
		2007	Random	0.98
MoskeyBasin	Deciduous Browse Available	2005	Random	0.99
		2006	Random	0.99
		2007	Random	0.99
	Deciduous Browse Consumed	2005	Oscillator	0.58
		2006	Oscillator	0.99
		2007	Random	0.99
	Conifer Browse Available	2005	Random	0.98
		2006	Random	0.99
		2007	Random	0.96
	Conifer Browse Consumed	2005	Random	0.99
		2006	Random	0.99
		2007	Random	0.95

Table 5. Changes in the form of semivariogram models from 1988 to 2007. Models from 1988-1990 are from Pastor et al. (1998). Only recently patterns of annual consumption switched to random, coincident with a drop in total forage consumption at Moskey Basin and Lane Cove. In contrast to 1988-1990 when patterns of available browse and consumed browse were correlated, patterns of available and consumed browse were uncorrelated from 2005-2007.

Location	Ecosystem Property	1988-1990	2005	2006	2007
Moskey Basin	Total Available Browse	Oscillator	Random	Random	Random
	Total Annual Consumption	Oscillator	Oscillator	Oscillator	Random
	Conifer Basal Area	Oscillator		Spherical	
	Resin Bag N Availability	Oscillator	Spherical	Spherical	
Lane Cove	Total Available Browse	Spherical	Random	Random	Random
	Total Annual Consumption	Spherical	Random	Random	Random
	Conifer Basal Area	Oscillator		Spherical	
	Resin Bag N Availability	Oscillator	Spherical	Spherical	

DISCUSSION

Patterns of browse availability and consumption

When the random or spherical models were most parsimonious with the data at the medium scale grids they were also most parsimonious with the data at the large scale grids. When the harmonic oscillator model applied to browse available or consumed, oscillations consistently dampened at distances longer than ~ 300-400 m. We also noted changes from oscillatory patterns of browse available and consumed to random distributions in as little as three years. These are very rapid changes in the form of landscape patterns of both browse consumption and availability during a time period that has seen no major disturbances in these valleys other than a declining moose population (Fig. 1).

In 2007 the moose population at Isle Royale was estimated at approximately 385 animals, the lowest estimate in 50 years (Allen 1976; Peterson 1977; Vuecetich and Peterson 2007). The low moose population and declining levels of annual consumption in these valleys may explain the current random distribution of browse consumption in both valleys as well as the lack of correlation between landscape patterns of browse availability and consumption. In contrast, when the moose population exceeded 1000 animals two decades ago, the spatial patterns of browse availability and consumption were strongly correlated (Table 5) (Pastor et al. 1998). Moose browsing (or the lack of browsing) could create rapid changes in landscape patterns of browse availability given the strong influence of moose on plant growth, morphology, and browse production shown in a number of studies (e.g. Bergström and Danell 1987, 1995; Danell and Huss-

Danell 1985; Brandner et al. 1990; Thompson and Curran 1993; Edenius et al. 1995; Pastor and Danell 2003; De Jager and Pastor 2008; Stolter 2008). Thus, changes in the spatial distribution of browse availability and consumption may arise from fluctuations in the moose population. As populations decline, spatial patterns of forage availability and consumption may become decoupled. This decoupling may in turn, allow patches of preferred species to recover from chronic high browsing pressure.

Patterns of Basal Area and Nitrogen Availability

While changes in landscape patterns of browse availability and consumption occur over relatively short time periods (1-3 years), changes in landscape patterns of tree basal area and nitrogen availability are likely to take much longer to occur. The spherical model fit the landscape patterns of plant basal area and nitrogen availability at both locations and across both spatial extents. At Lane Cove, the range was consistently on the order of ~200 m for plant basal area and nitrogen availability regardless of spatial extent. In contrast, the range was always greater than half the distance between the farthest pairs of points at Moskey Basin. Thus, patches of similar tree basal area and nitrogen availability were well-defined but randomly arranged at Lane Cove, but not at Moskey Basin. These patterns differ qualitatively from the oscillatory patterns of these properties two decades ago (Table 5) (Pastor et al. 1998). Thus, as for patterns of browse availability and consumption, patterns of tree basal area and nitrogen availability appear to be dynamic.

