NOTE TO USERS

This reproduction is the best copy available.

UMI®

THE SPATIAL STRUCTURE OF SMALL-MAMMAL POPULATIONS IN A MANAGED FOREST

by

Jeff Bowman
B.Sc.(Hons), Queen's University, 1992
M.Sc., Laurentian University, 1996

A thesis submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

in the Graduate Academic Unit of Biology

Supervisors: G. F. Forbes, Ph.D., Forestry and Environmental Management
T. G. Dilworth, M.Sc., Biology

Examining Board: R. Turner, Ph.D., Mathematics and Statistics, Chair
C. Bourque, Ph.D., Forestry and Environmental Management
D. Quiring, Ph.D., Forestry and Environmental Management

External Examiner: J. A. Bissonette, Ph.D., Utah State University

THE UNIVERSITY OF NEW BRUNSWICK

April, 2000

© Jeff Bowman, 2000

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-62168-5

Canadä

Abstract

I tested the hypothesis that there are processes contributing to the distribution and abundance of small mammals that are independent of the effects of resource variation. The prediction was that within the domain of dispersal, small-mammal populations would exhibit spatial structure that was independent of the distribution of resources. Systematic live-trapping surveys were conducted on nested grids at three spatial scales: (1) extent = 4900 ha, grain = 1000 m; (2) extent = 306 ha, grain = 250 m; and (3) extent = 31 ha, grain = 125 m. From 1996 to 1999, surveys were conducted on a landscape intensively managed for timber, and on a reference landscape. Spatial analysis of abundance data demonstrated that small-mammal populations (*Clethrionomys gapperi*, *Peromyscus maniculatus*, *Blarina brevicauda*, and *Napaeozapus insignis*) exhibited positive spatial autocorrelation at distances of between 133 and 533 m depending on the species and the landscape. No higher-order population structure was detected. Thus, variability in small-mammal abundance occurred over short distances (i.e., 133 - 533 m). Mean straight-line distances moved between sampling points by tagged animals were: 370 m (*Peromyscus maniculatus*; N = 44), 225 m (*Napaeozapus insignis*; N = 33), and 224 m (*Clethrionomys gapperi*; N = 23). Landscape context was not significantly related to the abundance of any species at radial extents > 250 m. Partial constrained ordination of small-mammal abundance matrices demonstrated that the amount of variation explained by spatial models was inversely proportional to the sampling grain, while the amount of variation explained by vegetation was consistent across scales. I suggest that fine-scale spatial structure existed within the small-mammal populations — a result of processes occurring over short distances.

Preface

This dissertation is written in articles format. For chapters of which I am not the only author, co-authors are noted on the title page. Some of these articles were accepted for journal publication prior to the completion of my dissertation. These published articles are identified with a foot note on the title page. Rights to reprint these articles were obtained from the copyright holders, and these letters of permission are included in Appendix 6.

Acknowledgements

This research project, like many, was a cooperative effort, and so there are many people to thank. First of all, my co-advisors Graham Forbes and Tim Dilworth deserve acknowledgement for their respective contributions. Both gave me valuable time and assistance whenever it was needed. Thank you. Thanks also to my other committee members, Tony Diamond and M.-A. Villard, both of whom were a big part of this project. Thanks to Warren Ballard for helping this project get started and bringing me to New Brunswick. Lots of other folks took part in initiating the SFMN 'Interstand Dynamics' project, all of whom deserve my thanks, especially: Stan Boutin, Gilles Couturier, Sue Hannon, Rich Moses, and Steve Young. Thanks to all of the funders, each of whom is listed on the next page, along with all of the technical assistants, without whom this work would have been impossible. Many have taken the time to read some or all of this material, and their thoughtful contributions are much appreciated: John Bissonette, Charles Bourque, Tony Diamond, Dan Keppie, Matt Litvak, Douglas Morris, Roger Powell, Dan Quiring, Rolf Turner, M.-A. Villard, and Tara Warren. Both at UNB and in the field, I had the good fortune of being surrounded by a great group of friends and co-conspirators. Special thanks go to John Gunn and Pete McKinley — may your boats always find the deep-water channel. Other friends at UNB include: Matt Betts, Julie Bourque, Hughie Broders, Crissy Corkum, Karen DeWolfe, Mark Edwards, Falk Huettmann, Jonathan Kierstead, Shawn Morrison, Rob Otto, Serge Rheaume, Lisa Sheppard, Tara Warren, and all the rest of the wildlifers. Finally, thanks to my family for all the support over the years, and especially thanks to Heather MacPherson....

Funders

Fraser Papers, Inc.
The Sustainable Forest Management Network
The Sir James Dunn Wildlife Research Centre
NSERC
Earth Works NB
The University of New Brunswick
The University of Alberta
The Atlantic Society of Fisheries and Wildlife Biologists
The NASA-MSU Professional Enhancement Program

Assistants

Steven Barber
Matt Betts
Bjorn Bostrom
Julie Bourque
Luc Bourque
Rick Curran
Rejean Duchesne
Alanda Fennimore
Carvell Fenton
Jaime Glenn
Trina Kilpatrick
Ben Kuttner
Slippery Dan Mazerolle
Jan Zip McPhee
Trista Michaud
Daniel Palm
Rob Pineo
Serge Protector Rheaume
Heather Sisk
Lisa Coyote Sheppard
Andy Sherpa Skibicki
Amanda Smith
Darren Sleep
Karen Woodard

Thanks to everyone

Table of contents

Page

List of tables

List of figures

Chapter 1

General introduction

Introduction

This dissertation is about the way that populations are distributed in space. My interest in this research began with a belief that organisms were scattered across the land in accordance with resources — the popular environmental-control model (Whittaker 1956). Ideas about environmental control have informed the design of many research projects. For example, it is common to assume that variation in the abundance of animals across sites is directly related to the varying quality of the sites (e.g., ideal-free habitat selection; Fretwell and Lucas 1970).

The environmental-control assumption is common in small-mammal ecology. Many empirical projects use small (< 2 ha) square quadrats with traps spaced 10-15 m apart. Population densities are estimated and related to vegetation within the quadrat, as if to suggest a causal link (Tevis 1956; Gashwiler 1959; Sims and Buckner 1973; Kirkland 1977; Martell and Radvanyi 1977; Miller and Getz 1977; Swan et al. 1984; Monthey and Soutiere 1985; Clough 1987; Parker 1989). This standard approach to studying animals seems not to recognize the potential importance of factors other than resource abundance in structuring animal populations. Quinn and Dunham (1983) suggested that patterns often are caused by multiple factors, including vertical and horizontal biotic relationships such as predation, competition, and dispersal. These processes can create spatial variation in the distribution of organisms that is independent of resource variation (Borcard et al. 1992).

The idea that populations can vary in space independently of the distribution of resources is not new. In fact, it is implicit in many theoretical discussions of genetics and population regulation in small mammals (e.g., Hansson 1977; Anderson 1980; Lidicker 1988). However, because so many empirical small-mammal studies follow a similar small-scale (< 2 ha) sampling protocol, there has been little ability to detect variations in space. Consequently, the amount and domain of spatial variation within small-mammal populations is unclear.

There has been considerable research into the spatial domain of habitat selection by small mammals. A number of authors conceptually differentiate microhabitat (i.e., features < a home-range) from macrohabitat (i.e., features > a home range) (e.g., Morris 1984; Morris 1989; Jorgensen and Demarais 1999). Generally, these studies suggest that small mammals respond behaviourally to microhabitat features, but select at the scale of macrohabitat (Morris 1987; Jorgensen and Demarais 1999). While this area of research is concerned with spatial domain, there is little consideration of non-resource-based spatial variability. There is often an assumption of environmental control.

One area of research that has demonstrated spatial variation within small-mammal populations is at the domain of a species' range. In recent years, studies have shown that a number of small-mammal species exhibit spatially-structured population dynamics across geographical regions (e.g., Steen et al. 1996; papers in Krebs 1997; Ranta et al. 1997). Spatial variation could also exist at scales smaller than a region (e.g., metapopulations; Krohne 1997; Goodwin and Fahrig 1998) although there is little empirical research within this domain. One of the few studies, by Krohne and Burgin (1990), demonstrates demographic heterogeneity within *Peromyscus leucopus* populations at an extent of < 3 ha. Morris (1992) detected a level of organization in *Peromyscus* populations at a distance of 140 m. Others (Patton and Feder 1981; Krohne and Baccus 1985; Adler 1987; Dickman and Doncaster 1987; Kelt et al. 94; Paillet and Butet 1996) have demonstrated the relative importance of local (fine-scale) processes for small-mammal populations.

The development of spatial analytical techniques has allowed ecologists to model processes that vary in space (e.g., Legendre and Fortin 1989; Borcard et al. 1992; Rossi et al. 1992; Thomson et al. 1996). These techniques generally involve the description of spatial pattern. Patterns which have structure (i.e., they are spatially non-random) can be considered synthetic models of underlying processes, such as dispersal or predation (Legendre and Fortin 1989; Borcard et al. 1992). As patterns have a scale, spatial analytical techniques can also be used to detect the scale of the underlying processes that spatial patterns represent (Legendre and Fortin 1989). Knowledge of the scale of a process, in turn, provides insight into the process.

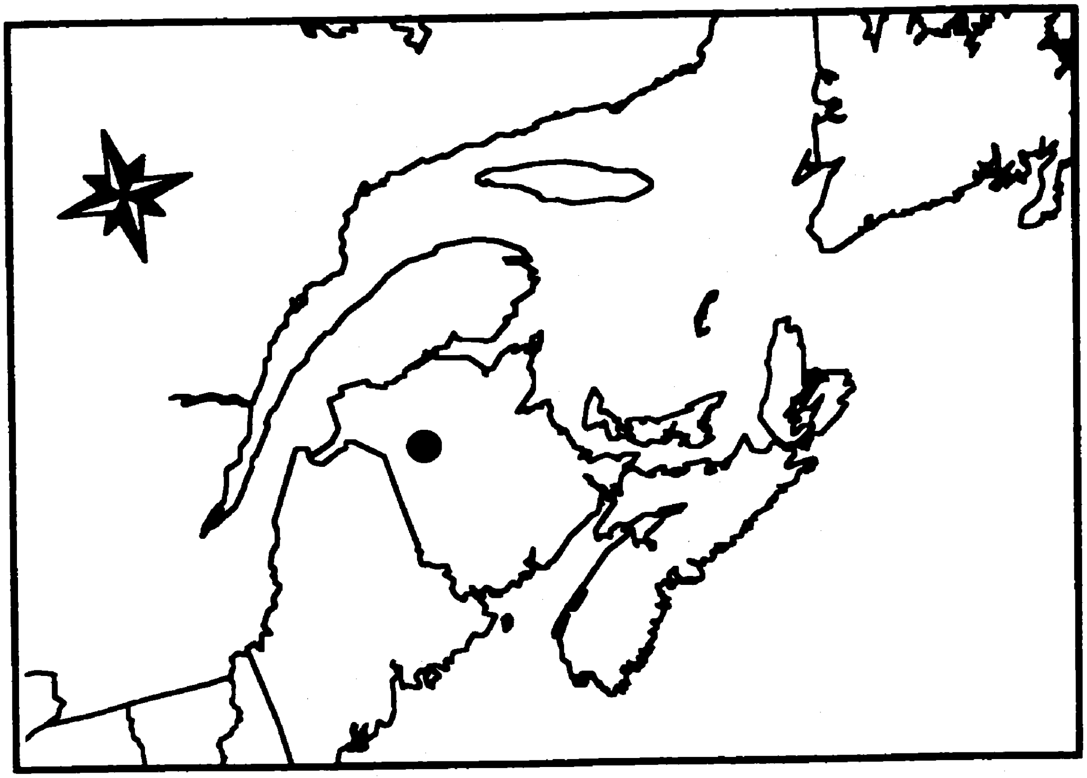
My approach with this research project was to test the prediction that there are processes contributing to the distribution and abundance of small mammals that are independent of the effects of resource variation. I modelled the spatial variation of small-mammal populations across a range of scales that had not previously been sampled in a systematic way. This approach provided unique insight into small-mammal population ecology. The broad objectives were threefold. First, I wanted to assess whether small-mammal populations exhibited spatial structure that was independent of the distribution of resources. The second objective was to determine the spatial scale(s) over which structure occurred. My final objective was to measure any discernable relationship between forest management practices and the spatial structure of small-mammal populations.

Study area

The study took place in the private industrial forest of Fraser Papers Inc. (47°N, 67°W), in the Appalachian forest of northwestern New Brunswick (Fig. 1.1). The area is within the Acadian forest region of Canada (Rowe 1972). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Common upland understory plants included hobblebush (*Viburnum alnifolium*), striped maple (*Acer pensylvanicum*), mountain maple (*Acer spicatum*) and an abundance of regenerating overstory species (beech, birch, and maple). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and in the most mesic sites, eastern white cedar (*Thuja occidentalis*). Lowland understory plants were often regenerating softwoods, as well as hardwood shrubs such as beaked hazel (*Corylus cornuta*), yellow birch, and white birch.

This dissertation is part of a larger research project within the Sustainable Forest Management Network (SFMN), A Network of Centres of Excellence. The objectives of the SFMN project included understanding the responses of wildlife to the structure of managed forests. Therefore, we selected two 4900-ha study areas representing opposite ends of the continuum of forest management intensities: (1) a reference area, with relatively little management disturbance (i.e., < 15% recent (< 15 years) clearcut or softwood plantation); and (2) an intensively managed area, where clearcuts and softwood plantations covered > 50% of the landscape. My research project took place within these two landscapes.

Fig. 1.1. Location of the study area (●) in the Appalachian highlands of New Brunswick, Canada.



Small mammals

Small-mammal species common in the study area included red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), woodland jumping mice (*Napaeozapus hudsonicus*), and short-tailed shrews (*Blarina brevicauda*) (Dilworth 1984). The habitat associations of these and other small mammals in northern forests have been researched, although some species (e.g., short-tailed shrews and deer mice) seem to defy prediction as they can occupy an array of cover types. General trends in habitat associations are as follows: Getz (1968) indicated that red-backed voles have high water requirements, and suggested that they should inhabit mesic sites. Others have confirmed this (Gunderson 1959; Kirkland and Griffin 1974; Nagorsen and Peterson 1981; Nordyke and Buskirk 1991; D'Eon and Watt 1994), also indicating associations with mature softwoods and decadent coarse woody debris. Woodland jumping mice are most abundant in areas with herbaceous cover (Whitaker and Wrigley 1972; Vickery 1981), and areas that are close to streams (Kirkland and Schmidt 1982). Deer mice are associated with disturbance and edge in all forest types and seem to decrease in abundance in mature forest (Nagorsen and Peterson 1981; Sekgororoane and Dilworth 1995). Short-tailed shrews seem to be habitat generalists, although they may tend more toward hardwood sites with abundant leaf litter than softwoods (Grant 1976; Dilworth 1984; Swan et al. 1984). Other small rodents that occur in the study area, but at lower densities include rock voles (*Microtus chrotorrhinus*), meadow voles (*Microtus pennsylvanicus*), meadow jumping mice (*Zapus hudsonius*), and southern bog lemmings (*Synaptomys cooperi*).

Layout of dissertation

A number of different methods were used depending on the objectives of each chapter. A summary of the chapter objectives is included below, and detailed methods are included in each chapter.

Chapter 2

A literature review, assessing the spatial scales typically used to study small mammals.

Chapter 3

An exploratory analysis of the spatial structure of small mammals captured within the reference and intensively managed landscapes. Carried out across a range of scales, these analyses demonstrated relevant scales of spatial variability for small mammals.

Chapter 4

A description of small-mammal movements, which can be considered an indication of the spatial extent of the process of dispersal.

Chapter 5

A correlative study of the effects of landscape context on small-mammal abundance. By using a range of spatial extents, the important extents were revealed.

Chapter 6

A variance partitioning approach which tested for spatial variability in small-mammal abundance that was independent of environmental variation.

Chapter 7

A synthesis of the results.

References

Adler, G. H. 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. Can. J. Zool. **65**: 903-912.

Anderson, P. K. 1980. Evolutionary implications of microtine behavioural systems on the ecological stage. The Biologist, **62**: 70-88.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, **73**: 1045-1055.

Clough, G. C. 1987. Relations of small mammals to forest management in northern Maine. Can. Field-Nat. **101**: 40-48.

D'Eon, R. G., and Watt, W.R. 1994. Small mammal habitat study first year results. Ontario Ministry of Natural Resources, Northeast Science and Technology. IR014.

Dickman, C. R., and Doncaster, C. P. 1987. The ecology of small mammals in urban habitats. I. Populations in a patchy environment. J. Anim. Ecol. **56**: 629-640.

Dilworth, T. G. 1984. The land mammals of New Brunswick. T. G. Dilworth, Fredericton, New Brunswick.

Fretwell, S. D., and Lucas, H. L., Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica, **19**: 16-34.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. J. Mamm. **40**: 128-139.

Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology, **49**: 276-286.

Goodwin, B. J., and Fahrig, L. 1998. Spatial scaling and animal population dynamics. *In*

Ecological scale: theory and applications. *Edited by* D. L. Peterson and V. T. Parker. Columbia University Press, New York, NY. pp. 193-206.

Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. Can. J. Zool. **54**: 2156-2173.

Gunderson, H. L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. **40**: 405-412.

Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. Oikos, **29**: 539-544.

Jorgensen, E. E., and Demarais, S. 1999. Spatial scale dependence of rodent habitat use. J. Mammal. **80**: 421-429.

Kelt, D. A., Meserve, P. L., and Lang, B. L. 1994. Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. J. Mammal. **75**: 890-904.

Kirkland, G. L., Jr., and Griffin, R. J. 1974. Microdistribution of small mammals at the coniferous-deciduous forest ecotone in northern New York. J. Mammal. **55**: 417-427.

Kirkland, G. L., Jr. 1977. Responses of small mammals to the clearcutting of northern Appalachian forests. J. Mammal. **58**: 600-609.

Kirkland, G. L., Jr., and Schmidt, D. F.. 1982. Abundance, habitat, reproduction and morphology of forest-dwelling small mammals of Nova Scotia and southeastern New Brunswick. Can. Field-Nat. **96**: 156-162.

Krebs, C. J. 1997. Vole cycles in Hokkaido: a time series goldmine. TREE, **12**: 340-341.

Krohne, D. T. 1997. Dynamics of metapopulations of small mammals. J. Mammal. 78: 1014-1026.

Krohne, D. T. and Baccus, R. 1985. Genetic and ecological structure of a population of *Peromyscus leucopus*. J. Mammal. 66: 529-537.

Krohne, D. T., and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, 82: 97-101.

Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio, 80: 107-138.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine "cycles". J. Mammal. 69: 225-235.

Martell, A. M., and Radvanyi, A. 1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Can. Field-Nat. 91: 41-46.

Miller, D. H., and Getz, L. L. 1977. Factors influencing the local distribution and species diversity of forest small mammals in New England. Can. J. Zool. 55: 806-814.

Monthey, R. W., and Soutiere, E. C. 1985. Responses of small mammals to forest harvesting in northern Maine. Can. Field-Nat. 99: 13-18.

Morris, D. W. 1984. Microhabitat separation and coexistence and separation of two temperate-zone rodents. Can. Field-Nat. 98: 215-218.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology, 68: 362-369.

Morris, D. W. 1989. The effect of spatial scale on patterns of habitat use: red-backed voles as an empirical model of local abundance for northern mammals. *In* Patterns in the structure of mammalian communities. *Edited by* D. W. Morris, Z.

Abramsky, B. J. Fox, and M. Willig. Spec. Publ. Mus. Tex. Tech Univ., Texas Tech University, Lubbock. pp. 23-32.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol. Ecol. **6**: 412-432.

Nagorsen, D. W., and Peterson, R. L. 1981. Distribution, abundance and species diversity of small mammals in Quetico Provincial Park, Ontario. Le Naturaliste Canadien, **108**: 209-218.

Nordyke, K. A., and Buskirk, S. W. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Can. Field-Nat. **105**: 330-334.

Paillet, G., and Butet, A. 1996. Spatial dynamics of the bank vole (*Clethrionomys glareolus*) in a fragmented landscape. Acta Oecologica, **17**: 553-559.

Parker, G. R. 1989. Effects of reforestation upon small mammal communities in New Brunswick. Can. Field-Nat. **103**: 509-519.

Patton, J. L., and Feder, J. 1981. Microspatial heterogeneity in pocket gophers: non-random breeding and drift. Evolution, **35**: 912-920.

Quinn, J. F., and Dunham, A. E. 1983. On hypothesis testing in ecology and evolution. Am. Nat. **122**: 602-617.

Ranta, E., Kaitala, V., Lindstrom, J., and Helle, E. 1997. The Moran effect and synchrony in population dynamics. Oikos, **78**: 136-142.

Rossi, R. E., Mulla, D. J., Journel, A. G., and Franz, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. **62**: 277-314.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forest Service, Department of Environment, Ottawa.

Sekgororoane, G. B., and Dilworth, T. G. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Can. J. Zool. 73: 1432-1437.

Sims, H. P., and Buckner, C. H. 1973. The effects of clearcutting and burning of *Pinus banksiana* forests on the populations of small mammals in southeastern Manitoba. Am. Midl. Nat. 90: 228-231.

Steen, H., Ims, R. A., and Sonerud, G. A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. Ecology, 77: 2365-2372.

Swan, D., Freedman, B., and Dilworth, T. 1984. Effects of various hardwood forest management practices on small mammals in central Nova Scotia. Can. Field-Nat. 98: 362-364.

Tevis, L. Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. J. Mammal. 37:189-196.

Thomson, J. D., Weiblen, G., Thomson, B. A., Alfaro, S., and Legendre, P. 1996. Untangling multiple factors in spatial distributions, lilies, gophers, and rocks. Ecology, 77: 1698-1715..

Vickery, W. L. 1981. Habitat use by northeastern forest rodents. Am. Midl. Nat. 106: 111-118.

Whitaker, J. O., Jr., and Wrigley, R. E. 1972. *Napaeozapus insignis*. Mammalian Species, 14: 1-6.

Whittaker, R. H. 1956. Vegetation of the Great Smokey Mountains. Ecol. Monogr. 26: 1-80.

Chapter 2

Spatial scales of trapping in small-mammal research

Abstract

We surveyed 127 published small-mammal trapping studies (*Peromyscus maniculatus* and *Clethrionomys gapperi*) to assess the range of sizes used in the design of trap arrays. The distribution of trap spacings was bimodal, with peaks at 10 and 15 m. The mean extent of trapping arrays was 1.8 ha for grids and 358 m for transects. Only 7 manuscripts mentioned prebaiting. The results suggest that many small-mammal studies are designed in a similar way, at small spatial scales. Larger-scale patterns and processes may occur undetected without larger-scale sampling designs.

Authorship: Jeff Bowman, Cristine Corkum, and Graham Forbes

Introduction

Ecological research often is carried out over a narrow range of relatively small spatial scales (Kareiva and Anderson 1989; Brown and Roughgarden 1990). This broad observation also may apply to small-mammal research. One consequence of working at small spatial scales is that larger-scale patterns and processes can be overlooked or misinterpreted (Wiens et al. 1993). For example, Wegner and Merriam (1990) showed that white-footed mice, *Peromyscus leucopus*, use agricultural fields surrounding forest fragments; a phenomenon that could have been overlooked without considering landscape context. Empirical small-mammal field studies commonly employ grid or transect arrays of traps, the design of which establishes the spatial scale of the study. We surveyed the literature to assess the range of trapping array sizes, and thus spatial scales, used in small-mammal research.

Materials and methods

We surveyed published studies of two common species: the red-backed vole, *Clethrionomys gapperi*, and the deer mouse, *Peromyscus maniculatus*. Five journals were chosen where studies of these two species were abundant: American Midland Naturalist, The Canadian Field-Naturalist, Canadian Journal of Zoology, Ecology, and Journal of Mammalogy. All field studies of *P. maniculatus* or *C. gapperi* published between 1960 and 1997 inclusive were selected for our analysis. From each published manuscript, we tabulated data on trap spacing, spatial extent of grid or transect, total trapnights of the study, length of trapping period, length of prebait period, and the number of grid or transect replicates. Areal units were converted to ha and length was converted to m. Some authors published multiple manuscripts using one field study, and in these cases we only included one sample. When multiple designs (e.g., transect and grid) were used in one study they were considered as separate samples. We carried out an exploratory analysis of the tabulated data.

Results and discussion

We surveyed 127 studies from 1960 to 1997 (Appendix 5). The majority of these studies (N = 80; Table 2.1) employed trapping grids rather than transects. Transect studies are limited in that density cannot be estimated (due to the lack of a finite area for the denominator of density calculations). The mean extent of the grids was 1.8 ha while the mean extent of transects was 358 m (Fig. 2.1; Table 2.1). More than 50 % of transects were < 300 m, and more than 50 % of grids were 1 ha or smaller (Fig. 2.1).

