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**Predicting the Survival of Woodland Species
in Human-altered Landscapes**

by

Kringen M. Henein BA., BSc.

A Thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

Doctor of Philosophy

Department of Biology
Ottawa-Carleton Institute of Biology
Carleton University
Ottawa, Ontario
June 23, 1995

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in human-altered landscapes"

submitted by

KRINGEN MARGARET HENEIN, B.A., B.Sc.

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

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Thesis Supervisor
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External Examiner

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We shall not cease from exploration

And the end of all our exploring

Will be to arrive where we started

And know the place for the first time.

T.S. Eliot,

"Little Glidding"

ABSTRACT

Rapid, large-scale anthropogenic landscape change increasingly challenges native species. The identification of factors affecting species persistence is needed to direct planning and land management.

I designed an individual-based simulation model to examine the relationship among 3 landscape elements (composition, configuration, connectivity) and the persistence of 2 woodland small mammals whose responses to habitat change lie towards opposite ends of a gradient.

I obtained habitat use and demographic and movement parameters for the less adaptable eastern chipmunk (*Tamias striatus*) from trapping and radio-telemetry studies in farmland near Ottawa. Chipmunks used woods and canopied fencerows, but not fields. Fencerow use was higher in summer than fall. Residents favoured woods. Daily movements of 400 m occurred in all sex/age groups. Linear ranges exceeded previous reports.

Model parameters for the more opportunistic white-footed mouse (*Peromyscus leucopus*) came from existing data from the same region. Mice also moved greater distances in farmland, but used corn and grain fields as well as wooded areas.

The simulations followed chipmunk and mouse populations over 25 years in landscapes with unique combinations of amount of woodland (10%, 30%, 50%), number of patches (2, 4, 8), and level of connectivity (high, intermediate, low, none).

Connectivity was the best predictor of population persistence for chipmunks. Long survival times and low extinction rates occurred in model landscapes with high and intermediate quality connectivity and with 30% or more woodland. Chipmunk populations in unconnected landscapes and in 8 patch landscapes with only 10% woodland and low connectivity suffered high extinction rates. Highly variable populations were at greater risk of extinction, especially when woodland habitat was low. For behaviourally inflexible species, maintenance of landscape connectivity when habitat loss and fragmentation occur is vital to survival.

Survival rates for mice were high in all landscape patterns. Since mice were not restricted to woods and fencerows, all landscapes were highly connected for them and provided over 78% usable habitat. For opportunistic species able to use novel resources, landscape change may not be limiting.

The response of species to human-altered landscapes is an essential factor in predicting population persistence.

ACKNOWLEDGMENTS

*No man is an island, entire of itself;
every man is a piece of the continent,
a part of the main. (John Donne)*

Many people generously assisted me with this project; without their help it could not have been completed. I would like to express my gratitude to all.

First, I wish to thank my supervisor, Gray Merriam, for his inspiration, his guidance, his patience, and above all his vision of landscape that provides the context for this study. I am grateful to my thesis advisors, Hans Damman and Scott Findlay, for their perceptive comments. Andrew Bennett took me under his wing in the field and showed me how to handle small mammals and organize a trapping program. His assistance and advice during the summer of 1989 was indispensable. Michael Smith taught me the intricacies of a GIS. John Wegner provided help with all aspects of the process from field work in electrical storms to literature searches in the library. He generously supplied me with data from his *Peromyscus leucopus* studies for my model, educated me in matters ecological and philosophical, and was always a source of wisdom and stability.

Several other people helped with the field work: thanks go to Chris Drummond, Dave Omond, Alfredo Rios, Kari Stuart-Smith, and Russell Walton for their cheerful assistance and good company. Members of Gray Merriam's lab provided emotional support and intellectual stimulation. I value their friendship and their encouragement. To Ron Fritz, Brett Goodwin, Karen Hawley, Andy McAllister, John Pedlar, Shealagh Pope, Phil Taylor, Etsuko Tsuchiya, Kurtis Trzcinski, Marc-Andre Villard, and Andrew Young : thanks for the memories. I would also like to thank Lenore Fahrig for her helpful suggestions and statistical advice, and all the members of her lab for their contribution to the enjoyable working atmosphere.

Five landowners kindly allowed me to set out livetraps and track chipmunks on their property. I wish to thank Murray Davidson, Donny Lowe, Gray and Aileen Merriam, Michael Merriam, and Lawrence Payne of Manotick, Ontario for the privilege of sharing their landscape for three summers.

My work was supported financially with grants from NSERC, a Tri-Council Secretariat Eco-scholarship, and graduate scholarships from Carleton University. I am grateful for this assistance.

I wish especially to recognise my family for their unfailing support and encouragement throughout the peaks and valleys of the project. To my husband, Jean-Claude, and my sons Colin and Patrick, a thousand thank-yous. You are a part of this product.

And finally, I am indebted to the many small mammals that entered the livetraps and wore the radio collars. Without their participation this work would not have been possible, so I dedicate the thesis to them and to their descendants. Long may they prosper.

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Chapter 1

General Introduction

*The major problems in the world are the result of the differences
between the way nature works and the way man thinks.*

Gregory Bateson

Human activity is restructuring landscapes at an unprecedented rate and spatial scale. Many past studies have shown how species function in areas of predominately natural habitat (Burt, 1940, Blair 1942, Harland et al. 1979), or are affected by natural disturbance (Heinselman 1973, Pickett and White 1985), but there is an increasingly urgent need to determine how species respond to fragmented human-altered environments. Predicting long-term survival of populations in mosaics requires an understanding of how the behaviours of resident organisms interact with the composition and configuration of the landscape. The ability to generate these predictions is vital to making informed decisions about current and proposed land use and to moderating our impact on the organisms with which we share the landscape.

Two hundred years ago most of the land in southeastern Ontario was forested (Guillet 1933, Scott 1979, White 1985). Today the majority of these forests have been cleared and most of the land outside urban areas has been put to agricultural use. Nevertheless, fragments of wooded land persist as woodlots, fencerows, and riparian strips along natural drainage features. These areas support a sometimes diverse flora (Middleton and Merriam 1983, Fritz and Merriam 1993, Bennett et al. 1994), and populations of native small mammals, birds, and arthropods (Wegner and Merriam 1979, Middleton and Merriam 1983, Yahner 1983, Henderson et al. 1985, Shalaway 1985, Burel 1991). How do native species respond to this drastically altered, heterogeneous landscape? Does the effect of the landscape pattern and structure on a population differ for species with different responses? Can the responses themselves be used as predictors of success in such landscapes? What are the important elements of landscape structure that affect population persistence? These questions are the focus of this thesis. I address them with an individual-based simulation model using parameters derived from empirical studies of two small mammals, *Tamias striatus* and *Peromyscus leucopus*, in a farmland mosaic.

Spatial and temporal heterogeneity:

Even in relatively pristine areas, forests are not homogeneous (Dwyer and Merriam 1981, Middleton and Merriam 1983, Mladenoff et al. 1993). It is likely that most species perceive their environment as a mosaic of patches, some with useful resources, some marginal, and some hostile (Addicott et al. 1987, Kolasa and Pickett 1991). The scale at which these patches are defined depends on the species' perspective rather than ours (Kotliar and Wiens 1990, With 1994), so the impact of change on the spatial components of an organism's habitat may not be immediately obvious to the human observer.

Conditions are rarely homogeneous on temporal scales either. In the short term, seasons cycle; on a longer time base, natural disturbances such as fire and insect outbreaks reset ecosystems; at a very large scale, climate changes can alter entire biomes (Holling 1986). However many species have persisted despite these challenges by developing strategies for dealing with uncertainty and variability (Southwood 1977, 1988, Hansson 1979), and most organisms occur in a narrower range of their environment than they are capable of tolerating (Haila and Levins, 1992).

Landscape changes then and now:

The important difference between the challenge of natural environmental variability and the effects of changes caused by recent human activity is related to the period of adjustment permitted the organisms. Changes to landscapes once occurred slowly over evolutionary time, allowing species to adapt gradually to the degree of uncertainty normal to their habitat through

natural selection (Southwood 1977, 1988, Greenslade 1982). Strategies were developed and perfected over millennia. Consider owls. The snowy owl (*Nyctea scandiaca*) of the tundra copes with boom and bust cycles in its main food supply, the lemming, by leaving its range in times of hardship (Batzli et al. 1980). These birds have been sighted as far south as North Carolina in low lemming years (Gross 1947). Other northern owls remain in their usual territories but switch to alternate prey and fail to breed in years of low vole levels (Korpimaki 1986). Where the risk of uncertainty has been low however, some species have become closely tuned to specific habitats and resource bases. An example is the spotted owl (*Strix occidentalis caurina*) of the American north-west. This bird requires three to seven square kilometres of 250-year-old coniferous forest for survival. Since fires are extremely rare in these forests, rapid change was not an historical problem for this species (Forsman et al. 1984, Lande 1988, Haila and Levins 1992).

Changes to landscapes now occur rapidly in areas where changes may be non-traditional, requiring an immediate behavioural change. For some species that have already developed flexibility through a history of coping with uncertainty, adjustment is feasible. Laurance (1991) found that edge-tolerant species were more adaptable and had higher rates of population success than interior species in anthropogenically disturbed areas. However, for some interior species like the spotted owl or, locally in eastern Ontario, the scarlet tanager (Villard 1991, Villard et al. 1992), reduction of traditional habitat from human activities such as logging or development will reduce the probability of population survival.

Resource changes:

Landscape changes alter the resource base of populations. This may be manifest as loss of all or part of an organism's traditional habitat, introduction of novel resources that may or may not be exploitable, and restructuring of the distribution of resources. Although the heterogeneity of the original habitat may be reduced due to loss of area (Wilcove et al. 1986, Karr 1990), the overall result is usually increased patchiness, since the matrix in which the habitat patches are embedded adds new elements to the landscape (Mladenoff et al. 1993). Three factors contribute to the success or failure of a species under these new conditions: 1) the composition of the landscape (i.e. the amount and type of resource patch; 2) the configuration of the landscape (i.e. the pattern, size, and number of these patches; and 3) the ability of the species to access enough resource patches to complete its life cycle and successfully reproduce (Dunning et al. 1992, Li and Reynolds 1993, Taylor et al. 1993). The latter depends on the behaviour of the organism as well as to the landscape pattern (Merriam 1984, Taylor et al. 1993).

