

**Fine scale movements of wetland small mammals:
An analysis of pattern and perspective**

by

DONNA DARLENE HURLBURT

BSc (Agriculture), Nova Scotia Agricultural College, 1993

**Thesis
submitted in partial fulfillment of the requirements for
the Degree of Master of Science (Biology)**

**Acadia University
Spring Convocation 1997**



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.

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 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.

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.

0-612-22030-3

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	ix
ACKNOWLEDGEMENTS	x
ABSTRACT	xiii
 CHAPTER 1. Trail Configuration And Complexity In Wetland Small Mammals: A Comparison Of Species Perception Based On Fine-Scale Movement.	
Introduction	1
Objectives	6
Materials And Methods	7
<i>Study Area</i>	7
<i>Trapping Procedures</i>	11
<i>Tracking Methods</i>	12
<i>Trail Analyses</i>	13
<i>Gait and Stride Analyses</i>	19
<i>Human Trails</i>	20
<i>Habitat Analyses</i>	20
Results	23
<i>Analyses of Trail Structure</i>	23
<i>Analyses of Trail Complexity</i>	23

<i>Human Trails</i>	24
<i>Behaviour of Fractal Dimensions Across Scales</i>	24
<i>Comparisons of <u>Microtus pennsylvanicus</u> and <u>Blarina brevicauda</u></i>	24
<i>Habitat Analysis</i>	25
Discussion	38
<i>Similarities And Differences In Perception</i>	38
<i>Limits To Extrapolating Information Across Scales</i>	42
<i>Relevance To Wildlife Management And Conservation</i>	44
Summary	45
CHAPTER 2: Part A - The Configuration And Complexity Of Meadow Vole (<i>Microtus Pennsylvanicus</i>) Movement In A Freshwater Wetland: A Comparison Of Fluorescent Powder And Bobbin Tracking.	
Introduction	47
Materials And Methods	49
<i>Study Area</i>	49
<i>Trapping Procedures</i>	49
<i>Tracking Methods</i>	50
<i>Trail Analyses</i>	52
Results	53
<i>Total Length</i>	53
<i>Trail Structure</i>	53
<i>Trail Complexity</i>	54
Discussion	57

<i>Trail Analyses</i>	57
<i>Logistics</i>	59
<i>Deleterious Effects</i>	63
Summary	64
CHAPTER 2: Part B - An Evaluation Of The Analysis Of Fine-Scale Movement Of Wetland Small Mammals	
<i>Data Collection</i>	65
<i>Data Analysis</i>	67
<i>Scale-Dependent and Scale-Independent Analyses</i>	68
CHAPTER 3. So Landscape Ecology Measures Up, Eh ? ... But Does It Measure Down?	
<i>Definition of landscape</i>	75
<i>General characteristics of landscapes</i>	76
<i>Microlandscapes</i>	80
<i>Organism - defined landscapes</i>	82
LITERATURE CITED	89
PERSONAL COMMUNICATIONS	97
APPENDIX 1	98
APPENDIX 2	105

LIST OF TABLES

Table	Page
1 Summary of the trophic status, size, lifestyle and locomotory behaviour of the six small mammal species used in this study.....	10
2 Summary of mean structural parameters of trails produced by six species of small mammals.....	27
3 Summary of mean structural parameters, subdivided by habitats, for <i>Blarina brevicauda</i> , <i>Zapus hudsonius</i> , and <i>Microtus pennsylvanicus</i>	28
4 Summary of mean complexity indices for trails produced by six species of small mammals.....	29
5 Summary of mean complexity indices, subdivided by habitats, for <i>Blarina brevicauda</i> , <i>Zapus hudsonius</i> , and <i>Microtus pennsylvanicus</i>	30
6 Complexity indices for human trails in meadow and alder habitats.....	31
7 Structural characteristics of meadow vole (<i>Microtus pennsylvanicus</i>) trails subdivided by sex, reproductive and non-reproductive conditions.....	32
8 Complexity of meadow vole (<i>Microtus pennsylvanicus</i>) trails subdivided by sex, reproductive and non-reproductive conditions.....	33
9 Relationships between weight and trail structure, and weight and trail complexity for meadow voles (<i>Microtus pennsylvanicus</i>) and short-tailed shrews (<i>Blarina brevicauda</i>).....	34

10	Mean habitat parameters for human-perceived habitats.	35
11	Mean number of small mammal captures per trap station in each wetland subclass.....	37
12	Structural characteristics of meadow vole (<i>Microtus pennsylvanicus</i>) bobbin and powder trails in meadow and alder habitats.....	55
13	ANOVA table for structural and complexity indices of meadow vole (<i>Microtus pennsylvanicus</i>) trails.....	56
14	Relationships between trail complexity indices for short-tailed shrews (<i>Blarina brevicauda</i>), meadow jumping mice (<i>Zapus hudsonius</i>) and meadow voles (<i>Microtus pennsylvanicus</i>). Trail complexity indices were not highly correlated.....	72

LIST OF FIGURES

Figure	Page
1 Schematic diagram of study site showing the arrangement of trapping grids, trap stations and habitats within the wetland.....	9
2 Illustration of movement parameters used in this study.....	16
3 Powder trail (Trail 246) of meadow vole (<i>Microtus pennsylvanicus</i>) in meadow.....	17
4 Bobbin trail (Trail 230) of meadow vole (<i>Microtus pennsylvanicus</i>) in meadow.....	18
5 Bobbin trail (Trail 23) of meadow vole (<i>Microtus pennsylvanicus</i>) which demonstrates the change in trail complexity at habitat boundaries.....	36
6 Powder trail (Trail 175) of meadow vole (<i>Microtus pennsylvanicus</i>) in meadow.....	73
7 Powder trail (Trail 220) of meadow jumping mouse (<i>Zapus hudsonius</i>) in meadow.....	74

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Tom Herman, for becoming a great friend and mentor. Furthermore, he always allowed me to speak my mind (without holding it against me) and always had an unwavering faith in my abilities.

I wish to acknowledge the more than eighty volunteers who assisted with trapping and tracking of small mammals; without them this project would never have been possible. Special thanks to the Shad Valley students (Summer 1995) and the Mammalogy classes of 1995 and 1996 for participating in field work. Deserving special recognition are Cindy Underhill, Jennifer Wright, Jeffie MacNeil, Tina Moore, Ann Powell, and Tom Herman for swampin' on a regular basis.

Special thanks go to Dr. Soren Bondrup-Nielsen, Dr. Phil Taylor, Dr. Gray Merriam and Dr. Vilis Nams for their intriguing discussion and ideas. Dr. Nams also kindly provided the program 'Fractal' with an unlimited amount of consultation time. Statistical advise was provided by Dr. Patrick Farrell, who assured me that it was OK to work with 'real' numbers.

Financial support was provided through Acadia Graduate Fellowships, Acadia Graduate Teaching Assistantships and Carl and Margaret McCarthy Scholarships in Wildlife Biology.

THE CALF - PATH

**One day, through the primeval wood,
A calf walked home, as good calves should;
But made a trail all bent askew,
A crooked trail as all calves do.**

**Since then two hundred years have fled,
And, I infer, the calf is dead.
But still he left behind his trail,
And thereby hangs my moral tale.**

**The trail was taken up next day
By a lone dog that passed that way;
And then a wise bell-wether sheep
Pursued the trail o'er vale and steep,
And drew the flock behind him, too,
As good bell-wethers always do.**

**And from that day, o'er hill and glade,
Through those old woods a path was made;
And many men wound in and out,
And dodged, and turned, and bent about
And uttered words of righteous wrath
Because 'twas such a crooked path.
But still they followed - do not laugh -
The first migrations of that calf,
And through this winding wood-way stalked,
Because he wobbled when he walked.**

**This forest path became a lane,
That bent, and turned, and turned again;
This crooked land became a road,
Where many a poor horse with his load
toiled on beneath the burning sun,
And traveled some three miles in one.
And thus a century and a half
They trod the footsteps of that calf.**

The years passed on in swiftness fleet,
The road became a village street;
And this, before men were aware,
A city's crowded thoroughfare;
And soon the central street was this
Of a renowned metropolis;
And men two centuries and a half
Trode in the footsteps of that calf.

Each day a hundred thousand rout
Followed the zigzag calf about;
And o'er his crooked journey went
The traffic of a continent.
A hundred thousand men were led
By one calf near three centuries dead.
They followed still his crooked way,
And lost one hundred years a day;
For thus such reverence is lent
To well established precedent.

A moral lesson this might teach,
Were I ordained and called to preach;
For men are prone to go it blind
Along the calf-paths of the mind,
And work away from sun to sun
To do what other men have done.
They follow in the beaten track,
And out and in, and forth and back,
And still their devious course pursue,
To keep the path that others do.

But how the wise old wood-gods laugh,
Who saw the first primeval calf!
Ah! Many things this tale might teach -
But I am not ordained to preach.

SAM WALTER FOSS

ABSTRACT

Six species of wetland small mammals (*Blarina brevicauda*, *Zapus hudsonius*, *Microtus pennsylvanicus*, *Sorex cinereus*, *Mustela erminea* and *Peromyscus leucopus*) were tracked using a powder that glows under UV light to reveal fine-scale movement patterns. Analysis of fine-scale movement revealed similarities in trail structure and complexity, in all but the smallest species, *Sorex cinereus*. Individuals within a species exhibited similar patterns of fine-scale movement regardless of age or reproductive condition. Despite measurable differences in habitat use and structure, trails did not differ significantly between alder and meadow habitats. It is speculated that similarities in trail structure and complexity may be attributed to similarities in morphology among species. Detailed examinations of trailing methods and movement analyses indicated that the methods were appropriate and did not bias significantly the results of the study. Data suggest that it may be more appropriate to study small mammal movement at the wetland subclass level rather than at finer scales; the factors that need to be considered before identifying the crucial scales of study were critically evaluated in a discussion of organism-defined landscapes. The organism-defined landscape is often suggested as a solution to conservation-based problems, but no one has discussed the difficulties with such an application.

CHAPTER ONE

Trail Configuration And Complexity In Wetland Small Mammals : A Comparison Of Species Perception Based On Fine-Scale Movement.

Introduction:

Scale refers to the spatial and temporal dimension at which any object or process is measured (Wiens 1989). The scales at which humans perceive and use landscapes may be irrelevant in determining the elements or processes in the landscape that are important to other organisms (Turner 1989). We observe the environment on a limited range of scales imposed on us by our perceptual capabilities, and by technological and financial constraints (Levin 1992). One must consider the perceptions of the organism in question rather than those of the investigator, to identify the aspects of the landscape that are important to other organisms (Wiens 1976). As well, ecologists must understand the relationships between the human-perceived heterogeneity of the physical environment and the heterogeneity that other species can sample and experience (Fahrig 1992, Wiens 1989). Heterogeneity, the scale-dependent complexity or variability of a system that can affect ecological processes, represents the complexity of the environment to which an organism can perceive and respond (Li and Reynolds 1995, With 1994b).

Ecologists have been slow in recognizing this issue of scale in ecological studies and have tended to observe landscape pattern and process at anthropocentric scales or in plots of tradition-bound sizes (Wiens and Milne 1989, Wiens *et al.* 1993). Of the first 99 studies published in Landscape Ecology, over seventy-five percent were conducted at

scales ranging from several hectares to many square kilometers - the scales at which humans perceive landscapes (Wiens 1992). Maurer (1985) states that this scale problem has prevented scientists from finding simple communities of birds. He suggested that the population unit exists at a much smaller scale than those scales commonly used for observing communities. Wiens *et al.* (1987) demonstrated that the scale of investigation influences the patterns that are detected in assemblages of birds in shrubsteppe habitats in North America. Karieva and Anderson (1988) examined ninety-seven manipulative field experiments published in Ecology between January 1980 and August 1986; they found 43% of the studies to have characteristic physical dimensions of less than one metre, and 75% to be below 10 metres, despite sizes and types of organisms studied. The scale at which studies are conducted may profoundly influence the conclusions of a study (Turner 1989).

To adopt an organism-centered view of the landscape, one must define the perceptive resolution of the organism, the range of spatial scales across which an organism views the landscape as heterogeneous (Crist *et al.* 1992, Johnson *et al.* 1992, With 1994b). Perception is a function of the sensory abilities of an organism and is modified by physiology and behavior (With 1994b).

Fine-scale animal movement patterns are ideal for assessing species' perceptions and responses to landscape heterogeneity, because they are strongly influenced by environmental structure and provide a spatial record that documents how and at what scales an organism interacts with spatially heterogeneous environments (Crist *et al.* 1992, Wiens and Milne 1989, With 1994b). Research on individual animal movements may

also provide explanations for the distribution and dynamics of populations, the links between various biotopes within larger ecosystems, and of the ecological functioning of the landscape (Johnson *et al.* 1991, Szaki and Liro 1991) (For detailed discussion of landscape concepts see Chapter 3).

Organisms are continuously affected by abiotic and biotic factors that influence their movement (Gaustestad and Mysterud 1993). Species that differ in size, morphology, and physiology frequently move at different rates and in different ways (With 1994a). Animal paths will frequently exhibit varying characteristics of movement (e.g. directionality, turning frequency and turning angles) among species and areas of different landscape structure (Johnson *et al.* 1992, With 1994a). Kolasa and Rollo (1991) found that vagile organisms perceive landscape heterogeneity at different scales than more sedentary animals. Weiss and Murphy (1988) suggest that stride size may contribute to an organism's perception of the environment. With (1994b) demonstrated that different life stages of grasshoppers possess different perceptions of landscape structure because of differences in physiology and nutrition. It is expected that other factors such as visual acuity, gait and sex are also important. It is plausible, however, that organisms of the same trophic levels, "life style" and locomotory behaviors will perceive the same environment at similar scales.

Similarities in responses among species to a landscape's heterogeneity are intriguing because they may suggest a general "set" of rules that determine how different organisms respond to landscape structure across a range of scales (With 1994b). If patterns at fine scales are representative of patterns at larger scales, then information

gained about small-scale patterns may be used to understand processes operating at broader scales (Gardner *et al.* 1989). This procedure, called extrapolation, is the process of transferring information from one scale to another (Turner and Gardner 1991).

The ability to extrapolate an organism's response to habitat heterogeneity to another organism may be limited; comparisons may have to be restricted to organisms of similar physiology and trophic status (Wiens *et al.* 1993). Although movement patterns may be similar in complexity, the causal factors underlying this complexity may be different (Johnson *et al.* 1992). It is known that events occurring on larger scales influence other events occurring at smaller scales, but it is unknown how this information is transferred between scales, and what information is lost or preserved as one moves from one scale to another (Levin 1992). Analyses of movement patterns from different species, within the same environment, may shed light on how different species perceive and use landscape patchiness and help determine the limits of the extrapolation of information between spatial scales.

Previous fine-scale studies of movement have primarily been centered upon the responses of insects to the vegetative heterogeneity of their habitat (*e.g.* Crist *et al.* 1992, Kareiva 1986, Wiens and Milne 1989, With 1994a, 1994b). Studies have shown that beetles of the same species (Wiens and Milne 1989) and of closely related species (Crist *et al.* 1992) respond to the mosaic patch structure of their environments in a non-random fashion, *i.e.* they exhibit repeatable patterns of movement when analyzed with scale-independent techniques. Crist *et al.* (1992) also reported that beetle movement responses to patch structure at small scales appeared to be similar to those at larger scales. With

(1994b) determined that a larger species of grasshopper exhibited different responses to landscape structure than smaller ones, suggesting that not all grasshoppers within a single environment perceived habitat patchiness at similar scales. Wiens *et al.* (1995) demonstrated that the pathway complexity of major taxa of beetles, grasshoppers and ants varied significantly, presumably due to differences in perception of environmental heterogeneity and differences in resource use.

There is a paucity of data concerning fine-scale movement responses of small mammals and larger organisms to habitat complexity. Small mammals form a significant portion of landscape biomass, energy flow and biodiversity, and consequently are of ecological importance. These organisms are abundant and move over spatial scales that can be easily measured by researchers. Small scale approaches permit easier experimental manipulation and easier replication of study plots (Wiens and Milne 1989). Small organisms with short generation times are probably more sensitive to environmental changes than the larger organisms sharing the same landscape (Wiens 1976). Small mammals, although often grouped together in ecological studies (Golley 1978), include species with a variety of life history strategies including feeding mode, activity patterns and behavior. It is expected that many species from this broad grouping will perceive and respond to spatial heterogeneity differently, and as a result, operate over different spatial scales.

Objectives:

The purpose of this study was to compare the fine-scale movement patterns of six species of small mammals to determine the spatial scales at which they perceive the spatial heterogeneity of a freshwater wetland and to determine the limits of scale extrapolation . The relevance of human-defined landscapes for managing animal habitat will be discussed. The following questions will be addressed:

1. Do different species of small mammals within a single wetland perceive the structure of the landscape at similar scales? Does perception vary with trophic status, age, sex, body size or habitat? What other factors may influence animal perception (*e.g.* step size, limb morphology and gait, or visual acuity)?
2. Do humans perceive the structure of that landscape at scales different than small mammals? Why or why not? What are the similarities and differences between small mammal- and human-defined landscapes? What implications does this have for conservation biology?
3. What are the limits of extrapolating small mammal movement patterns from one species to another?

Materials And Methods:

Study Area

Trapping and tracking of small mammals were conducted within a portion of a small freshwater wetland (as described by the National Wetlands Working Group 1988) in Greenwich, Nova Scotia (45° 05'N, 64° 23'W). This 1.5 ha wetland is surrounded by agricultural land and highway.

Trapping grids were set in two distinct locations of the study area separated by stream (Figure 1). The first area consisted of old-field meadow dominated by *Carex* spp., *Poa* spp. and *Solidago canadensis* adjacent to dense alder (*Alnus rugosa*) swamp. Alder understory consisted primarily of *Equisetum arvense*, sparse *Solanum nigrum* and *Impatiens capensis*. Several patches of reed canary grass (*Phalaris arundinaceum*) were interspersed throughout the alder swale and along the stream.

In addition to differences in physical structure, the second trapping area was more diverse in plant composition and stratification than Grid One. Grid Two was characterized by deep, narrow ditches running perpendicular to the stream. These trenches, presumably for land drainage, were spaced at approximately 20m intervals. The front half of the grid (i.e. along the stream) was dominated by old field meadow consisting primarily of *Carex* spp., *Poa* spp. and *Equisetum arvense*. Alders (*Alnus rugosa*) generally extended to the stream in the immediate vicinity of the ditches. Soil in this area was considerably wetter than in Grid One. The back portion of the grid was dominated by alder with occasional patches of *Typha latifolia* and *Dryopteris spinulosa*.

Alder understory was relatively barren, possibly due to supersaturation of the soil, with seasonal occurrences of *Impatiens capensis*.

Trapping from September to December 1994 and June to September 1995 revealed that this wetland supports a variety of small mammal species. Those trapped included: meadow vole (*Microtus pennsylvanicus*), meadow jumping mouse (*Zapus hudsonius*), house mouse (*Mus musculus*), white-footed mouse (*Peromyscus leucopus*), masked shrew (*Sorex cinereus*), short-tailed shrew (*Blarina brevicauda*), short-tailed weasel (*Mustela erminea*) and possibly pygmy shrew (*Sorex hoyi*). Other mammals known to reside in the study site included: star-nosed mole (*Condylura cristata*), raccoon (*Procyon lotor*), muskrat (*Ondatra zibethicus*), skunk (*Mephitis mephitis*) and bobcat (*Felis rufus*).