Although the mean trap spacing was 14 m, the distribution of spacings was bimodal, with peaks at 10 and 15 m (Fig. 2.2; Table 2.1). The convention of using 10- or 15-m trap spacing seems to be based in part on papers by Burt (1940), Calhoun (1948), Kikkawa (1964) and Smith et al. (1975). Calhoun (1948) presented a standardized protocol for the North American Census of Small Mammals, which used trap stations spaced 20, 50, or 100 ft apart. Note that 50 ft is approximately 15 m. Kikkawa (1964) suggested a 10-m spacing in a deciduous woodland, while Smith et al. (1975) indicated that 15 m is a good compromise for studying a range of species. The selection of a trap spacing should be based on the biology of the study species: spacings should be selected so that each animal has a trap within its home range. This is balanced against the extent of the trapping design and the number of traps logistically feasible. In practice, the extent of the trapping unit (grid or transect) and the spacing of traps are chosen as a compromise between wanting a large area covered in traps and wanting adequate coverage of that area (Tew et al. 1994). It seems that researchers have determined 10- or 15-m spacing to be a good compromise for studying *C. gapperi* or *P. maniculatus* populations.

We were surprised how rarely prebaiting has been practised by small-mammal researchers. Only 7 studies indicated that traps were prebaited. Other authors either did not mention prebaiting or specifically indicated that no prebaiting took place. Chitty and Kempson (1949) suggested that prebaiting is an important tool for avoiding the 'new object reaction' of rodents. Though there is evidence that more animals can be captured over a given trapping period by employing this technique (Chitty and Kempson 1949) it seems that prebaiting is not widely used, or at least not widely reported, in small-mammal studies.

Our survey revealed that most empirical studies of *C. gapperi* or *P. maniculatus* use similar, small-scale designs. Trapping grids are mostly < 2 ha in extent (or transects < 500 m), and traps are spaced 10- or 15-m apart. A number of (presumably) independent replicates are used to generate variance estimates (mean number of replicates = 24.0, median = 6; Table 2.1). We do not suggest that these small-scale studies are inadequate: they can be very effective for studying small mammals (e.g., Smith et al. 1975; Tew et al. 1994). Clearly, the scale of the trapping design must coincide with the scale of the processes being studied (Kareiva and Anderson 1989). What our findings do indicate, is that empirical small-mammal researchers infrequently address questions about large spatial scales. There is, however, a need for such questions since we cannot assume that population processes are restricted to small areas, particularly in light of recent work in landscape ecology.

Acknowledgements

The authors acknowledge the Sustainable Forest Management Network (NCE) for funding. JB and GF received additional funding from Fraser Papers Inc., and the Sir James Dunn Wildlife Research Centre. JB received scholarship funding from NSERC and the University of New Brunswick, and CC received support from the University of Alberta. Tony Diamond, Tim Dilworth, Roger Powell, and Marc-André Villard commented on the manuscript and Jan Murie gave some welcome assistance with the literature search.

References

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich. No. 45.

Brown, J. H., and Roughgarden, J. 1990. Ecology for a changing Earth. Bull. Ecol. Soc. Am. 71: 173-188.

Calhoun, J. B. 1948. North American Census of Small Mammals. Release No. 1, Announcement of Program. Rodent Ecology Project, John Hopkins University, Baltimore, Maryland.

Chitty, D. A., and Kempson, D. A. 1949. Prebaiting small mammals and a new design of live trap. Ecology, 30: 536-542.

Kareiva, P. M. and M. Anderson. 1989. Spatial aspects of species interactions: the wedding of models and experiments. *In* Community ecology. Lecture notes in biomathematics 77. *Edited by* A. S. Hastings. Springer, Berlin. pp. 35-50.

Kikkawa, J. 1964. Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus*. J. Anim. Ecol. 33: 259-299.

Smith, M. H., Gardner, R. H., Gentry, J. B., Kaufman, D. W., and O'Farrell, M. H. 1975. Density estimations of small mammal populations. *In* Small mammals: their productivity and population dynamics. *Edited by* F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge University Press, London. pp. 25-33.

Tew, T. E., Todd, I. A., and MacDonald, D. W. 1994. The effects of trap spacing on population estimates of small mammals. J. Zool., Lond. 233: 340-344.

Wegner, J., and Merriam, H. G. 1990. The use of spatial elements in a farmland mosaic by a woodland rodent. Biol. Conserv. 54: 263-276.

Wiens, J. A., Stenseth, N. C., Van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. Oikos, 66: 369-380.

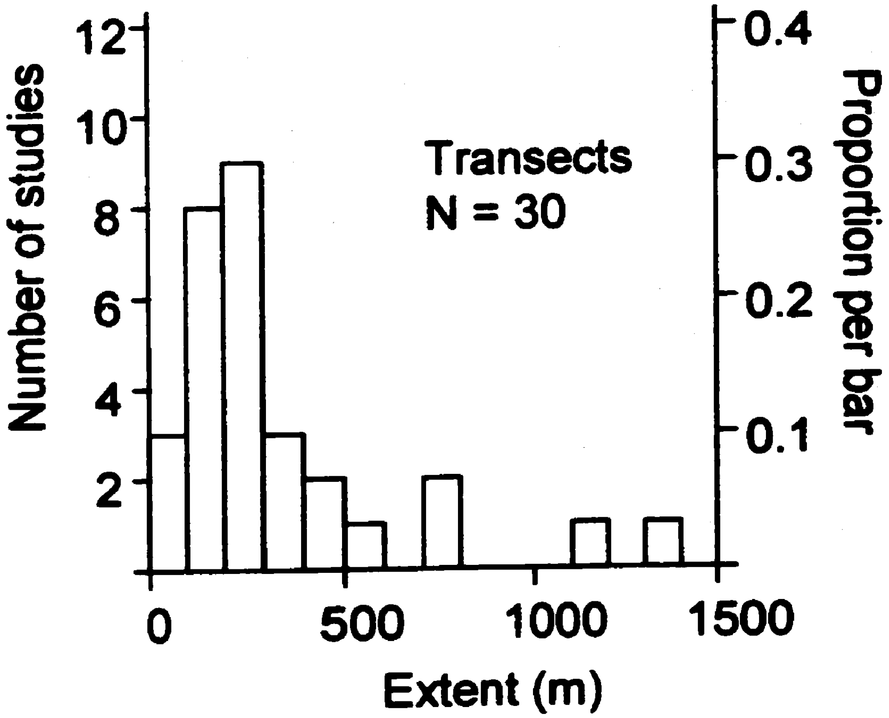
Table 2.1. Descriptive statistics of small-mammal trapping designs published between 1960 and 1997 in five journals*.

Variable	N**	Mean	Median	SE	Min	Max
Trap spacing (m)	114	14	15	0.6	2	45
Extent (grid; ha)	80	1.8	1.0	0.3	< 0.1	18
Extent (transect; m)	30	358	294	55.3	16	1309
Number of replicates	116	24	6	4.6	1	429
Length of trapping period (# nights)	68	4	3	0.3	2	14
Length of prebait period (# nights)	121	0.1	0.0	< 0.1	0	5
Total trapnights	112	11238	5346	1403	154	90000

* Field studies of *Peromyscus maniculatus* and/or *Clethrionomys gapperi* published in American Midland Naturalist, Canadian Field-Naturalist, Canadian Journal of Zoology, Ecology, or Journal of Mammalogy.

** Number of studies for which data was available

Fig. 2.1. Spatial extent of trapping arrays used in studies of *Clethrionomys gapperi* and/or *Peromyscus maniculatus* published in 5 journals (American Midland Naturalist, Canadian Field-Naturalist, Canadian Journal of Zoology, Ecology, and Journal of Mammalogy) between 1960 and 1997.


Transects
N = 30
Number of studies
12
10
8
6
4
2
Proportion per bar
0.4
0.3
0.2
0.1
0
500
1000
1500
Extent (m)

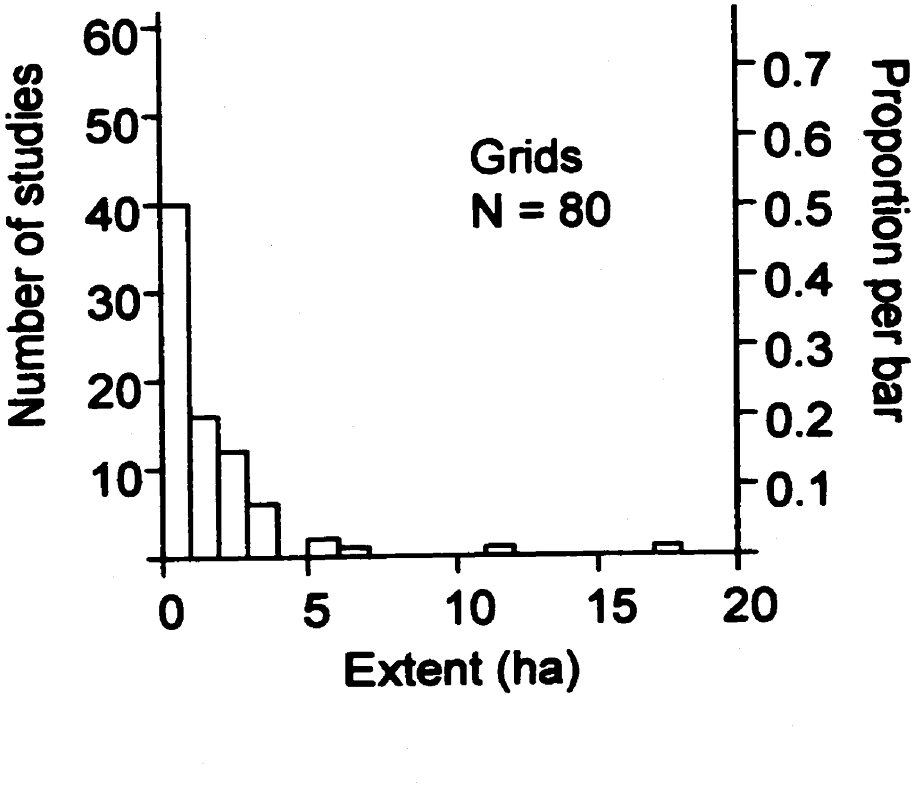
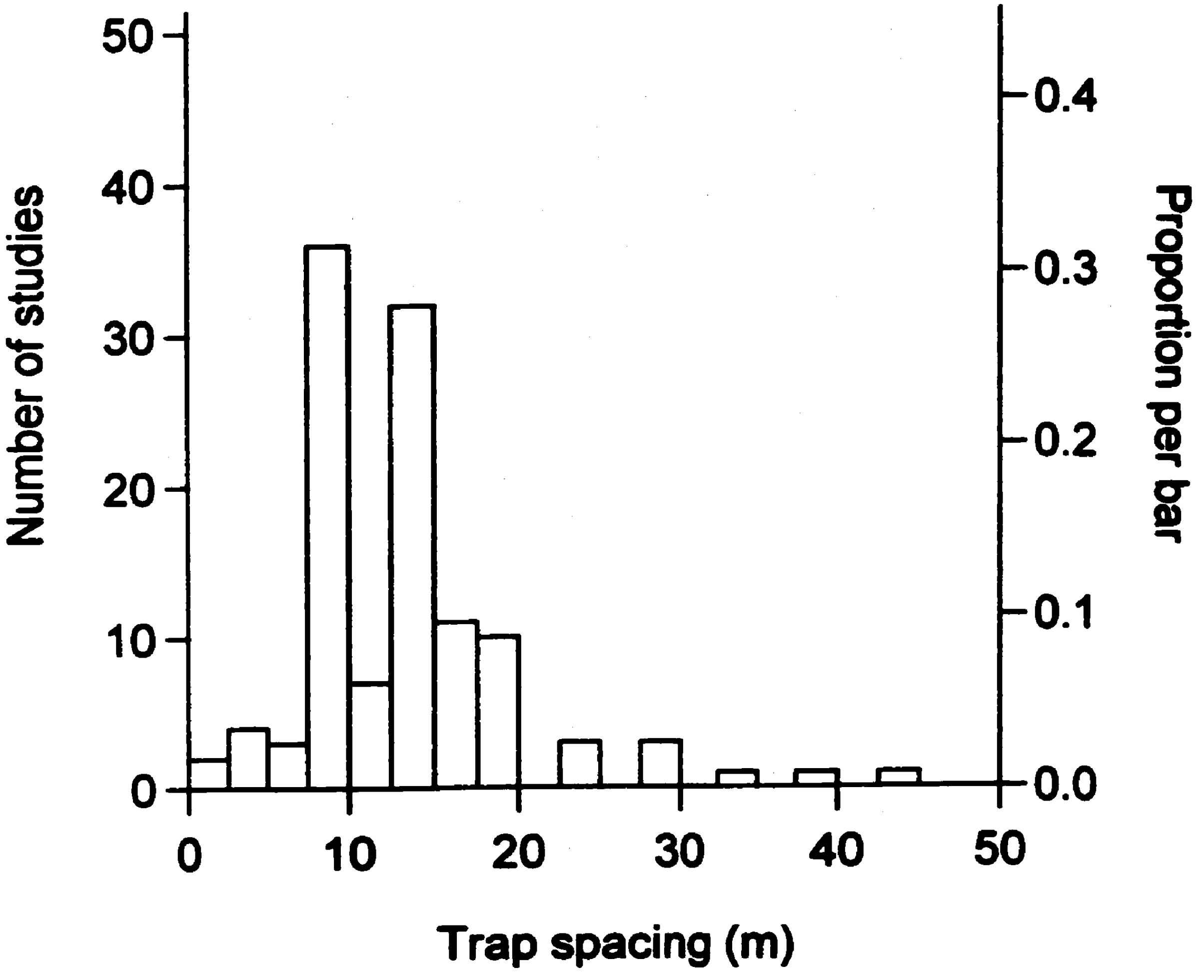

Grids
N = 80
Number of studies
60
50
40
30
20
10
Proportion per bar
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
5
10
15
20
Extent (ha)

Fig. 2.2. Trap spacing used in studies of *Clethrionomys gapperi* and/or *Peromyscus maniculatus* published in 5 journals (American Midland Naturalist, Canadian Field-Naturalist, Canadian Journal of Zoology, Ecology, and Journal of Mammalogy) between 1960 and 1997.


50
40
30
20
10
0
Number of studies
0.4
0.3
0.2
0.1
0.0
Proportion per bar
0
10
20
30
40
50
Trap spacing (m)

Chapter 3

The spatial scale of variability in small-mammal populations

Abstract

We studied small-mammal populations across a range of spatial scales to determine which scales were relevant to demographic variability. We predicted that a scale of variability in population structure would occur at the scale of dispersal, which has previously been described as < 200 m for some small-mammal species. Systematic live-trapping surveys were conducted on nested grids at three scales: (1) extent = 4900 ha, grain = 1000 m; (2) extent = 306 ha, grain = 250 m; and (3) extent = 31 ha, grain = 125 m. Prior to the present study, small mammal populations had not been systematically live-trapped across a similar range of scales. From 1996 to 1998, surveys were conducted on a landscape intensively managed for timber, and on a reference landscape. Spatial analysis of abundance data demonstrated that small-mammal populations (four species) exhibited positive spatial autocorrelation at distances of between 133 and 533 m depending on the species and the landscape. No higher-order population structure was detected. Thus, variability in small-mammal abundance occurred over short distances (i.e., 133 - 533 m).

Authorship: Jeff Bowman, Graham Forbes, and Tim Dilworth

Published in Ecography, 23: 314-320, 2000.

Introduction

Understanding the temporal and spatial scales at which organisms perceive and respond to their environment is a central issue in ecology (Wiens 1989). There has been a tendency by ecologists to study many phenomena within a narrow range of scales (Brown and Roughgarden 1990). A majority of empirical small-mammal research is done at spatial extents of < 2 ha (e.g., Burt 1940; Smith et al. 1975). The small, replicated plots that are often used are essential for many questions, but due to their size, they are not well-suited for understanding larger-scale patterns and processes.

In recent years, spatially-explicit field studies have demonstrated that a number of small-mammal species exhibit structured population dynamics across geographical regions (e.g., Steen et al. 1996; papers in Krebs 1997; Ranta et al. 1997a,b). At spatial scales smaller than a region, populations dynamics can create sub-regional structure (e.g., subpopulations and metapopulations; Krohne 1997; Goodwin and Fahrig 1998). There is little empirical research on the spatial structure of small-mammal populations at this sub-regional scale. Krohne and Burgin (1990) and Morris (1992) found that structure in small-mammal populations is, in part, a result of processes occurring at a scale of hundreds of metres. Morris (1992) detected a dispersal scale of 140 m for deer mice, *Peromyscus maniculatus* Wagner. Krohne and Burgin (1990) detected a scale of demographic heterogeneity in *P. leucopus* Rafinesque that is < 3 ha. Morris (1992) and Krohne and Burgin (1990) may be referring to the same process: *Peromyscus* populations are organised into small (100s of metres) patches. By patch, we mean an area of demographic homogeneity, or low variability. Krohne and Burgin's (1990) patchy structure is directly related to Morris' (1992) dispersal scale – dispersing animals must travel out of a patch to establish a territory (Krohne and Burgin 1990). Such patches are variously defined in the literature as demes (Anderson 1970; Lidicker 1975; Krohne 1997), operational demographic units (Merriam 1995), or subpopulations (Krohne 1997).

A spatially-explicit design was used to assess how populations were organised at scales not previously assessed in a systematic way. Our objective was to detect the spatial scale (or scales) of demographic variability in small-mammal populations, thereby identifying patch structure within the populations. Again, we use the term patch to describe areas of low demographic variability. We refrain from more traditional terms like deme, because of the population genetics connotation (Anderson 1970). In future studies we will relate patches of low variability in mammal abundance to landscape structure: a species-based approach to defining landscape elements. The present study was exploratory, necessary because few current data exist for us to make strong inferences about how populations of the relevant species were distributed in space. We assumed that the findings of Krohne and Burgin (1990) and Morris (1992) (concerning *Peromyscus*) apply broadly to other species of similar size. Therefore, we expected patchiness, or low variability, only at the finest grain in the study (125 m), which was finer than Morris' (1992) dispersal scale. We expected that our coarsest grain was too fine to detect any regional population dynamics (e.g., Steen et al. 1996).

Materials and methods

The study took place on the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of sugar maple *Acer saccharum* Marsh., yellow birch *Betula alleghaniensis* Britt., and American beech *Fagus grandifolia* Ehrh. Lowland sites were dominated by black spruce *Picea mariana* Mill., white spruce *Picea glauca* (Moench) Voss, and balsam fir *Abies balsamea* (L.) Mill.

Our long-term objectives included understanding the response of small-mammal populations to the structure of managed forests. Therefore, we selected two study areas representing opposite ends of the continuum of forest management intensities: (1) a reference area, with relatively little management disturbance (i.e., < 15% recent (< 15 years) clearcut or softwood plantation); and (2) an intensively managed area, where clearcuts and softwood plantations covered > 50% of the landscape. We systematically placed sample points 1000-m apart, in a square (8 x 8) grid, providing two 4900-ha, square grids (reference and managed) each with 64 sample points. Nested within these large grids were 8 x 8 grids with grains of 250 m (306 ha). In the reference area only, there was a third nested grid with a grain of 125 m (30 points, 5 x 6, 31 ha) (Fig. 3.1). For sampling reasons, points were not established within 50 m of roads or water bodies, so some irregularities existed in the shape of the grids. At the top end, our choice of scales was a logistical one; we could not survey more than 4900 ha. The finer scales were chosen for biological reasons with the smallest of these finer than Morris' (1992) dispersal scale. To our knowledge, this project (and a paired project in Alberta; Corkum et al. 1999) was the first where small mammals were systematically live-trapped over a similar range of spatial scales.

We trapped the sample points to estimate small-mammal abundance in spring and autumn beginning in autumn 1996 for the reference area and spring 1997 for the managed area (Table 3.1). Five Victor Tin-Cat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) were used to survey each sample point. One trap was placed at point center, and four other traps were placed at each cardinal direction, 35 m from center (Fig. 3.1 inset). The five-trap array was designed to survey a 50-m radius around each point. All traps were placed in 'most likely runway' positions and prebaited for three days with oats and sunflower hearts. Traps were then set for four consecutive nights. Therefore, a single point took seven days to sample: three nights of prebaiting and four nights of trapping. The number of sampling points precluded us from trapping all the points simultaneously. Trapping on the largest grids (1000-m grain) spanned three seven-day periods, while the smaller grids were trapped within one or two periods and we assumed a negligible temporal drift in the samples. Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, KA, USA) and released. Trapping success was expressed as number of individuals per species per point over four nights, considered a minimum estimate of abundance. Shrews were not marked and so trapping success for shrews was expressed as number of captures per point. Following Henttonen et al. (1985) we used autumn data (mid-August to mid-September) for studying spatial variability in small mammal populations.

Our statistical analysis of the small-mammal capture data was an initial, exploratory approach to describing the spatial structure of the sampled populations (Tukey 1980, Haining 1990). We used patterns of variability in abundance of small mammals as an index to demographic variability (Krohne and Burgin 1990). We assumed small-mammal populations were isotropic in their structure, and so we developed all-directional correlograms (Moran's I; Legendre and Fortin 1989) to study patterns of spatial autocorrelation for species abundances in each of the three reference-area study grids (125-m, 250-m, and 1000-m grains). Then, correlograms were developed for the managed area and contrasted with the patterns of autocorrelation in the reference landscape.

As data were counts, distributions departed from normality, so we conducted our analyses on square-root transformed data. Most techniques for surface pattern analysis (i.e., structure functions: correlograms, semivariograms, and covariograms) require assumptions of normality and stationarity but are robust to departures. Haining (1990) suggests that structure functions are useful exploratory tools for non-normal data providing interpretations are limited. We chose correlograms over the more popular semivariograms (Meisel and Turner 1998) because they are standardised, facilitating comparison among correlograms. Both methods are comparable, in that calculating Moran's I yields a correlogram that is very similar to the inverse of a semivariogram (Meisel and Turner 1998). A second reason for using correlograms was that they allow an objective test of significance. Significance was determined using the Bonferroni procedure (Legendre and Fortin 1989), and because our approach was exploratory, we relaxed requirements for global correlogram significance to alpha = 0.1 (Bonferroni-corrected)

(Steen et al. 1996). Distance classes were established with approximately equal numbers of pairs in each class. Data analysis was conducted using S-Plus 4.0 (MathSoft Inc., Seattle, WA, USA).

Results

From 1996 to 1998 we carried out 20980 multiple-capture trapnights, resulting in 5920 small-mammal captures. A range of species was captured, but we only conducted spatial analysis of the four most abundant species (Table 3.2). Populations of some species, especially deer mice and woodland jumping mice, *Napaeozapus insignis* Miller, exhibited considerable inter-annual fluctuations and for these species spatial analysis was not conducted during the lowest years (Table 3.2).

All species exhibited heterogeneous distributions on all of the grids that were sampled. (Figures 3.2 and 3.3 are representative of the type of outputs available from our spatial analysis approach.) However, we did detect significant positive spatial autocorrelation, which is an indication of the scale of patchiness, or low variability (Legendre and Fortin 1989). On the reference landscape during the fall of 1997, red-backed vole, *Clethrionomys gapperi* Vigors, populations exhibited no autocorrelation (i.e., high variability) at the two largest scales (grains = 1000 m and 250 m). At the finest grain (125 m), voles exhibited significant positive autocorrelation at 133 m (Fig. 3.2). Deer mice populations were also heterogeneous on all grids, however they exhibited a coarser-grained structure (than voles) with positive autocorrelation at 270 m - 275 m (Fig. 3.3). We note here that correlogram distance classes were not exactly equal to the operational grain sizes (e.g., 133 m vs 125 m) because of small irregularities in the shape of the grids.

Table 3.3 summarises the results of our spatial analyses for all species, landscapes, and years. There was no significant autocorrelation at the coarsest grain (1000 m), either in the reference or managed landscapes. Depending on species and landscape, autocorrelation was detected at distances ranging from 133 m to 533 m (Table 3.3). Significant patchiness was detected on the managed landscape for more species, and for larger distance classes than on the reference landscape at the mid-sized grain of 250 m (Table 3.3; Fig. 3.4).

