

Ecological Scale and Species-Habitat Modeling: Studies on the Northern Flying Squirrel.

by

Matthew Thompson Wheatley

B.Sc., University of Alberta, 1994

M.Sc., University of Alberta, 1998

A Dissertation Submitted in Partial Fulfillment of the
Requirements for the Degree of

DOCTOR OF PHILOSOPHY

In the Department of Biology

© Matthew Thompson Wheatley, 2010
University of Victoria

All rights reserved. This thesis may not be reproduced in whole or in part, by photocopy or other means, without the permission of the author.

Supervisory Committee

Ecological Scale and Species-Habitat Modeling: Studies on the Northern Flying Squirrel.

by

Matthew Thompson Wheatley

B.Sc., University of Alberta, 1994

M.Sc., University of Alberta, 1998

Supervisory Committee

Dr. Karl Larsen, Department of Biology
Co-Supervisor

Dr. Pat Gregory, Department of Biology
Co-Supervisor

Dr. John Taylor, Department of Biology
Departmental Member

Dr. Dave Duffus, Department of Geography
Outside Member

Dr. Richard Bonar, Hinton Wood Products (West Fraser Mills Ltd.)
Additional Member

Abstract

Supervisory Committee

Dr. Karl Larsen, Department of Biology

Co-Supervisor

Dr. Pat Gregory, Department of Biology

Co-Supervisor

Dr. John Taylor, Department of Biology

Departmental Member

Dr. Dave Duffus, Department of Geography

Outside Member

Dr. Richard Bonar, Hinton Wood Products (West Fraser Mills Ltd.)

Additional Member

Although scale is consistently identified as the central problem in ecology, empirical examinations of its importance in ecological research are rare and fundamental concepts remain either largely misunderstood or incorrectly applied. Due to the mobile and wide-ranging nature of wildlife populations, species-habitat modeling is a field in which much proliferation of multi-scale studies has occurred, and thus provides a good arena within which to test both scale theory and its application. Insufficient examination of a relevant breadth of the scale continuum could be an important constraint in all multi-scale investigations, limiting our understanding of scalar concepts overall. Here I examine several concepts of ecological scale by studying free-ranging populations of northern flying squirrels (*Glaucomys sabrinus*), purported to be a keystone species in northern forests. Coarse-grain digital forest coverage revealed that flying squirrels in the boreal and foothills of Alberta were not conifer specialists, rather forest generalists regarding stand type and age. Lack of coarse-grain scale effects led me to examine fine-grain data, including an assessment of scale domains using a novel continuum approach. Fine-grain data revealed important scale-related biases of trapping versus telemetry, namely that, at fine-grain scales, different habitat associations could be generated from the same data set based on methods alone. Then, focusing on spatial extent, I develop a true multi-scalar approach examining scale domains. First, I quantify only forest attributes across multiple extents, and demonstrate unpredictable scale effects on independent variables often used in species-habitat models. Second, including both independent (habitat) and dependent

(squirrel telemetry) variables in the same approach, I demonstrate that the relative ranking and strength-of-evidence among different species-habitat models change based on scale, and this effect is different between genders and among life-history stage (i.e., males, females, and dispersing juveniles). I term this the “continuum approach”, the results of which question the validity of many published species-habitat models. Lastly, I attempt to clarify why existing models should be scrutinized by reviewing common rationales used in scale choice (almost always arbitrary), outlining differences between “observational scale” and the commonly cited “orders of resource selection”, and making a clear distinction between multi-*scale* versus multi-*design* ecological studies.

Table of Contents

Supervisory Committee	ii
Abstract	iii
Table of Contents	v
List of Tables	vii
List of Figures	ix
Acknowledgments.....	xi
Dedication	xiii
Chapter 1. Ecology of northern flying squirrels, a scalar approach.....	1
The Intellectual Journey.....	1
Introduction.....	2
Why Scale?	3
Implications of ecological grain and extent	5
The Northern Flying Squirrel.....	8
Chapter 2. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: Northern flying squirrels in Alberta, Canada.....	11
Abstract	11
Introduction.....	12
Materials and Methods.....	15
Study Location	15
Site selection.	18
Sampling techniques	18
Landscape composition.....	19
Statistical analysis.....	20
Results.....	22
Discussion	29
Chapter 3. Differential space use inferred from live-trapping versus telemetry: Northern flying squirrels and fine spatial grain.	32
Abstract	32
Introduction.....	32
Study Area	36
Materials and Methods.....	37
Live-trapping and radio collaring	37
Radio tracking.....	38
Determination of space use.....	39
Vegetation Sampling.....	40
Statistical Analyses	41
Results.....	42
Spatial relationships: forage, nest, and capture sites.....	42
Spatially-explicit time budgets	42

Vegetation structure comparisons.....	43
Discussion.....	47
Chapter 4. Domains of scale in forest landscape metrics: Implications for species-habitat modeling.....	52
Abstract.....	52
Introduction.....	52
Materials and Methods.....	58
Landscape metrics.....	58
Observational scale and sample size.....	61
Plot sampling.....	61
Metric quantification and domains of scale.....	61
Results.....	62
Discussion.....	68
Conclusions.....	72
Chapter 5. A continuum approach linking ecological scale and wildlife-habitat models: Flying squirrels in Alberta, Canada.	74
Abstract.....	74
Introduction.....	74
Methods.....	79
Study area.....	79
Squirrel capture and telemetry.....	81
Results.....	92
Observational scale.....	92
Squirrel biology.....	97
Discussion.....	103
Ecological scale.....	103
Squirrel biology.....	105
Chapter 6. Factors limiting our understanding of ecological scale in wildlife-habitat studies.....	109
Abstract.....	109
Introduction.....	109
Choice of Observational Scale.....	111
Cross-scalar predictability.....	118
Spatial versus scalar observations.....	119
Pseudo-scales.....	120
Orders of resource selection versus observational scales.....	122
Solutions.....	124
Chapter 7. Contributions to knowledge.....	126
Literature Cited.....	130

List of Tables

Table 2-1. Captures per 100 trap-nights \pm SEM of northern flying squirrels in four forest types from northern and western Alberta, Canada. Captures are sorted by dominant habitat type at the 50 m spatial extent. Sample sizes are in brackets.....	23
Table 2-2. Mixed-model ANOVA results comparing flying squirrel relative abundance by habitat type over three spatial extents.	24
Table 4-1. Definitions of landscape metrics quantified in this study.	60
Table 4-2. Post-hoc multiple comparison results for Fractal Dimension among observational scales, demonstrating how differences among scales appear unpredictably as one moves up the scale continuum, particularly above the 512 ha observational extent.	65
Table 5-1. Average 90% kernel density home-range size estimate for adult flying squirrels over three summers of study near Hinton, Alberta (Canada). Kernels were created using behavioral-focal data, weighted using “total observational minutes” for each telemetry point.	85
Table 5-2. Definitions of independent variables generated for squirrel-habitat modeling in this study.	90
Table 5-3. Candidate models and their associated hypotheses tested in this study. Hypotheses are based on both published accounts and those considered probable through this study. Model numbers as designated here are used in the results to denote model ranks and best-model selections for each scale. (Model numbers begin at 2, an artefact of the spreadsheet and statistical software linkage whereby column 1 held variable titles).....	91
Table 5-4. Regression table for the two top-ranked models for adult males at the 0.32-ha scale. Note model number and scale denoted for each (see Table M for w_i ranks for all candidate models).....	99
Table 5-5. Regression table for the two top-ranked models for adult females at the 0.02-ha scale. Note model number and scale denoted for each (see Table M for w_i ranks for all candidate models).....	99
Table 5-6. Regression table for the two top-ranked models for adult females at the 1-ha scale. Note model number and scale denoted for each (see Table M for w_i ranks for all candidate models).....	100

Table 5-7. Regression table for the two top-ranked models for adult females at the 13-ha scale. Note model number and scale denoted for each (see Table M for w_i ranks for all candidate models).....	100
Table 5-8. Regression table for the two top-ranked models for dispersing juveniles at the 13-ha scale. Note model number and scale denoted for each (see Table M for w_i ranks for all candidate models).....	101
Table 5-9. Ranking based on w_i (Akaike weight) of all candidate models for male flying squirrels at the 0.32-ha scale.	101
Table 5-10. Ranking based on w_i (Akaike weight) of all candidate models for female flying squirrels at the 13-ha scale.....	102
Table 5-11. Ranking based on w_i (Akaike weight) of all candidate models for juvenile flying squirrels at the 13-ha scale.....	102
Table 6-1. Total counts and proportion of non-arbitrary spatial scales employed among different taxonomic groups for scalar ecology studies done over the last 2 decades. A total of 79 studies were reviewed from the journals Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology taken from issues published between 1993 and 2007.....	114
Table 6-2. Articles included in this review, listed chronologically within each taxonomic group. The proportion of non-arbitrary observational scales represents the number of scales selected using biological rational divided by the total number of scales used within each study.....	116

List of Figures

Figure 2-1. Average captures per 100 trap-nights of flying squirrels in three habitat categories from northern and western Alberta, Canada.....	25
Figure 2-2. Average captures per 100 trap-nights of flying squirrels in four habitat categories from forests in northern and western Alberta, Canada.....	26
Figure 2-3. Negative relationship between average stand height and flying squirrel abundance at the 300m spatial extent from forests in northern and western Alberta, Canada..	27
Figure 2-4. There was no relationship between average conifer composition and flying squirrel relative abundance at the 50 m spatial extent from forests in northern and western Alberta, Canada.	28
Figure 3-1. Average distances (± 1 SEM) between trap-capture sites, nest sites, and focal foraging areas for northern flying squirrels near Hinton, Alberta, Canada.	45
Figure 3-2. Average proportion (± 1 SEM) of flying squirrels' post-capture nocturnal activity budget spent at different distances from the capture site as determined via walk-in radio telemetry observations.....	46
Figure 3-3. Correspondence analysis of vegetation structure at trap-capture stations (circles) and at focal foraging areas (triangles) over 2 summers (white versus black) for northern flying squirrels near Hinton, Alberta, Canada.....	47
Figure 4-1. Informed versus naïve selection of observational scales for a multi-scale ecological study..	56
Figure 4-2. Location of study area in west-central Alberta showing examples of (a) 16ha; (b) 512ha; and (c) 8192ha sampling plot designs..	59
Figure 4-3. Average values and associated variation for nine landscape metrics across 15 spatial extents (while holding grain constant) in the foothills of west-central Alberta, Canada..	Error! Bookmark not defined.
Figure 4-4. Theorized relationship between observational scale, cumulative model variance (both dependent and independent variables), and subsequent fit of a predictive ecological model.....	71
Figure 5-1. Theoretical variance plot for both dependent and independent variables used to model a 2-variable relationship across 3 observational scales (A, B, and C).....	77

Figure 5-2. A visual example of the detail acquired from LiDAR in generating forest-structure for this study..	87
Figure 5-3. Plot of observational scale (extent) versus model support, with the best-supported single model noted along the bottom of each figure, and the best averaged 2-model combination listed along the top (see Table 5-3 for model details)..	96
Figure 6-1. Average proportion of non-arbitrary scales used in scalar ecology studies (bars, left y-axis), and the number of studies examined for each year (dotted line, right y-axis)..	115
Figure 6-2. A summary of commonly used sampling approaches to “multi-scalar” studies in ecology.	122

Acknowledgments

I really enjoyed doing this project. It has been a fulfilling intellectual experience. Though my progress ebbed and flowed consistent with parental and professional obligations, picking up where I left off was never a chore. This is mostly due to the support and assistance I received along the way from the people and organizations that showed genuine interest in this research.

This research was funded by a number of sources including the Natural Sciences Engineering and Research Council of Canada (NSERC) through an Industrial Postgraduate Scholarship to myself, and through NSERC Discovery grants to Karl Larsen. Hinton Wood Products (a division of West Fraser Mills Ltd.) was a key partner in terms of research direction and funding support. Other key sources of funding came from the Forest Resource Improvement Association of Alberta (FRIAA), the University of Alberta Challenge Grants in Biodiversity, the Alberta Sport, Parks, Recreation, and Wildlife Foundation of the Alberta Government, and the Canadian Wildlife Foundation. The genuine interest and encouragement of Rick Bonar (Hinton Wood Products) facilitated the genesis of this work.

I am indebted to the field assistants who actually agreed to work 7pm-4am in the middle of the forest. These adventurous souls included Corey Bird, Brian Purvis, Adam McCaffrey, Trina DeMonye, Barbara Koot, Andrea Pals, and Nissa Hildergrad. Thanks to all of you for the data.

A few key people inspired me during my time on-campus at UVic. Jason Fisher was an untiring sounding-board for ideas on ecological scale. Jason was fundamental in helping me develop my ideas and move from a student of landscape ecology to a practitioner. Thanks, Jake. John Taylor offered genuine enthusiasm for a genetic component of this work that, due to time constraints, I was unable to see to completion (though, I still have 4-year-old squirrel hair in the butter drawer of my fridge), but from which I unexpectedly learned so much. John also held bar-none the best graduate-level course I've ever taken: a detailed study of Darwin's *Origin of Species*. This was a highlight for me at UVic, and has forever shaped my thoughts on ecology. Thank you, John. And of course, I want to thank my supervisor Karl Larsen. Karl allowed me to pursue and develop my own ideas

in an encouraging and constructive environment and offered me all the latitude I needed to learn how to develop my own original research; this is the best contribution any teacher could offer a student. Thank you, Karl.

Lastly, I want to thank my family for their unending support. Thanks Dad, for your newfound interest in squirrels and the environment (and all the newspaper clippings that come with this). Thanks Mom, who I never have to ask. And thank you Wendy, my wife, who deserves co-author on this, not because she wrote it (she didn't, Karl, just to be clear), but because she was supportive in every way and allowed me to yammer on incessantly and with impunity about ecological scale. Thank you, Wendy. (and p.s., my cruise-vest does not smell like squirrel; it never did, and never will).

And in the final stages of writing, when things seemed stale and inspiration hard to find, my daughter Alexandria was born and everything took on new meaning (and along with this a slower writing pace!). Every day, Alex reminds me of why I endeavour to learn about Nature: it's so we can conserve it for her. If I had ever known this before, I clearly had forgotten it somewhere along the way. Thank you, Alex, for forever setting me straight.

Dedication

This thesis is dedicated to my daughter Alexandria.

Alex, through works like this may we hope to understand the forest enough to keep it a healthy, functioning, and familiar place for you to grow up and enjoy the same as I have. If you're reading this, put it down and go find a squirrel in the forest, for it will teach you far more than I ever could.

Chapter 1 Ecology of northern flying squirrels, a scalar approach.

The Intellectual Journey

The ecological-scale toolbox is pretty meagre. Even theoretical concepts have yet to progress beyond the thumbnail sketch. By-in-large, ecologists do not appear particularly concerned with this; multi-scale studies have increased in numbers, especially in the wildlife sciences, and many have empirically demonstrated some form of multi-scale or hierarchical resource selection in animals. The unfortunate progression of this science, however, has been a veritable dearth of methodology when it comes to scale and its implications for the fundamentals of species-habitat modeling. The GIS analyst will be the first to admit that scale really does matter, and I am one of these types. Over the past decade my work has been (almost exclusively) scalar and GIS-based, and I have quantified animal and forest-structure data in more ways and across more scales than the average researcher. As mundane as some of these analyses seemed, it was these ostensibly ordinary tasks that formed the foundation of my thoughts for this thesis, and highlighted to me those areas where new techniques and tools were needed to progress the science of species-habitat modeling forward. It is my intent herein to add at least one useful tool to the ‘ecological-scale toolbox’.

Given the relatively infant state of ecological scale as a research field, I did not have much to begin with, especially anything empirical in nature. As such, this thesis represents my evolution of thought as I tried one approach, and then refined it to develop the next. The reader will see this progression respectively in the thesis chapters. I begin with a contemporary multi-scale design in Chapter 2, which concludes little in terms of scale (but more regarding habitat use), and really sets the stage for my subsequent attempts to examine scale in a more fruitful way. In Chapter 3, I refine my approach to an ecological-grain focus, then progress towards the “continuum approach” which I espouse in Chapters 4 and 5; by doing so, I question validity of many wildlife-habitat studies published to date. In Chapter 6, I attempt to clarify why this situation exists, and suggest a way forward.

Thus, this thesis is an intellectual journey that reflects my increasing appreciation for landscape theory and empirical study design. My direction from beginning to end evolved, and truly reflects changes in my opinions as they were shaped by unappreciated knowledge (e.g., innovations in GIS-based land coverages like LiDAR) and feedback. My intent throughout is to remain true to the original objective: to add some innovative tools to the species-habitat modeling toolbox. At the very least this thesis should enable future researchers interested in ecological scale to begin with the premise that the “continuum approach” is important and has been empirically established, so let us start from there.

Introduction

Techniques used to predict animal abundance or occupancy largely are based on the concept of the ecological niche (e.g. Grinnell 1917; Hutchinson 1957; Chase and Leibold 2003): a species has a unique set of requirements that must be provided by its habitat for it to be present and persist there. The discipline of wildlife-habitat modeling stems directly from this and seeks to develop predictable relationships between important and measurable components of physical habitat and a species' occurrence or abundance (e.g. Verner et al. 1986). These relationships are then extrapolated across landscapes to produce use-maps, estimate habitat carrying capacity, or construct resource-selection-functions to inform land managers of the potential ecological implications surrounding management scenarios - will a population become isolated, extirpated, or unchanged as a consequence of land management? Such models allow science-based decisions to be made, backed by probability functions and quantified consequences, ideally in a visual-map format.

Most wildlife biologists are familiar with habitat-modeling concepts, at least in their most simple form, the most basic being the Habitat Suitability Index (HSI Models; Brooks 1997). Data on a species' occurrence are collected; these may be presence-absence, relative abundance, or detailed telemetry data, amongst other forms, including expert opinion in some cases (e.g. HSI's). Physical habitat is then measured at or surrounding locations where animal presence was sampled. Some researchers sample

randomly-selected or “available” habitat too, allowing an arsenal of statistical techniques to be applied to determine relationships (or lack thereof) between animal and habitat data. Models that are statistically significant are said to describe animal selection or preference, or when resources are used disproportionately to their availability, “use” is said to be “selective” (Manly et al. 2002). These functions are then extrapolated across a landscape with the assumptions that statistical relationships hold, at least for an area of interest and perhaps even for an entire landscape. In this sense, these models carry weight and have vital implications for species management and conservation. Model development, therefore, should be scrutinized.

This thesis is an attempt at such scrutiny, but with an equally important objective of further understanding the autecology of northern flying squirrels (*Glaucomys sabrinus*) on a managed landscape where the animal’s ecology is poorly described. These general objectives are not unique to studies of wildlife-habitat relationships; I will argue, however, that what is unique in my approach here is a true focus on ecological scale, and its implications for quantifying wildlife-habitat relationships, something that should be considered long before we develop core-use areas or choose a statistical paradigm with which to analyze them. From the number of apparent multi-scale studies in the literature, today the topic appears well-studied, but is, in practice, misunderstood or ignored altogether. This is a fact I hope has sobering implications for the reader, particularly as they see it play out empirically through the chapters of this thesis. What I offer here is a critical review of ecological scale along with empirical examples involving flying squirrels, in which I attempt to clarify the importance of scale in data collection and predictive model development. In this process, I also offer insights into flying squirrel ecology in Alberta forests, but it is all couched within the “science of scale” (Goodchild and Quattrochi 1997; Peterson and Parker 1998; Marceau and Hay 1999).

Why Scale?

Though treated rarely in ecology, explorations into scale can be traced back to the geographical sciences (for historical context see Gehlke and Biehl 1934 and Yule and Kendall 1950), specifically the modifiable areal unit problem (MAUP; Openshaw and

Taylor 1979; Openshaw 1984; Jelinski and Wu 1996). Whenever we address scale in ecology, we are in essence addressing the MAUP, which states that the spatial distribution of variables or their level of correlation in space can be entirely modified according to their level of aggregation, or more generally, the field of view used to collect and present spatial information. In ecology, this *field of view* is generally termed *observational scale* (e.g. Heneghan and Bolger 1998; Jost et al. 2005).

The size or extent of observational scale defines what is included or excluded in our analyses: the number of animal observations, the relative proportions of different habitat types, and the level of habitat heterogeneity essentially all form the fundamentals of how we perceive nature. Ecologists have adopted the terms “grain and extent” (see below; Gergel and Turner 2002; Mayer and Cameron 2003) when discussing these issues, but these are just components of the MAUP; sampling a larger area with less detail is different from sampling a smaller area with more or the same detail. The method (observational scale) with which we choose to view nature defines what we see and this is translated in full into our predictive models in the form of averages and their associated variation. Informed geographers will go on at length about how different metrics show different statistical characteristics contingent on scale. Even though so-called “multi-scale predictive models” are continuously produced in the wildlife sciences (see Wheatley and Johnson 2009 for a review), ecologists remain mute on the effects of scale on our science. Why is this?

Scale-focused research in wildlife biology has burgeoned in the almost 20 years since Wiens (1989) and Levin (1992) anointed “scale” as a top issue in ecology. There is now no shortage of multi-scale studies in the ecological literature (e.g. Benson and Chamberlain 2007; Coreau and Martin 2007; Graf et al. 2007; Limpert et al. 2007; Slauson et al. 2007; Thogmartin and Knutson 2007; Yaacobi and Rosenzweig 2007; amongst others), and both Wiens (1989) and Levin (1992) are arguably two of the most-cited papers in contemporary ecology (as of August 2010, cited 2,041 and 2,865 times respectively since their publication). Most wildlife studies now have scalar references, often presented in terms of hierarchy theory (Allen and Starr 1982) and meticulously

arranged in terms of species' "orders of resource selection" (*sensu* Johnson 1980; cited 1,394 times as of August 2010). Empirical evidence continues to build that most animals indeed show scale-dependent selection: animals either use different resources across scales, or are differentially related to habitat structure across scales, both reinforcing the hierarchical nature (ordering) of resource selection.

The two components of ecological scale are grain and extent (Gergel and Turner 2002; Mayer and Cameron 2003). Grain is the finest level of spatial resolution available, and extent is the physical size or duration of an ecological observation (Turner et al. 1989). In wildlife research, extent (physical size) is by far the most widely examined aspect of scale, particularly common in studies examining a species' response over "multiple spatial scales" from the micro-site or home range to the landscape level (the fourth through second orders of resource selection; Johnson 1980). When we quantify wildlife-habitat relationships, whether we address or ignore grain or extent has implications for both the nature and our interpretation of the resulting data. What exactly are these implications, and how are they a function of ecological scale? I explain each briefly below, and refer the reader to the appropriate chapters in this thesis where each topic is explored in detail.

Implications of ecological grain and extent

Measurement variation and scale selection

The first implication deals with measurement variation among scales. In building wildlife-habitat models, we select observational scales as best we can to be relevant to the biology of the organism we are studying. Often the first scale we choose is based on home range or something similar (e.g. core-use areas, iterations of various kernels, etc.), but we lack justification for choosing scales beyond this. Moreover, the justification offered in these circumstances often is non-scalar and arbitrary, largely based on Johnson's (1980) orders of resource selection (i.e., non-scalar), or through a researcher's best guess irrespective of the scale continuum (i.e., arbitrary). I learned this directly by doing, and I set the stage early in this thesis with my first attempt at scalar research in

Chapter 2, which is an empirical example of how even slightly uninformed scale selection can lead to frustrating results and lack of clear conclusions. This was a crucial first step in my intellectual journey because it clarified to me how futile uninformed scale selection can be, and it began my search for alternative methods to formally integrate scale into research design. Had I not completed Chapter 2 as such, I strongly suspect Chapters 4, 5, and 6 would not have precipitated. But, for me to truly understanding the inherent limitations of Chapter 2 (see Chapters 4, 5, and 6 for this), I needed to shift my focus away from extent and onto grain.

Ecological grain

The second implication deals with ecological grain, and how the choice of sampling methods become exceedingly important as fine-grained components of habitat are considered. An important consideration in the design of ecological studies is how chosen field methods relate to components of ecological scale, namely grain. Many recent field studies of northern flying squirrels (Carey et al. 1999; Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005) suggest that these animals respond to fine-grained components of habitat; however, these conclusions are reached using sampling methods (live-trapping using peanut butter as bait) that arguably draw animals in from adjacent areas beyond the grain size of measured habitat. Because researchers are dealing with fine grain metrics, the bias associated with methods used to enumerate animals must be consistent with that grain (e.g., the error associated with locating animals in space should be less than the grain size). I examine these issues in a methodological way in Chapter 3 by quantifying how different results can be obtained contingent on sampling methods alone. This, I believe, effectively demonstrates how grain matters in the study of animal habitat use. In this chapter I also offer insight into flying squirrel habitat selection, however couched in “ecological scale” it may be.

In the remainder of my thesis I focus on “ecological extent.” Extent is the theatre within which most scale research plays out, and is most commonly referred to as “plot size” or the “size of the experimental unit.” Moreover, I know of no multi-scale wildlife studies that have used multiple grains, only multiple extents, so there is arguably an analytical bias generally to focus on extent. And admittedly, ecological extent is how I

originally interpreted Figure 4 in Wien's (1989, pg 382, Fig. 4) original description of Domains of Scale, a fundamental scalar concept that I focus upon for most of my thesis.

Domains of Scale

The third implication of ecological grain and extent can be described using Wein's (1989) largely overlooked concept of Domains of Scale. Wiens (1989) introduced the idea of "scale domains" to the ecological literature and defined them as "portions of the scale spectrum within which process-pattern relationships are consistent regardless of scale." In essence, he was simply describing ecological thresholds using scalar language. By extension, however, his ideas also imply that researchers must be aware of how metrics scale along a scale continuum, including both dependent and independent variables used in wildlife-habitat modeling. Simply stated, if we are guessing at which observational scales to use, we are then entirely unaware of the scale continuum and whether two chosen scales are even within different domains, for if they are, we are likely building the same model twice; the problem is that we interpret them as different models built on different scales, when in fact they are not. To avoid this requires an *a priori* examination of the scale continuum that must inform the choice of observational scales used in multi-scale predictive modeling. I examine this issue in Chapters 4 and 5 where I empirically demonstrate how forest metrics change unpredictably along the scale continuum and then, in light of this, I quantify multi-scale habitat use of both adult and juvenile flying squirrels to demonstrate that, in fact, scale does matter: different results will appear from the same data entirely contingent on scale. These two chapters form the basis for what I term the "continuum approach" to species-habitat modeling. Demonstrating the empirical implications of this approach in a wildlife-habitat modeling context arguably is the premier contribution of this thesis.

Finally, in Chapter 6, I review where some key issues and misconceptions exist within the science of scale, and I suggest some ways forward for the improvement of species-habitat modeling in general.

The Northern Flying Squirrel

Use of a model study species to address ecological theory is a common approach (I once argued that even Darwin did this, but I now possess mixed feelings regarding this claim), and is a tradition I maintain in this thesis. I did this with caution, however, because I was dealing with a relatively unknown, nocturnal animal, so I included in my general objectives both advancements in ecological-scale theory and a broader understanding of autecological natural history. At the onset of this project it was apparent, at least to me, that both of these objectives were equally relevant, including the natural-history ones, and I will attempt here to explain why.

The well-known ecological relationship between mycorrhizal fungi, small mammals, and trees, is considered a keystone association in forested systems worldwide (Johnson 1996, Claridge 2002). Mycorrhizal fungi are symbiotic with the roots of woody vegetation. The fungi enhance the ability of roots to absorb soil nutrients and the roots provide fungi with carbohydrates from photosynthesis (Ingham and Molina 1991; Molina et al. 1992). Because hypogeous mycorrhizal fungi possess below-ground fruiting bodies (Burdson 1968; Korf 1973; Fogel and Trappe 1978), they rely on animals to disperse spores throughout the forest. Small mammals in particular seek out these fungi (basidiomes) for consumption and subsequently deposit the spores in new locations, primarily via their fecal pellets (Maser et al. 1978). The importance of this relationship to the function of forest ecosystem initially was outlined over three decades ago (see Fogel and Trappe 1978) and has become of interest to forest managers because tree growth and post-harvest regeneration is of both economic and ecological concern (e.g. Pilz and Perry 1984; Harvey et al. 1989; Dahlberg and Stenström 1991; Bradbury et al. 1998; Kranabetter 2004).

Maser et al. (1978) described relationships of the northern flying squirrel (*Glaucomys sabrinus*) with, and its reliance on, hypogeous fungi as a food resource. Northern flying squirrels are perhaps best known from the Pacific Northwest of the United States as a primary prey for threatened northern spotted owls (*Strix occidentalis*; see Carey et al. 1992), and where a significant component of the commercial logging industry was impacted by recovery efforts for the owls and their prey (see Carey 1995). As an important prey base and a primary dispersal agent for fungal spores, the flying squirrel

occupies what some contend to be a keystone ecological role in northern forested ecosystems (Maser et al. 1986; Carey et al. 1999). Several authors have described this squirrel-fungus relationship in the western United States (Maser et al. 1985; Waters and Zabel 1995; Loeb et al. 2000; Pyare and Longland 2001; Carey et al. 2002; Meyer et al. 2005) but only two studies detail this relationship from farther north in Canada (Currah et al. 2000; Vernes et al. 2004). Our knowledge of animal-fungus relationships in the forests of west-central Canada was limited (i.e., see Wheatley 2007a), as was our understanding of flying squirrel-habitat relationships in this area too.

At the onset of this study (spring 2004), flying squirrels generally were considered members of the mature-conifer-forest guild, mostly from studies based in the Pacific Northwest of North America (Maser et al. 1978; Smith and Nichols 2004). However, the Pacific Northwest is considerably different in climate and both physical and spatial forest structure compared with forests composing the remainder and majority of the flying squirrel's natural distribution (i.e., boreal Canada and interior Alaska; Wheatley et al. 2005). Further, observations of flying squirrel nest sites in west-central Alberta (many via woodpecker-nest searches, see Bonar 2000) indicated no clear relationship between flying squirrels and conifer forests, and the limited evidence linking them to conifer forests in Alberta was not strong (e.g., MacDonald 1995). Thus, purported flying-squirrel habitat associations in general in the foothills and boreal forests of Alberta were questioned. At the time, hand-held GPS technology became affordable and available, and time-tested telemetry methods from red squirrel research (e.g., Larsen and Boutin 1994) appeared completely feasible for the flying-squirrel system. It was this combination of relatively detailed night-time spatial information coupled with strong habitat-use telemetry data that set the stage for this thesis.

It was a primary objective of this thesis to clarify some simple species-habitat relationships for flying squirrels and forests in Alberta. However, these relationships are intermingled with analyses that examine sampling methods and observational-scale theory. The natural-history reader will have to extract habitat-use information from amongst my focus on scale, to the extent that two full chapters herein (Chapter 4 and 6) employ no squirrel data whatsoever. Nonetheless, I strongly submit that our understanding of flying-squirrel habitat use has increased greatly because of this research,

and I refer the reader to data presented within Chapters 2, 3, and 5 for relatively detailed habitat-use information on these animals.

Chapter 2 Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: Northern flying squirrels in Alberta, Canada.¹

Abstract

It is common practice to evaluate the potential effects of management scenarios on animal populations using Geographical Information Systems (GIS) that relate proximate landscape structure or general habitat types to indices of animal abundance. Implicit in this approach is that the animal population responds to landscape features at the spatial extent represented in available digital map inventories. Northern flying squirrels *Glaucomys sabrinus* are of particular interest in North American forest management because they are known from the Pacific Northwest as habitat specialists, keystone species of old-growth coniferous forest, and important dispersers of hypogeous, mycorrhizal fungal spores. Using a GIS approach I test whether the relative abundance of flying squirrels in northern Alberta, Canada, is related to old forest, conifer forest, and relevant landscape features as quantified from management-based digital forest inventories. I related squirrel abundance estimated through live trapping to habitat type (forest composition – conifer, mixedwood, and deciduous) and landscape structure (stand height, stand age, stand heterogeneity, and anthropogenic disturbance) at three spatial extents (50 m, 150 m, and 300 m) around each site. Relative abundances of northern flying squirrels in northern and western Alberta were similar to those previously reported from other regions of North America. Capture rates were variable among sites, but showed no trends with respect to year or provincial natural region (foothills versus boreal). Average flying squirrel abundance was similar in all habitats with increased values within mixedwood stands at large spatial extents (300 m), and within deciduous-dominated stands at smaller spatial extents (50 m). No relationship was found between

¹ This chapter has been published as “Wheatley, M., J.T Fisher, K. Larsen, J. Litke, and S. Boutin. 2005. Using GIS to relate small mammal abundance to landscape structure at multiple spatial extents: northern flying squirrels in Alberta, Canada. *Journal of Applied Ecology* 42:577-586” and is reproduced exactly here save for minor editorial differences (e.g., changing “we” to “I”) for the thesis version.

squirrel abundance and conifer composition or stand age at any spatial extent. None of the landscape variables calculated from GIS forest inventories predicted squirrel abundance at the 50 m or 150 m spatial extents. However, at the 300 m spatial extent I found a negative, significant relationship between average stand height and squirrel abundance. Boreal and foothill populations of northern flying squirrels in Canada appear unrelated to landscape composition at relatively large spatial resolutions characteristic of resource inventory data commonly used for management and planning in these regions. Flying squirrels do not appear clearly associated with old-aged or conifer forests; rather, they appear as a habitat generalists. This study suggests that northern, interior populations of northern flying squirrels are likely more related to stand-level components of forest structure such as food, micro-climate (e.g. moisture), and understory complexity, variables not commonly available in large-scale digital map inventories. I conclude that available digital habitat data potentially excludes relevant, spatially-dependent information and could be inappropriately used for predicting the abundance of some species in management decision making.

Introduction

Habitat structure and the juxtaposition of suitable and unsuitable habitats are known to affect the distribution of forest vertebrates (Rodríguez and Andrén 1999; Bowman et al. 2001; Reunanen et al. 2002). An understanding of relationships between animal distribution, habitat types, and landscape patterning is of considerable importance in applied ecology where management actions (e.g. forest harvesting) necessarily alter patch size, connectivity, and age distribution of habitats. Predictive models that describe relationships between animal populations and spatial habitat structure are commonly generated using Geographic Information Systems (GIS) (e.g. Arbuckle and Downing 2002; Gibson et al. 2004; Hatten and Paradzick 2002; Mackey and Lindenmayer 2001; Rowe et al. 2002; Verner et al. 1986) that evaluate species-specific responses to habitat heterogeneity, and quantify the spatial extent (Kotliar and Wiens 1990) at which a species uses or selects for landscape features (e.g. Johnson et al. 2004). Once quantified, responses can be modelled using GIS-based techniques such as Spatially Explicit

Population Dynamic Models that predict animal distribution based on the interaction between individual behavioral processes and landscape structure (Rushton et al. 1997; Rushton et al. 2000). These methods have become common to sustainable land management strategies, and increasingly form the basis for species-habitat management activities (see Rushton et al. 2004).

Digital GIS-based landcover inventories allow for efficient quantification of landscape structure at relatively large spatial extents (i.e. above forest stand level; Holloway et al. 2003; Jaberg and Guisan 2001; Jeganathan et al. 2004; Pearce et al. 2001; Osbourne et al. 2001; Suarez-Seoane et al. 2002), but their usefulness for animals that potentially respond to fine-scale habitat features can be limited because such high-resolution data rarely are incorporated into relatively large regional or provincial digital inventories (Engler et al. 2004). For management areas that rely heavily on digital forest inventories in decision-making processes, such as many North American forestry operations, understanding which animals respond to landscape features available on GIS is a key for effective and sustainable planning. Animals considered 'habitat specialists' are of particular interest in such a predictive modeling context because of their potential inability to tolerate significant changes in structural or spatial habitat attributes generated from management activities (Bright 1993). However, features of the landscape that define the functional landscape (Johnson et al. 2001; Kotliar and Weins 1990) and affect a species' distribution must be quantified and measurable at a relevant spatial extent on the GIS before this can be an effective approach (Levin 1992; Turchin 1996; Turner and Gardner 1991).

Northern flying squirrels (*Glaucomys sabrinus* Shaw) have become of particular interest to forest management in the United States and Canada (Carey 1995, 2000; Smith and Nichols 2003) because of their direct relationship to old-growth forest and fungal communities therein. Essential to growth of woody vegetation is its symbiotic relationship with nitrogen-fixing hypogeous mycorrhizal fungi; the fungus associates with roots and provides essential nutrients for tree growth: an obligatory relationship for both tree and fungus (Claridge et al. 2000). Generally, neither mycorrhizal fungi nor their hosts complete their life-cycle independently (Maser et al. 1978). Because the fungus is hypogeous (i.e. completely underground), it lacks above-ground fruiting bodies and relies completely on animals for spore dispersal – primarily microtines and tree squirrels (Carey

et al. 1999; North et al. 1997). Flying squirrels feed almost exclusively on hypogeous fungi (Currah et al. 2000; Maser et al. 1986) and unlike microtines disperse the spores through faecal deposits at spatial extents greater than the stand level. These animals are considered habitat specialists and, through their fungal relationships, a 'keystone' species of mature, coniferous forest (Maser et al. 1978; Smith and Nichols 2004). As a cavity nester and a prey species for many predators (including threatened owl species; Carey et al. 1992), its presence has been linked to old-growth coniferous forests and is considered to reflect ecosystem health (Carey 2000).

It is because of this link to old growth forests that the majority of research on this animal comes almost exclusively from forests in the Pacific Northwest of North America (e.g. Maser et al. 1978; Carey 2000; Ransome and Sullivan 2003; Smith and Nichols 2003) with reference to prey availability and recovery efforts for threatened northern spotted owls (*Strix occidentalis* Merriam) (Carey 1995). However, the Pacific Northwest is considerably different in climate and both physical and spatial forest structure compared to forests composing the remainder, and majority of the flying squirrel's natural distribution (i.e. boreal Canada, interior Alaska). Consequently, flying squirrel habitat associations are not known throughout most of its northern range, (but see McDonald 1995) particularly in the foothills and boreal regions of Canada where industrial development is increasingly widespread. Flying squirrels appear to be associated with mature, conifer forest attributes directly altered by contemporary, multi-pass forest harvesting (e.g. stand age, snag retention, understory development; see Carey 1995). This is a problematic association, and key industrial concern in northern and western Alberta, where harvest rotation age commonly is less than the average and natural ages of mature or old forests. Through rotational harvesting over time forest patches become younger in age and smaller in size.

The focus of this study was to relate flying squirrel abundance to parameters of forested landscape typically assessed and readily available via remote sensing using management-based GIS inventories. My objectives were (a) to compare squirrel abundance among broad habitat categories based on conifer and deciduous composition, and (b) to relate observed flying squirrel abundance to landscape structure around each sampling area at three spatial extents (300 m, 150 m, and 50 m). Based on this animal's

previously described association with old, conifer forests and stand-level forest attributes (see Carey 1995; McDonald 1995) I predicted that: 1) flying squirrels would be positively associated with conifer composition, stand height, and stand age, and negatively associated with younger, mixedwood stands dominated by a deciduous canopy and, 2) based on previous research suggesting stand-level associations between northern flying squirrels and habitat variables, any relationships to squirrel abundance would be found with landscape variables quantified at small spatial extents. To explore this I sampled northern flying squirrels within a range of conifer-dominated and deciduous-dominated forest types, from across northern and west-central Alberta encompassing 32 sites.