Population response:

An organism faced with a patchy environment must knit together enough resource patches to satisfy its needs (Addicott et al. 1987). As proposed by Dunning et al. (1992), this can be done by obtaining a specific resource in more than one patch of the same type (supplementation), or by obtaining different resources from a number of different patch types to satisfy the same need (complementation). Two behavioural elements are important here: the ability of the individual to move between the patches, and the degree to which it may adapt to use novel

resources. These will determine whether or not the organism's operational resource base is diminished.

An organism can move between resource patches if the matrix between the patches is permeable to it (i.e. if there are routes deemed usable by the organism), and if the distant patches are within its range. This interaction between landscape and organism has been termed connectivity by Merriam (1984), and in this sense it is a measure of the probability of an organism moving successfully within a particular landscape. Taylor et al. (1993) have stressed the importance of connectivity as an additional element of landscape structure along with composition and configuration (Dunning et al. 1992, Li and Reynolds 1993).

Danielson (1992) suggests that organisms faced with large tracts of unusable and sub-optimal habitat in a landscape may have difficulty encountering remaining areas of good quality habitat, settling instead in more accessible sink areas (defined by Pulliam (1988) as habitat where mortality exceeds reproductive success). Such a landscape exhibits low connectivity, and its potential productivity will not equal the sum of its parts.

The response of organisms to the presence of novel resources affects the degree to which changes in the connectivity, composition, and configuration of the new landscape affect the success of the population. For example, a woodland organism able to profit from the resource patches replacing the forest may not suffer any overall loss of habitat. Population response to changes in landscape resources may be of two types: numerical or functional (Holling 1959). The numerical response is detectable at the population level (i.e. it involves changes in the number of individuals within a population). When a species retains its traditional use of the

landscape in the face of fragmentation and habitat loss, population size is usually diminished by higher mortality or decreased fecundity, leading to increased risk of extinction. The functional response is a reaction of individual members of a population and includes resource switching, supplementation, and changes to movement patterns. Such a response may not be detectable in terms of population size, and species responding in this way may continue to thrive in the altered landscape.

Scale:

Choice of scale is vital to understanding population dynamics and predicting population success. The study area must include flows of individuals and resources important to the whole population. That is, it must be large enough to contain the resource areas used by individuals for important activities such as foraging, searching for mates, raising litters, and exploration. These areas, which may expand and contract temporally, are termed ecological neighbourhoods by Addicott et al. (1987). An organism's range is therefore dynamic and is a composite of its ecological neighbourhoods. Individuals whose neighbourhoods overlap with or are easily accessible to those of other individuals form sub-populations (breeding groups) within patches or groups of patches in the mosaic. Where landscape connectivity permits, these sub-populations occasionally exchange individuals. In this way, local extinction in one sub-population may be 'rescued' (Brown and Kodric-Brown 1977) by individuals from another (Middleton and Merriam 1981) and gene flow sufficient to preserve genetic diversity is maintained (Slatkin 1985, Merriam et al. 1989, McCauley 1995). At the landscape scale (Forman and Godron 1986, Turner 1989) the effective demographic unit, or population, is made up of these interacting sub-populations.

Inter-connected but demographically isolated patches subject to non-synchronous extinctions and recolonizations were first described by Andrewartha and Birch (1954). Such an arrangement was shown by den Boer (1968) to spread the risk of extinction in space. The term metapopulation was coined by Levins (1970) for a theoretical set of patches undergoing extinction and colonization. In his model, and in its successors (Roff 1974, Hanski 1985, Goodman 1987, Lande 1987, Wissel and Stocker 1991), all patches are assumed to be equal in size, quality, and accessibility, and the probability of extinction and recolonization at any patch is the same. A general result of these models is that increasing the number of local populations reduces overall extinction probability. However, departures from the model's theoretical assumptions give different results. Lefkovich and Fahrig (1985) varied the pattern of connectivity and found the geometry of the metapopulation to be important. The most stable arrangements were those forming more complex geometric figures. Henein and Merriam (1990) varied the quality of connectivity among patches and found that addition of a patch connected to other patches with low quality connections reduced the viability of the overall population. Verboom et al. (1991) varied patch size and quality, and showed that patch extinction rate increased as these variables diminished, while patch recolonization rate was positively related to the density of other nearby subpopulations. Urban and Shugart (1986) modelled demographics of birds in a habitat mosaic where patches were of varying size and accessibility. They varied natality rate and isolation effect. Their results suggest that to understand population dynamics in a habitat mosaic, three levels of complexity must be considered: at the landscape level, the landscape pattern constrains interactions at lower levels; at the patch level, patch population dynamics affect the success of the overall population as well as influencing individual demography; at the individual level, demographic behaviour ultimately drives the system. This integrated approach owes its origins to hierarchy theory (Allen and Starr 1982). Results of these studies suggest that predicting the

fate of populations requires consideration of spatial pattern, quality of landscape elements, the interaction of sub-populations, and local demographics.

Difficulties arise when an organism's relationship to the landscape is studied at the wrong scale. For example, animals in habitat mosaics where most patches are less than the size of a home range are not usually dispersing when they move between patches, so it is inappropriate to measure dispersal in terms of these movements (La Polla and Barrett 1993). How can we tell if the scale is appropriate? Important processes and interactions for target species in landscapes must be assessed prior to carrying out a spatial and temporal study, and this knowledge rather than anthropogenic perceptions of landscapes should guide the design (Addicott et al. 1987). In their paper on disturbance and scale of observation, Pickett et al. (1989) propose a hierarchical approach to levels of interaction. When a population in a patchy landscape is studied at the correct scale, the overall variation in the number present in the study area between comparable time periods will be relatively small, since the noise of individuals moving from patch to patch for resources (Dunning et al. 1992), and of winking sub-populations (Wilson 1975) will be screened out.

Study objective:

My objective is to analyse the effects of differences in landscape composition, configuration and connectivity on the population survival of a pair of small mammal species occupying different positions on a gradient of behavioural flexibility, and to develop some predictive ability for species with similar responses.

Study organisms:

I have chosen to look at the response of two woodland (Iverson et al. 1967) small mammals to the replacement of native forest by low intensity agriculture. I chose these species to represent two different reactions to fragmentation: an opportunistic response and a behaviourally inflexible response. The white-footed mouse, *Peromyscus leucopus*, has been found to use not only traditional wooded areas as habitat in the Ottawa area, but also certain types of crop fields. These animals readily move through, forage in, and nest in corn and small grain fields as well as wooded areas, and can even overwinter in the ploughed cornfields (Wegner and Merriam 1990, Merriam and Wegner 1992). They now fall toward the generalist end of the behavioural response gradient for use of space and novel resources. Studies by Henderson et al. (1985) and Wegner (unpub.) suggest that the eastern chipmunk, *Tamias striatus*, retains its traditional preference for woodland habitat in similar agricultural landscapes in the region. They found these animals in woodlots and fencerows, but not in crop fields. The chipmunk falls at the specialist end of the behavioural response gradient. These dissimilar responses to novel landscape patches suggest there will be differences in the success of the populations of these two representative species in agricultural landscapes.

Organization of the study:

There are two major components to this dissertation, a field component that was undertaken to measure parameters for a simulation model, and a theoretical component consisting of two versions of an individual-based, stochastic simulation model.

I conducted the field study to collect empirical data on the temporal and spatial use of landscape elements by chipmunks and on the scale of their movement in the farm mosaic. This information was required to supplement the literature, as only a few studies have been done on the species in an agricultural setting (Asher and Thomas 1985, Henderson et al. 1985). Results from the field component and some additional information from previous demographic studies were used to set realistic parameters for the model.

The first version of the model was designed to predict the success of a chipmunk population inhabiting a landscape with different sets of composition, configuration and connectivity over a period of twenty-five years. I varied the number of habitat patches, proportion of the landscape as habitat, and level of connectivity, and measured extinction rate and mean population survival. A second version of the model predicts success for white-footed mice in the same landscape. I modified the demographics and parameters of landscape use based on John Wegner's farmland study from the same region (Wegner and Merriam 1990, Wegner, unpub.) and the mouse literature. Simulations run for mice were compared to those for chipmunks in similar landscapes.

These sub-studies are presented and discussed in separate chapters that follow.

Chapter 2

The Field Study

*But ask now the beasts and they shall teach thee;
and the fowls of the air, and they shall teach thee;
or speak to the earth and it shall teach thee.*

Job 12: 7-8

INTRODUCTION

I studied chipmunks in 200 ha of farmland in Manotick, Ontario between May and October from spring 1989 to autumn 1991 to estimate parameter values for habitat use and movement patterns. I used capture-recapture methods and radio telemetry to monitor habitat selection, and I also quantified fencerow attributes to address the following questions about the population in the agricultural landscape:

Habitat:

- 1) What constitutes a high quality landscape element for chipmunks in the agricultural mosaic?
- 2) Are there differences in the use of woods and fencerows by residency status, sex and age?
- 3) What landscape elements are used as natal habitat and for overwintering?
- 4) Are there seasonal differences in landscape use?

Movement:

- 1) How large is a chipmunk's range?
- 2) What distances are moved on a daily basis?
- 3) Are there age or sex related differences in daily movement and range?
- 4) How often do individuals move between patches?
- 5) Do chipmunks tolerate conspecifics in fencerows?

Demographics:

- 1) What population sizes are achieved seasonally at the landscape level?
- 2) What proportion of animals are:
  - transients versus residents?
  - young versus adult?
  - male versus female?
- 3) What is the overwinter survival rate?
- 4) What is the pregnancy rate?

Henderson et al. (1985) found that chipmunks inhabiting woodlots in an agricultural mosaic moved along fencerows to recolonize local extinctions. However, detailed movement frequencies and distances, as well as structural attributes of suitable fencerows were not available. To build the model, I needed to learn more about how chipmunks use the farm landscape: the scale at which they operate, the landscape features they use or avoid, the temporal variations in their behaviour, the effects of age and sex differences, and the size and variance of their populations. Chipmunks have been the focus of many studies in wooded habitat (Allen 1938, Burt 1940, Blair 1942, Yerger 1953, Forsyth and Smith 1973, Pidduck and Falls 1973, Tryon and Snyder 1973, Roberts 1976, Elliott 1978, Yahner 1978a, 1978b, Getty 1981a, 1981b, Mares et al 1982, Lacki et al. 1984, White and Svendsen 1990, 1992, Kramer and Weary 1991), but their behaviour in agricultural mosaics has not been well documented despite their persistence in this type of landscape for at least 200 years.