Discussion

In this study we systematically sampled small-mammal populations over a broad range of spatial scales. Populations of small mammals were heterogeneously distributed on all grids (e.g., Figs. 3.2 and 3.3). The results are supported by finer-scale research suggesting that many population processes occur locally (e.g., Patton and Feder 1981; Adler 1987). In our study, positive autocorrelation occurred at distances ranging between 133 m and 533 m, depending on the species and the landscape (Table 3.3). The demographic variability in our study may have been related to: (1) the dispersal scale of 140 m for *Peromyscus maniculatus* detected by Morris (1992); and (2) the 3-ha scale of demographic heterogeneity detected by Krohne and Burgin (1990) for *P. leucopus*. While we studied a range of species, it is reasonable that similar processes were occurring. We suggest that dispersal operates at the same scale as demographic variability – it is exactly this variability that dispersers are trying to exploit. Dispersing individuals seek vacant territory

(Lidicker 1975; Krohne and Burgin 1990). This speculation raises a testable prediction: species with coarser spatial variability in population structure should disperse farther than species with finer spatial variability.

Our inability to detect any larger-scale patchiness suggests that, within the range of scales we studied, fine-scale (133 - 533 m) variation in resources, competition, and/or predator abundance affected the structure of the small-mammal populations. Thus, larger scale patterns were an aggregate of the fine-scaled variation. At even larger, regional scales, spatially-structured population fluctuations can occur in some species (e.g., Steen et al. 1996; Ranta et al. 1997a,b), suggesting a level of organisation beyond the local dynamics considered in our study (e.g., Goodwin and Fahrig 1998).

Much of the spatial structure that we detected in our small-mammal data might be explained by structure in available resources. We will conduct analyses to address this question, however, it is expected that some of the demographic variability occurred independently of habitat structure. Krohne and Burgin (1990) detected demographic heterogeneity in *P. leucopus* populations within apparently homogeneous hardwood stands, and we have observed demic structure in red-backed vole populations within much larger, (apparently) uniform softwood stands (Bowman *et al.* 1999).

Krohne and Burgin (1990) suggested that fine-scaled population aggregates (or patches) vary independently in space and time, depending on the abundance of resources or predators, which themselves fluctuate locally in space and time. Single patches are regulated by a single, dominant factor, but at the scale of the metapopulation, multiple factors regulate populations (Lidicker 1988). This may explain the difficulty researchers have had in trying to relate single factors to population regulation in small mammals

(Krohne and Burgin 1990). This also may contribute to the low proportion of variance explained in many small-mammal habitat use studies.

Our cross-scale design and analysis demonstrated that small-mammal populations exhibited spatial variability at distances of between 133 m and 533 m. The approach was useful for exploring the data, raising some questions about the spatial structure of small-mammal populations. In particular, one testable prediction was raised: species with coarser spatial variability in population structure should disperse farther than species with finer spatial variability.

Acknowledgements

Funding for this study was provided by Fraser Papers Inc., Canada's Sustainable Forest Management Network (NCE), NSERC, The Sir James Dunn Wildlife Research Centre, ACWERN, and Earth Works New Brunswick. We have great cooperators in the NCE project including Steve Young and Gilles Couturier at Fraser Papers Inc., Tony Diamond, Pete McKinley, John Gunn, and Mark Edwards at UNB, M.-A. Villard and Julie Bourque at the University of Moncton, and Stan Boutin, Sue Hannon, Rich Moses, Crissy Corkum, and Jason Fisher at the University of Alberta. Many technicians helped in the field and we are grateful to them. Hugh Broders, Tony Diamond, and M.-A. Villard gave thoughtful comments on the manuscript. Our study protocol was approved by the University of New Brunswick Animal Care Committee.

References

Adler, G. H. 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. Can. J. Zool. 65: 903-912.

Anderson, P. K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond. 626: 299-325.

Bowman, J., Forbes, G., and Dilworth, T. 1999. The spatial structure of small-mammal populations in a managed forest. *In* Science and practice: sustaining the boreal forest. *Edited by* T. S. Veeman, D. W. Smith, B. G. Purdy, F. J. Salkie and G. A. Larkin. Sustainable Forest Management Network, University of Alberta, Edmonton, AB. pp. 58-63.

Brown, J. H., and Roughgarden, J. 1990. Ecology for a changing Earth. Bull. Ecol. Soc. Am. 71: 173-188.

Burt, W. H. 1940. Territorial behaviour and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich., No. 45.

Corkum, C. V., Fisher, J. T., and Boutin, S. 1999. Investigating influences of landscape structure on small mammal abundance in Alberta's boreal mixedwood forest. *In* Science and practice: sustaining the boreal forest. *Edited by* T. S. Veeman, D. W. Smith, B. G. Purdy, F. J. Salkie and G. A.Larkin. Sustainable Forest Management Network, University of Alberta, Edmonton, AB. pp. 29-35.

Goodwin, B. J., and Fahrig, L. 1998. Spatial scaling and animal population dynamics. *In* Ecological scale: theory and applications. *Edited by* D. L. Peterson and V. T. Parker. Columbia University Press, New York, NY. pp. 193-206.

Haining, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press.

Henttonen, H., McGuire, A.D., and Hansson, L. 1985. Comparisons of amplitudes and frequencies (spectral analysis) of density variations in long-term data sets of *Clethrionomys* species. Ann. Zool. Fenn. 22: 221-227.

Kareiva, P. M., and Anderson, M. 1988. Spatial aspects of species interactions: the wedding of models and experiments. *In* Community ecology. Lecture notes in biomathematics 77. *Edited by* A. S. Hastings. Springer, Berlin. pp. 35-50.

Krebs, C. J. 1997. Vole cycles in Hokkaido: a time series goldmine. TREE, 12: 340-341.

Krohne, D. T. 1997. Dynamics of metapopulations of small mammals. J. Mammal. 78: 1014-1026.

Krohne, D. T., and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, 82: 97-101.

Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Lidicker, W. Z. Jr. 1975. The role of dispersal in the demography of small mammals. *In* Small mammals: their productivity and population dynamics. *Edited by* F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge University Press, Cambridge. pp. 103-128.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine "cycles". J. Mammal. 69: 225-235.

Meisel, J. E., and Turner, M. G. 1998. Scale detection in real and artificial landscapes using semivariance analysis. Landscape Ecol. 13: 347-362.

Merriam, H. G. 1995. Movement in spatially divided populations: responses to landscape structure. *In* Landscape approaches in mammalian ecology and conservation. *Edited by* W. Z. Lidicker, Jr. University of Minnesota Press, Minneapolis. pp. 64-77.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol. Ecol. **6**: 412-432.

Patton, J. L., and Feder, J. 1981. Microspatial heterogeneity in pocket gophers: non-random breeding and drift. Evolution, **35**: 912-920.

Ranta, E., Kaitala, V., and Lindstrom, J. 1997a. Dynamics of Canadian lynx populations in space and time. Ecography, **20**: 454-460.

Ranta, E., Kaitala, V., Lindstrom, J., and Helle, E. 1997b. The Moran effect and synchrony in population dynamics. Oikos, **78**: 136-142.

Smith, M. H., Gardner, R. H., Gentry, J. B., Kaufman, D. W., and O'Farrell, M. H. 1975. *In* Small mammals: their productivity and population dynamics. *Edited by* F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge University Press, Cambridge. pp. 25-33.

Steen, H., Ims, R. A., and Sonerud, G. A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. Ecology, **77**: 2365-2372.

Tukey, J. W. 1980. We need both explanatory and confirmatory. Am. Stat. **34**: 23-25.

Wegner, J., and Merriam, H. G. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biol. Conserv. **54**: 263-276.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecol. **3**: 385-397.

Table 3.1. Live-trapping grids surveyed during autumn in northwestern New Brunsick. Three grids (125-m, 250-m, and 1000-m grains) were located in a reference landscape. Two grids (250-m and 1000-m grains) were located in a managed landscape. Autumns when trapping was not conducted are indicated by 'nt'.

	1996	1997	1998
125-m reference	nt	t	t
250-m reference	t	t	t
1000-m reference	t	t	t
250-m managed	nt	t	t
1000-m managed	nt	t	nt

Table 3.2. Autumn capture rates (captures/100 trap nights) for small-mammal species captured in five study grids in northwestern New Brunswick. Listed in order of abundance in most abundant year.

Species	1996	1997	1998
**Peromyscus maniculatus* Wagner	0.81	22.30	3.62
**Clethrionomys gapperi* Vigors	5.17	9.92	18.83
**Blarina brevicauda* Say	4.24	9.63	17.76
**Napaeozapus insignis* Miller	3.64	0.25	2.95
Microtus chrotorrhinus Miller	0	0.16	0
Mustela erminea L.	0	0.14	0
Microtus pennsylvanicus Ord	0	0	0.07
Synaptomys cooperi Baird	0.04	0.02	0.02
Zapus hudsonicus Zimmerman	0	0.04	0
Sorex spp.	0	0.37	1.05

* indicates species selected for spatial analysis

Table 3.3. Distance classes (m) of positive autocorrelation from globally significant correlograms for small-mammal populations captured in autumn on five study grids in the forests of northwestern New Brunswick. A reference landscape contained three grids (125-m, 250-m, and 1000-m grains) and a managed landscape contained two (250-m and 1000-m grains). All grids were surveyed in 1996 (96), 1997 (97), and 1998 (98) unless indicated by 'nt' (not trapped). A hyphen '-' indicates that the correlogram was not globally significant.

	Reference landscape									Managed landscape					
	125-m			250-m			1000-m			250-m			1000-m		
	96	97	98	96	97	98	96	97	98	96	97	98	96	97	98
C. g.	nt	133	133	-	-	-	-	-	-	nt	267	267	nt	-	nt
P. m.	nt	270	350	-	275	275	-	-	-	nt	267	267	nt	-	nt
B. b.	nt	-	-	-	-	-	-	-	-	nt	533	-	nt	-	nt
N. i.	nt	-	270	-	-	275	-	-	-	nt	-	267	nt	-	nt

C. g. = *Clethrionomys gapperi*; *P. m.* = *Peromyscus maniculatus*; *B. b.* = *Blarina brevicauda*; and *N. i.* = *Napaeozapus insignis*.

Fig. 3.1. Layout of three study grids on a reference forest landscape in northwestern New Brunswick, Canada. Three nested scales were surveyed: A = 1000-m grain, 8 x 8 points, 4900 ha extent; B = 250-m grain, 8 x 8 points, 306 ha extent; and C = 125-m grain, 5 x 6 points, 31 ha. Each survey point consisted of an array of five traps (inset). The study design was duplicated on an intensively managed forest landscape, with the exception of C, which was omitted.

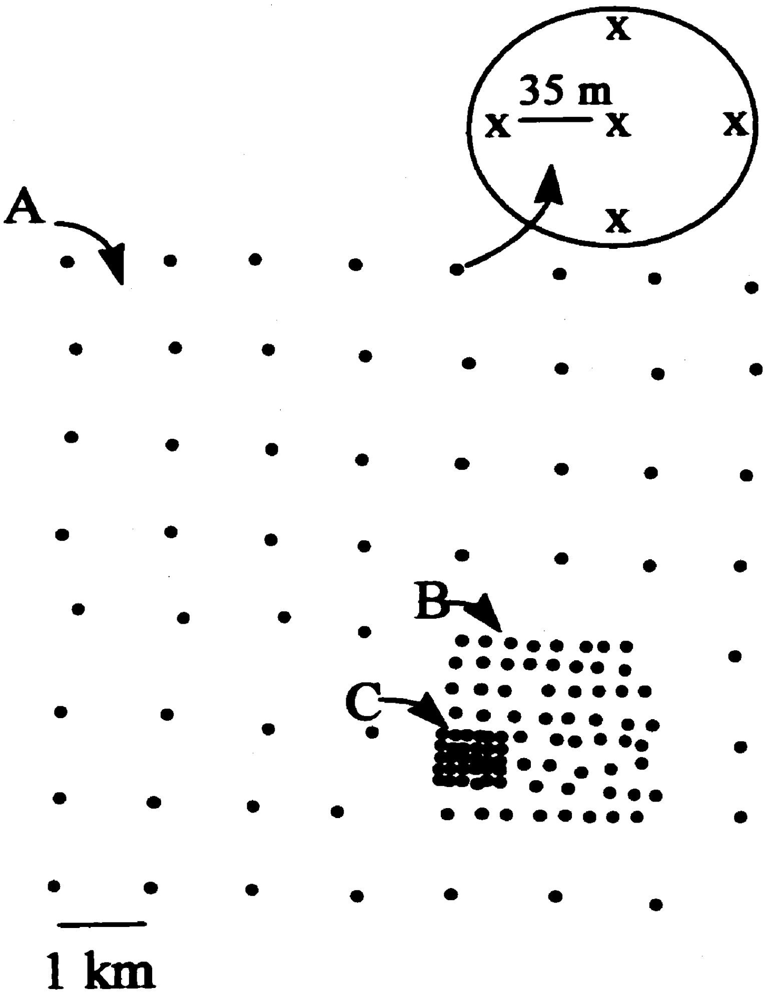

x
35 m
x
x
x
x
A
B
C
1 km

Fig. 3.2. Interpolated gray-scale maps and correlograms for autumn abundance of *Clethrionomys gapperi*, sampled at three spatial scales in a reference forest in New Brunswick. Three, nested survey grids are represented by: A (1000-m grain, 8 x 8 points, 4900 ha extent); B (250-m grain, 8 x 8 points, 306 ha extent); and C (125-m grain, 5 x 6 points, 31 ha extent). Abundance data range from 0 (white) to 12 (black) per survey point. Filled correlogram symbols indicate: (1) global correlogram significance; and (2) distance classes with significant autocorrelation.

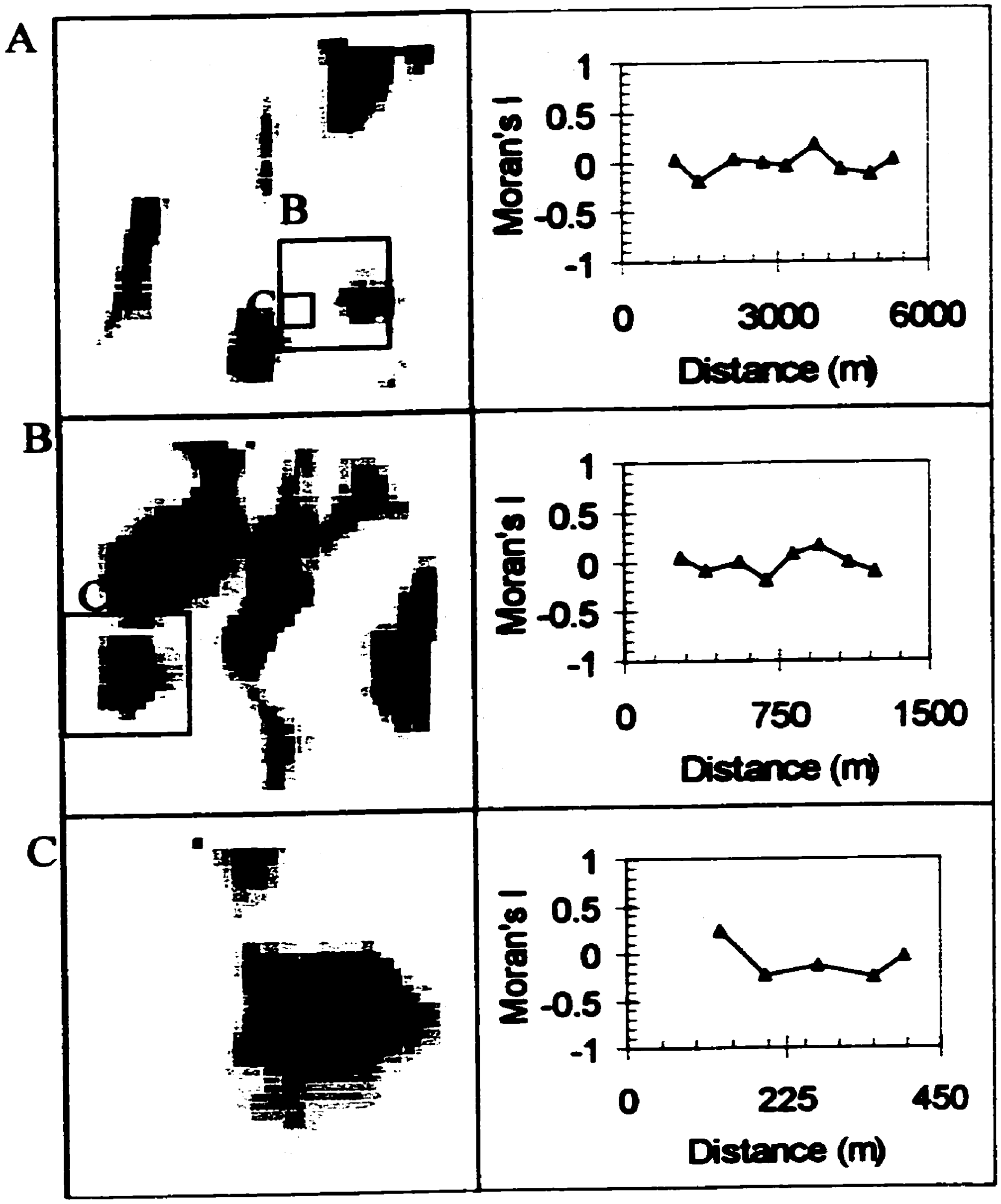

A
B
C
B
C
C
1
0.5
0
-0.5
-1
Moran's I
0
3000
6000
Distance (m)
0
750
1500
Distance (m)
0
225
450
Distance (m)

Fig. 3.3. Interpolated gray-scale maps and correlograms for autumn abundance of *Peromyscus maniculatus,* sampled at three spatial scales in a reference forest in New Brunswick. Three, nested survey grids are represented by: A (1000-m grain, 8 x 8 points, 4900 ha extent); B (250-m grain, 8 x 8 points, 306 ha extent); and C (125-m grain, 5 x 6 points, 31 ha extent,). Abundance data range from 0 (white) to 15 (black) per survey point. Filled correlogram symbols indicate: (1) global correlogram significance; and (2) distance classes with significant autocorrelation.

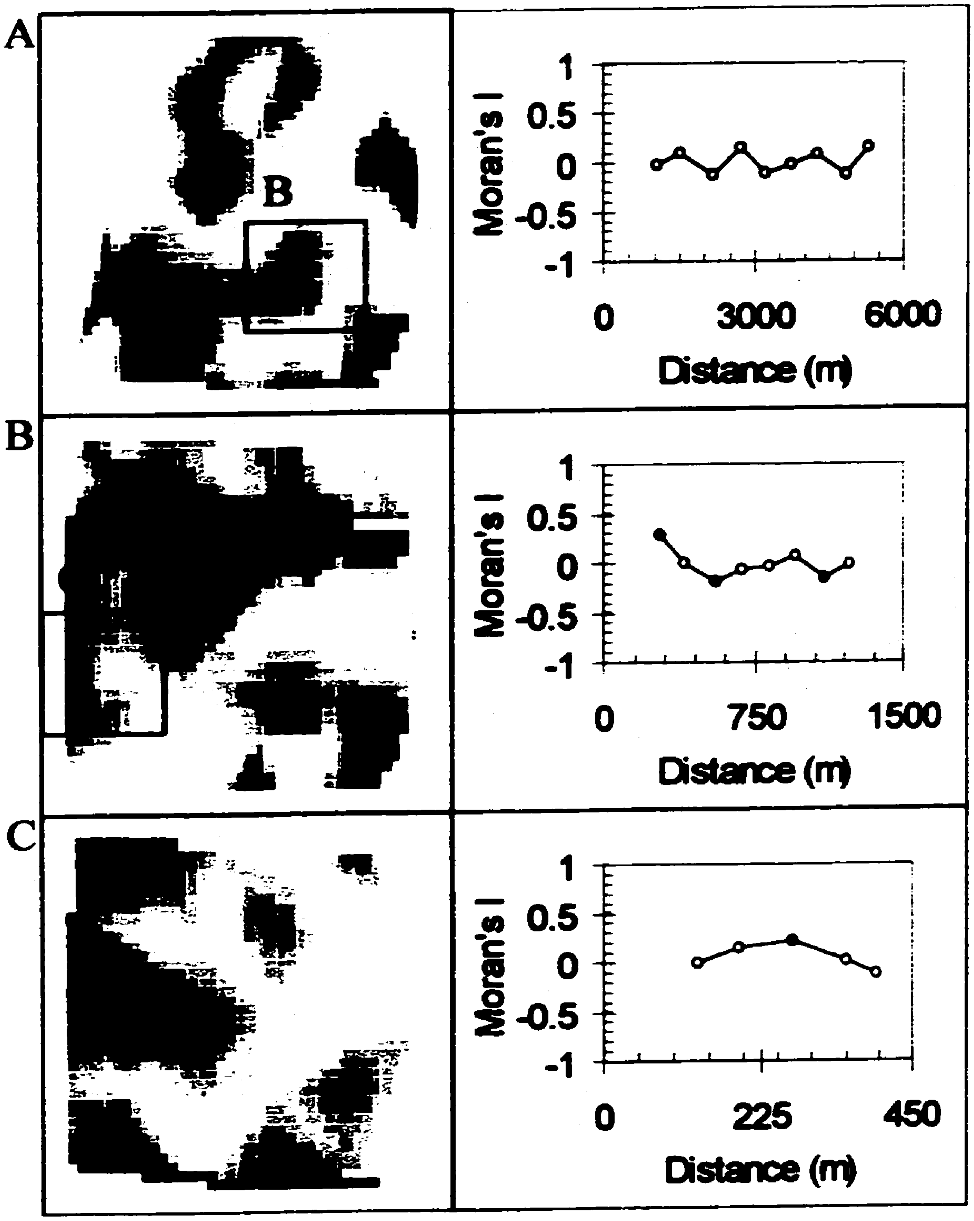
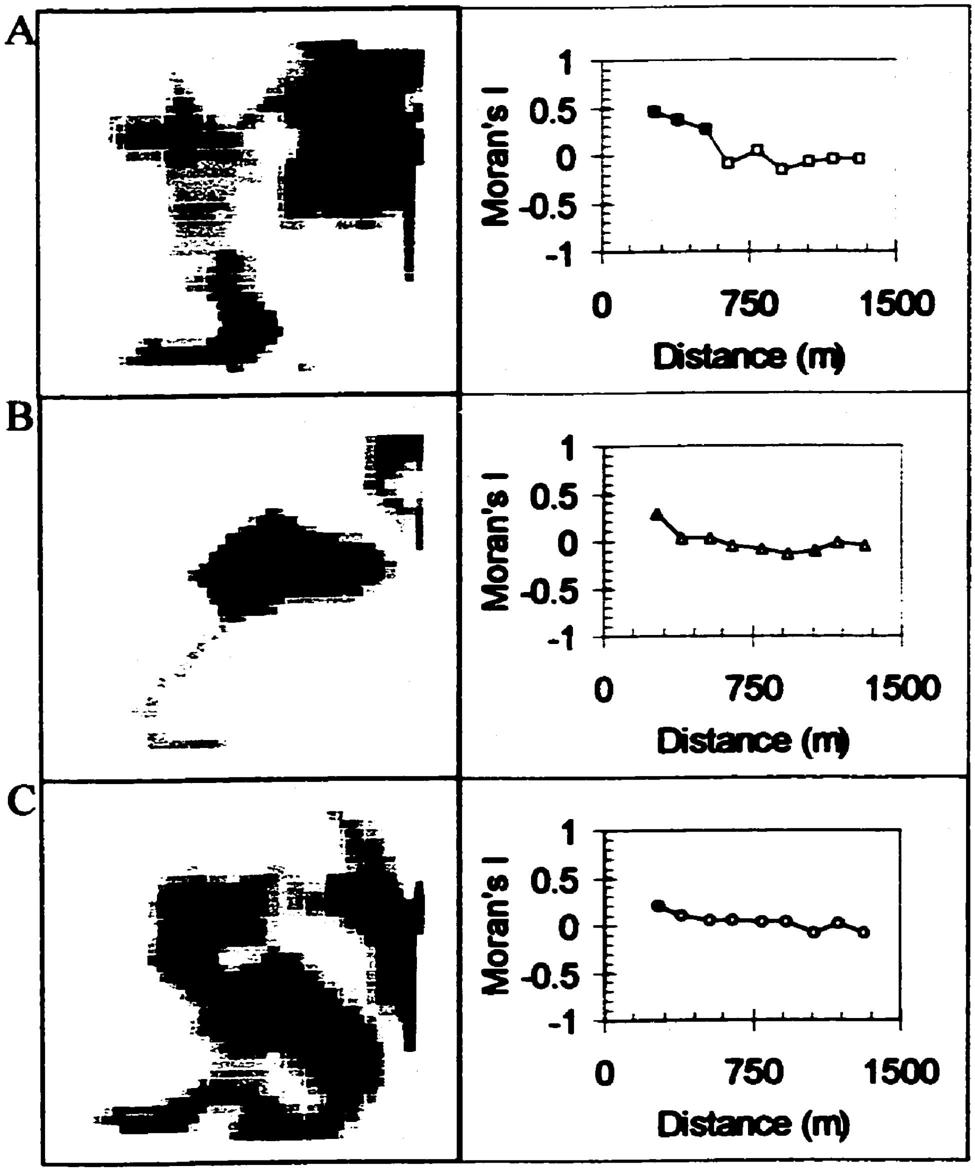

A
B
Moran's I
1
0.5
0
-0.5
-1
0
3000
6000
Distance (m)
B
Moran's I
1
0.5
0
-0.5
-1
0
750
1500
Distance (m)
C
Moran's I
1
0.5
0
-0.5
-1
0
225
450
Distance (m)

Fig. 3.4. Interpolated gray-scale maps and correlograms for autumn abundance of three small-mammal species in an intensively managed forest in New Brunswick, sampled on a systematic grid (250-m grain, 8x 8 points, 306 ha extent). The three species are: *Blarina brevicauda* (A), *Clethrionomys gapperi* (B), and *Peromyscus maniculatus* (C). Abundances range from 0 (white) to 11 (black) individuals per point. Filled correlogram symbols indicate: (1) global correlogram significance; and (2) distance classes with significant autocorrelation.