Materials and Methods

Study Location

This paper combines results from two studies that initially were separate, partially coordinated projects. Both employed identical live-trapping techniques and are pooled together here in one study. There are slight differences in sampling year and transect length among areas, but I account for these differences statistically and through capture per unit effort standardizations (see Statistical Analyses). Sampling was conducted across northern and west-central Alberta, Canada, within the boreal mixedwood and the foothill natural ecoregions (Strong 1992). Twenty-three sites were sampled in the boreal ecoregion: three near Fort McMurray (56° N 111° W), three near Lac La Biche (53° N 112° W), three near Athabasca (55° N 114.5° W), eight near Manning (57° N 118° W), and six near Grande Prairie (55° N 119° W). Nine sites were sampled in the foothills ecoregion near Hinton (53° N 117° W).

Boreal ecoregion

The boreal ecoregion of Alberta is a heterogeneous mixture of forest stands including trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* Moench) and jack pine (*Pinus banksiana* Lamb.) dominating upland areas, and stands of black spruce (*Picea mariana* Mill.), larch tamarack (*Larix laricina* K. Koch.), white birch (*Betula papyrifera* Marsh.) and balsam poplar (*Populus balsamifera* L.) dominating lowland areas. Extensive black spruce bogs, larch tamarack bogs and peatland are common in lowland areas. Stand age is a mixture of young forest (< 20 years) of both fire and harvest origin, and mature and old growth forest (> 20-100+ years) of fire origin. Both anthropogenic and natural disturbance features are widespread. Fire is the primary disturbance pattern, followed by extensive oil and gas seismic exploration and active forest harvesting. The general topography is undulating to level.

The forest canopies of deciduous-dominated stands consisted primarily of mature to old trembling aspen with average stand ages ranging from 62 – 107 yrs, and with understory shrub species including wild rose (*Rosa spp.*; Moss 1994), alder (*Alnus crispa* Pursh), and hazel (*Corylus cornuta* Marsh.). Deciduous snags in various stages of decay were numerous within these stands. Mixedwood stands had aspen-dominated canopies with roughly 40% white spruce, and a spruce-dominated sub-canopy with deciduous snags common. Dense understories consisted of rose, alder, hazel, cranberry (*Viburnum spp.*; Moss 1994), saskatoon (*Amelanchier alnifolia* Nutt.), and honeysuckle (*Lonicera spp.*; Moss 1994). Mixedwood canopy trees on average ranged from 61 - 103 years old. Conifer-dominated stands consisted primarily of mature white spruce (60-70% of canopy) averaging 67-111 years of age mixed with mature aspen (<25%). Immature understory species included aspen, balsam poplar, lodgepole pine, and alder all in low abundance. These stands had willow *Salix spp.* (Moss 1994) and bunch berry (*Cornus Canadensis* L.) at low densities in the understory, with dense coverage of Labrador tea (*Ledum groenlandicum* Oeder) and mosses (*Sphagnum spp.*; Ireland 1980). These stands contained many conifer snags and large coarse woody debris.

Within the boreal ecoregion I established five study sites (sites 1-5, Fig. 2-1) and trapped flying squirrels in three of the most common forested habitats found within each (24 boreal sampling transects total). I sampled in deciduous-dominated stands (primarily trembling aspen), deciduous-conifer mixedwood stands (trembling aspen mixed primarily with white spruce and to a lesser extent larch tamarack), and conifer-dominated stands (primarily white spruce). Live-trapping areas were established in mature and old forests that previously had not been logged.

Foothills Ecoregion.

The foothills ecoregion of Alberta consists of foothills running northwest to southeast along the front-range of the Rocky Mountains. The topography is moderate to steep, with elevation ranging from 1200 m to 1600 m. Coniferous forest 80-120 years old (*Pinus contorta* London, *Picea glauca*, *Picea mariana*, and *Abies spp.*; Moss 1994) covers over 80% of the area; smaller proportions of both younger and older stands, of both fire and logging origin, are dispersed throughout. Within the study area, large patches of mature lodgepole pine (*Pinus contorta*), white spruce, and mixed-lodgepole pine-white can be found.

Deciduous-dominated stands were similar in composition and age to those described from the boreal ecoregion. Lodgepole pine stands are the dominant feature within the foothills landscape (roughly 80% by area). These stands consisted of >70% lodgepole pine with an understory composition of alder (*Alnus crispa*), wild rye (*Elymus spp.*; Moss 1994), labrador tea, and mosses (*Ptilium* and *Sphagnum spp.*; Ireland 1980). Black spruce (*Picea mariana*) occupied a portion of the canopy, but at low densities. Immature white spruce and fir (*Abies balsamea* L.) were present at low densities. Standing, burnt snags were common features within pine stands. Spruce-fir stands consisted of roughly 30% spruce, and <70% fir (*Abies lasiocarp* Hook. and *Abies balsamea*). The understory was composed of sapling fir, feather moss (*Hylocomium spp.*; Ireland 1980), and wintergreen (*Pyrola spp.*; Moss 1994). Dense alder patches and lichens (*Alectoria*, *Brioria* and *Usnia spp.*; Kershaw, Pojar & Mackinnon 1998) were common in all spruce-fir stands.

Within the foothills ecoregion I established nine sampling transects distributed evenly within three of the most common habitat types; deciduous-dominated (trembling aspen), lodgepole pine (>70% pine), and mixed white spruce-fir. All sites were established in mature forest 95-181 years of age that previously had not been logged.

Site selection.

Study sites were selected using a stratified approach to encompass dominant landscape composition and natural heterogeneity for each area, including the most common habitat types by area and their associated disturbance levels. Flying squirrels are known to key into mature forest attributes (e.g. cavities and snags), thus I focused my efforts on stands > 60 years of age and older. Relative overstorey composition was assessed using Alberta Vegetation Inventory (AVI) maps – provincial government maps noting all forest polygons, including the stand density, age of origin, and dominant tree species assessed and digitized from 1:50 000 orthogonal aerial photos. Site selection criterion included primary and secondary canopy species composition (common, representative of the area, or of management concern), stand age (> 60 years of age), intersite proximity (spatially independent), and access.

Sampling techniques

Flying squirrels were sampled using live-trapping transects, and relative abundance was calculated as captures of unique animals per trap unit effort.

Eighteen transects were sampled near Ft. McMurray, Lac La Biche, Athabasca, and Hinton. All these transects (9 boreal, 9 foothill) were 1 km in length, each with 25 trapping stations placed at 40 m intervals. These were plotted to fit patch shape. Some were not straight lines, but transect direction was limited to 60 degrees of the original bearing. If seismic lines or roads were crossed, the width of the intersection was excluded from the transect length.

Fourteen transects were established near Manning and Grande Prairie consisting of two types. Six of these transects were straight lines, 450 m in length and located in Site

4. The remaining eight of these transects consisted of two 200 m parallel transects (100 m apart) but within the same stand. In all cases trapping stations were flagged at 50 m intervals so that ten trapping stations were established on all transects or pairs therein.

At each trapping station, two live traps (Model #201 or #102, Tomahawk Live Trap Company, Tomahawk, Wisconsin) were set: one on the ground at the base of a tree (diameter at breast height > 30 cm), and one in a tree >1m but <2 m above ground. The latter was attached to the trunk using aluminum nails. Rain covers (light ply-wood or plastic attached with elastic bands) covered at least half of the top and bottom of each trap and a handful of raw cotton or synthetic insulation was placed within. Both traps were placed within 10 m of the trapping station. I pre-baited for at least 4 days prior to setting traps by placing small amounts of peanut butter (<1 gram) on the top of each trap or at the base of flagged trap station trees.

Traps were baited with peanut butter and sunflower seeds, set between 1800 hrs and 2200 hrs, and checked the next morning between 0600 hrs and 1100 hrs for 4 to 7 consecutive nights depending on the study area. Captured animals were marked with either Monel #1 eartags (National Band and Tag Co., Newport, Kentucky) or dorsally with non-toxic, permanent ink. Our intent was to record the number of new captures per trapping effort; unique markings were not necessary. For Athabasca, Lac La Biche, and Fort McMurray trapping occurred from 10 June – 03 July 1997. For Grande Prairie and Manning trapping occurred from 15 June – 15 July 2001. For Hinton, trapping occurred from 17 June – 19 July 2003. When calculating the number of trap-nights, a correction factor of half a trapnight was subtracted for each trap found triggered without an animal (see Nelson & Clark 1973). No sampling areas were resurveyed between years.

Landscape composition

I quantified habitat around trapping transects by digitally capturing all mapped polygon features within 50 m, 150 m, and 300 m around the transect lines. Thus, GIS plots were long and narrow centred on the transect, and encompassed natural heterogeneity within sites. Choice of spatial extent sizes was based on observed stand-level movements of flying squirrels released from traps (approximately 50 m, or to encompass average

gliding distance reported by Vernes 2001), with the largest plot (300 m) chosen to encompass reported home range sizes of flying squirrels; see Cotton and Parker (2000). Plots were additive; larger plots included spatial features of smaller ones.

Digital inventory data were obtained from local forest companies and included all spatial features (forest polygons, openings, roads, water bodies, etc.) around all study areas from recent provincial air photos using provincial digitizing standards. For each forest polygon the acquired digital forest data included habitat composition recorded as percentage cover of the primary, secondary, and tertiary leading tree species, as well as polygon size (area), age (years), and height (m). To extract relevant habitat information, I converted within-polygon tree proportions to species-by-area measurements by multiplying the proportion of each species by the area for each polygon. This resulted in a tree-species-by-area measure for all GIS plots.

The forest system in northern Alberta is relatively sparse in tree diversity, so proportionally many species are the inverse of each other and autocorrelation of habitat variables is common. I wished to avoid testing uninformative hypotheses (Anderson et al. 2000) of correlated variables, so I limited variable generation to those pertaining directly to my hypotheses, to those currently predicted biologically important to flying squirrels, and to those relevant to management planning using GIS. Within each plot I calculated average stand age (yrs), average stand height (m), percentage conifer species by area, percentage non-forest openings by area, and heterogeneity (average polygon size in m^2 – see below). Anthropogenic openings were rare relative to natural openings (low wetlands, water bodies, etc.) so I pooled all openings into one non-forest category. Average polygon size was calculated as a measure of plot heterogeneity; homogeneous areas had larger average polygon size by area, heterogeneous plots had smaller average polygon size by area.

Statistical analysis

I employed two main approaches to examine squirrel relative abundance according to habitat structure or type: Analysis of Variance and stepwise regression.

Using habitat category as a fixed effect and year as a random effect, I compared squirrel abundance among areas using a mixed-model type III ANOVA, with habitat

blocked two different ways. First, based on the percentage conifer present around each trapping transect calculated separately for each of the three spatial extents, I blocked all study areas into three broad habitat categories: 1) conifer-dominated, 2) mixedwood, and 3) deciduous-dominated. Deciduous areas had on average <8% conifer, mixedwood areas had on average 40-50% conifer, and conifer-dominated areas had >85% conifer composition.

Secondly, I blocked all study areas into four more specific habitat types based on dominant canopy tree species. The habitat categories included 1) trembling aspen, 2) mixed aspen-spruce, 3) white spruce, and 4) lodgepole pine. Habitat categories had >80% composition of the leading tree species. Mixedwood sites consisted of between 40-47% spruce, the remainder being aspen-dominated. As spatial extent was increased, additional habitat patches were included within the GIS plots and some sites were reclassified into different habitat categories.

I used stepwise regressions to determine whether landscape composition was related to squirrel abundance independent of habitat categories. One regression was conducted for each of the three spatial extents. In all cases trapping transect was used as the experimental unit and 'captures per 100 trap-nights' was used as the dependent variable. Independent variables entered into each model included average tree height (m), average stand age (yrs), percentage conifer (% of area), percentage non-forest (% area), and average patch size (m²; a measure of heterogeneity). Year was included as a dummy variable. The criteria probability for F to enter the model was set to 0.05, and the probability criteria of F to remove from the model was set to 0.1.

In three cases, GIS plots were not spatially independent. To achieve spatial independence, I randomly dropped one site from each of three spatially-overlapping pairs (one site from the 150 m analysis, two sites from the 300 m analysis). I achieved temporal independence by sampling each study site once, sampling different sites among years, and statistically accounting for variability associated with year.

To achieve normality and reduce heteroscedasticity in the data, relative abundance of squirrels, average tree height, average stand age, and average patch size were transformed using the natural log function ($\ln x+1$). Proportion data were arcsin square root transformed. Analyses were completed using SPSS version 8.0.

Results

In total I marked 93 individual northern flying squirrels from 32 study sites over 5935 trap-nights and three mid-summer seasons of sampling. Relative abundance ranged from zero to 6.96 unique captures per 100 trap-nights with no clear trend for increased or decreased values among years or sampling regions, apart from slightly increased values at the Lac La Biche area in 1997 (Table 2-1). I recorded zero captures in nine of the 32 trapping transects over the three summer seasons of trapping but these zeros appeared unrelated to local habitat as classified within 50 m of the trapping transect (two spruce, four mixedwood, and three aspen sites).

At the 300 m spatial extent there was a trend for increased squirrel abundance in mixedwood habitat compared to conifer-dominated and deciduous-dominated habitats (Fig. 2-1), however, this was not statistically significant (see below). I did not find any association between flying squirrel abundance and habitat at the 50 m, 150 m, or 300 m spatial extents (Table 2-2; three-habitat comparisons). Additionally, there were no significant interactions between habitat and year at any spatial extent (all $P > 0.15$; Table 2-2).

Similarly, at the 300 m spatial extent there was a trend for increased squirrel abundance in mixedwood habitat compared to trembling aspen, white spruce, and lodgepole pine (Fig. 2-2). However, this was not statistically significant and sites were not extensively reclassified by habitat type at this level. I did not find any association between flying squirrel abundance and the four habitat categories at the 50 m, 150 m, or 300 m spatial extents (Table 2-2; four-habitat comparisons). Additionally, there were no significant interactions between habitat and year at any spatial extent (all $P > 0.14$).

Overall regression models at 50 m and 150 m spatial extents were not significant, and consequently no environmental variables entered these models. Stepwise multiple regression at the 300 m spatial extent was significant overall ($F_{[1,28]} = 2.1$, adjusted $r^2 = 0.20$, $P = 0.009$) with average stand height as the only significant factor predicting squirrel abundance ($t = -2.8$, $P = 0.009$; Fig. 2-3). Squirrel abundance was negatively associated with average stand height at the 300 m spatial extent. This relationship was derived from height data that ranged from 12 – 28 m.

I found little or no relationship between squirrel abundance and any of the other environmental parameters. Of note is the lack of any relationship between abundance and conifer composition (Fig. 2-4), a relationship that was equally disparate at all three spatial extents using conifer composition data that were roughly evenly distributed between zero and 100% among sampling areas. Similarly, I found no discernable relationship between abundance and stand age with forest age averages that ranged evenly among sites between approximately 60 to 181 years.

Table 2-1. Captures per 100 trap-nights \pm SEM of northern flying squirrels in four forest types from northern and western Alberta, Canada. Captures are sorted by dominant habitat type at the 50 m spatial extent. Sample sizes are in brackets.

Year	Site	Dominant Habitat Type at 50 m spatial extent			
		Trembling Aspen	Mixed Conifer	Lodgepole Pine	White Spruce
1997	Athabasca	1.45 (1)	2.52 (1)	--	0.69 (1)
	Ft. McMurray	2.80 (1)	0.71 (1)	--	0 (1)
	Lac La Biche	6.96 (1)	3.84 (1)	--	2.38 (1)
2001	Grande Prairie	0.28 \pm 0.23 (3)	1.20 \pm 0.6 (3)	--	--
	Manning	--	0.69 \pm 0.34 (6)	--	0.43 \pm 0.43 (2)
2003	Hinton	0.29 \pm 0.15 (3)	--	1.32 \pm 0.48 (3)	2.19 \pm 1.22 (3)

Table 2-2. Mixed-model ANOVA results comparing flying squirrel relative abundance by habitat type over three spatial extents.

Spatial Extent	Factors	ANOVA Comparisons	
		3 habitats	4 habitats
50 m	Habitat	$F_{2,24} = 0.28, P = 0.77$	$F_{3,23} = 0.15, P = 0.93$
	Year	$F_{2,24} = 1.00, P = 0.46$	$F_{2,23} = 0.91, P = 0.49$
	Hab x year	$F_{3,24} = 1.80, P = 0.16$	$F_{3,23} = 2.01, P = 0.14$
150 m	Habitat	$F_{2,23} = 0.24, P = 0.79$	$F_{3,22} = 0.14, P = 0.93$
	Year	$F_{2,23} = 0.96, P = 0.47$	$F_{2,22} = 0.98, P = 0.47$
	Hab x year	$F_{3,23} = 1.60, P = 0.21$	$F_{3,22} = 1.72, P = 0.19$
300m	Habitat	$F_{2,22} = 0.48, P = 0.65$	$F_{3,21} = 0.38, P = 0.77$
	Year	$F_{2,22} = 3.80, P = 0.15$	$F_{2,21} = 2.58, P = 0.23$
	Hab x year	$F_{3,22} = 0.58, P = 0.63$	$F_{3,21} = 0.99, P = 0.41$

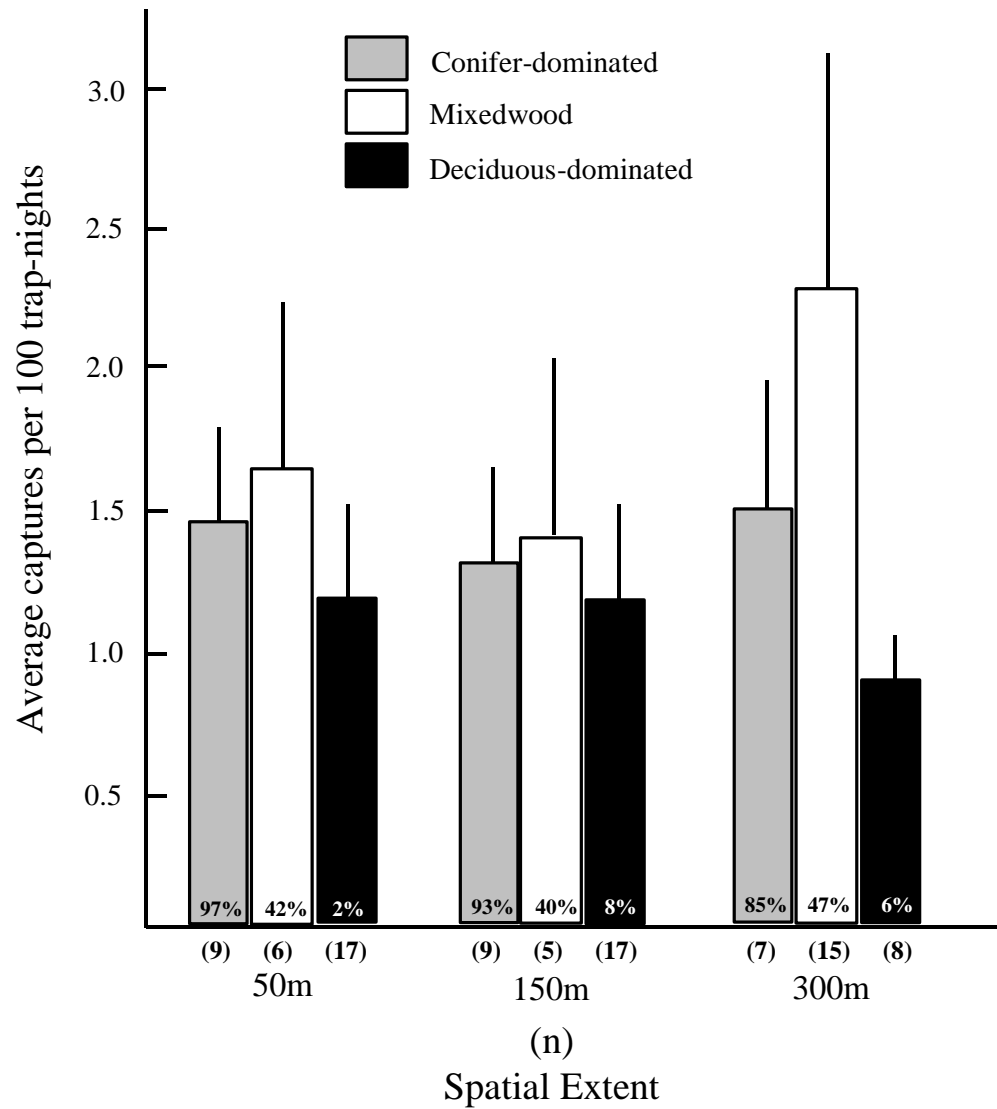


Figure 2-1. Average captures per 100 trap-nights of flying squirrels in three habitat categories from northern and western Alberta, Canada. As spatial extent was increased and additional habitat patches were included within larger sampling areas, some sites were reclassified into different habitat categories. Average conifer proportions for each category are listed as percentages at the bottom of each bar. Sample sizes (number of trapping transects) are in brackets below each bar and error bars indicate SEM.

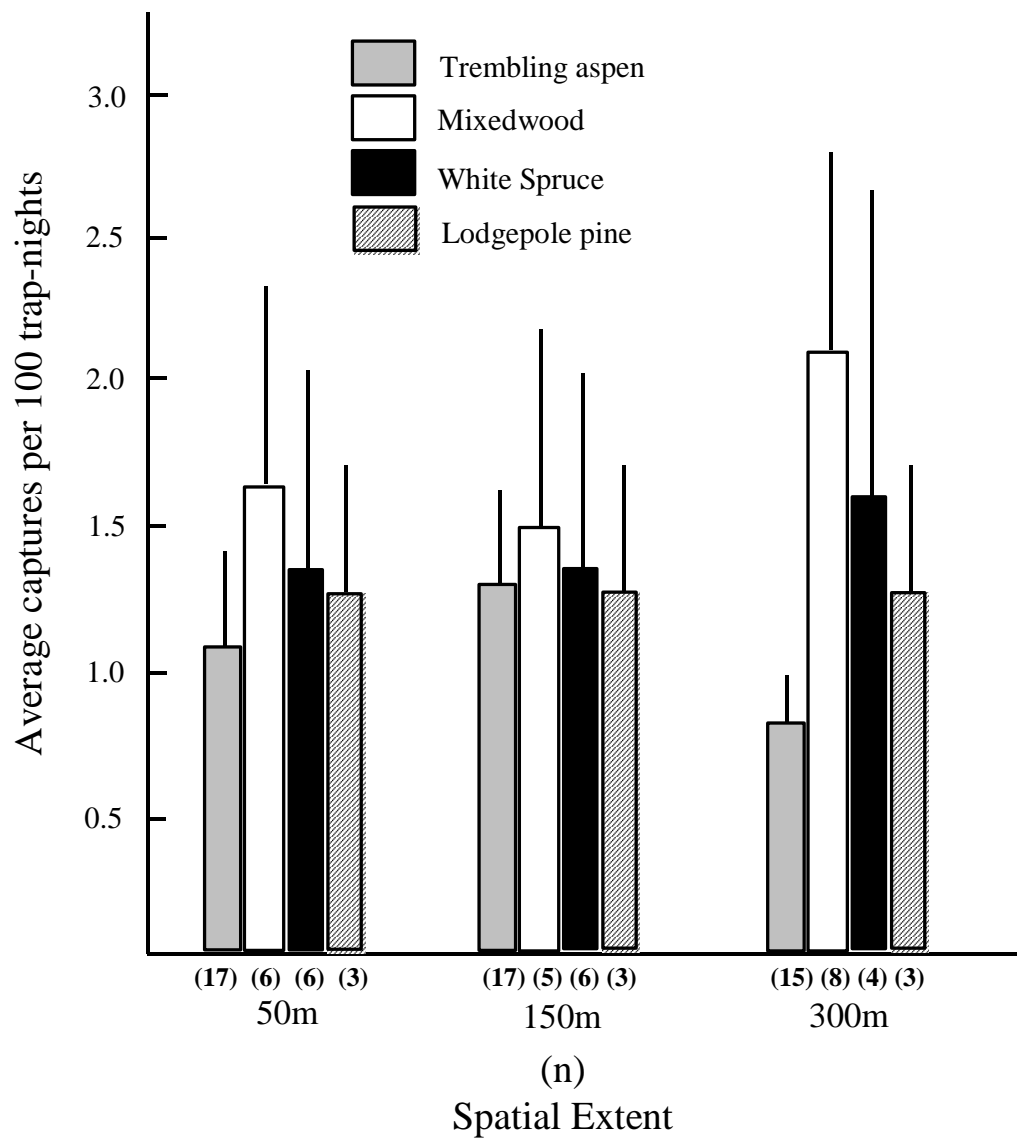


Figure 2-2. Average captures per 100 trap-nights of flying squirrels in four habitat categories from forests in northern and western Alberta, Canada. As spatial scale was increased and additional habitat patches were included within larger scales, some sites were reclassified into different habitat categories. Sample sizes (number of trapping transects) are in brackets below each bar and error bars indicate SEM.

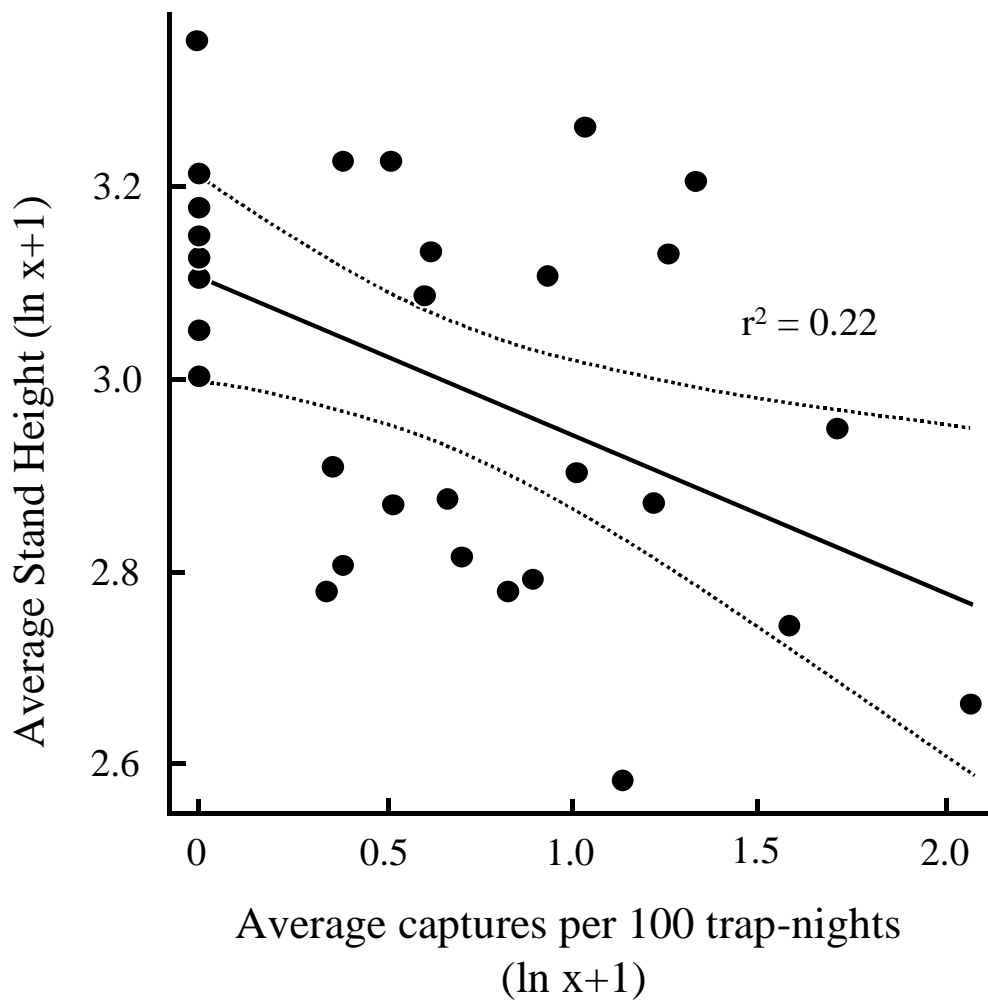


Figure 2-3. Negative relationship between average stand height and flying squirrel abundance at the 300m spatial extent from forests in northern and western Alberta, Canada. The transformed values of both variables ($\ln x + 1$) are plotted. Lines represent a best-fit linear regression with 95% confidence intervals.

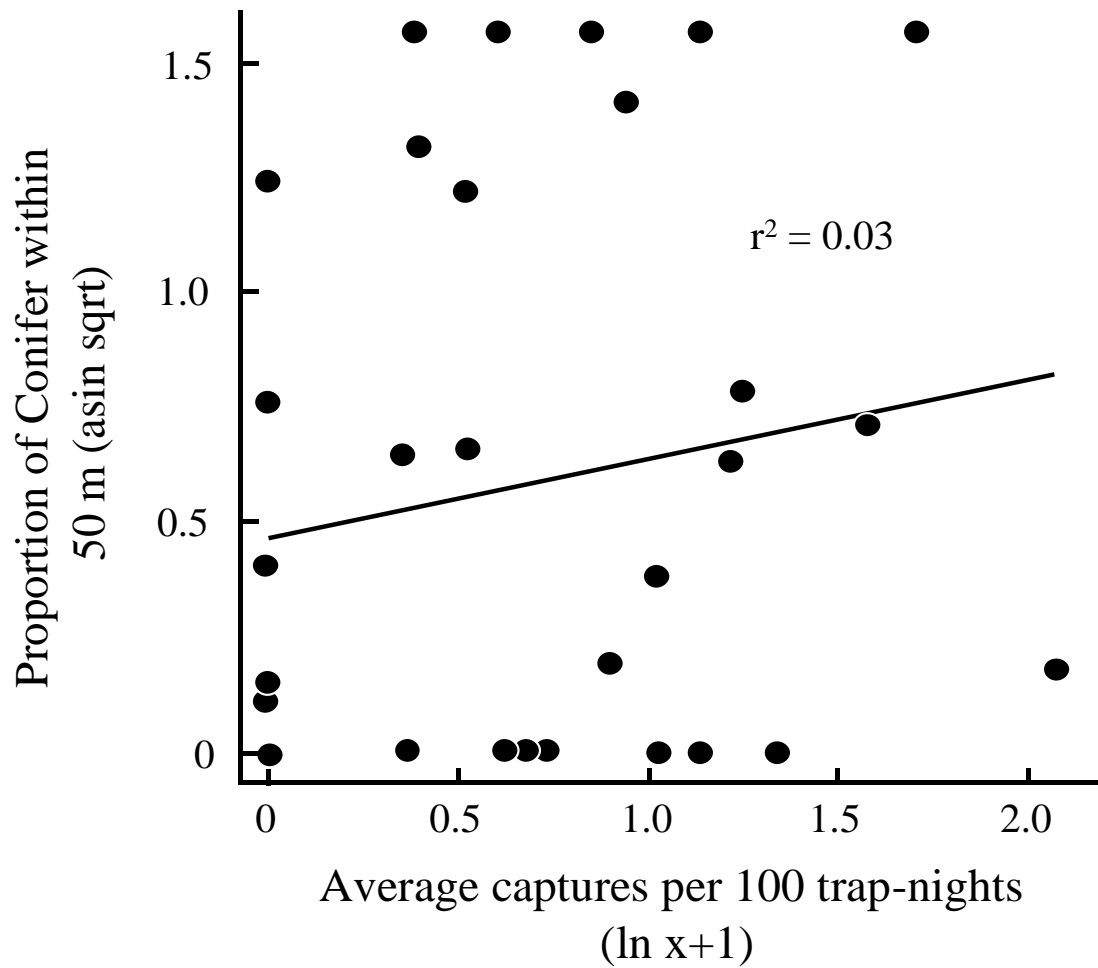


Figure 2-4. There was no relationship between average conifer composition and flying squirrel relative abundance at the 50 m spatial extent from forests in northern and western Alberta, Canada. Similar relationships were also found for the 150 m and 300 m spatial extents. The transformed values of both variables (\ln abundance + 1, and arcsin square root of conifer composition) are plotted. Solid line represents a best-fit linear regression.

Discussion

Flying squirrels were found in all habitats sampled but were not significantly associated with any particular habitat type, either conifer or deciduous-dominated, at any spatial extent. I found abundance completely unrelated to conifer composition, stand age (above 60 years), patch size, and non-forested openings at both large and small spatial extents. Abundance was unrelated to stand height at the 50 m and 150 m spatial extents, but showed a significant negative relationship (above 12 m) at the 300 m spatial extent. My prediction, namely that abundance would be positively related to stand age and conifer composition (see Carey 1995; McDonald 1995; Smith and Nichols 2003), or other components of older forests (e.g. stand age) at the stand level, was not supported.

Relating flying squirrel abundance to old-growth forest in Alberta is difficult. My results are consistent with somewhat uncommon literature suggesting northern flying squirrel abundance is not necessarily specific to conifer habitat or related to features of older forests; see Martin (1994) and Rosenberg and Anthony (1992). These animals can be found in younger, second growth forests, although it is not known whether these are breeding or persistent populations. Similarly, Waters and Zabel (1995) and Pyare and Longland (2002) found no correlation between flying squirrel abundance and either snags or cavities (contrary to Smith and Nichols 2004) – both prominent characteristics of old-growth or mature forests. I expected more animals to be found in mature stands with higher trees and larger gaps characteristic of older forests in our study areas, but response to average stand height was the reverse of my prediction and seen only at one spatial extent. Squirrel abundance in this study was similar across a continuum of habitats and stand ages, further suggesting that features other than those necessarily associated with habitat type or forest successional stage are driving flying squirrel abundance.

Increasingly, the occurrence of *G. sabrinus* is being linked to food abundance (Ransom and Sullivan 2004; Pyare and Longland 2002), specifically the abundance of truffles (Pyare and Longland 2002), the subterranean fruiting body of hypogeous fungus, identified as the primary food item in a relatively specific diet (Maser et al. 1986; Currah et al. 2000). Ransome and Sullivan (2004) present convincing evidence that food abundance is a significant, proximate mechanism driving flying squirrel abundance.

However, habitat features related to food abundance are most likely to occur at a higher resolution than average stand values available from digital forest inventory. If food is a significant proximate mechanism, then effectively modelling the abundance of *G. sabrinus* will be difficult: a clear link does not exist between hypogeous fungus and measurable habitat features or habitat types (but see Fogel 1976). Also unknown is the spatial distribution and abundance of these food items, but this is probably linked to stand-level moisture and temperature (Currah et al. 2000) - two variables below the resolution of digital forest inventory data, and typically spatially patchy within and among areas (Fogel 1976).

If proximate features affecting flying squirrel abundance show clumped or patchy spatial distributions, then this has implications for sampling techniques used to derive abundance measurements for this animal used in subsequent model predictions. Spatial and temporal heterogeneity in flying squirrel capture rates (trapping “hot spots”) among and within studies have been reported (Rosenburg et al. 1995; Cote and Ferron 2001; Pyare and Longland 2002; present study). Pyare and Longland (2002) found correlations between capture locations and truffle diggings of northern flying squirrels in eastern Canada, and they discuss how different species of hypogeous fungi fruit at different times and persist ephemerally. They suggest that these animals are exploiting microhabitats based on a combination of ephemeral fungi abundance and above-ground microhabitat characteristics that provide cover from predators, and that this results in patchy trap success over time and space. If flying squirrels are tracking ephemeral resources (Talou et al. 1990; Donaldson and Stoddart 1994; Pyare and Longland 2002) resulting in clumped population distributions that change over time and space, then commonly used sampling transects or grids will show “hit and miss” capture rates. Telemetry studies relating movements to resources, i.e. foraging dispersal, will help validate abundance data by relating capture locations to fine-scale habitat use, but because flying squirrels are nocturnal, movement studies are rare (although with the advent of GPS I now know of at least four movement studies on *G. sabrinus* in North America that should become available in the near future).

Of particular interest is how my results differ from those found in Alberta by McDonald (1995). Her capture rates were similar to those reported here; however, she

found positive associations between flying squirrel abundance and conifer density. Further, she found significantly more flying squirrels in older (≥ 120 years) versus younger forests (50-65 years). Although the forest stands sampled within my study included the range of spruce composition and stand age sampled by McDonald (1995), the overall range of habitats, spatial extent surrounding plots, and geographic area sampled here were greater. Habitat associations for flying squirrels appear to change significantly (i.e. were not detectable here), when examined over larger spatial extents, or a greater variety of forest types at larger grain. Differences in abundance-habitat relationships reported among studies could simply reflect differences in ephemeral resource use between study areas, or a completely different functional landscape contingent on the spatial extent examined.

The performance of predictive models will depend on the vagility of the organism being studied, the predictor variables selected, and the grain and spatial extent considered (Engler et al. 2004). The data used here to describe landscape composition appear above the grain of perception of *G. sabrinus*. This study highlights potential problems associated with assigning relative importance to habitat types, or landscape configurations, based on studies done at only one spatial extent or in one landscape context (Fisher et al. 2005). To date, I cannot assign a habitat preference to northern flying squirrels in Alberta, and successful management and conservation of this species will require further knowledge of within and among-patch movement patterns of individuals with reference to key in-patch features. Efforts to predict northern flying squirrel abundance using available GIS-based digital forest inventories in North America should be dissuaded unless digital resolution is increased above general habitat polygons.

Chapter 3 Differential space use inferred from live-trapping versus telemetry: Northern flying squirrels and fine spatial grain.²

Abstract

Small mammal space use is inferred from live-capture data or various methods of tracking, with differences between these methods potentially affecting the input and subsequent inferential abilities of resulting wildlife-habitat models. Unlike tracking via radio telemetry, live-trapping employs use of bait, known to change proximate animal density as evident in many food addition studies (the “pantry effect”), and conceivably biasing individuals’ space use, particularly if measured over small spatial extents in heterogeneous areas. To examine this, we analysed both trapping and telemetry data from northern flying squirrels (*Glaucomys sabrinus*) to assess whether different habitat associations are generated contingent on sampling method. I found, conditional on sampling method, 2 different space use patterns were identified from the same group of squirrels, and 2 significantly different sets of habitat model input were associated with each. Trap areas were not used post-capture; once enumerated, animals on average (n = 34) spent over 80% of their time from 100 – 200+ m, upwards of 800m, away from trap areas. Using telemetry and fine-grained habitat structure data, I found 33% of sampled squirrels used areas not identified via habitat-stratified trap effort (specifically black spruce habitat). I conclude that wildlife-habitat investigations dealing with fine spatial grain are likely to acquire different results using trapping versus telemetry, especially if animals are relatively mobile and habitat areas relatively heterogeneous.