The study concentrated on the movements of *Microtus pennsylvanicus*, *Zapus hudsonius*, *Peromyscus leucopus*, *Sorex cinereus*, *Blarina brevicauda* and *Mustela erminea*. These six species represent the spectrum of small mammal diversity within this wetland, demonstrating variation in trophic status (*e.g.* herbivorous, insectivorous and carnivorous), lifestyle (*e.g.* semi-fossorial, litter dwelling) and locomotory behavior (Table 1).

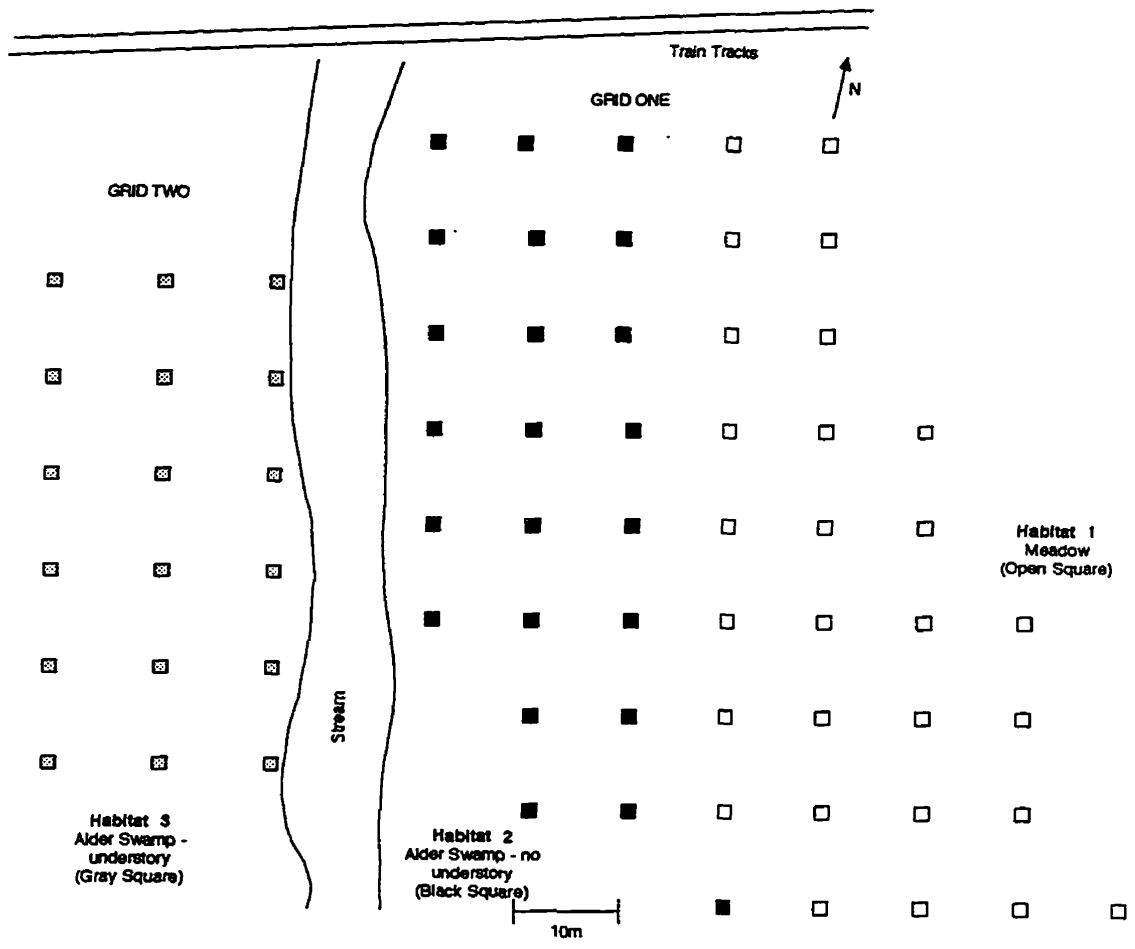


Figure 1. Schematic diagram of study site showing the arrangement of trapping grids, trap stations and habitats within the wetland. Each square represents one trap station with two traps.

Table 1. Summary of the trophic status, size, lifestyle and locomotory behaviour of the six small mammal species used in this study.

Species	Trophic Level	Weight Range (g)	Behaviour
Short-tailed Shrew (<i>Blarina brevicauda</i>)	Insectivore	13 - 25.5 g ¹	semi-fossorial, litter dwelling poorly developed vision, but can echolocate
Meadow Jumping Mouse (<i>Zapus hudsonius</i>)	Herbivore	13 - 23 g ¹	terrestrial & semi-saltatory hibernators, increased feeding in fall well developed vision
Meadow Vole (<i>Microtus pennsylvanicus</i>)	Herbivore	13 - 50 g ¹	terrestrial, use runways well developed vision
Masked Shrew (<i>Sorex cinereus</i>)	Insectivore	3 - 6.5 g ¹	terrestrial, litter dwelling poorly developed vision
White-footed Mouse (<i>Peromyscus leucopus</i>)	Herbivore	9.5 - 22.5 g ¹	terrestrial, semi-arboreal well developed vision
Short-tailed Weasel (<i>Mustela erminea</i>)	Carnivore	98 - 120 g ^{1,2} (Females) 130 - 206 g ³ (Males)	terrestrial, semi-fossorial well developed vision

1. The range of weights (for that particular species) from animals captured in this study.
2. Only female weasels were captured in this study.
3. Range of weights for male weasels was taken from Hall (1951).

Trapping Procedures

Small mammals were trapped from June 6 to October 19, 1995 using two trap grids of fifty-one (Grid 1) and eighteen (Grid 2) trapping stations respectively; trap stations were placed at 10m intervals. Two Ugglan live traps were placed at each station in small mammal runways in an effort to maximize captures. Small mammals were sampled for two four-day trapping sessions per month (in consecutive weeks) for a total of 4002 trap nights. Traps were checked twice daily, in early morning and late evening.

All rodents were permanently marked by unique toe clipping at their first capture. Shrews and weasels were not marked. At each capture, species, sex, age (juvenile, subadult, adult), reproductive condition and trap site were recorded. Body mass, measured to the nearest 0.5g, was recorded using a Pesola balance.

Dead animals were necropsied to determine reproductive condition. Skulls of dead *Blarina brevicauda* were cleaned and saved for age determination based on tooth wear (Morris 1972).

In an effort to obtain information on habitat use and perception of small mammals, a subset of animals was subject to one of two fine-scale trailing methods: 1) fluorescent powder tracking or 2) bobbin tracking. For the purposes of minimizing the number of factors that may confound the results, only powder trails from June 1995 to October 1995 were used for analyses investigating the perceptual differences between species. A detailed comparison of bobbin and powder tracking can be found in Chapter 2.

Tracking Methods

Powder tracking:

Each small mammal was placed in a plastic bag containing a uniquely coloured fluorescent pigment (Radiant Color, CA) and gently shaken until its fur was saturated with powder (DuPlantier *et al.* 1984, Lemen and Freeman 1985). In the case of multiple captures at a trap station, individual animals were powdered with different shades of pigment to avoid confusion during tracking. Animals were released within a 2 m radius of the trap station where they were captured, and release points highlighted with fluorescent tape labels. Traces of pigment were left behind as the organism moved through its habitat.

Powder trails were tracked at night using hand-held, longwave ultraviolet lamps (VWR Scientific Inc., San Gabriel, CA and Raytect, Middlefield, CT). All pathways were followed and marked with flagging tape until no traces of fluorescing powder could be seen. Systematic searches were conducted around the point of trail disappearance to detect further indication of movement.

Mapping:

Thread and flagging tape (powder) trails were mapped using a compass and measuring tape. A movement step was defined as any directional change greater than 5 cm in length. Visual observations of habitat use and apparent trail complexity were noted during this process.

More emphasis was placed on obtaining numbers of trails rather than lengths of trails because there could be statistical interdependences between consecutive moves within the same pathway (Turchin *et al.* 1991, Farrell, pers. comm.). All trails from a species within habitats were pooled for analyses since neither trail structure, nor trail complexity varied with trail length, season or time of day.

Trail Analyses

Trails were analysed using a variety of methods that quantified the configuration and complexity of movement pathways. Path configuration is thought to be indicative of the locomotory and sensory adaptations (perceptual capabilities) of organisms (Bell 1991). Mean move lengths (MML), mean move length orientation (MMLO) and mean turning angles (MTA) were calculated for each trail (Figure 2). Move lengths are the straight segments of individual pathways (Smith 1974) or the displacement between two turning angles (Turchin *et al.* 1991). A turning angle is the difference between the directions of two consecutive move lengths (Smith 1974, Turchin *et al.* 1991). Mean move length orientation is the mean orientation of all move lengths within a trail. This measure has limited use in determining perceptual differences among species at fine scales but has proven to be a quick way of assessing directionality in trails. Trails randomly traveling in all directions should have MMLO of approximately 180° .

Trail complexity was measured using fractal dimensions, turning rate per unit distance and a ratio of net movement [the distance from the first point to the last point of a pathway, i.e. straight line distance (SLD)] to gross movement [the sum of movement

steps or total distance (TD)]. The SLD/TD index ranges from 0 to 1; highly linear movement has a high SLD/TD value and highly convoluted movement has a low SLD/TD value (Bell 1991, Coughlin *et al.* 1992, Yeomans 1995).

The fractal dimension (d) of a movement pattern indexes the tortuosity of the pathway. Thus, the value of d will vary from 1.0, a straight line, to 2.0, a convoluted pattern that essentially fills the plane (Figure 3, Figure 4). Fractal dimensions are calculated using the divider's method which entails measuring the total length of the pathway at different ruler lengths. As the length of the ruler increases, the total length of the pathway decreases because more of the pathway's detail will be ignored (With 1994a, 1994b).

Fractal dimensions were calculated using Fractal version 1.7 (Nams 1996) using 15 replicates of 40 different step sizes between a minimum scale of 0.05m and a maximum scale of 10.00m.

Fractal dimension (d) may be a scale-dependent measure, meaning that it may be greater or lesser when the trail is viewed at different spatial scales. Trails are not fractal if they become straighter at smaller scales; trails are fractal if they exhibit a constant d over a range of scales. A trail which shows similar d across scales indicates that the organism is perceiving its habitat as similar across that range; if d changes at some point, it may indicate that at that particular scale the organism is viewing its habitat as different. The behaviour of how d changes with scale was examined for up to 15 randomly-chosen trails for each species to reveal possible differences in habitat use at particular scales.

All complexity and path configuration indexes were compared between species, sex, weight classes and habitat using Kruskal-Wallis One Way ANOVA on Ranks. In a number of instances, Mann Whitney U tests also had to be performed because the data did not meet the assumptions of the Kruskal-Wallis One Way Anova on Ranks. Results from both analyses are summarized in Appendix 1.

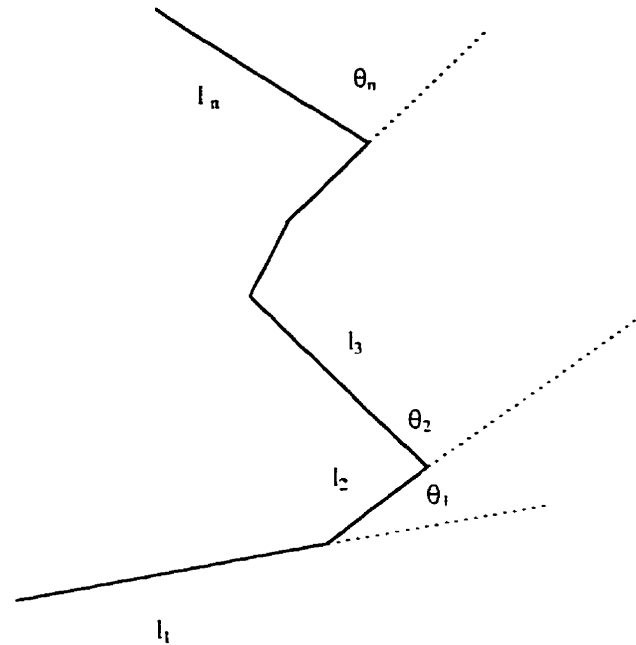


Figure 2. Illustration of movement parameters used in this study. Mean move length is the mean of distances traveled between each step length ($\sum l_1 + l_2 + l_3 + l_n \dots /n$). Net displacement is the straight line distance from the beginning of l_1 and the end of l_n . Mean turning angle is the mean change in direction between subsequent move lengths (Turning Angle (θ_1) = $\theta l_2 - \theta l_1$). Mean move length orientation is the mean compass bearings of move lengths within a trail.

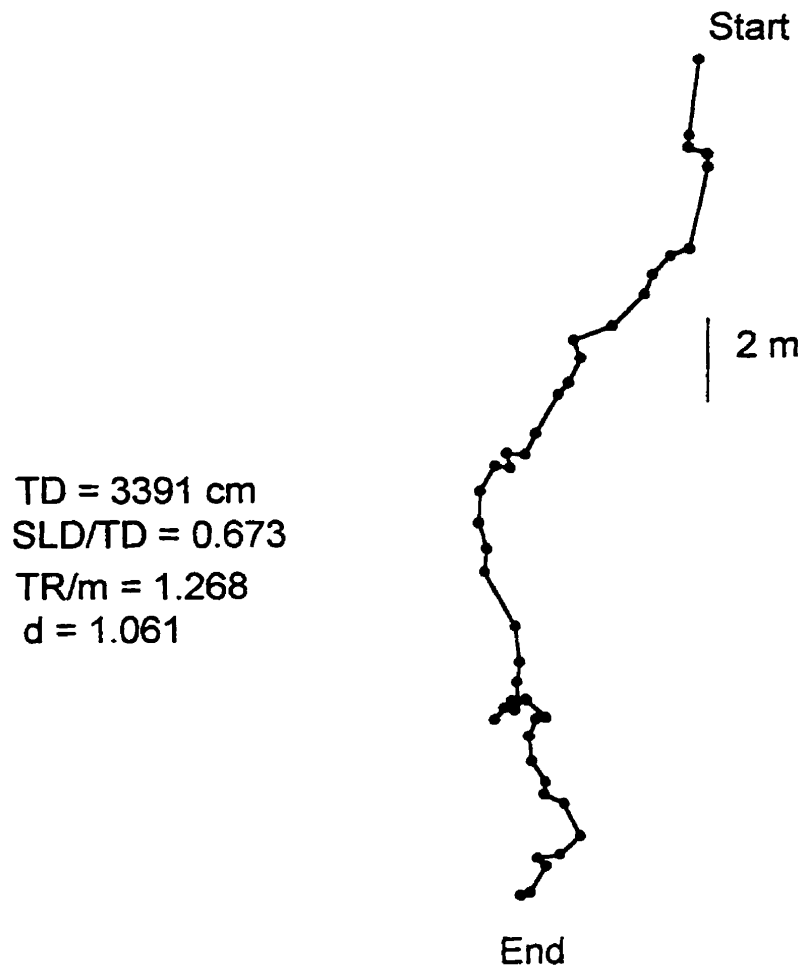


Figure 3. Powder trail (Trail 246) of meadow vole (*Microtus pennsylvanicus*) in meadow. This trail has a low degree of tortuosity.

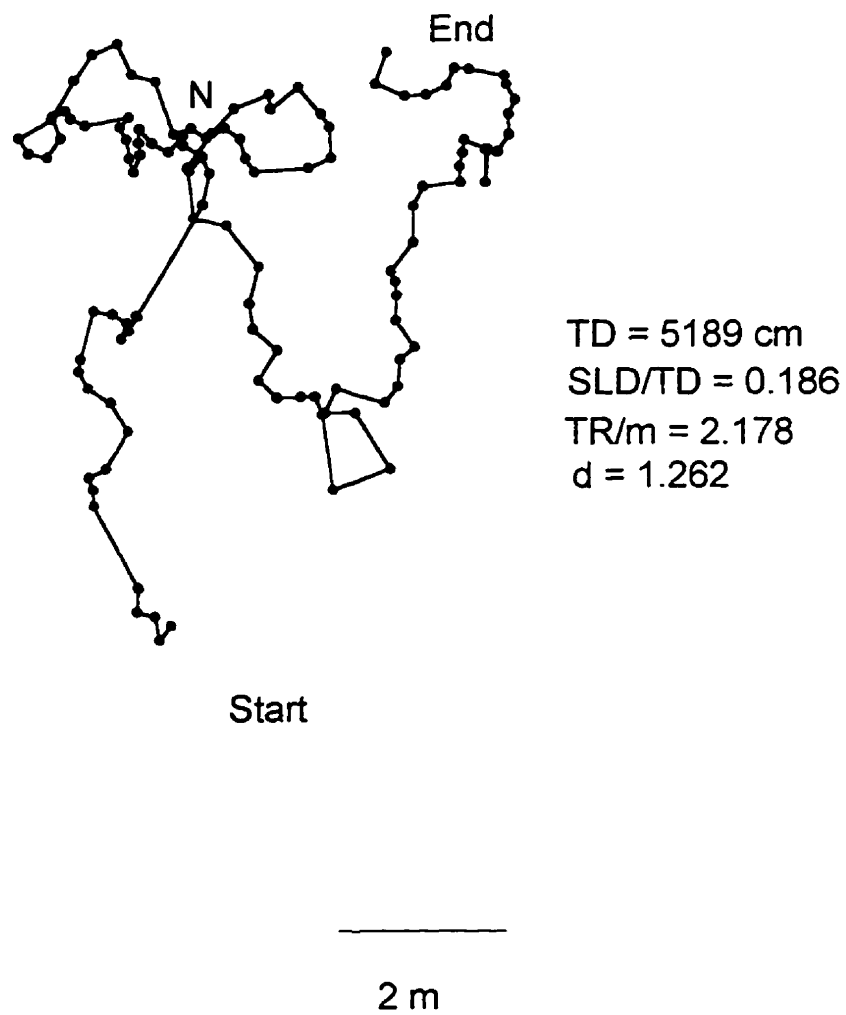


Figure 4. Bobbin trail (Trail 230) of meadow vole (*Microtus pennsylvanicus*) in meadow. N shows the location of a nest. This trail has a high degree of tortuosity.

Gait and Stride Analyses

Ten captive meadow voles (*Microtus pennsylvanicus*) and six short-tailed shrews (*Blarina brevicauda*) were subject to an extremely fine tracking method to reveal potential differences between gait and morphology of the two similarly-sized species. In addition, these measurements were used to determine if there were differences in perception between the two species that had not been detected due to limitations of the powder tracking method. Animals were released in a shallow tray of non-toxic ink in the corner of a behavioural observation arena (1.22 X 1.22 m) lined with large sheets of paper. Subsequent movement produced ink footprint trails in which detailed structure of the foot was evident.