A
Moran's I
1
0.5
0
-0.5
-1
0
750
1500
Distance (m)
B
Moran's I
1
0.5
0
-0.5
-1
0
750
1500
Distance (m)
C
Moran's I
1
0.5
0
-0.5
-1
0
750
1500
Distance (m)

Chapter 4

Distances moved by small woodland rodents within large trapping grids

Abstract

During a four-year small-mammal study in New Brunswick, Canada, we documented long-distance movements (> 125 m) for three species. Mean straight-line distances moved were: 370 m (*Peromyscus maniculatus*; N = 44), 225 m (*Napaeozapus insignis*; N = 33), and 224 m (*Clethrionomys gapperi*; N = 23). More woodland jumping mice, *N. insignis*, moved than any other species, relative to abundance: 9.4% of captures were made after a long-distance movement.

Authorship: Jeff Bowman, Graham Forbes, and Tim Dilworth

Introduction

Movement is an important process, which can contribute to the temporal and spatial structure of populations (Wiens et al. 1993). However, empirical descriptions of movements for small mammals are rare, in part, because of the methods used to sample populations (Howard 1960; Clark et al. 1988). Trapping grids frequently are too small in spatial extent to detect long-distance movements (e.g., Burt 1940; Smith et al. 1975; Wegner and Merriam 1990). Despite the difficulty of data collection, there are reports of long-distance movements for a variety of small-mammal species, for example: *Peromyscus maniculatus* (Howard 1960; Bowman et al. 1999), *Peromyscus leucopus* (Krohne et al. 1984; Wegner and Merriam 1990), *Napaeozapus insignis* (Ovaska and Herman 1988), *Dipodomys stephensi* (Price et al. 1994), *Reithrodontomys megalotis* (Clark et al. 1988), and papers in Kozakiewicz and Szacki (1995). These reports are an important source of data which can help ecologists to understand the process of dispersal (Kozakiewicz and Szacki 1995).

We carried out a four-year study of the spatial structure of small-mammal populations in a managed forest in New Brunswick, Canada. Our study design involved large (4900 ha) live-trapping grids which provided us with an opportunity to assess long-distance movements for three species. In this paper, we describe the magnitude and variability of long-distance movements made by: *Peromyscus maniculatus*, *Napaeozapus insignis*, and *Clethrionomys gapperi*.

Materials and methods

The study took place in the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*).

The study design is described in detail by Bowman et al. (2000). Two 4900-ha forested landscapes, one intensively managed, the other a reference, were systematically live-trapped using a set of nested grids. The two largest grids (one per landscape) had grains of 1000 m and extents of 4900 ha (8 x 8; 64 points each). Nested within each of the large grids was a smaller grid with a grain of 250 m and an extent of 310 ha (8 x 8; 64 points each), and, on the reference, there was a third grid with a grain of 125 m and an extent of 31 ha (5 x 6; 30 points). A total of 260 sample points were spread systematically across the two landscapes within these grids. At each point an array of 5 Victor Tincat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) was used to sample small-mammal populations. Traps were placed at point centre and 35-m from the centre on each compass ordinal; each trap was placed in a 'most likely runway' position. Traps were prebaited for three days with oats and sunflower hearts and then set for four consecutive nights. The trapping protocol was carried out twice per annum in spring (May - June) and autumn (August - September). Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag

(National Band and Tag Co., Newport, KA, USA) and released. Our protocol was approved by the University of New Brunswick Animal Care Committee.

We considered that an animal had moved if it was recaptured (i.e., with an ear tag) at a sample point where it had not been captured previously. The finest grain in our study was 125 m (i.e., the space between sample points on the 31 ha trapping grid) so 125 m was our definition of a long-distance movement. Shorter movements were not long enough to move an animal between sample points, and were not considered in our analysis. Movement distances were calculated as straight-line distances between the centres of the capture and recapture sample points. Calculations were made using digital maps of the study area and a Geographic Information System (GIS; Arc/View). All long-distance movements were summed across seasons and years (per species) to maximize our sample. In other words, we made no distinction between spring and autumn movements. We present descriptive analyses of the movement data that enable some comparison of the magnitude and variability of long-distance movements across species.

Results and discussion

The three most abundant rodents captured were red-backed voles, (*Clethrionomys gapperi*; 9.40 captures/100 trap nights (tn)), deer mice (*Peromyscus maniculatus*; 7.66 captures/100 tn), and woodland jumping mice (*Napaeozapus insignis*; 2.78 captures/100 tn). These three were the only species for which long-distance movements were witnessed. Relative to abundance, more woodland jumping mice moved between sampling points than any other species: 9.4% of captures occurred after long-distance movements, compared to 4.2% and 1.8% for deer mice and red-backed voles, respectively (Table 4.1).

These proportions were calculated by omitting captures on the two largest (1000-m grain) grids because no movements were ever recorded at the largest scale.

While distances moved were of similar magnitude among species, deer mice made longer movements than either woodland jumping mice or red-backed voles (Fig. 4.1, Table 4.1). The longest of these (1768 m) was reported by Bowman et al. (1999). Other authors recognize the ability of deer mice (and closely-related white-footed mice, *Peromyscus leucopus*) to move long distances. Howard (1960) recorded a movement of 1000 m for *P. maniculatus*, and Wegner and Merriam (1990) reported a movement by *P. leucopus* of > 1000 m. While Ovaska and Herman (1988) demonstrated a movement by a woodland jumping mouse of > 800 m, we are unaware of other studies reporting long-distance movements by either *N. insignis* or *C. gapperi*, with the exception of homing studies. For example, Bovet (1980) recorded successful homing by red-backed voles from as far as 600 m.

Two sources of error must be considered when interpreting these data. First, we have not corrected for the uneven distribution of trap pairs among different distance classes. The number of trap pairs varied with distance (Fig. 4.1) and in fact, appeared to bias our results long: there were fewer trap pairs at the shortest distances. This was further confounded by a second bias: the density of traps varied throughout the study grids as a result both of geometry and the nested trapping design. Rather than make questionable corrections against these two biases, we present unmodified data and caution the reader against over interpretation. Even with the inherent biases, these data are of value because of the scarcity of information on small-mammal movements (e.g., Wegner and Merriam 1990; Kozakiewicz and Szacki 1995).

We expect that many of the movements which we have operationally-defined as 'long-distance' are actually dispersal movements. Krohne and Burgin (1990) speculated on a relationship between dispersal and spatial population structure. Dispersing animals exploit openings caused by demographic heterogeneity — there is, according to this speculation, a relationship between the spatial scales of dispersal and population structure. Similarly, Morris (1992) suggested that there is a dispersal scale, which is a level of organization for populations. For example, Bowman et al. (2000) demonstrated that deer mouse, red-backed vole, and woodland jumping mouse populations exhibit patchy structure at distances of 133 - 350 m, on the same study landscapes as the movement data presented here. The magnitudes of the patchy structure and the dispersal movements are similar, supporting Krohne and Burgin's (1990) speculation that the spatial scales of dispersal and population structure are related.

Acknowledgements

The authors acknowledge financial support from Fraser Papers Inc., The Sustainable Forest Management Network, NSERC, The Sir James Dunn Wildlife Research Centre, and EarthWorks NB. We cooperated with Mark Edwards, Tony Diamond, Pete McKinley, John Gunn, M.-A. Villard, Julie Bourque, Sue Hannon, Stan Boutin, Crissy Corkum, Jason Fisher, Rich Moses, and many assistants: we thank them all. Tony Diamond and M.-A. Villard gave thoughtful comments on the manuscript.

References

Bovet, J. 1980. Homing behaviour and orientation in the red-backed vole, *Clethrionomys gapperi*. Can. J. Zool. **58**: 754-760.

Bowman, J., Forbes, G., and Dilworth, T. 2000. The spatial scale of variability in small-mammal populations. Ecography. **23**: 314-320.

Bowman, J., Edwards, M., Sheppard, L., and Forbes, G. 1999. Record distance for a non-homing movement by a deer mouse, *Peromyscus maniculatus*. Can. Field-Nat. **113**: 292-293.

Burt, W. H. 1940. Territorial behaviour and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich., No. 45.

Clark, B. K., Kaufman, D. W., Kaufman, G. A., Finck, E. J., and Hand, S. S. 1988. Long-distance movements by *Reithrodontomys megalotis* in a tallgrass prairie. Am. Midl. Nat. **120**: 276-281.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. **63**: 152-161.

Kozakiewicz , M., and Szacki, J. 1995. Movement of small mammals in a landscape: patch restriction or nomadism? *In* Landscape approaches in mammalian ecology and conservation. *Edited by* W. Z. Lidicker, Jr. University of Minnesota Press, Minneapolis. pp. 78-94.

Krohne, D. T. and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, **82**: 97-101.

Krohne, D. T., Dubbs, B. A., and Baccus, R. 1984. An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus*. Am. Midl. Nat. **112**: 146-156.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol. Ecol. **6**: 412-432.

Ovaska, K. and Herman, T. B. 1988. Life history characteristics and movements of the woodland jumping mouse, *Napaeozapus insignis*, in Nova Scotia. Can. J. Zool. **66**: 1752-1762.

Price, M. V., Kelly, P. A., and Goldingay, R. L. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi* Merriam) and implications for conservation. J. Mammal. **75**: 929-939.

Smith, M. H., Gardner, R. H., Gentry, J. B., Kaufman, D. W., and O'Farrell, M. H. 1975. *In* Small mammals: their productivity and population dynamics. *Edited by* F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge University Press, Cambridge. pp. 25-33.

Wegner, J. and Merriam, G. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biol. Conserv. **54**: 263-276.

Wiens, J. A., Stenseth, N. C., Van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. Oikos, **66**: 369-380.

Table 4.1. Distances moved by small woodland rodents within large trapping grids in New Brunswick, Canada.

Species[A]	Mean Dist. (m)	SE (m)	Max Dist. (m)	N	Percent[B]	J[C]	F[D]	M[E]
P. m.	370	55	1768	44	4.2	21	8	15
N. i.	225	22	607	33	9.4	3	10	20
C. g.	224	24	494	23	1.8	5	1	17

[A] *P. m.* = *Peromyscus maniculatus*; *N. i.* = *Napaeozapus insignis*; *C. g.* = *Clethrionomys gapperi*

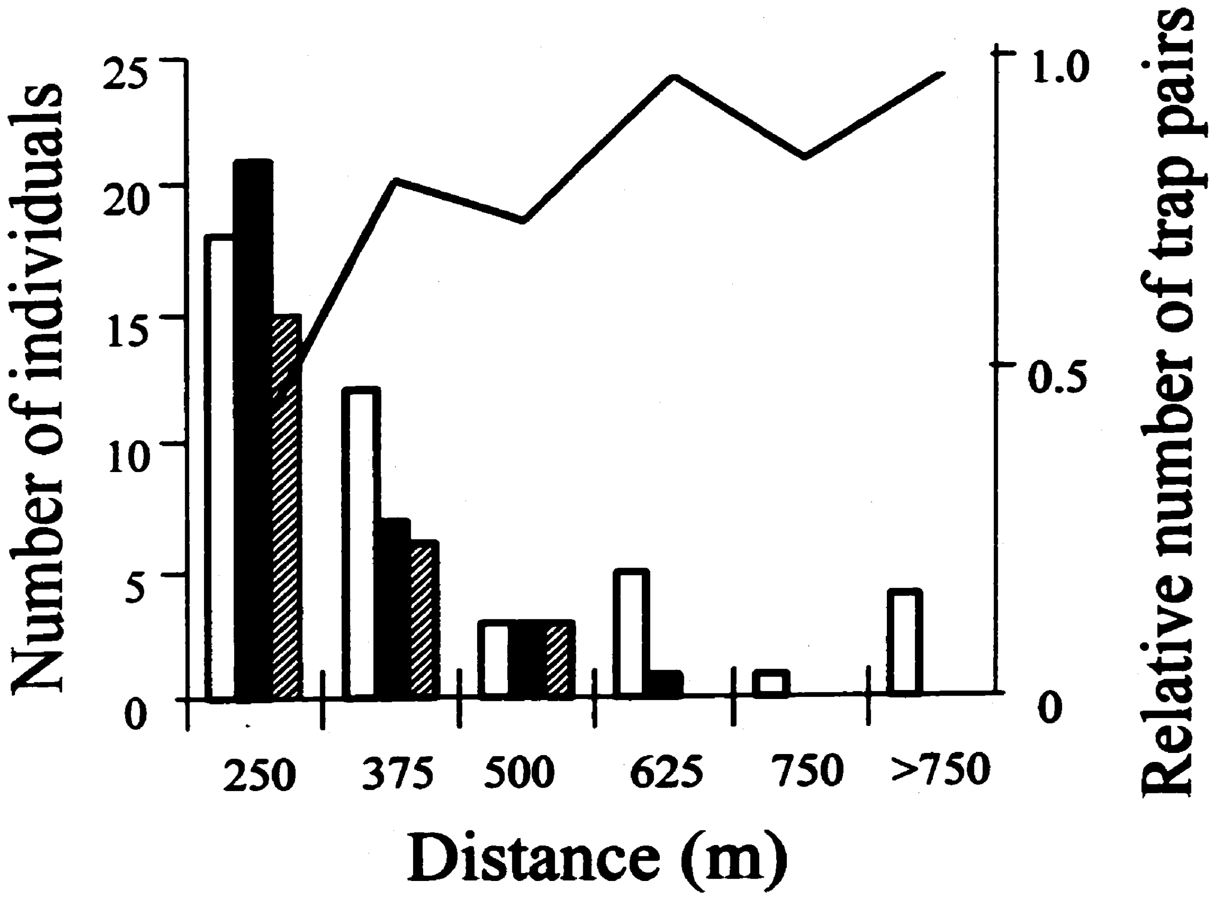
[B] Percentage of captures that had moved > 125 m.

[C] Juveniles and subadults

[D] Adult females

[E] Adult males

Fig. 4.1. Distribution of distances moved by woodland rodents within large trapping grids in New Brunswick, Canada. White bars are *Peromyscus maniculatus*, solid bars are *Napaeozapus insignis*, and hatched bars are *Clethrionomys gapperi*. The relative number of trap pairs within each distance class is indicated by the solid line.


Number of individuals
25
20
15
10
5
0
250
375
500
625
750
>750
Distance (m)
1.0
0.5
0
Relative number of trap pairs

Chapter 5

Landscape context and small-mammal abundance in a managed forest

Abstract

We assessed whether small-mammal abundance was related to landscape context, when context was considered independently of within-stand vegetation and at different spatial extents. The study took place in an industrial forest in northwestern New Brunswick, Canada. Within-stand vegetation models explained 9 - 32 % of the deviance in the abundance of individuals from the four most abundant species: *Clethrionomys gapperi*, *Peromyscus maniculatus*, *Blarina brevicauda*, and *Napaeozapus insignis*. Landscape context was related to the distributions of two species: *C. gapperi* were less abundant within contexts of softwood plantations; and *N. insignis* abundance was directly related to the amount of softwood forest. Variables measured at the largest radii of landscape context (500 m) were never significantly associated with the abundance of small mammals. Most species appeared robust to forest management with the exception of the negative relationship between *C. gapperi* and softwood plantations.

Authorship: Jeff Bowman, Graham Forbes, and Tim Dilworth

Accepted for publication in Forest Ecology and Management

Introduction

Forest management can influence populations of small mammals in at least two ways: (1) by altering conditions within forest stands; or (2) by altering conditions around stands (i.e., altering the landscape context). Although the effects on small-mammal populations of landscape context in managed forests are not well known, the within-stand effects of various forest management interventions have been studied and have generally indicated that small-mammal populations are robust. For example, Kirkland (1990) reviewed 21 published studies to demonstrate that in eastern North America, many small-mammal species respond positively to clear cutting. He suggested that this response is due to the increased amount of herbaceous understory foliage on recently cut sites. Similarly, a number of stand-scale studies have demonstrated that small-mammal populations either respond positively, or do not respond to selection (or partial) cutting (Swan et al. 1984; Monthey and Soutiere 1985; Medin and Booth 1989; Steventon et al. 1998). Broadly, it seems that there is a positive relationship between small-mammal populations and the amount of understory foliage. Thus, stand interventions which reduce the amount of herbaceous understory (e.g., herbicide application, mechanical site preparation, softwood plantations) also reduce populations of folivorous small mammals until such a time as the understory regrows (Langley and Shure 1980; Parker 1989; Lautenschlager 1993).

The removal of coarse woody debris (CWD) associated with some stand interventions (e.g., scarification) can be deleterious to small-mammal populations (see Harmon et al. 1986 and Freedman et al. 1996 for reviews). Dead logs are a source of fungi and mycophagous small mammals (e.g., *Clethrionomys*) use CWD for foraging

(Maser and Trappe 1984). The distribution of mycophagous small mammals has been linked to the distribution of CWD (Nordyke and Buskirk 1991; Bowman et al. 2000a).

The many studies of within-stand effects of forest management on small mammals demonstrate a wide range of often species-specific relationships. However, few studies assess these relationships at the scale of a forest landscape. By forest landscape, we refer to spatial extents larger than single forest stands. The studies that do exist suggest, like many within-stand studies, that small-mammal species often are robust to forest management. Rosenberg and Raphael (1986) did not detect a negative response by small mammals to forest fragmentation in the Rocky Mountains, suggesting instead that deer mice (*Peromyscus maniculatus*) respond positively to some edge and clearcut measures. Sekgororoane and Dilworth (1995) and Bayne and Hobson (1998) also found deer mice associated with edges. Other studies have suggested that deer mice and red-backed voles (*Clethrionomys gapperi*), two of the most common small-mammal species in eastern North America, are not adversely affected by the cumulative effects of stand interventions across forest landscapes (Yahner 1992; Bayne and Hobson 1998; Hayward et al. 1999). However, most studies of small-mammal populations have not considered the influence of landscape context independently of the effects of within-stand vegetation.

The spatial extents over which landscape context influences small-mammal populations will depend on the extents over which population processes of small-mammal species occur (e.g., Roland and Taylor 1997). Krohne and Burgin (1990) and Bowman et al. (2000b) have demonstrated that demographic variability in small mammal populations occurs over relatively short distances (100s of metres). These authors have suggested that the variability is a result of processes such as predation, habitat selection, and competition occurring locally (i.e., within 100s of metres). If such processes do indeed occur over small extents, then larger-scale landscape context should be relatively unimportant (e.g., Dickman and Doncaster 1987). The objective of this paper was to assess whether small-mammal abundance was related to management-induced landscape context, when context was considered independently of within-stand vegetation and at different spatial extents.

Materials and methods

Some aspects of the study design were also described by Bowman et al. (2000a,b). The study took place on the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick, Canada (47°N, 67°W). Upland sites were dominated by tolerant hardwood communities, with an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*P. glauca*), eastern white cedar (*Thuja occidentalis*), and balsam fir (*Abies balsamea*). We selected two study areas representing opposite ends of the continuum of forest management intensities: (1) a reference area, with relatively little management disturbance (i.e., < 15% recent (< 15 years) clearcut or softwood plantation); and (2) an intensively managed area, where clearcuts and softwood plantations covered > 50% of the landscape. We systematically placed sample points 1000-m apart, in a square (8 x 8) grid, providing two 4900-ha, square grids each with 64 sample points. For sampling reasons, points were not established within 50 m of roads or water bodies.

Small mammals

We trapped the sample points to estimate small-mammal abundance in spring and autumn, 1997. Five Victor Tin-Cat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) were used to survey each sample point. One trap was placed at point centre, and four other traps were placed at each cardinal direction, 35 m from centre. The five-trap array was designed to survey a 50-m radius around each point. All traps were placed in 'most likely runway' positions and prebaited for three days with oats and sunflower hearts. Traps were then set for four consecutive nights. Therefore, a single point took seven days to sample: three nights of prebaiting and four nights of trapping. The number of sampling points precluded us from trapping all the points simultaneously. During each season, trapping spanned three seven-day periods. Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, KA, USA) and released. Our protocol was approved by the University of New Brunswick Animal Care Committee. Trapping success was expressed as number of individuals per species per point over four nights, and this was considered a relative index of abundance. Shrews were not marked and so trapping success for shrews was expressed as number of captures per point.

Within-stand vegetation

Within-stand vegetation characteristics were sampled at each point using three 10- by 20-m quadrats. One quadrat was placed at the centre of the plot (offset 5 m to the west to avoid the effects of observer traffic at the point). Two other quadrats were placed 75-m from the centre at two of the following positions (selected randomly): north, southwest, southeast. Within each quadrat, trees ≥ 8 cm in diameter-at-breast-height (DBH) were counted, identified to species, and measured for DBH and decay class (1 = healthy live tree, 9 = decayed stump; Maser et al. 1979). Stems < 8 cm DBH were considered understory. Understory plants were sub-sampled on a 10- by 2-m transect within the quadrats. All woody understory stems were identified to species and stratified by height: 0.5 - 1 m, 1 - 2 m, 2 - 4 m, 4 - 6 m, and > 6 m. The ground layer (leaf litter, herbs, bare ground, bryophytes, lichens, and graminoids) in each quadrat was measured by subjectively assigning a value from 0 to 5 (0 = absent, 5 = very abundant). Coarse woody debris was measured along the two 20-m edges of each quadrat. Logs ≥ 8 cm diameter (mid-log) were tallied and measured for diameter, species (where possible), and decay class (1 = sound, 5 = highly decayed; Maser et al. 1979). Vegetation surveys were completed during July and August of 1997.

Landscape context

Digital forest inventories, based on 1996 aerial photographs, were obtained from the land owner and were used to describe the forest landscapes. We used a Geographic Information System (GIS; Arc/Info and Arc/View) to develop landscape metrics. We wanted metrics that would describe the effects of forest management on the landscape, at a range of spatial scales. We reclassified the landscapes into 6 coarse patch types: tolerant hardwood, partially-cut tolerant hardwood (< 15 years), softwood, mixedwood, clear cut (< 15 years), and plantation (< 15 years; included the oldest available). Most plantations were scarified and had received an application of herbicide, so we did not separately measure these effects. Buffers of varying radii (100 m, 250 m, 500 m) were established around each sample point and within each buffer the composition of patch types was calculated, as a proportion. We calculated total edge (m) within each buffer (related to disturbance linearly; Hargis et al. 1998). To calculate edges, landscapes were dissolved into three cover types: (1) plantation + clearcut; (2) road; and (3) all other types. Only management-induced edges (roads, clearcut + plantation vs other forest types) were included. We also included separate variables measuring amount of road edge (m) and clearcut + plantation edge (m) within each buffer. In addition, the distance to the nearest road was measured for each sample point. As roads are a result of forest management, we felt that distance to roads should also be related to management disturbance. Finally, we calculated the number of patches within each buffer (a richness measure) and Simpson's diversity index for each buffer.

Data analysis

A previous study (Bowman et al. 2000b) demonstrated that small-mammal populations at points 1000 m apart are not spatially autocorrelated. Therefore, we included all 128 sample points in parametric analyses.

A set of local vegetation variables was selected by performing a principal components analysis (PCA). We used the broken-stick model as a stopping rule for the PCA (Jackson 1993), keeping the original vegetation variable that was most strongly loaded onto each PCA axis. We did not use the actual PCA scores because many vegetation variables exhibited non-normal distributions. Thus, the PCA was just an exploratory tool used to select variables.