Introduction

The scale by which organisms perceive landscape structure will characterize their space use. However, a relevant understanding of space use only can be acquired using sampling methods congruent with a study animal’s so-called scale of landscape perception (*sensu*

² This chapter has been published as “Wheatley, M. and K. Larsen. 2008. Differential space use inferred from live-trapping versus telemetry: Northern flying squirrels and fine spatial grain. *Wildlife Research* 35 (5):425-433.” and is reproduced exactly here save for minor editorial differences (e.g., changing “we” to “I”) for the thesis version.

Wiens 1989). Scale is defined ecologically as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner et al. 1989, Gustafson 1998, Dungan et al. 2002, Schneider 2001), the constituents of which are the fundamentals of how we observe ecological systems; grain being the finest level of spatial resolution available, and extent the physical size or duration of an ecological observation (Turner et al. 1989). Observational scale should correspond to a species’ biology or hypothesized grain of habitat perception (Wiens 1989). Because this perception often is uncertain, it is generally described broadly as somewhere between large- or fine-scale or grain, a distinction that is routinely arbitrary, but with significant management implications: this defines the extent and intensity of field sampling used to relate species’ presence to habitat structure. For species operating at finer scales, habitat sampling becomes more intensive (i.e., increased grain, decreased extent), whereas less detailed more extensive habitat sampling generally is adequate for species operating at larger grain. But regardless of scale, similar assumptions must be made: (1) proximate structures surrounding points where animals are observed present are on average indicative of commonly used areas; and (2) bias resulting in animal presence among sampling points is inconsequential. Such assumptions become progressively more important when working at increasingly small grain and extent, particularly in heterogeneous areas or where animal motility promotes frequent inter-patch movement: if unused and used patches frequently are adjacent, sample methods and the exact placement of sampling points in space become highly relevant.

Wildlife-habitat models often utilize linear or logistic regression; the latter used most frequently (see Keating and Cherry 2004 and references therein). These techniques require live-capture data often acquired using baited capture stations along transects or within trapping grids to generate presence-absence indices of space use (see Carey et al. 1999, Lambert and Adler 2000, Bowman and Fahrig 2002, Pyare and Longland 2002, Ball et al. 2003, van der Ree et al. 2003, Gibson et al. 2004, Smith et al. 2004). However, animals do not enter traps without incentive. Bait in the form of food is almost always placed in traps. For instance in North American studies, peanut butter, typically mixed with various seeds, apple, or molasses are the most common mammalian live-capture bait. Often referred to as ‘the pantry effect’, numerical responses of small mammals to

food addition are well known (see Boutin 1990 for a review). Thus, it is conceivable that the presence of bait could translate into biased space use by animals attracted to it from adjacent habitat patches (patch, e.g., Manville et al. 1992), generating spurious relationships between space use and habitat structure. This bias would be especially pertinent for observations acquired at small spatial extents and while determining fine-grain or microhabitat use. Unless habitat is truly homogeneous (a rarity in nature) it is at these small scales where the probability is greatest of animals moving amongst and being (incorrectly) enumerated within different patch types. If a study animal is hypothesized to respond to habitat structure quantified at relatively small grains and extents (often termed micro-site or foraging scales; Moen and Gutierrez 1997, Welsh and Lind 2002, Zimmerman and Glanz 2000, Pyare and Longland 2002, Smith et al. 2004), issues of spatial sampling bias are exacerbated.

Except for sample-grid “edge effect” (Koford 1992, Sullivan and Klenner 1992, Carey et al. 1999) regarding demographic parameters (namely density), issues of spatial sampling bias generally are not addressed when building predictive models (but see Douglass 1988). Where bait bias has been examined (Douglass 1988, Manville et al. 1992), studies either lack replication (e.g., Douglass 1988) or do not report any spatial or temporal component of observation regarding the average distances (i.e. $N > 1$) individuals have traveled to access trap stations, or the proportion of time spent in proximity to the study area. Further, even though an animal is captured in a trap, uncertainty still prevails whether baited capture locations are representative of “used habitat” when compared to areas used by free-roaming unbaited animals. What we lack are spatial and temporal components better describing sample bias pertaining to bait attractiveness; whether bait-related biases occur consistently or “on average”; and over what spatial scales we can expect these biases to manifest.

Scale is arguably the central problem in ecology (Levins 1992), so it is crucial to understand the relative importance to acquired data of scale-dependent parameters, namely: (a) the mobility of the study animal; (b) the spatial time budget of animals in reference to appropriate landmarks (namely baited traps, nests, and natural foraging locations); and (c) patch heterogeneity acquired from quantified differences in habitat structure among used patches. These parameters form explicit biological definitions of an

animal's perception of ecological scale, habitat heterogeneity, and patch size, and provide spatial context to observations used to develop and refine predictive habitat models, particularly among landscapes that differ in patch size, quality, and connectivity. Such data rarely are reported in the literature in a methodological context, yet would afford us greater credibility in evaluating the utility of our sampling methods and the inferential abilities of resulting models.

An on-going study of northern flying squirrels (*Glaucomys sabrinus*) in Alberta, Canada (Wheatley et al. 2005; Wheatley 2007a) facilitated an appropriate examination of these scale-related sampling issues. Northern flying squirrels are considered a keystone species in northern forests (Carey et al. 1999). They inhabit a variety of forest types (Wheatley et al. 2005), are primary prey for nocturnal raptors (Carey et al. 1992), and consume and distribute spores of hypogeous fungi via their feces (Maser et al. 1978; Rosentreter et al. 1997; Wheatley 2007a) influencing both predator numbers and forest-tree productivity. Recently, these animals have been associated to fine-scale forest structure based on logistic regression models examining space use inferred from baited live traps (see Carey et al. 1999; Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005). Given the practical difficulties inherent in studying this nocturnal animal, and the apparent fine scale by which it perceives landscape (Pyare and Longland 2002; Smith et al. 2004; Wheatley et al. 2005), I question whether trapping alone is adequate to infer space use, or whether a more demanding and expensive radio telemetry technique is required to avoid bait biases and develop a meaningful fine-scale wildlife-habitat model. In this study, I use two different techniques acquiring two sets of habitat structure data associated with flying squirrel space use: one from trap-capture sites using baited live traps, and one from nocturnal foraging areas elucidated via radio telemetry. I examine the spatial relationships between trap-capture sites, foraging areas, and nest sites, and I spatially summarize the nocturnal time budgets of flying squirrels in reference to where they were live-captured and where they subsequently spent their time. I then quantify whether trapping versus telemetry produces differences in habitat data sampled from "used sites" over two years of study.

I ask: (1) what is the spatial relationship between baited capture locations, frequented foraging areas, and nest sites? (2) Are capture sites, on average, indicative of space use

and if so, what proportion of time is spent by squirrels in these areas post-capture? And (3) are there differences between habitat structures surrounding trap-capture locations versus known foraging areas? Can trapping versus telemetry result in different model input regarding animal space use and corresponding habitat structure?

Study Area

I sampled in the foothills of west-central Alberta, Canada within 50 km from the townsite of Hinton (53° N, 117° W) along the eastern slopes of the Rocky Mountains. Topography is moderate to steep, ranging from 1200 m to 1600 m ASL. Coniferous, deciduous, and mixed coniferous-deciduous forests (hereafter referred to as *mixedwood*) compose this region. Pure stands of upland lodgepole pine (*Pinus contorta*) are most common, followed by upland mixedwood forest, together forming roughly 70% of the landscape by area. Lowland black spruce (*Picea mariana*) bogs are widespread, and upland white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and poplar (*Populus balsamifera*) forest compose the remainder of the area. Mature stands are approximately 80 to 200+ years of age and are amongst a matrix of naturally burned areas 1 to >50 years of age, and areas of commercial forest management of varying size, intensity, and age (up to 55 years old).

I used available digital forest inventories in GIS (ArcView ver3.3) to generate a list of candidate study sites within 50-km from the townsite of Hinton. In previous research (Wheatley et al. 2005) we found no association between flying squirrel relative abundance and forest tree species, thus candidate sites here consisted of mature forest >70 years of age regardless of leading tree species. I avoided younger regenerating stands where squirrel capture was deemed tenuous *a priori*. Candidate sites had to be large enough to encompass a 1-km trapping transect, sampling methods directly comparable to our previous work with flying squirrels (Wheatley et al. 2005) and using similar trapping methods to other *Glaucomys* studies (Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005). The relatively large size of sample sites ensured they were representative of all forest types described above, encompassing several patch types and heterogeneity in both over- and under-story vegetation. Because my interests in space use were at the individual level, I used transects rather than grids to maximize total unique captures

(Pearson and Ruggiero 2003). I randomly selected sites from the candidate list and trapped each until at least 2 animals per transect were radio-collared (see below). I abandoned sites where no squirrels were captured within 2 weeks of trapping, and randomly selected new sites from the candidate list.

I sampled 10 study areas over two summers (2004-2005): four sites in 2004, and six sites in 2005. The four sites in 2004 consisted of two upland mixedwood areas; one site 50% within upland lodgepole pine and 50% within black spruce; and one site 60% within mixedwood forest and 40% within black spruce. The six sites in 2005 consisted of three upland mixedwood sites dominated by aspen and white spruce and each with 30% black spruce; one lodgepole pine site; one upland aspen site 20% within black spruce; and one upland white spruce site. Nine of the study sites were within 250 m of black spruce areas of at least 5 ha in size. Within all sites understory structure was variable along continua of shrub cover (*Alnus crispa*, *Salix* spp., and *Rosa acicularis*), downed wood, and canopy cover. Sites were at least 5-km apart, and no sites from Wheatley et al. (2005) were used in this study.

Materials and Methods

Live-trapping and radio collaring

All work conducted herein has been approved by the University of Victoria Animal Care Committee (#2004-023-1) and under research permit 11952 approved and issued by the Wildlife Animal Care Committee of the Alberta Fish and Wildlife Division. At each site I established a 1-km trapping transect. Transect start points were located randomly, and transect direction largely was determined by patch shape, such that traps were not placed in adjacent regenerating forest. Traps were placed systematically along transects every 40 m. At each trapping station I placed two live traps (Tomahawk live traps Model #201 or #102, Tomahawk Live Trap Company, Tomahawk, Wisconsin) approximately 20–40 m apart avoiding understory gaps and open patches, but perpendicular to the same side of the transect for a total of 50 traps per transect. I placed traps in trees (2-m high) or on downed logs (probable squirrel runways). Traps were covered with heavy-gauge

polyurethane and filled with cotton batting positioned so it did not obstruct the trap's treadle movement. Ten days prior to trapping, I pre-baited transects every second night with peanut butter. Consistent with published work (see Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005 and references therein), during trapping traps were baited with ~1 g of peanut butter mixed with rolled oats and sunflower seeds. I set traps from 2100h - 2300h, and checked them every 4 hours until 0800h from 10 June – 01 July in 2004, and from 18 May – 30 May in 2005.

I divided radio collars equally among sites by collaring all initial captures within the trapping period regardless of gender, but spaced to minimize autocorrelation such that animal home ranges were unlikely to overlap (approximately 300-600m apart; home-range size estimate; Witt 1992). I collared the initial 2 – 3 animals captured per site, and chose to collar animals based on order of capture, then regarding minimal spatial overlap with other collared animals. Sex-biased trapability was not apparent; roughly equal numbers of males and females were captured with equal trap effort.

Upon capture I fitted each animal with uniquely numbered metal ear tags (Monel #1, National Band and Tag Co., Newport, Kentucky). Using mesh-handling bags I fitted squirrels with collar-fixed radio transmitters (Model PD-2C transmitter, 2.7-g by wt, 2.1-cm crimp-fitted wire collar diameter, Holohil Systems Ltd., Carp, Ontario, Canada). All animals were released at site of capture. Collaring was done before juvenile emergence so that only resident adult squirrels known to be 1+ years of age were followed (note: juvenile phenology was known; as part of this study we collared and monitored juveniles pre-emergence as part of a dispersal project to be reported elsewhere).

Radio tracking

I allowed at least 1.5 weeks for animals to adjust to radio transmitters before sampling. As a fundamental component of my objectives, I halted trapping prior to and during radio tracking activities. Using a radio receiver (Model R1000, Communication Specialists Inc., Orange County, CA, USA) and directional 3-element aluminum antennae, I located animals between 2300h and 0400h by walk-in locations. Animals were followed repeatedly throughout the summer (see below) and upon each initial location I followed animals continuously for 15 minutes in 2004, and for 30 minutes in 2005 recording

multiple consecutive locations per animal (hereafter referred to as a “focal”). I followed animals for at least 10 focals each in 2004 (average 12 ± 0.4 SEM; minimum 150 minutes/animal), and at least 12 focals each in 2005 (average 15 ± 0.5 SEM; minimum 360 minutes/animal). In both years I followed each animal every two to three nights from mid-June until mid August rotating each individual’s sampling by evening time period (2200-0000h; 000-0200h; 0200-0400h). I found squirrels habituated to observer presence within three focals, often gliding within 2 m of an observer to forage or travel: thus, I considered any behavior changes from observer presence negligible and equal among focal squirrels.

During focals I recoded squirrel locations in UTM coordinates using handheld WAAS-enabled Global Positioning System receivers (Magellan SporTrack, Thales Navigation, San Dimas CA USA; Garmin GPS72, Garmin International, Olathe KA USA). I recorded locations only when GPS Estimated Position Error was <7 m, and most often during differential WAAS reception when position error was <3 m. I abandoned focals if satellite coverage was poor (i.e., >7 m). I recorded locations for every movement (tree-to-tree glides) during a focal, verifying location data using geo-referenced orthophotos in GIS, augmented with comparisons to digital coverage of all spatial features (edges, roads, openings, and trails). For each point location I recorded an associated time (in minutes) spent at each point. Because all data collection was nocturnal and through dense forest, I judged 1 minute the most precise unit for any given point location.

During daylight hours I recorded nest locations. Within sampling periods, each squirrel used from 1 to 7 nests (average 2.9 ± 0.22 SEM), so I located nests at least once per week to track changes in nest locations.

Determination of space use

To examine whether trap sites were in proximity to foraging sites, I determined “focal foraging areas” for each squirrel as follows. Using GIS, I generated a scatter plot of all UTM points collected for each squirrel. Corresponding to vegetation plot sizes used in recent flying squirrel microhabitat work (20m radius plots; Smith et al. 2004), I overlaid a 40-m x 40-m grid encompassing all UTM locations. I summed the total number of minutes each animal was observed within each 40-m² cell. I used total minutes and

number of visits to define “focal foraging areas” as cells where a squirrel had returned on >4 separate focals, and within which was spent $\geq 30\%$ of the individual’s total observed time. Within each focal foraging area, I used either the UTM point cluster (if present), or the grid-cell center if points were evenly dispersed as the focal foraging center. To avoid spatial autocorrelation in foraging areas, one of any two adjacent focal foraging areas was randomly dropped. Using GIS, I calculated all straight-line distances among initial capture sites, focal foraging area centers, and nest sites.

To examine what proportion of their time budgets squirrels spent in proximity to capture areas, I summed the proportion of observed time each squirrel spent at varying distances from their initial capture site. I partitioned each animal’s time budget into proportions within 20-m distance intervals (corresponding to vegetation plot radii distance; Smith et al. 2004) from capture sites, summing the proportion of time spent within each 20-m interval for each animal. Zeros were assigned to distance intervals where squirrels were altogether absent. I determined average proportions (% observed minutes) for each interval separately by gender, and also for both genders pooled.

Vegetation Sampling

I sampled environmental variables based on Payre and Longland (2002) and Smith et al. (2004) who used live-capture to suggest flying squirrels are linked to fine-scale forest structure. Around both initial capture sites and focal foraging area centers, I measured: shrub cover (%) and height (cm) by species; downed wood (% cover); canopy closure (% cover); average tree diameter at breast height (DBH); tree species composition (%); and snag and live tree density (stems per ha).

At each capture and foraging point, I established two circular 20-m diameter vegetation plots along the trap transect, one of which physically encompassed the trap/foraging point. Within plots: shrubs were defined as <5 m in height; trees >5 m height and >7 cm DBH regardless of species. Shrub cover and downed wood were estimated in percent cover within the plot circle. Average heights of the two dominant shrubs in each plot were recorded. Tree stems were counted by species, classified live or dead (snag), and DBH was measured (cm) for each. I determined tree species composition and stems per ha as species proportions and total stem counts respectively.

Using a spherical densiometer I determined canopy cover using an average of four readings, 1 facing each cardinal direction from the forage center or trap location. For final analyses, I randomly dropped one of any pair of highly correlated vegetation variables (>0.7 Pearson Correlation Coefficient).

Statistical Analyses

To compare distances between capture, forage, and nest sites (hereafter referred to as the *Distance Metric*), I used a mixed model nested Analysis of Variance (PROC GLM in SAS version 8.02, SAS Institute Inc., Carey, North Carolina, USA). Main factors included Distance Metric (trap-to-forage, trap-to-nest, nest-to-forage), Gender, and the interaction of Distance-Metric-by-Gender. Because there were three different distance metrics per squirrel for both genders, I included a nested random factor of Squirrel-within-Gender which was used as the denominator to calculate appropriate F-ratios regarding fixed and random factors (Gotelli and Ellison 2004). To compare time budget data among years and genders, I used a three-factor ANOVA (PROC GLM in SAS) with Year, Gender, and Distance Category as main effects. Thus, for this comparison the factor of interest is the three-way interaction of Year by Gender by Distance Category. For all ANOVAs alpha was set at a traditional 5%.

To graphically explore vegetation data acquired from trap versus focal foraging areas, I used Correspondence Analysis (CA; Legendre and Legendre 2003). On the resulting bi-plot I calculated 75% confidence ellipses around separate treatment groups of “traps” and “focal foraging areas,” with passive environmental variables showing strength and direction of vegetation components separating plots. To statistically compare whether vegetation around trap-captures differed significantly compared to vegetation around focal foraging areas, I used Multiple-Response Permutation Procedure (MRPP; McCune and Grace 2002). Because I compared differences within a multi-variant relationship among 85 sample plots, natural variation was predicted to be relatively high. Thus, for this comparison I set MRPP alpha less conservatively at 10%. I chose this alpha for its common use in conventional statistics, while allowing for a reduced type II error (Zar 1999). Here, a true difference among means is implied where significant differences are reported; however, I provide exact P-values so readers may judge probabilities relative to

their own standards of significance. All CA and MRPP analyses were done in PC-ORD (version 4.3; McCune and Grace 2002). Bi-plot ellipses were calculated using R, package *vegan* (www.r-project.org).

Results

For two summers I followed a total of 34 individual flying squirrels: 21 males and 13 females. I followed seven females and nine males in 2004 each for at least 150 minutes over 10 – 15 focals (average 12 focals ± 0.4 SEM), and six females and twelve males in 2005 each for at least 360 minutes over 12 – 17 focals (average 15 focals ± 0.5 SEM).

Spatial relationships: forage, nest, and capture sites

Average straight-line distances between trap-capture stations, nests, and focal foraging areas extended further for males than for females (Figure 3-1), but distances were not statistically different between genders (nested ANOVA; Gender $F_{1,32} = 2.45$, $P = 0.13$). From the nest, animals traveled furthest to reach trap-capture sites relative to natural foraging areas, with travel distances upwards of 526 m (max. nest-to-trap distance) and 705 m (max. forage-to-trap distance). Animals traveled the shortest distances between nests and forage areas, on average some 45-55 m closer than nest-to-trap distances (Figure 3-1). Some nest and forage sites were by chance within 8 m and 64 m of trap locations respectively (minimum distances observed) resulting in relatively large variability about the means, and no statistical differences among individual distance metrics between genders (nested ANOVA, Distance Metric x Gender $F_{2,32} = 0.10$, $P = 0.90$) or when pooling genders (nested ANOVA, Distance Metric $F_{2,32} = 0.67$, $P = 0.52$). The furthest distances were traveled to reach non-natural landmarks (traps).

Spatially-explicit time budgets

Once enumerated in traps, both male and female flying squirrels spent less than 2% of their time on average within 20 m of the trap-capture site, and spent $\geq 80\%$ of their time 100-m+, and upwards of 780 m, away from the site of first capture (Figure 3-2a and 3-2b). Males traveled on average longer distances than females to access traps (i.e. >620 m;

Figure 3-2a and 3-2b), with a maximum distance from a respective trap site of 888 m for males versus 589 m for females, evident in the longer right skew of the male's versus the female's time-by-distance plot (Figure 3-2a and 3-2b); however, this was not statistically significant (ANOVA, Year x Gender x Distance Category $F_{39,1199} = 0.853$, $P = 0.726$). Because of this similarity, these data were pooled to reveal a similar pattern (Figure 3-2c): trap-capture sites were not considered "used habitat" post-capture.

Vegetation structure comparisons

When comparing habitat structure surrounding trap versus foraging areas, similar trends were observed in both 2004 and 2005 (Figure 3-3, white versus dark symbols), but trends within each year alone were not statistically significant (MRPP, alpha = 10%, probability of a smaller or equal delta $P = 0.24$ for 2004; $P = 0.57$ for 2005). Because similar trends were observed among years, I pooled these data. Upon pooling, differences between vegetation structures around trap versus foraging areas became statistically significant (see below). No differences were found in habitat structure associated with males versus females (MRPP, alpha = 10%, probability of a smaller or equal delta $P = 0.29$). Because the same trend was visible among years, I present one correspondence analysis pooling both years and genders (but see Schooley 1994).

In the correspondence analysis, together axis one and two (Figure 3-3) explained 56% of the variability in vegetation structure among plots. Axis one accounted for 40% of the variation while axis two explained 16%. Environmental variables accounting for the most variability and separating the treatments of trap versus forage areas included black spruce trees, willow shrub cover, tree-sized willow, and alder shrub cover. Because these variables plotted equidistant from both axes, environmental gradients among areas are best explained using both axes one and two. An additional 11% variability was explained along axis three; however axis three included similar explanatory variables from axes one and two (e.g. tree-sized willow), so axis three is not considered herein.

Trap-capture areas were more clustered in ordination space relative to foraging areas (Figure 3-3). They clustered close to the plot origin, along a gradient from upland spruce and aspen forests with low *S. canadensis* shrub cover (to the left of axis one), to lodgepole pine forests with dense alder shrubs (to the right of axis one). Little separation

of trap-capture areas occurred along the second axis, reflected in the relatively small 75% confidence ellipse for trap-capture areas. Operationally, animals were captured only within forest stands characterized as coniferous or deciduous upland forests.

Comparatively, focal foraging area plots clustered less, showing more variability in ordination space. One environmental gradient absent from trap-capture plots is apparent in foraging plots; namely a gradient from upland forest to lowland black spruce forest, characterized by dense black spruce trees, thick willow shrub cover, increased tree density, increased snag density, and higher volumes of CWD (from the origin to the top right of Figure 3-3). Because of this black spruce gradient, the 75% confidence ellipse for focal foraging areas is relatively large. This gradient represents 11 separate squirrels consistently foraging in black spruce areas (33% of sampled animals; six from 2004, and five from 2005). Because of this, I found a significant difference between the vegetation surrounding capture locations versus foraging areas (MRPP, alpha = 10%, probability of a smaller or equal delta $P = 0.10$). The use of lowland black spruce habitat was only identified from telemetry-based foraging data.

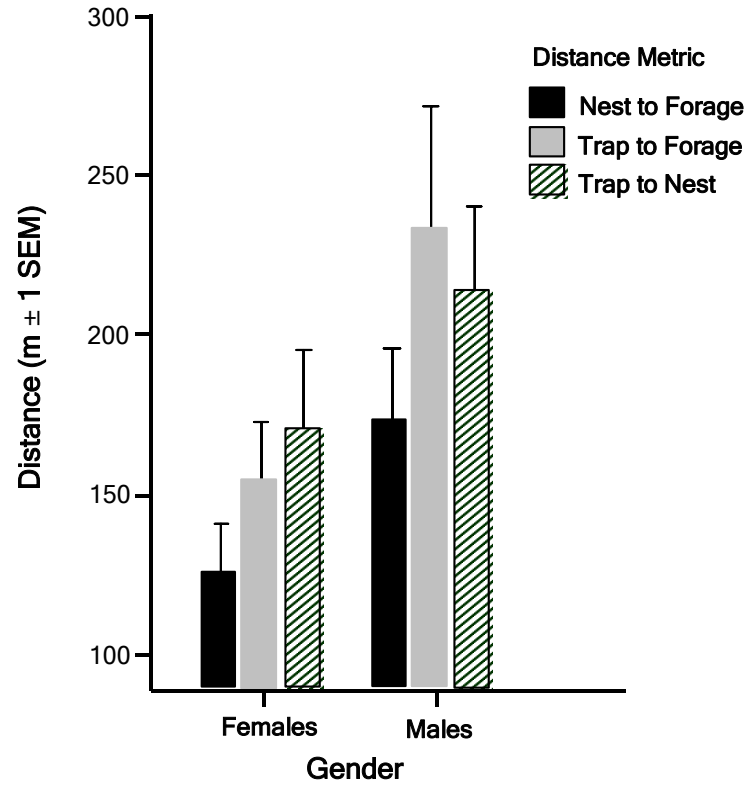


Figure 3-1. Average distances (± 1 SEM) between trap-capture sites, nest sites, and focal foraging areas for northern flying squirrels near Hinton, Alberta, Canada.

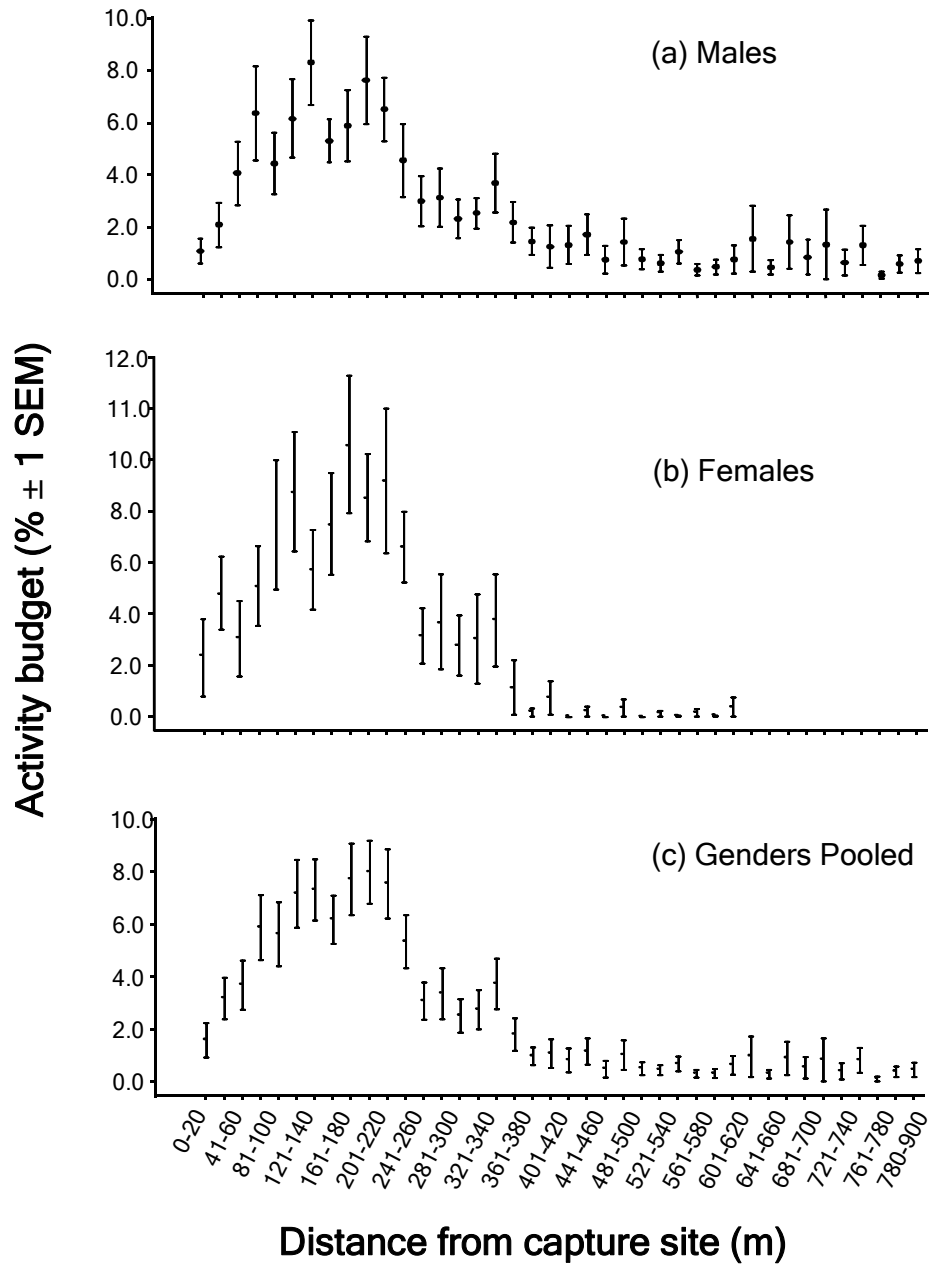


Figure 3-2. Average proportion (± 1 SEM) of flying squirrels' post-capture nocturnal activity budget spent at different distances from the capture site as determined via walk-in radio telemetry observations. For each distance category, $n = 21$ for (a) males, $n = 13$ for (b) females, and $n = 34$ for (c) genders pooled.

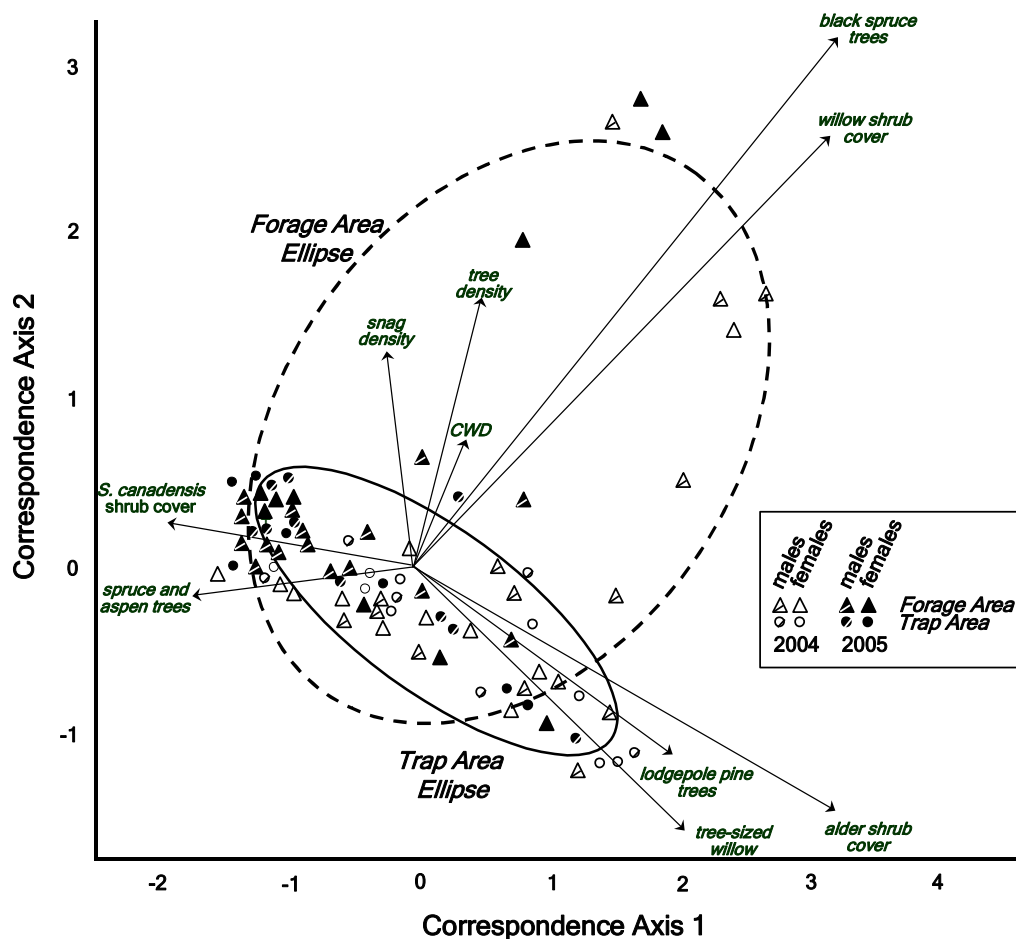


Figure 3-3. Correspondence analysis of vegetation structure at trap-capture stations (circles) and at focal foraging areas (triangles) over 2 summers (white versus black) for northern flying squirrels near Hinton, Alberta, Canada. Confidence ellipses (75%) are plotted for the two groups as well as passive environmental variables (arrows) to show the strength and direction of environmental gradients among plots in ordination space. Sample sizes are $n = 34$ trap-capture stations and $n = 51$ focal foraging areas.

Discussion

Using fine-grain habitat data, I identified one used-habitat gradient from radio telemetry absent from trapping data, representing one-third of radio-collared animals, and effectively generated two statistically different sets of candidate model input. As such, I suggest use of data from baited live-traps versus radio tracking could produce different inferences regarding fine-scale space use for any habitat selection analysis, and the

magnitude of this difference will necessarily depend on the relative habitat heterogeneity of the study area and inter-patch movement abilities of the study animal.

I argue my results are not simply an artefact of sampling invasiveness. It is conceivable squirrels might have avoided trap areas post-capture in favor of areas with less human interaction further from trap lines. However, I found squirrels to habituate to human presence during telemetry within the first 3 focals, often foraging and traveling within meters of observers. When I removed radio transmitters, I caught most collared squirrels in the same traps where they were initially handled and collared, which I interpreted as a learned behavior whereby squirrels returned to known food locations during trap sessions. Spatial aversions to handling sites were not evident. Further, I found no instances where data collected during the first 3 focals were spatially anomalous forming peripheries or outlier areas within final data sets, giving me little reason to suspect avoidance of either trap areas or observer presence post-capture.

Similarly, my results are not an artefact of an unstratified trapping bias. One-third of my focal squirrels used black spruce habitat, yet even though I trapped within this habitat type, I did not catch squirrels there; possibly implying either patch adjacency effects in trapping, or habitat-specific trapability. At least one-fifth of my traps were completely within black spruce roughly in accordance to habitat availability, so there were no clear deficiencies in trap stratification. If considering even larger spatial extents, nine of the 10 study sites were within 250 m of black spruce areas suggesting squirrels were lured from these areas into baited traps (Figure 3-2), implying a habitat-adjacency effect in trap captures. Pyare and Longland (2002) related flying squirrels to fine-grained habitat structure within 10 m of traps (similar to Smith et al. 2004 and Smith et al. 2005) and describe their sampling grids adjacent to second- and old-growth habitat patches, similar in context to my trap-capture sites being in proximity to black spruce. Their traps could have lured animals from other patch types similar to what I have observed here. In the same way, patch adjacency might also account for the lack of association between habitat type and flying squirrel relative abundance found by Wheatley et al. (2005), though their use of increased spatial extents reduced the spatial relevancy of trap placement and patch adjacency in general. My results could suggest habitat-specific trapability whereby traps are either avoided or somehow not noticed by squirrels in black spruce, but I lack data to

explore this. Habitat-specific trapability would be a complex interaction of habitat structure and possibly predator densities (among other factors).

Although I used transect sampling, I suspect similar results would be obtained using grid sampling too. Differences between transects versus grids are not commonly reported, but known differences include that transects capture more individuals (Pearson and Ruggiero 2003) and sample more community diversity than grids (Steele et al. 1984; Pearson and Ruggiero 2003); whereas grids sample traditional demographics (density, dispersion, home ranges, etc.) better than transects (Bujalska 1989). Because of their length and shape, transect will sample more habitat heterogeneity, including a greater diversity of microhabitat (as sampled here), better than grids. Here, I used transects to maximize the number of individuals captured per trap effort across as much habitat diversity as possible while controlling for spatial independence among individual collared squirrels. That said, it remains to be tested whether results similar to mine would be acquired using trapping grids. For trapping-grid studies, avoiding spatial autocorrelation among individual animals would essentially require a single trapping grid per non-overlapping home range. I know of no such study. Further, published studies (Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005) have sampled multiple animals within grid sizes corresponding to single-squirrel home ranges (1.5 ha to 14 ha; Cotton and Parker 2000; Witt 1992; Menzel et al. 2006), precluding proper study designs to examine these questions (i.e. no spatial independence among observations). Trap encounter rates per squirrel would be higher on a grid, and perhaps by chance food (bait) availability on grids with higher trap densities might be more congruent with natural movement patterns of sampled squirrels, resulting in lower movement distances than those reported here. However, issues of spatial independence cannot be set aside, and similar questions remain; namely how far have animals traveled to reach these traps, and are traps placed in areas the animals would normally use? Answers to these questions have remained almost entirely uncertain for both transects and grids.

Live-trapping and radio tracking both have biases and practical limitations. Radio tracking is labor-intensive, often imposing operational constraints on sample size, locations per animal, observation independence (but see De Solla et al. 1999), and statistical power. Location accuracy can be habitat or terrain specific (North and

Reynolds 1996; D'Eon et al. 2002), or too low when using indirect techniques such as triangulation (Nams 1989; Samuel and Kenow 1992), particularly when telemetry error exceeds the average grain size of habitat patches (White and Garrott 1986; Nams 1989). More notably, to avoid bait-related biases in space use, trapping must cease during radio tracking, thus reproductive activity cannot sufficiently be monitored, and space use cannot be linked to habitat quality (i.e., reproduction, survival, and resource availability; Van Horne 1983, Wheatley et al. 2002). Nonetheless, for species whose general habitat associations are unclear and likely fine-grained, a precise telemetry program augmented with scale-appropriate habitat characterization forms an important initial pattern-seeking step towards reliably documenting space use.

Comparatively, to infer space use via live-trapping, one requires careful consideration of sampling effort and spatial bias. Traps must be placed systematically among habitat types adequately sampling the biotic community, and spaced according to the landscape mobility of the target species: something we often know little about *a priori* (e.g. data such as Figure 3-2 herein). Habitat heterogeneity, and thus trap placement, becomes increasingly important as extent decreases and finer-grained habitat structures are considered. Unfortunately, analyses examining how variation in habitat variables changes from large to fine grain or scale (e.g. Johnson et al. 2004) are not widespread, and confined primarily to the jargon of the geographical and remote-sensing sciences (e.g. Wu 1999; Saura and Martinez-Millan 2001). If bait causes a numerical response (pantry effect), the distance animals travel to enter traps, and whether traveling associates them with otherwise unused space, is an important source of bias, especially when using linear transects or where sample-grid edge effect is a concern. Inversely, bait availability could inhibit animal movement, encouraging animals to stay within trapping grids, and may be (incorrectly) interpreted as decreased space use. Movement, home range size, or dispersal distances inferred via live trapping (e.g. Dobson 1979; Clout and Efford 1984; Ellis et al. 1997; Ransome and Sullivan 2003) could be misleading if a bait-based spatial bias lured otherwise dispersed animals back to trapping areas for further enumeration. In this study, trapping lured animals in from distances beyond the sampled stand, habitat-specific trapability appeared evident, and trapping alone failed to detect significant portions of space use.