For each trail, stride length and the relative orientation of each stride were determined. Stride is the distance from where one footprint appears in a trail to the next point that a footprint made by the same foot appears. This measurement was recorded from the same point on the first print to the same point on the second. Stride during a normal walk equals the body length of the mammal from its hips to shoulders and is directly indicative of the animal's size (Halfpenny 1986). Turning angles were calculated by taking the absolute difference in orientation between subsequent strides and should reflect differences in morphology. Minimum turn size and stride length may help to clarify the differences and similarities observed in powder trails of the two species.

The mean and standard error were calculated for turning angles and stride lengths within a trail. Mean values between species were compared using Mann Whitney U tests at $p \leq 0.05$.

Human Trails

Six trails produced by people checking trap lines were mapped in October 1995 using the same methods as used for mapping the trails of small mammals. These trails were generated by over 80 people throughout the trapping season. Trail parameters were compared to determine if humans and small mammals differ in perception between habitats.

Data were compared with movement parameters from other species using Kruskal-Wallis One Way ANOVA on Ranks.

Habitat Analyses

The study site appeared to have several different wetland subclasses (Milton *et al.* 1995): meadow (Grid One), shrub swamp with no understory (Grid One), shrub swamp with grass understory (Grid Two) (Figure 1). Habitat structure was measured and compared between subclasses to determine if these areas were different using variables that were thought to be important to the organisms in the study. In addition, species diversity (mean number of species per trap) and mean number of small mammals captured per station were compared between wetland subclasses to determine if small mammals were using these areas differently.

The movement pattern of small mammals is a function of plant structure, soil variability and cover (Getz 1961, Getz 1971, Getz 1989, Peles and Barrett 1996, Pruitt 1953). Plant structure, soil moisture, soil penetrability, litter depth and leaf area index were measured and compared between wetland subclasses. The decision to use these variables was based on the natural history of the organisms in question; thus, these factors are thought to be important to the organism when moving through its environment.

All variables were measured three times (approx. 6 weeks between each session) throughout the trapping season at four random locations within a 2m radius of each trap station. These variables could not be measured at finer spatial and temporal scales due to an increase in habitat disturbance. It is difficult to obtain habitat information that is relevant to the organism until analyses of the trail had been completed. An understanding of the spatial and temporal processes influencing the movement of small mammals should precede the design of a sampling scheme to estimate the appropriate parameter (Turner *et al.* 1989).

Soil moisture content (% relative saturation) was estimated using a calibrated Kelway Soil® Acidity and Moisture Probe. Soil penetrability was measured by a pocket penetrometer which measures the resistance of the soil to a spring-loaded steel rod. Fossorial mammals (*e.g.* short-tailed shrews) may prefer areas of the study site where the soil is less compact and less resistant to digging.

Cover at small mammal level was estimated using two different measures. Litter depth was determined by measuring (to the nearest mm) from the top of the litter to bare

ground using a ruler. Leaf coverage was estimated by a LAI-2000 Plant Canopy Analyzer® at ground level. Measurements, made above and below the vegetation, were used to determine canopy light interception at 5 angles from which Leaf Area Index was computed using a model of radiative transfer in vegetative canopies (Norman and Campbell 1989). The derivation of the radiation transfer model and the assumptions associated with the use of LAI are summarized in Appendix 2.

Habitat parameters, species diversity and trap captures were compared between habitats using One Way Analysis of Variance. Significant differences in species diversity and trap captures between habitats may indicate that small mammals are using and possibly perceiving these environments as different. Differences in habitat may cause variation in movement patterns of small mammals between habitats.

Although analyses revealed that small mammals perceived these three habitats as different (Table 10), trails from both alder swamp habitats were pooled. It was necessary to use the same subclasses as used in wetland classification schemes to make comments about the problems with habitat classification for non-human species. This decision was also based on the limitations of having small sample sizes from several species in alder habitats. Trail structure and complexity did not vary within species between these two alder swamp areas.

Results:

Analyses of Trail Structure -

Differences among species for MTA ($p=0.799$) and MMLO ($p=0.231$) were not significant using Kruskal-Wallis One Way ANOVA (Table 2; Appendix 1). MML was significantly smaller in the smallest species, *Sorex cinereus*, than in all other small mammal species. In addition, MML was significantly larger in *Microtus pennsylvanicus* than in its potential predator, *Mustela erminea* ($p=0.047$).

Kruskal-Wallis One Way ANOVA on Ranks revealed that differences within species between habitats for MTA ($p=0.725$), MML ($p=0.237$) and MMLO ($p=0.314$) were not significant (Table 3, Appendix 1).

Analyses of Trail Complexity -

SLD/TD and fractal d did not differ significantly between species (Table 4; Appendix 1). TR was significantly higher in *Sorex cinereus* than all other species, except for *Peromyscus leucopus*. TR also was significantly higher in *Microtus pennsylvanicus* than in *Blarina brevicauda* ($p=0.020$). TR is summarized for all species in Table 4 and Appendix 1.

Kruskal-Wallis One Way ANOVA on Ranks revealed that differences within species between habitats for SLD/TD ($p=0.293$), TR ($p=0.255$) and fractal dimension ($p=0.124$) were not significant (Table 5, Appendix 1).

Human Trails:

Human trails exhibited significantly longer MML and larger MTA ($p < 0.05$) than the six small mammal species (Table 2; Appendix 2). Trails were also more directed (Table 4; Appendix 1); however, human trail parameters may not be directly comparable to small mammal trails due to differences in data collection and motivational forces.

In contrast to most small mammals studied, human trails tended to be more complex in alder than in meadow but not significantly ($0.20 > p > 0.05$) (Table 6).

Behaviour of Fractal dimensions across scales -

There were no obvious trends in plots of fractal dimension and step size for any species. Fractal dimension behaviour tended to vary from trail to trail within any particular species; trails from the same individual also varied. Fractal dimension behaviour did not vary with length of trail.

*Comparisons of *Microtus pennsylvanicus* and *Blarina brevicauda* -*

Trail Structure and Complexity:

Kruskal-Wallis One Way ANOVA on Ranks revealed that MTA ($p = 0.134$), MML ($p = 0.275$), MMLO ($p = 0.705$), SLD/TD ($p = 0.473$), TR ($p = 0.139$) and fractal d ($p = 0.554$) did not differ significantly among sexes, or reproductive and non-reproductive adult meadow voles (Table 7; Table 8).

Neither trail structure, nor trail complexity was related to mass of individual *Microtus pennsylvanicus* or *Blarina brevicauda* (Table 9). Smaller sized short-tailed

shrews and meadow voles tended to have similar MMLs and MTAs as larger individuals. Indicating a possible change in orientation mechanism, MMLO was significantly different in larger shrews than smaller shrews. MMLO did not differ with mass of individual meadow voles.

Although trail complexity tended to decrease as mass of individual *Blarina brevicauda* and *Microtus pennsylvanicus* increased, this trend was not significant for all complexity indices at $p \leq 0.05$.

Gait and stride analysis:

Stride length of meadow voles (77.48 ± 0.97 mm, $n=36$) was significantly longer than that of short-tailed shrews (64.21 ± 1.03 mm, $n=18$, $p=2.703 \times 10^{-19}$). Mean turning angle did not differ between voles (19.15 ± 1.72 , $n=36$) and shrews (21.69 ± 3.58 , $n=18$, $p=0.262$).

Habitat Analysis -

Habitat parameters, species diversity and total animals per trap were pooled from all sampling periods within each of the three habitats since values were similar throughout a habitat over time. One Way Analysis of Variance revealed that all habitat parameters, species diversity and trap captures varied significantly between habitats at $p \leq 0.05$ (Table 10) and suggested that small mammals are using these habitats differently and possibly perceiving them as different. This was supported further by a number of trails where

meadow voles moved from the alder swale to the meadow (Figure 5). Trail complexity increased considerably at the apparent boundary between the two habitats.

Different habitats appeared to vary in importance to different species (Table 11); for example, all meadow jumping mice ($n=31$), except one, were captured in alder immediately adjacent to the stream.

Table 2. Summary of mean structural parameters of trails produced by six species small mammals. Human trail parameters are also shown but may not be directly comparable to small mammal trails because of differences in data collection and motivational factors.

Species	MTA \pm se (°)	n	MMLO \pm se (°)	n	MML \pm se (cm)	n
<i>Blarina brevicauda</i>	99.3 \pm 9.05	35	185.1 \pm 8.45	36	43.2 \pm 2.26	36
<i>Zapus hudsonius</i>	98.6 \pm 9.86	18	173.8 \pm 9.67	18	46.6 \pm 3.02	18
<i>Microtus pennsylvanicus</i>	91.2 \pm 5.28	68	179.9 \pm 5.46	68	40.6 \pm 1.45	68
<i>Sorex cinereus</i>	106.4 \pm 28.14	8	142.5 \pm 22.31	8	26.2 \pm 3.10	8
<i>Mustela erminea</i>	75.7 \pm 11.81	4	147.5 \pm 10.67	4	56.6 \pm 11.09	4
<i>Peromyscus leucopus</i>	82.2 \pm 37.57	3	204.3 \pm 15.19	3	58.3 \pm 9.85	3
<i>Homo sapiens</i>	91.2 \pm 30.37	6	182.4 \pm 3.05	6	218.9 \pm 23.12	6

Legend: MTA (Mean Turning Angle), MMLO (Mean Move Length Orientation), MML (Mean Move Length), se (\pm 1 standard error), n (Number of trails).

Table 3. Summary of mean structural parameters, subdivided by habitats, for *Blarina brevicauda*, *Zapus hudsonius* and *Microtus pennsylvanicus*. Trails in alder habitat include all trails produced in the alder swale in Grid One and in all of Grid Two.

Species	Habitat	MTA \pm se (°)	n	MMLO \pm se (°)	n	MML \pm se (cm)	n
<i>Blarina brevicauda</i>	Field	96.6 \pm 8.98	26	176.1 \pm 10.84	26	44.5 \pm 2.86	26
	Alder	107.1 \pm 24.80	9	208.5 \pm 8.15	10	39.7 \pm 3.20	10
<i>Zapus hudsonius</i>	Field	N/A	1	N/A	1	N/A	1
	Alder	95.5 \pm 9.91	17	172.4 \pm 10.14	17	46.9 \pm 3.19	17
<i>Microtus pennsylvanicus</i>	Field	94.7 \pm 8.19	35	178.0 \pm 7.82	35	39.6 \pm 1.54	35
	Alder	91.9 \pm 8.98	33	173.9 \pm 9.16	34	40.0 \pm 2.65	34

Legend: MTA (Mean Turning Angle), MMLO (Mean Move Length Orientation), MML (Mean Move Length), se (\pm 1 standard error), n (Number of trails)

Table 4. Summary of complexity indices for trails produced by six species of small mammals. Human trail parameters are also shown, but may not be directly comparable to small mammal trails because of differences in data collection and motivational factors.

Species	SLD/TD \pm se	n	TR/m \pm se	n	d \pm se	n
<i>Blarina brevicauda</i>	0.56 \pm 0.04	35	2.19 \pm 0.16	35	1.14 \pm 0.03	20
<i>Zapus hudsonius</i>	0.58 \pm 0.05	17	2.50 \pm 0.53	18	1.12 \pm 0.03	16
<i>Microtus pennsylvanicus</i>	0.61 \pm 0.02	68	2.46 \pm 0.09	67	1.11 \pm 0.01	41
<i>Sorex cinereus</i>	0.68 \pm 0.07	8	3.49 \pm 0.32	8	1.13 \pm 0.04	7
<i>Mustela erminea</i>	0.58 \pm 0.08	4	2.08 \pm 0.37	4	1.11 \pm 0.03	4
<i>Peromyscus leucopus</i>	0.53 \pm 0.22	3	1.73 \pm 0.34	3	1.10 \pm 0.04	3
<i>Homo sapiens</i>	0.87 \pm 0.03	6	0.47 \pm 0.05	6	1.01 \pm 0.01	6

Legend: SLD/TD (Straight Line Distance to Total Distance Ratio), TR (Turning Rate per meter), d (Fractal dimension), se (\pm 1 standard error), n (Number of trails)

Table 5. Summary of mean complexity indices, subdivided by habitats, for *Blarina brevicauda*, *Zapus hudsonius* and *Microtus pennsylvanicus*. Trails in alder habitat include all trails produced in the alder swale in Grid One and in all of Grid Two.

Species	Habitat	SLD/TD±se	n	TR/m±se	n	d±se	n
<i>Blarina brevicauda</i>	Field	0.54±0.05	25	2.22±0.21	25	1.17±0.04	15
	Alder	0.62±0.07	10	2.10±0.18	10	1.12±0.02	8
<i>Zapus hudsonius</i>	Field	N/A	1	N/A	1	N/A	1
	Alder	0.60±0.04	16	2.51±0.56	17	1.12±0.03	14
<i>Microtus pennsylvanicus</i>	Field	0.57±0.03	35	2.48±0.12	35	1.12±0.01	33
	Alder	0.65±0.03	33	2.43±0.15	32	1.09±0.01	23

Legend: SLD/TD (Straight Line Distance to Total Distance Ratio), TR (Turning Rate), d (Fractal dimension), se (± 1 standard error), n (Number of trails)

Table 6. Complexity indices for human trails in meadow and alder habitats.

Index	Alder mean±se	Meadow mean±se	p
SLD/TD	0.82±0.05	0.92±0.01	0.104
TR/m	0.56±0.03	0.38±0.04	0.076
d	1.05±0.02	1.01±0.00	0.193

Legend: SLD/TD (Straight Line Distance to Total Distance Ratio), TR (Turning Rate), d (Fractal dimension), se (± 1 standard error)

Table 8. Trail complexity of meadow voles (*Microtus pennsylvanicus*) subdivided by sex, reproductive (R)¹ and non-reproductive (N)² conditions.

		SLD/TD _{±se}	n	TR/m _{±se}	n	d _{±se}	n
Females	R	0.57 _{±0.05}	14	2.73 _{±0.20}	14	1.12 _{±0.02}	14
	N	0.53 _{±0.57}	3	3.10 _{±0.67}	3	1.09 _{±0.04}	3
Males	R	0.62 _{±0.05}	21	2.13 _{±0.15}	21	1.12 _{±0.02}	15
	N	0.69 _{±0.07}	4	2.32 _{±0.19}	4	1.09 _{±0.02}	4
Juveniles ³		0.65 _{±0.04}	13	2.55 _{±0.23}	12	1.08 _{±0.01}	10

Legend: SLD/TD (Straight Line Distance to Total Distance Ratio), TR (Turning Rate), d (Fractal dimension), se (\pm 1 standard error), n (Number of trails)

1. Female voles were considered reproductive if they were \geq 25 grams (adult) and were pregnant, lactating, had a copulatory plug or a perforated vagina. Male voles were considered reproductive if they were \geq 25 grams (adult) and had enlarged, scrotal testes.
2. Female voles were considered non-reproductive if they were \geq 25 grams (adult) and were not pregnant, not lactating and had a unperforated vagina. Male voles were considered non-reproductive if they were \geq 25 grams (adult) and had abdominal testes.
3. Voles were considered juvenile if they were $<$ 25 grams and showed no sign of reproductive activity.

Table 7. Trail structural characteristics of meadow voles (*Microtus pennsylvanicus*) subdivided by sex, reproductive (R)¹ and non-reproductive (N)² conditions.

		MTA _{+se} (°)	n	MMLO _{+se} (°)	n	MML _{+se} (cm)	n
Females	R	85.36 _{+9.32}	24	176.98 _{+10.91}	25	36.93 _{+1.77}	14
	N	84.50 _{+25.43}	3	180.59 _{+25.58}	3	34.26 _{+7.35}	3
Males	R	90.27 _{+10.19}	21	166.87 _{+10.77}	21	46.02 _{+3.53}	21
	N	153.527 _{+27.37}	4	171.121 _{+17.37}	4	40.084 _{+1.84}	4
Juveniles ³		104.376 _{+15.74}	13	188.444 _{+14.85}	13	37.457 _{+3.44}	13

Legend: MTA (Mean Turning Angle), MMLO (Mean Move Length Orientation), MML (Mean Move Length), se (\pm 1 standard error), n (Number of trails)

1. Female voles were considered reproductive if they were \geq 25 grams (adult) and were pregnant, lactating, had a copulatory plug or a perforated vagina. Male voles were considered reproductive if they were \geq 25 grams (adult) and had enlarged, scrotal testes.
2. Female voles were considered non-reproductive if they were \geq 25 grams (adult) and were not pregnant, not lactating and had a unperforated vagina. Male voles were considered non-reproductive if they were \geq 25 grams (adult) and had abdominal testes.
3. Voles were considered juvenile if they were $<$ 25 grams and showed no sign of reproductive activity.

Table 9. Relationships between mass (g) and trail structure, and mass and trail complexity for meadow voles (*Microtus pennsylvanicus*) and short-tailed shrews (*Blarina brevicauda*).

	R ²	Adj R ²	n	F	p
<i>Blarina brevicauda</i>					
Wt. vs. TD (cm)	0.0002	-0.0310	34	0.0069	0.9343
Wt vs. MTA (°)	0.0010	-0.0334	31	0.0292	0.8655
Wt vs. MMLO (°)	0.0984	0.0702	34	3.4916	0.0709
Wt vs. MML (cm)	0.0015	-0.0297	34	0.0488	0.8265
Wt vs. TR/m	0.0164	-0.0144	34	0.5328	0.4707
Wt vs. SLD/TD	0.0205	-0.0101	34	0.6706	0.4189
Wt vs. d	0.0186	-0.0304	22	0.3800	0.5445
<i>Microtus pennsylvanicus</i>					
Wt. vs. TD (cm)	0.0173	0.0026	69	1.1794	0.2814
Wt vs. MTA (°)	0.0000	-0.0151	68	0.0001	0.9904
Wt vs. MMLO (°)	0.0029	-0.0120	69	0.1969	0.6587
Wt vs. MML (cm)	0.0062	-0.0087	69	0.4146	0.5218
Wt vs. TR/m	0.0082	-0.0071	67	0.5370	0.4663
Wt vs. SLD/TD	0.0029	-0.0122	68	0.1943	0.6608
Wt vs. d	0.0125	-0.0058	56	0.6837	0.4119

Legend: TD (Total length of trail), MTA (Mean Turning Angle), MMLO (Mean Move Length Orientation), MML (Mean Move Length), TR (Turning Rate), SLD/TD (Straight Line Distance to Total Distance Ratio), d (Fractal dimension), Wt (Mass)

Table 10. Mean habitat parameters for human-perceived habitats. Habitat parameters were pooled from each trap station and from all three sampling periods.