Changes in landscape patterns of tree basal area derive from long-term changes in plant growth and mortality. The repeated browsing of saplings of aspen, birch, and other preferred browse species curtails their height growth and leads to their mortality (Krefting 1974; Risenhoover and Maas 1987; Heinen and Sharik 1990; McInnes et al. 1992; Edenius et al. 1995; McLaren 1996; Persson et al 2005; De Jager and Pastor 2008). Thus, plant species composition tends to shift toward dominance by unbrowsed or lightly browsed conifers as heavily browsed deciduous species either die from direct moose browsing or from competition for light with the unbrowsed conifers. Such changes in the landscape patterns of plant species composition, in turn, affect nitrogen availability because of the deposition of conifer litter with low nitrogen to lignin ratios (Pastor et al. 1993, 1998). Low nitrogen to lignin ratios can slow decomposition rates and decrease soil fertility in areas where annual moose browsing is high. How the impact of heavy moose browsing on individual trees merges into changes in larger scale landscape patterns of plant basal area isn't well known. But because the patterns that we have shown here differ from those in 1988-1990, it appears as though the spatial distribution of these properties changes within two decades of time.

Beaver also cut large diameter trees from the valley bottoms, especially aspen, and by opening gaps in the forest canopy could therefore create or alter spatial patterns of basal area, nitrogen availability, and browse production. There are abandoned beaver ponds and meadows in the valley bottoms at both Lane Cove and Moskey Basin. The absence of beaver cutting farther upslope may be responsible for the higher total basal area that we observed in the extended grids because these contain grid points located

farther from the valley bottoms than those in the medium scale grids (Fig. 2, Table 1). However, spatial patterns of these properties did not differ between the two scales of grids in either valley. Additionally, during this study (2005-2007), we did not observe any trees freshly cut by beaver in these valleys. Thus, while long-term changes in plant basal area could possibly result from beaver activity, the short-term changes that we observed in patterns of browse availability most likely cannot be accounted for by any current beaver activity.

Diffusive instability and the dynamics of landscape patterns

Explicit conditions for the stability of the type of patchy spatial heterogeneity that we have shown in this and other studies (Pastor et al. 1998) are given by reaction-diffusion or diffusive instability models (Murray 1980; Okubo 1980; Kareiva 1982; Kareiva and Shigesada 1983; Pastor et al. 1998; Pastor 2005). It has been suggested that diffusive instability might be the source of spatial heterogeneity in ecosystems where herbivores exert strong control over species composition and nutrient cycling (Pastor 2005) because herbivores and plants often interact nonlinearly with each other and also disperse at different rates across landscapes. Depending on the growth rates of the interacting populations and the rate at which the populations disperse, spatial heterogeneity can either be created or destroyed because the strength of the interactions between the two populations can be modified by the different rates of movement of the two populations (Turing 1952).

At Isle Royale, plant populations disperse by seed and moose populations diffuse across landscapes in search of preferred forage. Pastor et al. (1998) proposed the following equations to describe the coupling of moose foraging pressure with the growth of deciduous and conifer biomass along with the diffusion of these organisms through space:

$$\begin{aligned}\frac{\partial S_1}{\partial t} &= r_1 S_1 (1 - a_{11} S_1) + a_{12} S_1 S_2 + a_{13} S_1 S_3 + D_1 \frac{\partial^2 S_1}{\partial x^2} \\ \frac{\partial S_2}{\partial t} &= r_2 S_2 (1 - a_{22} S_2) + a_{21} S_1 S_2 + a_{23} S_2 S_3 + D_2 \frac{\partial^2 S_2}{\partial x^2} \\ \frac{\partial S_3}{\partial t} &= r_3 S_3 (1 - a_{33} S_3) + a_{31} S_1 S_3 + a_{32} S_3 S_2 + D_3 \frac{\partial^2 S_3}{\partial x^2}\end{aligned}$$