The choice of sampling method used to relate animal presence to habitat structure should be influenced primarily by the spatial grain and extent of the target species' movement characteristics, and necessarily related to the grain of hypothesized "used" habitat structure. As finer-grained habitat components are considered, precisely where animals are located in space becomes increasingly important, spatial bias in sampling must be minimized, and more precise methods must be considered. A sampling program based solely on live-capture may not be sufficient, if not entirely misleading. Regardless of how many habitat variables can be generated from GIS, even analyses using multiple spatial extents and a correctly stratified design will fall short if sampling methods are not congruent with the extent and grain of interest. Unfortunately, without detailed and extensive vegetation sampling, this often is not possible below a certain inherent grain of habitat structure, and it is below this grain that these issues truly become relevant. As researchers venture further into spatial analyses where habitat variables can be quantified *ad libitum* using GIS and high-resolution remote sensing (e.g. laser-based LiDAR; Lim et al. 2003), careful attention must be given to sampling bias and exactly how animals are located, especially when considering fine habitat grain and small spatial extents.

Chapter 4 Domains of scale in forest landscape metrics: Implications for species-habitat modeling.³

Abstract

Observational scale defines the field-of-view used to quantify any set of data, and thus has profound implications on the development and interpretation of species-habitat models. However, most multi-scale studies choose observational scales using criteria unrelated to how metrics quantify along the scale continuum; scale choice is either arbitrary or via orders of resource selection irrespective of potential among-scales differences in mean or variation. Here, I use GIS to examine these issues for 9 forest-landscape metrics across 15 observational extents (while holding grain constant) and demonstrate how associated averages and variation change markedly and unpredictably across observational scale continua, emphasizing that *a priori* selection of 2 “different” scales cannot be done intuitively, arbitrarily, or based on orders of resource selection. Evaluation of the scale-domain continuum is a critically absent step in the building and interpretation of all multi-scale ecological models.

Introduction

Collection and interpretation of ecological data is largely a function of scale. There are now no shortages of multi-scale studies in the ecological literature (e.g., Slauson et al., 2007; Graf et al., 2007; Limpert et al., 2007; Benson and Chamberlain, 2007; Yaacobi and Rosenzweig, 2007; Coreau and Martin, 2007; Thogmartin and Knutson, 2007; amongst others), and particularly abundant are those focusing on wildlife-habitat modeling (see Wheatley and Johnson, 2009 for a more thorough review). But, finding ones that address the fundamentals of “the scale issue” (Marceau, 1999) as it pertains to these models and their subsequent predictions is difficult. In ecological modeling, these fundamentals are essentially twofold: 1) the choice of appropriate observational scales

³ This chapter has been published as “Wheatley, M. 2010. Domains of scale in forest landscape metrics: Implications for species-habitat modeling. *Acta Oecologica* 36: 259-267” and, save for minor editorial changes to figure sizes, is reproduced in published form herein.

and the quantitative implications of these choices, and 2) designing studies that progress our ability to extrapolate pattern and process among scales (e.g., Turner et al., 1989; Jarvis, 1995). Both of these issues are discussed in some detail by Wiens (1989) who framed them in terms of domains of scale, which are “portions of the scale spectrum within which process-pattern relationships are consistent regardless of scale” (p. 392; Fig. 4 in Wiens, 1989). When addressing scale in ecology, and particularly in landscape ecology where we quantify landscapes over multiple spatial scales (mainly using Geographical Information Systems (GIS); e.g., Hatten and Paradzick, 2003; Weir and Harestad, 2003; Fisher et al., 2005; Wheatley et al., 2005), identifying scale domains should be fundamental to the design and interpretation of resulting predictive models. To do this, however, requires an empirical summary of a metric’s behavior (i.e., means and variance, or medians) along a sufficient span of the scale continuum, including a wide range of potential observational scales. Yet, researchers largely choose observational scales arbitrarily or using constructs entirely removed from any metric’s scale continuum; namely Johnson’s (1980) orders of resource selection. I argue herein why this is detrimental to our interpretation of predictive ecological models, especially those quantifying wildlife-habitat relationships.

Though treated rarely in ecology, explorations into scale can be traced back to the geographical sciences (for historical context see Gehlke and Biehl, 1934 and Yule and Kendall, 1950), specifically the Modifiable Areal Unit Problem (MAUP; Openshaw and Taylor, 1979; Openshaw, 1984; Jelinski and Wu, 1996). Whenever we address scale in ecology, we are in essence addressing the MAUP, which states that the spatial distribution of variables or their level of correlation in space can be entirely modified according to their level of aggregation; or more generally, the field of view used to collect and present spatial information. In ecology, this field of view is generally termed “observational scale” (e.g., Heneghan and Bolger, 1998; Jost et al., 2005). The size or resolution of observational scale defines what is included or excluded in our analyses, whether this is the number of animal observations, or the relative proportions of different habitat types, or the level of heterogeneity we choose to include within the extent of our data. When discussing scale, ecologists have adopted the terms “grain and extent” (Gergel and Turner, 2002; Mayer and Cameron, 2003), but these are just components of

the MAUP: sampling a bigger area with less detail is different than sampling a smaller portion of the same area with more or less detail. In other words, the size of one's sample plot or study area (extent), in combination with sampling intensity (i.e., level of detail; grain or time span) defines resultant values and associated variation for both dependent and independent variables. In theory, relatively incremental changes in either grain or extent should not produce drastic changes in these values; hence the idea of domains of scale (Wiens, 1989) or areas of no appreciable change along the scale continuum. It follows for multi-scale studies, therefore, that an examination of domains of scale vis-à-vis observational scale choice along this continuum should form a key step in the collection and interpretation of ecological data. This is particularly important in ensuring redundant models are not built on the same domain and incorrectly interpreted as different models on different scales (e.g., Fig. 4-1). Yet, this practice has been entirely overlooked. Wildlife-habitat research is a good field within which to highlight approaches to multi-scale studies. Because study taxa are mobile and range over multiple scales, this field of study has produced more multi-scale studies than most, including the geographical sciences (Wheatley and Johnson 2009).

What are the prevalent methods for observational scale choice in wildlife research? There are two common approaches. In the first, an initial scale is chosen usually based on something biological (home-range size, movement distance, etc.; e.g., Pedler et al., 1997; Hall and Mannan, 1999; Naugle et al., 1999; Terry et al., 2000; Gabor et al., 2001; Bond et al., 2002; Wheatley et al., 2005; White et al., 2005; amongst others) with 2 other scales selected such that one is above and one is below the first scale; often termed the landscape and the micro-site respectively (e.g., Moen and Gutierrez, 1997; Welsh and Lind, 2002; Zimmerman and Glanz, 2000). The second approach employs Johnson's (1980) orders of resource selection (e.g., Mace et al., 1996; Santos and Beier, 2008; Deppe and Rotenberry, 2008; Kittle et al., 2008; Tucker et al., 2008; amongst others), whereby observational scales are based upon the first through fourth hierarchical orders of resource selection; corresponding to feeding items, core-use areas, home ranges, and geographical distributions respectively. Habitat is quantified and predictive models are built at each chosen scale and conclusions are made regarding a species' multi-scale response to habitat.

In the context of ecological scale (*sensu* Wiens, 1989; also see Turner et al., 1989) these approaches have critical flaws potentially affecting our understanding of multi-scale wildlife patterns, if not wildlife-habitat relationships in general. None of these approaches formally recognize the scale continuum; that is, the empirical behavior in both mean and variation of an observed metric (dependent or independent variable) amongst a series of consecutive observational scales (grain, extent, or time). An understanding of the quantitative scale continuum implies a researcher has evidence-based rationale behind selecting two observational scales purported to be different. To do this implies an understanding of a metric's domains of scale. Current scale-selection methods deal only in absolute categories that are chosen either arbitrarily or based upon "fundamental units" (namely orders of resource selection) that are entirely removed from any examination of the scale continuum for any measured metric. Academically these are phrased as accounting for different hierarchical levels of ecosystem processes (Allen and Starr, 1982; O'Neill et al., 1986), but in reality none offer empirical validation behind observational scale choice. What if a researcher naively chooses observational extents that are all within the same scale domain? If so, and in the context of wildlife-habitat modeling, the habitat features measured would all be consistent from the micro-site to the landscape regardless of observational scale (Fig. 4-1). How might this affect subsequent model interpretation, particularly if we assume *a priori* based on constructs unrelated to the scale continuum that we are choosing *de facto* different observational scales, but in fact are not (i.e., naïve scale selection; Fig. 4-1)?

Given the current abundance of multi-scale wildlife studies published to date, it is interesting that not a single study has interpreted or evaluated cross-scalar models in a domain-of-scale gradient context by using scale continua. Even an initial evaluation of scale continua might give insight into ecological processes. A species' "selection" elucidated through multi-scale wildlife-habitat predictive models may simply represent "habitat coping", whereby animals are not selecting as much as simply dealing with the habitat-scale continuum, where their movements or densities (for instance) are more consistent with context-specific landscape physiognomy such as habitat gaps, or min-max values of patch sizes. To know this, however, we must examine the habitat-scale continuum for scale domains. What might domains of scale look like for wildlife-habitat

metrics, and how might we identify them *a priori* in the context of predictive modeling?
 Can variation alone separate 2 scale domains or provide insight into model interpretation?

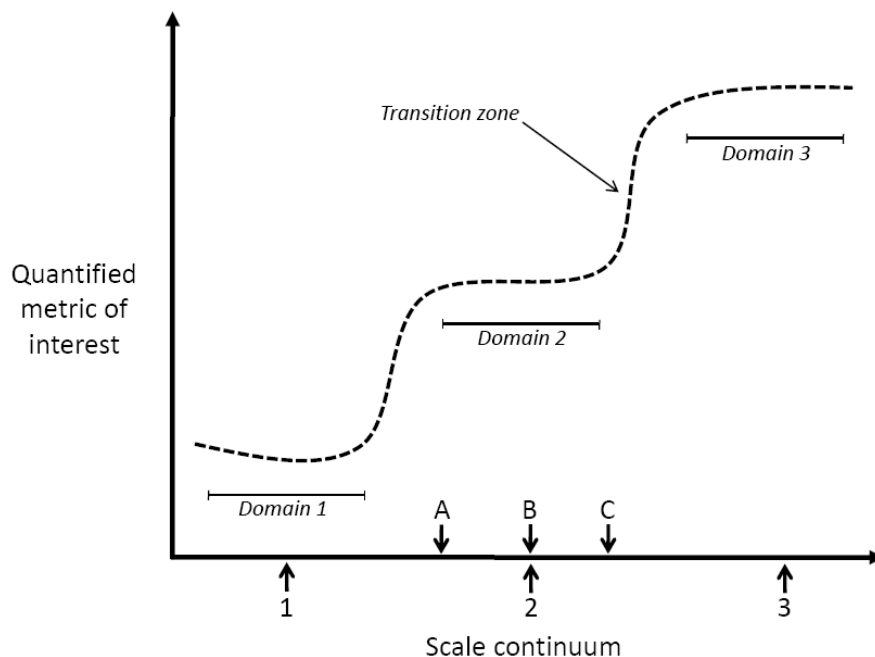


Figure 4-1. Informed versus naïve selection of observational scales for a multi-scale ecological study. If a researcher is interested in examining whether dependent variables respond differently among multiple scales, it becomes sensible to know whether variables are in fact being quantified among scales that are known to be different. An informed selection of scales (shown above as the numbers 1, 2, and 3) implies the researcher understands how a metric of interest changes (or doesn't change) along the scale continuum. A naïve selection of scales (shown above as the letters A, B, and C) implies the opposite whereby observational scales are chosen based on criteria removed from the scale continuum, commonly orders of resource selection or entirely arbitrary means. In the most parsimonious case (i.e., a univariate model), building and comparing naïve models built on scales A, B, and C would essentially result in comparisons of the same model among the same observational scale, which fundamentally corrupts the final interpretation as the researcher incorrectly assumes different scales were examined and concludes there is no effect of scale for the process being studied.

Though unapparent in the wildlife literature (and perhaps in the ecological literature in general), these ideas are neither particularly novel nor new. Wiens (1989) is arguably one of the most cited papers in contemporary ecology (cited 1391 times as of 2009 according to Web of Science) but ironically there is an entire absence of studies suggesting what an operational domain of scale might look like, let alone how ecologists might identify or quantify one domain from another (but see Nams et al., 2006). Geographers and landscape ecologists might argue the identification of scale domains is a developed topic (e.g., Wu, 1999; Hay et al., 2001; Saura and Martinez-Millan, 2001; Wu et al., 2002; Saura, 2004; Wu, 2004), forming a branch of their science exploring pixel sizes, map scales, and minimum map units (to name a few); however, application (or lack thereof) of this concept in ecological modeling suggests otherwise. For instance, scale-specific examinations of landscape metrics (e.g., Wu et al. 2002; Wu 2004) have yet to report scale-specific variation along a scale continuum. Along with mean values, associated variation largely defines whether 2 measurements (i.e., scales) are different, so without examining variance an assessment or interpretation of scale domains is not possible. Despite the widespread use of multi-scale designs in ecology, we still lack basic empirical insight into some fundamentals of scale. It has been suggested that a science of scale be established (Goodchild and Quattrochi, 1997; Peterson and Parker, 1998; Marceau and Hay, 1999), and that remote sensing and GIS be used as powerful tools for studying scale effects (Meentemeyer and Box, 1987; Marceau and Hay, 1999). A full science of scale should seek answers to the following interrelated questions regarded as the basic components of the scale issue (from Goodchild and Quattrochi, 1997): (a) the role of scale in the detection of patterns and processes, and its impact on modeling; (b) the identification of domains of scale (invariance of scale) and scale thresholds and the proper methods with which to delineate among domains; and (c) scaling, and the implementation of multi-scale approaches for analysis and modeling.

What follow is an examination of the first two points above, specifically to identify cross-scale patterns and their variance structures and to determine whether domains of scale are apparent for common landscape metrics (and typical wildlife-habitat metrics) for the forested areas in the foothills of Alberta, Canada. I first develop a visual representation of average values and associated variation for landscape metrics across a

scale continuum of observational extents. I then use a multiple-comparisons technique to define domains of scale for each metric. I also question whether scale breaks are simply artefacts of observational extent or inherent landscape characteristics, and I offer insight into the interpretation of cross-scale metric plots, something I argue should be fundamental to multi-scale ecological studies. Herein I deal only with observational extent; however, the same concepts apply for changes across observational grain or time, and their associated scale continua.

Materials and Methods

I quantified landscape metrics from a 1-million ha forested area in the foothills of Alberta, Canada (Fig. 4-2), corresponding to the administrative boundaries of a long-standing provincial Forest Management Area. Centered on the townsite of Hinton, Alberta (53° N, 117° W), ecological details of the study area can be found in Wheatley et al. (2002, 2005) and Wheatley (2007a, 2007b). Recent (c. 2001) digital forest inventory exists for the entire 1-million ha area (Fig. 4-2); save for municipalities, industrial mine sites, and provincial protected areas (blank areas in Fig. 4-2). Because it is management-based, this inventory is relatively detailed, derived and digitized from aerial orthophotography with minimum polygon sizes of <0.5 ha.

Landscape metrics

I selected a suite of metrics of broad relevance to resource managers, including metrics commonly reported in the literature and employed in natural areas management, but specifically those most relevant to forest management and wildlife-habitat modeling (Table 4-1). My intent was to include metrics based on both spatial and non-spatial forest patch characteristics; the former structured by polygon area and perimeter, the latter by within-polygon forest metrics. There are no existing hypotheses suggesting how either of these two metric types should scale, so they were both included herein.

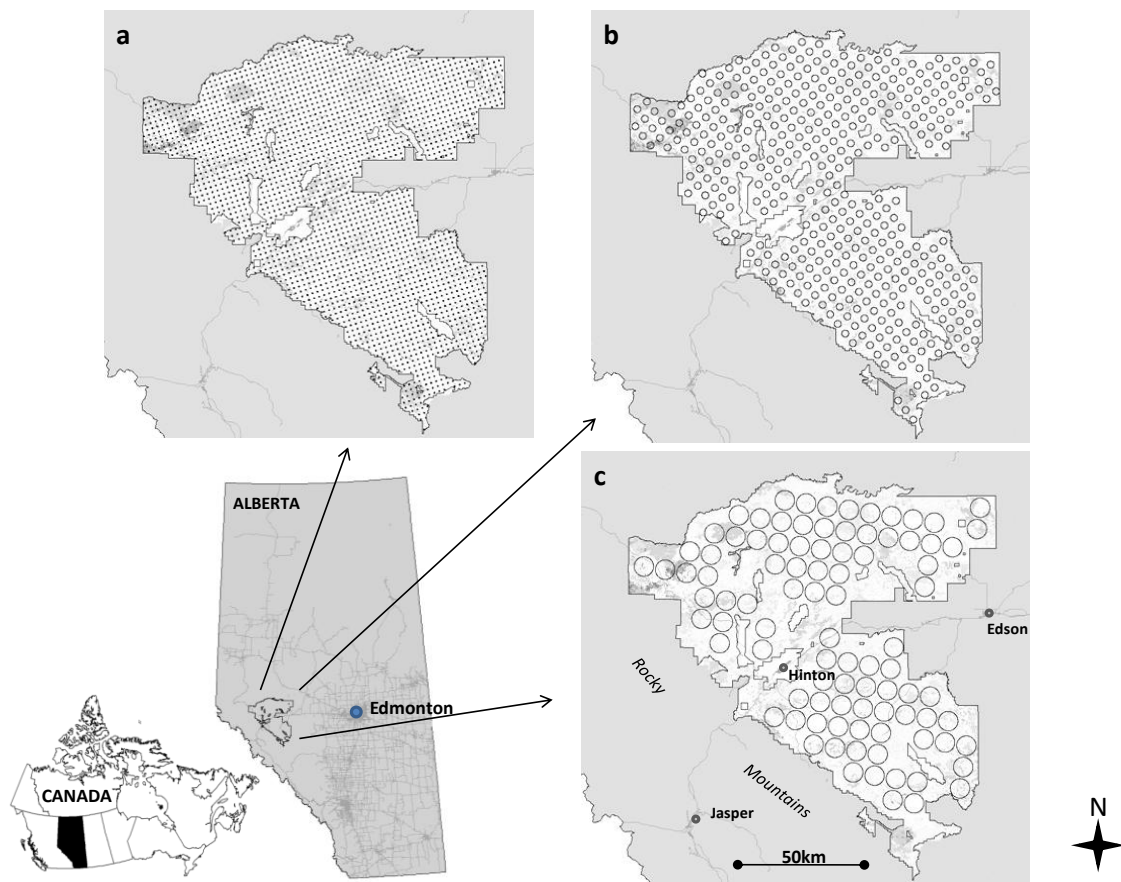


Figure 4-2. Location of study area in west-central Alberta showing examples of (a) 16ha; (b) 512ha; and (c) 8192ha sampling plot designs. Because of data un-availability for certain sites, delineated white zones were excluded from the study (protected areas, municipalities, and mine sites). Grey lines within each map are primary roads and highways.

Table 4-1. Definitions of landscape metrics quantified in this study.

Metric	Description
Gap density (#/ha)	Total number of gaps within each sampling area, divided by the sampling area. Gaps were defined as non-forest (e.g., roads, clearings, cutblocks, seismic, water, etc.) plus harvested areas with regenerating trees ≤ 1 m height.
Gap size (ha)	Total area of gaps divided by the number of gaps within each sampling area.
Patch size (ha)	Total area of unique patches (including gaps) divided by the number of unique patches within each sampling area.
Patch density (#/ha)	Total number of unique patches (including gaps) within each sampling area, averaged over all sampling areas within each scale.
Patch age (yrs)	Sum total of all non-gap patch ages divided by the number of non-gap patches within each sampling area.
Patch height (m)	Sum total of all non-gap forest patch heights divided by the number of non-gap patches within each sampling area.
Mean shape index	A measure of shape complexity. Sum of each patches' perimeter divided by the square root of its area, divided by the number of patches (McGaril and Marks 1994).
Perimeter-to-area ratio	A measure of shape complexity. The sum of each patch's perimeter/area ratio divided by the total number of patches in a sampling area.
Fractal dimension	Equals 2-times the logarithm of patch perimeter divided by the logarithm of patch are. A fractal dimension greater than 1 for a 2-dimensional patch indicates a departure from Euclidean geometry (i.e., an increase in shape complexity).

Observational scale and sample size

I define scale as “spatial extent” and hold grain constant throughout (but see Dungan et al. 2002 for further detail on scale definitions). I use observational extents ranging from 0.5 ha upwards to 8192 ha in size. I selected the lower limit of extent size (0.5 ha) based on minimal size of map units. The largest extent was determined based on sample size; with a maximum extent of 8192 ha, only 34 spatially independent plots can fit within the study area (Fig. 4-2, panel c), and this was initially considered a lower limit for plot sample size. Extents chosen in between were simply multiples of 2 (0.5, 1, 2, 4, 8...8192).

Plot sampling

Using Avenue Script in GIS (ArcView 3.3), I spaced circular sampling plots systematically throughout the entire study area (Fig. 4-2). Sample-plot size corresponded to the chosen observational-extent sizes. Starting points were selected randomly and sampling-plot edges were at least 3km apart chosen to be greater than single forest-patch widths. Plots were spaced in a square pattern directionally oriented using a randomly selected compass bearing. Using this method the total number of plots varied, thus I randomly selected $n = 100$ for use in metric summaries. This subsampling ensured equal sample sizes among observational extents.

Metric quantification and domains of scale

To quantify forest metrics, I selected all forest polygons that wholly or partially fell within any given sample plot. Selected polygons were then clipped such that only the portions within the sampling plots were retained. Once clipped, both the area and perimeter of all captured polygons were recalculated. In essence, this recalculation is what defines the metrics for each extent, and is also the foundation of the MAUP. Metrics were generated using a combination of spatial analysis routines (written based on ArcView v3.x Spatial Analyst) and the Regional Analysis function of Patch Analyst, an extension to ArcView available on-line (<http://flash.lakeheadu.ca/~rrempel/patch>). The final metrics are presented as overall averages, all with $n = 100$ plots (save for the 2

largest scales, see above), and with associated variation in standard deviations also plotted for each spatial extent.

A formal quantitative definition for a Domain of Scale has yet to be proposed. Initially my intent was to base domain breaks on standard analysis of variance (ANOVA) with an associated post-hoc multiple comparison (e.g., LSD) whereby significant differences among scales in mean values were to represent different domains of scale. However, variation for all metrics quantified herein was strongly associated with scale, thereby violating a basic assumption of parametric statistics, namely homogeneity of variance among groups. Thus, I first conducted a non-parametric ANOVA (Kruskal-Wallis; KW) to determine whether differences existed among observational scales for each metric. For those with significant overall group KW tests, I determined domains of scale based on multiple non-parametric KW comparisons among all potential combinations of observational scales for each metric. To account for experiment-wise error of multiple statistical tests, I used a Bonferroni alpha correction for 105 comparisons per metric and an initial alpha of 5%, resulting in alpha being set at 0.04% (i.e., significant tests had $P < 0.0004$). According to these tests, extents that were statistically similar were grouped as being within the same domain of scale (parametric LSD post-hoc methods rendered similar results).

Results

I measured nine landscape metrics over 15 spatial extents. Of these, the two metrics patch age and patch height did not scale and had a single domain from the smallest to the largest spatial extent (non-significant overall KW comparisons; patch age $\chi^2 = 14.1$, $df = 14$, $p = 0.440$; patch height $\chi^2 = 19.3$, $df = 14$, $p = 0.151$). Six metrics had at least three domains of scale, some upwards of nine domains (Fig 4-3; gap density, gap size, mean shape index, patch size, patch density, and perimeter-to-area ratio; significant overall KW comparisons all with $p < 0.001$). Domains of scale in these six metrics were defined as observational scales that were statistically unique and did not transition in terms of similarities to scales either above or below on the scale continuum. That is, unique domains had only single lowercase letters (see Fig 4-3). I refer to scales with double lowercase letters (see Fig 4-3) as “transition zones” (sensu Weins 1989, Fig 4A) along

the scale continuum wherein empirical similarities exist to adjacent scales. Delineating interpretable domains of scale for Fractal Dimension was impractical for graphing purposes. As observational scale increased above 512 ha for this metric (Table 4-2) transition zones became increasingly common such that one might argue most of this metric's scale continuum is one large transition zone whereby each observational extent is both similar and different to other extents, and not predictably. Selection of a unique scale domain in this instance was difficult.

In general, variation (standard deviation) decreased as observational scale increased; though this was not a consistent decrease for all metrics (Fig. 4-3). For instance, fractal dimension and patch density showed both increases and decreases in variance as extent increased, but with unpredictable variance peaks along the scale continuum. In some cases variation peaked in the middle of the scale continuum (e.g., forest gap size, patch density) or began increasing again at the largest observational scale (e.g., patch density).

In most cases, a visual interpretation alone of the number of scale domains would be insufficient to understand where differences (unique domains or transition zones) occurred along the scale continuum. For some metrics, marked differences in either average values or associated variation were apparent at the 0.5 ha extent relative to larger extents (e.g., gap size, gap density, perimeter-to-area ratio, mean shape index), indicating either a break in scale domains, or an artefact of observational sample extent, and some form of statistical interpretation would be required to delineate these domains. For instance, the 0.5, 1, and 2 ha scales for gap density all appear visually to be different, but only represent 2 statistical domains of scale. Somewhat unexpectedly, domains of scale reappeared unpredictably along the scale continuum for the perimeter-to-area ratio metric. In this instance, domain "b" applied only to 1 ha, 32 ha, and 128 ha, but not to the extents in-between (likewise for domain "a" in perimeter-to-area ratio). Without an examination of these metrics' scale continua, multi-scale use of them in a modeling context would be entirely uninformed.

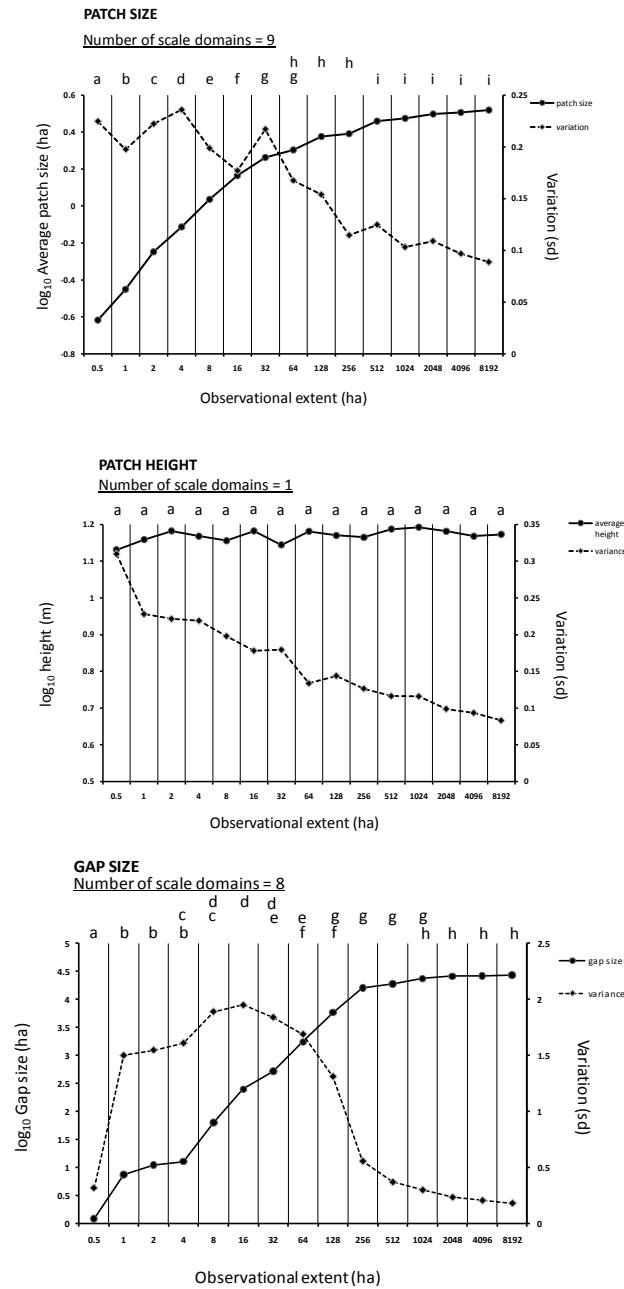


Figure 4-3. Average values and associated variation for nine landscape metrics across 15 spatial extents (while holding grain constant) in the foothills of west-central Alberta, Canada. The number of scale domains within each metric is denoted for each figure using lower-case alphabet, as determined using Kruskal-Wallis non-parametric post-hoc tests. For all extents but 2 (see text), $n=100$ plots per scale. Number of scale domains for Fractal Dimension is reported in text (Table 4-2).

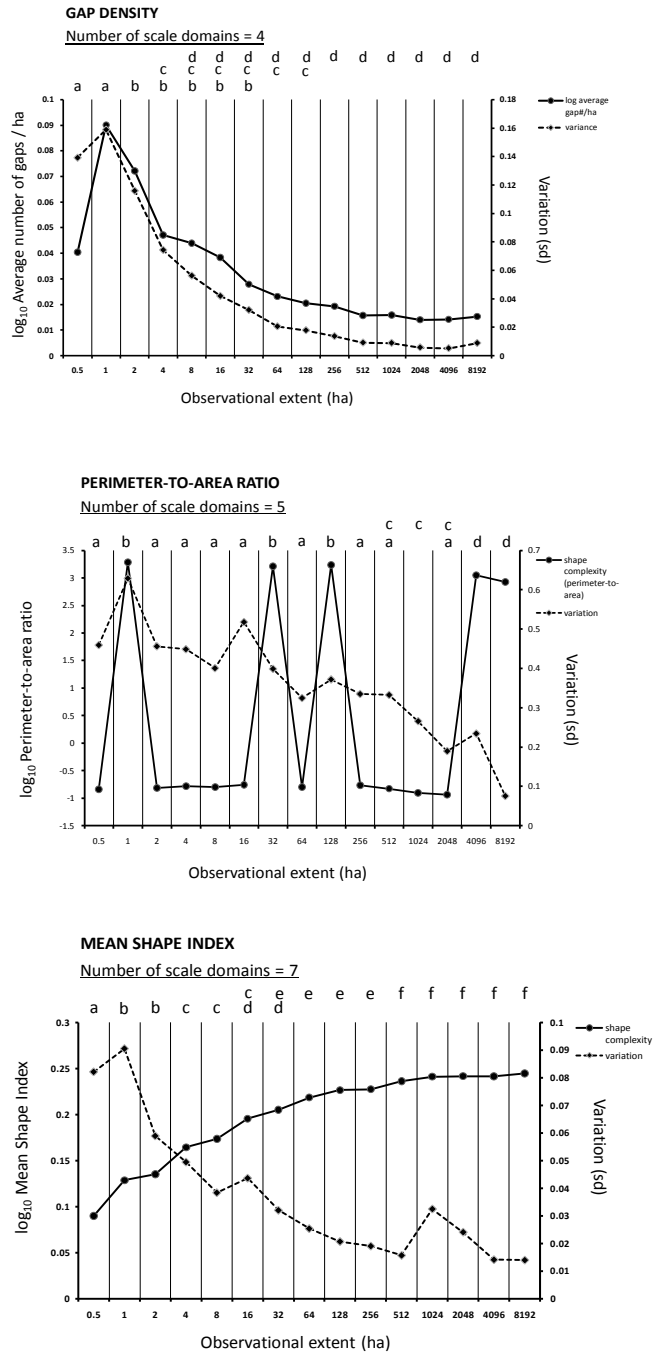


Figure 4-3 continued.

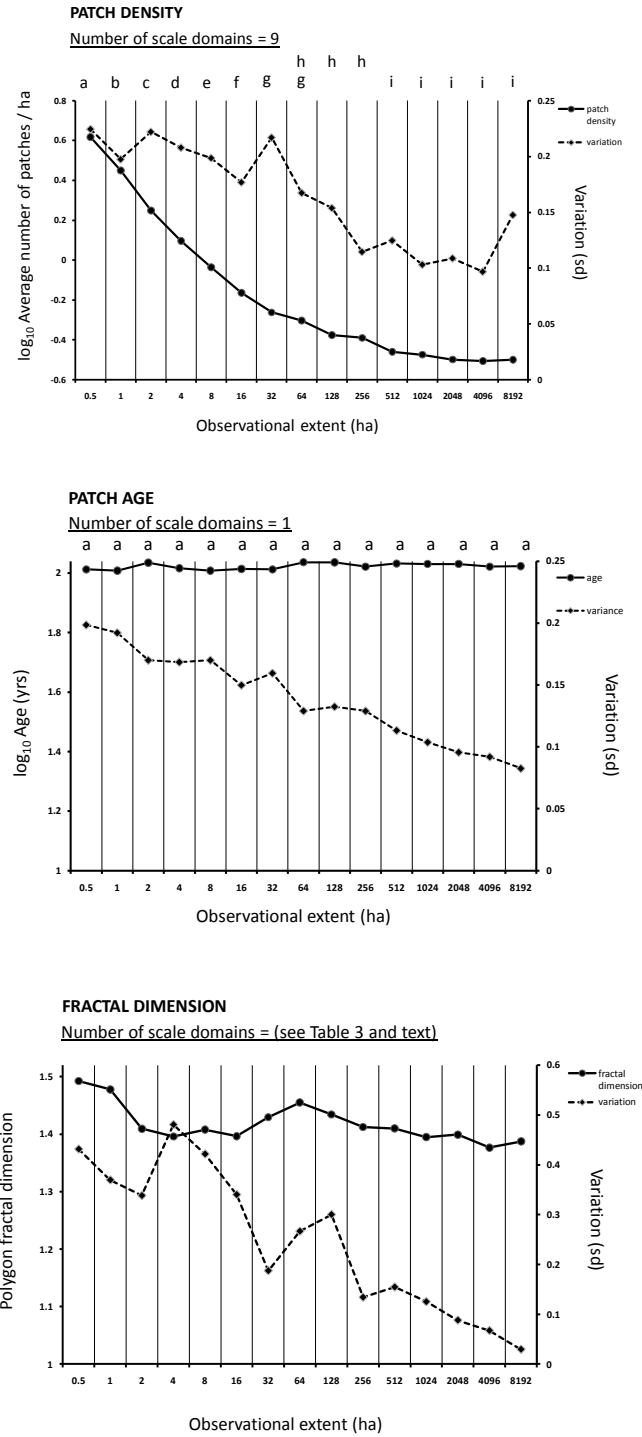


Figure 4-3 continued.

Table 4-2. Post-hoc multiple comparison results for Fractal Dimension among observational scales, demonstrating how differences among scales appear unpredictably as one moves up the scale continuum, particularly above the 512 ha observational extent.

scale	0.5	1	2	4	8	16	32	64	128	256	512	1024	2048	4096	8192
0.5		0.400	0.180	0.172	0.083	0.375	0.134	0.074	0.110	0.399	0.739	0.954	0.783	0.251	0.525
1			0.700	0.675	0.456	0.882	0.484	0.311	0.485	0.897	0.396	0.186	0.123	0.009	0.092
2				0.808	0.757	0.445	0.904	0.814	0.895	0.243	0.050	0.019	0.008	*	0.019
4					0.600	0.492	0.732	0.744	0.897	0.193	0.024	0.003	0.001	*	0.013
8						0.265	0.940	0.951	0.646	0.124	0.026	0.002	*	*	0.017
16							0.305	0.231	0.526	0.675	0.153	0.033	0.007	*	0.005
32								0.988	0.523	0.09+	0.008	0.001	*	*	*
64									0.537	0.071	0.003	*	*	*	*
128										0.338	0.022	0.001	*	*	*
256											0.192	0.013	*	*	*
512												0.177	0.017	*	0.015
1024													0.341	0.020	0.011
2048														0.028	0.311
4096															0.688
8192															

*significant differences with alpha = 0.04% (using a Bonferroni correction on 5% for 105 comparisons)

Discussion

Given the unpredictable nature of the scale-domain relationship among metrics observed herein, basing “different” scale selection on either orders of resource selection or by arbitrary means would be tenuous at best, and would represent naïve scale selection (see Fig. 4-1) especially in the absence of an evidence-based scale-continuum examination. Of the nine metrics examined, all but three showed identifiable domains of scale as determined using post-hoc tests. Cross-scale changes in metric values, and subsequent identification of multiple domains was most evident for metrics whose final values were based on the area and perimeter of polygons; metrics such as forest height and age did not scale. Most metrics were found to possess multiple domains of scale unapparent in visual inspections of individual scale graphs, and smaller domains at the 0.5 ha or 1 ha scales were potential artifacts of observational sampling scale, and likely entirely misrepresent the scalar nature of the specific metric at those observational extents (e.g., forest gaps). One metric (fractal dimension) appeared not to scale, and above 512 ha several transition zones appeared making the identification of scale domains difficult, and perhaps suggesting one large transition zone (at least based on methods used herein). Examination of the scale continuum revealed intriguing insight for each metric, including the number of unique observational scales (domains) and associated transition zones.

Although I used multiple Kruskal-Wallis post-hoc tests here as a method to define domains of scale, this might not suffice in other contexts. Where variance is more similar among scales, a parametric test concerning means and variance would be more powerful in delineating scale domains (i.e., versus a non-parametric test dealing with medians, as done here). Further, it would be prudent to relate domain-defining methods to the biology of the system in question. If using statistical domain-delineating methods, this relationship largely would be defined through adjustments to alpha. A difference of 20 ha in average patch size among two scales may be statistically significant, but may not represent a biologically meaningful difference. A 20 ha difference may be important to a red squirrel (*Tamiasciurus hudsonicus*) or a pine marten (*Martes Americana*), but not a large-ranging species like caribou (*Rangifer tarandus*). How variance, sample size, and alpha are combined into biologically meaningful indices used to define domains of scale

is a decision that lies entirely with the researcher, and a seemingly unavoidable level of subjectivity. The implication of this is a wholly open-ended area of research in ecological scale.