	Habitat 1 ^a (n=204) mean±1se	Habitat 2 ^b (n=276) mean±1se	Habitat 3 ^c (n=216) mean±1se	p
Soil Penetrability (kg/cm ²)	1.53±0.08	1.13±0.10	0.82±0.82	8.056 X 10 ⁻⁶
Soil Moisture (% relative saturation)	44.38±1.42	44.72±1.32	27.71±3.14	7.111 X 10 ⁻⁸
Litter Depth (cm)	7.21±0.38	5.11±0.91	2.90±0.19	1.481 X 10 ⁻⁵
Leaf Area Index	7.84±0.27	6.60±0.16	7.25±0.22	0.006
Total Animals Captured (mean number per trap)	18.23±1.08	5.63±0.84	12.00±2.23	3.573 X 10 ⁻⁹
Species Diversity (mean number of species per trap)	2.57±0.09	2.32±0.24	2.83±0.38	0.027

a. Grid One - Meadow

b. Grid One - Alder swamp without understory

c. Grid Two - Alder swamp with understory

se (± 1 standard error), n = number of samples per habitats

TD = 2710 cm
SLD/TD = 0.314
TR/m = 2.768
d = 1.213

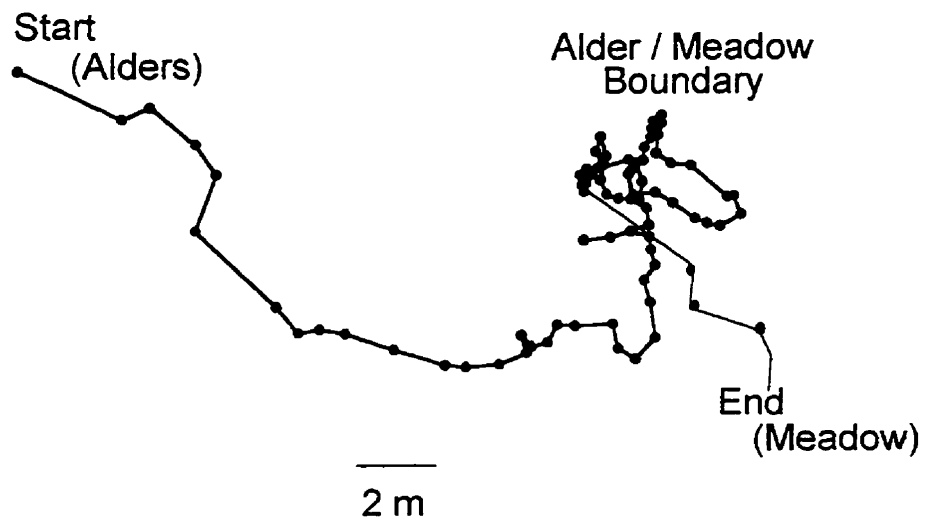


Figure 5. Bobbin trail (Trail 23) of meadow vole (*Microtus pennsylvanicus*) which demonstrates the change in trail complexity at habitat boundaries.

Table 11: Mean number of small mammal captures per trap station in each wetland subclass.

	Habitat 1 (17 stations) mean±se	n	Habitat 2 (23 stations) mean±se	n	Habitat 3 (18 stations) mean±se	n	p
Bb	5.000±0.806	95	1.211±0.387	23	2.389±0.549	43	6.532X10 ⁻⁵
Mp	9.526±1.332	181	5.105±1.414	97	9.111±1.557	164	0.001
Zh	0.053±0.053	1	0.526±0.193	10	0.944±0.262	17	0.001
Sc	0.947±0.281	18	1.684±0.459	32	1.722±0.456	31	0.346
Me	0.105±0.072	2	0.053±0.053	1	0.056±0.056	1	0.659
Pl	0.056±0.056	5	0.263±0.263	5	0.263±0.150	3	0.973

Legend: Bb (*Blarina brevicauda*), Mp (*Microtus pennsylvanicus*), Zh (*Zapus hudsonius*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*), se (\pm 1 standard error), n (Number of captures)

Discussion:

Similarities And Differences In Perception

In general, movement parameters were similar between the small mammal species in this study, despite differences in trophic levels and behaviours. In addition, differences in movement between reproductively active and reproductively inactive male and female meadow voles were not significant, despite reports of reproductively active and reproductively inactive meadow voles having different levels of activity (Webster and Brooks 1981).

Similarities in movement patterns suggest that these small mammal species are perceiving the wetland habitat in a similar manner (With 1994a). This is possible since adults of four of the six species are roughly the same size: *Blarina brevicauda*, *Zapus hudsonius*, *Microtus pennsylvanicus* and *Peromyscus leucopus*. *Sorex cinereus* tends to have smaller move lengths and turning angles and increased measures of complexity than the others. With (1994a) suggested that a species that exhibits increased complexity in movement trails is interacting with patch structure at a finer resolution than other species. This is an expected response in the masked shrew due to its diminutive body size; its adult body size is at least 4-5X smaller than adults (Table 1) and 2-3X smaller than juveniles of the other species. It is also possible that measurements were biased by mapping *Sorex cinereus* trails more finely than other trails. However, if anything, estimates are thought to be conservative, because it should be more difficult to detect tight turning angles in smaller species, and *Sorex cinereus* had a significantly higher turning rate per meter than other species.

This trend was also evident in short-tailed shrews and meadow voles (Table 9) where smaller individuals tended to have larger MMLs and MTAs than their larger counterparts. Smaller short-tailed shrews and meadow voles generally produced more tortuous trails than larger individuals (Table 9); however, mass only accounted for a very small amount of the total variation. Analysis of stride and gait failed to reveal any further insight about differences between these two species; it is known that meadow voles are larger than short-tailed shrews as supported by the stride size comparisons in this study.

Mustela erminea are considerably larger than the other five species (Table 1) and tended to lope when moving (pers. observ.) but movement structure and complexity, with the exception of MTA, were not significantly different from those of other species (Table 2, Table 4) suggesting that weasels do not move faster than the other species being studied (With 1994a). Species that move faster tend to have longer MML and larger MTA than slower species (Johnson *et al.* 1992, With 1994a, With 1994b). MTA values were smaller than other species despite larger body size. This value would be expected to be slightly higher if the sample of weasels was not female-biased. It is plausible that predators (e.g. weasels) may have to search for their prey (e.g. small rodents) at the same scales that prey use to move throughout their environment during routine activities. Larger organisms, such as weasels, may have to be able to move at small spatial scales. Sexual dimorphism in movement pattern may be a means of partitioning food resources for male and female weasels residing in the same area; males may move at larger scales than females to prey on larger organisms.

Peromyscus leucopus also exhibits a significantly higher MTA. This may be due to a small sample size (n=3), but is more apt to reflect a real phenomenon since all white footed mice were juveniles between 10-14 g. Intuitively, juvenile mice would be expected to move differently than adult mice because of differences in size and the absence of motivational forces due to reproduction. Smaller organisms are expected to exhibit increased complexity in movement (With 1994a), as shown in masked shrews (Table 4). Juvenile rodents are only 2X smaller than adults rodents; whereas, masked shrews are 4-5X smaller than adults of the other species (Table 1). Size dimorphism between juvenile and adult rodents may not be great enough to show this phenomenon in trail complexity. The absence of reproductive influences in juvenile white-footed mice may not be a factor that contributes to significantly higher MTA, since comparisons between reproductively active and inactive meadow voles have failed to reveal any differences in trail structure or complexity.

Despite the similarity in movement structure and complexity among species, species diversity and trap capture measurements suggested that small mammal species are using, and perhaps perceiving, alder and meadow habitats differently (Table 11). In addition, it appeared that small mammal species sharing the same habitat tended to partition their environments vertically rather than horizontally, and as a result, should be perceiving their environment as different. In alder habitat, for example, *Blarina brevicauda* tended to move under leaf litter, while *Zapus hudsonius* moved over it. *Peromyscus leucopus* also moved over the litter but spent a large proportion of their time (up to 50% of trails) traveling up into trees and along branches. In the meadow, *Blarina*

brevicauda traveled under leaf litter while *Sorex cinereus* traveled through it. Generally, *Microtus pennsylvanicus* used permanent runway systems in the meadow. In a few cases, voles traveled over the surface of the litter, but these were mostly adult males who were apparently dispersing; these animals were often new to the area in which they were traveling. *Mustela erminea* traveled over, through and under the litter often within the same trail. Differences in habitat use were not revealed in the analysis of fine-scale movement.

It is possible that the environment constrains the divergence of locomotory behaviours (and subsequent fine-scale movement pathways) in small mammals. Due to their small size and limited body plan, small mammals may exhibit fewer options in locomotion. If this is the case, further research should reveal that locomotory variation increases in groups of mammals with more variable body form.

Gunnarsson (1992) suggested that the fractal dimension of natural habitats may influence the body size distribution in spiders. Since body sizes of small mammals are similar in this study site, it is possible that habitats within this wetland have similar degrees of complexity (i.e. similar fractal dimensions) despite being noticeably different. Theoretically, similarities across habitats should lead to similarities in the groups of species living there.

It is also possible that the similarities noted between different species are not real because of inherent limitations in methodology. Trailing methods may have influenced naturally occurring behaviour (refer to Chapter 2 - Part A) or analyses failed to reveal actual differences in how species are perceiving their environment (refer to Chapter 2 -

Part B). As suggested by Johnson *et al.* (1992), movement patterns may be similar but the underlying causal factors may differ.

Perhaps, most importantly, it was assumed that each wetland subclass (*i.e.* meadow and alder swamp) was perceived as homogeneous throughout by all six species. Although this assumption is fairly common in wildlife management practices, different microhabitats undoubtedly exist and vary in importance to different groups within species (*e.g.* age and sex) and between species. It is concluded that at fine-scales, these species are perceiving the environment as similar; however, this may not be the case at larger spatial scales, since there is evidence of differences in habitat use at the wetland subclass level.

Limits To Extrapolating Information Across Scales

Despite observing similarities in movement between species, I believe that the ability to extrapolate information across scales remains a challenge. Wiens *et al.* (1995) suggested that similarities in d among species suggest that their movements may be described by a common model; however, we do not know why movement patterns in these species are similar; we can only speculate. To date, scaling rules have not been developed and the limits to extrapolation have been difficult to identify. Before making predictions across scales, Turner *et al.* (1989) suggest that four factors need to be addressed: identification of scales, understanding of the importance of parameters at

different scales, translation of information across scales and empirical testing of the methods and predictions across scales. The first two factors have barely been addressed in these commonly studied small mammal species. To begin making predictions across scales, we must identify the scales at which organisms or processes operate. All too frequently we are limited by logistical and analytical methodology (Chapter 2), in addition to our own perceptual biases. Furthermore, we do not understand how the variables influencing processes change with changes in scale. Shifts in the relative importance of variables may occur across ranges of scale (Wiens *et al.* 1993) and/or among species.

Scientists have used two methods to translate information across scales. The objective of the top-down method is to identify the constraints that are important at each scale. This approach can use the ideas of hierarchy theory to extrapolate between scales. The bottom-up approach begins with the individual or entity-based measurements and adds appropriate constraints to explain the resultant phenomena at broader scales. The objective here is to use information that is available at fine scales to predict phenomena at broader scales for which empirical data are lacking.

It is hypothesized that the extrapolations between fine and broad scales may not be symmetrical. It may be easier to scale from smaller to larger grain sizes or extent than to scale down to finer levels of resolution. In the absence of detailed knowledge, scaling down to finer levels may not be possible unless the concept of self-similarity can be applied. Depending on the specific questions to be addressed, both top-down and bottom-up approaches may have to be considered. If one focuses on only large scales, patterns and processes at finer scales may not be perceived due to filtering or averaging

effects; whereas, those occurring at much broader scales may be overlooked simply because the focus is at a smaller spatial unit (Risser 1987).

Relevance To Wildlife Management And Conservation

Landscape ecologists should consider a number of important questions when studying landscape patterns. Are traditional methods of patch identification based on visual assessment (*e.g.* wetland classification) adequate for drawing ecological inferences? Which spatial and temporal scales provide meaningful information about the effects of spatial patterns on ecological processes? Further, do current approaches to the description of spatial pattern provide essential information; if not, which approaches will provide it?

Despite numerous habitat classification schemes based on biotic and abiotic factors, habitat managers and ecologists have relied on dominant structural features, neglecting many minor structural components and patterns in the abiotic environment (*e.g.* microclimate) which may be important to other species (Chen *et al.* 1996, R. Milton, pers. comm.). For example, the two alder habitats in this study were shown to differ significantly in understory vegetation, soil moisture and small mammal numbers and diversity; however, the current wetland classification scheme used in Nova Scotia would identify both areas as shrub swamp and fail to identify the differences between them (Milton *et al.* 1995). This wetland scheme is actually more detailed than the national scheme (T. Power, pers. comm.).

Current classification schemes also ignore the spatial relationship of patches and the effects of temporal scales. Classification schemes are based on features that are present over long terms. Subtle changes in habitat over shorter time periods may be more relevant to many shorter-lived non-human species.

The importance of large spatial and temporal scale (human-sized) studies is recognized; after all, that is the range of scales at which land use and habitat disturbance occur; however, studies should be conducted at a variety of scales, some of which are important to the organism or process being studied. It is necessary to examine critically the ecology and behaviour of the organism before choosing scales for study.

In this community of small mammals, it may have been possible to set the grain of movement study at the wetland subclass level rather than at 5 cm increments within wetland subclasses. Similar studies in similarly classified wetlands may provide further insight into this possibility.

SUMMARY:

Six species of wetland small mammals (*Blarina brevicauda*, *Zapus hudsonius*, *Microtus pennsylvanicus*, *Sorex cinereus*, *Mustela erminea* and *Peromyscus leucopus*) were tracked using a fluorescent powder that glows under UV light to reveal patterns of movement structure and complexity within and between species. Analysis of fine-scale movement in small mammals revealed similarities in trail structure and complexity, in all but the smallest species, *Sorex cinereus*. Despite measurable differences in habitat use and structure, trail structure and complexity did not differ

significantly within species between alder and meadow habitats. It is speculated that these small mammal species may be constrained by similarities in their morphologies and as a result fail to demonstrate differences in locomotory patterns. It is concluded that at fine-scales (those within a wetland subclass), these species are perceiving the environment as similar; however, this may not be the case at larger spatial scales, since there is evidence of differences in habitat use at the wetland subclass level. Studies of small mammal movement at the wetland subclass level may be more appropriate and less labor intensive.

CHAPTER TWO - PART A

The Configuration And Complexity Of Meadow Vole (*Microtus Pennsylvanicus*) Movement In A Freshwater Wetland: A Comparison Of Fluorescent Powder And Bobbin Tracking.

Introduction:

Small mammals are secretive, mostly nocturnal and difficult to observe (Boonstra and Craine 1986, Goodyear 1989, Lemen and Freeman 1985); as a result, it is difficult to obtain information on fine-scale movements of this group of organisms. The ability to address questions on perception and scale of habitat use by animals may be limited by the methods used to track and analyze movement pathways. Traditionally, radio telemetry and intensive grid trapping have been used to obtain information about movements of small mammals. Neither of these methods reveal the precise paths nor the microhabitat selection of the organism in question (Goodyear 1989, Lemen and Freeman 1985), and are of little use in determining the perceptual differences between small mammal species. The primary objective of this experiment was to determine if bobbin and powder tracking are equally effective methods in determining fine-scale movement and habitat use of meadow voles in wetland habitats.

Recently, these two methods of fine-scale tracking have gained popularity with ecologists for determining movement and habitat use of mammals. Powder tracking entails covering the organism with a powder that fluoresces under UV light. As the organism moves through its habitat, it leaves a trail of pigment on the substrate and vegetation along its path that can be followed at night using ultraviolet lights (Lemen and Freeman 1985). Spool-and-line (bobbin) tracking involves the attachment of a spool of fine thread to an animal. The thread flows freely as the animal moves through its habitat, leaving a trail of thread behind (Anderson *et al.* 1988, Boonstra and Craine 1986, Miles *et al.* 1981). Both of these methods provide continuous detail on the movements of small

mammals giving accurate information on the precise route traveled which then can be used to interpret spacing behavior, predator avoidance and foraging (Boonstra and Craine 1986, Lemen and Freeman 1985). Both techniques are relatively cheap to use (Anderson *et al.* 1988, Boonstra and Craine 1986, Lemen and Freeman 1985, Miles *et al.* 1981) and neither requires the constant presence of an observer (Anderson *et al.* 1988, Lemen and Freeman 1985, Goodyear 1989).

Goodyear (1989) believes that most methods of tracking small mammals influence their behavior due to the continued presence and effects of the trailing method and/or observer. This issue is of particular importance in this study, which assumes that trails represent normally occurring activities. In previous studies, there has been little attempt to determine the extent of influence of tracking methods on fine-scale movement.

Anderson *et al.* (1988) reported that thread trails obtained from bandicoots (*Echymipera kalubu*) portrayed normal bandicoot behavior and were not influenced by stresses associated with capture and handling. Miles *et al.* (1981) questioned the influence of bobbins on the normal behavior and movements of a variety of Brazilian forest mammals, but failed to provide any further insight. Mikesic and Drickamer (1992) found that the application of fluorescent powder to wild house mice (*Mus musculus*) tended to reduce activity in the lab for up to twenty-four hours following application; this change in activity was presumed to be due to increased grooming. Stapp *et al.* (1994) found that the use of fluorescent powders for tracking studies had few pathological effects on deer mice (*Peromyscus maniculatus*).

Materials And Methods:

Study Area

Trapping and tracking of meadow voles (*Microtus pennsylvanicus*) was conducted within a portion of a small freshwater wetland (as described by the National Wetlands Working Group 1988) in Greenwich, Nova Scotia (45° 05'N, 64° 23'W). This 1.5 ha wetland is surrounded by agricultural land and highway.

Trapping grids were set in a meadow dominated by *Carex* spp., *Poa* spp. and *Solidago canadensis* adjacent to dense alder (*Alnus rugosa*) swale adjacent to a stream. Alder understory consisted primarily of *Equisetum arvense*, sparse *Solanum nigrum* and *Impatiens capensis*. Several patches of reed canary grass (*Phalaris arundinaceum*) were interspersed throughout the alder swale and along the stream.

Trapping Procedures

Meadow voles were trapped during October 1995 and 1996 in previously existing trapping grids used for a larger study. Two Ugglan live traps were placed at each station in small mammal runways when possible to maximize captures. Traps were checked twice daily, in early morning and late evening. Voles were censused for a total of 174 trap nights in 1995 and 120 trap nights in 1996.

All meadow voles were permanently marked by toe clipping at their first capture. At each capture, sex, age (juvenile, subadult, adult), reproductive condition and trap site

were recorded. Body mass, measured to the nearest 0.5 g, was recorded using a Pesola spring balance.

A subset of adult meadow voles was subject to one of two fine-scale trailing methods: 1) fluorescent powder tracking or 2) bobbin tracking.

Tracking Methods

Powder tracking:

Each small mammal was placed in a plastic bag containing a uniquely coloured fluorescent pigment (Radiant Color, CA) and gently shaken until its fur was saturated with powder (Lemen and Freeman 1985). In the case of multiple captures at a trap station, individual animals were powdered with different shades of pigment to avoid confusion during tracking. Animals were released within the field or alder habitats; release points were highlighted with fluorescent tape labels. Traces of pigment were left behind as the organism moved through its habitat.

Powder trails were tracked at night using hand-held, long wave ultraviolet lamps (VWR Scientific Inc., San Gabriel, CA and Raytect, Middlefield, CT). All pathways were followed and marked with flagging tape until no traces of fluorescing powder could be seen. Systematic searches were conducted around the point of trail disappearance to detect further indication of movement.