where S_1 , S_2 , and S_3 are moose, deciduous, and conifer biomass density respectively; r_i are the respective growth rates; a_{ij} are the per capita effects of species j on i for each two-way interaction; and D_1 , D_2 , and D_3 are the diffusion coefficients of moose, deciduous, and conifer species respectively. Because moose are solitary browsers, their diffusion depends on the gradient of food supply ($\partial S_2 / \partial x^2$) rather than on the gradient of its own population density. Both plant species have a positive effect on moose biomass ($a_{12} S_2$ and $a_{13} S_3$), moose consumption has a negative effect on both plant species ($-a_{21} S_1$ and $-a_{31} S_1$), and moose prefer deciduous over conifer species ($a_{12} > a_{13}$). The term ($a_{33} S_3$) describes the increase in seedling establishment with increasing shade-tolerant conifer biomass, while seedling establishment of shade intolerant deciduous species is negatively related to its own biomass. In this model spatial patchiness arises from the differential rates of diffusion and the magnitudes, signs, and asymmetries of the interaction terms (Okubo 1980).

Okubo (1980) and Murray (1980) show that for spatial heterogeneity of the interacting species to be stable in such systems three conditions must be met: (1) The diffusion rate of the predator must be greater than that of the prey and greater than some function of the ratio of the per capita mortality of the predator to per capita growth of the prey; (2) The growth of the prey must involve a positive feedback with its own population or with some underlying ecosystem property; and (3) an increase in predator density decreases prey density through consumption, and therefore predators regulate their own density.

During time periods with average to high moose population densities the diffusion rate of the moose population, as they search for their preferred forage, will almost always be greater than the diffusion rate of vegetation. The growth of the plant populations through plant litter-nutrient availability interactions is a plausible positive feedback which sustains plant growth. Finally, it is reasonable to expect moose to have a detrimental impact on the growth of plant biomass. Thus, most of the time conditions 1-3 should be met and we would expect landscape pattern stability in the moose-forest-soil ecosystem of Isle Royale. However, these conditions may not always hold, especially during periods of extremely low moose populations. If the moose population decreases substantially and nears extinction (as has been the recent case at Isle Royale, Fig. 1), then the effect of the moose population on the plant populations would decrease and the rate of dispersal of the moose population would essentially slow. If this is the case, the diffusion rate of the moose population may become slower than a conceivable function of the ratio of per capita moose mortality to per capita plant growth. Then the plant

populations will simply diffuse without interacting with moose and spatial heterogeneity would become unstable and be replaced by spatial homogeneity. During the past few years the moose population has been extremely low, consumption has been consistently low at Lane Cove and declined in 2007 at Moskey Basin and landscape patterns of browse availability and consumption have decoupled in both valleys. It is possible that previously depressed plant populations have been allowed to disperse to a homogenous or random distribution as they have been released from browsing pressure. Therefore, the condition that the herbivore population disperses faster than the plant populations may not hold when populations approach extinction. This is a possible mechanism for changes from patterned to random landscape distributions following population declines.

Studies have demonstrated unimodal responses of biomass of deciduous species to moose browsing where plant growth is greatest at moderate consumption rates. For example, De Jager and Pastor (2008) found unimodal responses of birch in northern Sweden and of aspen in the same valleys that we studied in this paper. Thus, the third condition for pattern stability, that increases in herbivore density ought to decrease plant growth, may not hold for some deciduous plant species. Replacing the negative effects of increases in the herbivore population on deciduous plant growth with a quadratic equation may change the conditions for stability considerably.

Therefore, it appears as though the moose-forest-soil ecosystem of Isle Royale may at times meet the conditions for stable landscape heterogeneity, but at other times may not. The changes that we have observed from 1988-1990 (Pastor et al. 1998) to now, two decades later, may be driven by extreme fluctuations in the moose population and/or

from unimodal plant responses to different browsing rates. However, more investigation is needed into this and other herbivore dominated ecosystems to determine precisely how the stability of landscape patterns of different ecosystem properties is influenced by fluctuations in population density.