This subjectivity is important when structuring axes' length and detail to visually represent cross-scalar patterns. Nams, Mowat & Panian (2006) are among the first to empirically discuss domains of scale in wildlife-habitat modeling. They show graphical (non-statistical) representations of how grizzly bear habitat selection "peaks" at different scales and, based on these peaks, conclude that different domains must exist for bear habitat use (also see Johnson et al. 2004; p.875). However, the degree to which any plotted series of data will "peak" on a graph is entirely a function of axis precision, and associated min-max axes values. For instance, had I constrained the y-axis for fractal dimension to between 1.3 and 1.5, the metric would have graphically appeared to cross multiple domains of scales, when in fact statistics argue otherwise (also see Nams and Bourgeois, 2004:1741). Simply plotting confidence intervals (e.g., Nams et al., 2006) to delineate differences graphically is not sufficient either. Due to outliers, two means with non-overlapping confidence limits can still be statistically similar. It is important to note also that variance structure observed among scales in this study would preclude most approaches using parametric statistics to delineate domains of scale. For all metrics, variance was not homogeneous among scales, so domain-delineating methods must account for this while maintaining some biological relevancy to the system of study. Researchers must be careful in how they define and present a system's domains of scales, whether working graphically or statistically.

Perhaps one of the most important features to understand in a cross-scale study is whether some metrics show repeating domains of scale along the scale continuum. Gap density, for instance, has similar domains of scale for the 0.5 ha and 32 ha plot sizes, and (more strikingly) also between 16 ha and 8192 ha (also see Table 2 for fractal dimension). Both pairs of observational scales are similar to "core-use" versus "landscape" scales used in wildlife research (e.g., La Sorte et al., 2004; Manning et al., 2006; Meyer et al., 2002; Thogmartin and Knutson, 2007), considered entirely different observational scales or orders of resource selection (e.g., Huggard et al., 2007), yet they are both within the same domain of scale. Similarly, and perhaps more evident, are scales

“a” and “b” in the perimeter-to-area metric. Both of these repeat and render similar values across the entire scale continuum. Interpretation of two selection models using forest gaps built at (say) 2 ha versus 2048 ha (i.e. on the same domain of scale) is facilitated by knowing the relative differences of the independent variables among extents, including locations of potential transition zones. If the same model structure or fit is found at both extents, one of these may be a function of observational extent or, alternatively, something quite interesting may be happening ecologically in the system, the final interpretation of which would be assisted by the researcher understanding the similarities in scale domains among seemingly disparate observational extents, sometimes referred to as the robustness of the landscape metric (Saura and Martinez-Millan, 2001).

The same argument applies for understanding cross-scale variance structure and where metric values asymptote along the scale continuum. In forest gap size, there is a clear peak in variance roughly in the middle of the x-axis. Sixteen ha appears to be the most variable observational extent relative to others. Thus a selection model built at 8192 ha would have to account for significantly less variation relative to a model built at 16 ha; however, we generally do not interpret our habitat- selection models in this context. Understanding apparent asymptotes and peaks in variance along the independent-variable scale continuum should appeal to wildlife-habitat ecologists: these are what structure our selection models and their subsequent model fit, yet we do not even partially interpret them as such (see Fig. 4-4 for graphical explanation).

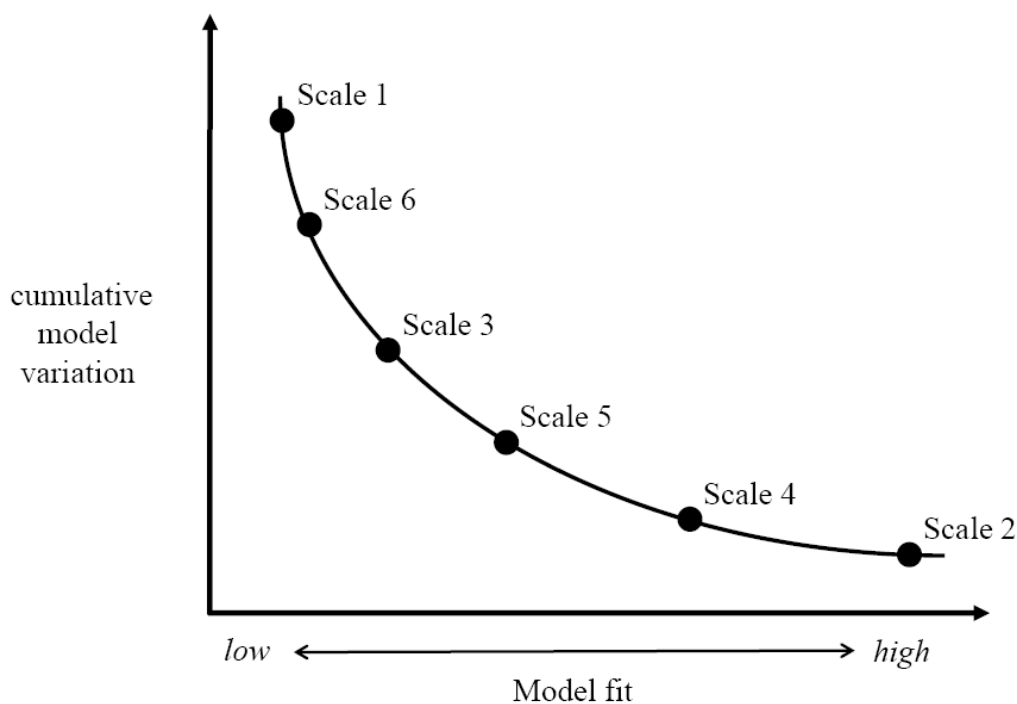


Figure 4-4. Theorized relationship between observational scale, cumulative model variance (both dependent and independent variables), and subsequent fit of a predictive ecological model. Predictive models describe how much variation in one variable(s) can be explained by another set of variables. As shown in this study, variation is scale specific and largely unpredictable across the scale continuum (see Fig. 4-3). Therefore, the overall fit of predictive models could be a function of either (a) something ecologically interesting across scales, or (b) an unpredictable scale-variance relationship resulting in either large or small scale-specific cumulative variance within a few specific observational scales. In this example, two consecutive scales (1 and 2) show disparate predictive-model abilities even though they are adjacent along the scale continuum. This disparity could be a function of scale-specific variance either from an artefact of scale, an unpredictable variance peak along the scale continuum, or a characteristic strategy of the study organism. Without an examination of the scale continuum, model interpretation is arguably only speculation among these alternatives.

A key aspect of scale-continua examination is the ability to identify potential artefacts of observational scale size. An artefact of sampling scale can be defined as an instance where acquired metric values are more characteristic of observational scale than the landscape's actual physiognomy. To identify these requires interpretation of both the average metric values and their associated variance. In this study there are several examples of potential artefacts at smaller sampling extents where there are marked changes in either metric values or their variation as one progresses from the 0.5 ha extent upwards to the 16 ha extent (e.g., forest gaps, gap size, mean shape index, patch size, and perimeter-to-area ratio). Identifying where sampling artefacts end and reality begins along the scale continuum might be evaluated examining raw data in a frequency histogram context. For instance, variation associated with gap size would indicate that most gaps in the study area are less than 64 ha in size, above which a marked drop in variance suggests entire gaps are being sampled within larger plot scales. And as one samples below 1 ha, an associated marked drop in variance suggests most gaps quantified at this extent are simply homogeneous 0.5 ha subsamples of larger gaps >0.5 ha in size: a bona fide artefact of observational sampling scale. Aspects of scale artefacts are only apparent when compared relative to other scales: interpreted as single scales, we are unaware whether or to what extent variance is structuring our independent variables and ultimately the subsequent fit of our predictive models.

Conclusions

Habitat metrics can change over a scale continuum to form different domain structures, and often in an unpredictable fashion. As such, understanding the nature of this change should be a key step in building and interpreting multi-scale predictive models. To this end, the development of cross-scale ecological studies and the choice of observational scales employed therein should go beyond an organism's implied "perception of the world" to also include an evaluation of how metrics of interest might themselves scale, and whether single or multiple domains of scale are involved. Exactly how this is evaluated depends on how researchers define a domain (statistically) or present it graphically, and whether a metric's scalar behavior is representative of actual landscape features, or simply an artefact of observational sampling scale. Further, we should not

expect these relationships to be similar across broad landscape types (e.g., tundra versus forest versus grassland, etc.). I suspect these scale relationships are context-specific, but quantifying this remains an open area for further research in ecological scale. But regardless, an examination of both the independent and dependent variables' cross-scale variation could give additional credence not only to the rationale behind observational scale choice, but also to the final model-fit-interpretation of predictive species-habitat models.

Chapter 5 A continuum approach linking ecological scale and wildlife-habitat models: Flying squirrels in Alberta, Canada.

Abstract

Ecological scale has been identified as a central and/or unifying concept in ecology, yet few empirical studies exist quantifying its importance in various contexts. Recent studies have demonstrated unpredictable effects of observational scale (extent) on the across-scale quantification and subsequent variance structure of forest-landscape metrics commonly used in species-habitat modeling. However, the empirical implications of these scaling effects for the construction and interpretation of species-habitat models remain to be fully examined. Using field-telemetry data on both adult and dispersing-juvenile northern flying squirrels and LiDAR-derived fine-grain forest structure data, I construct and rank the same set of candidate species-habitat models across a continuum of 14 biologically relevant spatial extents. I found differential relative model support (via AIC and Akaike weights) contingent upon scale, whereby upwards of seven different best models could be generated with varying levels of support among the 14 observational scales. Similarly, I found both the best model and its relative support to change along the scale continuum differently for males, females, and dispersing juveniles. Because most multi-scale studies choose observational scales arbitrarily, my results question the validity of many published habitat models. I conclude that the “continuum approach” to species-habitat modeling and an understanding of model relativity among scales are critically absent but fundamental steps in the building and interpretation of all multi-scale ecological studies.

Introduction

Though scale is being considered with increasing frequency, it is still a relatively emergent concept in ecology. Scale has been espoused as the central, unifying problem in ecology (Levin 1992), and fundamental to all ecological investigations (Wiens 1989). Several authors have urged for more focus on scale *per se* (Sandel and Smith 2009 and

references therein) including the addition of scale as an explicit factor in investigations (Meetenmyer and Box 1989; Weins 1989; Wheatley 2010). However, our general understanding of ecological scale remains limited (Wheatley and Johnson 2009), even though the empirical implications of scale for any ecological investigation is potentially profound (e.g., Wheatley 2010). In fact, for the wildlife sciences, scale choice most often is arbitrary or based on constructs largely removed from the scale continuum (Wheatley and Johnson 2009), and this is particularly evident in the literature on species-habitat predictive modeling. Can the explicit inclusion of scale improve or support ecological inference? In this study, I attempt to address these issues in an empirical, predictive-modeling context.

Scale is defined ecologically as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner et al. 1989, Gustafson 1998, Schneider 200, Dungan et al. 2002). The constituents of this are the fundamentals of how we observe ecological systems, with *grain* being the finest level of spatial resolution available, and *extent* the physical size or duration of an ecological observation (Turner et al. 1989). Because funding is limited and studies are mostly short-term (2-5 yrs), ecologists generally do not address time-scale issues in most instances. However, with the advent of spatial analyses and GIS, we are now able to empirically address grain and extent and their potential implications on wildlife science.

In terms of species-habitat modeling, there are two fundamental scale issues that require empirical examination: (1) how ecological variables and their associated variance quantify along a scale continuum, and what implications this scaling effect (or lack thereof) might have on ecological investigation; and (2) how the ecologist’s choice of observational scale might affect scientific results and the subsequent interpretation of predictive species-habitat models. As the former has been addressed in some detail elsewhere (e.g., Wheatley and Johnson 2009, Wheatley 2010; and for related examples not focusing on scale variance, see Wu 1999, Hay et al. 2001, Saura and Martinez-Millan 2001, Wu et al. 2002, Saura 2004, Wu 2004), herein I focus on the latter.

Choice of scale size, addressed here as observational extent or physical size of a sample plot, has implications for both means and associated variance along a scale continuum (Wheatley 2010). Thus, in a univariate context, an examination of among-

scale variance can be useful for choosing observational-scale size and interpreting models built at each scale. In a multivariate context, however, this quickly becomes complex primarily because there are differential among-scale changes in averages and variance for both dependent and independent variables along the scale continuum (Figure 5-1).

Further, when comparing several multivariate candidate models (e.g., via ROC scores, AIC weights, etc.), their subsequent support-ranks (i.e., relativity) will change across scales too. That is, the best-ranked model at scale A may not be the best-ranked at scale B, an effect that likely will be unpredictable among scales, too. The most direct way to examine this potential relativity is to rank and compare identical lists of candidate models among a relevant cross-section of the scale continuum. In this study, I use detailed radio-telemetry data on northern flying squirrels (*Glaucomys sabrinus*), combined with LiDAR-based (Verling et al. 2008, Seavy et al. 2009) forest structure data, to examine empirical implications of scale to habitat-model selection along a biologically relevant range of the scale continuum.

The northern flying squirrel is considered a key component of forested systems in North America (see Smith 2007 for a review). Research from the Pacific Northwest has documented close associations between flying squirrels and older forests (Carey et al. 1999), including a foraging and spore-dispersal mutualism with mycorrhizal fungus (Maser et al. 1986; Currah et al. 2000; Wheatley 2007a), whereby squirrels both consume and disperse fungal spores, thereby enhancing fungal-associated nutrient uptake of woody vegetation and subsequent forest health. As such, flying squirrels have become of interest to forest management, particularly in commercially harvested areas where tree regeneration and long-term sustainability of forest systems is both environmentally and economically important.

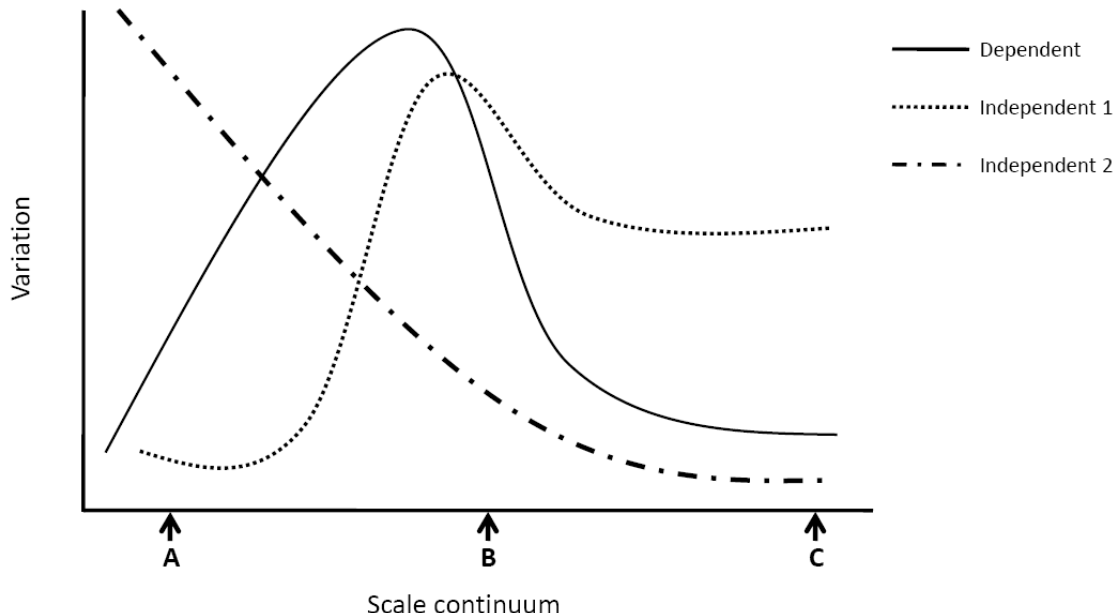


Figure 5-1. Theoretical variance plot for both dependent and independent variables used to model a 2-variable relationship across 3 observational scales (A, B, and C). In a univariate context using independent variable #1, and due to cumulative variance alone, one would predict better model fit using data quantified at scale A (variance minimum) versus scale C (variance average) versus scale B (peak variance). Adding another variable (independent variable #2) can change the relative model fit among scales such that scale C produces the strongest model, particularly if the selection coefficient for variable #2 is strong. Predicting this relativity among scales becomes exceedingly complex when accounting for *multiple candidate models* within each scale. At this stage, the importance of scale is most directly examined using a continuum approach comparing relative model fit for the best-ranked models among observational scales.

Previous research has linked these animals to a number of different habitat types, primarily consisting of old-growth conifer (e.g., Carey 1995) or some landscape-level conifer component (e.g., Carey 2000; Cote and Ferron 2001; Loeb et al. 2000; Mitchell 2001; Smith and Nichols 2003), while others have noted them as habitat generalists (e.g., Wheatley et al. 2005). Increasingly, however, many studies have concluded that relatively fine-grain within-stand components of forest structure are important in

predicting flying squirrel presence (Pyare and Longland 2002; Smith et al. 2004; Wheatley et al. 2005), though these assertions generally are inferred indirectly through trapping data which, at fine scales, can be problematic (Wheatley and Larsen 2008; also see Holloway and Malcom 2006). Additionally, these inferences are based on single-scale approaches to vegetation sampling, and thus are potentially based on spurious correlations between trapping data and scale-specific vegetation variance (Wheatley 2010). Herein, I use advancements in remote sensing (i.e., LiDAR) to acquire fine-grain (1-m² pixel grain) forest-structure data, enabling a powerful test for relationships between squirrel movements and fine-grain forest components while analytically accounting for the effect of scale on resulting models.

I had two primary objectives in this study. My first objective was to empirically demonstrate the continuum approach to species-habitat model selection on an actual animal system. I concluded elsewhere that “without an examination of the scale continuum, model interpretation is arguably only speculation among (a) a characteristic strategy of the study animal; (b) scale artefacts, or; (c) unpredictable variance peaks along the scale continuum” (Wheatley 2010, Fig 4). Until an example(s) of the consequences of this phenomenon are demonstrated empirically in a study of species-response modeling, this point will remain somewhat esoteric. Herein I examine the implications of the spatial-extent continuum to the ranking and selection of multiple candidate habitat-use models for the northern flying squirrel. Based on the unpredictable nature of the scale continuum observed elsewhere (Wheatley 2010), I predict that observational scale will largely determine whether models are found to be statistically significant, and will also determine the relative rank of candidate models examined at each scale.

Using this process, my second objective was to develop useful species-habitat relationships for flying squirrels in the foothills of west-central Alberta, Canada, specifically based on animal-telemetry and fine-grain habitat data, examining whether fine-grain forest structure is useful in predicting squirrel presence, and to inform forest management regarding the conservation of this purported “keystone” species. My hypotheses outlining potential squirrel-habitat relationships are outlined below (See Methods – *Statistical analyses and model selection*); I predict that observational scale will dictate the level to which each hypothesis is supported by the data.

Methods

Study area

Site description

I sampled in the foothills of west-central Alberta, Canada within 50 km of the townsite of Hinton (53° N, 117° W) along the eastern slopes of the Rocky Mountains. Topography is moderate to steep, ranging from 1200 m to 1600 m ASL. Pure stands of upland lodgepole pine (*Pinus contorta*) are most common, followed by upland mixed deciduous-conifer forest, together forming roughly 70% of the landscape by area. Lowland black spruce (*Picea mariana*) fens are widespread, and upland white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and poplar (*Populus balsamifera*) forest compose the remainder of the area. Further site descriptions of this area can be found elsewhere (Wheatley et al. 2002; Wheatley 2007a; Wheatley 2007b; and Wheatley and Larsen 2008).

In these forests, vertical and horizontal fine-grain structure is largely a function of tree-stem density, shrub cover, and open-ground patchiness irrespective of dominant tree species. Although present, coarse woody debris is not a prevailing feature. Canopy trees tend to be >15 m in height, ranging upwards of 30 m high, and average from 20 – 50 cm diameter-at-breast-height depending on species. Mature forests are of fire origin, thus have dominant sub-canopies of shade-tolerant trees. In pine stands, sub-canopies typically consist of black spruce or fir (*Abies lasiocarpa*), while in deciduous stands sub-canopies consist mainly of white spruce. Shrub complexity among stands varies depending on the dominant shrub species. Within pine stands, shrub complexity can vary within areas from low complexity (dominated by *Ledum groenlandicum*) to high (dominated by *Alnus crispa*). Within spruce or deciduous-dominated stands, shrub complexity is more uniform, dominated by shrub-sized aspen and poplar, but mostly consists of *Shepherdia canadensis* and *Salix spp.* Open areas within the forest are

primarily natural gaps in forest canopy where grasses dominate, or are remnants of gas-exploration trails (seismic lines) or reclaimed/abandoned logging roads or cutblocks.

Site selection

I used available digital forest inventories in GIS to generate a list of candidate study sites within 50-km of the townsite of Hinton. In previous research (Wheatley et al. 2005) I found no association between flying squirrel relative abundance and forest tree species; thus candidate sites here consisted of mature forest >70 years of age regardless of leading tree species. I avoided younger regenerating stands where squirrel capture was deemed tenuous *a priori*. Candidate sites had to be large enough to encompass a 1-km trapping transect, sampling methods directly comparable to my previous work with flying squirrels (Wheatley et al. 2005) and trapping methods similar to other *Glaucomys* studies (Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005). The number of sample sites ensured representation of all forest types described above, encompassing several patch types and heterogeneity in both over- and under-story vegetation. Because my interests in space use were at the individual level, I used transects rather than grids to maximize total unique captures (Pearson and Ruggiero 2003). I randomly selected sites from the candidate list and trapped each until at least 2 animals per transect were radio-collared (see below). I abandoned sites where no squirrels were captured within two weeks of trapping, and randomly selected new sites from the candidate list.

I sampled 16 study areas over three summers (May – September, 2004-2006): four sites in 2004, six sites in 2005; and six sites in 2006. Sites were approximately 5-km apart, and no sites from Wheatley et al. (2005) were used in this study. Of the 16 sites, five were dominated by white spruce, with patches of trembling aspen as co-dominant or sub-canopy, and with shrub understories dominated by *S. canadensis* and *A. crispa*. Five sites were dominated by white spruce with sub-canopies of black spruce including adjacent patches of pure black spruce wet areas, and with understories dominated by dwarf birch (*Betula pumula*), *Salix spp.*, and *A. crispa*. Three sites were dominated by trembling aspen with a white spruce sub-canopy, with *S. canadensis* and shrub-sized trembling aspen as shrub cover. Two sites were dominated by lodgepole pine with a black spruce

understory including thick patches of alder shrub cover, and one site consisted of a white spruce-balsam fir mixed canopy, with a shrub-sized balsam fir understory.

Squirrel capture and telemetry

Adult capture

At each site I established a 1-km trapping transect. Transect start points were located randomly, and transect direction largely was determined by patch shape. Traps were placed systematically along transects every 40 m. At each trapping station I placed two live traps (Tomahawk live traps Model #201 or #102, Tomahawk Live Trap Company, Tomahawk, Wisconsin) approximately 20–40 m apart for a total of 50 traps per transect. Depending on trap-site conditions I placed traps in trees (approx. 2-m high), on downed logs, or directly on the ground at the base of trees. Traps were covered with heavy-gauge polyurethane and filled with cotton batting (without obstructing the trap's treadle movement). Ten days prior to trapping, I pre-baited all trap locations with approximately 2 g of peanut butter every second night. To capture animals, traps were baited with ~1 g of peanut butter mixed with rolled oats and sunflower seeds (see Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005). I set traps from 2100h - 2300h, and checked them every 4 hours until 0800h from 10 June – 01 July in 2004; from 18 May – 30 May in 2005; and from 23 May – 21 June 2006.

I divided radio collars equally among sites, collaring the initial 2 – 3 animals captured per site but spacing the collars to minimize autocorrelation among collared animals (approximately 300-600m apart; home-range size estimate; Witt 1992). Sex-biased trapability was not apparent. Upon capture I fitted each animal with uniquely numbered metal ear tags (Monel #1, National Band and Tag Co., Newport, Kentucky). Using mesh-handling bags, I fitted squirrels with collar-fixed radio transmitters (Model PD-2C transmitter, 2.7 g by weight, 2.1-cm crimp-fitted wire collar diameter, Holohil Systems Ltd., Carp, Ontario, Canada). All animals were released at site of capture. Adults were captured and collared several weeks prior to juvenile emergence from the nests.

Juvenile capture

Upon capture, the reproductive condition of adult females was assigned based on nipple condition (Layne 1954; Becker 1992; Wheatley et al. 2002) into one of five categories; long and pink (engorged and lactating); long and dark (beginning to wean but still lactating); medium dark (weaning); small and dark (completely weaned or not lactating); small and pink (no past reproduction). For females in the first three reproductive categories, nests were located immediately post-collaring via radio telemetry and during daylight hours. Telemetry enabled us to identify individual nests, either within tree cavities, witches' broom, or as individual grass dreys. For grass dreys and witches-broom nests, I climbed the nest tree and placed juveniles into a cloth handling bag. For each juvenile I determined gender and weight, and I fitted those >50 g with collar-fixed radio transmitters (Model BD-2C transmitter, 1.6 g by weight, Holohil Systems Ltd., Carp, Ontario, Canada), then returned them directly to the natal nest. Litters located within cavity nests largely prevented me from physically entering the natal nest. For these cavity nests, nocturnal monitoring was used to determine when juveniles were mobile and able to independently exit the nest. Once initial emergence was observed, I then visited the cavity nests during daylight hours and physically tapped the nest tree, flushing out the juveniles into padded butterfly nets (rim opening 50 x 100 cm), at which time I assessed genders and weight, fitted radio transmitters, and then returned juveniles directly to the natal nest. Following these sessions, the adult female often relocated the litter to a different nearby nest, but I observed no deleterious effects from this: each squirrel frequented from 1 to 7 nests (average 2.9 ± 0.22 SEM) regularly during my study, necessitating routine daytime nest checks (at least once per week) to track these normal location changes.

Squirrel telemetry and behavioral focals

I allowed at least 1.5 weeks for animals to adjust to radio transmitters before sampling. I halted trapping prior to and during radio tracking activities, especially any pre-baiting activities (see Wheatley and Larsen 2008). Using a radio receiver (Model R1000, Communication Specialists Inc., Orange County, CA, USA) and directional 3-element

aluminum antenna, I located animals between 2300h and 0400h by walk-in locations assisted by 6-bulb LED headlamps and GPS navigation. Animals were followed repeatedly throughout the summer (see below) and upon each initial location I followed animals continuously for 15-min in 2004, and for 30-min in 2005 and 2006 recording multiple consecutive locations per animal (hereafter referred to as a “focal”). In all years I followed each animal every two to three nights from mid-June until mid-August, rotating each individual’s sampling by evening time period (2200-0000h; 000-0200h; 0200-0400h). I found squirrels habituated to observer presence within three focals, often gliding within 2 m of an observer to forage or travel: thus, I considered any behavior changes from observer presence negligible and equal among focal squirrels.

During focals I recorded squirrel locations in UTM coordinates using handheld WAAS-enabled Global Positioning System receivers (Magellan SporTrack, Thales Navigation, San Dimas CA USA; Garmin GPS72, Garmin International, Olathe KA USA). I recorded locations only when the GPS Estimated Position Error was <7m, and most often during differential WAAS reception when position error was <3m. I abandoned focals if satellite coverage was poor (i.e., >7m). I recorded locations for every movement (tree-to-tree glides) during a focal, verifying post-focal location data using geo-referenced orthophotos in GIS, augmented with comparisons to digital coverage of all spatial features (edges, forest gaps, roads, openings, and trails). For each point location I recorded an associated time (in minutes) spent at each point. Because all data collection was nocturnal and through dense forest, I judged 1 minute the most precise unit for any given point location.

Scale selection - upper and lower limits

The upper limit of the scale continuum was selected based on summer telemetry observations of adult flying squirrels recorded from 2004 – 2006 (Table 5-1). For each animal, telemetry data were converted into 90% kernel home range estimates. Flying squirrel behavioral observations showed multiple centers of activity within home ranges; thus a modified adaptive kernel approach was used. Because telemetry data were timed behavioral observations (versus individual-fix data), I required a method of weighting

telemetry points by the total squirrel-observation minutes per point such that when generating kernel shapes, heavier weights were given to points with higher total observation minutes. Software to apply observational weights only is available for a fixed kernel approach (weighted adaptive kernels were unavailable), thus two software packages were used: one to calculate a single-parameter per-animal smoothing factor, and one to generate a weighted per-animal fixed-kernel home range estimate. First, using the Home Range Extension for ArcView (Rogers and Carr 1998), a per-animal single-parameter smoothing-function value was calculated using the square-root of the mean variance in the x and y coordinates, known as h_{ref} (Silverman 1986; Worton 1989, 1995) as follows:

$$h_{ref} = n^{-1/6} \sqrt{\frac{var_x + var_y}{2}}$$

where n is the number of telemetry points, var_x is the variation in lateral animal movement, and var_y is the variation in longitudinal animal movement (Worton 1995). Second, using Hawth's Tools (Beyer 2004), kernel polygons were generated using a bivariate normal (Gaussian) fixed-kernel density estimator, while applying an observational weight (total minutes) to each telemetry point, and while using an individual h_{ref} for each animal. The polygon areas for all final kernels were generated and kernels with multiple polygons were summed into a single area-measure for each animal. The upper range of these estimates constituted the upper range of the observational-scale continuum used here, while the lower limit was set based on the minimum grain of the available habitat data (see *Habitat sampling* below).

Table 5-1. Average 90% kernel density home-range size estimate for adult flying squirrels over three summers of study near Hinton, Alberta (Canada). Kernels were created using behavioral-focal data, weighted using “total observational minutes” for each telemetry point.

Year	Males ^a			Females ^b		
	n	90%KDE \pm sd (ha)	Range (ha)	n	90%KDE \pm sd (ha)	Range (ha)
2004	7	13.4 \pm 8.1	5.4 – 26.8	9	6.3 \pm 3.0	2.6 – 10.4
2005	13	13.4 \pm 7.6	3.2 – 27.7	7	8.9 \pm 4.7	4.0 – 19.1
2006	4	14.2 \pm 8.3	8.3 – 26.5	9	9.9 \pm 5.3	3.1 – 20.8
Yrs pooled	24	13.5 \pm 7.5	3.2 – 27.7	25	8.3 \pm 4.6	2.6 – 20.8

^a One outlier removed from sample (70.5 ha KDE)

^b One outlier removed from sample (0.4 ha KDE)

Univariate 2-factor ANOVA using YEAR and GENDER as main fixed effects showed no differences among year (Year $F_{2,49} = 1.63$, $P = 0.41$; YEAR \times GENDER $F_{2,49} = 0.23$, $P = 0.80$) and significant differences among gender (GENDER $F_{1,49} = 7.4$, $P = 0.009$).

Quantifying habitat composition

My objectives required a method to generate continuous data on habitat architecture (i.e., physical structure), whereby the same metrics could be quantified along a continuum of observational extents. Thus, I used laser altimetry, most commonly known as Light Detection and Ranging (LiDAR). LiDAR is a relatively new source of geospatial data that can provide fine-grained information on both 2- and 3-D physical structure of terrestrial ecosystems (Vierling et al. 2008; also see review by Lefsky et al. 2002). Lidar is a remote sensing method that obtains extremely detailed surface terrain data. The laser is part of an airborne scanning system that emits and receives laser pulses towards the earth surface (thousands per second) at known angles. The system measures laser-return time (in nanoseconds) for the purpose of calculating object distances from the LiDAR emitting instrument. Surface elevations are derived by accurately recording the two-way laser-pulse travel time in combination with positioning and orientation information obtained from the onboard GPS and GPS base-stations on the ground surface.

For all study sites sampled herein, LiDAR data were available at a 1-m² pixel grain in 2 forms, bare-earth and full-feature, both with >1.3 laser hits/m². The bare-earth data represent a continuous surface model – an evenly spaced grid of points with elevations

derived from where the x-y position transects the triangulated irregular network (TIN) created from the classified ground measured points, whereby all vegetation, structures, and above-ground features have been removed through post-processing of the raw data. Using the bare-earth data as a zero-elevation surface DEM, I used the full-feature LiDAR to determine the top height (in meters) representing the highest laser return for each 1-m² pixel throughout the study area. Subtracting the bare-earth from the full-feature LiDAR returned a forest-structure coverage with a resolution of 1 m and a stated vertical accuracy of 4 cm. Vegetation heights were then classified into four groups considered representative of the general forest structure throughout the area: ground (0 – 0.09 m), shrubs (0.1 – 5 m), subcanopy (5 – 15 m), and canopy (15+ m). Using a mobile ArcPad handheld unit, resultant raster coverages were ground-truthed to verify habitat classifications and to verify geolocations of fine-grained structures such as ground openings, shrub patches, and individual tree or tree-patch locations to approximately 3 - 5 m GPS accuracy (unit position-error readings were generally <3 m during ground truthing). Further, resultant classifications were verified using georeferenced high-resolution (<5 m pixel) color ortho imagery of all areas. Final coverages used for analyses were found to be accurate; for instance, shrub features <1 m in height were clearly identified in the derived forest-structure coverage both along trails <6 m wide, and within forest gaps. Similarly, accuracy was found in terms of stratification of the forest canopy, generating an accurate digital inventory across the entire study area (Figure 5-2). Variations on the abovementioned height-class theme did not produce accurate representations of forest structure consistent with ortho imagery or known forest-patch structure.

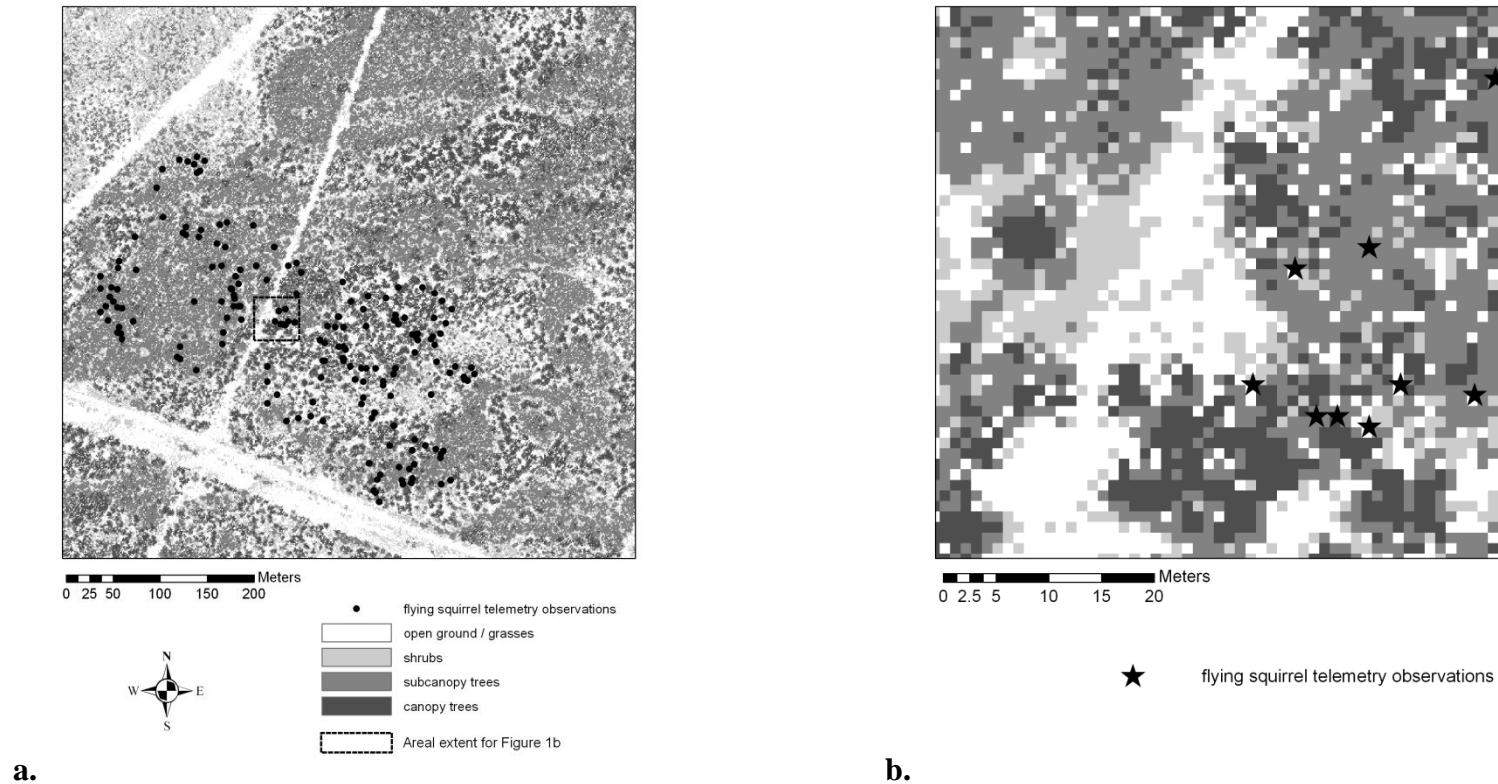


Figure 5-2. A visual example of the detail acquired from LiDAR in generating forest-structure for this study. (a) Telemetry data (black dots) for one adult male flying squirrel displayed atop the classified LiDAR surface. (b) Enlarged view of the dotted square from panel “a” showing fine-grain detail, including 2-m gaps in a forest trail, individual tree-tops, and ground or shrub-covered areas as ecotones between forested and non-forested areas. Digitizing this grain of forest data enables a true scalar approach without limitations of the smallest scale size, or of variables changing due to coverage-availability among scales (see Wheatley and Johnson 2009, or Figure 6-2 of this thesis).

Wet areas mapping

Fine-scale gradients in soil moisture levels are thought to be indicative of species-specific abundance of hypogeous fungi (Trappe 1977; Amaranthus and Perry 1987; Amaranthus et al. 1994), a primary food resource of flying squirrels (Maser et al. 1986, Carey et al. 1999; Wheatley 2007a). Because each fungus has its own set of physiological characteristics (Trappe 1977), some do better in dry areas and some flourish in moist areas. In combination with fine-grain forest structure (e.g., coarse wood debris, shrub cover, host-plant type; Molina and Trappe 1982, Deacon et al. 1983, Amaranthus et al. 1994; Harmon et al. 1994, Visser 1995, Smith et al. 2004), moisture level is considered one important predictor of ectomycorrhizal community types. Existing digital stream coverages (single-line features) were too coarse grained and thus uninformative regarding small-scale squirrel movements, particularly in indicating soil-moisture gradients along a 1 m² pixel surface. Therefore, I used a LiDAR-derived depth-to-moisture layer created at the same grain as the forest inventory. Wet-areas mapping was acquired for all study areas, consisting of depth-to-moisture estimates from hydrological models derived using a combination of LiDAR-based surface-water-flow modeling (Murphy et al. 2008) and a cartographic depth-to-water map (*sensu* Murphy et al. 2009). The resulting output classifies a 1 m² raster surface into depth-to-water measurement categories from potential surface water; 0 – 0.25 cm; 0.26 – 0.50 cm; 0.51 – 3 m; 3 – 4 m; and >4 m. To simplify for analytical purposes, I grouped classes 1 through 3 (from potential surface water; 0 – 0.25 cm; and 0.26 – 0.50 cm) into a single “moist” layer, and everything > 0.51 m depth-to-water into a “dryer” layer. For every sampling plot, I thus calculated the percentage area of each plot that was “moist” and denote this as the “wet area” independent variable.