Eastern chipmunks are diurnal, semi-fossorial small mammals, of the family Sciuridae, that traditionally have inhabited the forests of eastern North America (Snyder 1982). In the Ottawa area they are active between March and November (Smith and Smith 1972), and spend the winter in underground burrows where stockpiles of seeds, nuts, and acorns sustain them between periods of torpor (Yerger 1955, Snyder 1982). They are solitary animals; males and females maintain separate burrows (Yahner 1978b). Most breed once in early spring, although some animals may instead breed in summer, and rarely, a chipmunk may breed twice in the same year, once in spring and again in summer (Yerger 1955, Smith and Smith 1972). The spring breeding period is about 4 weeks, from early March to mid-April in the Ottawa area, and the summer breeding occurs between mid-June and late July (Smith and Smith 1972). Svendsen and Yahner (1979) found that 90% of the females in their study produced a litter. Gestation is 31 days (Burt 1940). Young are born in the female's burrow and remain below ground for 5 to 7 weeks (Smith and Smith 1972, Pidduck and Falls 1973).

Litter sizes may range from 1 to 9 (Yerger 1955, Smith and Smith 1972, Roberts 1976) and conform to a truncated normal distribution with a mean of between 4 and 5 (Snyder 1982). In our area, Smith and Smith (1972) counted uterine scars and found a mean of 4.9; Pidduck and Falls (1973) counted emergent young and resident females in spring and estimated litter sizes averaging 4.3. Some studies found a sex ratio favouring males (Burt 1940, Blair 1942), while others reported more females than males (Yerger 1955). Individuals become sexually mature at about 11 months; most spring-born females breed the following spring and most summer-born females breed in the following summer (Smith and Smith 1972). The average lifetime of chipmunks in the wild is estimated at 2 or 3 years (Allen 1938, Burt 1940), although Allen (1938) reported a captive animal attaining the age of eight.

The rule of solitary habitation is broken only while a mother is raising young. Snyder (1982) reports that mothers become intolerant of their offspring within two weeks of the emergence from the natal burrow, and the young disperse and establish their own home area. Roberts (1976) found that most of these juvenile movements were less than 40 m, the average radius reported for a home range by White and Svendsen (1992). Chipmunk home ranges in woodland are dynamic, varying among years, seasons, and individuals (Yerger 1953, Forsyth and Smith 1973, Getty 1981a,b, Mares and Lacher 1987), and they overlap except in core areas (Yerger 1953, Dunford 1970, Yahner 1978a, Mares and Lacher 1987). Individuals of both sexes defend their core areas, which have a radius of about 15 m, centred on the burrow, but they may tolerate each other to a distance of .5 m when outside the core (Dunford 1970, Yahner 1978a, 1978b). Home range sizes reported in the literature run from 445 m² (Forsyth and Smith 1973) to 9193 m² (Roberts 1976). However, variability in the number of captures and the methods used to make home-range calculations renders inter-study comparison difficult. Within studies, chipmunk home range sizes have been found to vary inversely with the availability of food (Mares et al. 1976, Kramer and Weary 1991), water (Bowers et al. 1990), and population density (Forsyth and Smith 1973, Mares et al. 1982).

An individual's linear range, calculated as the distance between the two most distant captures (Stickel 1954), may also be used as a measure of extent of landscape use. Yerger (1953) reported chipmunk linear ranges varying from 20 to 230 m. Dunford (1970) studied a population in a second-growth deciduous "hedgerow" in Ithaca, New York, and found linear ranges of 70 m. Roberts (1976) measured a linear range of 509 m for one female chipmunk, and found that some animals made long sallies outside their home areas to exploit particular food sources. Adult males have been found to have larger home ranges and to make longer movements than adult

females (Yerger 1953, Yahner 1978a, Lacki et al. 1984), but Mares et al. (1980) and Getty (1981a) found more variability among individuals than between sexes. Clearly, chipmunk range sizes and movements, even within forest habitat, have not been fully described.

METHODS

Study area:

The study site, which is subdivided into five low intensity farms, lies just east of the Rideau River, approximately 30 km south of Ottawa, Canada (45°14' N, 75°39' W), within the Great Lakes - St. Lawrence Forest Region of Canada (Rowe 1977). Thirty percent of this landscape is woodland, divided among four patches ranging in size from 2.5 to 25 ha. These woodlots are dominated by sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), eastern white cedar (*Thuja occidentalis*), basswood (*Tilia americana*) and white elm (*Ulmus americana*). The other 70% of the landscape consists of pasture and hay fields, crop fields planted in corn (*Zea mays*), oats (*Avena sativa*), and buckwheat (*Fagopyrum esculentum*), farm buildings and lanes, a creek, and a network of fencerows. The fencerows are unmanaged; they probably regenerated spontaneously after the original clearing of the land about 150 years ago (Fritz and Merriam 1993) and persist through neglect. Some fencerows contain low stone walls built of rocks removed from the fields, but most have old rail or wire fences. Fencerows are of varying widths and vegetation types. Some are merely narrow grassy margins less than a metre wide, but many support mature shrubs and trees and are up to ten metres wide. There is much heterogeneity in structure, species composition and width within fencerows. The most common trees and tall shrubs in the fencerows are white ash, hawthorn (*Crataegus* spp.), white elm, nannyberry (*Viburnum lentago*), choke cherry (*Prunus virginiana*), dogwood (*Cornus* sp.), white oak (*Quercus alba*), and aspen (*Populus tremuloides*). Two vines, Virginia creeper (*Parthenocissus vitacea*) and grape (*Vitis riparia*) are also widespread and may dominate locally.

Trapping procedures:

Chipmunks were trapped in 4 woodlots and 18 fencerows in the study area between May and October 1989, and the same 4 woodlots and 14 of the 18 fencerows during the same period in 1990. The landscape, with trap locations indicated, is shown in figure 2.1. I used Sherman-type live traps containing dacron wool bedding and baited with a mixture of rolled oats, honey and peanut butter formed into 2 cm balls.

Two woodlots had grids of 7 rows by 5 columns, and the other 2 had grids of 5 rows by 5 columns. The traps in the grids were placed 20 m apart. Fencerows represented a range of vegetation types, widths and distances from woodlots. There were 10 traps per fencerow, spaced 10 m apart and placed along the midline of the fencerow vegetation.

There were 5 two-week trapping sessions in 1989. Each of the first 4 sessions consisted of 4 days trapping in woods during the first week and 4 days trapping in fencerows the second week. Traps were opened in the morning of the first day, checked morning and evening thereafter, and closed on the evening of the fourth day. The sessions began May 29, June 26, July 24, and August 28. The fifth session ran for 4 days only beginning September 25. Traps were opened in the morning and closed in the evening to protect animals from overnight hypothermia. The first 2 days traps were open in the woods, the last 2 days in fencerows. Three-hundred traps were set in each session, 120 in woods and 180 in fencerows for a total of 5400 trap days.

In 1990 I conducted 6 trapping sessions. For each session, two woodlots and half the fencerows were censused in the first week, and the other two woodlots and remaining fencerows in the second week. The sessions began May 7, May 29, July 3, July 30, August 29, and September 25. There were 240 traps set in each session in 1990, 120 in the woods and 120 in the fencerows, totalling 4800 trap days.

Captured chipmunks were transferred from the live trap to plastic mesh bags for handling. On first capture, a numbered monel ear-tag was attached to each ear for identification. At that time and at each following capture, a chipmunk's identity, weight, sex and reproductive condition was recorded along with the trap location, date and time. Chipmunks were identified as young of the year, adult, or uncertain age based on categories derived by Pidduck and Falls (1973) in Algonquin Park and Chaffey's Locks, Ontario.

- 1) Young of the year: non-reproductive animals weighing less than 85 g at first capture.
- 2) Adults: animals in reproductive condition or animals falling into any of the following categories: animals weighing more than 100 g, animals captured in May, animals captured in June and weighing at least 85 g, and animals captured for a second year.
- 3) Uncertain age: non-reproductive animals weighing more than 85 g but less than 100 g at first capture and first trapped in July or later.

Chipmunks were designated resident, temporary resident, or transient depending on their trapping history. Individuals captured in the same fencerow or woodlot during two or more trapping sessions were called resident. Temporary residents were those present during one

session only, but trapped more than once in the same area (i.e. 2 or more captures in a woodlot, in a fencerow, or in adjoining fencerows or woods and fencerows). Transients were trapped only once in a particular fencerow or wood, and never recaptured.

Radio-tracking procedures:

Animals were selected for radio monitoring based on age, sex, and location. Forty chipmunks were successfully radio tracked (16 or more relocations) over the study period: 10 young males, 10 adult males, 10 young females and 10 adult females. These individuals came from all parts of the landscape. Selected animals were anaesthetized by placing them in a large container with a small amount of medical grade ethyl ether. They were observed carefully and when sedated, they were fitted with a collar bearing a radio transmitter. I used type BD-2GC collars designed and built by Holohil Systems Ltd., Woodlawn, Ontario. The transmitter is a crystal controlled 2 stage design, pulsed by a multivibrator. The transmitter and battery are sealed in an inert, waterproof epoxy coating. This package measures 18 x 8 x 6 mm. An antenna made of stranded stainless steel wire coated with black nylon protrudes from the package. In the field, the antenna can be passed through a flexible PVC tube and threaded through a hole in the transmitter housing to form a loop that can be fastened securely with a brass crimp, and serves as the collar. These transmitters weighed about 2 g, had a range of 100 m and a life of about 90 days. Signals were picked up with Merlin 12 receiving sets built by Custom Electronics, Urbana, Utah and hand-held Yagi antennas. When the collared chipmunks recovered from the anaesthetic, they were released at point of capture.

Chipmunks were located twice a day, in the morning and in the late afternoon. Their position was determined by triangulation and recorded as a set of cartesian coordinates on a map drawn from an air photograph of the landscape. Signals could be received even when the chipmunk was in a burrow. Collars did not appear to restrict the behaviour of the chipmunks. Lactating females continued to return to their burrows and tend their young; the confirmed mortality rate was only 5%, and one animal overwintered wearing a collar and was recaptured in good condition in the spring.