Small-mammal data were counts, so we used Poisson regressions (from the family of Generalized Linear Models [GLMs]) to build optimal models relating the abundance of small mammals (by species and season) to local vegetation characteristics. Optimal models were those explaining the most deviance in the response variable. Significance of these regression models was determined using analysis of deviance tables (alpha = 0.05). Deviance residuals from these regressions were saved and used as new variables, representing small mammal distributions independent of the effects of local vegetation. This new set of variables was regressed (using Gaussian GLMs; the deviance residuals had Gaussian distributions) against the set of landscape metrics, to measure the independent effects of landscape context on the distribution of small mammals. Compositional variables that were proportions were arcsine transformed.

Results

During 5120 trapnights, we made 1500 captures of > eight species (see Bowman et al. 2000a). We only carried out statistical analyses of the four most abundant species: deer mice; red-backed voles; short-tailed shrews, *Blarina brevicauda*; and woodland jumping mice, *Napaeozapus insignis*. Statistical analyses were not carried out on *N. insignis* data from autumn because of low abundance.

Analysis of 114 different sample points demonstrated that all four species were significantly related to within-stand vegetation characteristics. Depending on species and season, between 9 and 32 % of the deviance in small-mammal distributions was explained by vegetation (Table 5.1).

Small-mammal species were distributed similarly among cover types in both spring and autumn (Table 5.2). Generally, red-backed voles and woodland jumping mice were most abundant in softwood sites, while deer mice and short-tailed shrews were most abundant in hardwood stands and in clear cuts. No species was abundant in plantations.

When the effects of within-stand vegetation were removed from small-mammal abundances, two species were significantly related to variables describing landscape context. In both spring and autumn, red-backed voles were negatively associated with the amount of plantation. The best model (i.e., most explained deviance) for this relationship was for a 250-m radius in spring and a 100-m radius in autumn (Table 5.3). Woodland jumping mice were positively associated with the amount of softwood within a 100-m radius of sampling points (Table 5.3). No species were significantly related to any edge variables at any radius, nor to the distance of the nearest road. Nor were there any significant relationships with the richness or diversity of patches.

Discussion

Our results were indicative of the resource generalism of many small-mammal species. Although within-stand vegetation was always significantly related to species-specific small-mammal abundance, a relatively low amount of deviance was explained (between 9 and 32%; Table 5.1).

Landscape context was related to the distributions of two species: *C. gapperi* and *N. insignis*. Although context was important, it was never important at the largest radius of 500 m (Table 5.3). We believe that this is consistent with the suggestion of Krohne and Burgin (1990) and Bowman et al. (2000b) that processes occur locally to structure small-mammal populations in space. Bowman et al. (2000b) found *C. gapperi* and *N. insignis* populations spatially autocorrelated at scales of 275 m or less, depending on the landscape.

The negative relationship between *C. gapperi* and the amount of plantation accords with other studies that find red-backed voles to be negatively related to forest management indices. Mills (1995) found western red-backed voles (*C. californicus*) to be more abundant in interiors than forest edges and similarly, Sekgororoane and Dilworth (1995) found that *C. gapperi* are most abundant in forest interiors compared to forest-clearcut edges. Although some studies have not indicated a negative association between red-backed voles and managed forests (e.g., Kirkland 1990; Yahner 1992; Bayne and Hobson 1998), Nordyke and Buskirk (1991) suggested that *C. gapperi* is an indicator of old-growth conditions in the Rocky Mountains because of a positive relationship with decadent coarse woody debris. We also found a relationship between red-backed voles and coarse woody debris (Bowman et al. 1999; Bowman et al. 2000a) and this may explain, in part, why voles were negatively-related to plantations. Although young plantations might be suitable for voles (Parker 1989), in our study area plantations had received site preparation (e.g., scarification and herbicide) that removed much of the structure and forage.

Woodland jumping mice were more abundant during spring in landscapes with softwood forest (Table 5.3). At a continental scale, the distribution of this species is related to the distribution of hemlock, spruce, and balsam fir (Banfield 1984), and there is a microhabitat relationship between softwood species and woodland jumping mice (e.g., Vickery 1981).

Our data do not support studies that find a positive relationship between small-mammal species (particularly deer mice) and edge (Rosenberg and Raphael 1986; Bayne and Hobson 1995; Sekgororoane and Dilworth 1995). Deer mice in our study were related to hardwood understory variables in both spring and fall (Table 5.1). Hardwood shrubs are themselves often associated with edges, so an affinity by deer mice for shrubby sites could be the basis for the apparent relationship between deer mice and edge.

The study demonstrated that in managed forest, four small-mammal species were significantly related to local vegetation variables. Two of the species demonstrated weak relationships to landscape context at spatial extents of 100 and 250 m. Highlighted were the resource generalism of small mammals and the robustness of many small-mammal species in the face of intensive forest management. Further studies should be carried out to study red-backed vole population structure in forests perforated by softwood plantations.

Acknowledgements

We received funding for this research from Fraser Papers Inc., the Sustainable Forest Management Network (NCE), NSERC, and the Sir James Dunn Wildlife Research Centre. We collaborated with many colleagues including Gilles Couturier, Steve Young, Tony Diamond, Pete McKinley, John Gunn, Mark Edwards, Lisa Sheppard, M.-A. Villard, Julie Bourque, Sue Hannon, Stan Boutin, Rich Moses, Jens Roland, Phil Taylor, Crissy Corkum, and Jason Fisher. We thank our many helpful colleagues and technicians for their support. Tony Diamond and Tara Warren made helpful suggestions on the manuscript.

References

Banfield, A. W. F. 1984. The mammals of Canada. University of Toronto Press, Toronto.

Bayne, E. M., and Hobson, K. A. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. Can. J. Zool. **76**: 62-69.

Bowman, J., Sleep, D., Forbes, G., and Edwards, M. 2000a. The association of small mammals and coarse woody debris at log and stand scales. For. Ecol. Manage. **129**: 119-124.

Bowman, J., Forbes, G., and Dilworth, T. 2000b. The spatial scale of variability in small-mammal populations. Ecography. **23**: 314-320.

Bowman, J., Forbes, G., and Dilworth, T. 1999. The spatial structure of small-mammal populations in a managed forest. *In* Science and practice: sustaining the boreal forest. *Edited by* T. S. Veeman, D. W. Smith, B. G. Purdy, F. J. Salkie and G. A.Larkin. Sustainable Forest Management Network, University of Alberta, Edmonton, AB. pp. 58-63.

Dickman, C. R., and Doncaster, C. P. 1987. The ecology of small mammals in urban habitats. I. Populations in a patchy environment. J. Anim. Ecol. **56**: 629-640.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J. S., Johnson, G., and Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. **4**: 238-265.

Hargis, C. D., Bissonette, J. A., and David, J. L. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecol. 13: 167-186.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K., Jr., and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.

Hayward, G. D., Henry, S. H., and Ruggiero, L. F. 1999. Response of red-backed voles to recent patch cutting in subalpine forest. Cons. Biol. 13: 168-176.

Jackson, D. A. 1993. Stopping rules in principle components analysis: a comparison of heuristical and statistical approaches. Ecology, 74: 2204-2214.

Kirkland, G. L. Jr., 1990. Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos, 59: 313-320.

Krohne, D. T., and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, 82: 97-101.

Langley, A. K. Jr., and Shure, D. J. 1980. The effects of loblolly pine plantations on small mammal populations. Am. Midl. Nat. 103: 59-65.

Lautenschlager, R. A. 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. Can. J. For. Res. 23: 2286-2299.

Maser, C., Anderson, R. Cromack, K. Jr., Williams, J. T., and Martin, R. E. 1979. Dead and down woody material. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J. W. Thomas. USDA Agricultural Handbook 553.

Maser, C., and Trappe, J. M. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164. Pacific Northwest For. and Range Exp. Station, Portland, Oregon.

Medin, D. E., and Booth, G. D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. USDA For. Serv. Gen. Tech. Rep. INT-408. Intermountain Research Station, Ogden, Utah.

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Cons. Biol. **9**: 395-403.

Monthey, R. W., and Soutiere, E. C. 1985. Responses of small mammals to forest harvesting in northern Maine. Can. Field-Nat. **99**: 13-18.

Nordyke, K. A., and Buskirk, S. W. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Can. Field-Nat. **105**: 330-334.

Parker, G. H. 1989. The effects of reforestation upon small mammal communities in New Brunswick. Can. Field-Nat. **103**: 509-519.

Roland, J., and Taylor, P. D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature **386**: 710-713.

Rosenberg, K. V., and Raphael, M. G. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. *In* Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. *Edited by* J. Verner, M. L. Morrison, and C. J. Ralph. University of Wisconsin Press, Madison. pp. 263-272.

Sekgororoane, G. B., and Dilworth, T. G. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Can. J. Zool. **73**: 1432-1437.

Steventon, J. D., MacKenzie, K. L., and Mahon, T. E. 1998. Responses of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. For. Chron. **74**: 703-713.

Swan, D., Freedman, B., and Dilworth, T. G. 1984. Effects of various hardwood forest management practices on small mammals in central Nova Scotia. Can. Field-Nat. **98**: 362-364.

Vickery, W. L. 1981. Habitat use by northeastern forest rodents. Am. Midl. Nat. **106**: 111-118.

Yahner, R. H. 1992. Dynamics of a small mammal community in a fragmented forest. Am. Midl. Nat. **127**: 381-391.

Table 5.1. Results of generalized linear models relating vegetation variables to mammal abundances in northwestern New Brunswick. Variables are all counts and are listed in order of entry. Relationships are significant at: $P < 0.001$ (+++), $P < 0.01$ (++), or $P < 0.05$ (+). All relationships are positive. For all regressions, $N = 114$.

	Spring 1997		Autumn 1997	
Species*	Variable	Deviance (%)	Variable	Deviance (%)
C. g.	Softwood shrubs < 1 m	13.3^{+++}	Spruce stems	14.5^{+++}
	Hardwood shrubs 2 - 4 m	5.3^{+}	Hardwood shrubs > 6 m	4.4^{+}
	Balsam fir snags	5.7^{+}	Softwood shrubs < 1 m	2.3^{+}
			Beech stems	4.2^{+}
P. m.	Hardwood shrubs 4 - 6 m	3.8^{+}	Sugar maple stems	7.0^{++}
	Balsam fir stems	6.5^{+}	Beech shrubs 4 - 6 m	2.6^{+}
			Balsam fir stems	2.8^{+}
B. b.	Hardwood shrubs 2 - 4 m	9.4^{++}	Sugar maple shrubs < 1 m	11.0^{+++}
			Hobblebush** shrubs < 1 m	4.2^{+}
			Total stems	4.1^{+}
N. i.	Total snags	15.6^{+++}	(No analysis)	
	Yellow birch shrubs < 1 m	10.1^{++}		
	Coarse woody debris	6.0^{+}		

* *C. g.* = *Clethrionomys gapperi*; *P. m.* = *Peromyscus maniculatus*; *B. b.* = *Blarina brevicauda*; and *N. i.* = *Napaeozapus insignis*

** *Viburnum alnifolium*

Table 5.2. Mean number of individuals (± 95% confidence interval) captured by season in major stand types during a small-mammal trapping project in northwestern New Brunswick in 1997. The sampling design was systematic, so some trapping grids were intersected by > 1 stand-type. These intersected samples were excluded from the summary.

Species*	Season	Hardwood (N = 43)	Softwood (N = 18)	Plantation (N = 13)	Clear cut (N = 8)	Partial cut (N = 10)
C. g.	Spring	0.7 ± 0.5	1.9 ± 1.2	0.1 ± 0.2	0.3 ± 0.3	0.6 ± 0.6
	Autumn	1.5 ± 0.8	4.3 ± 1.8	0.4 ± 0.4	1.4 ± 1.3	0.7 ± 0.5
P. m.	Spring	0.8 ± 0.3	0.4 ± 0.3	0.2 ± 0.2	1.0 ± 1.2	0.3 ± 0.4
	Autumn	3.8 ± 1.0	2.5 ± 1.4	1.3 ± 1.5	4.1 ± 3.3	5.0 ± 2.3
B. b.	Spring	0.5 ± 0.3	0.1 ± 0.2	0.2 ± 0.3	0.4 ± 0.4	0.0 ± 0.0
	Autumn	2.5 ± 0.8	1.6 ± 0.7	0.7 ± 0.5	1.9 ± 1.2	4.7 ± 3.2
N. i.	Spring	0.1 ± 0.1	0.6 ± 0.5	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0
	Autumn	0.0 ± 0.1	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.00	0.0 ± 0.0

* *C. g.* = *Clethrionomys gapperi*; *P. m.* = *Peromyscus maniculatus*; *B. b.* = *Blarina brevicauda*; and *N. i.* = *Napaeozapus insignis*.

Table 5.3. Results of Generalized Linear Models relating landscape context variables to mammal abundances in northwestern New Brunswick. Mammal (response) variables are abundances with local vegetation trends removed through regression. Relationships are significant at: $P < 0.01$ (– –) or $P < 0.05$ (+, –). Direction of relationships is indicated by + or – signs. For all regressions, N = 114.

	Spring 1997		Autumn 1997	
Species*	Variable	Deviance (%)	Variable	Deviance (%)
C. g.	Plantation (250 m)***	4.3 –	Plantation (100 m)**	7.2 – –
P. m.	No significance		No significance	
B. b.	No significance		No significance	
N. i.	Softwood (100 m)**	4.8 $^+$	(No analysis)	

* *C. g.* = *Clethrionomys gapperi*; *P. m.* = *Peromyscus maniculatus*; *B. b.* = *Blarina brevicauda*; and *N. i.* = *Napaeozapus insignis.*

** Variable calculated within a 100-m radius

*** Variable calculated within a 250-m radius

Chapter 6

The spatial component of variation in small-mammal abundance at three scales

Abstract

We studied small-mammal populations across a range of spatial scales to determine if populations exhibited spatial variability that was independent of the distribution of vegetation. Between 1996 and 1999, systematic live-trapping surveys were conducted on nested grids at three scales: (1) extent = 4900 ha, grain = 1000 m; (2) extent = 306 ha, grain = 250 m; and (3) extent = 31 ha, grain = 125 m. The four most abundant species were *Clethrionomys gapperi*, *Blarina brevicauda*, *Peromyscus maniculatus*, and *Napaeozapus insignis*. The amount of variation in the small-mammal matrices explained by spatial models was inversely proportional to the sampling grain, while the amount of variation explained by vegetation was consistent across scales. We suggest that fine-scale spatial structure occurs in small-mammal populations — a result of processes occurring over short distances.

Authorship: Jeff Bowman, Graham Forbes, and Tim Dilworth

Introduction

Spatial variability in population attributes has often been related to variable resource quality (e.g., environmental control, Whittaker 1956; ideal-free habitat selection; Fretwell and Lucas 1970). However, Quinn and Dunham (1983) suggested that patterns are often caused by multiple factors, including vertical and horizontal processes such as predation and competition. For example, Krohne and Burgin (1990) demonstrated demographic heterogeneity in *Peromyscus leucopus* within a forest that the authors perceived to be homogenous. Krohne and Burgin's (1990) study and others (Anderson 1970; Krohne and Baccus 1985; Cooke 1997) suggest that demographic structure which is independent of resource use can exist within populations. This structure reflects a level of organization, equivalent to a local or sub-population (Krohne 1997; Goodwin and Fahrig 1998).

The idea that populations can vary in space independently of the environment is not new. In fact, it is implicit in many theoretical discussions of genetics and population regulation in small mammals (e.g., Hansson 1977; Anderson 1980; Lidicker 1988). However, the scale over which such variability occurs has been addressed infrequently by empiricists. Some suggest that small-mammal populations can exhibit spatial heterogeneity over relatively short distances of hundreds of metres (Krohne and Burgin 1990; Bowman et al. 2000). Krohne and Burgin (1990) suggested that sub-populations (demographic units in their language) arise such that exploitable variation in population structure exists within the spatial domain of dispersal. For example, Morris (1992) demonstrated a dispersal scale of 140 m for *Peromyscus maniculatus*.

The development of spatial analytical techniques has allowed ecologists to model processes that vary in space (e.g., Legendre and Fortin 1989; Borcard et al. 1992; Rossi et al. 1992; Thomson et al. 1996). These techniques generally involve the description of spatial pattern. Patterns which have structure (i.e., they are not random) can be considered synthetic models of underlying spatial processes, such as dispersal or predation (Legendre and Fortin 1989; Borcard et al. 1992). As patterns have a scale, spatial analytical techniques can also be used to detect the scale of the underlying processes that spatial patterns represent (Legendre and Fortin 1989).

We tested the prediction that processes occurring independently of the effects of resource variation contribute to the distribution and abundance of small mammals. Our objectives were: (1) to assess whether small-mammal populations exhibited spatial structure that was independent of the distribution of resources; and (2) to determine the spatial scale(s) over which structure occurred. The study was carried out at three different scales within a 4900-ha landscape, with our finest grain smaller than Morris' (1992) dispersal scale.

Materials and methods

The study took place on the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*).

The overall study design was described in detail by Bowman et al. (2000). The present study was carried out on a 4900-ha forested landscape that was managed with a low intensity for forest products (e.g., < 15% recent clear cuts or softwood plantations). A set of nested grids was used to sample the 4900-ha landscape for small mammals (Fig. 3.1). The largest grid had a grain of 1000 m and an extent of 4900 ha (8 x 8; 64 points). Nested within the large grid was a smaller grid with a grain of 250 m and an extent of 310 ha (8 x 8; 64 points) and a third grid with a grain of 125 m and an extent of 31 ha (5 x 6; 30 points). A total of 141 sample points were spread systematically across the landscape within these grids. At each point an array of 5 Victor Tincat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) was used to sample small-mammal populations (Fig. 3.1 inset). Traps were placed at point centre and 35-m from the centre on each compass ordinal; each trap was placed in a 'most likely runway' position. Traps were prebaited for three days with oats and sunflower hearts and then set for four consecutive nights. The trapping protocol was carried out twice per annum in spring (May - June) and autumn (August - September) beginning in autumn 1996 until spring 1999. The number of sampling points precluded us from trapping all the points simultaneously. Trapping on the largest grids (1000-m grain) spanned three seven-day periods, while the smaller grids were trapped within one or two periods and we assumed a negligible temporal drift in the samples. Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, KA, USA) and released. Our protocol was approved by the University of New Brunswick Animal Care Committee.

Vegetation characteristics were sampled at each point using three 10- by 20-m quadrats. One quadrat was placed at the centre of the plot (offset 5 m to the west to avoid the effects of observer traffic at the point). Two other quadrats were placed 75-m from the centre at two of the following positions (selected randomly): north, southwest, southeast. Within each quadrat, trees ≥ 8 cm in diameter-at-breast-height (DBH) were counted, identified to species, and measured for DBH and decay class (1 = healthy live tree, 9 = decayed stump; Maser et al. 1979). Stems < 8 cm DBH were considered understory. Understory plants were sub-sampled on a 10- by 2-m transect within the quadrats. All woody understory stems were identified to species and stratified by height: 0.5 - 1 m, 1 - 2 m, 2 - 4 m, 4 - 6 m, and > 6 m. The ground layer (leaf litter, herbs, bare ground, bryophytes, lichens, and graminoids) in each quadrat was measured by subjectively assigning a value from 0 to 5 (0 = absent, 5 = very abundant). Coarse woody debris was measured along the two, 20-m edges of each quadrat. Logs ≥ 8 cm diameter (mid-log) were tallied and measured for diameter, species (where possible), and decay class (1 = sound, 5 = highly decayed; Maser et al. 1979). Vegetation surveys at each point were completed during July and August of 1997.

Patterns of variability in abundance of small mammals were used as an index to demographic variability (Krohne and Burgin 1990; Bowman et al. 2000). Small-mammal data were counts, so abundances were square-root transformed prior to parametric analysis. Matrices of small-mammal abundance were related to vegetation and spatial location in direct gradient analyses using canonical correspondence (CCA; ter Braak 1986). We used the method of partial constrained ordination (Borcard et al. 1992) to partition variance in the small-mammal matrices into four parts: (1) variation related to vegetation and independent of any spatial effects; (2) variation related to space and independent of any vegetation effects; (3) variation related to both spatial and vegetation effects (i.e., shared variance); and (4) unexplained variation. A set of 20 vegetation variables was developed by examining a correlation matrix of variables and subjectively eliminating one variable where $r > 0.6$. Spatial structure was estimated using a set of two-dimensional geographical co-ordinates in a cubic polynomial (Borcard et al. 1992):

$$Z = b_1 X + b_2 Y + b_3 XY + b_4 X^2 + b_5 Y^2 + b_6 X^2 Y + b_7 XY^2 + b_8 X^3 + b_9 Y^3 \quad (1)$$

where Z is spatial variation in small-mammal abundance, X is longitude and Y is latitude in Cartesian co-ordinates. The cubic polynomial was used because it has some ability to model non-linearities. Our decision to use more vegetation variables than spatial variables was conservative: bias resulting from unequal numbers of variables would have underestimated the spatial, rather than the vegetation, component.

Partial constrained ordination was carried out using CANOCO (ter Braak 1988). For each small-mammal matrix, the optimal vegetation model was determined using the forward selection procedure available in CANOCO. Spatial models were determined in the same way. Partial ordinations were carried out by removing effects of the spatial model from the vegetation model, and vice-versa. Significance of models was assessed using Monte-Carlo permutation tests with $p < 0.05$.

Results

During 16320 trapnights, the most abundant species were *Clethrionomys gapperi* (9.40 captures per 100 tn), *Blarina brevicauda* (7.89 captures per 100 tn), *Peromyscus maniculatus* (7.66 captures per 100 tn), and *Napaeozapus insignis* (2.78 captures per 100 tn) (Table 6.1). These four, abundant species were included in the ordination analyses, with the exceptions of *P. maniculatus* from autumn 1996 and *N. insignis* from autumn 1997 due to insufficient abundance those seasons.

In each autumn that we sampled, vegetation models explained a significant amount of variation in the small-mammal species matrix at every spatial scale (Table 6.2). However, the spatial models were only significant at the 125-m and 250-m grains, and never at the 1000-m grain. There was little variation in small-mammal abundance that was shared by both the vegetation and spatial models (Table 6.4). No models lost significance during partial ordinations.

The spring data revealed results that were very similar to results from the autumn. Vegetation models explained a significant amount of variation in the small-mammal species matrix with the exception of the 1000-m grain during spring 1997 (Table 6.3). Spatial models from spring analyses were always significant at the 125-m grain, but only significant during spring 1999 at the 250-m grain. Spatial models were never significant in spring at the 1000-m grain (Table 6.3). Again, as in the autumn, no models lost significance during the partial ordinations, indicating that little of the variation in the small-mammal matrices was shared by both the vegetation and spatial matrices (Table 6.4).

Regardless of season or scale, vegetation explained more variance in the small-mammal matrices than either the spatial or the shared (spatial-vegetation) components (Table 6.4; Fig. 6.1). The 95% confidence intervals for the mean amount of variation in small-mammal matrices explained by vegetation overlapped across the three scales (Table 6.4). The spatial models explained more variance at the 125-m grain than either of the coarser grains (Table 6.4; Fig. 6.1).

Discussion

Small-mammal populations in our study exhibited spatial variability that was independent of the distribution of vegetation. Spatial structure was most important at our finest sampling grain of 125 m (Fig. 6.1). These results are consistent with the notion that sub-population structure occurs within the spatial domain of dispersal (Krohne and Burgin 1990). For example, mean long-distance movements made by species in the present study ranged from 224 m (*C. gapperi*) to 370 m (*P. maniculatus*) (Bowman et al. submitted). A time series of the spatial patterns of red-backed vole abundance reveals that while the scale of spatial structure was consistent, the actual patterns were, temporally, remarkably dynamic. For example, there was not one site within the 125-m grain sampling grid that was consistently occupied by red-backed voles (Fig. 6.2). The fine-scale structure that we observed suggests that vertical and horizontal processes, such as predation and competition, can act over a short distance to create spatial structure within small-mammal populations (Krohne and Burgin 1990; Bowman et al. 2000).

While the amount of variation in the small-mammal matrices explained by the spatial models was inversely proportional to sampling grain, the amount of variation explained by vegetation was consistent across scales (Table 6.4, Fig. 6.1). In other words, the portion of population structure that we attribute to resource-use was constistent across scales. This suggests a linear transfer of the resource-use component across the scales that we sampled (Wiens et al. 1993; Kelt et al. 1994). However, the vegetation variables contributing to models were not consistent across scales. We think that this was a consequence of the restricted range problem — vegetation diversity inevitably increased with grid size (e.g., Stohlgren et al. 1997).