It is also unclear how patterns of ecosystem properties at finer scales (e.g. sapling biomass or forage production) merge with patterns of other ecosystem properties at other scales (e.g. plant species composition and soil fertility). This is an especially important consideration in plant-herbivore systems because herbivores typically range across large areas and make foraging decisions across a range of temporal and spatial scales (Senft et al. 1987). The nature of time-lags of changes among landscape patterns is also unknown and constitutes additional challenges for landscape ecological studies.

It also remains to be seen whether the landscape patterns that we have shown here or their dynamics are energetically unfavorable for moose, or if spatial patterns that are energetically problematic are replaced with patterns that correspond with more positive energy balances as the moose population fluctuates. Continued efforts to improve spatially explicit herbivore-ecosystem models like that of Moen et al. (1997, 1998) should help to determine when landscape patterns become problematic for herbivores and in turn determine how landscape patterns respond to population oscillations. Meanwhile, continued monitoring of ecosystem properties across large landscapes and across time periods long enough to capture animal population dynamics should continue to provide empirical data on how landscape patterns and animal populations interact with each other.

Chapter IV: Discussion of the thesis

SYNTHESIS AND SIGNIFICANCE

In the opening chapter I posed four questions that have guided the study of spatially dynamic ecosystems over the past 25 years. These questions also guided my work as a graduate researcher: 1) How do we characterize spatial heterogeneity from the viewpoint of specific organisms? 2) What ecological processes are responsible for the spatial heterogeneity present in ecosystems? 3) How do organisms respond to spatial heterogeneity in terms of their ecology, evolution, and behavior? 4) How do we account for spatial heterogeneity in the management and conservation of species and ecosystems? In this chapter I discuss how the results from the studies in Chapters 2 and 3 contribute to resolving a few of the general questions in landscape and ecosystems ecology.

How do we characterize spatial heterogeneity from the viewpoint of specific organisms?

Ecologists typically characterize landscapes as patchy. The use of the term “patch” to describe landscapes implies a relatively discrete pattern. While patches may vary widely in size and shape, the main idea is that some areas are relatively homogenous relative to other areas. As Kotliar and Wiens (1990) point out, patch boundaries ought to be defined by objective criteria such as the relative rate of change in a variable of interest per unit of space because then comparisons of patch structure can be made between different systems.

In Chapter 2, I applied the recently developed mechanistic foraging models of Spalinger and Hobbs (1992) and Hobbs et al. (2003) to show how the size of patches as

perceived by animals can be predicted by quantitative models of intake rate. Relative to foraging animals, a patch is a discrete spatial unit that differs from the surrounding area by a change in feeding rate (Senft et al. 1987, Bailey et al. 1996, Searle et al. 2005). As they appear to foraging herbivores, food concentrated patches consist of vegetation within d^* (m) of an individual plant. d^* is a threshold distance separating two different sets of foraging processes which are described in detail in Chapter 2 and by Spalinger and Hobbs (1992) and Hobbs et al. (2003). This definition combines the density and spatial arrangement of plants in space with the geometry of plant canopies and explicit foraging mechanisms to define patch boundaries across the landscape. In Chapter 2 I showed how the size of patches as perceived by browsing herbivores can change from summer when they forage on large bites of leafy plant material, to winter when browsers switch to feeding on smaller woody plant material and with differences in past browsing intensity. In winter, moose appear to view patches as being more dispersed, especially in areas with high past rates of browsing and low plant density. In such situations, forage appears as isolated fragments within what were perceived as large food concentrated patches during summer. This appearance of fragmentation occurs without any change in the location of plant stems, but because of how previous browsing and changes in season have altered the geometry of the plant tissue available, which in turn regulates bite mass and consequently the time animals spend processing bites. Therefore, the small scale changes in twig length in cm, bite mass in g, and d^* in m propagate upward to the 10-50m scale of larger patches because they determine which mechanisms control intake rate and the distribution of those mechanisms across the landscape.