Measurements of fencerow variables:

Elements of fencerow quality were determined by correlating fencerow use by chipmunks (number of individuals captured in 1989) with the measures of fencerow features taken during the summer of 1989. Data from 1989 alone were used because fencerows trapped in 1989 covered a greater range of features than the smaller sample of 1990. The following features were measured:

- 1) The width of the fencerow was measured at 1 m and 2 m above the ground at each trap site. These values were averaged over the ten trap sites for each fencerow.
- 2) Vegetation types at each trap site were determined by estimating the percentage cover (in 10% cover-class intervals) of various plant types in a 5 m transverse slice of fencerow centred on the trap. These results also were averaged for each fencerow. Vegetation types included large trees (> 10 m height), small trees (4-10 m), tall shrubs (1.5-4 m), low shrubs (< 1.5 m), tall vines (1.5-4 m), low vines (< 1.5 m), grasses, herbs.

3) Three non-living structural features were assessed in the same way:

- i) the presence of litter**
- ii) rocks**
- iii) logs or fence rails.**

4) Four variables representing linear continuity were measured:

- i) the distance to the nearest wood from the proximal end of the trapline**
- ii) percentage of that distance as gaps (lengths of fencerow > 5m lacking trees or shrubs),**
- iii) the overall length of the shortest path between two woods containing the fencerow, and**
- iv) The percentage of this path containing gaps. Typically gaps were sections of grassy or herbaceous vegetation.**

5) Floristic richness was determined for each fencerow by counting the number of different species of trees and tall shrubs (1.5–4m) present within the trapping area of each fencerow.

Statistical analysis and home range calculation:

Movement behaviour:

I used SAS (SAS Institute 1990) for all statistical tests on movement behaviour. Maximum probability of a type I error was set at 5% for all hypotheses tested. I tested the null hypotheses that range length, largest single move, and average distance moved between sightings were not related to age or sex. The dependent variables were log-transformed when necessary

to meet the assumptions of the parametric analyses. In addition, I tested the null hypothesis that no significant differences existed in range lengths of animals with different patterns of landscape use, i.e. those sighted exclusively in woods, those sighted exclusively in fencerows, those using both woods and fencerows with woods predominating, and those using both woods and fencerows with fencerows predominating. Range length was log-transformed for this analysis. Where significant ANOVAs existed, a Scheffé pair-wise comparison was run to identify significant differences among variables.

Home range:

I estimated home ranges for animals recorded exclusively in woodlots in the telemetry study, to compare them with home ranges reported in large tracts of woodland in the literature. I used a minimum area polygon method because this is the one most commonly reported in studies of chipmunks in forest habitat. The calculations were made using a SAS program from White and Garrot (1990).

Fencerow characteristics:

I used correlation and non-parametric (Kruskal-Wallis) one way analysis of variance to test for presence or absence of a significant relationship between the number of individual chipmunks captured in each fencerow in 1989 and the fencerow features (width, vegetation types, structural components, linear continuity, and floristic richness) identified above. Variables were log-transformed where this improved the fit of the correlations. Models of one or more variables explaining the relative abundance of chipmunks in fencerows were obtained from step-wise multiple regression analyses. I also ran a principal components analysis of fencerow components and structure to group related fencerow features into orthogonal factors, and I tested

the null hypothesis that the presence of chipmunks in fencerows was not correlated with these factors. The underlying assumption in these analyses is that the frequency at which chipmunks are captured in a fencerow reflects their assessment of its quality.

Use of landscape elements:

I used Chi-square goodness of fit tests (Zar 1984) to determine if chipmunk use of landscape elements was independent of residency type, age, sex, and season. Maximum probability of a type I error was set at 5%. The tests included landscape elements used (woods only, fencerows only, woods and fencerows) by:

- 1) residency type (resident, temporary resident, transient), 3 X 3 contingency table.
- 2) age (young, adult), 3 X 2 contingency table.
- 3) sex (male, female), 3 X 2 contingency table.
- 4) season (spring, summer, fall), 3 X 3 contingency table.

RESULTS

There were 615 captures of 126 individual chipmunks (72 males, 54 females) over 5400 trap days in 1989, and 719 captures of 131 individuals (72 males, 59 females) occurred over 4800 trap days in 1990. Forty-nine per cent of the individuals captured over the two field seasons were residents, and 25% were transients (table 2.1). Thirty-two per cent were adult when first captured, and 68% were young or of uncertain age (table 2.2).

Radio-tracking from 1989 to 1991 produced a data set of 40 individuals, evenly divided among age and sex, having 16 or more sightings each. There were 1760 sightings for these animals with a mean of 44 ± 15.30 sightings per individual. Twenty-six of these individuals were first captured in woods, the other 14 were first captured in a fencerow (table 2.3).

LANDSCAPE:

1) Assessing landscape quality:

Chipmunks were present in all 4 woodlots. All ages and sexes were represented. Seventy per cent of sightings of radio-collared animals (table 2.3) and 60% of all captures (table 2.4) occurred in woods. Sixty-six per cent of all chipmunks and 81% of resident

No chipmunk was ever recorded in a field over the 3 years of radio-tracking. However, many animals were found in fencerows. Fifty-nine per cent of all individuals in the mark-recapture study and 70% of those in the telemetry study were recorded at least once in a fencerow. All sex/age groups and residency classes were represented (table 2.2, table 2.5), but there was considerable variation in number of captures, number of individuals captured, and intensity of use by different residency classes among the fencerows sampled. This suggests differences in fencerow quality from the animals' perspective.

Forty-eight per cent of individuals captured in fencerows over the two years were residents, 30% were temporary residents, and 22% were transients (table 2.5). Temporary residents, those individuals captured more than once but only in a single trapping session, are a difficult class to interpret. They may include residents that suffered early mortality, or were trap-shy, as well as transients that paused briefly on their way through the landscape. Since their status was ambiguous, their relationship with fencerow features has not been analysed separately, although they are included in all analyses involving total individuals. Their identification is to ensure a distinction between residents and transients.

Attributes of the fencerows sampled are shown in table 2.6 (see Bennett et al. 1994, Fritz and Merriam 1994 for a description of the species composition of these fencerows, and figure 2.1 for location of individual fencerows). Some fencerows supported a continuous cover of large older trees and tall shrubs. They were relatively wide and structurally complex (e.g. 'H', 'L', and 'Q'). Others were dominated by shrubs and smaller, younger trees (e.g. 'C', 'D', and 'P'). Several were narrow with few or no woody species and were dominated by herbs and grasses (e.g. 'I', 'O', and 'R'). Fencerow attributes are summarized as follows:

a) width:

Fencerow width at 1 m above the ground ranged from 1.4 m to 9.7 m with a mean width of $5.57 \text{ m} \pm 2.34$. Width at 2 m varied from 1.4 m to 10.7 m with a mean width of $5.64 \text{ m} \pm 2.43$.

b) vegetation type:

Tree cover ranged from 0 to 52%, shrub cover from 0 to 72%, vines from 0 to 50%, grass from 11 to 90%, and herbs from 9 to 27%.

c) structural components:

For 17 of 18 fencerows, ground cover by logs ranged from 0 to 13%. Fencerow 'A' had 60% log cover. Five fencerows had 24% or higher cover of rocks, while all others had less than 5%. Coverage by litter was between 5 and 75%. Litter was significantly positively correlated with the presence of shrubs, trees, and vines, while vines and logs were significantly positively correlated ($p < 0.05$).

d) linear continuity:

The distance to the nearest wood from the closest trap site was quite variable among the fencerows, ranging from 1 m to 690 m. The median distance was 75 m. Twelve of 18 fencerows had no gaps in the path to the nearest wood. The rest contained gaps representing from 7 to 38% of the path. Paths between woodlots containing the sample fencerows were from 218 m to 1735 in length, with a mean of 783.78 ± 379.0 . Six of these had no gaps. The others had gaps ranging from 3 to 51% of the distance.

e) floristic richness:

There were 29 different species of trees and shrubs present at the sampled sites. Floristic richness varied from 0 to 18 with a mean of 9.06 species $\pm$ 4.29.

Chipmunks were not found equally in all fencerows. Few animals were captured in the narrow, grassy fencerows while both residents and transients were present in wider, more complex fencerows with woody vegetation. Table 2.7 shows that overall captures ranged from 44 (13 individuals) in fencerow 'B', a structurally complex fencerow within 90m of a woodlot, to 0 in fencerow 'O', an open grassy margin along a wire fence, 690m from a woodlot.

Table 2.8 shows the correlations between the number of individual chipmunks (residents, transients and total individuals) trapped in fencerows in 1989 and the fencerow attributes. I used number of individuals rather than number of captures for the correlation to control for individual differences, since by definition, transients were captured only once, while some residents were trapped repeatedly.

a) width:

There was a strong positive correlation of residents with width at 2m ($R^2 = 0.62$, $p < 0.006$) and with width at 1m ($R^2 = 0.58$, $p < 0.01$).

b) type of vegetation:

All classes of animals were significantly positively correlated with woody vegetation in the form of trees and taller shrubs ($p < 0.03$ to $p < 0.001$). This suggests that these attributes are important correlates of fencerow quality for all chipmunks. Residents

showed a stronger relationship with the presence of tall trees ($R^2 = 0.71$, $p < 0.001$) and short trees ($R^2 = 0.69$, $p < 0.001$) than the other classes. Residents were also positively related to the presence of vines taller than 1.5m ($R^2 = 0.49$, $p < 0.04$) and negatively related to grass ($R^2 = -0.54$, $p < 0.02$).

c) structural attributes:

Residents showed a positive relationship with the presence of litter in the fencerow ($R^2 = 0.55$, $p < 0.02$). Transients and total individuals showed no significant relationship with any structural components.

d) linear continuity:

The proportion of the path to the nearest woodlot composed of gaps was an important negative correlate of all classes of chipmunk, and thus continuity of cover in this pathway enhances fencerow quality. Residents related more strongly to this attribute ($R^2 = -0.62$, $p < 0.006$) than did transients ($R^2 = -0.58$, $p < 0.01$), but chipmunks in general were more likely to use fencerows that were continuous extensions of woodlots ($R^2 = -0.62$, $p < 0.006$). Transients, residents, and total individuals showed a strong negative relationship with the proportion of gaps in the route between two woods incorporating the fencerow (transients: $R^2 = -0.69$, $p < 0.002$; residents: $R^2 = -0.48$, $p < 0.04$; total individuals: $R^2 = -0.62$, $p < 0.006$). Transients also correlated negatively with the length of the path between 2 woodlots incorporating the fencerow ($R^2 = -0.69$, $p < 0.002$), suggesting that preferred routes through the landscape tend to be short in length, and to provide a continuous cover of woody vegetation.

e) floristic richness:

Residents were significantly related to the floristic richness of fencerows ($R^2 = 0.54$, $p < 0.02$). Those fencerows with higher numbers of species of trees and shrubs had more captures of resident chipmunks. Transients and total individuals were not significantly related to this factor.