At each of the spatial scales we sampled, there was a large amount of unexplained variation in the small-mammal matrices (Fig. 6.1). Some of this nugget variation may have resulted from inadequate sampling of small-mammal, vegetation, and spatial matrices. For example, the spatial matrix was constrained to a cubic polynomial. However, we think that much of the unexplained variation can be attributed to the resource generalism of the small-mammal species in our study (e.g., Grant 1976; Kozakiewicz 1995; Morris 1996). The four species in this study are all wide-ranging, and exhibit a variety of habitat associations across their ranges (Dilworth 1984). Another possible source of variation was landscape context (Turner 1989), although Bowman et al. (in press) demonstrated that context is not an important factor for small-mammal populations within this forested study area.

Acknowledgements

We received financial support from the Sustainable Forest Management Network, Fraser Papers Inc., NSERC, the Sir James Dunn Wildlife Research Centre, and Earthworks NB. We collaborated on the project with many folks and we thank them all, especially Gilles Couturier, Steve Young, Tony Diamond, Pete McKinley, John Gunn, Mark Edwards, Lisa Sheppard, M.-A. Villard, Julie Bourque, Sue Hannon, Stan Boutin, Crissy Corkum, Rich Moses, and Jason Fisher.

References

Anderson, P. K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond. **626**: 299-325.

Anderson, P. K. 1980. Evolutionary implications of microtine behavioural systems on the ecological stage. The Biologist, **62**: 70-88.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, **73**: 1045-1055.

Bowman, J., Forbes, G., and Dilworth, T. 2000. The spatial scale of variability in small-mammal populations. Ecography. **23**: 314-320.

Bowman, J., Forbes, G. and Dilworth, T. In press. Landscape context and small-mammal abundance in a managed forest. For. Ecol. Manage.

Bowman, J., Forbes, G. and Dilworth, T. Submitted. Distances moved by small woodland rodents within large trapping grids. Can. Field-Nat.

Cooke, J. L. 1997. A spatial view of population dynamics. *In* Wildlife and landscape ecology: effects of pattern and scale. *Edited by* J. A. Bissonette. Springer, New York. pp. 288-309.

Dilworth, T. G. 1984. The land mammals of New Brunswick. T. G. Dilworth, Fredericton, New Brunswick.

Fretwell, S. D., and Lucas, H. L., Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica, **19**: 16-34.

Goodwin, B. J., and Fahrig, L. 1998. Spatial scaling and animal population dynamics. *In* Ecological scale: theory and applications. *Edited by* D. L. Peterson and V. T. Parker. Columbia University Press, New York. pp. 193-206.

Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. Can. J. Zool. 54: 2156-2173.

Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. Oikos, 29: 539-544.

Kelt, D. A., Meserve, P. L., and Lang, B. K. 1994. Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. J. Mammal. 75: 890-904.

Kozakiewicz, M. 1995. Resource tracking in space and time. *In* Mosaic landscapes and ecological processes. *Edited by* L. Hansson, G. Merriam, and L. Fahrig. Chapman and Hall, London. pp. 136-147.

Krohne, D. T. 1997. Dynamics of metapopulations of small mammals. J. Mammal. 78: 1014-1026.

Krohne, D. T. and Baccus, R. 1985. Genetic and ecological structure of a population of *Peromyscus leucopus*. J. Mammal. 66: 529-537.

Krohne, D. T. and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, 82: 97-101.

Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio, 80: 107-138.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine “cycles”. J. Mammal. 69: 225-235.

Maser, C., Anderson, R. Cromack, K. Jr., Williams, J. T., and Martin, R. E. 1979. Dead and down woody material. *In* Wildlife habitats in managed forests: the Blue

Mountains of Oregon and Washington. *Edited by* J. W. Thomas. USDA Agricultural Handbook 553.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscape. Evol. Ecol. 6: 412-432.

Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. Ecology, 77: 2352-2364.

Quinn, J. F., and Dunham, A. E. 1983. On hypothesis testing in ecology and evolution. Am. Nat. 122: 602-617.

Rossi, R. E., Mulla, D. J., Journel, A. G., and Franz, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62: 277-314.

Stohlgren, T. J., Chong, G. W., Kalkhan, M. A., and Schell, C. D. 1997. Multiscale sampling of plant diversity: effects of minimum unit size. Ecol. Appl. 7: 1064-1074.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis in ecology. Ecology, 67: 1167-1179.

ter Braak, C. J. F. 1988. CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis, and redundancy analysis. Agricultural Mathematics Group, Ministry of Agriculture and Fisheries, Wageningen, The Netherlands.

Thomson, J. D., Weiblen, G., Thomson, B. A., Alfaro, S., and Legendre, P. 1996. Untangling multiple factors in spatial distributions, lilies, gophers, and rocks. Ecology, 77: 1698-1715.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. **20**: 171-198.

Whittaker, R. H. 1956. Vegetation of the Great Smokey Mountains. Ecol. Monogr. **26**: 1-80.

Wiens, J. A., Stenseth, N. C., Van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. Oikos, **66**: 369-380.

Table 6.1. **Relative abundance (captures/100 trap nights) of four small-mammal species captured from 1996 to 1999 in northwestern New Brunswick, Canada.**

Species*	Autumn 96	Spring 97	Autumn 97	Spring 98	Autumn 98	Spring 99
C. g.	5.17	6.38	9.92	7.24	18.83	7.56
P. m.	0.81	4.13	22.30	3.05	3.62	6.54
B. b.	4.24	2.04	9.63	1.83	17.76	13.87
N. i.	3.64	2.08	0.25	6.98	2.95	1.73

* *C. g.* = *Clethrionomys gapperi*; *P. m.* = *Peromyscus maniculatus*; *B. b.* = *Blarina brevicauda*; and *N. i.* = *Napaeozapus insignis*

Table 6.2. Results of canonical correspondence analysis (CCA) of autumn small-mammal distributions (1996-1998) in northwestern New Brunswick. Small-mammal community included *Clethrionomys gapperi*, *Peromyscus maniculatus*[A], *Blarina brevicauda*, and *Napaeozapus insignis*[B]. Variables are listed in order of entry into models. Unless otherwise indicated, vegetation variables are counts. NS indicates $p > 0.05$.

Grain (m)	Year	N	Vegetation model	$F^{C, E}$	Spatial model	$F^{D, E}$
125	96	--	(NA)	--	(NA)	--
	97	30	Mean decay class of logs	3.58**	XY	2.56*
			Betula alleghaniensis shrubs			
	98	30	All coarse woody debris	3.60**	Y^2	5.06**
			All stems			
250	96	64	*Picea* spp. stems	3.43**	XY^2	3.48**
			Acer saccharum shrubs			
			All snags			
	97	64	All coarse woody debris	3.03*	--	NS
			Mean decay class of logs			
	98	64	All snags	4.59**	Y	4.38**
			All coarse woody debris		X	
			Mean decay class of logs			
			Logs decay class 5			

Table 6.2 continued over

Table 6.2 continued

Grain (m)	Year	N	Vegetation model	F[C, E]	Spatial model	F[D, E]
1000	96	61	*Acer saccharum* stems	5.50**	–	NS
			Fagus grandifolia shrubs			
			Hardwood shrubs			
			Viburnum alnifolium shrubs			
			All snags			
	97	59	*Picea* spp. stems	4.91**	–	NS
			All stems			
			Logs decay class 2			
			Softwood shrubs			
	98	60	Softwood shrubs	2.46*	–	NS
			Abies balsamea stems			

A) *P. maniculatus* was not included in autumn 1996 models due to low abundance

B) *N. insignis* was not included in autumn 1997 models due to low abundance

C) Vegetation model

D) Spatial model

E) Monte-Carlo permutation test; * $p < 0.05$; ** $p < 0.01$

Table 6.3. Results of canonical correspondence analysis (CCA) of spring small-mammal distributions (1997-1999) in northwestern New Brunswick. Small-mammal community included *Clethrionomys gapperi*, *Peromyscus maniculatus*, *Blarina brevicauda*, and *Napaeozapus insignis*. Variables are listed in order of entry into models. Unless otherwise indicated, vegetation variables are counts. NS indicates $p > 0.05$.

Grain (m)	Year	N	Vegetation model	$F^{A,C}$	Spatial model	$F^{B,C}$
125	97	30	*Abies balsamea* stems	4.40**	XY	4.49**
			Acer saccharum stems			
			Acer saccharum shrubs			
			Betula alleghaniensis shrubs			
	98	30	Softwood shrubs	2.49*	Y	3.65*
			All stems			
	99	30	Logs decay class 4	3.09*	Y	2.30*
			Betula alleghaniensis stems			
250	97	64	Hardwood shrubs	2.72**	--	NS
			All stems			
			Logs decay class 3			
			Acer saccharum shrubs			

Table 6.3 continued over

Table 6.3 continued

Grain (m)	Year	N	Vegetation model	$F^{A,C}$	Spatial model	$F^{B,C}$
250	98	64	All stems	4.11**	–	NS
			Acer saccharum stems			
	99	64	Logs decay class 1	3.07*	Y	5.25*
			Logs decay class 5			
			Mean log diameter			
1000	97	56	–	NS	–	NS
	98	62	All herbs	2.85**	–	NS
			Mean log diameter			
			Picea spp. stems			
			All stems			
			All shrubs			
	99	55	Softwood shrubs	4.11**	–	NS
			Abies balsamea stems			

A) Vegetation model

B) Spatial model

C) Monte-Carlo permutation test; * $p < 0.05$; ** $p < 0.01$

Table 6.4. **Results of partial constrained ordination (canonical correspondence) expressed as variance in small-mammal distributions explained (%) by: vegetation (with spatial effects removed), spatial co-ordinates (with vegetation effects removed), and a shared spatial - vegetation component. Small-mammal community included *Clethrionomys gapperi*, *Peromyscus maniculatus*[A], *Blarina brevicauda*, and *Napaeozapus insignis*[B].**

		Autumn			Spring			
Matrix	Grain (m)	96	97	98	97	98	99	95% C. I.[C]
Vegetation	125	–	16	17	42	16	19	22.0 ± 9.8
	250	18	15	21	23	18	12	17.7 ± 3.1
	1000	49	28	8	0	30	15	21.5 ± 11.2
Space	125	–	4	24	7	11	6	11.1 ± 6.9
	250	6	0	10	0	0	6	3.6 ± 3.3
	1000	0	0	0	0	0	0	0
Shared	125	–	5	< 1	15	1	< 1	4.2 ± 4.9
	250	1	0	3	0	0	2	1.1 ± 1.2
	1000	0	0	0	0	0	0	0

A) *P. maniculatus* was not included in autumn 1996 models due to low abundance

B) *N. insignis* was not included in autumn 1997 models due to low abundance

C) Mean ± 95% confidence interval

Fig. 6.1. Variance in the abundance of small mammals in a forest landscape attributed to: (1) an unexplained component; (2) a spatial component (with vegetation effects removed); (3) a shared spatial - vegetation component; and (4) a vegetation component (with spatial effects removed). Amounts are means of samples taken during spring and autumn (1996-1999). Standard errors are indicated by error bars. Sampling was carried out at three spatial scales (grains = 125 m, 250 m, and 1000 m).

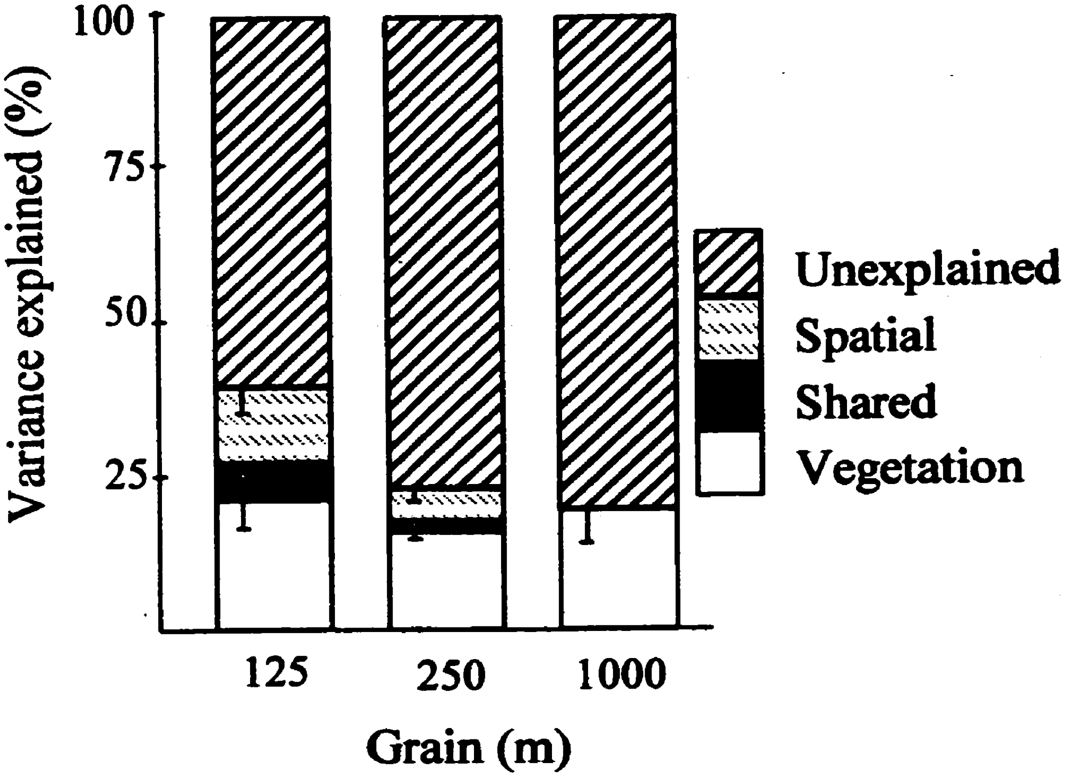
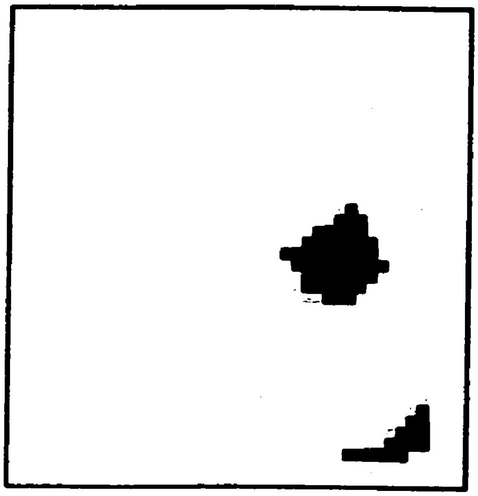
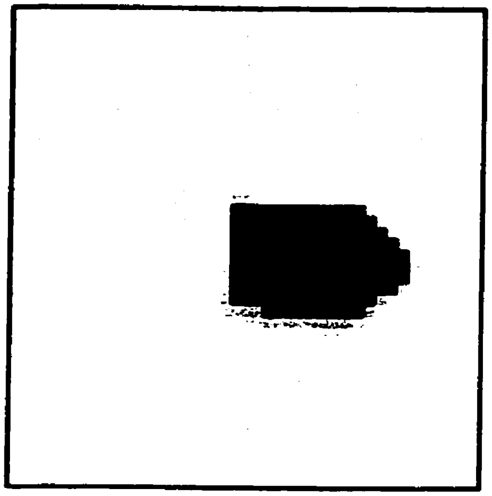

Variance explained (%)
100
75
50
25
125
250
1000
Grain (m)
Unexplained
Spatial
Shared
Vegetation

Fig. 6.2. Interpolated gray-scale maps for the abundance of *Clethrionomys gapperi* duringfive consecutive trapping sessions in New Brunswick, Canada. Samples were taken on a 31 ha grid (5 x 6; 125-m grain) during: (A) spring 1997; (B) autumn 1997; (C) spring 1998; (D) autumn 1998; and (E) spring 1999. Abundances range from 0 (white) to 12 (black) per survey point.

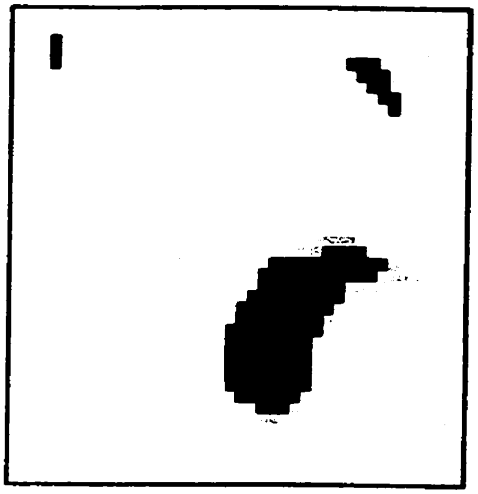
A



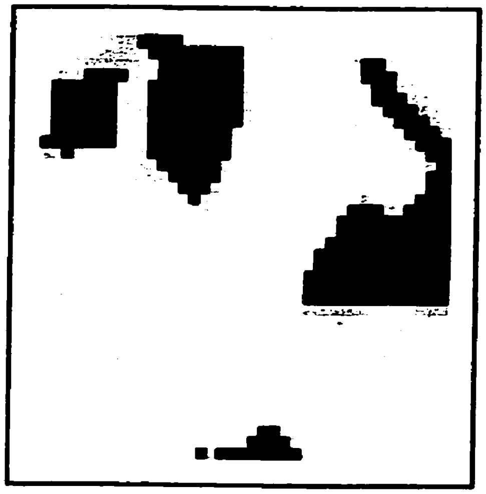
B



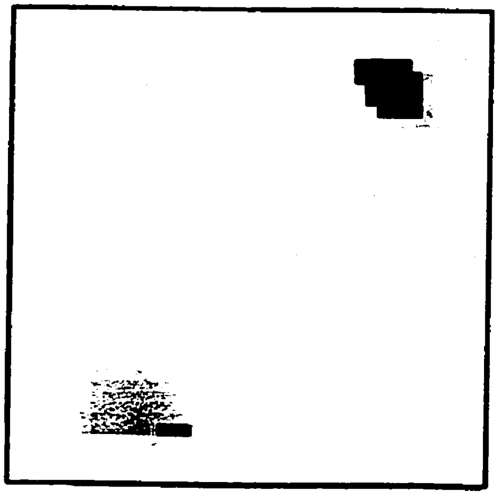
C



D



E



Chapter 7

Synthesis

This dissertation demonstrated that small-mammal populations in northwestern New Brunswick exhibited structure within the spatial domain of dispersal. Abundances were autocorrelated over distances of between 133 and 533 m depending on the species and the landscape (Chapter 3). Some of this spatial structure occurred independently of the distribution of resources (Chapter 6). The mean straight-line distances moved by animals between sampling points were: 224 m (*Clethrionomys gapperi*); 225 m (*Napaeozapus insignis*); and 370 m (*Peromyscus maniculatus*) (Chapter 4). The abundances of two species (*C. gapperi* and *N. insignis*) were related to landscape context variables at extents of 250 m or less (Chapter 5).

The results suggest that there is a level of organization in small-mammal populations within a 133 - 533 m spatial domain. Theoreticians have referred to such a level as a demographic unit, a subpopulation, a deme, or a local population (Lidicker 1975; Krohne 1997). My findings are consistent with Krohne and Burgin's (1990) report of demographic heterogeneity in a population of *Peromyscus leucopus* within a 3-ha trapping grid. Krohne and Burgin (1990) speculated that processes act locally to create variation, and dispersers exploit that variation. Thus, variation exists within the spatial domain of dispersal.

A number of processes could create spatial structure that exists independently of the distribution of resources. These include vertical processes, such as predation, and horizontal processes, such as competition (Quinn and Dunham 1983). For example, a weasel (*Mustela erminea*) could extinguish a local population of red-backed voles, *C.*

gapperi, while leaving a neighbouring vole population (in otherwise equivalent vegetation) to persist (Debrot and Mermod 1983). Such an event would create variation within vole populations over short distances.

A time series of the spatial patterns of small-mammal abundance reveals that while the scale of spatial structure was consistent, the actual patterns were, temporally, remarkably dynamic (Fig. 6.2). Thus, I envision a scenario whereby the processes are dynamic in time as well as in space. A site that is "good habitat" one year is not necessarily good the next year. Weasel home ranges shift over time, thus the effects of predation shift (Debrot and Mermod 1983). For example, there was not one site within the 125-m grain sampling grid that was consistently occupied by red-backed voles (Fig. 6.2). Temporal and spatial patterns of abundance fluctuate within a range of natural variability.

The notion of a level of organization in small-mammal populations within a 133 - 533 m spatial domain has implications for censusing small mammals. Although small, the size of subpopulations within my study were generally larger than trapping grids traditionally used in small-mammal research (i.e., < 2 ha; Chapter 2). While the scale of spatial structure in small-mammal populations likely varies across regions, these results reinforce the idea that populations are not distributed purely through environmental control. Subtle variations in small-mammal demographics should be encompassed by trapping regimes, and researchers should recognize that single subpopulations might be controlled by different processes (Lidicker 1988; Krohne and Burgin 1990). All of this argues for pilot studies prior to small-mammal research projects in areas where spatial population parameters are not known.

This dissertation has not dealt explicitly with the possibility of regional population dynamics. While there is no evidence that small mammals in New Brunswick exhibit such large-scale fluctuations, small mammals in other regions certainly do (Steen et al. 1996; papers in Krebs 1997; Ranta et al. 1997). The kind of fine-scale spatial structure that I detected (i.e., local dynamics) could occur in the presence of larger-scale structure (i.e., regional dynamics) as a nested hierarchy of population dynamics (Urban et al. 1987; Goodwin and Fahrig 1998). It would be interesting to test whether populations that are known to exhibit regional dynamics also exhibit spatial structure at finer scales, and vice-versa.

One of the objectives of the dissertation, to measure any discernible relationship between forest management and the spatial structure of small-mammal populations, was only partially achieved. The project was designed with an experimental harvest in mind, and post-harvest sampling that has yet to be completed. It is clear that small mammals fluctuate in time and in space within a range of variability. An analysis of the effects of forest management should test whether management creates fluctuations that are outside of that range, and this was not accomplished. However, I have demonstrated that red-backed voles were the species that most obviously responded in a negative way to forest management. Vole abundances were negatively related to landscapes that were dominated by softwood plantations (Chapter 5), and in such an intensively managed context, vole distributions were coincident with decayed coarse woody debris (Appendix 2). Management prescriptions that reduce structure in vegetation and woody debris are not good for red-backed voles. The fine scale of local population dynamics that I detected suggests that small mammals should be somewhat robust to forest management, and indeed this seemed to be the case (Chapter 5). Such local dynamics, by definition, do not require a lot of space. For example, small buffer strips were large enough to contain local populations of red-backed voles (e.g., Bowman et al. 1999; Chapter 3). Provided that forest remnants, like buffer strips, are connected to larger source areas, small mammals should remain extant in landscapes that are managed at reasonable levels of intensity. However, this question merits further research. In Appendix 1, I have included more forest management considerations.

References

Bowman, J., Forbes, G., and Dilworth, T. 1999. The spatial structure of small-mammal populations in a managed forest. *In* Science and practice: sustaining the boreal forest. *Edited by* T. S. Veeman, D. W. Smith, B. G. Purdy, F. J. Salkie and G. A. Larkin. Sustainable Forest Management Network, University of Alberta, Edmonton, AB. pp. 58-63.

Debrot, S., and Mermod, C. 1983. The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.). Oecologia, **59**: 69-73.

Goodwin, B. J., and Fahrig, L. 1998. Spatial scaling and animal population dynamics. *In* Ecological scale: theory and applications. *Edited by* D. L. Peterson and V. T. Parker. Columbia University Press, New York, NY. pp. 193-206.

Krebs, C. J. 1997. Vole cycles in Hokkaido: a time series goldmine. TREE, **12**: 340-341.

Krohne, D. T. 1997. Dynamics of metapopulations of small mammals. J. Mammal. **78**: 1014-1026.

Krohne, D. T., and Burgin, A. B. 1990. The scale of demographic heterogeneity in a population of *Peromyscus leucopus*. Oecologia, **82**: 97-101.

Lidicker, W. Z. Jr. 1975. The role of dispersal in the demography of small mammals. *In* Small mammals: their productivity and population dynamics. *Edited by* F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge University Press, Cambridge. pp. 103-128.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine "cycles". J. Mammal. **69**: 225-235.

Quinn, J. F., and Dunham, A. E. 1983. On hypothesis testing in ecology and evolution. Am. Nat. **122**: 602-617.

Ranta, E., Kaitala, V., Lindstrom, J., and Helle, E. 1997. The Moran effect and synchrony in population dynamics. Oikos, **78**: 136-142.

Steen, H., Ims, R. A., and Sonerud, G. A. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. Ecology, **77**: 2365-2372.

Urban, D. L., O'Neill, R. V., and Shugart, H. H., Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists to understand spatial patterns. Bioscience, **37**: 119-127.