Independent variable (habitat) calculations

Surrounding every recorded squirrel observation I quantified habitat structure at 14 different observational extents. These extents corresponded to the habitat-data minimum

grain and the limitations of handheld GPS accuracy for following squirrels (0.01 ha) to the estimated maximum average kernel home range size for flying squirrels calculated in this study (17 ha; Table 5-1). Observational scales examined here were; 0.01 ha; 0.02 ha; 0.04 ha; 0.08 ha; 0.16 ha; 0.32 ha; 0.64 ha; 1 ha; 2 ha; 5 ha; 7 ha; 10 ha; 13 ha; and 17 ha. Observational scales were generated in GIS by placing non-overlapping contiguous hexagons across the entire study area, then retaining only hexagons containing squirrel observations. This way, placement of hexagons was unbiased relative to any given single observation or group of observations. Within each hexagon, I calculated the following independent variables (Table 5-2): proportion of ground, shrubs, subcanopy, canopy, and wet area; the largest patch (% area; a measure of connectivity); and the number of patches (a measure of forest heterogeneity). Metrics were generated using a combination of spatial analysis routines (written based on ArcView v3.x Spatial Analyst) and both the Class and Landscape Analysis function of Patch Grid within Patch Analyst, an extension to ArcView available on-line (<http://flash.lakeheadu.ca/~rrempel/patch>). The dependent variable for each hexagon was “total observed squirrel minutes.” For larger observational extents, some hexagons captured >1 individual squirrels (e.g., dispersing juvenile siblings), in which case I standardized these by dividing total minutes by the number of squirrels in each hexagon before relating this metric to the independent variables. Multiple squirrels within a single hexagon were uncommon, and there were never >2 animals/hexagon.

Statistical analysis and model selection

To relate the dependent variable (squirrel minutes) to several independent variables (forest structure, moisture), I generated 18 hypothesis-based candidate models describing potential ecological relationships between squirrel movements and habitat structure (Table 5-3). Combinations of independent variables were screened *a priori* for among-variable correlations (multicollinearity), such that highly correlated variables (i.e., Pearson’s correlation coefficient >0.7) were not forced together into the same model. Using the statistical package R (available on-line at www.r-project.org), model and coefficient significance was tested using a general linear model, direct / forced multiple

regression (\log_{10} transformed dependent variable, non-transformed independent variables; Gaussian error distribution). I used the Akaike information criterion, and Akaike weights to rank and choose the most parsimonious model(s) for each spatial extent such that the fewest variables explain the greatest amount of variation. Akaike weights provide a normalized comparative score for all specified models and are interpreted as the approximate probability that each model is the best model of the set of proposed models (Anderson et al. 2000; Burnham and Anderson 2002). I tested the same 18 models at all 14 spatial extents separately for adult males, adult females, and juveniles (genders combined), and the best scale(s) within which to model squirrel-habitat relationships were chosen based on the highest obtained Akaike weight observed along the spatial continuum. For interpretation of individual model output regarding variable significance levels, I used an alpha of 10% but also report exact P-values so readers may judge these relative to their own standards of significance.

Table 5-2. Definitions of independent variables generated for squirrel-habitat modeling in this study.

Independent Variable	Initialism	Description
Ground	ground	Total area of ground cover divided by the total sampling-plot area (percentage).
Shrubs	shrub	Total area of shrub cover divided by the total sampling-plot area (percentage).
Sub-canopy	subcan	Total area of sub-canopy cover divided by the total sampling-plot area (percentage).
Canopy	can	Total area of canopy cover divided by the total sampling-plot area (percentage).
Wet-Area	wetarea	Total area of wet-area cover divided by the total sampling-plot area (percentage).
Largest Patch Index	LPI	Equal to the percent of the sampling plot that is made up of the largest patch. When the entire sampling plot is composed of a single patch, the LPI = 100.
Number of Patch Types	NUMP	Total number of spatially unique patches within the sampling plot. A measure of heterogeneity.

Table 5-3. Candidate models and their associated hypotheses tested in this study.

Hypotheses are based on both published accounts and those considered plausible through this study. Model numbers as designated here are used in the results to denote model ranks and best-model selections for each scale. (Model numbers begin at 2, an artefact of the spreadsheet and statistical software linkage whereby column 1 held variable titles).

Model No.	Included variables	Hypothesis
2	can, NUMP	Large trees and forest complexity facilitates movement for efficient foraging (long glides), and heterogeneous patchy forest provides complexity and cover to avoid predation.
3	can, NUMP, LPI	Similar to Model 2, with the addition of patch connectivity: high trees, forest complexity, and connectivity enhance general movement of individuals.
4	can, subcan	Squirrels are associated with developed understories characteristic of complex, mature forests, where characteristic fungal food sources are abundant, and predation risk is minimized (e.g., Holloway and Malcom 2006).
5	subcan, shrubs	Within-stand horizontal structure provides cover while foraging.
6	shrubs, wetarea, year	Squirrels key into annual mycorrhizal fungi blooms associated with either wet or dry areas (fungal communities are assumed different among moisture levels; Trappe 1977; Amaranthus and Perry 1987; Amaranthus et al. 1994)
7	ground, can	Large trees and gap openings facilitate gliding.
8	shrubs, ground	Squirrels key into mycorrhizal fungi that is associated with open areas and shrub cover irrespective of moisture levels.
9	wetarea, can	Squirrels prefer black spruce bogs (i.e., Wheatley and Larsen 2008).
10	can, ground, shrubs	Squirrels prefer habitat near ecotones to facilitate all aspects of foraging, gliding, and nesting.
11	LPI, NUMP	Patch complexity facilitates both foraging and nesting, and connectivity facilitates movement among patch types minimizing multi-patch crossings.
12	wetarea	Squirrels prefer wetter areas for the characteristic forest structure and availability of fungal communities associated with these habitats.
13	wetarea, year	Squirrels identify areas based on moisture conditions characteristic of fungal communities associated either with wet or dry habitats; however, the locations and availability of these areas changes among years.

14	LPI	Squirrels are associated with non-edge core-habitats regardless of forest age.
15	can, shrubs, wetarea	Squirrels prefer black spruce-willow forests (i.e., Wheatley and Larsen 2008, top-right of Fig 3; Figure 3-3 in this thesis).
16	can, shrubs, wetarea, LPI	Squirrels prefer unfragmented black spruce-willow forests (i.e., Wheatley and Larsen 2008, top-right of Fig 3; Figure 3-3 in this thesis), indicative of many nest sites and foraging areas observed throughout the study.
17	can, LPI	Squirrels are associated with non-edge mature core-forests (i.e., forest-age specific).
18	shrubs	Shrub cover was a strong driver of the CA in Wheatley and Larsen (2008) thus may largely drive fine-grain animal occurrence.
19	shrubs, subcan, wetarea, can	Mycorrhizal fungi are consistently best in forests that are older, moister, and more complex.

Results

Over three summers (May – September) in 2004, 2005, and 2006, I followed 24 adult males, 25 adult females, and 15 dispersing juveniles in 16 different study areas. In 2004, I followed adult animals for an average of 8 (± 1.5 SD) focals each (average 135 ± 41 SD total minutes/animal; range 77 – 261 minutes/animal); in 2005, an average of 10 (± 2.2 SD) focals each (average 325 ± 108 SD minutes/animal; range 124 – 721 minutes/animal); and in 2006, an average of 12 (± 3.5 SD) focals each (average 435 ± 173 SD minutes/animal; range 46 – 631 minutes/animal). I followed juveniles in 2005 and 2006 only. In 2005, I followed juveniles for an average of 20 (± 2.7 SD) focals each (average 563 ± 188 SD minutes/animal; range 338 – 1028 minutes/animal), and in 2006 I followed juveniles for an average of 8 (± 3.0) focals each (average 90 ± 42 SD minutes/animal; range 33 – 140 minutes/animal).

Observational scale

Males

For adult male flying squirrels, the strongest support for a single model relative to all other potential candidate models was found at the 0.32 ha observational extent (Figure 5-3). Model support for any given best model decreased at both higher and lower extents, indicating that outside the 0.32 ha spatial extent, model support becomes diluted among all candidate models, in some cases almost in equal proportions (e.g., 5 ha extent; Figure 5-3). Approximately similar (and moderate) model support was found for best models at the 0.01 ha and 13 – 17 ha extents. The weakest model support was found for data analyzed at the 2 – 10 ha spatial extents, indicating relatively poor relationships for most models at those scales.

Selecting the best two models in a model-averaging context increased relative model support differently along the scale continuum. For most spatial extents, combining the top two models increased relative model support almost 2-fold over the best single model, an effect most pronounced on either side of the 0.32 ha scale, where combined model support effectively approached 1.0 (or 100%).

For male squirrels, depending on what scale data were quantified within, there were 7 potential best models (Figure 5-3; models #6, 8, 11, 12, 13, 14, and 18) ranging from site-specific variables (e.g., model #6) to more landscape-scale variables (e.g., model #11). For the 0.32 ha scale, the best supported single model was #13, and the strongest averaged model was the combination of the top two models #13+6, forming a combined Akaike weight of >0.98. Model #13 appeared six times as the best model along the scale continuum (Figure 5-3) but with Akaike weights differing in some instances upwards of 3-fold depending on scale (e.g., 0.32 ha versus 7 ha scales). Other models appeared multiple times but with similar Akaike-weight support among scales (e.g., model #6; Figure 5-3).

Females

For adult (breeding) females, the strongest support for a single model was found at multiple spatial extents and inconsistently along the entire scale continuum (Figure 5-3).

Approximately equal peaks in single-model support were found at 0.02 ha (model #16), 1 ha (model #13), 5 ha (model #2), 10 ha (model #2). In contrast, support for a single model was not apparent between 0.04 ha and 0.64 ha, and was equally absent at the 2- and 7-ha extents. Further, different models were ranked best overall among scales, producing a total of 5 different best models contingent on scale. The effect of model-averaging the best two models varied among scales. In some instances model support almost doubled (e.g., 0.04 – 0.16 ha scales) whereas for other scales this effect was negligible (e.g., 2, 7, and 17 ha scales). The strongest support for model-averaging was found at the 1 ha, 10 ha, and 13 ha scales, where all Akaike weights approached 1.0. For females, a single peak or a clear pattern in model support among scales was not apparent.

For adult females, similar peaks in single-model support were evident among scales, yet each represented different best models. Peaks in single-model support were observed at the 0.02 ha, 1 ha, 5 ha, and 10 ha, but represented models #16, 13, 2, 2, and 2 respectively, and all had similar Akaike weights between 0.6 and 0.7. Combining the top two models for an averaged model produced peaks at the 1 ha, 10 ha, and 13 ha, and again these were for two different model combinations: model #13+6 for the 1 ha scale, and model #2+3 for the 10 ha and 13 ha scales (Figure 5-2). Selection of either single or averaged models was scale dependent.

Dispersing juveniles

For dispersing juvenile squirrels, the strongest support for a single model relative to all other scales was found at the 13 ha spatial extent (Figure 5-3). Model support for either single or combined-averaged models decreased on either side of the 13 ha scale. Roughly equal model support was observed from 0.01 ha through the 0.32 ha scales, but this was in support of 4 different best models (#16, 19, 10, and 4) among 6 observational extents. Support for any candidate model was not apparent at the 0.64 ha, 1 ha, and 7 ha scales. Overall for dispersing juveniles, and similar to both males and females, eight different models were ranked as the best model contingent on scale.

Model averaging of the top two models produced a trend in Akaike weights identical to that observed for the single-model approach (Figure 5-3). However, addition

of a second model increased model support most for smaller scales (below 0.64 ha) relative to larger ones. Similar to the single-model approach, the peak in model-averaged support remained at 13 ha.

The best supported single model for juveniles at 13 ha was model #2. Addition of model #3 increased the Akaike weight from 0.6 to >0.9. Interestingly, the same model (#2) is both a peak (13 ha) and a trough (7 ha) in juvenile-model support along the scale continuum (Figure 5-3).

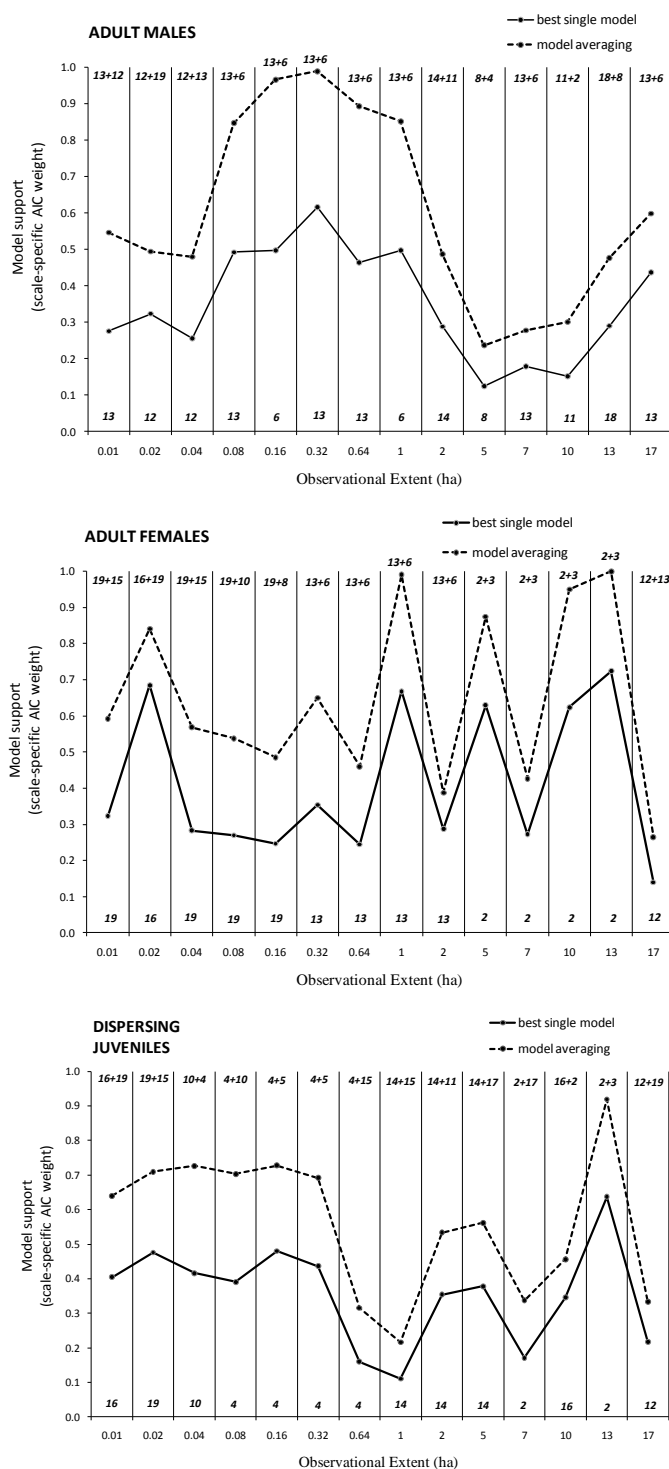


Figure 5-3. Plot of observational scale (extent) versus model support, with the best-supported single model noted along the bottom of each figure, and the best averaged 2-model combination listed along the top (see Table 5-3 for model details). Different models are selected depending on scale, whether choosing a single best model (solid black line) or averaging 2 models (dotted grey line). Further, different models are selected among scales differently depending on gender and life-history stage (adults versus juveniles).

Squirrel biology

Males

The best-supported models for male flying squirrels were found at the 0.32 ha observational extent, and included model #13 and model #6 (Table 5-3). Model #13 ($P < 0.001$) indicated a negative association with wet area ($P = 0.08$), and significant year effects (year two and three, both $P < 0.002$; Table 5-4), thus accounting for potential year effects improves model explanatory power. Of note is the negative selection coefficient associated with wet areas, indicating that squirrels spent more time within dryer areas. The addition of model #6 ($P < 0.001$; Table 5-4) improved overall averaged-model support (Figure 5-3) but included a non-significant variable “shrubs” (shrubs $P = 0.31$; Table 5-4). The selection coefficient for shrubs was negative, indicating a weak tendency for squirrels to spend more time in areas devoid of shrubs.

Females

Support for either single or averaged models was evident for females at multiple spatial scales (Figure 5-3). Strong relative support for single models was observed at the 0.02 ha, 1 ha and 13 ha spatial extents, and included models #16 and 19 (0.02 ha; Table 5-5), #13 and 6 (1 ha; Table 5-6) and #2 and 3 (13 ha; Table 5-7). Starting at the smallest scale, the best model at the 0.02 ha scale was model #16 ($P < 0.001$; Table 5-5) indicating positive and significant relationships with canopy cover ($P < 0.001$), shrub cover ($P = 0.0025$), patch size ($P = 0.015$), and a negative association with wet areas ($P = 0.078$). The next-best model at this scale is Model #19 ($P < 0.001$), indicating almost identical relationships, except that patch size is replaced by a positive association with subcanopy ($P = 0.088$; Table 5-5). At the 1 ha scale, the best model was #6 ($P < 0.001$; Table 5-6) but, aside from significant year effects, this model contained no statistically significant forest-structure variables. Similar results were found for the next-best model (#13; Table 5-6) at this scale, too. At the 13 ha scale, the best model was #2 ($P < 0.001$; Table 5-7), indicating a negative and significant association with tree canopy, and a positive (and

weak; see regression coefficient for canopy; Table 5-7) association with the number of patch types ($P < 0.001$). The second-best model at this scale (model #3; $P = 0.0021$; Table 5-7) indicated almost identical relationships, but with the addition of patch size (non-significant; $P = 0.79$). Tree canopy and shrubs appeared important for females at smaller scales (i.e., 0.02 ha), whereas canopy and number of patches (heterogeneity) appeared important for females at larger scales (i.e., 13 ha). Intermediate scales (e.g., 1 ha) were somewhat uninformative regarding female habitat use and forest structure.

Dispersing juveniles

Support for a single (or combined) model for dispersing juveniles peaked at the 13 ha scale (Figure 5-3) with models #2 ($P = 0.013$) and #3 ($P = 0.28$; Table 5-8). Model #2 indicated a negative association between juveniles and canopy cover ($P = 0.031$), and a positive association with the number of patch types (patch heterogeneity; $P < 0.001$). The second-best model at this scale indicated similar relationships but included a non-significant association with patch size ($P = 0.56$; Table 5-8). At smaller scales there was less support for any single model (e.g., particularly from 0.64 – 7 ha scales).

In general, ΔAIC from the best to the second-best models always was < 2 for males (Table 5-9), females (Table 5-10) and juveniles (Table 5-11), suggesting that model averaging of the top two models is not useful in this context (i.e., given the AIC log-likelihood calculation, 2 is the default). Most of the second-ranked models were either non-significant overall or contained non-significant additional variables. Thus, it is arguable that interpretation of habitat use is best done using only the top-ranked model for each scale.

Table 5-4. Regression table for the two top-ranked models for adult males at the 0.32-ha scale. Note model number and scale denoted for each (see Table 5-9 for w_i ranks for all candidate models).

Model 13, Scale: 0.32 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	1.56	0.10	15.51	<0.001
Wetarea	-0.21	0.12	-1.72	0.085
Year three	0.48	0.12	3.76	<0.001
Year two	0.33	0.11	3.02	0.0025
Null deviance: 667.76 on 582 degrees of freedom				
Residual deviance: 646.68 on 579 degrees of freedom				
Model 6, Scale: 0.32 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	1.64	0.12	12.97	<0.001
Shrubs	-0.40	0.41	-0.99	0.31
Wetarea	-0.18	0.12	-1.50	0.13
Year three	0.49	0.13	3.83	<0.001
Year two	0.32	0.11	2.98	0.0029
Null deviance: 667.76 on 582 degrees of freedom				
Residual deviance: 645.57 on 578 degrees of freedom				

Table 5-5. Regression table for the two top-ranked models for adult females at the 0.02-ha scale. Note model number and scale denoted for each.

Model 16, Scale: 0.02 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	0.71	0.12	5.94	<0.001
Canopy	0.80	0.20	3.92	<0.001
Shrubs	0.50	0.16	3.03	0.0025
Wetarea	-0.10	0.06	-1.76	0.078
Largest Patch Index	0.0040	0.0016	2.42	0.015
Null deviance: 1360.6 on 1451 degrees of freedom				
Residual deviance: 1336.0 on 1447 degrees of freedom				
Model 19, Scale: 0.02 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	0.76	0.13	5.77	<0.001
Shrubs	0.74	0.22	3.30	<0.001
Subcan	0.28	0.16	1.70	0.088
Wetarea	-0.12	0.059	-2.14	0.032
Canopy	0.77	0.21	3.65	<0.001
Null deviance: 1360.6 on 1451 degrees of freedom				
Residual deviance: 1338.7 on 1447 degrees of freedom				

Table 5-6. Regression table for the two top-ranked models for adult females at the 1-ha scale. Note model number and scale denoted for each.

Model 6, Scale: 1 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	2.37	0.20	11.51	<0.001
Shrubs	0.43	0.59	0.73	0.46
Wetarea	-0.18	0.24	-0.78	0.43
Year three	0.76	0.19	3.81	<0.001
Year two	0.59	0.20	2.94	0.0035
Null deviance: 270.61 on 209 degrees of freedom				
Residual deviance: 245.67 on 205 degrees of freedom				
Model 13, Scale: 1 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	2.46	0.16	14.59	<0.001
Wetarea	-0.21	0.23	-0.90	0.36
Year three	0.81	0.18	4.35	<0.001
Year two	0.60	0.20	3.03	0.0027
Null deviance: 270.61 on 209 degrees of freedom				
Residual deviance: 246.31 on 206 degrees of freedom				

Table 5-7. Regression table for the two top-ranked models for adult females at the 13-ha scale. Note model number and scale denoted for each (see Table 5-10 for w_i ranks for all candidate models).

Model 2, Scale: 13 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	2.42	0.048	4.63	<0.001
Canopy	-6.79	1.41	-4.78	<0.001
Number of patches	0.00027	0.000052	5.36	<0.001
Null deviance: 124.87 on 60 degrees of freedom				
Residual deviance: 75.78 on 58 degrees of freedom				
Model 3, Scale: 13 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	2.34	0.074	3.22	0.0021
Canopy	-6.99	1.61	-4.32	<0.001
Number of patches	0.00027	0.000052	5.22	<0.001
Largest patch index	-0.0042	0.0016	-0.26	0.79
Null deviance: 124.87 on 60 degrees of freedom				
Residual deviance: 75.68 on 57 degrees of freedom				

Table 5-8. Regression table for the two top-ranked models for dispersing juveniles at the 13-ha scale. Note model number and scale denoted for each (see Table 5-11 for w_i ranks for all candidate models).

Model 2, Scale: 13 ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	1.34	0.51	2.62	0.013
Canopy	-7.31	3.24	-2.25	0.031
Number of patches	0.000355	0.000078	4.52	<0.001
Null deviance: 84.70 on 34 degrees of freedom				
Residual deviance: 50.78 on 32 degrees of freedom				
Model 3, Scale: 13ha				
Parameter	Estimate	Standard Error	t value	<i>P</i>
(Intercept)	0.94	0.87	1.08	0.28
Canopy	-6.94	3.34	-2.07	0.046
Number of patches	0.00037	0.00085	4.40	<0.001
Largest patch index	0.0097	0.017	0.58	0.56
Null deviance: 84.7 on 34 degrees of freedom				
Residual deviance: 83.59 on 32 degrees of freedom				

Table 5-9. Ranking based on w_i (Akaike weight) of all candidate models for male flying squirrels at the 0.32-ha scale.

Model#	Variables in model	Rank	0.32ha AIC	Δ_i	Akaike Weight w_i
13	wetarea, year	1	1724.9	0.0	0.6157
6	shrubs, wetarea, year	2	1725.9	1.0	0.3734
12	wetarea	3	1736.0	11.1	0.0024
15	can, shrubs, wetarea	4	1737.0	12.1	0.0015
9	wetarea, can	5	1737.5	12.6	0.0012
5	subcan, shrubs	6	1738.0	13.0	0.0009
4	can, subcan	7	1738.1	13.1	0.0009
19	shrubs, subcan, wetarea, can	8	1738.2	13.2	0.0008
18	shrubs	9	1738.3	13.4	0.0007
16	can, shrubs, wetarea, LPI	10	1738.8	13.9	0.0006
14	LPI	11	1739.6	14.7	0.0004
10	can, ground, shrubs	12	1739.7	14.8	0.0004
8	shrubs, ground	13	1740.0	15.1	0.0003
7	ground, can	14	1740.4	15.5	0.0003
2	can, NUMP	15	1741.4	16.5	0.0002
11	LPI, NUMP	16	1741.5	16.6	0.0002
17	can, LPI	17	1741.6	16.7	0.0001
3	can, NUMP, LPI	18	1743.4	18.5	0.0001

Table 5-10. Ranking based on w_i (Akaike weight) of all candidate models for female flying squirrels at the 13-ha scale.

Model#	Variables in model	Rank	13haAIC	Δ_i	Akaike Weight w_i
2	can, NUMP	1	194.3	0.0	0.7236
3	can, NUMP, LPI	2	196.3	1.9	0.2762
11	LPI, NUMP	3	211.6	17.3	0.0001
9	wetarea, can	4	216.2	21.9	0.0000
4	can, subcan	5	216.7	22.3	0.0000
15	can, shrubs, wetarea	6	216.9	22.6	0.0000
7	ground, can	7	217.6	23.3	0.0000
19	shrubs, subcan, wetarea, can	8	217.9	23.6	0.0000
17	can, LPI	9	218.2	23.8	0.0000
10	can, ground, shrubs	10	218.4	24.1	0.0000
16	can, shrubs, wetarea, LPI	11	218.7	24.4	0.0000
5	subcan, shrubs	12	221.1	26.7	0.0000
18	shrubs	13	221.7	27.4	0.0000
14	LPI	14	222.5	28.2	0.0000
12	wetarea	15	222.6	28.2	0.0000
8	shrubs, ground	16	223.0	28.7	0.0000
13	wetarea, year	17	223.5	29.1	0.0000
6	shrubs, wetarea, year	18	225.2	30.9	0.0000

Table 5-11. Ranking based on w_i (Akaike weight) of all candidate models for juvenile flying squirrels at the 13-ha scale.

Model#	Variables in model	Rank	1haAIC	Δ_i	Akaike Weight w_i
2	can, NUMP		120.4	0.0	0.6367
3	can, NUMP, LPI		122.0	1.6	0.2822
11	LPI, NUMP		124.5	4.2	0.0787
14	LPI		135.1	14.7	0.0004
8	shrubs, ground		135.8	15.4	0.0003
12	wetarea		135.9	15.5	0.0003
18	shrubs		136.2	15.8	0.0002
7	ground, can		136.5	16.2	0.0002
17	can, LPI		137.0	16.6	0.0002
9	wetarea, can		137.3	17.0	0.0001
5	subcan, shrubs		137.3	17.0	0.0001
10	can, ground, shrubs		137.4	17.0	0.0001
4	can, subcan		137.5	17.1	0.0001
13	wetarea, year		137.8	17.4	0.0001
15	can, shrubs, wetarea		138.0	17.6	0.0001
19	shrubs, subcan, wetarea, can		139.2	18.9	0.0001
16	can, shrubs, wetarea, LPI		139.6	19.3	0.0000
6	shrubs, wetarea, year		139.6	19.3	0.0000

Discussion

These findings lend empirical support to the assertions of Wheatley and Johnson (2009) and Wheatley (2010) that an empirical examination of the scale continuum is a critical but absent step in the building and interpretation of all multi-scale ecological models. I found differential model support (via AIC and Akaike weights) contingent upon scale, whereby upwards of seven different best models could be generated with varying levels of support among the 14 observational scales. Similarly, I found both the best model and its relative support to change along the scale continuum differently for males, females, and juveniles. These findings enabled me to choose models with the highest among-scale support from the most apparently relevant scales, and discount scales where model support was relatively poor. An examination of relative model fit along a scalar continuum enhances one's ability to detect scalar peaks in model support, adding credence to the rationale behind observational scale choice, and also to the scalar interpretation of the resulting "best" predictive model. I discuss these results in terms of ecological scale in the context of interpreting the best-ranked species-habitat model.

Ecological scale

How does this approach differ from multi-scale approaches already prevalent in the literature? There are two primary differences. First, I selected observational scale size based on a biologically relevant scale continuum, with upper and lower limits set to a quantified average home range size and the lower limit determined by the grain of available habitat data. And, within this continuum I examined identical variables and candidate models among all observational scales, constituting a true multi-*scale* study rather than a multi-*design* study, the latter stating little about scalar processes (Wheatley and Johnson 2009; also see Chapter 6 this thesis).

Second, I completed the same model selection analyses along the whole scale continuum, facilitating a relative comparison of among-scale best models, their corresponding model fit, and potential domain structure. Generally, multi-scale studies published to date have selected only two or three arbitrarily chosen scales, often with no

biological anchor, and inferences are generated by contrasting and comparing results derived from this narrow window of observational scales (often based on orders of resource selection, *sensu* Johnson 1980; see Wheatley and Johnson 2009). For example, for flying squirrels, two plausible micro-site and home-range scales could be 0.04 ha and 10 ha respectively. When used in a traditional two-scale multi-scale approach, one would conclude similar and weak associations among scales (scale invariance; Figure 5-3, males), when in fact better-supported models exist from the same data set, just at different adjacent scales (i.e., true scale variance). A narrow scale window could easily produce misleading, spurious results, an accusation arguably appropriate for most multi-scale studies published to date, and something that fundamentally questions the scientific state of multi-scale animal ecology.

The scale-continuum approach enables identification of key observational scales (i.e., peaks in model fit), and also an assessment of scale domains (*sensu* Weins 1989; also see Wheatley 2010) or sections of the scale continuum within which pattern and process are predictable. Examples here can be seen for females between 5 ha and 13 ha (Figure 5-3; all model #2), or for juveniles between 0.08 and 0.64 ha (Figure 5-3; all model #4), even including information on how model fit for the same model can change within the same scale domain (e.g., juveniles 0.08 ha versus 0.64 ha, Figure 5-3), or how model fit can change almost an order of magnitude among adjacent scales (e.g., juveniles 13 ha versus 17 ha, Figure 5-3). Examining a biologically relevant section of the scale continuum enables relative comparisons of model selection, model fit, and potential occurrence of scale domains, all important in the final interpretation and conclusions for any multi-scale study.

Linking the selected best models to cross-scale variance of both dependent and independent variables is a key next step in advancing our interpretation of multi-scale studies. In theory, this is relatively simple in a univariate context (e.g., see Wheatley 2010, Fig 4; or this thesis, Figure 4-4), whereby low-variance data sets would produce tighter-fit models, or in a logistic-regression context whereby only the independent variable scales. However, such an interpretation quickly becomes exceedingly complex with multi-variate models and continuous dependent variables (i.e., not zero and 1 logistic variables that do not change along the scale continuum), particularly as both

dependent and independent variables and their associated variance change differently among scales. As model fit is observed to change along a scale continuum, we must question whether this is a function of basic animal behavior or an artefact of variance associated with scale-specific independent variable structure (*sensu* Wheatley 2010), or dependent-variable cross-scale variance. That is, are we observing habitat use where animal behaviors overcome potential limitations of physical habitat structure? Or, are animals simply coping, whereby observed peaks in habitat-model fit are associated with some form of independent-variable variance structure (e.g., average patch size determines animal movement distances)? Currently we lack formal techniques to decouple ‘habitat use’ from ‘habitat coping’, but these can be developed only via an empirical examination of a biologically relevant section of the scale continuum; thus the continuum approach espoused here should form a key step in this process.

Squirrel biology

To make inferences regarding squirrel habitat use, I assume that peaks in model support along the scale continuum identify observational scales within which animals perceive their proximate environment more so relative to other scales. Further, because models reflect out-of-nest behavioral focals, the data collected herein do not address nest-site habitat per se (though a significant portion of observations were arguably in proximity to nest sites; see this thesis, Figure 3-1, black bars). It follows then that adult males perceive proximate habitat structure differently than either females or dispersing juveniles, whereby relevant scales for males < females ≤ dispersing juveniles. From a behavioral perspective, this might reflect different life-history requirements among lone males, nursing females, and weaning / dispersing juveniles.

Daily space use for lone males, particularly post-breeding-season and with no parental-care duties, theoretically would be driven by optimal foraging and predation avoidance. However, the best-supported models suggest otherwise, whereby males ostensibly use more open drier areas with lower shrub cover; there were no other clear relationships to forest-structure variables, particularly pertaining to predation avoidance (e.g., complex closed forest, etc.). This relationship was found along a scale domain from 0.08 – 1 ha,

with a peak therein at 0.32 ha (Figure 5-3), suggesting that this relationship is best quantified within this domain, and that (a) male squirrels perhaps function intentionally at these scales, or (b) fine-grain habitat is somehow structured on average at scales around or approximating 0.32 ha and squirrels respond accordingly.

For males, the *a priori* hypothesis supported by the data (Table 5-3) is that male squirrels choose areas based on characteristic moisture conditions indicative of either wet- or dry-associated fungal communities, and that these areas change annually in both availability and location. If my hypotheses hold, then the data not only suggest that fungal-associated foraging over-rides general forest structure for predicting male-squirrel space use, but that the fungal communities targeted therein (see Wheatley 2007a) are indicative of dry areas with relatively low shrub or downed-wood cover. This contradicts most published accounts of flying squirrel micro-site preference or small-scale space use (positive shrub and downed-wood relationships; Carey et al. 1999; Pyare and Longland 2002; Smith et al. 2004; Smith et al. 2005; Holloway and Malcolm 2006). Further, the comparable plot scale used in previous studies (20-m diameter circular plot; roughly 0.03 ha; e.g., Pyare and Longland 2002; Smith and Nichols 2004) was discounted herein in favour of the 0.32 ha plot size (Figure 5-3). Therefore, different conclusions among studies are either an artefact of sampling strategies and scale, or reflect a true geographic difference among populations. Because a continuum of scales was not sampled elsewhere, this discrepancy cannot be sorted; however, because selection and interpretation of the best models chosen herein was done relative to the whole scale continuum, I can be sure that scale is not the lurking variable (*sensu* Sandel and Smith 2009) driving my results, and that differences among studies are perhaps largely an artefact of scale.

Daily space use for breeding females in theory would be constrained by energetic demands of lactation and by the time required to nurse young within proximity of the natal nest. For females, there were three characteristic scales (0.02 ha, 1 ha, and 13 ha), each with relatively strong w_i weighting (Figure 5-3); however only the 0.02 ha and 13 ha-scale models contained significant forest-structure variables (Tables 5-6, 5-7, and 5-8) and thus are the focus here (e.g., see Arnold 2010). Model support at the 0.02 ha scale may be a function of nursing young and remaining within proximity of the nest,

particularly since neither nursing juveniles nor their mothers spent > 2 hours afield before returning to the nest ostensibly to nurse (M. Wheatley, unpublished data). The *a priori* hypothesis supported at the 0.02 ha scale (Table 5-3; model #16) is that females prefer unfragmented forests (large patch sizes imply at this scale relative connectivity) with developed over- and under-stories indicative of many nest sites and foraging areas observed throughout this study (i.e., Wheatley and Larsen 2008, top-right of Fig 3, therein quantified as dense black spruce-willow forests; this thesis Figure 3-3). Similar model support was found at the larger 13 ha scale, where the *a priori* hypothesis (Table 5-3; model #2) was that large trees and forest complexity facilitate movement for efficient foraging (long glides) and heterogeneous, patchy forests provide cover and forest complexity to avoid predation while foraging. However, I found a negative association with canopy cover, observed in the field as relatively long-range foraging bouts into younger regenerating stands where I often observed females consuming tree sap and cambium from regenerating lodgepole pine saplings <3m in height. Thus female space use appears truly to be multi-scale, whereby there is simultaneous selection for both safe nest sites, and younger open forests for foraging. This type of multi-scale response has yet to be quantified in this context for any animal (see Wheatley and Johnson 2009 for a review).

Juvenile flying squirrels generally are not philopatric (at least from European evidence; Selonen et al. 2007; Hanski and Selonen 2008); thus dispersing juveniles, in theory, should function at larger scales and respond to forest structure relevant to more landscape-level dispersal cues. The *a priori* hypothesis supported by these data is the same for adult females at the 13 ha scale (large trees and forest complexity facilitates safe among-patch movement), with the same caveat being a negative relationship with canopy cover. Unlike females, juveniles were not observed foraging on tree stems within younger forests; however, they did explore these areas during dispersal bouts outside of the natal territory. Feeding observations for juveniles indicate that these bouts are not to exploit resources, but rather are exploratory forays whereby juveniles are gaining knowledge of the surrounding landscape at the home-range scale, information that would partially inform the proximate choice to disperse or remain philopatric.

In terms of forest management, my results do not suggest that these animals are constrained to older forests except for nest requirements. Generally, flying squirrels in this system appear able to effectively utilize variable-aged stands and traverse or forage within numerous forest types. Previous research has linked flying squirrels to older-growth conifer forests (see Smith 2007 for a review), and scientists have suggested that to sustain flying squirrel populations managers should conduct selective harvesting to maintain older-forest characteristics such as snags, old-stand patches, shrub cover, and coarse woody debris (e.g., Carey 2000; Holloway and Malcom 2006; Smith 2007 and references therein). My results suggest that different forest attributes are required depending on squirrel gender and age. Whether forest managers can effectively create such features through logging will vary among regions; features such as moisture levels and shrub cover, found significant herein, typically are not managed effectively through commercial timber-harvesting techniques. However, features such as patch size, patch types, sub-canopy and canopy-cover can be generated through various management prescriptions including both clear and partial/selective harvest, and effective replanting. As long as nest sites are retained, flying squirrels in this system appear able to exploit a mosaic of forest habitats (Wheatley et al. 2005), of both natural and harvest-regenerating origin and appear capable of persistence under existing management regimes in the foothills of west-central Alberta.

Chapter 6 Factors limiting our understanding of ecological scale in wildlife-habitat studies.⁴

Abstract

Multi-scale studies ostensibly allow us to form generalizations regarding the importance of scale in understanding ecosystem function, and in the application of the same ecological principles across a series of spatial domains. Achieving such generalizations, however, requires consistency among multi-scale studies not only in across-scale sample design, but also in basic rationales used in the choice of observational scale, including both grain and extent. To examine the current state of this science, here I review 79 multi-scale wildlife-habitat studies published since 1993. I summarize rationales used in scale choice and also review key differences in scale-specific experimental design among studies. I found on average that 70% of the observational scales employed in wildlife-habitat research were chosen arbitrarily with no biological connection to the system of study, and with no consideration regarding domains of scale for either dependent or independent variables. Further, I found it common to change either both grain and extent, or the entire suite of independent variables across scales, making cross-scale extrapolations and generalizations impossible. I discuss these sampling limitations by clarifying the differences between multi-*scale* versus multi-*design* studies, including the distinction between *spatial* versus *scalar* observations, and how these may differ from the commonly cited “orders of resource selection”. I conclude by reviewing both existing and suggested alternatives to reduce the arbitrary nature of observational scale choice prevalent in today’s wildlife literature.