Defining patches using quantitative models of rates of ecological processes, however, does not resolve the problem of hierarchical patch structure. In Chapter 2, I identified patches that exceeded the size of the fine scale grids (14X14 m) (Fig. 3, *Introduction*) and probably encompassed areas that were on the order of 50-100 meters during summer where there had been little browsing pressure. But in Chapter 3, I examined the spatial distribution of available forage, plant species composition, and soil fertility across the large scale grids (Fig 3, *Introduction*). These analyses revealed patches that are on the order of 200-400 meters, but the size and distribution of which change over time with changing moose population density. Therefore patches defined by short-term intake rate are nested within patches of total forage biomass and plant community assemblage across the landscape. At the larger scales, herbivores decide where to forage by selecting for certain plant community compositions and their feeding rates are controlled by plant chemistry and cell wall structure which influence digestion rate (Van Ballenberghe and Miquelle 1990, Risenhoover 1987). These decisions and processes occur much less frequently than the decisions and processes that occur at finer scales. Therefore the mechanisms that regulate the intake rates of ungulates depend on the time scale at which we observe the animal, consequently, patch definitions also depend on which process the animal is involved in. Defining spatial heterogeneity by changes in the rates of ecological processes thus only solves part of the problem. The problem that remains is that what appears as spatial heterogeneity at one scale, may not lead to changes in rates of ecological processes at other scales. Clearly, further investigation is needed into how changes in the rates of ecological processes and spatial heterogeneity at

fine scales are linked to heterogeneity at other scales. In the case of moose, I showed how changes in the geometry of plant canopies at fine scales can constrain foraging rates at scales 20-50 m. But additional questions remain, such as how are changes in feeding rates that occur across 20-50 m areas linked to changes in feeding rates over longer time periods and across larger landscapes where animals make different foraging decisions?

What ecological processes are responsible for the spatial heterogeneity present in ecosystems?

It is well known that ecological processes are spatially heterogeneous due to variation in abiotic conditions (i.e. climate, topography, substrate) (Jenny 1941, Turner and Chapin 2005). But it is less well known how biotic interactions modify, amplify, and/or remove heterogeneity from landscapes. The presence of ungulate herbivores in nearly every terrestrial ecosystem worldwide (Fritz and Loison 2006) and their influence on primary productivity, nutrient cycles, and the distribution of other plants and animals (Duncan et al. 2006) has led to their consideration as the main drivers for forming the structure and function of terrestrial ecosystems (Hobbs 1996, Persson et al. 2000, Danell et al. 2006). From past studies at Isle Royale and elsewhere we have learned that the high energy requirements and selective foraging of moose can have significant impacts on plant community composition, rates of nutrient cycling, and the spatial distribution of these properties across boreal forest landscapes (McInnes et al. 1992; Pastor et al. 1993; Pastor and Naiman 1997; Pastor et al. 1998; Persson et al. 2005a and b). I've further shown here and elsewhere (De Jager and Pastor 2008) that moose influence the geometry of tree

canopies of deciduous and conifer species differently and that these differences at the scale of the tree crown result in changes in herbivore feeding rates and perceptions at scales that are orders of magnitude larger. These changes most likely further influence the foraging behavior of moose across landscapes and lead to the type of spatial pattern dynamics that I investigated in Chapter 3.

As moose populations fluctuate, the distribution of their foraging pressure changes. It appears as though when populations get extremely low, their foraging pressure is reduced and becomes spatially random. Plants which had been suppressed by prior browsing are then allowed to regrow and spatial distributions of browse availability eventually become random. The distribution of other higher level properties such as plant community composition and soil fertility also appear to change but more slowly. However, it is unclear how changes in patterns at these larger scales emerge from changes that occur at finer scales. Future studies should reveal more precisely how patterns at different scales interact with each other over time with changes in population density and herbivore foraging.