Appendix 1

Preliminary forest management considerations

Introduction

The Sustainable Forest Management Network (NCE) project, of which my dissertation is a part, is just beginning to fulfill its potential as regards the study of forest management effects on wildlife. The NCE project was designed with the intention of an experimental harvest after the initial sampling. In effect, my dissertation represents the initial sampling of the small-mammal component. A greater understanding of the effects of forest management on small mammals could be achieved with future resampling of the study areas. The reference study area (Haley Brook) is currently being harvested, so future sampling could yield information on short- and long-term responses to a variety of harvesting activities. Resampling the intensively managed study area (Big Cedar) in the future could provide insight into the long-term responses of small-mammals to plantations (i.e., What happens to the structure of plantations as they age?).

Regardless of future work, the current project has yielded some interesting points. We demonstrated that small-mammal populations exhibit spatial dynamics over a relatively small area (e.g., 133-533 m; Chapter 3). The fine spatial scale of dynamics suggests that small mammals should be somewhat robust to forest management, and indeed this seemed to be the case (Chapter 5). Such local dynamics, by definition, do not require a lot of space. For example, small buffer strips were large enough to contain local populations of small mammals (e.g., Chapter 3). Only red-backed voles, *Clethrionomys gapperi*, were negatively-related to a forest-management index (the amount of plantation within a 250-m radius of the sampling point; Bowman et al. in press; Chapter 5). None of the small mammals that I studied could be considered an indicator of mature forest conditions: all were abundant in a variety of cover types including recent clearcuts (Bowman et al. in press; Chapter 5). I have detailed a few considerations below.

Coarse woody debris

Several studies indicate that small mammals (and red-backed voles in particular) use coarse woody debris (CWD) extensively for foraging, travelling, and nesting (e.g., Ure and Maser 1982; Nordyke and Buskirk 1991). In the intensively managed Fraser study area (Big Cedar), we found that red-backed voles were more abundant in stands with decayed CWD (Bowman et al. 2000; Appendix 2). The intensively managed landscape had 0.76 decayed logs/sample plot, while the reference area (Haley Brook) had 3.06 decayed logs/sample plot (Bowman et al. in press b; Appendix 2). We suggest that voles were possibly limited by the amount of CWD on the intensively managed landscape. Intensive-forest management often results in a loss of CWD, in part as a result of site preparation techniques and this seems to be the case in the Big Cedar area. Coarse woody debris is an important structural feature to retain for small mammals.

Plantations

The current (young) age classes of softwood plantations are not suitable habitat for red-backed voles or woodland jumping mice, *Napaeozapus insignis* (Bowman et al. in press; Chapter 5). This is in contrast to naturally-regenerated sites which are used frequently by both species (Bowman et al. in press a; Chapter 5). It seems that there are two main reasons why plantations are not suitable: (1) mechanical site preparation of plantations reduces coarse woody debris (see above); and (2) the even age structure means that as plantation canopies close, growth of ground-layer vegetation is limited (Parker 1989). Ground-layer vegetation provides small-mammals with forage and cover. As there were no mature plantations within Fraser's freehold to sample during our study, only time can tell whether the simplified structure of plantations will change with increasing age. This is a strong argument for future resampling. For now, the data suggests that plantations should be used with caution, and that structure within plantations (e.g., CWD) should be maximized.

Rare species

Species which were too rare to be dealt with quantitatively were not adequately considered in this dissertation. Six species occurred in the study areas at such low population densities: (1) the meadow vole, *Microtus pennsylvanicus*; (2) the meadow jumping mouse, *Zapus hudsonius*; (3) the rock vole, *Microtus chrotorrhinus*; (4) the southern bog lemming, *Synaptomys cooperi*; (5) the arctic shrew, *Sorex arcticus*; and (6) the Gaspé shrew, *Sorex gaspensis*. Two of these, the meadow vole and the meadow jumping mouse are primarily early-successional species (Dilworth 1984), suggesting that they are not likely at risk from forest management. The other four species use mature forests to a greater extent. These forest-using species could be at risk from forest management without our knowledge because of their naturally low densities in the area. For example, we never caught a rock vole in the intensively managed Big Cedar area, although we captured several in the reference area. The Gaspé shrew is of particular concern because it has the most restricted range of these rare species and has been listed as vulnerable (COSEWIC 1997).

References

Bowman, J., Forbes, G., and Dilworth, T. In press. Landscape context and small-mammal abundance in a managed forest. For. Ecol. Manage.

Bowman, J., Sleep, D., Forbes, G., and Edwards, M. 2000. The association of small-mammals and coarse woody debris at log and stand scales. For. Ecol. Manage. **124**: 119-124.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 1997. Unpubl., Can. Wildl. Serv., Ottawa.

Dilworth, T. G. 1984. Land mammals of New Brunswick. T. G. Dilworth, Fredericton, NB.

Nordyke, K. A., and Buskirk, S. W. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Can. Field-Nat. **105**: 330-334.

Parker, G. H. 1989. Effects of reforestation on small mammal communities in New Brunswick. Can. Field-Nat. **103**: 509-519.

Ure, D. C., and Maser, C. 1982. Mycophagy of red-backed voles in Oregon and Washington. Can. J. Zool. **60**: 3307-3315.

Appendix 2

The association of small mammals and coarse woody debris at log and stand scales

Abstract

Coarse woody debris is an important structural element in forests. We empirically investigated the relationships between small mammals and coarse woody debris decay stage at two different scales: individual logs and forest stands. There were no significant relationships between small mammals and individual logs of different decay classes. We investigated the stand scale using areas with contrasting management intensities (a reference area and a more intensively managed area). No significant relationships were found between small mammal abundance (any species) and either mean decay class of logs in a stand, or overall abundance of logs. There was evidence of a landscape context effect. Red-backed voles, the most abundant microtine in the region, were significantly related to the abundance of the most decayed logs. This relationship was only significant on the intensively managed landscape, where highly decayed logs were rare.

Authorship: Jeff Bowman, Darren Sleep, Mark Edwards, and Graham Forbes

Published in Forest Ecology and Management, 129: 119-124, 2000

Introduction

There is a growing awareness that it is critical to retain coarse woody debris (CWD) in managed forests as habitat for many species of animal, including small mammals (Harmon et al. 1986; Freedman et al. 1996). A number of studies have empirically explored the relationship between small mammals and CWD, most often at a microhabitat scale. Several species, such as *Clethrionomys gapperi*, *C. californicus*, *Peromyscus maniculatus*, *P. leucopus*, and *Microtus pinetorum* use downed logs and stumps for travelling, foraging, and nesting (e.g., Miller and Getz 1977; Hayes and Cross 1987; Graves et al. 1988; Planz and Kirkland 1992; Tallmon and Mills 1994; and McMillan and Kaufman 1995; but see Barry et al. 1990, Mills 1995).

While the distribution of woody debris is important for small mammals, it may be the decay stage of the CWD that determines its use. Maser et al. (1979), Ure and Maser (1982), and Maser and Trappe (1984) have all indicated that there is an important relationship between fungi, decayed CWD, and mycophagous small mammals. Logs in an advanced stage of decay might provide microenvironments for small mammals to forage and nest (*sensu* Freedman et al. 1996). However, studies are few and results are not conclusive. For example, Tallmon and Mills (1994) found that *C. californicus* are associated with decayed logs, but Hayes and Cross (1987), also studying *C. californicus*, found no relationship with decayed logs. Gunderson (1959) demonstrated a positive association between rotting stumps and *C. gapperi*. Nordyke and Buskirk (1991) developed a predictive model directly relating log decay and *C. gapperi* abundance: 49% of variation in vole abundance is explained by the stage of log decay. Their study was at the forest stand scale, and did not address whether voles were actually associated with decayed logs within the stands.

We studied the relationship between decay stage of coarse woody debris and its use by small mammals. Use was assessed at two scales: (1) individual logs; and (2) forest stands. We predicted that small forest mammals would be closely associated with logs that were in an advanced stage of decay, as decadent logs should be good substrates for nesting, travelling, and foraging. We expected positive relationships between log decay and small-mammal abundance at both log and stand scales.

Materials and methods

The study took place on the Private Industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°22'N, 67°25'W). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghenensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*).

Individual Logs

Using *a priori* knowledge of the small mammal community gained during a concurrent study (Bowman et al. 1999), we selected three mature coniferous forest stands (primarily spruce and fir) with similar small mammal communities. Selected stands occurred in a forest with low management intensity (< 15% recent plantations or clearcuts). Stand variability was minimized by selecting stands of equal age, tree species composition, location relative to drainage, and CWD distribution. In each of the three stands line transects were conducted to select logs for small mammal sampling. Selected logs met the following requirements: (1) > 10 m from adjacent log; (2) > 3 m in length; and (3) > 20 cm in diameter. We selected five logs in each stand from each of the five Maser scale decay classes (1 = sound, 5 = highly decayed; Maser et al. 1979). This approach left 25 logs around a central point in each stand, each log a minimum of 10 m from an adjacent log. Seventy-five logs were sampled over three stands.

The small mammal abundance at each log was sampled with a Sherman live trap. Traps were placed along the side of the log, in the 'most likely runway'. Traps were prebaited for three days with a mixture of oats and sunflower hearts. We conducted two trapping sessions, on 17 July and 1 August 1998. Traps were set for five consecutive days, and checked each morning and evening. Captures were weighed, identified as to sex and reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, KA, USA), and released at the same site.

We report trapping success for the log-scale study as number of captures/100 trap nights. The data did not appear normally distributed, so we analyzed for differences in small-mammal captures per log class using non-parametric Kruskall-Wallis analysis of variance. We only used small mammal species in analysis if the species was captured at a rate > 1.0 capture per 100 trap nights.

Forest Stands

We selected stands using a stratified systematic approach. We first selected two different study areas: (1) a reference area, with relatively low management intensity (recent clearcuts and plantations < 15% of the landscape); and (2) an intensively managed area, where clearcuts, and softwood plantations covered > 50% of the landscape. Note that the log-scale study took place within the reference area. These two areas represent opposites in the continuum of management intensity. Both areas were 4900 ha in extent. We placed sample points 1 km apart, in a square (8 x 8) grid: therefore, we had two square grids (reference and managed) each with 64 systematic sample points. In practice though, some points had missing data and for this analysis we had N = 115 different forest stands, representing a variety of stand types.

At each point we sampled coarse woody debris in six 20-m transects. Two paired transects were located at point centre, while two other transects were located 70-m north and two were located 70-m south of the center. All logs > 8 cm in diameter and 1 m in length that crossed a transect were tallied. Different minimum diameters for CWD at the log and stand scales were chosen (8 cm vs 20 cm); we wanted to characterize all the logs in the stand, and so we were more inclusive at this scale. There was no intention to quantitatively compare results from the two scales, so this difference should not be an issue. Logs were identified to species (where possible), and assigned a Maser-scale decay class. Logs from all six transects were summed from each sample point for statistical analysis.

We sampled the stands for small mammals from 10 May to 10 June, and from 15 August to 15 September 1997. Five Victor Tin Cat repeating live traps (Woodstream Corp., Lititz, PA, USA) were used to survey each stand. One trap was placed at point center, and four other traps were placed in the cardinal directions at 35 m from center. All traps were placed in 'most likely runway' positions. All traps were prebaited for three days with oats and sunflower hearts. Traps were then set for four consecutive nights. Handling protocol was the same as at the log scale. The number of forest stands precluded us from trapping all the stations at once, so instead we prebaited and trapped all 115 stands within a four-week period.

Trapping success at the stand level was expressed as number of individuals per stand, considered a minimum estimate of abundance in each stand. Again, data did not appear normally distributed, so we proceeded with non-parametric analysis. Spearman rank correlations were used to explore the relationships between CWD variables and small mammal abundance. We only used small mammal species in analysis if the species was captured at a rate > 1.0 individual per 100 trap nights. We conducted analyses on the reference and managed landscapes separately, and on the combined sample.

Results

Individual Logs

A total of 741 trap nights at the log scale resulted in 142 captures of six species (Table A2.1). No significant relationships between any species of small mammal and the decay class of logs where they were captured were evident (Fig. A2.1). Further, there was no relationship between the total capture success of all species and log decay class (Fig. A2.1).

Forest Stands

A total of 5120 trap nights at the stand scale resulted in 1500 captures of 1015 individuals from eight species (Table A2.1). Spearman correlations demonstrated that there was no relationship between the mean decay class of logs from 115 different stands, and the number of individuals captured in those stands. This was consistent for all species and regardless of season or study landscape (Table A2.2; Fig. A2.2). Figure A2.2 is representative of our results for the correlation of small mammal abundance and mean decay class. For simplicity, we present only results in Table A2.2 from our analysis of the combined study landscapes. The reference and managed landscapes were also analyzed separately, demonstrating no significant relationships. Using the same statistical approach, we detected no relationship between the abundance of CWD and the number of individuals captured in a stand (Table A2.2).

We also assessed whether relationships existed between small mammal species and the abundance of particular decay classes. Only class 5 logs (the most decayed) were significantly related to small mammal abundance, and so only class 5 logs will be discussed further here. When we considered the landscape context, we detected a positive relationship between the abundance of class 5 logs and the number of red-backed voles captured. On the intensively managed landscape, voles were significantly correlated with class 5 logs, both in spring ($r_s = 0.51$, $N = 58$, $P < 0.001$) and fall ($r_s = 0.40$, $N = 58$, $P < 0.01$). The relationship was not significant on the reference landscape in spring ($r_s = -0.07$, $N = 57$, $\underline{P} > 0.05$) or fall ($r_s = 0.04$, $N = 57$, $P > 0.05$).

Discussion

We detected no relationship between the decay stage of logs and the use of individual logs by small mammals. Thus, our work supports the conclusion of Hayes and Cross (1991) who find no relationship between small mammal activity at individual logs and log decay, using two classes of logs (hard vs soft). Although we found that logs of all decay stages were used with equal intensity by small mammals, we suggest that the reasons for small mammals using logs would vary with decay stage. For example, red-backed voles will nest in rotted logs, while using the surface of sound logs as runways (Bowman, pers. obs.). Our study design did not tease apart these differences. We restrict our interpretation to say that the overall use of logs was consistent regardless of decay stage.

We have considered that small mammals were attracted artificially to logs by baited traps. However small mammals are generally only attracted to traps from a small radius (e.g., Hayes and Cross 1987) and in most cases this would mean they were already associated with the log.

At the stand scale, our study demonstrated no relationship between the abundance of any small-mammal species and either the abundance or mean decay class of logs, regardless of season or landscape (Table A2.2). Most studies that link the distribution of small-mammal species to the distribution of downed logs (e.g., Gunderson 1959; Doyle 1987; Tallmon and Mills 1994) have dealt with microhabitat, whereas the stand-scale component of our study provided a broader view. Microhabitat associations may not translate across scales (Wiens et al. 1993). The results of our stand-scale study reflected the notoriously broad niches and the variable response to forest management of many small-mammal species (e.g., Martell and Radvanyi 1977; Clough 1987; Steventon et al. 1998).

Red-backed voles are linked to old-growth conditions, including decayed logs, by Nordyke and Buskirk (1991) and our findings at the stand scale add to their study. Nordyke and Buskirk modelled *Clethrionomys gapperi* abundance as a function of mean CWD decay stage in forest stands. We cannot support their model outright, based on our findings. However, we did detect an interesting relationship between *Clethrionomys* and decayed logs that may add to our understanding. Highly decayed logs were abundant in our reference landscape (Table A2.3). We believe that this abundance is why we found no relationship between *Clethrionomys* and log decay (*sensu* Nordyke and Buskirk 1991) in the reference area, either at the log or stand scales: CWD decay was not a limiting factor. On the intensively managed landscape highly decayed logs were rare (i.e., possibly limiting; Table 3). This is a result of silviculture practices which reduce the amount of mature forest and protective overhead cover, characteristics associated with highly decayed CWD (Gore and Patterson 1986; Sturtevant et al. 1997). In particular, the practice of scarification removes a lot of CWD (Freedman et al. 1996). Many planted sites in the managed landscape were scarified. When class 5 logs were rare, a relationship with red-backed voles became apparent. In other words, the model of Nordyke and Buskirk (1991) may only apply to contexts where decayed CWD is relatively rare.

It is possible that the relationship between *Clethrionomys* and decayed logs is related to moisture balance. Red-backed voles have demanding water requirements (Getz 1968) and this is believed to be a major reason why they are associated with mature forests, which are often high in moisture content (Franklin et al. 1981). These areas are also the last areas in a managed forest to have an abundance of decayed logs (Maser 1990).

We suggest that future work could explore the causality of relationships at both the log and stand scales. By isolating managed forests, where decayed logs are rare due to silviculture activities, the relationships between red-backed voles and class 5 logs could be explored experimentally.

Acknowledgements

The project was supported by Fraser Papers Inc., NSERC, Canada's Sustainable Forest Management Network (NCE), Earth Works New Brunswick, and the Sir James Dunn Wildlife Research Center. Steve Young, Gilles Couturier, Tim Dilworth, Tony Diamond, Pete McKinley, John Gunn, Mark Edwards, M.-A. Villard, Sue Hannon, Stan Boutin, Rich Moses, and Crissy Corkum all collaborated on aspects of the NCE project. Many technicians also contributed and we thank them all. Hugh Broders and two anonymous reviewers made helpful suggestions on the manuscript.

References

Bowman, J., Forbes, G., and Dilworth, T. 1999. The spatial structure of small-mammal populations in a managed forest. *In* T. S. Veeman, D. W. Smith, B. G. Purdy, F. J. Salkie, G. A. Larkin (eds.). Science and practice: sustaining the boreal forest. Sustainable Forest Management Network, University of Alberta, Edmonton, Alberta. pp. 58-63.

Barry, R. E. Jr., Heft, A. A., and Baummer, T. E. 1990. Spatial relationships of syntopic white-footed mice, *Peromyscus leucopus*, deer mice, *Peromyscus maniculatus*, and red-backed voles, *Clethrionomys gapperi*. Can. Field-Nat. **104**: 387-393.

Clough, G. C. 1987. Relations of small mammals to forest management in northern Maine. Can. Field-Nat. **101**: 40-48.

Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus*, *Microtus oregoni* and *M. richardsoni*. Am. Midl. Nat. **118**: 258-265.

Franklin, J. F., Cromack, C. K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. U. S. Dep. Agric. Gen. Tech. Rep. PNW-118.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J. S., Johnson, G., and Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. **4**: 238-265.

Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology, **49**: 276-286.

Gore, J. A., and Patterson, W. A., III. 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. Can. J. For. Res. **16**: 335-339.

Graves, S., Maldonado, J., and Wolff, J. O. 1988. Use of ground and arboreal microhabitats by *Peromyscus leucopus* and *Peromyscus maniculatus*. Can. J. Zool. **66**: 277-278.

Gunderson, H. L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. **40**: 405-412.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. Jr., and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133-302.

Hayes, J. P., and Cross, S. P. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. Can. Field-Nat. **101**: 543-546.

Martell, A. M., and Radvanyi, A. 1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Can. Field-Nat. 91: 41-46.

Maser, C. 1990. The redesigned forest. Stoddard Publishing Co., Toronto, Ontario.

Maser, C., Anderson, R., Cromack, K., Jr., Williams, J. T., and Martin, R. E. 1979. Dead and down woody material. *In* J. W. Thomas (ed.). Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Agricultural Handbook 553. pp. 78-95.

Maser, C., and Trappe, J. M. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164. Pacific Northwest For. and Range Exp. Station, Portland, Oregon.

McMillan, B. R., and Kaufman, D. W. 1995. Travel path characteristics of white-footed mice (*Peromyscus leucopus*). Can. J. Zool. 73: 1474-1478.

Miller, D. H., and Getz, L. L. 1977. Factors influencing local distribution and species diversity of forest small mammals in New England. Can. J. Zool. 55: 806-814.

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Cons. Biol. 9: 395-403.

Nordyke, K. A., and Buskirk, S. W. 1991. Southern red-backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Can. Field-Nat. 105: 330-334.

Planz, J. V., and Kirkland, G. L., Jr. 1992. Use of woody ground litter for travel by the white-footed mouse, *Peromyscus leucopus*. Can. Field-Nat. 106: 118-121.

Steventon, J. D., MacKenzie, K. L., and Mahon, T. E. 1998. Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. For.

Chron. 74: 703-713.

Sturtevant, B. R., Bissonette, J. A., Long, J. N., and Roberts, D. W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. 7: 702-712.

Tallmon, D. A., and Mills, L. S. 1994. Use of logs within home ranges of California red-backed voles on a remnant of forest. J. Mammal. 75: 97-101.

Ure, D. C., and Maser, C. 1982. Mycophagy of red-backed voles in Oregon and Washington. Can. J. Zool. 60: 3307-3315.

Wiens, J. A., Stenseth, N. C., Van Horne, and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. Oikos. 66: 369-380.

Table A2.1. **Species caught during a small-mammal research project in northwestern New Brunswick, expressed as: (A) captures/100 trap nights; and (B) individuals/100 trap nights.**

Species	Logs^A	Stands^B	
	August 1998	**May 1997**	**August 1997**
Clethrionomys gapperi	5.4	4.6	9.4
Peromyscus maniculatus	1.9	2.8	14.7
Napaeozapus insignis	4.7	1.1	<1.0
Zapus hudsonius	---	---	<1.0
Microtus pennsylvanicus	3.7	<1.0	<1.0
Microtus chrotorrhinus	---	<1.0	<1.0
Synaptomys cooperi	---	<1.0	<1.0
Blarina brevicauda	2.0	1.7	9.7
Sorex spp.	<1.0	<1.0	<1.0

Table A2.2. Spearman correlation coefficients for relationships between small mammal abundance in 115 forest stands and: (1) mean decay class of logs in the same stands; or (2) number of logs in the stands. No relationships were significant ($P > 0.05$, $N = 115$)

	Mean Decay Class		Number of Logs	
Species	Spring	Fall	Spring	Fall
C. gapperi	-0.03	0.01	-0.03	0.12
P. maniculatus	0.02	0.06	-0.04	0.18
N. insignis	0.15	0.08	0.01	0.01
B. brevicauda	-0.11	-0.01	-0.05	0.04

Table A2.3. The abundance of highly decayed logs (Maser scale class 5 ; Maser et al. 1979) in reference and intensively managed forests. The distributions were significantly different ($P < 0.001$; two sample Kolmogorov-Smirnov test).

Forest	Mean No. Class 5 Logs	SD
Reference	3.06	3.35
Managed	0.76	1.30

Fig. A2.1. Kruskal-Wallis rank sums for species captured adjacent to logs assigned 1 of 5 different Maser et al. (1979) decay classes. No relationships were statistically significant ($P > 0.05$, $N = 75$).