Results of the stepwise multiple regression of total individuals, residents, and transients trapped in fencerows in 1989 on fencerow attributes are shown in table 2.9. Two vegetation factors best predicted the number of residents: tall trees (49.8%) and vines > 1.5 (25.3%). Together they explained 75.1% of the variance for residents. The model for transients contained 2 factors that were significant at $p < 0.05$ and together explained 61.3% of the variance. These included two measures of linear continuity (% of the path between woodlots as gaps (47.4%) and length of path between woodlots (13.9%)).

Table 2.10a shows the results of a principal components analysis. Four orthogonal factors for which the eigenvalues of the covariance matrices were greater than 1 were obtained from the fencerow features measured. Together these factors explained 80% of the total variance. The first axis represents wide, structurally complex fencerows dominated by woody vegetation and explains 48% of the variance; the second axis is low shrubs and vines (15% of the variance), the third isolation (11%), and the fourth herbs (6%). Residents, transients, and total individuals were all significantly related to factor 1 (table 2.10b). Residents had the strongest relationship, with a level of significance of 0.01. Transients and total individuals related to factor 1 at a level of 0.05. Factor 1 contains components from all categories of attributes measured. None of the other three factors was significantly related to the chipmunk

data. This result provides a simple measure of high quality versus low quality fencerows for chipmunks in general. High quality fencerows will tend to be wider, contain more woody vegetation and less herbaceous vegetation, support a greater variety of tree and shrub species, and have fewer gaps in the pathway to woodlots along which they lie.

2) Use of woods versus fencerows by residency type, age, and sex:

I tested whether captures of individual chipmunks in woods only, fencerows only, or a combination of woods and fencerows were related to residency type (resident, temporary resident, transient), age, and sex. Transients were trapped equally in woods and in fencerows in both 1989 and 1990 (table 2.5). However, there was a significant difference in capture locations between residents and temporary residents in 1990 (table 2.11, $\chi^2=15.25$, $df=2$, $p<0.001$). The exclusive use of fencerows was higher than expected for temporary residents, and lower than expected for residents. Twenty-nine per cent of residents used both woods and fencerows, 53% used woods only, and 18% used fencerows only. Eleven per cent of temporary residents used both woods and fencerows, 34% used woods alone, and 44% used fencerows alone. There was no significant relationship between use of landscape elements and residency type in 1990.

I then tested whether the use of landscape elements was independent of age and sex. In 1989, use of fencerows, woods, or a combination of both was significantly different for adults and young (table 2.12, $\chi^2=7.28$, $df=2$, $p<0.05$). More young chipmunks than expected were captured exclusively in fencerows, while fewer adults used fencerows alone. Adults were more likely than expected to use a combination of woods and fencerows, while young used this

category less than expected. There was no significant interaction between age and use of landscape elements in 1990, or for sex and use of landscape elements for either year.

Twelve of 40 animals in the radio-telemetry study (30%) were located in a single woodlot and were never sighted in fencerows; thirteen (32%) used a single woodlot and a single fencerow; twelve (30%) used a single woodlot and more than one fencerow; two used only fencerows and one used two woodlots and two fencerows. In contrast to the mark-recapture study, there were no significant differences in use of woods, fencerows or a combination of the two between adults and young chipmunks, however there was a significant interaction between sex and use of landscape elements (table 2.13, $\chi^2 = 7.4$, $df=2$, $p<0.05$). Eighty-five per cent of males used a combination of woods and fencerows, while for females, 45% used only woods, 45% used a combination of woods and fencerows, and 10% used fencerows exclusively.

3) Use of landscape elements for nesting and overwintering:

Fencerows as nesting sites for chipmunks:

All 10 adult females in the radio-telemetry study were pregnant or lactating when first captured. From frequency of sightings and from direct observations, I infer that 8 individuals had natal burrows in woods and 2 had natal burrows in fencerows (chipmunk 1734 in fencerow 'C' and chipmunk 1861 in fencerow 'P'). Both individuals nesting in the fencerows were known to be in their third summer, having been first captured as young animals in 1989, and again as adults in 1990. They were always captured in the vicinity of these 2 fencerows, and never captured or sighted in woods. The following evidence suggests that females 1734 and 1861 successfully raised litters in fencerows. In 1990, 3 juveniles were trapped in fencerow 'P' and

2 juveniles were trapped in fencerow 'C'. In July 1991, a juvenile captured in fencerow 'C' was fitted with a radio collar. This animal subsequently used the same fencerows as the adult resident in 'C'.

Fencerows as overwintering sites for chipmunks:

Indirect evidence for overwintering in fencerow burrows comes from trapping data in 1989 and 1990. The 2 females discussed above were captured in late September 1989 in their home fencerows and were recaptured, lactating, in the same fencerows in early May of 1990. Since females often remain in the hibernaculum burrow to raise their spring litter (Svendsen and Yahner (1979), this suggests that females 1737 and 1861 overwintered in fencerows.

4) Seasonal variation in landscape use by chipmunks:

Table 2.14 shows the seasonal population levels in woods and fencerows over the 2 years of trapping. Overall, 79 individuals were trapped in spring, 170 in summer, and 117 in fall. I tested if capture locations (woods only, fencerows only, or a combination of both) differed for summer and fall sessions. In 1989 there was a significant difference in capture locations between the two seasons (table 2.15, $\chi^2 = 24.01$, $df = 4$, $p < 0.001$). Fewer chipmunks than expected were captured in woods alone in the summer, while significantly more were captured in fencerows alone or in woods and fencerows during that period. In the fall, more individuals than expected were captured in woods alone and fewer in fencerows alone or in combinations of woods and fencerows. This suggests an expansion of the population into the fencerows in summer, and a withdrawal back into traditional woodland in fall. Use of the landscape did not vary significantly among the seasons in 1990.

MOVEMENT:

Radio-tracking data provides comparative information on the frequency and extent of movements of individuals in the different sex/age groups. I calculated average distances moved between sightings, the size of the largest single move, and a linear range representing the distance between the two most widely separated sightings for all individuals sighted over 15 times. For individuals recorded only in woods, I report home ranges calculated as minimum area polygons to permit comparison with home ranges reported in forest landscapes.

1) How mobile are chipmunks on a daily basis? Does this differ significantly by age or sex?

Chipmunk locations were monitored twice a day. Distances between sightings were highly variable, ranging from a minimum of zero, where the individual was located at the identical place to the previous sighting, to a maximum of 457 m. Figure 2.2 shows the frequency distribution for the length of moves between sightings. Fifty per cent of all moves were over distances less than 40 m and 25% of moves were 80 m or more.

I tested whether the distance moved between sightings depended on sex, age, or sex/age group. Since moves measured for the same individual are not considered independent observations, I used a repeated measures analysis modified to accommodate different numbers of observations among individuals. Table 2.16a shows the mean average moves for these classes. Differences between males and females and between young and adults were not significant. Among sex/age classes, adult females had a somewhat smaller mean average move, with less variability among individuals than the other sex/age groups, likely a reflection of the need for

females to remain close to the burrow while raising pups. This was not statistically significant (table 2.16b), however there was a probability of a making a type II error of 0.33 due to the small sample size and the high within group variability. Differences among individuals (representing the error term in this test) were significant ($p < 0.0001$) and accounted for most of the variation observed in the movement data.

Table 2.17a shows the mean longest single move made by males, females, adults, and young. I tested whether the size of the longest single move depended on sex and age. There were no significant differences for AGE, SEX, or AGE*SEX (table 2.17b). At least one individual in every sex/age group moved more than 400 m between consecutive sightings. These long moves were often made over the course of a single day. For example, the young male with the longest single move (457 m) travelled this distance between 10:00am and 7:00pm of the same day. This gives an indication of the mobility of these animals in an agricultural landscape.

2) How large is a chipmunk's range? Does this differ among ages and sexes?

Most animals moved back and forth within a defined area rather than moving directionally through the landscape. I measured observed range length (Stickel 1954) for each animal by calculating the linear distance between the two most widely spaced locations where the animal was sighted (table 2.18a). The largest linear range recorded was 902 m. This range belonged to the same young male whose longest single move was 457 m. The range of even this mobile individual was no larger than twice the longest move. The smallest range size was 92 m for a young female.

I tested whether the linear range size depended on sex and age (table 2.18b). The main effect of SEX was significant ($p < 0.0482$). The average range size for males was 360.00 ± 200.87 m, while female range size averaged 257.69 ± 139.91 m. There was no significant difference in linear range size between young and adult chipmunks, but again, the power of the test was low due to the high amount of variability among individuals.

Table 2.19a shows mean linear range sizes for chipmunks based on the habitat in which they were found. I tested whether linear range sizes differed significantly for chipmunks using different combinations of habitats (table 2.19b). The independent variable LANDUSE had 4 levels: woods only; fencerows only; both woods and fencerows (mostly woods); both fencerows and woods (mostly fencerows). The model was significant ($p < 0.0001$). Chipmunks sighted only in woods had significantly smaller range lengths than did animals using fencerows either as exclusive habitat or as a supplement to woodland. This suggests that animals living in traditional woodland move shorter distances in the landscape, and thus have smaller neighbourhoods than those making use of fencerow habitat, although overall resource area may be similar.

Home range sizes, determined as convex minimum area polygons, were calculated for 12 individuals recorded only in woods in the telemetry study (Table 2.20). Number of sightings varied from 16 to 76, and the home ranges varied from 26,050 m² to 2,350 m². The average home range measured 11,037.50 m² with a standard deviation of 6,749.25. The relationship between number of sightings and size of home range was not linear.

3) How often do sub-populations exchange individuals?

Observed exchanges of individuals between woodlots were rare. I recorded only 4 over the three years of the study. One young male with a radio collar travelled from woodlot 3 to woodlot 1. This individual went back and forth between these two woodlots several times over the observation period. Three animals from the trapping study moved between woodlots. In each case the move was temporary. In 1990, a young male who was frequently captured in woodlot 3 was trapped in woodlot 1; he subsequently returned to woodlot 3 and was recaptured there. A young female moved along fencerows from woodlot 3 to woodlot 2 in the summer of 1989, and was recaptured in woodlot 3 soon after. An adult male moved from woodlot 1 to woodlot 4, and back to woodlot 1 during a 24 hour period in the spring of 1989. No adult females were recorded moving between woodlots.