Bobbin tracking:

Nylon thread quilting bobbins (Pylon-2) were obtained from Culver Textile Corporation, New Jersey. Each bobbin was approximately 3-3.25 cm long, 1 cm wide and held about 125 m of thread. Heat shrink tubing (PVC and Thermafit) was melted around each bobbin, leaving one end open to allow thread to unwind freely. The other end of the tubing was tapered to allow for easier attachment to the animal. The entire thread tracking apparatus weighed on average 2.31 ± 0.02 grams. This represents approximately 5-9 % of an adult meadow vole's body mass.

Thread trailers were glued to the central rump area of adult (≥ 25 g) meadow voles with a variety of 'superglues'; the open end of the bobbin was pointed towards the posterior end of the animal. Unlike previous studies using bobbins (*e.g.* Anderson *et al.* 1988, Boonstra and Craine 1986, Miles *et al.* 1981), this method did not require anesthetizing or shaving of the animal. After allowing sufficient time for the glue to set, voles were placed in a bucket to watch for behavioural responses to the bobbin and to ensure its proper placement. The free end of the thread was secured to vegetation at the point of release and marked with flagging tape for future reference. Thread trails were excavated and followed within 14 days of bobbin attachment in an attempt to prevent thread breakage.

Release points:

Meadow voles were rarely captured in the alder habitat, thus in order to compare tracking methods between habitats, it was often necessary to release voles from the

meadow into the less preferred and less familiar alder habitat. It was thought that structure and complexity of trails may vary between familiar and unfamiliar surroundings and confound our results. To test for this phenomenon, Kruskal-Wallis (significance level at $p \leq 0.05$) was used to compare trail structure and complexity among the following groups: 21 voles released within 2 m of the capture site in the meadow, 5 released within 2 m of the capture site in the alders, 9 released in what was assumed to be unfamiliar surroundings (at least 60 m away from where the animal was captured) in the meadow, and 21 released in the unfamiliar alder habitat.

Mapping:

Thread and flagging tape (powder) trails were mapped using a compass and measuring tape. A movement step was defined as any directional change greater than 5 cm in length. Visual observations of habitat use and apparent trail complexity were also noted during this process.

Trail Analyses

Trails were analysed using a variety of methods that quantified the configuration and complexity of movement pathways as described in Chapter One.

Trails from 1995 and 1996 were pooled for analyses. All path configuration and complexity indexes were compared between habitats and trailing methods using a Two-Way Analysis of Variance (ANOVA).

Results:

A total of 31 powder trails and 27 bobbin trails were obtained from both sampling periods. Of the 27 bobbin trails, 14 were terminated because the bobbin had fallen off the animal, 11 ended due to string breakage, and one thread trail could not be followed any farther because the vole traveled underground below dense alder roots. One bobbin had been deliberately removed due to improper attachment to the vole.

Total Length:

Bobbin trails were significantly longer in 1995 (21.14 ± 5.42 m, $n=12$) than in 1996 (11.28 ± 3.36 m, $n=15$). Differences in length of powder trails between years were not significant ($p \leq 0.05$) (15.46 ± 1.52 m ($n=17$) in 1995 and 16.81 ± 1.34 m ($n=14$) in 1996). Overall, bobbin trails were longer than powder trails (Table 12); however, the total length of bobbin trails was highly variable, making this method less predictable in the quantity of information that would be obtained. Differences in trail length between habitats were significant in 1995 at 33.67 ± 9.31 m ($n=5$, $p \leq 0.05$) in alder and 13.88 ± 1.59 m ($n=24$, $p \leq 0.05$) in field. All other structural and complexity variables did not differ between years and were pooled for analyses. Descriptive statistics of trail structure and complexity for trailing methods and habitats are summarized in Table 12.

Trail Structure:

Differences in MML, MMLO and MTA between trailing methods were not significant at $p=0.900$, $p=0.429$ and $p=0.96$ respectively. MML was significantly longer

in alder habitat than in meadow ($p=0.029$). MMLO ($p=0.220$) and MTA ($p=0.414$) did not differ between habitats. Two-way ANOVAS revealed that most of the variation in trail structure could be attributed to differences in habitats rather than methods (Table 13), although the data also suggest that bobbin trails tend to have more variable structure than powder trails (Table 12).

Trail Complexity:

Turning rate was significantly higher ($p=0.034$) in meadow than in alder habitat. Fractal dimensions were significantly higher in bobbin trails than in powder trails ($p=0.016$). SLD/TD ($p=0.347$) and TR ($p=0.932$) did not vary between trailing methods. Most of the variation in trail complexity can be attributed to differences in trailing methods rather than habitat (Table 12; Table 13).

Table 12: Structural characteristics of meadow vole (*Microtus pennsylvanicus*) bobbin and powder trails in meadow and alder habitats.

	Bobbin-Meadow (mean±se)	n	Bobbin-Alder (mean±se)	n	Powder-Meadow (mean±se)	n	Powder-Alder (mean±se)	n
TD (cm)	1132.47±343.12	15	2009.00±535.59	12	1420.75±118.07	16	1806.80±156.89	15
MML (cm)	33.31±2.85	14	43.82±4.97	11	35.46±2.09	16	40.78±4.16	14
MMLO (°)	203.14±12.85	14	200.02±8.68	11	204.51±10.26	16	182.53±6.68	15
MTA (°)	72.62±10.71	13	67.57±10.57	10	74.08±6.52	16	64.93±7.08	15
SLD/TD	0.57±0.15	12	0.46±0.07	10	0.51±0.03	15	0.48±0.06	15
TR/m	3.31±0.43	14	2.27±0.25	11	2.95±0.23	16	2.67±0.23	15
d	1.13±0.02	11	1.15±0.04	11	1.11±0.02	16	1.06±0.01	15

Legend: TD (Total length of trail), MML (Mean Move Length), MMLO (Mean Move Length Orientation), MTA (Mean Turning Angle), SLD/TD (Straight Line Distance to Total Distance Ratio), TR (Turning Rate), d (Fractal Dimension), se (± 1 standard error), n (Number of trails)

Table 13. ANOVA table for structural and complexity indices of meadow vole (*Microtus pennsylvanicus*) trails.

Index	Source of variation	df	SS	F ratio	p
MML (cm)	Method	1	2.73	0.02	0.900
	Habitat	1	860.07	5.04	0.029
	Method*Habitat	1	92.57	0.54	0.465
	Error	52	8882.29	---	---
MMLO (°)	Method	1	891.14	0.64	0.429
	Habitat	1	2162.17	1.54	0.220
	Method*Habitat	1	1218.76	0.87	0.356
	Error	52	72937.60	---	---
MTA (°)	Method	1	4.54	0.01	0.946
	Habitat	1	659.81	0.68	0.414
	Method*Habitat	1	55.00	0.06	0.813
	Error	50	48654.15	---	---
TR/m	Method	1	0.01	0.01	0.932
	Habitat	1	5.92	4.73	0.034
	Method*Habitat	1	1.88	1.50	0.227
	Error	51	63.87	---	---
SLD/TD	Method	1	0.04	0.90	0.347
	Habitat	1	0.00	0.00	0.993
	Method*Habitat	1	0.02	0.43	0.517
	Error	48	1.92	---	---
d	Method	1	0.03	6.28	0.016
	Habitat	1	0.00	0.31	0.579
	Method*Habitat	1	0.01	2.32	0.135
	Error	49	0.27	---	---

Legend: MML (Mean Move Length), MMLO (Mean Move Length Orientation), MTA (Mean Turning Angle), TR (Turning Rate), SLD/TD (Straight Line Distance to Total Distance Ratio), d (Fractal dimension)

Discussion:***Trail Analyses -***

Trail length may be confounded by a variety of behavioural, technical and environmental factors. Responses to handling stress may vary; some meadow voles may move further than others simply because of individual differences in behaviour. Small-scale aspects of the landscape, undetectable by humans, may also influence the total distance moved by voles.

Trail structure and complexity did not vary significantly among release points; thus, movements were similar in familiar and unfamiliar habitat. Alternatively, this may suggest that voles are familiar with the entire study site and that their range of movement can be quite extensive.

The length of trail may also be dependent on habitat. Bobbin trails may be longer in the alder habitat because there is less vegetation that could potentially break the thread; similarly powder trails could be longer in alder because there is less vegetation on which the powder could wear off.

The color of the fluorescent powder may affect the total length of the trail. In fall, in this particular wetland environment, green powder was easier to follow than other colors such as pink or yellow. Previous experience in this study site has shown that this tends to vary with season; for instance, green is hard to track in the summer when many horsetails and grasses naturally fluoresce green under UV light.

The brand of superglue used to attach bobbins to the animals may influence the results of the study. The usefulness of the glue is dependent on a variety of factors such

as temperature and the habitat through which the animal is traveling. Researchers should try several brands of glue before choosing one, to ensure that the bobbin does not adhere to the animal for too long or too short a time and that they obtain the required amount of information. In this study, the use of a different brand of super glue in 1996 contributed to the increased rate of bobbin trails with short total distances.

The reduced size of MTA in the field can be attributed to increased vegetation density. Animals would turn more frequently in more complex habitats with increased stem densities. Since animals turn more frequently, move lengths would be shorter in complex habitats and longer in open habitats such as alder as supported by this study (Table 12; Table 13).

The differences in fractal dimension between powder and bobbin trails may be attributed to one tracking method interfering with the animal's natural behaviour more than the other. In this study, it is possible that bobbins altered vole movement more than powder since bobbin trails have more variability in trail structure. Bobbin attachment requires longer handling time and causes more stress and irritation than the other method. It causes an area of localized disturbance which is apt to bother the vole more than powder which is evenly dispersed over the animal's body. It would be difficult to examine the effect of bobbin attachment in more detail in the field without influencing the animal's natural behaviour any further; however, the absence of a control group (*i.e.* trails of voles without tracking devices) makes conclusions difficult. Increased sample size may shed light on the effects of bobbin attachment compared to powder application.

Movement in the field was expected to be more complex than in alder because field vegetation is more structurally diverse and has a higher density of stems (Wiens and Milne 1989, With 1994). This increased complexity would require the animal to turn more frequently if it were looking for the path of least resistance. Although this pattern was evident in turning rate between habitats, it was not found in the other indices of trail complexity. This discrepancy may be explained by the fact that each index measured trail complexity at different spatial scales; TR measured trail complexity at scales of one metre or less, SLD/TD measured complexity at total trail length and fractal dimensions incorporate trail complexity at a wide range of scales. The SLD/TD index may have been an inappropriate measure of complexity since trail length is most likely attributed to the type of habitat and the trailing method rather than the behaviour of the animal. Fractal dimensions are expected to be more indicative of overall trail tortuosity than the other two methods because they incorporate trail complexity at a range of scales (Crist *et al.* 1992, Wiens and Milne 1989, With 1994a) (refer to Chapter 2 - Part B).

Logistics -

Both tracking methods were successful in producing continuous records of meadow vole movement and habitat use in meadow and alder habitats. In association with a larger study, these methods provided insight into predator/prey dynamics, nesting behaviour, home range size and interspecific and intraspecific interactions of voles in their natural habitat. Movements could be followed in both sparsely and densely vegetated wet habitats and I was able to track large numbers of animals simultaneously.

Unfortunately due to the secretive nature of the organism, neither method allows the researcher to determine the periodicity and duration of stops. These trails do not represent the temporal sequence of moves made by the animal, unless the animal moves at a constant rate (Bell 1991). As a result, it can not be determined if either method reduced the activity of the voles in their natural environment. Studies by Mikesic and Drickamer (1992) demonstrated that house mice covered with fluorescent powder exhibited reduced running wheel activity up to 6 hours after application, presumably due to an increase in grooming. They speculate that free-living animals may face enough other pressures that they are less influenced by the powder than animals in a laboratory setting.

In addition, both methods are limited in the duration in which they can be used to track small mammals; powder eventually wears off and bobbins have a limited amount of thread. Animals can be tracked repeatedly upon recapture to reveal longer term habitat use and movement provided the tracking method is not detrimental to the vole's health or behaviour.

Both types of trails may persist throughout a seasonal study period. Powder trails were tracked over a month from when the animals were released and powdered. One particular trail persisted for 31 days in a frequently flooded drainage ditch. Despite being exposed to several heavy bouts of rain, this trail was one of the longest at 28.36 m. In general, powder trails become harder to follow over time, which results in shorter trails. Thread trails also persist for long periods if not disturbed. Entire trails can be destroyed if a person or large animal becomes entangled in the thread. Thread trails are also susceptible to breakage by vegetation or ants (Miles *et al.* 1981) but the trail can often be

picked up at distances <15cm away in dense field vegetation. Thread trails can also be removed and discarded at the end of the experiment.

Both methods result in short-term destruction of habitat. Tracking requires crawling intensively through vegetation to look for powder or thread trails. During the summer months, in a larger corresponding study, the study site was permitted two weeks to recuperate between tracking sessions. This recovery period may have to be extended during cooler months when the vegetative growth is reduced. Neither method may be suitable for long term studies or studies that require minimal habitat disturbance.

Several other factors should be considered before choosing a method of fine-scale tracking for small mammals. Both methods are reasonably inexpensive. Powder costs about \$12 (Cdn) per can, which is enough to powder 75 to 100 small mammals. Powder tracking also requires the purchase of an ultraviolet light, which can cost up to \$200 (Cdn) depending upon the particular unit. Bobbins cost \$197.50 per box which contains enough bobbins for approximately 90 to 100 animals. Heat shrink tubing and superglue are relatively inexpensive and available at most hardware stores.

Bobbin tracking can only be conducted during the day. Although powder tracking is generally completed at night, it can also be conducted during the day under a heavy, dark blanket (McShea and Gilles 1992). It is difficult (and potentially dangerous) to track small mammals in wet environments in the dark.

Some colors of powder are easier to detect than others. Horsetails (*Equisetum* spp.) stems, lichens and insects tend to fluoresce blue or green under UV lights. Many of

the powder colors available appear similar under UV light; of 10 available colors in this study, only 4 could be distinguished from each other in the field.

On several occasions it was difficult to distinguish similarly-colored powder trails because powder residue had remained from earlier trails. Halfpenny (1992) noted the persistence of powder in the environment for over 2 years in shady, protected areas. He warned of the potential for fluorescent powder to contaminate the environment and suggested that researchers take measures to avoid the release of the initial heavy load of powder when the animal first touches the ground. He also used hand-held vacuum cleaners to clean up powder trails. It is note-worthy that intensive tracking in a small area may contribute to such contamination problems. Residual powder may have an impact on later, unrelated studies in the same area.

Powder tracking can be used successfully on a variety of species, regardless of age or size. Powder can be used on animals as small as masked shrews (*Sorex cinereus*) (Teferi and Herman 1995, Chapter One). Bobbins were only used on adult meadow voles > 25 g, due to the size and bulky shape of the trailing apparatus. Although not available commercially, smaller scaled-down bobbins could have been created for tracking smaller animals. It is expected that either method would have little influence on the behaviour and movement of larger small mammals; several short-tailed weasels (*Mustela erminea*) were successfully tracked using fluorescent powder throughout the duration of the larger accompanying study (refer to Chapter One).

Deleterious effects -

There was no direct evidence that either tracking method increased the animal's susceptibility to predation, although it is plausible that either may have slowed animals down, and in the case of bobbins, made it more difficult for animals to hide in confined spaces. To date, no one has studied the susceptibility of brightly colored mice to predation by larger mammals or birds of prey (Mullican 1988).

It has been suggested that the use of fluorescent powder on small mammals may contribute to respiratory ailments due to the ingestion and inhalation of powder particles (Stapp *et al.* 1994) . Despite the frequent re-powderings of some individual animals, we saw no harmful effects of the powder on study animals, although detailed examinations of respiratory systems were not conducted. Bobbin tracking resulted in hair loss up to 1.5 cm by 1 cm on the rump of meadow voles, preventing any further tracking of individuals that had been subject to this method. During cooler weather, such hair loss could result in heat loss and eventual death of the animal.

A major concern with any tracking method is the influence of the method on behaviour. Trauma from the handling process and subsequent exposure to the attachment of the bobbin or the powdering process may affect subsequent behaviour and movement patterns upon release. Trail complexity, however, was not significantly different between subsequent trailings of individuals suggesting that the effects of handling are short-lived. There may also be subtle effects on social status and foraging (Key and Woods 1996).

Summary:

Using fluorescent powder and bobbin tracking, the fine-scale movements of adult meadow voles (*Microtus pennsylvanicus*) were examined in a wetland environment. Both methods were effective in demonstrating aspects of microhabitat use and behaviour; however, tests comparing trail structure and trail complexity revealed that the bobbin method produced patterns that were more variable and unpredictable than the powder method. Further analyses suggest that animals with bobbin attachments tended to exhibit more complex movement patterns. Most of the variation in trail structure could be attributed to differences in habitat rather than differences in trailing method. It is expected that the choice of either method will depend on financial and technical logistics and the specific questions under study.

CHAPTER TWO - PART B

An Evaluation Of The Analysis Of Fine Scale Movement Of Wetland Small Mammals.

The ability to identify which spatial and temporal scales should be studied to provide meaningful information about the effects of spatial patterns on ecological processes is limited. It is a challenge to deal with fine-scale movement data so that it 1) is compatible with statistical analysis and computer modelling, 2) accurately represents the movement of the organism (Wiens *et al.* 1993) and 3) does not create a deluge of information. Researchers should be aware of the range of challenges to be faced during the data collection and data analysis phases of movement studies.

Data Collection:

Problems with data collection lie primarily in three areas: grain of measure, imposition of artificial scale constraints and the maintenance of simplicity.

The usefulness of distance and orientation data may be limited by the observer's perspective, and may not accurately depict the movement response of the organism to the heterogeneity which it perceives and to which it responds. The resolution used to collect data must be relevant to the organism in time and space and be useful in isolating different behavioural sequences, although we may be limited by our methodology and apparatus (Chapter 2 - Part A). There are three major components of data collection in which this problem is especially evident: determination of the temporal sequence of moves,

definition of move length, and definition of turn.

Pathways must be divided into a number of straight line units and directions for recording and analysis; unfortunately it is rare for a trail to have regular stop points that would assist in defining discrete segments (Turchin *et al.* 1991). The usual method for digitizing pathways is to record the coordinates of the organism at set time intervals and connect the successive positions with straight lines (e.g. Kareiva and Shigesada 1983). It is nearly impossible to use this strategy for organisms that are secretive and not readily observed (*in sensu* Bell 1991). Generally, the track will not accurately represent the temporal sequence of moves made by the animal, unless the animal moves at a constant rate (Bell 1991), where it would be possible to partition the path into moves of time rather than space (Tourtellot *et al.* 1991). Unfortunately, subdividing the trail at regular time intervals (Kareiva and Shigesada 1983) will produce turns where the animal did not turn, especially if the time intervals are too long (Turchin *et al.* 1991; Wiens *et al.* 1993). Too short intervals may produce turns that do not correspond to actual behavioural events (Turchin *et al.* 1991) and increase the sampling effort required for each trail. One can assume that at small spatial scales, movement data will be collected at a varying rate.