How do organisms respond to spatial heterogeneity in terms of their ecology, evolution, and behavior?

Defining spatial heterogeneity by changes in rates of ecological processes can yield quantitative predictions of how the distribution of landscape features influence the ecology and fitness of individuals. Moose and other herbivores respond to heterogeneity in forage distribution by changes in their feeding rate. But as I have stressed throughout

this dissertation, moose and other herbivores also influence heterogeneity. The changes that moose have imposed on the spatial distribution of ecosystem properties at Isle Royale have occurred within the span of my graduate studies and well within the lifetime of a single moose. This suggests that moose pass on environments to their offspring that are structurally and functionally different from the ones they inherited. Moose therefore modify the selection pressures that their offspring face. Animals that adapt to landscape heterogeneity by maintaining or improving their food intake rate stand to benefit both ecologically and evolutionarily.

Although bites of plant tissue seem much too small to have a consequence to animal evolution, most herbivores harvest thousands of bites every day, the consequences of these actions are compounded over days, seasons, and lifetimes with potentially large evolutionary consequences (Shipley 2007). Moose and other animals recognize the energetic value of harvesting large bites. A number of studies have indicated that moose select larger twig diameters, and hence larger bite sizes, as the number of stems per patch declines and as the distance between patches increases (Vivas and Saether 1987, Shipley and Spalinger 1995, Shipley et al. 1998). Furthermore, herbivores have adapted mouth anatomy that allows them to maximize bite size on their selected forage plants. Grazers, which tend to have wider muzzles and incisor arcades than browsers, feed on dense swards of grasses and can attain larger bite sizes by biting deeper and wider into short swards of grass. In contrast, browsers can insert narrower muzzles into plant canopies to crop more efficiently (Shipley 2007).

However, plants also respond to browsing by replacing lost tissue. Some plants have adapted to high historic browsing pressure by sprouting thorns, developing smaller leaves and twigs, or branching at wide angles, all of which decrease the available bite size and may allow some plants to avoid future herbivory (Greenwood and Atkinson 1977; Cooper and Owen-Smith 1986; Belovsky et al. 1991; Myers and Bazely 1991; Vivås et al. 1991; Milewski et al. 1991; Gowda 1996; Bond et al. 2004). But these adaptations also depend on the relative strengths of other selection pressures in the environment. Shade intolerant early successional species like aspen and birch have adapted the capacity to grow quickly into the forest canopy. These same species have some capacity to respond positively to browsing in the short-term (Chapter 2; Danell et al. 1985; Danell and Huss-Danell 1985; Bergstrom and Danell 1987; Fornara and Du Toit 2007; De Jager and Pastor 2008). Whereas shade tolerant late successional species are adapted to low light environments, grow much more slowly, and do not appear to respond to browsing in the short term (Chapter 2; Brandner et al. 1990; Edenius et al. 1991; Thompson and Curran 1993; Millard et al. 2001; Persson et al. 2005; De Jager and Pastor 2008). This may allow the shade tolerant species to avoid repeat browsing. Moose and other herbivores may take advantage of the faster growth of the deciduous species by annually revisiting them (Pastor and Danell 2003). This creates plants with “pruned” growth forms and maintains them within the height reach of most herbivores. However, over the long-term, heavily browsed plants are eventually replaced by less palatable plants (Krefting 1974; Risenhoover and Maass 1987; McInnes et al. 1992; Thompson et al. 1992).

The solitary nature of most browsing herbivores may be a co-evolved adaptation to forested ecosystems that tend to respond “negatively” to high levels of herbivory (Pastor et al. 2006). In contrast to browsing, grazing tends to stimulate the production of grass growth and rates of nutrient cycling (Sinclair and Norton-Griffiths 1979; McNaughton et al. 1997). It has been suggested that grazing herbivores form dense herds in order to take advantage the “positive” effects of grazing on plant growth and nutrient cycling (McNaughton 1984). Thus, browsing herbivores and grazing herbivores appear to have co-evolved different anatomical structures (e.g. mouths) as well as social behaviors in response to differences in the growth form of woody and herbaceous plants.