4) Do chipmunks exclude conspecifics from fencerows?

Over the two year trapping period, there were 22 incidents of two adult chipmunks captured in the same fencerow at the same time.

In 7 of these cases, the two individuals were both adult females, in 6 cases they were both adult males, and in the other 9 cases the pair consisted of an adult female and an adult male. Thus 14% of captures of adults in fencerows occurred with a conspecific present.

DEMOGRAPHICS:

Trapping data were used to answer the following questions about chipmunk demographics in the agricultural mosaic. Answers to these questions were necessary to estimate parameters for the simulation, but are not intended to represent a comprehensive study of chipmunk autecology.

1) What population levels are achieved seasonally?

Table 2.21 shows the population levels reached in spring, summer, and fall for adults and for the group including young animals and those of unknown age in 1989 and 1990. Seasonal means over the 2 years were 39.5 ± 7.78 in spring, 85.0 ± 1.41 in summer, and 58.5 ± 2.12 in fall. The overall population in this landscape doubles from spring to summer, largely due to the recruitment of juveniles, but drops off again in the fall to 1.5 times the original spring population, perhaps because chipmunks become more difficult to trap in fall (Smith and Smith 1972). This lack of trappability may be related to winter food gathering and burrow preparation, and is more marked in adults than younger individuals. The ratio of known adults to known young in summer and fall was 1:1.7. However, individuals of unknown age made up approximately 26% of the summer population over the 2 years, and 44% of the fall population. Tryon and Snyder (1973) suggest that the majority of these "unknowns" are young chipmunks, immigrants or floaters, trying to establish residency. Qualitative assessment of these animals in my study support this view, suggesting that the estimate of young chipmunks used in the adult to young ratios is likely conservative and might be as high as 1:3 in the fall.

2) What proportion of animals are transient versus resident, young versus adult, and male versus female:

Over the two years of the trapping study, 49% of individuals captured were classed as residents and 25% were classed as transients. The remaining animals were classed as temporary residents. There were 82 adults and 175 young or unknown aged animals over the two years, which represents a ratio of 1 adult to 2.13 young and unknown aged individuals. Male chipmunks made up 56% of the total population, while females made up 44%, which is a ratio of 1.27 males to 1 female. This difference was not significant ($\chi^2 = 3.76$, $df = 1$, $p > 0.05$).

3) What is the overwinter survival rate?

Survival rates were calculated from the 1989 and 1990 trapping data. Individuals known to have been present in the landscape in 1989 that were recaptured in 1990 were winter survivors. The population size at the end of 1989 was estimated as all individuals trapped between August 28 and September 28, 1989 as well as any additional 1989 individuals recaptured in 1990. Based on these criteria, there were 60 individuals known alive in the fall of 1989, and 38 of these were recaptured in 1990. This gives a minimum estimate of overwinter survival of 63%.

4) What is the reproductive rate?

I used the 1990 trapping data to estimate the weekly pregnancy rate in the population. Ten out of 12 females present in the four week period from early May to early June were pregnant, representing an overall pregnancy rate for that period of 80% or 0.4 pregnancies per

female per week. Before mid-July there were 44 young chipmunks in the population, suggesting a surviving litter size of 4.4 individuals. In July, I recorded 2 additional pregnancies, and by the end of the month, 4 new juveniles were captured. The pregnancy rate for the summer period was 20%, or 0.2 pregnancies per female that had not bred in spring per week. One of the spring mothers was lactating again in the late summer. From this evidence, I estimated the probability of a female producing a second litter at 0.1 pregnancies per female that had produced a spring litter per week.

DISCUSSION

POPULATION-LANDSCAPE DYNAMICS:

The field study was undertaken to investigate chipmunk population dynamics in the agricultural landscape for the purpose of assigning appropriate values to parameters in the simulation model. Information about population structure, habitat use, distances moved, seasonality and demographics was collected to supplement existing knowledge of chipmunk behaviour in more traditional settings, published in the literature. I discuss the most pertinent findings and provide a summary at the end of the section.

The network of woods and fencerows in the low intensity agricultural study landscape supports a seasonally dynamic, persistent population of chipmunks. Although chipmunks have traditionally favoured forest habitat, they survive in this agricultural mosaic by making a living in woodland fragments and/or complex wooded fencerows, and they move among these habitats along fencerows that provide good cover.

The chipmunk population is distributed in this landscape as a set of overlapping neighbourhoods (*sensu* Addicott et al. 1987), composed of remnant woodland habitat, linear habitat in fencerows, and fencerow corridors. The focal areas for members of the population change in locus, composition, and extent as requirements and resources shift in time and space. Woodlots provide concentrated areas of traditional habitat but fencerows can also function as habitat patches in their own right, and are seasonally important elements in this landscape.

Animals raised litters and overwintered in both woods and fencerows. They moved along fencerows, between woods and fencerows, and between woods. Captures in fencerows were biased towards young animals and temporary residents, but transients were captured with equal frequency in woods and fencerows.

There were no recorded permanent moves from one woodlot to another, which suggests that this population may behave as a single, spatially dynamic demographic unit rather than a set of discrete sub-populations experiencing occasional one-way dispersal events, as proposed by metapopulation theory (Fahrig and Merriam 1985, Hanski and Gilpin 1991). However, although known inter-patch forays were infrequent, the overall mobility of the population suggests that the opportunity to detect and make use of under-utilized resources and empty habitat exists (Snyder 1982, Johnson 1989). Large numbers of transient animals and the appearance of untagged adults late in the season are indirect evidence of exchange with areas outside the study site. Therefore, woodlots suffering overwinter losses will be repopulated, either from within the landscape or outside.

Habitat:

One of the purposes of this study was to identify quality habitat for chipmunks in the farm landscape. That is, to determine which landscape elements chipmunks used and which they avoided. Habitat quality is subjective and varies with the needs of the individuals, with the presence or absence of predators, and with the seasons. A chipmunk locating a home burrow has different requirements, restrictions, and priorities than a chipmunk travelling across the landscape; a chipmunk preparing to overwinter may be more concerned with drainage conditions at a site than a chipmunk searching for food. Van Horne (1983) considers habitat quality to be

a function of survival and reproductive success rather than density alone. Patches in which mortality exceeds reproduction are defined as 'sinks' regardless of numbers of inhabitants (Pulliam 1988). However, these areas may contribute significantly to the persistence of a population by providing habitat for immature animals during seasonal peaks, and acting as sources of individuals for vacancies in prime patches. From a population perspective, these areas may be functionally high quality. Assessment of quality in this study is based on number of individuals captured, but nesting and overwintering success are validators.

Woods:

Not surprisingly, chipmunks considered woods good habitat. They have traditionally been reported to prefer late successional, mature forests with dense canopies and little herbaceous vegetation (Svendsen and Yahner 1979, but see Bennett et al. 1994). All four woodlots in my study area supported reproductive chipmunks, and a few individuals restricted their neighbourhoods to woods alone. The high proportion of reproductive females present in woods in the spring suggests that most successful overwintering took place there (Svendsen and Yahner 1979).

Fencerows:

Fencerow habitat supplements woodland for this population, especially in mid season when the population is at its largest. It provides refuge for travellers through the landscape and it may be successfully used for permanent residency.

The higher proportion of young chipmunks that were captured exclusively in fencerows in the mark-recapture study suggests fencerow habitat is often used by animals of lower status.

Svendsen and Yahner (1979) studied a chipmunk population in a hillside woods with a narrow wooded strip along a rocky outcrop, and also found evidence of this. Juveniles occupied the narrow strip of woods along the outcrop while adults occupied the main woodlot.

Temporary residents were found more frequently in fencerows than woodlots and transients were captured as often in fencerows as in woods. Males in the telemetry study were more likely than females to use fencerows as part of their neighbourhood, possibly a reflection of the need to search the landscape for females during periods of reproductive activity (Yahner 1978a, Galloway and Boonstra 1989).

Although residents used woods more frequently than fencerows, many residents used fencerows and woods in combination, and a few used fencerows exclusively. Several females successfully bred in fencerows. One resident female raised litters in two consecutive years in a fencerow dominated by shrubs and small trees, using surrounding fencerows as supplementary habitat, and was never sighted in the nearby wood.

Generally, chipmunks were found more often in those fencerows most resembling woodland. These were structurally complex, wider fencerows with canopy, shrub, vine and litter cover and high linear continuity. They provided not only a reliable passage through the mosaic, but food, refuge, and nesting sites. They were not merely corridors, but important components of the neighbourhood - habitat patches in their own right.

The elements of quality were more precisely defined, and explained more of the variation in chipmunk presence when fencerow features were related specifically to the presence of

residents or transients. Several studies of species living in linear habitats have shown a relationship between specific elements of the habitat and the presence of residents (Yahner 1983, Osborne 1984, Lindenmayer et al. 1993). Residents in the study landscape responded most strongly to the presence of canopy cover in the fencerow itself. The presence of transients was most strongly related to the absence of gaps in the pathway from the fencerow to the nearest woodlot, and in the pathway between two woods that included the fencerow. Transients passing through the area may not require the same level of food and nesting resources, but cover and refuge will be important in unfamiliar territory (Merriam and Lanoue 1990, Clarke et al. 1993).

Non-habitat:

Chipmunks were absent from narrow, grassy fencerows lacking in canopy trees or shrubs. Although movement through pasture or crop fields is possible (Forsyth and Smith 1973, Henderson et al. 1985), no chipmunk was ever observed in these areas during either trapping or radio tracking. This is consistent with the findings of Wegner and Merriam (1979). The negative association of chipmunks to fencerows with extensive gaps in tree and shrub cover supports the prediction of Forman and Godron (1986) that lack of continuity in linear landscape elements can be a deterrent to their use for movement in the landscape for some species.

Seasonality:

van Apeldoorn et al. (1992) suggest that functions of habitat elements may differ seasonally. Seasonal differences in habitat use were evident from the 1989 data in my study (table 2.14). Chipmunks increased their use of fencerows in summer, but were captured more often in woodlots in spring and fall. This expansion and contraction of landscape use may have

been related to the presence of plentiful resources in fencerows in mid season and the need for more sheltered woodland habitat for overwintering and early season natality.

Failure to observe a summer expansion into fencerows in 1990 similar to that in 1989 may have been due to variability in food production between the two years, but these variables were not measured. Whatever the cause, it is an example of the unpredictability of the system, and the necessity for flexibility in the population.