In the case of small mammal movement, it is necessary to choose the minimum length of straight line units or move lengths (Bell 1991). If move lengths are too large, trail detail may be lost; if move lengths are too small, they will require increased effort in recording and computation by the researcher. Collecting at the highest resolution possible may not be worthwhile since the high resolution of trails will actually emphasize the variability of the data (Tourtellot *et al.* 1991) and may reveal translatory movements due

to gait rather than turns associated with actual changes in orientation (Bell 1991).

Kitching and Zalucki (1982) suggest that for any trail there is a hypothetical level of resolution which uses the largest move length that retains the features of an animal's behavior in which an investigator is interested; however, using longer move lengths would require longer trails. This optimal scale of observation may differ between species.

Mean turning angle and turn rate result from the size of move length (*i.e.* resolution) used in the study. Turning rate is a locomotory measure used to detect a change in orientation; however, it must be remembered that each turn is composed of gait noise and intentional course change (Bell 1991; Tourtellot *et al.* 1991).

Data Analysis:

In addition, there are a number of concerns associated with the statistical analysis of angular data. Most studies have failed to recognize that angle data vary widely and generally do not fit normal distributions, because they range from 0 to 360° (Cain 1989; Kitching and Zalucki 1982). Consecutive moves within a trail may not be independent (Cain 1989). Autocorrelated data require special non-parametric statistics since directional angles are circular rather than linear (Batschelet 1981; Mardia 1972). This can be prevented by using individual trails, rather than the steps within each individual pathway, as replicates as in this study (Wiens *et al.* 1993).

Scale-Dependent And Scale-Independent Analyses:

Movement at small scales tends to be influenced by foraging and/or thermoregulation, whereas, at larger scales, animals tend to move in response to social factors or habitat changes across habitat boundaries. This scale-dependent movement behaviour, and the fact that animals vary in size, vagility, physiology and life history characteristics has made it difficult to compare movement processes among species within and between habitats (Crist *et al.* 1992).

Organisms differing in size, morphology or taxonomy move at different rates and trace different movement paths. Because movement pathways are strongly influenced by environmental structure, they may reflect differences in how organisms perceive habitat. Comparisons between species are complicated by the scale-dependence of movement (Wiens *et al.* 1995) and resultingly, scale-dependent measures tend to vary significantly between species and with variations in habitat heterogeneity.

Fractal analyses are thought to alleviate some of these concerns. Fractal analyses are assumed by many to be scale-independent measures of movement which will allow researchers to examine movement pathways across a range of spatial scales (Crist *et al.* 1992; Wiens and Milne 1989; Wiens *et al.* 1995; With 1994a, b). These measures are less sensitive to measurement scale and may facilitate perceptual comparison between species with different body sizes, movement rates and locomotory gaits (Wiens *et al.* 1995; With 1994a, b).

Turchin (1996) is concerned about the key assumption of the fractal approach, in which it is assumed that the estimated fractal dimension is constant over some

biologically relevant range of scales. Fractal analysis assumes that a pathway several centimetres long will have the same degree of tortuosity as a path several hundred metres long. These criticisms are crucial when using data at small scales to gain information about large scales; however, he concludes that we can not calculate just one single fractal dimension for a trail unless self-similarity across a range of scales is demonstrated. This conclusion was based on the fact that the calculation of one overall d does not fit with correlated random walk models.

Correlated random walks behave like linear movement ($d=1$) at small spatial scales, specifically at the scale that corresponds to the organism's body size, and like Brownian motion ($d=2$) at very large scales. Fractal dimensions of simulated paths resulting from correlated random walks tend to grade smoothly from $d=1$ to $d=2$ as the spatial scale is increased. These models assume that travel has no directionality, that turn angle is chosen randomly and equally, and that the environment in which animals move is homogeneous and lacks barriers (Nams, pers. comm.); such models have been successful in modelling movement patterns on the large scale (Kareiva 1983), but less successful on the small scale because such assumptions often are not met. At small scales mammals appear to move towards specific points and move to avoid obstacles (pers. observ.); The range of MMLO for all small mammal species fail to support the assumption that trails are random in respect to direction. MMLO ranges tended to be narrow and were never evenly dispersed between 0 and 360°.

Thus far, I have deliberately avoided the use of the terms 'scale-dependent' and 'scale-independent' in this thesis. 'Scale-dependent' measures do not necessarily change

with the size of the organism; for example, weasels are larger but do not exhibit different trail structure from much smaller mammals. In the case of fractal dimensions, they may or may not be scale-independent (Turchin 1996, Nams 1995) depending upon the behaviour of d with ruler size.

Measures of trail complexity for *Blarina brevicauda*, *Zapus hudsonius* and *Microtus pennsylvanicus* were not highly correlated (Table 14), perhaps due to inherent problems with each measure. Theoretically, measures that incorporate trail complexity at multiple scales should not be related to those measures that are dependent on the size of the organism; as demonstrated by the insignificant relationship between TR and d , and SLD/TD and TR. Neither SLD/TD, nor fractal d differed significantly among different sized species (Table 4, Appendix 1) indicating that they are 'scale-independent' measures. As a result, SLD/TD and d should be, and are, significantly related (Table 14). In addition, fractal dimensions failed to show any consistent pattern with changes in step size indicating that they are 'scale-independent'.

There are inherent limitations associated with complexity indices, some of which may be situation-dependent. Researchers may want to examine their particular situation critically before choosing appropriate measures of trail complexity; for example, SLD/TD gives very poor information on the tortuosity of a trail. All paths having the same length and net displacement will have the same tortuosity value even though they may have very different degrees of tortuosity (Dicke and Burrough 1988). This is demonstrated in Figure 5 and Figure 6 where the trails appear quite different but have similar SLD/TDs.

TR is dependent on move length size (Dicke and Burrough 1988), so longer MMLs should lead to a decrease in TR (*e.g.* weasels have lower TR than masked shrews).

Fractal analysis incorporates tortuosity at all scales, although it does not provide information on orientation or directionality (Dicke and Burrough 1988). Fractal analysis fails to identify the causal factors underlying similarities in complexity. Fractal dimensions may be similar, but the response of the organisms to their environment may be quite different (Johnson *et al.* 1992, Wiens *et al.* 1995, With 1994a). In this study, the behaviour of fractal dimension with changes in step size appeared to vary from trail to trail. Close examination of these plots would probably be useful for demonstrating the range of differences in individual fine-scale movement within a species.

In general, measures of movement structure and complexity, in this study, failed to reveal differences in the structure and pattern of small mammal movement despite differences in size, morphology and behaviour between species (Refer to Chapter 1). It is possible that fine scale movement for all six species is within a narrow range and that measures dependent on the organisms size may be more revealing about perceptual differences than fractal analysis; however, fractal dimensions may be more useful for comparisons between highly divergent groups of organisms.

Table 14. Relationships between trail complexity indices for short-tailed shrews (*Blarina brevicauda*), meadow jumping mice (*Zapus hudsonius*) and meadow voles (*Microtus pennsylvanicus*). Trail complexity indices were not highly correlated.

	<i>Blarina brevicauda</i>	<i>Zapus hudsonius</i>	<i>Microtus pennsylvanicus</i>
SLD/TD vs. TR			
Adj R square	0.047	0.011	0.003
R square	0.075	0.073	0.018
n	35	17	67
F	2.670	1.183	0.176
Sign. F	0.112	0.294	0.676
SLD/TD vs. d			
Adj R square	0.134	0.080	0.357
R square	0.174	0.150	0.369
n	23	14	56
F	4.410	2.123	31.592
Sign. F	0.048	0.171	6.867E-07
TR vs. d			
Adj R square	-0.047	-0.083	-0.015
R square	0.001	0.001	0.003
n	23	14	56
F	0.020	0.007	0.176
Sign. F	0.889	0.934	0.676

Legend: SLD/TD (Straight Line Distance to Total Distance Ratio), TR/m (Turning Rate), d (Fractal dimension), n (Number of trails)

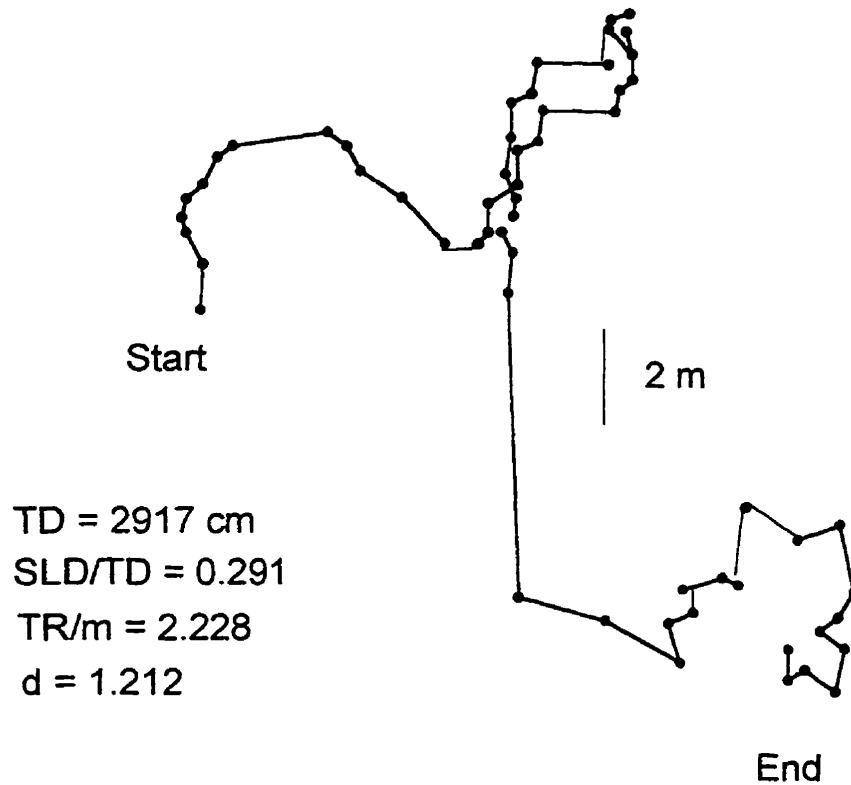


Figure 6. Powder trail (Trail 175) of meadow vole (*Microtus pennsylvanicus*) in meadow. See Figure 7 for a trail with similar complexity but of quite different structure. Indices of trail complexity fail to reveal such differences among trails when used alone. Complexity indices should be combined with indices of trail structure to determine perceptual differences among groups of organisms.

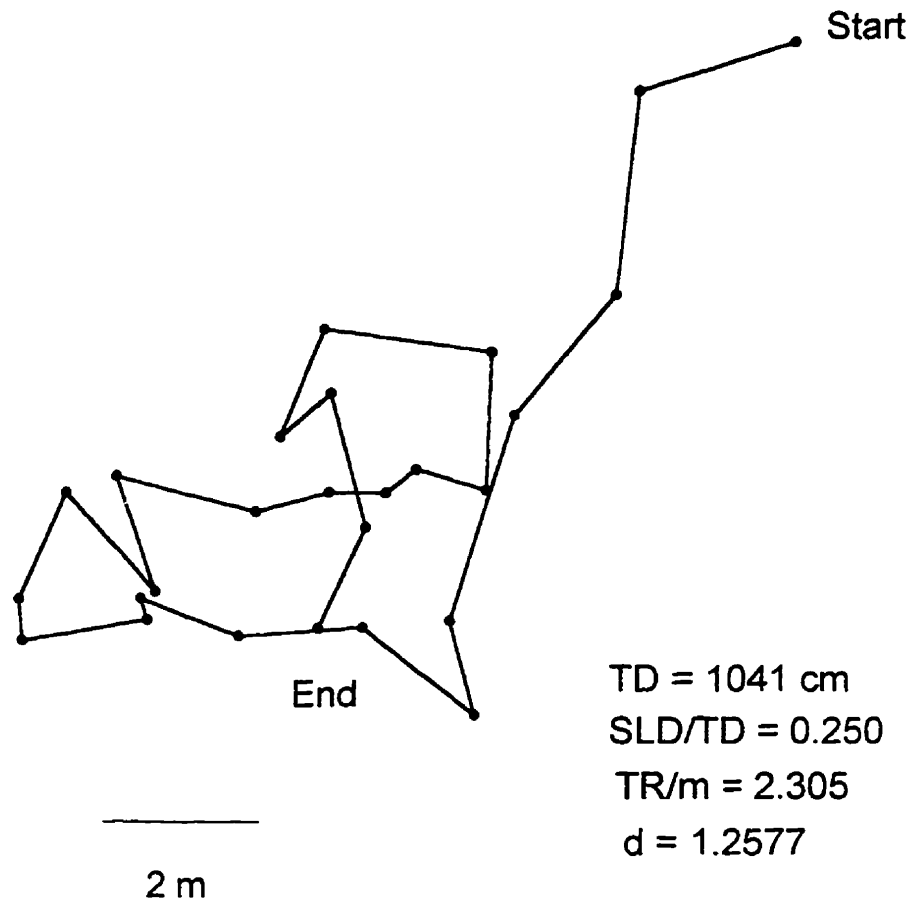


Figure 7. Powder trail (Trail 220) of meadow jumping mouse (*Zapus hudsonius*) in meadow. See Figure 6 for a trail with similar complexity but of quite different structure. Indices of trail complexity fail to reveal such differences among trails when used alone. Complexity indices should be combined with indices of trail structure to determine perceptual differences among groups of organisms.

CHAPTER 3

So Landscape Ecology Measures Up, Eh? ... But Does It Measure Down?

“...the concept continues to elude me. Perhaps one reason for this is that I persist in seeing it not as a scenic or ecological entity but as a political or cultural entity; changing in the course of history....I have come to the point where instead of trying to establish distinctions between landscapes, I try to discover similarities...[and am] more concerned with...perceiving the universe which presumably lies behind diversity.”

(J.B. Jackson)

Definition of landscape:

The term landscape has become a buzzword of the 1990's, but due to the term's long history and interdisciplinary background, it requires careful definition and use. The definition of landscape is problematic because landscapes can be observed from many different points of view, and various disciplines focus on different processes operating at different temporal and spatial scales (Sauer 1967; Urban *et al.* 1987). Currently, within the field of landscape ecology, there appear to be two main approaches to defining landscapes; these approaches primarily reflect differences in scale.

The first defines landscapes in terms of human perception and land use (Berleant 1992; Eckbo 1975; Hansson & Angelstam 1991; Sauer 1967; Zube 1987); these landscapes generally range in size from a few hectares to many square kilometers (Wiens 1989; Wiens 1992). Berleant (1992) defined such a landscape as an “...intellectual, moral and aesthetic statement of man”. We unavoidably approach the study of landscapes from

an anthropocentric point of view, seeing only the boundaries and discontinuities in nature that seem important to us (Wiens 1985).

The second approach focuses on the non-random, repeated patterns of landscape structure that appear to occur at all scales (Forman and Godron 1981) and does not restrict landscapes to large scales. Studies of landscapes from this perspective focus on the configuration of elements or patches in relation to one another in the overall mosaic and how landscape structure influences a variety of ecological patterns and processes (Lidicker 1995; Wiens & Milne 1989; Wiens *et al.* 1993). Forman and Godron (1986) define such a landscape as "...a heterogeneous land area composed of a cluster of interacting components that is repeated in a similar format throughout." There is nothing in this perspective of landscape ecology that limits it to landscapes perceived at human-sized scales (Wiens 1989) and these ideas should apply to any scale of investigation.

Both approaches to landscape ecology are complementary as they both recognize landscapes as spatial mosaics with discrete elements. The combination of both views has resulted in the proposal of a variety of landscape properties (some of which are included below) by landscape ecologists; these characteristics must be general since they must hold true at all spatial and temporal scales and in all regions and environments. A coherent paradigm for landscape ecology has yet to emerge (Lidicker 1995; Wiens *et al.* 1993).

General characteristics of landscapes:

Landscapes are distinct, bounded units with specific ecological characteristics which can be broadly classified as structure, function and change (Forman and Godron

1981; Turner and Gardner 1991). The arrangement or structural pattern of landscape elements is a major determinant of functional flows and movements through the landscape, and of changes in its pattern and process over time (Forman 1995).

Structure -

Structure refers to the spatial relationships between landscape components or elements (Turner and Gardner 1991). Landscapes are heterogeneous; they are structurally different from one another because of the variation in distribution of species, energy and materials among landscape elements (Forman and Godron 1986) which include patches, corridors and matrices. These structural differences lead to functional differences in landscapes due to the variation in the flows of species, energy and materials (Forman and Godron 1986). Studies of landscape structure investigate the distribution of energy, nutrients and organisms in relation to the quantity, types and configurations of landscape elements (Forman and Godron 1981; Turner and Gardner 1991).

Patches are defined as non-linear surface areas which differ in appearance from surrounding material (Forman and Godron 1986). Patches, consisting of plant and animal assemblages, vary in size, shape, heterogeneity and boundary characteristics. Patches are classified by their origins and can be separated into disturbance, remnant, environmental resource, planted and habitation patches. Patches can also be defined from the perspective of the organism being studied or the questions being asked (*e.g.* foraging theory).

Corridors are narrow strips of land that are structurally different from the matrix located on either side. They are characterized by sharp microclimatic and soil gradients from side to side. Corridors may be isolated but generally they connect patches of similar vegetation. Examples include roads, railways, dykes, ditches, power lines, hedge rows and stream beds; their functions can be summarized as transportation, protection, resources and aesthetics.

The matrix is the binding element that surrounds and cements the landscape together. The matrix can be distinguished from a patch because it exceeds the total area of any particular patch type; it is more connected than other elements and it has more control over landscape dynamics than other elements.

Function -

Landscape functions, both natural and human, are the fluxes of energy, nutrients and species among landscape elements (Forman and Godron; Lidicker 1995). Functional attributes of landscapes are not easily described since landscape dynamics create structure and landscape structure determines dynamics (Forman 1995; Forman and Godron 1986; Risser 1987). This area of landscape ecology is just starting to develop (Risser 1990). Processes vary in their effects and importance at different spatial and temporal scales in the landscape, and the relationships between spatial patterns and processes are not restricted to single or particular scales (Risser 1987).

Forman and Godron (1986) identify several vectors for the flow of energy, nutrients and species between landscape elements: wind, water, flying animals, terrestrial

animals and humans. The forces that drive these flows are broadly classed as diffusion, mass flow and locomotion (Forman and Godron 1986; Risser 1987; Risser 1990).

Due to the traditional, more human-oriented background of landscape ecology, large scale processes that influence landscape structure have been described in detail. Geologic, hydrologic, climatic and human processes have been identified as important in regulating landscape structure and function (Forman and Godron 1981; Forman and Godron 1986). Smaller scale processes have yet to be clearly summarized. Risser (1990) attempts to combine large and small scale processes through his identification of three causal mechanisms for landscape function. First, landscape flows vary over short and long temporal scales, so long-term studies are necessary. Second, geological processes, including climate, and the short and long term interactions between geological and ecological processes are important. Finally, it is necessary to combine both natural and human based processes and energy flows. Human disturbance of natural landscapes alters dynamics due to the introduction and alteration of patches and dynamics (Wiens 1985).