Introduction

Most ecologists now agree that scale is important when acquiring and interpreting ecological data. Scalar aspects of ecological observation and analysis have become

⁴ This chapter has been published as “Wheatley, M. and C. Johnson. 2009. Factors limiting our understanding of ecological scale. *Ecological Complexity* 6:150-159” and is reproduced here in published form, save for minor editorial adjustments for thesis format (e.g., changing “we” to “I”).

common over the last two decades, and now figure prominently in prioritizing research objectives (Levin 1992), designing organism-centered sampling methods (Wiens 1989), and extrapolating process from observed patterns (Turner et al. 1985; Turner 2005). These ideas have inspired a growing number of “multi-scalar analyses” intent on describing ecological phenomena at more than one observational scale. Unfortunately, increased interest in ecological scale has not resulted in new or innovative understanding of basic questions in scalar ecology. We still lack the ability to predict across observational scales, which ultimately hinders progress from observed patterns to known mechanisms and processes. I argue that this inability stems from arbitrary and inconsistent cross-scale study design. To demonstrate this, I review and summarize a large sample of peer-reviewed literature that focuses on the application of scaling principles to wildlife-habitat models. I examine the rationale used by researchers to choose observational scales; evaluate the most commonly used approaches to multi-scale ecological studies; and from this, I summarize some limitations in scale research that require innovation and improvement.

Why use more than one observational scale? Most ecologists likely consider this question rhetorical, but approaches to and interpretations of multi-scale analyses suggest otherwise. The impetus for multi-scale studies should be two-fold. First, the same ecological process might show different patterns if observed at different scales. If we study a system at an inappropriate scale, we may not detect its actual dynamics, but may instead identify patterns that are artefacts of scale (Wiens 1989). The inability to distinguish emigration from mortality in many live-capture studies, for instance, is an artefact of trapping-grid scale. Second, not all aspects of an animal’s biology can be observed using one observational scale. For example, different observational scales are required for local foraging versus natal dispersal. These are practical sampling reasons for using multiple observational scales, but there is also a fundamental theoretical reason that receives almost no attention: namely, the ability to *predict* patterns and processes across scales. Because ecological data are always limited, the ability to scale-up or scale-down in our predictions is crucial, particularly in conservation and management of wide-ranging species. But, despite a growing number of apparent scale-focused studies, empirical support for ecological scaling techniques remains elusive.

Why are we still largely unable to extrapolate across scales (Levin 1992; Heuvelink 1998; Clark et al. 2001; Peters and Herrick 2004)? There are arguably several reasons, the most notable in the literature being our varied definitions of scale (e.g. Dungan et al. 2002), but perhaps the most elementary involve basic study design, and specifically the rationales used in choosing observational scales. Every scalar study must begin with the selection of a relevant scale, defined in ecological contexts as “the spatial or temporal dimension of an object or process, characterized by both grain and extent” (Turner et al. 1989, Gustafson 1998, Dungan et al. 2002; also see Schneider 2001). The constituents of grain and extent are the fundamentals of how we observe ecological systems; grain referring to the finest level of spatial resolution available in a data set, and extent to the physical size or duration of an ecological observation (Turner et al. 1989). Ideally, these both are selected based on relevant information regarding a species’ biology, or grain of perception (Wiens 1989), but often this is unknown and scalar references are arbitrary. With rare exception the number of scales employed is limited, meaning much weight rests upon rationales used in scale selection. Therefore, it is important to clarify rationales employed in selecting observational scales. If choices are largely arbitrary, published results may reflect scale artifacts and, by examining irrelevant or redundant scales of observation, may entirely miss true scalar processes. Patterns observed across scales will form the bases of hypotheses exploring underlying processes (Swihart et al. 2002), so an important distinction is whether these are derived from arbitrary/anthropocentric versus biological/organism-centered study designs. Similarly, it is worth examining whether cross-scalar experimental designs are consistent among studies. Both of these factors largely define our ability to produce scalar extrapolations and generalizations within the “science of scale” (Goodchild and Quattrochi 1997).

Choice of Observational Scale

To quantify how observational scales have been chosen for study, I reviewed all multi-scale articles from a sample of journals that publish scalar studies: *Landscape Ecology*, *Journal of Wildlife Management*, and *Journal of Applied Ecology*. My focus was on wildlife-habitat research: because study taxa are mobile and range over multiple scales, this field of study has produced more multi-scale studies than most, including the

geographical sciences. It is from these studies where scalar insights will be generalized into the broader ecological literature. I used Web of Science to search for articles identifying “spatial” or “scale” in their abstract; then, I chose those claiming to have employed >1 observational scale. I analyzed each paper and determined the rationale for selecting the number and dimensions of each spatial scale. I considered choice of scale non-arbitrary if the authors provided a link between scale (grain or extent) and some aspect of the organism’s biology (e.g. movement parameters, home range, dispersal area, foraging distance, etc.), even if cited from previous research. If authors chose a scale because they “felt it to be representative...” or “considered it a good compromise...” I scored these as arbitrary. I noted taxonomic class and field of study (population or community). In total, I reviewed 79 multi-scale wildlife-habitat studies published between 1993 and 2007. I summarized trends in choice of scale over time and among taxonomic and research sub-disciplines (i.e. population versus community ecology). Additionally, I compared and summarized the experimental design employed for each study.

The majority of studies I reviewed were premised on arbitrary choice of scale (Table 6-1; Figure 6-1). Over the 14-year review period, only 29% (± 5 SEM) of the observational scales I examined had a biological rationale for their use. Although variation around each annual mean was relatively high (Figure 6-1), in no single publication year did >50% of the scales have direct biological links to the species being studied. The number of multi-scalar studies has generally increased over time, with a peak in 1995 and 2004 (Figure 6-1). When viewed by taxonomic class, the majority of scalar studies have been completed on birds and mammals (Table 6-1), with mammalogy showing the highest proportion of non-arbitrary scale choice, though still only 45% on average. Most scale work has been done at the population versus the community level and the majority of observational scales (approximately 60-80%) were chosen arbitrarily (Table 6-2). Regardless of publication year or field of study, using arbitrary scales of observation clearly is pervasive.

How might the choice of observational scale affect our understanding of ecological scale? Most studies justify at least one observational scale anchored to something biological (home range or core areas, etc.), and then arbitrarily choose one larger and one

smaller scale (i.e. 2/3 arbitrary = ~70%; the average finding of this review; Table 6-2). With data deficiencies common in ecology, some might argue all we can do is arbitrarily select scales. Eventually, however, patterns from these studies must drive process-focused hypothesis-based research. Absent from this literature is concern whether arbitrarily chosen scales are even on different scale domains (Wiens 1989) than others employed in the same study. Currently, existing scale research is poised to proceed to this stage on patterns that might largely be artefacts of scale alone, from studies principally employing either anthropocentric or arbitrary scales of observation. Arbitrary scale choice will inhibit our ability to make cross-scale predictions, which essentially is the primary reason for doing multi-scale analyses.

Table 6-1. Total counts and proportion of non-arbitrary spatial scales employed among different taxonomic groups for scalar ecology studies done over the last 2 decades. A total of 79 studies were reviewed from the journals Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology taken from issues published between 1993 and 2007.

Year	Taxa			
	Birds	Herps	Inverts	Mammals
1994			1	
1995	1			1
1996	1		1	1
1997	1			1
1998	2			
1999	4			2
2000			1	3
2001	1			2
2002	4	1		1
2003	1	1	1	3
2004	1	2	1	5
2005	8	1	1	6
2006	8			4
2007	3		1	3
Total count	35	5	7	32
Proportion of non-arbitrary scales (\pm SEM)	23% \pm 6	0	0	45% \pm 7

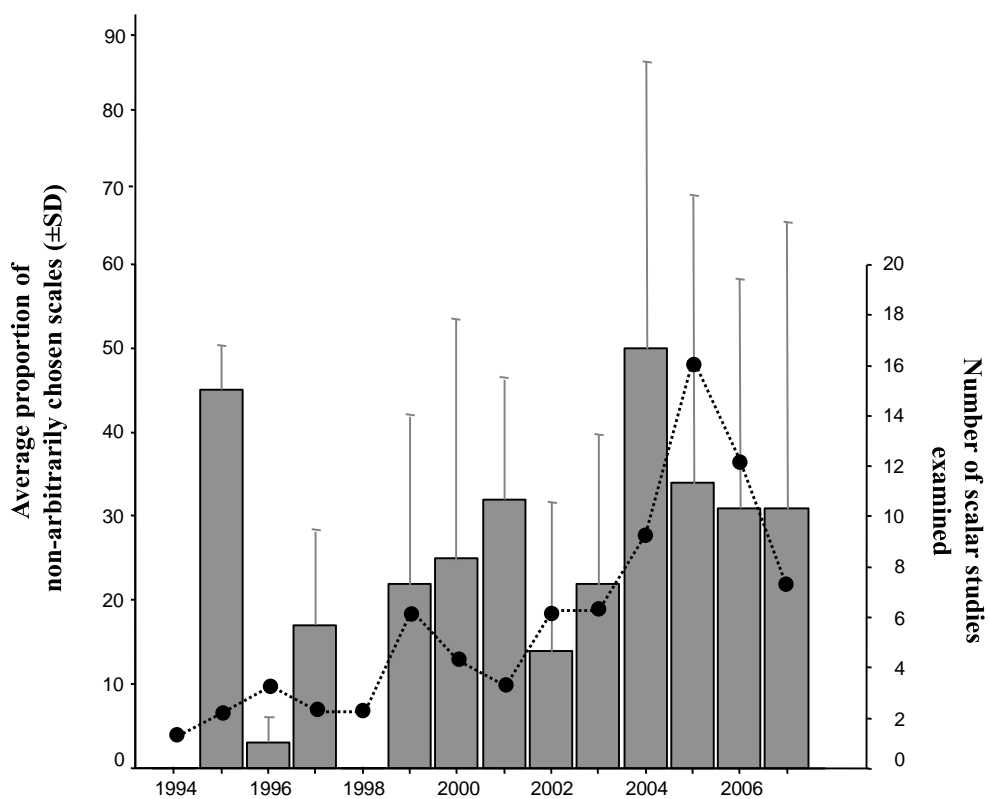


Figure 6-1. Average proportion of non-arbitrary scales used in scalar ecology studies (bars, left y-axis), and the number of studies examined for each year (dotted line, right y-axis). A total of 79 studies were reviewed from the journals *Landscape Ecology*, *Journal of Wildlife Management*, and *Journal of Applied Ecology* taken from issues published between 1993 and 2007.

Table 6-2. Articles included in this review, listed chronologically within each taxonomic group. The proportion of non-arbitrary observational scales represents the number of scales selected using biological rational divided by the total number of scales used within each study.

Field of Study	Proportion of Non-arbitrary observational scales	Citation
Birds		
Community	0	Naugle et al. 1999
	0	Powell and Steidl 2002
	50	La Sorte et al. 2004
	0	Cleary et al. 2005
	0	Dunford and Freemark 2005
	0	James et al. 2006
	50	Koper and Schmiegelow 2006
	0	Huettmann and Diamond 2006
	67	Coreau and Martin 2007
	0	Thogmartin and Knutson 2007
Population	40	Baker et al. 1995
	0	Squires and Ruggiero 1996
	33	Moen and Gutierrez 1997
	0	Steeger and Hitchcock 1998
	0	Dellasala et al. 1998
	0	Hall and Mannan 1999
	0	Thome et al. 1999
	100	Miller et al. 1999
	20	Daw and DeStefano 2001
	0	Thompson and McGarigal 2002
	20	Fuhlendorf et al. 2002
	0	Meyer et al. 2002
	14	Hatten and Paradzick 2003

	100	Whittingham et al. 2005
	0	Driscoll et al. 2005
	50	Manzer and Hannon 2005
	50	Blakesley et al. 2005
	0	Graf et al. 2005
	0	Bayne et al. 2005
	25	Miles et al. 2006
	0	Mahon and Martin 2006
	0	Sharp and Kus 2006
	0	Li et al. 2006
	100	Manning et al. 2006
	100	Graf et al. 2007
Reptiles/Amphibians		
Community		
	0	Welsh and Lind 2002
	0	Martin and McComb 2003
	0	Price et al. 2005
	0	Fischer et al. 2004
Population		
	0	Russell et al. 2004
Invertebrates		
Community		
	0	Duffield and Aebisher 1994
	0	Cowley et al. 2000
	0	Fleishman et al. 2003
	0	Chust et al. 2004
	0	Schweiger et al. 2005
	0	Yaacobi et al. 2007
Population		
	0	Lesna et al. 1996
Mammals		
Community		
	50	Wallace et al. 1995
	50	Gabor et al. 2001
	100	Johnson et al. 2004a
	50	Holloway and Malcolm 2006
Population		
	8	Bowyer et al. 1996

0	Pedlar et al. 1997
0	Taylor et al. 1999
33	Bowers and Dooley 1999
0	Terry et al. 2000
0	Zimmerman and Glanz 2000
100	Schaefer et al. 2000
25	Apps et al. 2001
67	Bond et al. 2002
67	Chamberlain et al. 2003
0	Weir and Harestad 2003
50	Gosselink et al. 2003
100	Johnson et al. 2004b
100	Atwood et al. 2004
33	Lopez et al. 2004
67	Apps et al. 2004
67	Wheatley et al. 2005
0	White et al. 2005
100	Anderson et al. 2005
50	Said and Servanty 2005
33	Wallace and Crosthwaite 2005
100	Fisher et al. 2005
100	Gustine et al. 2006
14	Watrous et al. 2006
33	Telesco and Van Manen 2006
50	Slauson et al. 2007
0	Limpert et al. 2007
0	Benson and Chamberlain 2007

Cross-scalar predictability

Cross-scalar predictability should be the paramount question in scalar ecology, but is missing from almost all multi-scale studies I reviewed. This is not a new concept. Wiens (1989), for example, clearly outlined why the identification of “domains of scale” is key to our understanding of ecological systems. He contends if the scale spectrum is not

continuous (i.e. every change in scale does not bring with it changes in patterns and processes), there may be domains of scale over which patterns and processes are predictable. If we can predict how observations will change among domains (the space between known break-points), we may be able to extrapolate observations among scales. For instance, rather than measuring animal density in 10 30-hectare forests, we might only measure density in 10 2-hectare forests, and then scale up. The logistical implications are striking, but the theoretical implications carry even more weight: points where pattern and process change along a scale continuum likely identify key shifts in ecological processes. Why is this not a primary objective of multi-scale studies? Based on our literature review, I submit this happens from researchers confounding *spatial* and *scalar* approaches, combined with a misconception between *orders of resource selection* (Johnson 1980) and *scales of observation*.

Spatial versus scalar observations

Ecologists must clearly distinguish between *spatial* and *scalar* observations. This distinction exists in various forms (e.g. Pickett et al. 1994, Stern 1998, Dungan et al. 2002), but in practice the two are used interchangeably creating an ambiguity that has sobering implications for scalar sampling design, analysis, and interpretation. *Spatial* sampling deals with x-y locations in space, and observations generally consist of patch occupancy, distance-to, or time-budget measurements quantifying observational variation irrespective of grain or extent. Unless initially quantified as zero, variation in *spatial* observations will not change with changes in extent. However, an object's referenced position in space most likely will vary with changes in grain; but this would then represent a *scalar* sampling design.

A *scalar* sampling design deals with changes in either grain or extent: to make scalar inferences, changes in one cannot accompany changes in the other, and independent variables must remain consistent across scales (e.g. Figure 6-2A and 6-2B). If grain and extent are changed simultaneously, one cannot decouple the importance of each if patterns change among observational scales. Often when this occurs (e.g. Dellasala et al. 1998; Terry et al. 2000; Zimmerman and Glanz 2000; Gabor et al. 2001; Chamberlain et

al. 2003; Lopez et al. 2004; Mahon and Martin 2006; Benson and Chamberlain 2007), it is the smallest scale that is spatial rather than scalar (e.g. Figure 6-2C). For instance, measurements of habitat proportions within core areas or home ranges are common in multi-scale studies (Apps et al. 2001; Gosselink et al. 2003; Wheatley et al. 2005; amongst others). But, when scaling down to individual animal locations (often termed micro-site or foraging scales; Moen and Gutierrez 1997; Welsh and Lind 2002; Zimmerman and Glanz 2000), a tendency exists to switch from habitat proportions to proportion of locations within habitats (e.g. Chamberlain et al. 2003), the latter denoting a change from scalar to spatial sampling (e.g. Figure 6-2C). Similarly, nest-sites often are used as focal points for multi-scale studies, whereby habitat proportions are summarized around each nest. Although “nests” versus “landscapes” are treated as separate scales, individual nests often are described in both non-spatial and non-scalar terms (e.g. nest height, tree diameter, slope, aspect, etc.; Figure 6-2D) without reference to any particular grain or extent (e.g. Squires and Ruggeiro 1996), and are not scales in and of themselves. Because both grain and extent are changed simultaneously among observations, or are not referred to at all, these types of designs prevent cross-scale comparisons or generalizations. They are in effect multi-*design* studies, not multi-*scale* studies, and are only partially relevant to scalar ecology.

Pseudo-scales

Problems can still manifest when grain or extent are controlled across observational scales. For instance, using multiple replicates of the same plot size to scale up and quantify habitat over larger scales (e.g. Figure 6-2E; Hall and Mannar 1999; Weir and Harestead 2003; Cleary et al. 2005) is not a valid multi-scalar approach. Such techniques simply capture average habitat variation at a single extent from several equal-sized plots (e.g. Figure 6-2E), effectively masking changes in variation among scales (i.e. the metric of interest). In a related sense, quantification of used-versus-available habitat must be done using similar extents for both used *and* available habitat, such that variation associated with *smaller* core areas (used habitat) is not compared directly to variation associated with arbitrarily defined, *larger* study areas (available habitat; Figure 6-2F). Because we expect different variance structures associated with each change in extent

(e.g. the modifiable area unit problem, or MAUP; Openshaw 1984), different extents cannot be compared directly in this respect.

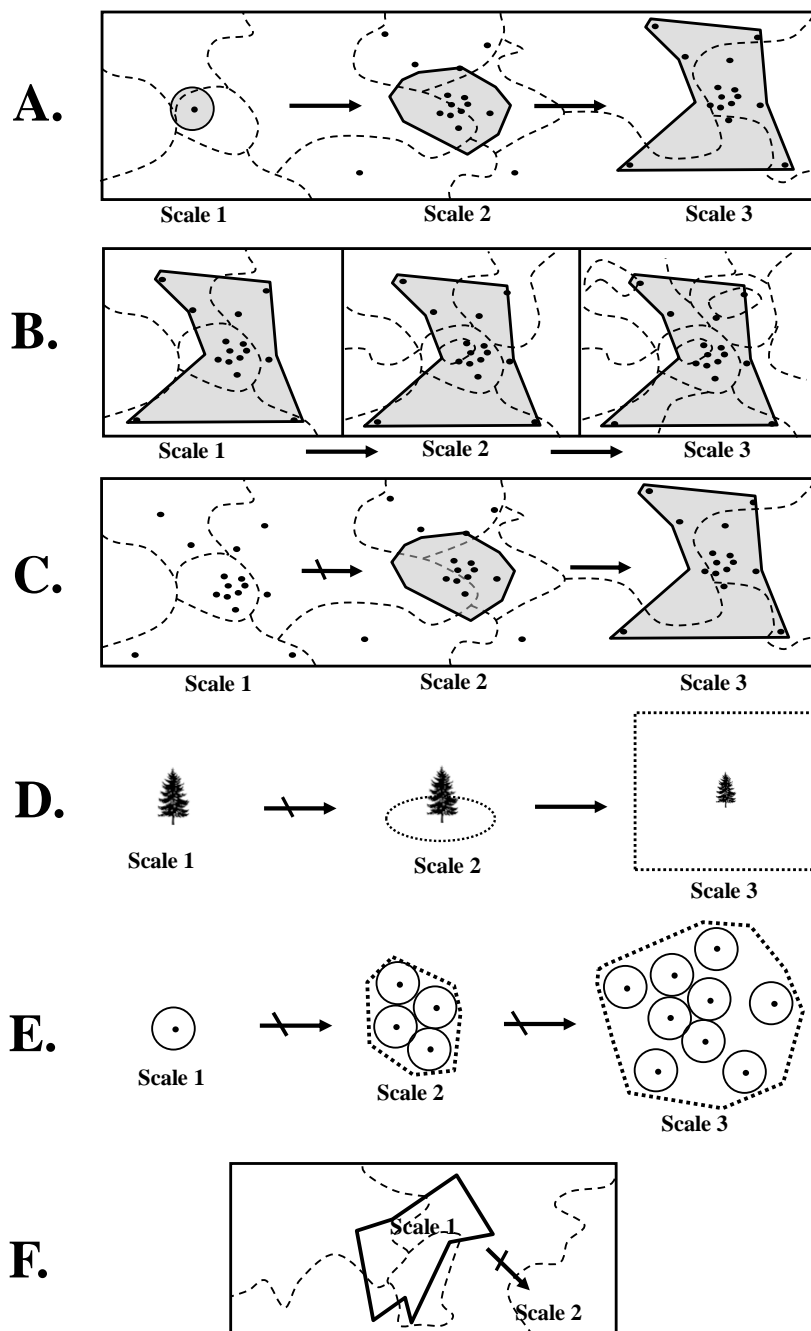


Figure 6-2. See next page for caption.

Figure 6-2. A summary of commonly used sampling approaches to “multi-scalar” studies in ecology.

Scales denoted in quotations are either non-scalar (broken arrow denoted in figure) or do not constitute appropriate multi-scalar comparisons. **(A) Multi-scalar extent approach:** A truly scalar approach where habitat structure is summarized around animal locations (black dots) at varying spatial extents (gray areas) and grain is held constant. In this approach, the variation associated with habitat structure at multiple scales is captured, and can thus be legitimately compared among scales. In this example, the same habitat variables are quantified around a single point (scale 1), then around a cluster of points (e.g. kernel-based core area; scale 2), then around a home range (e.g. MCP; scale 3). **(B) Multi-scalar grain approach:** Similar to 1A above; a true scalar approach where only grain is altered to make changes in scale, but extent is held constant. **(C) Mixed spatial-scalar approach:** In this approach, scale 1 is examined by comparing the proportion of points falling within different habitat polygons to a random distribution of points. Larger scales are then examined using the same methods as 2A above. Though purported as multi-scalar (3 scales), this approach in fact only examines 2 scales: the smallest “scale” is not scalar; it is spatial: no variation in habitat structure is captured at the smallest “scale”. **(D) Multi-scalar nest-trees:** Commonly used to evaluate nest sites at multiple scales, this approach is similar to 2B above, whereby non-scalar metrics (e.g. DBH, nest height, aspect, nest type) of individual nest trees are measured at the smallest “scale”, then larger scales are evaluated by quantifying different habitat variables (usually landscape metrics such as patch size, patch type by area, etc) at larger scales. Scale 1, the smallest “scale” in this approach, is in fact non-scalar, and is often also non-spatial. **(E) Invariant plot size:** This approach attempts to quantify habitat characteristics over increasingly larger areas, beginning at a single animal point location and progressively including larger numbers of points over larger areas. However, to cover larger areas inclusive of several points, multiples of the same plot size are used, effectively only quantifying habitat variation at a single scale. **(F) Compositional-type analysis:** Habitat within a “used area” (e.g. a core area; scale 1) is compared to habitat available throughout the study area (scale 2), effectively comparing habitat and its associated variability quantified at 2 different scales; the core use area (smaller scale) to the study area (larger scale). This approach is only scalar if used- and available-habitat plots are equal in size such that increases/decreases in scale are applied equally to both.

Orders of resource selection versus observational scales

One of the most-cited papers in multi-scalar wildlife-habitat studies is Johnson’s (1980) article on resource use-versus-availability and orders of resource selection. Most authors use this context when describing their choice of observational scale, from micro-site (4th-order selection) to landscape-scale (1st or 2nd-order selection). Johnson (1980) presents some statistical methodology to account for how used versus available resources can be quantified. In doing so he also presents a hierarchical method to define and rank

resources used at different orders of selection. Johnson (1980) argues this hierarchy would have a unifying nature for habitat-use studies, allowing disparate studies to become comparable once organized within the hierarchy.

Though I agree with this in theory, based on its citation use Johnson's hierarchical approach largely has been misinterpreted as a scalar approach, or a method to choose relevant scales and their associated independent variables. Many studies citing this work conceptualize observational scales and selection orders as the same things, perhaps because higher-order selection originally was defined in more spatial terms (i.e. actual food items at a feeding site; 4th-order selection; Johnson 1980, p.69). The result of this misconception is that higher selection orders are sampled *spatially* and are in fact also non-scalar, whereas lower orders of selection are sampled within and in reference to defined spatial extents (e.g. home ranges, plot sizes, study areas, etc.). Unlike lower orders of selection, many third- or fourth-orders of selection in wildlife-habitat studies entirely lack a spatial grain or extent (e.g. Squires and Ruggiero 1996; Moen and Gutierrez 1997; Steeger and Hitchcock 1998; Hall and Mannan 1999; Terry et al. 2000; Zimmerman and Glanz 2000; Gabor et al. 2001; Chamberlain et al. 2003; Lopez et al. 2004; Sharp and Kus 2006; amongst others). Failure to identify a grain or extent results in an operational inability to generalize across scales, because no common data are measured. Scaling up or down is impossible. This removes nothing from the validity of these studies in other respects, but they are not examining ecological scale, merely observing different phenomena in different ways within the same study (i.e. multi-*design* studies).

Orders of selection are conceptually useful, particularly in logic used to compare seemingly disparate resource-use studies, but they arguably encourage researchers to change both grain and extent, and the suite of variables observed among scales in their sample designs. When viewed strictly in scalar terms as multiple extents or grains, the focus then becomes changing only scale and not the independent variables measured among scales. Only then can we observe how the same variables change with changes in scale, and only then can we identify relevant domains of scale.

Solutions

How can we choose relevant scales of observation in the absence of organism-centered clues to scalar starting points? Methods for scale selection do exist, but most require organism data *a priori*. For example, first-passage time, defined as the time required for an animal to cross a circle with a given radius, can be a measure of how much time an animal uses within a given area, which will be scale dependent. A plot of variance in first-passage time versus spatial scale can reveal the scale at which the animal concentrates its search effort (Fauchald and Tveraa 2003) and perhaps perceives habitat structure. Similarly, frequency-based methods such as kernel densities (e.g. Seaman and Powell 1996) can be used to define focal areas within which habitat structure likely influences an animal's behavior and thus, from the size of these focal areas, can define starting points for observational scale. Movement analyses also can help determine biologically relevant observational scales. Curve-fitting models of movement distances (e.g. Sibly et al. 1990; Johnson et al. 2002) can suggest small versus large scales in reference to a study animal's behavior, or examination of walk parameters (e.g. random, Levy flight, etc.; but see Edwards et al. 2007) can suggest both grain (focal areas) and extent (movement distances in-between). All of these, however, require detailed animal data at the onset which is not generally available.

In the absence of available animal data, how might we proceed to identify a justifiable observational scale? How big should the trapping grid be, or how far around a sampling transect should we quantify habitat structure? The most relevant clues in these situations are direct examination of variability associated with habitat structure *per se* among scales. Natural scalar breaks in average habitat values and their associated variation can give strong clues towards how an animal might *have* to perceive habitat structure. There might be clear breaks in the habitat-scale continuum within which animals are forced to cope, and which may help structure habitat-use hypotheses including choice of biologically relevant scales. This may suggest domains of scale within which changes in sampling extent will not generate significant changes in habitat structure. For example, homogeneous or monotonically scaling habitat proportions, or large average gaps between suitable patch types, if known, can suggest both a starting and end point for scale choice based on habitat scaling alone. At the least, this may help rule out redundant

scales where one should not expect new habitat relationships to form relative to other (similar) scales. The same logic can be used to interpret existing habitat models in scalar contexts. If a significant habitat model is found at one scale and not another, is this because the animal is in fact responding to habitat at that scale, or does that scale simply represent the grain and extent for which a given habitat variable inherently shows the least variation? Our interpretation is always the former, and never the latter (but see Johnson et al. 2004a), even though sophisticated techniques to examine within-plot mean and variance are well established in the literature (see Dale et al. 2002). A simple examination of the independent variables' cross-scale variation could give additional credence not only to the rationale behind choice of observational scale, but also to the final interpretation of statistically significant habitat models.

From this review three main ideas arise as suggestions to improve research in ecological scale. First, ecologists wishing to incorporate scale must be judicious to clarify multi-*scale* from multi-*design* studies. A simple examination of the literature on the number of multi-scale studies is misleading; many of these change both grain and extent, or the whole suite of independent variables among scales, which violates a truly scalar approach. These studies do not investigate scale *per se*, but rather ask different questions using different methods about different processes among what are misinterpreted as different scales (also see Mayer and Cameron 2003). Second, ecologists must decide *a priori* whether they can truly ask scalar questions using relevant scales of observations, or whether they are simply guessing at scale and fishing for scalar patterns irrespective of either; (a) the spatial grain and extent of hypothesized life history traits of an organism; or (b) an examination of the habitat-scale continuum to identify potential scale domains of habitat parameters hypothesized to be important to the study species. Rather than obfuscate the potential importance of scale through arbitrary study design, research efforts might best be directed in full to a single scale until a more informed rationale for multi-scale study can be generated. Lastly, we must clarify exactly why we employ multiple scales of observation: it should always be to improve our abilities in cross-scalar predictability, and to determine at what scales certain processes are relevant and among what scales we see breaks in these processes. To do this, however, requires consistent sampling of similar independent variables across different scales of observation.

Chapter 7 Contributions to knowledge

Chapter 1 outlines the general thesis and clarifies its flow and connectedness among chapters. Original contributions to scientific knowledge are found in chapters 2 through 6, which I outline briefly below.

Chapter 2 provides arguably the first explicit consideration of the impact of observational scale on contemporary GIS-based wildlife-habitat modeling. It also provides the most geographic-extensive empirical account of flying squirrel habitat associations from both foothills and boreal forests of central Canada. I generally found weak relationships between squirrel abundance and landscape structure and, rather than concluding that this was an ecological reality, I suggested that observational scale may play a key role affecting model output and I provided a general way forward to examine this issue in future studies. Prior to this study, neither extent nor grain were implicated directly as potentially primary drivers of species-habitat model output. In terms of squirrel-habitat relationships (and all potential scale-related bias equal among sampling plots), this study is the first to clearly dispel a common belief that flying squirrels are most strongly related to mature conifer forests. My data suggest that they are forest generalists and can be found in a wide variety of both conifer and deciduous forests, with no clear relationship to stand age or forest type.

Chapter 3 represents the first empirical comparison of spatial bias associated with the two most common small-mammal sampling methods, namely live-trapping and radio telemetry. Both techniques are used almost interchangeably to generate species-habitat models, and I argue here that, if dealing with habitat data of relatively fine ecological grain, both techniques will generate different habitat-use patterns. My primary hypothesis is related to trap bait and a potential “pantry effect” that draws animals into sampling areas, and my methods represent the only spatial test of small-mammal sampling-method bias between different field techniques. The key finding here is a quantified difference in observed habitat-use patterns acquired from trapping versus telemetry on the same squirrel populations, and an empirical warning of these issues when dealing with fine-

grain habitat data. As part of this test, I also generate the most detailed fine-grain habitat-use data to date on flying squirrels in central Canada (versus coarse-grain in Chapter 2), further outlining their habitat-generalist tendencies and their abilities to exploit a variety of forest types.

Chapter 4 is the first empirical demonstration of the importance of observational scale (extent) in the quantification of forest landscape metrics, including both average values and associated variances. Although similar examinations can be found in the landscape ecology literature, none have ever reported across-scale variances, nor have they related this to subsequent analyses like habitat modeling. As multi-scale wildlife studies proliferate (e.g., see Chapter 6) arbitrary quantification of habitat metrics among scales must be dealt with as a formal step in the model-building process. I approach this issue using two related concepts: first, an explicit focus on scale-related variance, and second, how this variance underpins the architecture of scale domains. I demonstrate how associated averages and variation change markedly and unpredictably across observational scale continua, making scale domains difficult to predict or choose qualitatively, and emphasizing that *a priori* selection of two “different” scales cannot be done intuitively, arbitrarily, or based on orders of resource selection. I conclude by suggesting that an empirical evaluation of the scale-domain continuum is a critically absent step in the building and interpretation of all multi-scale ecological models.

Chapter 5 is the first full application of what I term the “continuum approach” to wildlife-habitat modeling, and clearly demonstrates how different modeling results can be generated from the same data set based on observational scale alone. I quantify both dependent (squirrel telemetry) and independent (habitat metrics) data across 14 observational extents, and then using AIC-based model selection techniques, I identify the best-supported models for all observational scales. As hypothesized from Chapter 4, different models are supported among scales, likely directly related to scale-specific variance structure. More important, however, I found different levels of support (strength of evidence) for the best models among scales from the same data set, suggesting that all habitat-use models and the strength of these models are subject to observational-scale

choice (something mostly done arbitrarily). As such, these results provide empirical validation of the continuum approach to model selection, and question the validity of many published habitat-use models. Lastly, this chapter provides additional habitat-use information for both adult and dispersing-juvenile flying squirrels, and is one of only a few studies to date to employ LiDAR-derived forest-structure data in a wildlife context.

Chapter 6 evaluates the most common approaches to multi-scale wildlife-habitat studies, and attempts to clarify some fundamental concepts in scalar ecology to help improve future efforts in this field. I review 79 multi-scale studies from the primary literature (since 1993) and summarize the rationales used in observational-scale choice. I found the majority of studies examined (79%) selected scales arbitrarily, and none employed any techniques resembling the continuum approach espoused in Chapters 4 and 5 herein. Thus, the conclusions of most published studies are subject to scale-related sampling issues and are potentially spurious. Further, I identified a probable root of these issues in the confusion between “spatial” versus “scalar” observations, and the incorrect interpretation and application of “orders of resource selection” rather than empirical-observational scales (of either grain or extent). I conclude by clarifying the difference between what I term “multi-scale” and “multi-design” studies, and how we will advance the science of scale only with a clear understanding of these two very different approaches.

Through this research, I also revealed some new insights into flying squirrel ecology in a geographic region where we knew little about this species. First, I confirmed that flying squirrels are not conifer specialists in the forests of Alberta, and that this moniker is best restricted for now to the coastal forests of North America, and specifically the Pacific Northwest. Second, I found this generalist association not only for coarse-grain forest classes, but also for fine-grained forest attributes, whereby flying squirrels clearly used lodgepole pine, spruce, aspen, and black spruce forest both for foraging and nesting. At a fine-grain scale, I also found them associated with understory shrub cover, including *Shepherdia*, *Salix*, and *Alnus*, but this was not consistent among all analyses. Third, additional examinations based on LiDAR data showed that the best supported models for

adult male squirrels were at intermediate spatial extents, and contained negative selection coefficients for both shrub cover and ground moisture, contradicting most published habitat-use studies of flying squirrels and relating males to more open areas with perhaps fungal communities indicative of dryer sites. The inverse was found for adult females, relating these animals to developed over- and under-stories with relative connectivity among patch types found at both small and large spatial extents (i.e., truly multi-scale), possibly due to the energetic foraging constraints of lactation (large scale) and their consequent proximity to nesting sites (small scale). Juveniles were found associated with patch connectivity and complexity at larger spatial extents, consistent with hypotheses regarding dispersal forays and information-gathering activities.

In Chapter 1, I state my objective of adding at least one useful tool to the ecological scale toolbox. In this vein, I submit that the primary contribution of this thesis is an empirical construction and validation of the continuum approach to species-habitat model selection. The approach is functionally a relative comparison of model support across a relevant range of spatial extents (or grains). It allows researchers to identify peaks in habitat-use (i.e., model support, given the available data) at different scales; these are peaks that easily can be missed (or found) even with relatively small changes in observational-scale size. Rather than selecting a few arbitrary observational scales, the ‘science of scale’ will be greatly advanced through comparisons of scale relativity, and evaluating model support along a relevant and sufficient breadth of the scale continuum.

Literature Cited

- Amaranthus, M.P. and Perry, D.A. (1987) Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. *Canadian Journal of Forest Research*, 17, 944-950.
- Amaranthus, M.P., Trappe, J.M., Bednar, L., and Arthur, D. (1994) Hypogeous fungal production in mature douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Canadian Journal of Forest Research*, 24, 2157 – 2165.
- Allen, T.F.H. and Starr, T.B. (1982) *Hierarchy: perspectives for ecological diversity*. University of Chicago Press, Chicago, USA.
- Anderson, D.P., Turner, M.G., Forester, J.D., Zhu, J., Boyce, M.S., Beyer, H., and Stowell, L. (2005) Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management*, 69, 298-310.
- Anderson, D.R., Burnham, K.P. and Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, 64, 912-923.
- Apps, C.D., McLellan, B.N., Kinley, T.A., and Flaa, J.P. (2001) Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *Journal of Wildlife Management*, 65, 65-77.
- Apps, C.D., McLellan, B.N., Woods, J.G., and Proctor, M.F. (2004) Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management*, 68, 138-152.
- Arbuckle, K.E. and Downing, J.A. (2002) Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 310-316.
- Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, 74, 1175-1178.
- Atwood, T.C., Weeks, H.P., and Gehring, T.M. (2004) Spatial ecology of coyotes along a suburban-to-rural gradient. *Journal of Wildlife Management*, 68, 1000-1009.

- Baker, B.W., Cade, B.S., Mangus, W.L., and McMillen, J.L. (1995) Spatial analysis of sandhill crane nesting habitat. *Journal of Wildlife Management*, 59, 752-758.
- Ball, S.J., Lindenmayer, D.B., and Possingham, H.P. (2003) The predictive accuracy of population viability analysis: a test using data from two small mammal species in a fragmented landscape. *Biodiversity and Conservation*, 12, 2393-2413.
- Bayne, E.M., Van Wilgenburg, S.L., Boutin, S., and Hobson, K.A. (2005) Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. *Landscape Ecology*, 20, 203-216.
- Becker, C. D. (1992) Proximate factors influencing the timing and occurrence of reproduction in red squirrels, *Tamiasciurus hudsonicus*. Ph.D. dissertation, University of Alberta, Edmonton, Alberta, Canada.
- Benson, J.F. and Chamberlain, M.J. (2007) Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *Journal of Wildlife Management*, 71, 117-126.
- Beyer, H. L. (2004) Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- Blakesley, J.A., Noon, B.R., and Anderson, D.R. (2005) Site occupancy, apparent survival, and reproduction of California spotted owls in relation to forest stand characteristics. *Journal of Wildlife Management*, 69, 1554-1564.
- Bonar, R.L. (2000) Availability of Pileated Woodpecker cavities and use by other species. *Journal of Wildlife Management*, 64, 52 – 59.
- Bond, B.T., Burger, L.W., Leopold, B.D., Jones, J.C., and Godwin, K.D. (2002) Habitat use by cottontail rabbits across multiple spatial scales in Mississippi. *Journal of Wildlife Management*, 66, 1171-1178.
- Boutin, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, 68, 203-220.
- Bowers, M.A., and Dooley, J.L., (1999) A controlled, hierarchical study of habitat fragmentation, responses at the individual, patch, and landscape scale. *Landscape Ecology*, 14, 381-389.