Despite the apparent preference for woods in the fall, evidence suggests that successful overwintering occurred in fencerows. Two females were observed raising litters in fencerow burrows in early spring 1990. There is a strong likelihood that they also overwintered there (Svendsen and Yahner 1979). Fencerow natal sites may be important sources of young animals for the population, helping to reduce woodlot isolation and the effects of habitat loss due to woodland fragmentation.

MOVEMENT:

The scale of fragmentation and the mobility of a species must be related if survival is to occur (Lord and Norton 1990, Wiens 1995). Movement within the landscape is basic to the persistence of this population, because no single patch can provide enough resources for all members for all seasons. Distances between resource areas are greater here than in forests, despite the heterogeneity present even in continuous woodland.

The large spatial scale at which this study was done, and the use of radio-telemetry to follow individual chipmunks over a period of weeks to months have permitted better estimates of daily moves and patterns of population movement than mark-recapture studies based on low recapture rates and areas limited by grid size (Mares et al. 1980).

Males and females, young individuals and adults could all move over 400 m between sightings (i.e., over a period of 8 to 12 hours). Ten per cent of all moves were greater than 140 m. (figure 2.2). Moves of this magnitude suggest dispersal events, but these moves were usually followed by a return to the animal's central area of activity, and were therefore sallies rather than permanent moves. Lidicker (1986) calls such movements excursions, and distinguishes them from dispersal, which is defined as a move to a new home area followed by reproduction.

There are several theories as to why these excursions, or exploratory movements, occur. Lidicker (1986) and Johnson (1989) believe that exploratory movements may be precursors to long distance dispersal. A dispersing individual may make sallies of increasing length over a period of time before making a permanent move. I did not observe any permanent long-distance moves of residents within the study landscape, but the presence of large numbers of individuals of uncertain age later in the season suggests exchanges with other populations occur.

Baker (1986) believes that individuals explore to familiarize themselves with the landscape. The resource base is assessed, refuge areas are expanded, empty burrow systems are discovered, ripening food sources are located, and other individuals are censused. Clarke et al. (1993) found that chipmunks took refuge from predators much more rapidly and successfully in

familiar sites. Baker further suggests that young, pre-reproductive animals are especially motivated to explore their surroundings. The longer moves made by young chipmunks in my telemetry study compared to adults (table 2.16a) may thus be directly related to their future success, since knowledge of what is out there is vital to surviving in a dynamic landscape. Although Roberts (1976) found juveniles established their first burrows less than 40 m from the natal site, distances moved in the agricultural landscape suggest longer excursions are necessary here to locate suitable vacant areas.

A homing event in the population illustrates a situation in which familiarity with the landscape may serve an individual well. A female, displaced over a kilometre from her home fencerow for radio-collaring, escaped and returned home over 2 days through the fencerow network, although she was afforded no visual clues on the outgoing trip, being enclosed in a livetrapp. Homing ability in this species has been described by Seidel (1961), who found it to be much stronger in adults than juveniles. It is possible that a knowledge of the landscape acquired through exploration is a contributing factor to success in homing events.

The relationship between food availability and exploration has been noted by Kramer and Weary (1991), who found that the amount of time chipmunks spent exploring increased as food density decreased. They suggest that when food sources are inconsistent, as occurs in unpredictable landscapes, it is advantageous to devote time to locating potential new sources. The dispersion of resources in the agricultural landscape for chipmunks, (who do not take advantage of novel food sources in crop fields), increases the need not only for exploration but for longer moves during everyday resource gathering. The evidence that home range size in chipmunks is related to food density (Mares et al. 1976), and water availability (Bowers et al. 1990) is likely

related to this need to move greater distances in search of resources. In my study, average distance between captures (i.e. everyday movements) exceeded the estimate of home range diameter reported in some studies (Yerger 1953, Smith and Forsyth 1973, Mares and Lacher 1987). There was considerable variation among individuals, but one young female moved an average distance between captures greater than distances travelled to new home sites in Yahner's study (1978a).

Linear range sizes:

The large ranges I observed are directly related to fragmentation, since resources are less centralized in fragmented landscapes than in continuous ones, and several different patches may be required over the season to supply basic needs (O'Neill et al. 1988, Dunning et al. 1992). Ims et al. (1993) studied voles in a habitat mosaic and found voles increased their home ranges to take in more than one patch. Knitting together resource patches to create functional but not necessarily contiguous home areas has also been observed in red squirrels in isolated wooded patches in the Netherlands (Celada et al. 1994). Supplementation and complementation of resources near the burrow with those in other landscape elements occurred frequently in the chipmunk population as evidenced by the number of individuals using both woodland and fencerow habitat. The longer moves required are reflected in greater linear ranges for these individuals. Average linear range lengths in my population were twice as long for every age/sex class as those reported by Roberts (1976), who detected longer movements than any other study I have found.

Home range measurements have traditionally been made to determine an individual's sphere of influence and the extent of its movement in the landscape. Many studies of chipmunk home ranges have used the convex minimum area polygon calculation to determine home range extent (Yerger, 1953, Forsyth and Smith 1973, Mares et al. 1976, Svendsen and Yahner 1979, Mares and Lacher 1987); however this method is unsuitable for data taken from fencerows, since too much unusable habitat would be included. Direct comparison of my results with those of other studies using area-based measures of home range was therefore not possible.

Home range comparisons:

I used the linear ranges to compare landscape use within my own study between animals using woods alone and those using fencerows. The ranges of individuals recorded in woods alone were half the size of ranges of individuals using fencerows or a combination of woods and fencerows, suggesting that animals using fencerow habitat for resources must be prepared to move greater distances over a season. When I compared average minimum area polygon home ranges for those same woodland animals with similarly calculated home ranges reported in the literature, I found the ranges of the agricultural woodland dwellers in my study to be more than twice as large as home ranges reported for animals in natural woodland.

To what extent are these apparent differences in movement patterns and landscape use the result of limitations in the sampling techniques? All the literature estimates were based on captures in grids, and measurement of an animal's movement pattern is restricted by the size of the trapping grid (Faust 1971), the distance between traps (Hayne 1950), and the number of captures (Mares and Lacher 1987). Therefore, estimates from the literature studies are probably

low. The ability of telemetry to detect movements unbiased by grid size or trap locations permits a more accurate assessment of landscape use, and is a factor in the difference in range size detected, as is the larger number of sightings used in the calculation. However I doubt whether these can account for the magnitude of the differences obtained. It is clear that chipmunks move greater distances and have larger ranges in the agricultural mosaic than have been reported in other work.

Conspecifics:

One of the questions asked in this study was whether or not chipmunks would tolerate each other within the same fencerow. This has important implications for the utility of fencerows as travel routes. Although chipmunks maintain separate burrow systems and are solitary except for mother-offspring groupings during the post natal period (Snyder 1982), they are not always antagonistic (Dunford 1970), and may benefit from alarm calls of nearby conspecifics (Burke da Silva et al. 1994). Many chipmunks were captured and observed in proximity although they were not interacting. Conspecifics frequently occurred in the same fencerow, even as adults. Dunford (1970) observed a population of chipmunks in a 6 m wide strip of deciduous "hedgerow" and found that, although their linear home ranges overlapped extensively, the individuals only defended the non-overlapping areas around burrow entrances. Yahner (1978b) studied interactions in chipmunks and found that animals were territorial within 15 m of their burrows in woods, but tolerated conspecifics to a distance of 0.5 m on neutral ground. Bowers and Adams-Manson (1993) set out plates of seed for chipmunks in an arboretum, and found that plates placed within 1 m of a burrow were defended but those placed at a distance of 10 m or more were outside the defended area. Getty (1981b) found chipmunks practice encounter

avoidance, moving in common areas in ways that minimize contact. Since my traps were 10 m apart in the fencerows, a capture of two chipmunks in adjacent traps was consistent with these previous findings. There was no indication of chipmunks excluding each other from fencerows during the period of my study.

DEMOGRAPHICS:

Demographic values specific to chipmunks in a fragmented agricultural landscape were important for developing the simulation model. The parameters used in the model will be discussed in more detail in the next section, but I will mention here some insights gained from the mark-recapture and telemetry studies, and how they relate to existing knowledge about chipmunks.

Stability:

There was little variation in size and composition between the 1989 and the 1990 populations. The population size in this landscape was comparable to that studied by Henderson et al. (1985) in a similar 4 km² agricultural landscape. This suggests a stable population at low risk of extinction (Pimm et al. 1988).

Seasonal population levels:

The number of individuals in the population more than doubled from spring to summer when the majority of the young were recruited, and declined slightly in fall, entering winter at

a size 50% larger than the spring level. This is similar to the population levels reported by White and Svendsen (1990).

Sex ratio:

There were more males than females captured in this population. Some past studies have also found larger numbers of males (Burt 1940, Blair 1942), but several others have reported more females (see Yerger 1955, Tryon and Snyder 1973). I wondered if females in my study were less trappable during the period they were raising their young, as this might bias the captures towards males. However, the ratios remained similar and in favour of males in all three seasons and in both years.

Residents and transients:

The ratio of residents to transients in my study was similar to that found by White and Svendsen (1990). There were twice as many residents as transients over the study period. The transient class likely includes long distance dispersers, a group difficult to identify. From the large distances that resident animals in my study could move in a matter of hours, it follows that long distance dispersers may be virtually unrestricted if suitable pathways exist through the landscape. This movement is especially adaptive in fragmented landscapes, since the strong likelihood of breeding for females that survive long distance moves can help to prevent genetic drift (Slatkin 1985, White and Svendsen 1990).

Age cohorts:

Yerger (1955) found a ratio of 2.4 young to 1 adult chipmunk in his study population during the summer. In my study, this age distinction is blurred by the presence of animals of uncertain age. The ratio of young plus uncertain age individuals to adults in summer was almost three to one in my study. Although many individuals of uncertain age were not reproductive, suggesting that they were indeed 'young', some were obviously older animals. The true ratio of young to adult may approach that of Yerger's population.

Longevity:

Chipmunks are considered relatively long-lived small mammals. Allen (1938) suggests 2 to 3 years is not unusual in the wild, while Tryon and Snyder (1973) calculated an overall mean longevity of 1.3 years at first capture in their nine year study. In my population, I found two animals in 1991 that had survived into their third year. However, many fail to make it past their first year.