How do we account for spatial heterogeneity in the management and conservation of species and ecosystems?

In parts of the world moose and other herbivores occur in populations dense enough to depress productivity and nutrient cycling rates and even cause local extinction of favored plant species. But in other areas, these herbivores are on the verge of extinction and are in need of conservation (Danell et al. 2006). Whether the conservation concern is the habitat or the animal population, or both, it is becoming clear that simple, traditional measures of food resources, such as forage abundance and nutritional quality, are inadequate for explaining the complex feedbacks between herbivores and ecosystems. The multi-scale nature of the interactions among foraging behavior, ecosystem properties, and population and landscape dynamics; will require an approach that considers the feedbacks among properties at different spatial scales. While manipulating habitat

structure at one scale may influence herbivores one way, manipulating habitats at other scales may influence herbivores in other ways. Therefore, managers need to consider the interrelationships among plant geometry, bite mass, plant spacing, and plant community composition across forested landscapes in order to fully appreciate the way herbivores will respond to habitat manipulations.

There is and has always been a fundamental mismatch in the scales at which ecological studies and management actions are carried out (Hobbs 2003). Ecological studies in general and studies of herbivore foraging in particular are traditionally carried out at fine scales where mechanisms responsible for processes can be carefully controlled. But management actions take place at much larger scales, often over several hundred square kilometers. These are also the scales at which populations interact with landscapes. However, as I have shown and discussed throughout this dissertation, often, decisions and outcomes at fine scales can constrain dynamics that play out across larger scales. A greater attention to linking the multiple-scale foraging dynamics of herbivores to their population dynamics is greatly needed if conservation strategies are to be based on a solid understanding of animal-habitat relationships.

FUTURE DIRECTIONS

The need to integrate knowledge across spatial scales has emerged from this and other works as a fundamentally important task for ecologists. If we want to understand the natural history of organisms like moose, if we want to understand how spatially dynamic systems function, and if we want to begin making management decisions based

on understanding how organisms interact with spatially dynamic systems, then integrating knowledge across scales is imperative. Spatially explicit models that link multi-scale animal foraging behavior and population dynamics with the spatial spread of plant and soil attributes is perhaps the most promising approach to integrating knowledge across scales. Such models allow researchers to test hypothesis at multiple scales, incorporate feedbacks among plants, animals, and soil fertility, and even predict the outcome of different management actions. Unfortunately, as the level of detail in spatially explicit models increases, the influence of small errors in parameter estimates also increases. From my investigations in Chapter 2, it is clear that there is a need for field tests of the food processing and travel rates of moose and any other animal for which such models are constructed. Such field tests would give us a much better understanding of d^* and make it possible for additional studies of the relationship between d^* and moose foraging behavior. Do moose forage within d^* ? A simple but informative study would be to construct frequency histograms of distances between plants that moose have selected bites from during different seasons and compare the distance between selected bites to estimates of d^* . The more precise estimates of the food processing and travel rates of moose or any other animal as well as field tests of foraging behavior could then be incorporated into spatially explicit models to test the outcome of different foraging strategies that consider d^* .

Landscape ecology is still searching for general principles of landscape dynamics (Turner et al. 2001). As Wiens (2008) points out, the complexities and contingencies of landscapes may make the search for generalizations difficult and that principles that

apply in one system may not apply everywhere. Hobbs and Lindenmayer (2007) therefore suggest that landscape ecologists develop “contingent” principles and theories that apply to landscapes that share common features. If this is the case, then it is imperative that characterization of spatial heterogeneity be based on rates of ecological processes in order to determine if landscapes in fact share common landscape features. It is also important that comparisons of landscape be made at multiple spatial scales in order to control for scale-dependant landscape patterns. Greater attention to these factors ought to enhance comparisons between different landscapes and hasten the development of a widely accepted body of landscape ecological theory.

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