Certain landscape elements and configurations are more conducive to fluxes than others (Forman 1995; Taylor *et al.* 1993). Highly heterogeneous areas have higher probabilities of containing unsuitable elements than more homogeneous areas and are predicted to have greater resistance to flow (Forman 1995). Heterogeneous landscapes have more boundaries and thus, more flows across boundaries within the landscape. These landscapes support more edge species which cross boundaries more frequently (Forman and Godron 1986). Kozakiewicz and Szacki (1995) suggest that species dynamics increase in highly heterogeneous areas. Such areas have smaller patches which

are apt to provide only one required resource and individual organisms have to move to more patches to obtain all their necessary requirements. Heterogeneity may also inherently stimulate mobility because different patches provide something new for animals to explore (Kozakiewicz and Szacki 1995).

Change -

Change is the alteration in structure and function of the landscape mosaic over time (Risser 1987) caused by natural and human processes. Landscapes are characterized by their relatively stable structure and slow, gradual change (Zonneveld 1989); resilience of the landscape depends both on its structure and history of exposure to particular disturbances (Forman 1995; Forman and Godron 1986). Disturbances are discrete events in time which disrupt landscape structure and process (Pickett and White 1985).

Microlandscapes:

Recently studies have attempted to define landscapes from the perspective of other species (*e.g.* Wiens and Milne 1989; With 1994a, 1994b). Unfortunately, there seems to be more to this than simply adjusting the scale at which we view nature, for we also tend to emphasize those factors with which our senses, primarily vision, are in tune (Wiens 1985). Other organisms perceive environmental mosaics in quite different ways and unless we adopt an organism-centred approach, we are unlikely to discern the elements of patch structure and dynamics that are important to them (Wiens 1985).

Landscapes adjusted to non-human organisms, at less than kilometer-wide scales, are called microlandscapes (Wiens 1989). Microlandscape scales would depend upon factors such as species rareness, age class, size of organism, mobility, environmental heterogeneity and duration of study (Wiens 1989).

Meentemeyer and Box (1987) suggest that small scale approaches have more variables to consider than larger scales. The most important variables are chemical and biotic rather than abiotic, such as the large, physical landform characteristics that are important at large scales. Temporal scale is more important at small scales than larger scales and small landscapes have fewer emergent properties.

Microlandscapes have several advantages over larger scale landscape approaches: measurements may be taken at a level of detail that is difficult to obtain at broader scales, sample sizes or sampling intensity can be increased, and experiments can be easily manipulated and replicated (Barrett *et al.* 1995; Meentemeyer and Box 1987; Wiens 1989; Wiens *et al.* 1993).

A potential application of microlandscape studies may be the ability to extrapolate ecological findings from microlandscapes to landscapes of broader scales. Extrapolation refers to the process of estimating unknown values from a set of known values (Turner *et al.* 1989). The ways in which spatial scales influence large scale pattern and process could be determined by observing microlandscapes that operate at smaller, more manageable spatial and temporal scales.

We frequently transfer information from human systems to the systems of other organisms and assume that differences are linear and can simply be corrected by adjusting

scale size, but the value of such extrapolations has yet to be determined. The usefulness of extrapolation will be limited by the ability to transfer information between systems at different scales; one must consider whether both systems behave the same way despite being at different scales. Wiens *et al.* (1993) believe that the extrapolation of responses of one organism to another is not always possible and that comparisons may have to be restricted to organisms of similar physiology and trophic status; the concept of extrapolation has not been taken any farther than its applications in animal movement (Wiens and Milne 1989; With 1994a, 1994b).

The purpose of this essay is to investigate several developing aspects of landscape ecology and to develop a general procedure to define landscapes from the perspective of organisms. This approach will incorporate the ideas of both existing landscape paradigms.

Organism-defined landscapes:

Many landscape ecologists (Hansson and Angelstam 1991; Kotliar and Wiens 1990; Wiens 1985; Wiens 1989; Wiens 1992; Wiens and Milne 1989; With 1994a,b) have suggested the need to consider landscapes from the perspectives of other species if we wish to implement successful management and conservation strategies (Hansson and Angelstam 1991).

To date, no one has suggested a complete approach for defining such landscapes. Several studies focused on the consequences of heterogeneity on the movement of ground insects, in particular, ants (Crist and MacMahon 1991; Crist and Wiens 1994), beetles

(Crist *et al.* 1992; Wiens and Milne 1989) and grasshoppers (With 1994a, b). By analyzing the complexity of movement pathways, these studies have attempted to assess the range of scales at which these organisms found vegetation structure and composition heterogeneous.

There are several problems with these initial approaches to defining microlandscapes. Firstly, landscape structure may have been defined in a manner that is irrelevant to the organisms under study. To my knowledge, only With (1994b) examined movement pathways at a variety of spatial and temporal scales to determine the minimum scale at which movement could be measured, before collecting data for her study. With (1994a, b) used a maximum spatial scale of 25 m² and a maximum temporal scale of 30 minutes; she provides no justification for the use of these particular scales nor what relevance they may have for the organism. Also, movements may have been influenced by other combinations of habitat factors such as ground temperature, moisture and humidity, in addition to vegetation structure and composition. Relevant habitat factors are apt to be species or question specific.

Secondly, the movements studied were mechanistic elements of foraging, home range space use, spatial distributions of populations, dispersal behaviour and community interactions (With 1994a). In developing conservation strategies, it is necessary to identify the scales at which each of the above processes occur and the elements of the landscape which generate the scale of habitat use. It is not enough to identify the minimum and maximum scales of the perceptual range since organisms do not necessarily respond to all scales between them (Kotliar and Wiens 1990). To manage or conserve a

species, it is necessary to have identified and maintained all of the resources necessary for their survival.

I believe that organism-defined landscapes should give consideration to the following: range of the organism's perspective resolution (*i.e.* grain and extent); spatial and temporal scales at which life-sustaining processes (*e.g.* foraging and reproduction) occur and the elements of the landscape that are intrinsic to these processes; and the influence of human and natural disturbances that occur or influence the landscape at scales between the grain and extent. This approach incorporates all of the characteristic features of landscape including structure, function and change. This model is directly applicable to the individual or perhaps, the species view of landscapes, but it can be easily adapted for population and community landscape approaches. Natural history is an inherent characteristic of this model.

The range of scales within which an organism responds falls between particular scales of grain and extent (Kotliar and Wiens 1990). Grain is the smallest scale at which an organism can respond (Norton and Lord 1990; Turner *et al.* 1989; Wiens 1990; With 1994a) or perhaps, distinguish patches (Kotliar and Wiens 1990). At patches less than grain size, organisms view the environment as homogeneous (Kotliar and Wiens 1990).

Initially, I thought grain size would be constrained by the size of an individual's pace or step, however, it has been suggested that other processes may occur at finer scales; for example, deer are frequently observed foraging at intervals smaller than one pace (Nams, pers. comm.). This lower limit of response is set by physiological (*e.g.* size, age, locomotory adaptations) and perceptual abilities (*i.e.* sensory acuity) of the

organism; and may be constrained at larger scales by behaviour and life-sustaining processes (Kotliar and Wiens 1990; Turner *et al.* 1990; Wiens 1989; With 1994a). One must identify the scales of sensory perceptions, locomotion, and life processes before choosing the smallest scale of the group as the grain scale.

Extent refers to the largest scale of heterogeneity to which an organism responds. This upper limit is determined by the lifetime range of the individual (Kotliar and Wiens 1990; Turner *et al.* 1990; With 1994b). To determine this scale of response, it is necessary to have natural history and movement data for the entire lifetime of the organism.

The survival of individual organisms is dependent on the ability to find food, suitable microclimates, and to avoid predation. The lifetime size of an individual's range is dependent on the availability of mates, ability to disperse, locomotory behaviour and possibly species density. Each of these processes can be defined in terms of an ecological neighbourhood as suggested by Addicott *et al.* (1987). Ecological neighbourhoods are defined by: an ecological process; a temporal scale appropriate to that process; and an organism's activity or influence during that process. In addition, I believe it is necessary to identify the components of the environment that are essential for that process, for example, resource patches and functional corridors between patches. This model is applicable to both mobile and sessile organisms and will allow for easier comparisons between studies at different scales, geographic locations and between species.

The role of human and natural disturbances is a necessary consideration when defining a landscape. Humans have a great impact on patch dynamics, through

fragmentation; we tend to reduce average patch size, increase distances between patches and decrease area:edge ratios (Urban *et al.* 1987; Wiens 1985). Although most human disturbance originates at large scales, it is necessary to identify any influences it may have on other organisms living at smaller scales. Naturally occurring disturbances such as seasonal flooding or fire may have an impact on habitat use by organisms.

The concept of home range may or may not contribute to the definition of an organism's landscape. In general, a home range is an area where an animal lives and carries out its daily activities (Brown and Orians 1970; Burt 1943; Sanderson 1966); however, the components of the organism's habitat and the processes that are included in the home range tend to vary from study to study. The usefulness of home range information may be limited by the ability to determine the actual processes, landscape elements and the temporal scales of the study.

Like most ecological models, this landscape approach may have some limitations.

1. The landscape unit may not be a logistically feasible unit of study in ecology.

This approach to organism-defined landscapes is apt to be limited by its complex, multilayered definition. Detailed descriptions and data are not readily available for many species, especially those that are rare and long-lived. Data are frequently lacking for species that are subject to management and conservation strategies.

The definition of landscape will be further complicated because perspectives are bound to differ between individuals of varying age classes, sexes, sizes and breeding conditions. Numerous studies of small mammals have demonstrated differences in dispersal behaviour between sexes and between breeding conditions within sexes

(Bondrup-Neilsen, pers. comm.). Age classes often differ in size, behaviour and life stage; for example, With (1994b) found that adult and nymphal grasshoppers interact with landscape structure in different ways. It is extremely difficult to define landscapes from the perspectives of all groups within a species.

2. Organism - defined landscapes may not have distinct boundaries as necessary by definition. Sometimes the regions that influence organisms may exceed the individual's lifetime range, for example, mobility of edible resources in the case of sit and wait predators; allelopathic organisms that produce deleterious by-products which are carried by water or air; or organisms that attract their consumers or mutualistic foragers from a wide region (Addicott *et al.* 1987).

3. Our ability to define other organism's landscapes may be limited. Due to our limited range of perception, we may not be able to determine the elements of the environment that are important to other species. We may be limited to assessing species - perceived heterogeneity mechanistically through movement patterns. It is impossible for humans to remove their perceptual biases from ecological studies.

4. Landscapes may not be real functional units of organization to other species and may be restricted to human use and perception. Human landscapes are greatly influenced by culture and aesthetic value (Nassauer 1995) and are identified by technological devices such as satellite imagery which increase our natural scale of perception (Kolars and

Nystuen 1974). Once again, we may simply be forcing our views on other species, and the landscape approach may be a limited management and conservation tool.

In conclusion, I believe it is necessary to develop the concept of organism-defined landscapes further. These approaches are often recommended by landscape ecologists as a solution to conservation-based problems, but no one has discussed the actual definition or potential limitations of the application. Landscapes still appear to reflect human perceptions and activities. Numerous patterns in the landscape are not produced by natural processes and disturbances. Research linking human perceptions with ecological conditions add an important dimension to landscape ecology, for understanding both a determinant of present patterns and as an indicator of alternative futures (Forman 1986). If landscapes are irrelevant levels of organization to other species, we should be placing our efforts elsewhere.

LITERATURE CITED:

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A. 1987. Ecological neighborhoods: Scaling environmental patterns. *Oikos* 49:340-346.

Anderson, T.J.C., Berry, A.J., Amos, J.N., and Cook, J.M. 1988. Spool-and-line tracking of the New Guinea Spiny Bandicoot, *Echymipera kalubu* (Marsupialia, Peramelidae). *Journal of Mammalogy* 69:114-120.

Barrett, G.W., Peles, J.D. and Harper, S.J. 1995. Reflections on the use of experimental landscapes in mammalian ecology. In Lidicker, W.Z, Jr. (ed.). Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, Minneapolis, pp. 157-174.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, London.

Bell, W.J. 1991. Searching Behaviour: The behavioural ecology of finding resources. Chapman and Hall, London.

Berleant, A. 1992. The Aesthetics of Environment. Temple University Press, Philadelphia, pp. 1-24.

Boonstra, R. and Craine, I.T.M. 1986. Natal nest location and small mammal tracking with a spool and line technique. *Canadian Journal of Zoology* 64:1034-1036.

Cain, M.L. 1989. The analysis of angular data in ecological field studies. *Ecology* 70:1540-1543.

Chen, J., Franklin, J.F. and Lowe, J.S. 1996. Comparison of abiotic and structurally defined patterns in a hypothetical forest landscape. *Conservation Biology* 10:854-862.

Childs, S.B. and Buchler, E.R. 1982. Misuse of orientation statistics. *Canadian Journal of Zoology* 60:475-477.

Coughlin, D.J., Strickler, J.R. and Sanderson, B. 1992. Swimming and search behaviour in clownfish, *Amphiprion perideraion*, larvae. *Animal Behaviour* 44:427-440.

Crist, T.O. and MacMahon, J.A.. 1991. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. *Insectes Sociaux* 38:379-396.

Crist, T.O. and Wiens, J.A. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos* 69:37-46.

- Crist, T.O., Guertin, D.S., Wiens, J.A. and Milne, B.T.** 1992. Animal movements in heterogeneous landscapes: An experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6:536-544.
- Daughtry, C.S.T. and Hollinger, S.E.** 1984. Cost of measuring leaf area index of corn. *Agronomy Journal* 76:836-841.
- Dicke, M. and Burrough, P.A.** 1988. Using fractal dimensions for characterizing the tortuosity of animal trails. *Physiological Entomology* 13:393-398.
- Dunning, J.B., Danielson, B.J. and Pulliam, H.R.** 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175.
- DuPlantier, J.M., Cassaing, J; Orsini, P. and Croset, H.** 1984. Utilisation de poudres fluorescentes pour l'analyse des déplacements des petits rongeurs dans la nature. *Mammalia* 48:293-298.
- Eckbo, G.** 1975. Qualitative values in the landscape. In Zube, E.H.; Brush, R.O. and Fabos, J.G. (eds.), Landscape Assessment: Values, Perceptions, and Resources. Dowden, Hutchinson and Ross, Inc., Pennsylvania, pp. 31-37.
- Fahrig, L.** 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41:300-314.
- Forman, R.T.T.** 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* 10:133-142.
- Forman, R.T.T. and Godron, M.** 1981. Patches and structural components for a landscape ecology. *BioScience* 31:733-739.
- Forman, R.T.T. and Godron, M.** 1986. Landscape Ecology. John Wiley & Sons, New York.
- Fourcassie, V., Coughlin, D. and Traniello, J.F.A.** 1992. Fractal analysis of search behavior in ants. *Naturwissenschaften* 79:87-89.
- Gagliuso, R. and McComb, W.C.** 1992. Designing landscapes for wildlife and timber. In G. Wood and B. Turner (eds.), Integrating forest information over space and time. Proc. Int. Union For. Res. Org. Conf. ANUTECH Pty. Ltd. Canberra, Australia. Pp. 379-388

- Gardner, R.H., O'Neill, R.V., Turner, M.G. and Dale, V.H.** 1989. Quantifying scale-dependent effects of animal movement with simple percolation models. *Landscape Ecology* 3:87-96.
- Gaustestad, A.O. and Mysterud, I.** 1993. Physical and biological mechanisms in animal movement processes. *Journal of Applied Ecology* 30:523-535.
- Getz, L.L.** 1961. Notes on the local distribution of *Peromyscus leucopus* and *Zapus hudsonius*. *American Midland Naturalist* 65:486-500.
- Getz, L.L.** 1971. Microclimate, vegetation cover, and local distribution of the meadow vole. *The Transactions of the Illinois State Academy of Science* 64:9-21.
- Getz, L.L.** 1989. A 14 year study of *Blarina brevicauda* in East Central Illinois. *Journal of Mammalogy* 70:58-66.
- Golley, F.B.** 1978. Role of small mammals in ecosystems. In Snyder, D.P. (ed.). Populations of Small Mammals Under Natural Conditions. The University of Pittsburgh, Pittsburgh. Pp. 76-78.
- Goodyear, N.C.** 1989. Studying fine-scale habitat use in small mammals. *Journal of Wildlife Management* 53:941-946.
- Gunnarsson, B.** 1992. Fractal dimension of plants and body size distribution in spiders. *Functional Ecology* 6:636-641.
- Halfpenny, J.** 1986. A Field Guide to Mammal Tracking in North America. Johnson Publishing Company, Colorado.
- Halfpenny, J.C.** 1992. Environmental impacts of powdertracking using fluorescent pigments. *Journal of Mammalogy* 73:680-682.
- Hall, E.R.** 1951. American Weasels. University of Kansas Publishing, Museum of Natural History 4:1-466.
- Hansson, L. and Angelstam, P.** 1991. Landscape ecology as a theoretical basis for nature conservation. *Landscape Ecology* 5:191-201.
- Hunter, M.L., Jr.** 1987. Managing forests for spatial heterogeneity to maintain biological diversity. *Trans. North Am. Wildl. and Nat. Resour. Conf.* 52:61-69.
- Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O.** 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7:63-75.

- Kareiva, P.** 1983. Analyzing insect movement as a correlated random walk. *Oecologia (Berl.)* 56:234-238.
- Kareiva, P.** 1986. Patchiness, dispersal, and species interactions: Consequences for communities of herbivorous insects. In Diamond, T. and Case, T.J. (eds.). Community Ecology. Harper and Row Publishers, New York. Pp.192-206.
- Kareiva, P. and Anderson, M.** 1988. Spatial aspects of species interactions: the wedding of models and experiments. In Hastings, A. (ed.). Community Ecology. Springer-Verlag, New York. Pp.38-54.
- Key, G.E. and Woods, R.D.** 1996. Spool-and-line studies on the behavioural ecology of rats (*Rattus* spp.) in the Galapagos Islands. *Canadian Journal of Zoology* 74:733-737.
- Kitching, R.L. and Zalucki, M.P.** 1982. Component analysis and modelling of the movement process: Analysis of simple tracks. *Researches in Population Ecology* 24:224-238.
- Kolars, J.F. and Nystuen, J.D.** 1974. City space - Concepts of scale. Human Geography - Spatial Design in World Society. McGraw-Hill Book Co., New York. Pp.17-34.
- Kolasa, J. and Rollo, C.D.** 1991. Introduction: The heterogeneity of heterogeneity: a glossary. In Kolasa, J. and S.T.A. Picketts (eds.). Ecological Heterogeneity. Springer-Verlag, New York. Pp.1-23.
- Kotliar, N.B. and Wiens, J.A.** 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253-260.
- Kozakiewicz, M. and Szacki, J.** 1995. Movements of small mammals in a landscape: Patch restriction or nomadism. In Lidicker, W.Z., Jr (ed.). Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, Minneapolis. Pp. 157-174.
- Lemen, C.A. and Freeman, P.W.** 1985. Tracking mammals with fluorescent pigments: A new technique. *Journal of Mammalogy* 66:134-136.
- Levin, S.A.** 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Li, H. and Reynolds, J.F.** 1995. On definition and quantification of heterogeneity. *Oikos* 73:280-284.