- Bowman, J., and Fahrig, L. (2002) Gap crossing by chipmunks: and experimental test of landscape connectivity. *Canadian Journal of Zoology*, 80, 1556-1561.
- Bowman, J., Forbes, G. and Dilworth, T. (2000) Landscape context and small-mammal abundance in a managed forest. *Forest Ecology and Management*, 140, 249-255.
- Bowyer, R.T., Kie, J.G., and VanBallenberghe, V. (1996) Sexual segregation in black-tailed deer: Effects of scale. *Journal of Wildlife Management*, 60, 10-17.
- Bradbury, S.M., Danielson, R.M., and Visser, S. (1998) Ectomycorrhizas of regenerating stands of lodgepole pine (*Pinus contorta*). *Canadian Journal of Botany*, 76, 218 – 227.
- Bright, P.W. (1993) Habitat fragmentation - problems and predictions for British mammals. *Mammal Review*, 23, 101-111.
- Brooks, R.P. (1997) Improving habitat suitability index models. *Wildlife Society Bulletin*, 25, 163-167.
- Bujalska, G. (1989) Trap line and trap grid as methods of estimation of population parameters in the bank vole inhabiting Crabapple Island. *Acta Theriologica*, 34, 325-337.
- Burdsall, H.H. Jr. (1968) A revision of the genus *Hydnocystis* (Tuberales) and of the hypogeous species of *Geopora* (Pezizales). *Mycologia*, 60, 496-525.
- Burnham, K. P., and Anderson, D. R. (2002) Model selection and multi-model inference: A practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Carey, A. B. (1995) Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications*, 5, 648-661.
- Carey, A.B. (2000) Effects of new forest management strategies on squirrel populations. *Ecological Applications*, 10, 248-257.
- Carey, A.B., Horton, S.P and Biswell, B.L. (1992) Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs*, 62, 223-250.
- Carey, A.B., Kershner, J., Biswell, B. and Domínguez de Toledo, L. (1999) Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs*, 142, 1-71.

- Chamberlain, M.J., Conner, L.M., Leopold, B.D., and Hodges, K.M. (2003) Space use and multi-scale habitat selection of adult raccoons in central Mississippi. *Journal of Wildlife Management*, 67, 334-340.
- Chase, J.M., and Liebold, M.A. (2003) *Ecological Niches*. University of Chicago Press, Chicago, IL.
- Chust, G., Pretus, J.L., Ducrot, D., and Ventura, D. (2004) Scale dependency of insect assemblages in response to landscape pattern. *Landscape Ecology*, 19, 41-57.
- Claridge, A.W., Cork, S.J. and Trappe, J.M. (2000) Diversity and habitat relationships of hypogeous fungi. I. Study design, sampling techniques and general survey results. *Biodiversity and Conservation*, 9, 151-173.
- Clark, J. S., Macklinand, E., and Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, 68, 213-235.
- Cleary, D.F.R., Genner, M.J., Boyle, T.J.B., Setyawati, T., Angraeti, C.D., and Menken, S.B.J. (2005) Associations of bird species richness and community composition with local and landscape-scale environmental factors in Borneo. *Landscape Ecology*, 20, 989-1001.
- Clout, M.N., and Efford, M.G. (1984) Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). *Journal of Animal Ecology*, 53, 737-749.
- Coreau, A. and Martin, J.L. (2007) Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example. *Landscape Ecology*, 22, 747-764.
- Coté, M. and Ferron, J. (2001) Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. *Canadian Journal of Forest Research*, 31, 1805-1815.
- Cotton, C.L. and Parker K.L. (2000). Winter habitat and nest trees used by northern flying squirrels in subboreal forests. *Journal of Mammalogy*, 81, 1071-1086.
- Cowley, M.J.R., Wilson, R.J., Leon-Cortes, J.L., Gutierrez, D., Bulman, C.R., and Thomas, C.D. (2000) Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *Journal of Applied Ecology*, 37, 60-72.

- Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M. and Larsen K.W. (2000) Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. *Canadian Journal of Botany*, 78, 1514-1520.
- Dahlberg, A., and Stenstrom, E. (1991) Dynamic changes in nursery and indigenous mycorrhiza of *Pinus sylvestris* seedlings planted out in forest and clearcuts. *Plant and Soil*, 136, 73 – 86.
- Dale, M.R.T., Dixon, P., Fortin, M.J., Legendre, P., Myers, D.E., and Rosenberg, M.S. (2002) Conceptual and mathematical relationships among methods for spatial analysis in ecology. *Ecography*, 25, 558-577.
- Daw, S.K., and DeStefano, S. (2001) Forest characteristics of northern goshawk nest stands and post-fledging areas in Oregon. *Journal of Wildlife Management*, 65, 59-65.
- Deacon, J.W., Donaldson, S.J., and Last, F.T. (1983) Sequences and interactions of mycorrhizal fungi on birch. *Plant and Soil*, 71, 257 – 262.
- De Solla, S.R., Bonduriansky, R., and Brooks, R.J. (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, 68, 221-234.
- Dellasala, D.A., Anthony, R.G., Spies, T.A., and Engel, K.A. (1998) Management of bald eagle communal roosts in fire-adapted mixed-conifer forests. *Journal of Wildlife Management*, 62, 322-333.
- D'Eon, R.G., Serrouya, R., Smith, G., and Kochanny, C.O. (2002) GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin*, 30, 430-439.
- Dobson, F.S. (1979) An experimental-study of dispersal in the California ground-squirrel. *Ecology*, 60, 1103-1109.
- Donaldson, R. and Stoddart, M. (1994) Detection of hypogeous fungi by Tasmanian bettong. *Journal of Chemical Ecology*, 20, 1201-1207.
- Douglass, R.J. (1988) The Use of Radio-Telemetry to Evaluate Microhabitat Selection by Deer Mice. *Journal of Mammalogy*, 70, 648-652.

- Driscoll, M.J.L., Donovan, T., Mickey, R., Howard, A., and Fleming, K.K. (2005) Determinants of wood thrush nest success: A multi-scale, model selection approach. *Journal of Wildlife Management*, 69, 699-709.
- Duffield, S.J., and Aebisher, N.J. (1994) The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter-wheat. *Journal of Applied Ecology*, 31, 263-281.
- Dunford, W., and Freemark, K. (2005) Matrix matters, Effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecology*, 20, 497-511.
- Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M., and Rosenberg M. S. (2002) A balanced view of scale in spatial statistical analysis. *Ecography*, 25, 626-640.
- Ellis, B.A., Mills, J.N., Childs, J.E., Muzzini, M.C., McKee, K.T. Jr, Enria, D.A., and Glass, G.E. (1997) Structure and floristics of habitats associated with five rodent species in an agroecosystem in Central Argentina. *Journal of Zoology*, 243, 437-460.
- Engler, R., Guisan, A. and Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, 41, 263-274.
- Fauchald, P. and Tveraa, T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, 84, 282-288.
- Fischer, J., Lindenmayer, D.B., and Cowling, A. (2004) The challenge of managing multiple species at multiple scales: Reptiles in an Australian grazing landscape. *Journal of Applied Ecology*, 41, 32-44.
- Fisher, J.T., Boutin, S., Hannon, S.J. (2005) The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales. *Landscape Ecology*, 20, 73-82.
- Fleishman, E., Betrus, C.J., and Blair, R.B. (2003) Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA. *Landscape Ecology*, 18, 675-685.
- Fogel, R. (1976) Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas fir stand. *Canadian Journal of Botany*, 54, 1152-1162.

- Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., and Shackford, J.S. (2002) Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology*, 17, 617-628.
- Gabor, T.M., Hellgren, E.C., and Silvy, N.J. (2001) Multi-scale habitat partitioning in sympatric suiforms. *Journal of Wildlife Management*, 65, 99-110.
- Gehlke, C.E. and Biehl, K. (1934) Certain effects of grouping upon the size of the correlation coefficient in census tract material. *Journal of the American Statistical Association Supplement*, 29, 169-170.
- Gergel, S.E. and Turner, M.G. (2002) *Learning landscape ecology: A practical guide to concepts and techniques*. Springer New York.
- Gibson, L.A., Wilson, B.A., Cahill, D.M. and Hill, J. (2004) Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology*, 41, 213-223.
- Goodchild, M.F. and Quattrochi, D.A. (1997) Scale, multiscaling, remote sensing, and GIS. *Scale in Remote Sensing and GIS* (eds. D.A Quattrochi, and M.F. Goodchild), CRC Press, pp. 1-11.
- Gosselink, T.E., Van Deelen, T.R., Warner, R.E., and Joselyn, M.G. (2003) Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. *Journal of Wildlife Management*, 67, 90-103.
- Gotelli, N.J. and Ellison, A.M. (2004) *A primer of Ecological Statistics*. Sinauer Associates.
- Graf, R.F., Bollmann, K., Bugmann, H. and Suter, W. (2007) Forest and landscape structure as predictors of capercaillie occurrence. *Journal of Wildlife Management*, 71, 356-365.
- Graf, R.F., Bollmann, K., Suter, W., and Bugmann, H. (2005) The importance of spatial scale in habitat models: Capercaillie in the Swiss Alps. *Landscape Ecology*, 20, 703-717.
- Grinnell, J. (1917) The niche-relationships of the California Thrasher. *The Auk*, 34, 427-433.
- Gustafson, E.J. (1998) Minireview: Quantifying Landscape Spatial Pattern: What Is the State of the Art? *Ecosystems*, 1, 143-156.

- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. (2006) Interpreting resource selection at different scales for woodland caribou in winter. *Journal of Wildlife Management*, 70, 1601-1614.
- Hanski, I.K., and Selonen, V. (2008) Female-biased natal dispersal in the Siberian flying squirrel. *Behavioral Ecology*, 20, 60 – 67.
- Hall, L.S., and Mannan, R.W. (1999) Multiscaled habitat selection by elegant trogons in southeastern Arizona. *Journal of Wildlife Management*, 63, 451-461.
- Harmon, M.E., Sexton, J., Caldwell, B.A., and Carpenter, S.E. (1994) Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. *Canadian Journal of Forest Research*, 24, 1883–1893.
- Harvey, A.E, Larsen, M.J., Jurgensen, M.F., and Jones, E.A. (1989) Nitrogenase activity associated with decayed wood of living northern Idaho conifers. *Mycologia*, 81, 765-771.
- Hatten, J.R. and Paradzick, C.E. (2003) A multiscaled model of southwestern willow flycatcher breeding habitat. *Journal of Wildlife Management*, 67, 774-788.
- Hay, G. J., Marceau, D. J., Dube, P., Bouchard, A. (2001) A multiscale framework for landscape analysis: Object-specific analysis and upscaling. *Landscape Ecology*, 16, 471-490.
- Heneghan, L. and Bolger, T. (1998) Soil microarthropod contribution to forest ecosystem processes; the importance of observational scale. *Plant and Soil*, 205, 113-124.
- Heuvelink, G.B.M. (1998) Uncertainty analysis in environmental modelling under a change of spatial scale. *Nutrient Cycling in Agroeco-systems*, 50, 255-264.
- Holloway, G.J., Griffiths, G.H. and Richardson, P. (2003) Conservation strategy maps: a tool to facilitate biodiversity action planning illustrated using the heath fritillary butterfly. *Journal of Applied Ecology*, 40, 413-422.
- Holloway, G.L., and Malcolm, J.R. (2006) Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. *Journal of Wildlife Management*, 70, 1735-1745.
- Huettmann, F., and Diamond, A.W. (2006) Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic. *Landscape Ecology*, 21, 1089-1108.

- Huggard, D.J., Klenner, W., Kremsater, L., Dunsworth, G. (2007) Dispersal-based indices and mapping of landscape connectivity. *BC Journal of Ecosystems and Management*, 8, 14-28.
- Hutchinson, G.E. (1957) The multivariate niche. *Cold Spring Harbor Symposium on Quantitative Biology*, 22, 415-421.
- Ingham, E.R., and Molina, R. (1991) Interactions among mycorrhizal fungi, rhizosphere organisms, and plants. In Barbosa, P., Krischik, V.A., and Jones, C.G. (eds.) *Microbial mediation of plant-herbivore interactions*. John Wiley & Sons.
- Ireland, R.J. (1980) Checklist of the mosses of Canada. Canadian Botanical Association, National Museums of Canada, Ottawa, Ontario, Canada.
- Jaberg, C. and Guisan, A. (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology*, 38, 1169-1181.
- James, W.C., Smallwood, K.S., Morrison, M.L., and Loffland, H.L. (2006) Influence of mammal activity on nesting success of passerines. *Journal of Wildlife Management*, 70, 522-531.
- Jarvis, P.G. (1995) Scaling processes and problems. *Plant, Cell, and Environment*, 18, 1079-1089.
- Jeganathan, P., Green, R.E., Norris, K., Vogiatzakis, I.N., Bartsch, A., Wotton, S.R., Bowden, C.G.R., Griffiths, G.H., Pain, D. and Rahmani, A.R. (2004) Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhinoptilus bitorquatus* in scrub jungle: an application of a new tracking method. *Journal of Applied Ecology*, 41, 224-237.
- Jelinski, D.E. and Wu, J. (1996) The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology*, 11, 129-140.
- Johnson C.J., Parker K.L. and Heard D.C. (2001) Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. *Oecologia*, 127, 590-602.
- Johnson, C.J., Boyce, M.S., Mulders, R., Gunn, A., Gau, R.J., Cluff, H.D., and Case, R.L. (2004) Quantifying patch distribution at multiple spatial scales: Applications to wildlife-habitat models. *Landscape Ecology*, 19, 869-882.

- Johnson, C.J., Seip, D.R. and Boyce, M.S. (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, 41, 238-251.
- Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65-71.
- Jost, C., Devulder, G., Vucetich, J.A., Peterson, R.O. and Ardit, R. (2005) The wolves of Isle Royale display scale-invariant satiation and ratio-dependent predation on moose. *Journal of Animal Ecology*, 74, 809-816.
- Keating, K.A. and Cherry, S. (2004) Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management*, 68, 774-789.
- Kershaw, L.J., Pojar, J. and Mackinnon A. (1998) *Plant of the Rocky Mountains*. Lone Pine Publishing, Edmonton, Alberta, Canada.
- Kittle, A.M., Fryxell, J.M., Desy, G.E., and Hamr, J. (2008) The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, 157, 163-175.
- Koford, R. R. (1992) Does supplemental feeding of red squirrels change population density, movements, or both? *Journal of Mammalogy*, 73, 930-932.
- Koper, N., and Schmiegelow, F.K.A. (2006) A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. *Landscape Ecology*, 21, 1045-1059.
- Korf, R.P. (1973) *Discomycetes and Tuberales*. In: Ainsworth, G.C., Sparrow, F.K., Sussman, A.S. (eds.), *The Fungi: An Advanced Treatise*, Vol. 4A. Academic Press, London and New York.
- Kotliar, N.B. and Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59, 253-260.
- Kranabetter, J.M. (2004) Ectomycorrhizal community effects on hybrid spruce seedling growth and nutrition in clearcuts. *Canadian Journal of Botany*, 82, 983 – 991.
- La Sorte, F.A., Mannan, R.W., Reynolds, R.T., Grubb, T.G. (2004) Habitat associations of sympatric red-tailed hawks and northern goshawks on the Kaibab Plateau. *Journal of Wildlife Management*, 68, 307-317.

- Lambert T.D., and Adler, G.H. (2000). Microhabitat use by a tropical forest rodent, *Proechimys semispinosus*, in central Panama. *Journal of Mammalogy*, 81, 70-76.
- Layne, J. N. (1954) The biology of the red squirrel, *Tamiasciurus hudsonicus* (Bangs), in central New York. *Ecological Monographs*, 21, 227 – 267.
- Lefsky, M.A., Cohen, W.B., Parker, G.G., and Harding, D.J. (2002) Lidar remote sensing for ecosystem studies. *Bioscience*, 52, 19 – 30.
- Legendre, P., and Legendre, L. (2003) *Numerical Ecology*. 2nd English edition. Elsevier Science BV, Amsterdam.
- Lesna, I., Sabelis, M., and Conijn, C. (1996) Biological control of the bulb mite, *Rhizoglyphus robini*, by the predatory mite, *Hypoaspis aculeifer*, on lilies: Predator-prey interactions at various spatial scales. *Journal of Applied Ecology*, 33, 369-376.
- Levin, S.A. (1992) The problem with pattern and scale in ecology. *Ecology*, 73, 1943-1967.
- Li, X.H., Li, D.M., Ma, Z.J., and Schneider, D.C. (2006) Nest site use by crested ibis: Dependence of a multifactor model on spatial scale. *Landscape Ecology*, 21, 1207-1216.
- Lim, K., Treitz, P., Wulder, M., St-Onge, B., and Flood, M. (2003) LiDAR remote sensing of forest structure. *Progress in Physical Geography*, 27, 88-106.
- Limpert, D.L., Birch, D.L., Scott, M.S., Andre, M. and Gillam, E. (2007) Tree selection and landscape analysis of eastern red bat day roosts. *Journal of Wildlife Management*, 71, 478:486.
- Loeb, S.C., Tainter, F.H., and Cazares, E. (2000) Habitat associations of hypogeous fungi in the southern Appalachians: Implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *The American Midland Naturalist*, 144, 286 – 296.
- Lopez, R.R., Silvy, N.J., Wilkins, R.N., Frank, P.A., Peterson, M.J., and Peterson, M.N. (2004) Habitat use patterns of Florida Key deer: Implications of urban development. *Journal of Wildlife Management*, 68, 900 – 908.

- Mace, R.D., Waller, J. S., Manley, T.L., Lyon, L.J., Zuuring, H. (1996) Relationships Among Grizzly Bears, Roads and Habitat in the Swan Mountains Montana. *Journal of Applied Ecology*, 33, 1395 – 1404.
- Mackey, B.G. and Lindenmayer, D.B. (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, 28, 1147-1166.
- Mahon, C.L., and Martin, K. (2006) Nest survival of chickadees in managed forests: Habitat, predator, and year effects. *Journal of Wildlife Management*, 70, 1257-1265.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P. (2002) *Resource Selection by Animals*, 2nd Edition, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Manning, A.D., Lindenmayer, D.B., Barry, S.C., Nix, H.A. (2006) Multi-scale site and landscape effects on the vulnerable superb parrot of south-eastern Australia during the breeding season. *Landscape Ecology*, 21, 1119-1133.
- Manville, C.J., Barnum, S.A, and Tester, J.A. (1992) Influence of bait on arboreal behavior of *Peromyscus leucopus*. *Journal of Mammalogy*, 73, 335-336
- Manzer, D.L., and Hannon, S.J. (2005) Relating grouse nest success and corvid density to habitat: A multi-scale approach. *Journal of Wildlife Management*, 69, 110-123.
- Marceau, D.J. and Hay, G.J. (1999) Proceedings of the International Workshop on Scaling and Modeling in Forestry: Applications in Remote Sensing and GIS, March 19-21, Montréal, Canada, Department of Geography, University of Montreal, 180 p.
- Marceau, D.J. (1999) The scale issue in social and natural sciences. *Canadian Journal of Remote Sensing*, 25, 347-356.
- Martin, K. J. (1994) Movements and habitat characteristics of northern flying squirrels in the central Oregon Cascades. MSc. thesis, Oregon State University, Corvallis, Oregon, USA.
- Martin, K.J., and McComb, B.C. (2003) Amphibian habitat associations at patch and landscape scales in the central Oregon Coast Range. *Journal of Wildlife Management*, 67, 672-683.

- Maser, C., Maser, Z., Witt, J. and Hunt, G. (1986) The northern flying squirrel: a mycophagist in southwest Oregon. *Canadian Journal of Zoology*, 64, 2086-2089.
- Maser, C., Trappe, J.M. and Nussbaum, R.A. (1978) Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, 59, 799-809.
- Mayer, A.L., and Cameron, G.N. (2003) Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landscape and Urban Planning*, 65, 201-217.
- McCune, B., and Grace, J.B. (2002) Analysis of ecological communities. (MjM Software Design, Gleneden Beach, Oregon.)
- McDonald, L. (1995) Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. Relationships between stand age, stand structure, and biodiversity in Aspen Mixedwood Forests in Alberta (ed. Stelfox, J.B.), Pp. 227-240. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta, and The Canadian Forest Service (Project No. 0001A), Edmonton, Alberta, Canada.
- Meentemeyer, V., and Box, E.O. (1987) Scale effects in landscape studies. *Landscape Heterogeneity and Disturbance* (ed. Turner, M.G), Springer-Verlag, pp. 15-34.
- Menzel, J.M., Ford, W.M., Edwards, J.W., and Terry, T.M. (2006) Home range and habitat use of the Vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA. *Oryx*, 40, 204-210.
- Meyer, C.B., Miller, S.L., and Ralph, C.J. (2002) Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the US west coast. *Landscape Ecology*, 17, 95-115.
- Miles, A.C., Castleberry, S.B., Miller, D.A., and Conner, L.M. (2006) Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *Journal of Wildlife Management*, 70, 1191-1199.
- Miller, D.A., Hurst, G.A., and Leopold, B.D. (1999) Habitat use of eastern wild turkeys in central Mississippi. *Journal of Wildlife Management*, 63, 210-222.

- Mitchell, D. (2001) Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). *American Midland Naturalist*, 146, 439 – 443.
- Moen, C.A., and Gutierrez, R.J. (1997) California spotted owl habitat selection in the central Sierra Nevada. *Journal of Wildlife Management*, 61, 1281-1287.
- Molina, R., and Trappe, J.M. (1982) Patterns of Ectomycorrhizal Host Specificity and Potential among Pacific Northwest Conifers and Fungi. *Forest Science*, 28, 423 – 458.
- Molina, R., Massicotte, H., and Trappe, J.M. (1992) Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In Allen, M.F. (ed.) *Mycorrhizal Functioning: an Integrative Plant-Fungal Process*. New York : Chapman and Hall.
- Moss, E.H. (1994) *Flora of Alberta, Second Edition*. University of Toronto Press, Toronto, Ontario, Canada.
- Murphy, P.N.C., Ogilvie, J., Meng, F., and Arp, P. (2008) Stream network modelling using lidar and photogrammetric digital elevation models: a comparison and field verification. *Hydrological Processes*, 22, 1747 – 1754.
- Murphy, P.N.C., Castonguay, M., Ogilvie, J., Nasr, M., Hazlett, P., Bhatti, J., and Arp, P. (2009) A geospatial and temporal framework for modeling gaseous N and other N losses from forest soils and basins, with application to the Turkey Lakes Watershed Project, in Ontario, Canada. *Forest Ecology and Management*, 258, 2304 – 2317.
- Nams V.O., and Bourgeois, M. (2004) Fractal dimension measures habitat use at different spatial scales: an example with marten. *Canadian Journal of Zoology*, 82, 1738-1747.
- Nams, V.O. (1989) Effects of radiotelemetry error on sample size and bias when testing for habitat selection. *Canadian Journal of Zoology*, 67, 1631-1636.
- Nams, V.O., Mowat, G., and Panian, M.A. (2006) Determining the spatial scale for conservation purposes - an example with grizzly bears. *Biological Conservation*, 128, 109-119.

- Naugle, D.E., Higgins, K.F., Nusser, S.M., and Johnson, W.C. (1999) Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecology*, 14, 267-276.
- Nelson, L., Jr. and Clark, F.W. (1973) Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy*, 54, 295-298.
- North, M., Trappe, J.M. and Franklin, J. (1997) Standing crop and animal consumption of fungal sporocarps in Pacific Northwest Forests. *Ecology*, 78, 1543-1554.
- North, M.P., and Reynolds, J.H. (1996). Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *Journal of Wildlife Management*, 60, 639-653.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B., and Allen, T.F.H. (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey.
- Openshaw, S. and Taylor, P.J. (1979) A million or so correlated coefficients: Three experiments on the modifiable areal unit problem. *In* *Statistical Applications in the Spatial Sciences* (eds. Wrigley, N. and Bennet, R.J.), Pion, London.
- Openshaw, S. (1984) The Modifiable Areal Unit Problem. *Concepts and Techniques in Modern Geography*, 38, 40 p.
- Osborne, P.E., Alonso, J.C. and Bryant, R.G. (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, 38, 458-471
- Pearce, J.L., Cherry, K., Drielsma, M., Ferrier, S. and Wish, G. (2001) Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. *Journal of Applied Ecology*, 38, 412-424.
- Pearson, D.E., and Ruggiero, L.F. (2003) Transect versus grid trapping arrangements for sampling small-mammal communities. *Wildlife Society Bulletin*, 31, 454-459.
- Pedlar, J.H., Fahrig, L., and Merriam, H.G. (1997) Raccoon habitat use at 2 spatial scales *Journal of Wildlife Management*, 61, 102-112.
- Peters, D.P.C., and Herrick, J.E. (2004) Strategies for ecological extrapolation. *Oikos*, 106, 627 - 636.
- Peterson, D.L. and Parker, V.T. (eds.) (1998) *Ecological Scale: Theory and Applications*. Columbia, University Press, New York.

- Pilz, D.P., and Perry, D.A. (1984) Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. *Canadian Journal of Forest Research*, 14, 94 – 100.
- Powell, B.F., and Steidl, R.J. (2002) Habitat selection by riparian songbirds breeding in southern Arizona. *Journal of Wildlife Management*, 66, 1096 - 1103.
- Price, S.J., Marks, D.R., Howe, R.W., Hanowski, J.M., and Niemi, G.J. (2005) The importance of spatial scale for conservation and assessment of anuran populations in coastal wetlands of the western Great Lakes, USA. *Landscape Ecology*, 20, 441-454.
- Pyare, S. and Longland W.S. (2002) Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forest Research*, 32, 1016-1024.
- Pyare, S. and Longland, W.S. (2001) Mechanisms of truffle detection by northern flying squirrels. *Canadian Journal of Zoology*, 79, 1007-1015.
- Ransome, D.B. and Sullivan T.P. (2003) Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. *Canadian Journal of Forest Research*, 33, 587-596.
- Ransome, D.B. and Sullivan T.P. (2004) Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *Journal of Mammalogy*, 85, 206-215.
- Reunanen, P., Nikula, A., Mönkkönen, M. Hurme, E. and Nevala, V. (2002) Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. *Ecological Applications*, 12, 1188-1198.
- Rodgers, A. R. and Carr, A. P. (1998) HRE: the Home Range Extension for ArcView™: user's manual. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research. Thunder Bay, Canada.
- Rodríguez, A. and Andrén, H. (1999) A comparison of Eurasian red squirrel distribution in different fragmented landscapes. *Journal of Applied Ecology*, 36, 649-662.
- Rosenberg, D. K. and Anthony, R. G. (1992) Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology*, 70, 161-166.

- Rosenberg, D.K., Overton, W.S., and Anthony, R.G. (1995) Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management*, 59, 252-261.
- Rosentreter, R, Hayward, G., and Wicklow-Howard, M. (1997) Northern flying squirrel seasonal food habits in the interior conifer forests of central Idaho, USA. *Northwest Science*, 71, 97-102.
- Rowe, D.K., Shankar, U., James, M. and Waugh, B. (2002) Use of GIS to predict effects of water level on the spawning area for smelt, *Retropinna retropinna*, in Lake Taupo, New Zealand. *Fisheries Management and Ecology*, 9, 205-216.
- Rushton, S.P., Lurz, P.W.W., Fuller, R. and Garson, P.J. (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology*, 34, 1137-1154.
- Rushton, S.P., Lurz, P.W.W., Gurnell, J. and Fuller, R. (2000) Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology*, 37, 997-1012.
- Rushton, S.P., Ormerod, S.J. and Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, 41, 193-200.
- Russell, K.R., Mabee, T.J., and Cole, M.B. (2004) Distribution and habitat of Columbia torrent salamanders at multiple spatial scales in managed forests of northwestern Oregon. *Journal of Wildlife Management*, 68, 405-417.
- Said, S., and Servanty, S. (2005) The influence of landscape structure on female roe deer home-range size. *Landscape Ecology*, 20, 1003-1012.
- Samuel, M.D., and Kenow, K.P. (1992) Evaluating habitat selection with radio-telemetry triangulation error. *Journal of Wildlife Management*, 56, 725-734.
- Sandel, B., and Smith, A.B. (2009) Scale as a lurking factor: incorporating scale-dependence in experimental ecology. *Oikos*, 118, 1284 – 1291.
- Santos, M.J., Beier, P. (2008) Habitat selection by European badgers at multiple spatial scales in Portuguese Mediterranean ecosystems. *Wildlife Research*, 35, 835-843.
- Saura, S. and Martinez-Millan, J. (2001) Sensitivity of landscape pattern metrics to map spatial extent. *Photogrammetric Engineering and Remote Sensing*, 67, 1027-1036.

- Saura, S. (2004) Effects of remote sensor spatial resolution and data aggregation on selected fragmentation indices. *Landscape Ecology*, 19, 197-209.
- Schaefer J.A., Morellet, N., Pepin, D., and Verheyden, H. (2008) The spatial scale of habitat selection by red deer. *Canadian Journal of Zoology*, 86, 1337-1345.
- Schaefer, J.A., Bergman, C.M., and Luttich, S.N. (2000) Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*, 15, 731-739.
- Schneider, D.E. (2001) The rise of the concept of scale in ecology. *BioScience*, 51, 545-553.
- Schooley, R.L. (1994) Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management*, 58, 367-374.
- Schweiger, O., Maelfait, J.P., Van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., and Bugter, R. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, 42, 1129-1139.
- Seavy, N.E., Viers, J.H., and Wood, J.K. (2009) Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height. *Ecological Applications*, 19, 1848 – 1857.
- Selonen, V., Hanski, I.K., Desrochers, A., (2007) Natal habitat-biased dispersal in the Siberian flying squirrel. *Proceedings of the Royal Society B; Biological Sciences*, 274, 2063 - 2068.
- Sharp, B.L., and Kus, B.E. (2006) Factors influencing the incidence of cowbird parasitism of least Bell's vireos. *Journal of Wildlife Management*, 70, 682-690.
- Silverman, B.W. (1986) *Density estimation for statistics and data analysis*. Chapman and Hall, London, England.
- Slauson, K.M., Zielinski, W.J. and Hayes, J.P. (2007) Habitat selection by American martens in coastal California. *Journal of Wildlife Management*, 71, 458-468.
- Smith, W.P. (2007) Ecology of *Glaucomys sabrinus*: Habitat, demography, and community relations. *Journal of Mammalogy*, 88, 862 – 881.

- Smith, W.P. and Nichols J.V. (2003) Demography of the Prince of Whales flying squirrel, and endemic of southeastern Alaska temperate rain forest. *Journal of Mammalogy*, 84, 1044-1058.
- Smith, W.P. and Nichols, J.V. (2004) Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. *Journal of Mammalogy*, 85, 663-674.
- Smith, W.P., Gende, S. M., and Nichols, J. V. (2005) The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. *Ecological Applications*, 15, 689-700.
- Smith, W.P., Gende, S. M., and Nichols, J.V. (2004) Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. *Journal of Mammalogy*, 85, 663-674.
- Squires, J.R., and Ruggiero, L.F. (1996) Nest-site preference of northern goshawks in southcentral Wyoming. *Journal of Wildlife Management*, 60, 170-177.
- Squires, J.R., DeCesare, N.J, Kolbe, J.A., Ruggiero, L.F. (2008) Hierarchical den selection of Canada lynx in western Montana. *Journal of Wildlife Management*, 72, 1497-1506.
- Steege, C., and Hitchcock, C.L. (1998) Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. *Journal of Wildlife Management*, 62, 1349-1358.
- Steele, B.B., Bayn, R.L., and Val Grant, C. (1984) Environmental monitoring using populations of birds and small mammals: analyses of sampling effort. *Biological Conservation*, 30, 157-172.
- Strong, W.L. (1992) Ecoregions and ecodistricts of Alberta. Vol. 1. Alberta Forestry, Lands and Wildlife, Land Information Services Division, Resource Information Branch, Government of Alberta, Edmonton, Alberta, Canada.
- Suárez-Seoane, S., Osborne, P.E. and Alonso, J.C. (2002) Large scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. *Journal of Applied Ecology*, 39, 755-771.
- Sullivan, T. P. and Klenner, W. (1992). Response to Koford: red squirrels and supplemental feeding. *Journal of Mammalogy*, 73, 933-936.

- Talou, T., Gaset, A., Delmas, M., Kulifaj, M. and Montant, C. (1990) Dimethyl sulfide: the secret for black truffle hunting by animals? *Mycological Research*, 94, 277-278.
- Taylor, J.S., Church, K.E., Rusch, D.H., and Cary, J.R. (1999) Macrohabitat effects on summer survival, movements, and clutch success of northern bobwhite in Kansas. *Journal of Wildlife Management*, 63, 675-685.
- Telesco, D.J., and Van Manen, F.T. (2006) Do black bears respond to military weapons training? *Journal of Wildlife Management*, 70, 222-230.
- Terry, E.L., Mclellan, B.N., and Watts, G.S. (2000) Winter habitat ecology of mountain caribou in relation to forest management. *Journal of Applied Ecology*, 37, 589-602.
- Thogmartin, W.E. and Knutson, M.G. (2007) Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. *Landscape Ecology*, 22, 61-75.
- Thome, D.M., Zabel, C.J., and Diller, L.V. (1999) Forest stand characteristics and reproduction of northern spotted owls in managed north-coastal California forests. *Journal of Wildlife Management*, 63, 44-59.
- Thompson, C.M., and McGarigal, K. (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecology*, 17, 569-586.
- Trappe, J.M. (1977) Selection of fungi for ectomycorrhizal inoculation in nurseries. *Annual Review of Phytopathology*, 15, 203 – 222.
- Tucker, S.A., Clark, W.R., Gosselink, T.E. (2008) Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. *Journal of Wildlife Management*, 72, 1114-1124.
- Turchin, P. (1996) *Movement and Spatial Population Dynamics*. John Wiley, New York, New York, USA.
- Turner, M.G. and Gardner, R.H. (eds.) (1991) *Quantitative methods in landscape ecology: an introduction*. Springer-Verlag, New York, New York, USA.
- Turner, M.G., Dale, V.H. and Gardner, R.H. (1989) Predicting across scales: theory development and testing. *Landscape Ecology*, 3, 245-252.

- van der Ree, R., Bennett, A.F., and Gilmore, D.C. (2003) Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. *Biological Conservation*, 115, 241-249.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, 47, 893-901.
- Verner, J., Morrison, M.L., and Ralph, C.J. (eds.) (1986) *Wildlife 2000: Modeling relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- Vernes, K. (2001) Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. *Journal of Mammalogy*, 82, 1026-1033.
- Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S., and Clawges, R.M. (2008) Lidar: shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment*, 6, 90 – 98.
- Visser, S. (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist*, 129, 389 – 401.
- Wallace, L.L., and Crosthwaite, K.A. (2005) The effect of fire spatial scale on Bison grazing intensity. *Landscape Ecology*, 20, 337-349.
- Wallace, L.L., Turner, M.G., Romme, W.H., O'Neill, R.V., and Wu, Y.G. (1995) Scale of heterogeneity of forage production and winter foraging by elk and bison. *Landscape Ecology*, 10, 75-83.
- Waters, J.R. and Zabel C. J. (1995) Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management*, 59, 858-866.
- Watrous, K.S, Donovan, T.M, Mickey, R.M., Darling, S.R., Hicks, A.C., and Von Oettingen, S.L. (2006) Predicting minimum habitat characteristics for the Indiana bat in the Champlain Valley. *Journal of Wildlife Management*, 70, 1228-1237.
- Weir, R.D. and Harestad, A.S. (2003) Scale-dependent habitat selectivity by fishers in south-central British Columbia. *Journal of Wildlife Management*, 67, 73-82.
- Welsh, H.H., and Lind, A.J. (2002) Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou Region of California and Oregon. *Journal of Wildlife Management*, 66, 581-602.

- Wheatley, M. (2007a) Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. *Northwest Science*, 81, 265-273.
- Wheatley, M. (2007b) Relating body size of red squirrels to different conifer cone morphologies within the same geographic location. *Journal of Mammalogy*, 88, 220-225.
- Wheatley, M. (2010) Domains of scale in forest landscape metrics: Implications for species-habitat modeling. *Acta Oecologica*, 36, 259-267.
- Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., and Boutin S. (2005) Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. *Journal of Applied Ecology*, 42, 577-586.
- Wheatley, M., and Johnson, C. (2009) Factors limiting our understanding of ecological scale. *Ecological Complexity*, 6, 150-159.
- Wheatley, M., and Larsen, K.W. (2008) Differential space use inferred from live trapping versus telemetry: Northern flying squirrels and fine spatial grain. *Wildlife Research*, 35, 425-433.
- Wheatley, M., Larsen, K.W., and Boutin, S. (2002) Does density reflect habitat quality for red squirrels during a spruce cone failure? *Journal of Mammalogy*, 83, 716-727.
- White, C.G., Schweitzer, S.H., Moore, C.T., Parnell, I.B., and Lewis-Weis, L.A. (2005) Evaluation of the landscape surrounding northern bobwhite nest sites: A multiscale analysis. *Journal of Wildlife Management*, 69, 1528-1537.
- White, G.C., and Garrott, R.A. (1986) Effects of biotelemetry triangulation error on detecting habitat selection. *Journal of Wildlife Management*, 50, 509-513.
- Whittingham, M.J., Swetnam, R.D., Wilson, J.D., Chamberlain, D.E., and Freckleton, R.P. (2005) Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: Implications for conservation management. *Journal of Applied Ecology*, 42, 270-280.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, 3, 385-397.

- Worton, B. J. (1989) Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, 70,164 – 168.
- Worton, B. J. (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, 59, 794 - 800.
- Wu, J. (1999) Hierarchy and scaling: Extrapolating information along a scaling ladder. *Canadian Journal of Remote Sensing*, 25, 367-380.
- Wu, J. (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology*, 19, 125-138.
- Wu, J., Shen, W., Sun, W., Tueller, P.T. (2002) Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology*, 17, 761-782.
- Yaacobi, G., Ziv, Y. and Rosenzweig, M.L. (2007) Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape Ecology*, 22,687-703.
- Yule, G.U. and Kendall, M.G. (1950) *An Introduction to the Theory of Statistics*. Griffin.
- Zimmerman, G.S., and Glanz, W.E. (2000) Habitat use by bats in eastern Maine. *Journal of Wildlife Management*, 64, 1032-1040.