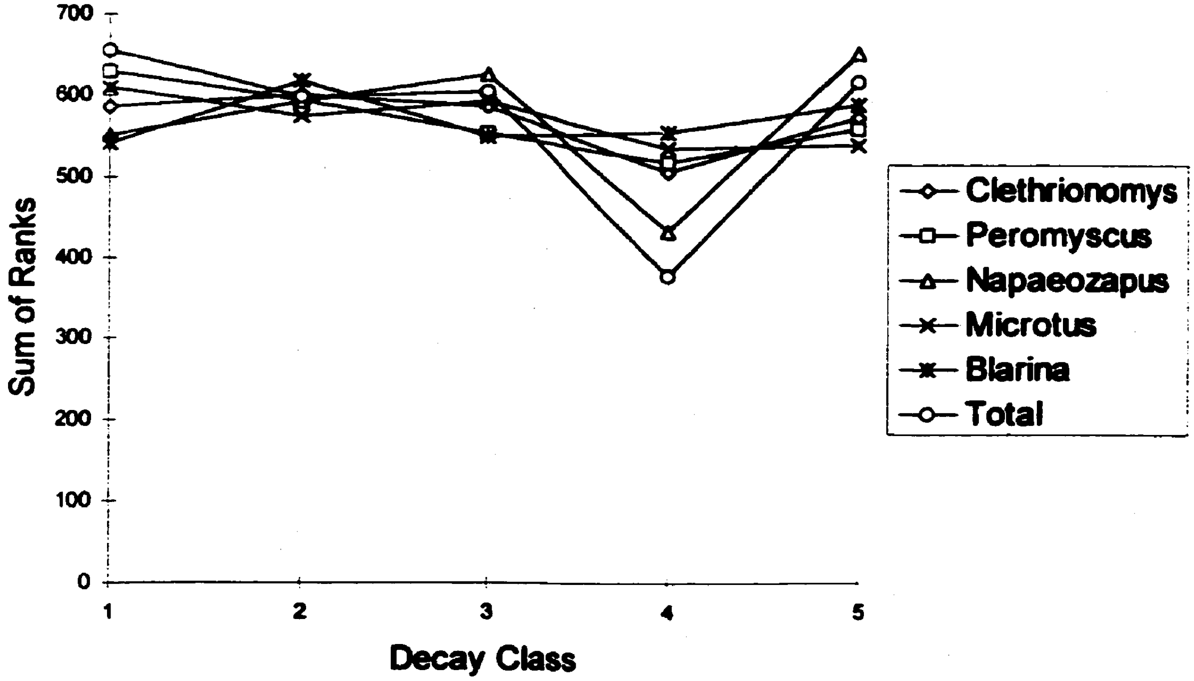
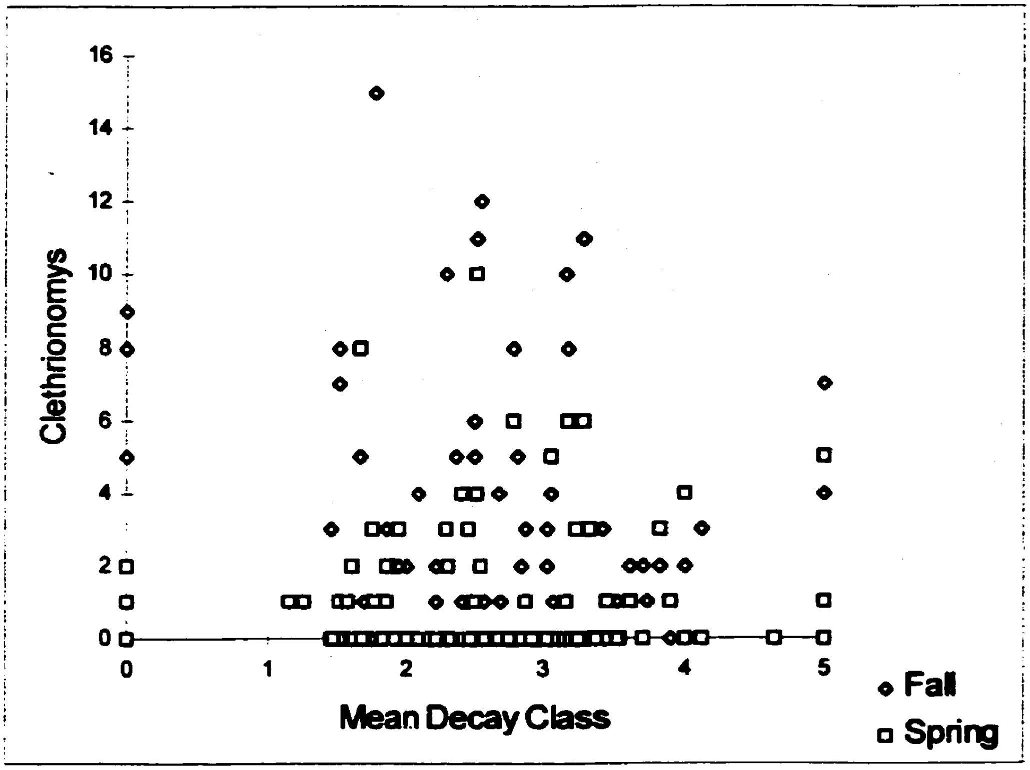

700
600
500
400
300
200
100
0
Sum of Ranks
1
2
3
4
5
Decay Class
Clethrionomys
Peromyscus
Napaeozapus
Microtus
Blarina
Total

Fig. A2.2. Relationship between mean decay class of logs and abundance of *Clethrionomys gapperi* in 115 different forest stands in New Brunswick. The relationship was not significant in spring ($r_s = -0.03$, $N = 115$, $P > 0.05$) or fall ($r_s = 0.01$, $N = 115$, $P > 0.05$).


Clethrionomys
16
14
12
10
8
6
4
2
0
0
1
2
3
4
5
Mean Decay Class
◆ Fall
□ Spring

Appendix 3

Record distance for a non-homing movement by a deer mouse, *Peromyscus maniculatus*

Abstract

We report a record distance of 1768 m for a non-homing movement by a Deer Mouse, *Peromyscus maniculatus.*

Authorship: Jeff Bowman, Mark Edwards, Lisa Sheppard, and Graham Forbes

Published in the Canadian Field-Naturalist, 113: 292-293, 1999

During a study of the spatial structure of small mammal populations in northwestern New Brunswick (47° N, 67° W) we observed a long distance movement by a Deer Mouse, *Peromyscus maniculatus*. The project design required large, nested trapping grids (grains of 125 m, 250 m, and 1000 m) and consequently we were capable of assessing long range, non-homing movements. On 9 September 1997 we captured a subadult, male Deer Mouse (weight = 15 g). The mouse was marked with a 1-g monel ear tag (National Band and Tag Co., Newport, Kansas, USA) and released at the same site. The site was a second-growth tolerant hardwood stand. Sixteen days later, on 24 September 1997, we recaptured the mouse at a trap that was a straightline distance of 1768 m away. The mouse weighed 18 g and was in good condition at recapture. The recapture site was dominated by mature softwoods (*Picea* spp. and *Abies balsamea*). Approximately half of the 516 small mammals that were captured and marked during 1997 were recaptured multiple times at the same site. Animals not recaptured had either moved, become trap shy, or been depredated. Only 24 individuals were detected moving distances > 125 m. We have no evidence that the acts of handling and marking small mammals are themselves sufficient to stimulate a long-distance movement.

To our knowledge this is the longest reported distance for a non-homing movement by a Deer Mouse. Howard (1960) reports a movement of 1000 m, and Wegner and Merriam (1990) report movement by the closely-related *Peromyscus leucopus* of > 1000 m. Long-distance homing movements by Deer Mice have been reported (Murie 1963; Furrer 1973). Teferi and Millar (1993) report the longest of these at 1980 m.

We suspect, based on time of year, age class, and weight of the mouse that this movement represents a dispersal. High densities of Deer Mice (10-fold increase from the same month a year previous; J. C. Bowman and G. Forbes, unpublished data) may have been the incentive for such a long-distance displacement. This observation supports recent suggestions (e.g., Kozakiewicz and Szacki 1995) that small mammals are more vagile than previously believed.

Acknowledgements

We acknowledge financial support from Fraser Papers Inc., NSERC, and the Sustainable Forest Management Network of Centres of Excellence.

References

Furrer, R. K. 1973. Homing of *Peromyscus maniculatus* in the Channelled Scablands of east-central Washington. J. Mammal. **54**: 466-483.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. **63**: 152-161.

Kozakiewicz, M. and Szacki, J. 1995. Movement of small mammals in a landscape: patch restriction or nomadism? *In* Landscape approaches in mammalian ecology and conservation. *Edited by* W. Z. Lidicker, Jr. University of Minnesota Press, Minneapolis, USA. pp. 78-94.

Murie, M. 1963. Homing and orientation of deer mice. J. Mammal. **44**: 338-349.

Teferi, T., and Millar, J. S. 1993. Long distance homing by the deer mouse, *Peromyscus maniculatus*. Can. Field-Nat. **107**: 109-111.

Wegner, J., and Merriam, G. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biol. Conserv. **54**: 263-276.

Appendix 4

Annotated list of small mammals from Victoria County, New Brunswick

Rodents

Red-backed vole, *Clethrionomys gapperi*

Very common (> 2000 captures)

Distributed throughout boreal North America, these voles were the most common species during the study. Primarily forest dwellers, red-backed voles were abundant in moist softwood stands with plenty of structure (*e.g.*, woody debris). Red-backed voles use rotted stumps and logs for nesting, travelling, and foraging. Consequently, intensively managed sites lacking in structural diversity (*e.g.*, plantations) were frequently without red-backed voles. A small number (< 2%) of voles captured were of a dark, or melanistic phase. One individual exhibiting partial albinism was captured.

Deer mouse, *Peromyscus maniculatus*

Very common (> 2000 captures)

With a continent-wide distribution, deer mice are true habitat generalists: we captured them in every type of site during the study, regardless of forest type or age. Habitat generalism allows this species to accommodate human activity (*e.g.*, they commonly nest in buildings). Deer mouse populations demonstrated a tendency to irrupt during the study: year-to-year changes in abundance were as much as ten-fold. This species was recently implicated as a vector for Sin Nombre (hanta) virus.

Woodland jumping mouse, *Napaeozapus insignis*

Common (> 700 captures)

The North American distribution of these mice is limited to the Hemlock and Spruce-Fir forests of the east. We found woodland jumping mice to be most abundant in shrubby sites with a softwood component. This mouse closely resembles the meadow jumping mouse but can be distinguished by its white-tipped tail.

Rock (or yellownose) vole, *Microtus chrotorrhinus*

Rare (9 captures)

Rock voles are uncommon across much of their range, which is coincident with the boreal forest in North America. Rarity is likely due to habitat specificity — rock voles are thought to be associated with rocky sites (as the name suggests). We captured these voles primarily in softwood riparian sites. A number were captured at one site, on the side of a steep ravine. No association with rocks was detected during our study.

Southern bog lemming, *Synaptomys cooperi*

Rare (8 captures)

Southern bog lemmings are distributed throughout southeastern Canada and the northeastern United States, but are uncommon throughout much of this range. We captured lemmings in moist, softwood sites. They resemble red-backed voles and meadow voles but are differentiated by smaller size and short tail (less than the length of hind legs).

Meadow vole, *Microtus pennsylvanicus*

Rare (6 captures)

Commonly distributed in grasslands across much of North America, these voles were rarely captured in our forested study area. Meadow voles eat grass seed, and this limits their distribution to sites where forage is available. The meadow voles that we did capture were in grassy, creekside sites, or recently disturbed sites.

Meadow jumping mouse, *Zapus hudsonius*

Rare (2 captures)

Meadow jumping mice are widely distributed across the boreal forest region of Canada and the northern United States, however, they are associated with sites having grassy or herbaceous cover. Both individuals captured during our study were in the same white spruce plantation, which had a thick layer of grass.

Insectivores

Short-tailed shrew, *Blarina brevicauda*

Very common (> 2000 captures)

Widely distributed across boreal and temperate North America, these shrews were abundant in a variety of sites during our study. However, short-tailed shrews were most closely associated with hardwood sites: it was apparent that hardwood leaf litter made a good substrate for burrowing. Short-tailed shrews are notable for using echolocation, and for having toxic saliva which can incapacitate prey.

Note on *Sorex* shrews:

First, our trapping methodology was not designed to capture *Sorex* shrews. Captures were incidental, thus I expect that *Sorex* species listed below were more abundant than our data suggest. Second, identifications of shrews to date are based on external morphology, rather than more accurate skull and dental characteristics. For this reason, numbers of captures should only be considered as estimates.

Masked shrew, *Sorex cinereus*

Common (> 40 captures)

The most common *Sorex* shrew across most of its distribution of the northern United States, Canada, and Siberia. Occasionally we captured masked shrews in moist riparian sites, however they were frequently associated with softwood plantations. Previous researchers have speculated that masked shrews succeed in plantations because these sites offer a high density of insects.

Smoky shrew, *Sorex fumeus*

Common (> 20 captures)

The distribution of smoky shrews is limited to the northeastern United States and Southeastern Canada. Through much of this range these shrews occupy deciduous sites with abundant leaf litter. Likely more common in the study area than our captures indicate (see note about *Sorex* shrews).

Arctic shrew, *Sorex arcticus*

Rare (< 10 captures)

Arctic shrews are widely distributed through the northern United States, Canada, and Siberia. We captured a few specimens which are archived at the University of New Brunswick, but these shrews were probably more abundant in the study area than our sample suggests (see note about *Sorex* shrews). Arctic shrews occupy moist forested habitats and are important predators of insect larvae. Easily differentiated from other shrews by tricoloured markings.

Pygmy shrew, *Sorex hoyi*

Rare (< 10 captures)

The smallest mammal in North America, pygmy shrews are widely distributed across the northern United States and Canada. Inhabit moist, grassy sites within forests. External features suggest that we captured a small number of these tiny shrews.

Gaspé shrew, *Sorex gaspensis*

Rare (< 10 captures)

This species is listed as vulnerable by COSEWIC, largely because it has a range that is restricted to the northern Appalachians. Gaspé shrews are similar to *Sorex dispar* of the southern Appalachians, both species occupying moist talus slopes and stream beds. Based on external features, I suspect that we captured a few Gaspé shrews, although this can not be confirmed until skull features are analyzed. Skulls are archived at the University of New Brunswick.

Note about species not captured

There are a couple of species whose distributions are thought to coincide with our study area, but were not captured during our study. These include the water shrew, *Sorex palustris*, and the star-nosed mole, *Condylura cristata*. Our study design was not intended to capture these two species: they were undoubtedly in the area, even though none were captured in > 25000 trap nights.

Appendix 5

Empirical field studies of *Peromyscus maniculatus* and/or *Clethrionomys gapperi* published between 1960 and 1997 (N = 127)*

Abbott, H. G., and Quink, T. F. 1970. Ecology, **51**: 271-278.

Anderson, D. C., and MacMahon, J. A. 1985. J. Mammal. **66**: 581-589.

Anderson, D. C., MacMahon, J. A., and Wolfe, M. 1980. J. Mammal. **61**: 500-519.

Barry, R. E., Jr., Heft, A. A., and Baummer, T. E. 1990. Can. Field-Nat. **104**: 387-393.

Batzli, G. O. 1968. J. Mammal. **49**: 239-250.

Beck, A. M., and Vogl, R. J. 1972. J. Mammal. **53**: 336-346.

Beer, J. R. 1961. J. Mammal. **42**: 174-180.

Belk, M. C., Smith, H. D., and Lawson, J. 1988. J. Mammal. **69**: 688-695.

Bovet, J. 1980. Can. J. Zool. **58**: 754-760.

Bowers, M. A., and Smith, H. D. 1979. Ecology, **60**: 869-875.

Brown, L. N. 1963. J. Mammal. **44**: 189-202.

Brown, L. N. 1967. Ecology, **48**: 677-689.

Buckner, C. A., and Shure, D. J. 1985. J. Mammal. **66**: 299-307.

Carter, N. E., and Brown, N. R. 1974. Can. Field-Nat. **88**: 363-364.

Clark, B. K., and Kaufman, D. W. 1990. Can. J. Zool. **68**: 2450-2454.

Clark, B. K., Kaufman, D. W., Kaufman, G. A., and Finck, E. J. 1987. J. Mammal. **68**: 158-160.

Clough, G. C. 1964. Can. Field-Nat. **78**: 80-89.

Clough, G. C. 1987. Can. Field-Nat. **101**: 40-48.

D'Anieri, P., Leslie, D. M., Jr., and McCormack, M. L., Jr. 1987. Can. Field-Nat. **101**: 547-550.

Douglass, R. J. 1989. J. Mammal. **70**: 648-652.

Doyle, A. T. 1990. J. Mammal. **71**: 14-23.

Drickamer, L. C. 1987. J. Mammal. **68**: 702-703.

Drickamer, L. C., and Capone, M. R. 1977. Am. Midl. Nat. **98**: 376-381.

Drickamer, L. C., and Paine, C. R. 1992. Am. Midl. Nat. **128**: 360-365.

Edwards, R. L. 1963. Can. Field-Nat. **77**: 1-12.

Etnier, D. A. 1989. Can. Field-Nat. **103**: 353-357.

Fleherty, E. D., and Navo, K. W. 1983. J. Mammal. **64**: 367-379.

Freedman, B., Poirier, A. M., Morash, R., and Scott, F. 1988. Can. Field-Nat. **102**: 6-11.

Fuller, W. A. 1977. Can. J. Zool. **55**: 42-51.

Gabbut, P. D. 1961. Ecology, **42**: 518-525.

Galindo, C., and Krebs, C. J. 1985. Can. J. Zool. **63**: 1870-1879.

Garman, S. L., O'Connell, A. F., Jr., and Connery, J. H. 1994. Can. Field-Nat. **108**: 67-71.

Gashwiler, J. S. 1970. Ecology, **51**: 1018-1026.

Geluso, K. N. 1971. J. Mammal. **52**: 605-607.

Gentry, J. B., Odum, E. P., Mason, M., Nabholz, V., Marshall, S., and McGinnis, J. T. 1968. J. Mammal. **49**: 539-541.

Gottschang, J. K. 1965. J. Mammal. **46**: 44-52.

Grant, P. R. 1976. Can. J. Zool. **54**: 2156-2173.

Grant, W. E., Birney, E. C., French, N. R., and Swift, P. M. 1982. J. Mammal. **63**: 248-260.

Halvorson, C. H. 1982. Ecology, **63**: 423-433.

Hansen, L. P., and Warnock, J. E. 1978. Am. Midl. Nat. **100**: 416-423.

Hoffman, G. R. 1960. Ecology., **41**: 571-572.

Holbrook, S. J. 1978. J. Mammal. **59**: 18-26.

Holbrook, S. J. 1979. J. Mammal. **60**: 528-542.

Innes, D. G. L., and Bendell, J. L. 1989. Can. J. Zool. **67**: 1318-1323.

Iverson, S. L., and Turner, B. N. 1972. Am. Midl. Nat. **88**: 440-445.

Kaufman, G. A., Kaufman, D. W., and Finck, E. J. 1988. Ecology. **69**: 342-352.

Kirkland, G. L., Jr. 1976. Am. Midl. Nat. **95**: 103-110.

Kirkland, G. L., Jr. 1977. J. Mammal. **58**: 601-609.

Kirkland, G. L., Jr., and Griffin, R. J. 1974. J. Mammal. **55**: 417-427.

Kirkland, G. L., Jr., and Malinowski, E. A. 1984. Can. Field-Nat. **98**: 440-443.

Kirkland, G. L., Jr., and Schmidt, G. L., Jr. 1982. Can. Field-Nat. **96**: 156-162.

Kirkland, G. L., Jr., Snoddy, H. W., and Amsler, T. A. 1996. Am. Midl. Nat. **135**: 253-260.

Knight, T. W., and Morris, D. W. 1996. Ecology, **77**: 1756-1764.

Kotler, B. P. 1985. J. Mammal. **66**: 374-378.

Krebs, C. J., and Wingate, I. 1976. Can. Field-Nat. **90**: 379-389.

Krefting, L. W., and Ahlgren, C. E. 1974. Ecology, **55**: 1391-1398.

Kritzman, E. B. 1974. J. Mammal. **55**: 172-188.

Kucera, E., and Fuller, W. A. 1978. J. Mammal. **59**: 200-204.

Long, C. A. 1964. Can. Field-Nat. **78**: 197-199.

Manville, R. H. 1961. Can. Field-Nat. **75**: 108-109.

MacMahon, J. A., Parmenter, R. R., Johnson, K. A., and Crisafulli, C. M. 1989. Am. Midl. Nat. **122**: 365-387.

Manville, R. H. 1961. Can. Field-Nat. **75**: 108-109.

Marinelli, L., and Neal, D. 1995. Can. Field-Nat. **109**: 403-407.

Marinelli, L., and Millar, J. S. 1989. Can. J. Zool. **67**: 412-417.

Martell, A. M. 1983. Can. J. Zool. **61**: 958-969.

Martell, A. M. 1983. Can. J. Zool. **61**: 970-980.

Martell, A. M. 1984. Can. Field-Nat. **98**: 223-226.

Martell, A. M., and Radvanyi, A. 1977. Can. Field-Nat. 91: 41-46.

Mastrota, F. N., Yahner, R. H., and Storm, G. L. 1989. Am. Midl. Nat. **122**: 388-393.

Matson, J. O. 1982. J. Mammal. **63**: 73-84.

Merkt, J. R. 1981. Can. J. Zool. **59**: 589-597.

Merritt, J. F., and Merritt, J. M. 1978. J. Mammal. **59**: 576-598.

Mihok S. 1979. Can. J. Zool. **57**: 1520-1535.

Mihok, S., and Fuller, W. A. 1981. Can. J. Zool. **59**: 2275-2283.

Millar, J. S., Innes, D. G. L., and Loewen, V. A. 1985. Can. Field-Nat. **99**: 196-204.

Miller, D. H., and Getz, L. L. 1977. Can. J. Zool. **55**: 806-814.

Miller, D. H., and Getz, L. L. 1977. J. Mammal. **58**: 1-16.

Monthey, R. W., and Soutiere, E. C. 1985. Can. Field-Nat. **99**: 13-18.

Morris, D. W. 1983. Can. J. Zool. **61**: 1517-1523.

Morris, D. W. 1984. Can. J. Zool. **62**: 1540-1547.

Morris, D. W. 1996. Ecology, **77**: 2352-2364.

Morris, R. D. 1969. J. Mammal. **50**: 291-301.

Morrison, M. L., and Anthony, R. G. 1989. Can. J. Zool. **67**: 805-811.

Nordyke, K. A., and Buskirk, S. W. 1991. Can. Field-Nat. **105**: 330-334.

O'Farrell, M. J. 1980. J. Mammal. **61**: 589-605.

Parker, G. R. 1989. Can. Field-Nat. 1989. **103**: 509-519.

Parren, S. G., and Capen, D. E. 1985. J. Mammal. **66**: 36-44.

Pasitschniack-Arts, M., and Gibson, J. 1989. Can. Field-Nat. **103**: 70-74.

Patric, E. F. 1962. J. Mammal. **43**: 200-205.

Perrin, M. R. 1981. Am. Midl. Nat. **106**: 102-110.

Petticrew, B. G., and Sadlier, M. F. S. 1974. Can. J. Zool. **52**: 107-118.

Pitts, W. D., and Barbour, M. G. 1979. Am. Midl. Nat. **101**: 38-48.

Powell, R. A., and Brooks, W. S. 1981. J. Mammal. **62**: 397-400.

Probst, J. R., and Rakstad, D. S. 1987. Can. Field-Nat. **101**: 362-368.

Racey, G. D., and Euler, D. L. 1982. Can. J. Zool. **60**: 865-880.

Radvanyi, A. 1970. Ecology, **51**: 1102-1105.

Radvanyi, A. 1975. Can. Field-Nat. **89**: 53-57.

Ramirez, P., Jr., and Hornocker, M. G. 1981. J. Mammal. **62**: 400-403.

Richens, V. B. 1974. Can. Field-Nat. **88**: 191-196.

Rickard, W. H. 1960. Ecology, **41**: 99-106.

Seabloom, R. W., Scwab, R. G., and Loeb, S. C. 1994. Can. J. Zool. **72**: 2238-2243.

Sekgororoane, G., and Dilworth, T. 1995. Can. J. Zool. **73**: 1432-1437.

Sheppe, W. 1967. Can. Field-Nat. **81**: 81-98.

Smith, D. A., and Speller, S. W. 1970. Can. J. Zool. **48**: 1187-1199.

Soper, J. D. 1961. Can. Field-Nat. **75**: 171-219.

Sullivan, T. P. 1980. Can. J. Zool. **58**: 2252-2259.

Swan, D., Freedman, B., and Dilworth, T. 1984. Can. Field-Nat. **98**: 362-364.

Tamsitt, H. Jr. 1960. Can. Field-Nat. **74**: 147-150.

Tamsitt, H. Jr. 1962. Can. Field-Nat. **76**: 71-78.

Turner, B. N., Perrin, M. R., and Iverson, S. L. 1975. Can. J. Zool. **53**: 1004-1011.

Van Horne, B. 1981. Can. J. Zool. **59**: 1045-1061.

Vaughan, T. A. 1974. J. Mammal. **55**: 764-795.

Verme, L. J., and Ozoga, J. J. 1981. Can. Field-Nat. **95**: 253-256.

Vickery, W. L., Iverson, S. L., Mihok, S., and Schwartz, B. 1989. Can. J. Zool. **67**: 8-13.

Waters, J. H. 1961. J. Mammal. **42**: 263-265.

Watts, C. H. S. 1970. J. Mammal. **51**: 341-347.

Whitaker, J. O., Jr. 1966. J. Mammal. **47**: 473-486.

Whitaker, J. O., Jr. 1967. Ecology, **48**: 867-872.

Wolff, J. O. 1985. Can. J. Zool. **63**: 2657-2662.

Wolff, J. O., and Dueser, R. D. 1986. Can. Field-Nat. **100**: 186-191.

Wrigley, R. E. 1969. Can. Field-Nat. **83**: 201-211.

Wrigley, R. E. 1974. Can. Field-Nat. **88**: 21-39.

Yahner, R. H. 1982. J. Mammal. **63**: 440-445.

Yahner, R. H. 1983. J. Mammal. **64**: 380-386.

Yahner, R. H. 1992. Am. Midl. Nat. **127**: 381-391.

---

* In 5 journals: American Midland Naturalist; Canadian Field-Naturalist; Canadian Journal of Zoology; Ecology; and Journal of Mammalogy