- Lidicker, W.Z., Jr.** 1995. The landscape concept: Something old, something new. In Lidicker, W.Z., Jr. (ed.). Landscape Approaches in Mammalian Ecology. University of Minnesota Press, Minnesota. Pp. 3-19.
- Mardia, K.V.** 1972. Statistics of Directional Data. Academic Press, London.
- Maurer, B.A.** 1985. Avian community dynamics in desert grasslands: Observational scale and hierarchical structure. *Ecological Monographs* 55:295-312.
- McShea, W.J. and Gilles, A.B.** 1992. A comparison of traps and fluorescent powder to describe foraging for mast by *Peromyscus leucopus*. *Journal of Mammalogy* 73:218-222.
- Meentemeyer, V. and Box, E.O.** 1987. Scale effects in landscape studies. In Turner, M.G. (ed.). Landscape Heterogeneity and Disturbance. Springer-Verlag, New York. Pp. 15-34.
- Mikesic, D.G. and Drickamer, L.C.** 1992. Effects of radiotransmitters and fluorescent powders on activity of wild house mice (*Mus musculus*). *Journal of Mammalogy* 73:663-667.
- Miles, M.A., De Souza, A.A. and Povoia, M.M.** 1981. Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. *Journal of Zoology*, London 195:331-347.
- Milton, R., Melanson, R. and Power, T.** 1995. Geographic Information System Wetlands Data Base Specifications. Nova Scotia Department of Natural Resources, Wildlife Division, Kentville, Nova Scotia.
- Morris, P.** 1972. A review of mammalian age determination methods. *Mammal Review* 2:69-104.
- Mullican, T.R.** 1988. Radiotelemetry and fluorescent pigments: A comparison of techniques. *Journal of Wildlife Management* 52:627-631.
- Nams, V.O.** 1996. The Vfractal: A new estimator for fractal dimension of animal movement paths. *Landscape Ecology* (in press).
- Nassauer, J.I.** 1995. Culture and changing landscape structure. *Landscape Ecology* 10:229-237.
- National Wetlands Working Group.** 1988. Wetlands of Canada. Polyscience Publications, Montreal.

Norton, D.A. and Lord, J.M. 1990. On the use of 'grain size' in ecology. *Functional Ecology* 4:719-720.

Norman, J.M. and Campbell, G.S. 1989. Canopy structure. In Percy, R.W., Ehleringer, H.A., Mooney, H.A. and Rundel, P.W. (eds.). Plant Physiological Ecology: Field Methods and Instrumentation. Chapman and Hall, New York. Pp. 301-325.

Petit, L.J., Petit, D.R. and Martin, T.E. 1995. Landscape-level management of migratory birds: looking past the trees to see the forest. *Wildlife Society Bulletin* 23:420-429.

Pickett, S.T.A. and White, P.S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando.

Pruitt, W.O., Jr. 1953. An analysis of some physical factors affecting the local distribution of the short-tailed shrew (*Blarina brevicauda*) in the northern part of the lower peninsula of Michigan. Miscellaneous Publication No. 77, University of Michigan.

Quimby, D.C. 1951. The life history and ecology of the jumping mouse, *Zapus hudsonius*. *Ecological Monographs* 21:61-95.

Risser, P.G. 1987. Landscape ecology: State of the art. In Turner, M.G. (ed.). Landscape Heterogeneity and Disturbance. Springer-Verlag, New York. Pp.3-14.

Risser, P.G. 1990. Landscape pattern and its effects on energy and nutrient distribution. In Zonneveld, I.S. and Forman, R.T.T. (eds.). Changing Landscapes: An Ecological Perspective. Springer-Verlag, New York. Pp.45-56.

Rowe, J.S. 1988. Landscape ecology: The study of terrain ecosystems. In Moss, M.R. (ed.), Landscape Ecology and Management. Polyscience Publications Inc., Montreal. Pp.35-42.

Sauer, C.O. 1967. The morphology of landscape. In Leighly, J. (ed.). Land and Life - A Selection from Writings of Carl Orwin Sauer. University of California Press, California. Pp. 315-350.

Smith, J.N.M. 1974. The food searching behaviour of two european thrushes I. Description and analysis of search paths. *Behaviour* 48:276-302.

Stapp, P., Young, J.K., VandeWoude, S. and Van Horne, B. 1994. An evaluation of the pathological effects of fluorescent powder on deer mice (*Peromyscus maniculatus*). *Journal of Mammalogy* 75:704-709.

- Szacki, J. and Liro, A.** 1991. Movements of small mammals in the heterogeneous landscape. *Landscape Ecology* 5:219-224.
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G.** 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.
- Teferi, T. and Herman, T.B.** 1995. Epigeal movement by *Sorex cinereus* on Bon Portage Island, Nova Scotia. *Journal of Mammalogy* 76:137-140.
- Tourtellot, M.K., Collins, R.D. and Bell, W.J.** 1991. The problem of movelength and turn definition in analysis of orientation data. *Journal of Theoretical Biology* 150:287-297.
- Turchin, P., Odendaal, F.J. and Rausher, M.D.** 1991. Quantifying insect movement in the field. *Environmental Entomology* 20:955-963.
- Turchin, P.** 1996. Fractal analyses of animal movement: A critique. *Ecology* 77:2086-2090.
- Turner, M.G.** 1989. Landscape Ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.
- Turner, M.G. and Gardner, R.H.** 1991. Quantitative methods in landscape ecology: An introduction. In Turner, M.G. and R.H. Gardner (eds.). Quantitative Methods in Landscape Ecology. Springer-Verlag, New York. Pp.3-14.
- Turner, M.G., Dale, V.H. and Gardner, R.H.** 1989. Predicting across scales: Theory development and testing. *Landscape Ecology* 3:245-252.
- Urban, D.L., O'Neill, R.V. and Shugart, H.H., Jr.** 1987. Landscape ecology. *BioScience* 37:119-127.
- Webster, A.B. and Brooks, R.J.** 1981. Daily movements and short activity periods of free-ranging meadow voles, *Microtus pennsylvanicus*. *Oikos* 37:80-87.
- Weiss, S.B. and Murphy, D.D.** 1988. Fractal geometry and caterpillar dispersal: or how many inches can inchworms inch? *Functional Ecology* 2:116-118.
- Wiens, J.A.** 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81-120.
- Wiens, J.A.** 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

- Wiens, J.A.** 1992. What is landscape ecology, really? *Landscape Ecology* 7:149-150.
- Wiens, J.A., Rotenberry, J.T. and Van Horne, B.** 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. *Oikos* 48:132-147.
- Wiens, J.A. and Milne, B.T.** 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* 3:87-96.
- Wiens, J.A., Crist, T.O. and Milne, B.T.** 1993. On quantifying insect movement. *Environmental Entomology* 22:709-715.
- Wiens, J.A., Stenseth, N.C., Van Horne, B. and Ims, R.A.** 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369-380.
- Wiens, J.A., Crist, T.O., With, K.A. and Milne, B.T.** 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology* 76:663-666.
- Wiens, J.A.** 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In Pickett, S.T.A. and P.S. White (eds.). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando Pp.169-193.
- Wiens, J.A.** 1990. On the use of 'grain' and 'grain size' in ecology. *Functional Ecology* 4:720.
- With, K.A.** 1994a. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9:25-36.
- With, K.A.** 1994b. Ontogenetic shifts in how grasshoppers interact with landscape structure: An analysis of movement patterns. *Functional Ecology* 8:477-485.
- Yeomans, S.R.** 1995. Water-finding in adult turtles: Random search or oriented behaviour? *Animal Behaviour* 49:977-987.
- Zalucki, M.P. and Kitching, R.I.** 1982. The analysis and description of movement in adult *Danaus plexippus* L. (Lepidoptera: Danainae). *Animal Behaviour* 80:174-198.
- Zonneveld, I.S.** 1988. Landscape ecology and its application. In Moss, M.R. (ed.). Landscape Ecology and Management. Polyscience Publications Inc., Montreal. Pp. 3-15.
- Zonneveld, I.S.** 1989. The land unit - A fundamental concept in landscape ecology, and its applications. *Landscape Ecology* 3:67-86.

PERSONAL COMMUNICATIONS:

Bondrup-Nielsen, S. Department of Biology, Acadia University, Wolfville, N.S.

Farrell, P. Department of Mathematics, Acadia University, Wolfville, N.S.

Milton, R. Department of Natural Resources, Kentville, N.S.

Nams, V.O. Department of Biology, Nova Scotia Agricultural College, Truro, N.S.

Power, T. Department of Natural Resources, Kentville, N.S.

APPENDIX 1:

Results of Kruskal-Wallis One Way Anova on Ranks and
Mann Whitney U Tests for Trail Comparisons Among Species.

Mean Move Length:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc	yes	<0.05		
Hs vs. Mp	yes	<0.05		
Hs vs. Bb	yes	<0.05		
Hs vs. Zh	no	>0.05		
Hs vs. Me	Do Not Test		yes	0.0095
Hs vs. Pl	Do Not Test		yes	0.0238
Pl vs. Sc	yes	<0.05		
Pl vs. Mp	no	>0.05		
Pl vs. Bb	Do Not Test		no	0.1470
Pl vs. Zh	Do Not Test		no	0.2090
Pl. vs.Me	Do Not Test		no	0.8570
Me vs. Sc	yes	<0.05		
Me vs. Mp	Do Not Test		yes	0.0472
Me vs. Bb	Do Not Test		no	0.2500
Me vs. Zh	Do Not Test		no	0.5800
Zh vs. Sc	yes	<0.05		
Zh vs. Mp	Do Not Test		no	0.0700
Zh vs. Bb	Do Not Test		no	0.3540
Bb vs. Sc	yes	<0.05		
Bb vs. Mp	Do Not Test		no	0.1480
Mp vs. Sc	no	>0.05		

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

SLD/TD Index:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc	Do Not Test		no	0.0593
Hs vs. Mp	Do Not Test		yes	0.0022
Hs vs. Bb	Do Not Test		yes	0.0023
Hs vs. Zh	Do Not Test		yes	0.0018
Hs vs. Me	Do Not Test		yes	0.0190
Hs vs. Pl	no	>0.05	no	0.0952
Pl vs. Sc	Do Not Test		no	0.6303
Pl vs. Mp	Do Not Test		no	0.6996
Pl vs. Bb	Do Not Test		no	1.0000
Pl vs. Zh	Do Not Test		no	1.0000
Pl vs. Me	Do Not Test		no	0.8571
Me vs. Sc	Do Not Test		no	0.6828
Me vs. Mp	Do Not Test		no	0.7400
Me vs. Bb	Do Not Test		no	0.9820
Me vs. Zh	Do Not Test		no	0.9640
Zh vs. Sc	Do Not Test		no	0.1900
Zh vs. Mp	Do Not Test		no	0.6603
Zh vs. Bb	Do Not Test		no	0.8074
Bb vs. Sc	Do Not Test		no	0.2062
Bb vs. Mp	Do Not Test		no	0.4626
Mp vs. Sc	Do Not Test		no	0.3974

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

Fractal Dimension:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc	Do Not Test		yes	0.0023
Hs vs. Mp	Do Not Test		yes	0.0025
Hs vs. Bb	Do Not Test		yes	0.0014
Hs vs. Zh	Do Not Test		yes	0.0017
Hs vs. Me	Do Not Test		yes	0.0190
Hs vs. Pl	Do Not Test		yes	0.0476
Pl vs. Sc	Do Not Test		no	1.0000
Pl vs. Mp	Do Not Test		no	0.9629
Pl vs. Bb	Do Not Test		no	0.6812
Pl vs. Zh	Do Not Test		no	0.8668
Pl. vs.Me	Do Not Test		no	0.8571
Me vs. Sc	Do Not Test		no	0.9273
Me vs. Mp	Do Not Test		no	0.5631
Me vs. Bb	Do Not Test		no	0.9691
Me vs. Zh	Do Not Test		no	0.6033
Zh vs. Sc	Do Not Test		no	0.7893
Zh vs. Mp	Do Not Test		no	0.9929
Zh vs. Bb	Do Not Test		no	0.7623
Bb vs. Sc	Do Not Test		no	0.9779
Bb vs. Mp	Do Not Test		no	0.4562
Mp vs. Sc	Do Not Test		no	0.9767

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

Turning Rate:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc	yes	<0.05		
Hs vs. Mp	yes	<0.05		
Hs vs. Bb	Do Not Test		yes	<0.0001
Hs vs. Zh	Do Not Test		yes	0.0015
Hs vs. Me	no	>0.05		
Hs vs. Pl	Do Not Test		yes	0.0238
Pl vs. Sc	no	>0.05		
Pl vs. Mp	Do Not Test		no	0.0926
Pl vs. Bb	Do Not Test		no	0.3864
Pl vs. Zh	Do Not Test		no	0.5136
Pl. vs.Me	Do Not Test		no	0.6286
Me vs. Sc	Do Not Test		yes	0.0283
Me vs. Mp	Do Not Test		no	0.4773
Me vs. Bb	Do Not Test		no	0.8713
Me vs. Zh	Do Not Test		no	0.9661
Zh vs. Sc	Do Not Test		yes	0.0042
Zh vs. Mp	Do Not Test		no	0.1391
Zh vs. Bb	Do Not Test		no	0.9476
Bb vs. Sc	Do Not Test		yes	0.0015
Bb vs. Mp	Do Not Test		yes	0.0196
Mp vs. Sc	Do Not Test		yes	0.0032

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

Mean Move Length Orientation:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc			no	0.2824
Hs vs. Mp			no	0.9932
Hs vs. Bb			no	0.8153
Hs vs. Zh			no	0.5709
Hs vs. Me			yes	0.0190
Hs vs. Pl			no	0.3810
Pl vs. Sc			no	0.1939
Pl vs. Mp			no	0.3231
Pl vs. Bb			no	0.5800
Pl vs. Zh			no	0.1450
Pl. vs.Me	not significantly		no	0.1143
Me vs. Sc	different between		no	0.9333
Me vs. Mp	species	0.2312	no	0.1278
Me vs. Bb			no	0.1095
Me vs. Zh			no	0.1363
Zh vs. Sc			no	0.1410
Zh vs. Mp			no	0.5540
Zh vs. Bb			no	0.4038
Bb vs. Sc			no	0.0702
Bb vs. Mp			no	0.5407
Mp vs. Sc			no	0.0663

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

Mean Turning Angle:

	Kruskal-Wallis		Mann-Whitney	
	yes / no	prob.	yes / no	prob.
Hs vs. Sc			no	0.2824
Hs vs. Mp			no	0.3410
Hs vs. Bb			no	0.2032
Hs vs. Zh			no	0.2433
Hs vs. Me			no	0.6095
Hs vs. Pl			no	0.9048
Pl vs. Sc	not significantly		no	0.9212
Pl vs. Mp	different between	0.7987	no	0.7481
Pl vs. Bb	species		no	0.5883
Pl vs. Zh			no	0.6511
Pl. vs.Me			no	1.0000
Me vs. Sc			no	0.6828
Me vs. Mp			no	0.7098
Me vs. Bb			no	0.3667
Me vs. Zh			no	0.4187
Zh vs. Sc			no	0.7599
Zh vs. Mp			no	0.3510
Zh vs. Bb			no	0.8880
Bb vs. Sc			no	0.7669
Bb vs. Mp			no	0.4087
Mp vs. Sc			no	0.8199

Legend: Bb (*Blarina brevicauda*), Zh (*Zapus hudsonius*), Mp (*Microtus pennsylvanicus*), Sc (*Sorex cinereus*), Me (*Mustela erminea*), Pl (*Peromyscus leucopus*)

APPENDIX 2

**Assumptions Associated With LAI and the Derivation of
Radiation Transfer Model**

LEAF AREA INDEX

Assumptions:

LAI calculations are based on four assumptions about the measured canopy:

1. The foliage is black. It is assumed that the below canopy readings do not include radiation that has been reflected or transmitted by foliage.
2. The foliage elements are small compared to the area of view of each ring.
3. The foliage is randomly distributed within certain foliage-containing elements. These envelopes might be parallel tubes (a row crop), a single ellipsoid (an isolated bush), an infinite box (turf grass), or a finite box with holes (deciduous forest with gaps).
4. Foliage is azimuthally randomly oriented. That is, it does not matter how the foliage is inclined, but the leaves should be facing all compass directions.

No real canopy conforms exactly to these assumptions. Foliage is never random, but is clumped along stems and branches, and is not "black". Many species exhibit some degree of heliotropism, which violates the azimuthal randomness assumption. However, many canopies can be considered random, and living foliage does have low transmittance and reflectance below 490 nm.

Studies have revealed that the model works well even if the assumptions are not exactly met if the proper measurement techniques are used (Daughtry and Hollinger 1984).

LAI calculations:

The optical sensor of the LAI-2000 consists of a fisheye lens and an optical system. The fisheye lens “sees” a hemispherical image, which the optical system focuses onto a photodiode detector made up of five concentric rings. Each detector ring views a different portion of the canopy or sky centered on one of the 5 view angles. The fraction of the diffuse incident radiation that passes through a plant canopy, for each of the view angles can be expressed as

$$\frac{\text{Diffuse intensity below the canopy at view angle } \emptyset}{\text{Diffuse intensity below the canopy at view angle } \emptyset} = T(\emptyset)$$

$T(\emptyset)$ is the probability of diffuse non-interceptance for a given view angle (ring) called the gap fraction; it is analogous to transmittance. $T(\emptyset)$ depends on the foliage orientation, foliage density and pathlength through the canopy in the same way that light transmittance through a solution depends upon extinction coefficient, absorber concentration and pathlength, i.e. according to the Beer-Lambert Law.

$$T(\emptyset) = \exp(-G(\emptyset) \mu S(\emptyset)) \text{ or,}$$

$$-\ln T(\emptyset) = G(\emptyset) \mu S(\emptyset) \quad (\text{equation 1})$$

where $G(\emptyset)$ is the fraction of the foliage projected toward angle \emptyset , μ is the foliage density (m^2 foliage per m canopy; analogous to concentration) and $S(\emptyset)$ is the pathlength through the canopy for each view angle, \emptyset . Miller gives an exact solution for foliage density, μ :

$$\mu = -2 \int \frac{\ln(T(\theta))}{S(\theta)} \sin \theta d\theta \quad (\text{equation 2})$$

The ratio $\ln(T(\theta))/S(\theta)$ is called the contact number (m^{-1}). Equation 2 can be applied to any general canopy shape (rows, isolated plants, etc.) as long as $S(\theta)$ is known. For full cover canopy of height z , $S(\theta)=z/\cos\theta$ and $\text{LAI}=\mu \cdot z$, so equation 2 may be rewritten

$$\text{LAI} = -2 \int \ln(T(\theta)) \cos \theta \sin \theta d\theta \quad (\text{equation 3})$$

The LAI-2000 implements this equation by numerical integration using the 5 measured angles. The detector geometry fixes the value of $\sin \theta d\theta$ for each ring allowing computation of a constant weighing factor $w(\theta_i)$ for each ring. The numerical integration then becomes

$$\text{LAI} = -2 \sum \ln(T(\theta_i)) \cos \theta_i w(\theta_i) \quad (\text{equation 4})$$

where the subscript i refers to each of the detector rings with view angle centered at θ_i