Overwinter survival:

Tryon and Snyder (1973) suggest that much of the mortality northern populations suffer occurs in winter. Overwinter survival from 1989 to 1990 was relatively high (63%) in my population compared to other studies (Yerger 1955, Tryon and Snyder 1973). Successful overwintering in this area requires a well insulated, well drained burrow system stocked with enough non-perishable, high quality food to sustain the animal from November to April during

non-torpid periods. Overwinter survival undoubtedly varies with factors such as length and severity of winter, food production in the previous summer, and condition of the animal in the fall. Chipmunks born late in the season may be particularly vulnerable. Only 2 of 11 juveniles first captured in the late summer were recaptured the following spring.

Reproduction:

Most chipmunk births occur in spring, but two breeding seasons have been reported in this area (Yerger 1955, Smith and Smith 1972, Pidduck and Falls 1973). In my 1990 population, 80% of adult females gave birth in spring, 20% gave birth in fall, and one individual produced a litter in both seasons. This is consistent with the observations of Smith and Smith (1972), although Pidduck and Falls (1973) found much variation from year to year.

SUMMARY:

- 1) The chipmunk population in the 200 ha agricultural landscape is organized as a set of dynamic, overlapping neighbourhoods.
- 2) Chipmunks use woods and some fencerows for resource gathering, refuge, nesting, overwintering, and travel. They do not use fields.
- 3) Fencerows with good canopy cover and few open stretches are selected over sparsely vegetated ones. Chipmunks can raise litters, and may overwinter in some of these fencerows. Such fencerows are termed high quality.
- 4) There may be seasonal shifts in habitat preference. Woods were favoured in spring and fall, especially by resident adults. Fencerows may be more heavily used in summer, especially by temporary residents and young animals.
- 5) Individuals from any sex/age class can make long distance moves of over 0.4 km in 8 hours and return.
- 6) No permanent long distance moves within the landscape were observed, but many exploratory moves were made.

7) Linear ranges are generally larger in the agricultural landscape, whether in woods or fencerows, than have been reported in the literature for forest habitat.

8) Home ranges within the agricultural landscape were larger when they fell exclusively in fencerows or a combination of woods and fencerows than when they were in woods alone.

9) Chipmunks tolerate conspecifics in fencerows.

10) The study population varied little in size and makeup between the two years of trapping. Population size doubled in the summer. The sex ratio favoured males. Residents outnumbered transients two to one. Young animals outnumbered adults by more than two to one in mid season.

11) Overwinter survival was generally quite high (63%) in this population, but individuals born late in the season were an exception; they had a survival rate of less than 20%.

12) There were two breeding seasons in 1990, early spring and mid summer. The majority of females bred only in spring, a few did not breed until summer, and one individual bred in both spring and summer.

Table 2.1

Number of individual chipmunks trapped in 1989 and 1990 by residency type, sex, and age

	All Individuals			Residents			Temporary Residents			Transients		
	Total	1989	1990	Total	1989	1990	Total	1989	1990	Total	1989	1990
Males												
adults	46	23	23	22	8	14	12	9	3	12	6	6
young	52	30	22	24	14	10	17	10	7	11	6	5
uncertain	46	19	27	21	9	12	10	3	7	15	7	8
total	144	72	72	67	31	36	39	22	17	38	19	19
Females												
adults	36	21	15	20	11	9	9	5	4	7	5	2
young	45	24	21	24	13	11	11	4	7	10	7	3
uncertain	32	9	23	15	3	12	9	2	7	8	4	4
total	113	54	59	59	27	32	29	11	18	25	16	9
All												
adults	82	44	38	42	19	23	21	14	7	19	11	8
young	97	54	43	48	27	21	28	14	14	21	13	8
uncertain	78	28	50	36	12	24	19	5	14	23	11	12
individuals	257	126	131	126	58	68	68	33	35	63	35	28
captures	1334	615	719									
trap days	10200	5400	4800									

Table 2.2

**Number of individual chipmunks trapped in woods only, fencerows only,
and in both woods and fencerows in 1989 and 1990 by age and sex**

	woods	fencerows	woods and fencerows	total
1989				
adults				
males	9	3	11	23
females	6	6	9	21
total	15	9	20	44
young				
males	7	16	7	30
females	12	7	5	24
total	19	23	12	54
uncertain age				
males	5	8	6	19
females	5	3	1	9
total	10	11	7	28
1990				
adults				
males	13	6	4	23
females	8	4	3	15
total	21	10	7	38
young				
males	11	8	3	22
females	9	7	5	21
total	20	15	8	43
uncertain age				
males	9	12	6	27
females	12	8	3	23
total	21	20	9	50

Table 2.3
Use of fencerows and woodlots by radio-collared chipmunks including location of original capture, and the presence of individuals in one or both habitat types by sex and age.

	Number of Individuals	First captured in		Use of landscape			Most sightings	
		woods	fencerows	woods only	fencerows only	woods only	fencerows only	
Males								
adults	10	7	3	1	0	9	1	
young	10	4	6	2	0	4	6	
total	20	11	9	3	0	13	7	
Females								
adults	10	9	1	6	1	3	2	
young	10	6	4	3	1	6	4	
total	20	15	5	9	2	14	6	
All								
adults	20	16	4	7	1	12	3	
young	20	10	10	5	1	14	10	
total	40	26	14	12	2	27	13	
Sightings								
woods							1232	
fencerows							528	
total							1760	

Table 2.4

Number of chipmunk captures in fencerows and in individual woodlots in 1989 and 1990

	fencerows	all woodlots	woodlot 1	woodlot 2	woodlot 3	woodlot 4
1989						
total captures	259	337	57	96	124	60
total individuals	82	83	16	26	26	15
trapping effort	3240	2160	630	450	450	630
1990						
total captures	262	457	136	119	119	83
total individuals	69	86	21	19	24	22
trapping effort	2400	2400	700	500	500	700
1989 and 1990						
total captures	521	794	193	215	243	143
total individuals	151	169	37	45	50	37
trapping effort	5640	4560	1330	950	950	1330
size of woodlot (ha)		52	5	25	20	2

Table 2.5

Number of individual chipmunks captured in woods only, in fencerows only, and in both woods and fencerows in 1989 and 1990 by residency type

	woods	fencerows	woods and fencerows	total individuals
1989				
residents	17	12	29	58
temporary residents	10	13	10	33
transients	17	18	0	35
total individuals	44	43	39	126
1990				
residents	36	12	20	68
temporary residents	12	19	4	35
transients	14	14	0	28
total individuals	62	45	24	131
1989 and 1990				
residents	53	24	49	126
temporary residents	22	32	14	68
transients	31	32	0	63
total individuals	106	88	63	257

Table 2.6

Fencerow attributes - 1989

F/R	W1m	W2m	DISN	DISP	GAPN	GAPP	TTRE	STRE	TSHR	TVIN	SSHR	SVIN	GRAS	HERB	LOGS	LITT	ROCK	FRICH
A	7.5	7.9	50	405	0	7	4	35	65	50	45	29	11	13	60	73	2	11
B	4.6	4.4	88	405	0	7	6	21	36	31	38	19	41	10	13	30	4	9
C	6.3	5.2	300	870	7	3	1	10	47	46	59	32	18	9	3	53	3	10
D	3.6	3.8	390	1070	28	12	0	12	69	31	35	12	39	17	2	44	3	7
E	4.4	5.1	50	510	0	15	12	42	36	2	22	14	62	17	11	24	4	10
F	5.4	5.2	60	218	0	0	8	33	59	4	34	16	36	12	13	45	3	10
G	4.7	5.9	70	535	0	0	9	38	57	9	36	16	36	12	2	32	33	9
H	7.9	6.6	80	535	0	0	8	48	72	15	36	11	12	10	12	75	3	12
I	1.4	1.4	50	1020	30	41	0	0	0	0	8	11	90	10	0	10	1	0
J	3.9	3.9	50	1120	0	46	3	13	19	0	11	40	52	19	2	9	54	6
K	4.5	4.5	270	675	0	16	0	2	13	7	18	17	82	13	1	10	0	6
L	7.9	8.5	235	775	0	0	15	52	65	19	41	12	26	11	11	60	24	11
M	5.7	5.7	1	775	0	0	8	35	67	3	45	9	17	10	10	72	1	18
N	8.9	8.8	370	975	7	12	2	23	63	27	46	20	31	12	13	54	2	13
O	2.7	2.7	690	1285	38	51	1	7	80	0	13	10	74	20	2	5	32	1
P	8.1	8.3	135	830	0	6	3	11	58	0	40	15	47	15	1	43	3	11
Q	9.7	10.7	70	1735	0	0	11	38	69	36	26	15	12	10	5	73	28	13
R	3	3	50	370	18	12	0	4	26	7	47	20	50	27	4	29	1	6

LEGEND

W1m width (m) of fencerow at 1 metre height
W2m width (m) of fencerow at 2 metre height
DISN distance (m) to nearest wood from closest trap
DISP distance (m) of path between 2 woods through fencerow
GAPN % of path to nearest wood as gaps
GAPP % of path between 2 woods through fencerow as gaps

TTRE % cover of tall trees (> 10m)
STRE % cover of short trees (4 - 10m)
TSHR % cover of tall shrubs (1.5 - 4m)
SSHR % cover of short shrubs (< 1.5m)
TVIN % cover of tall vines (1.5 - 4m)
SVIN % cover of short vines (< 1.5m)

GRAS % cover of grass
HERB % cover of herbs
LOGS % cover of logs
LITT % cover of litter
ROCK % cover of rocks
FRICH floristic richness

Table 2.7
Use of fencerows by chipmunks in 1989 from trapping data

fencerow id	number of captures	number of individuals	residency status in fencerow		
			resident	temporary residents	transients
A	18	4	2	1	1
B	44	13	3	6	4
C	12	3	1	0	2
D	13	6	1	3	2
E	19	8	3	1	4
F	25	12	1	2	9
G	39	17	1	9	7
H	18	6	2	0	4
I	0	0	0	0	0
J	1	1	0	0	1
K	0	0	0	0	0
L	14	5	2	0	3
M	13	6	1	1	4
N	18	2	1	0	1
O	0	0	0	0	0
P	17	8	1	3	4
Q	27	8	4	2	2
R	0	0	0	0	0

Table 2.8

Correlation coefficients and p values for the relationship between fencerow attributes
and the use of fencerows by resident and transient individual chipmunks

N = 18 fencerows, * = $p < 0.05$, ** = $p < 0.01$

Attribute	Residents		Transients		All individuals	
	R ²	p<	R ²	p<	R ²	p<
Width						
at 1m above ground	0.58	0.01 *	0.20	0.42	0.23	0.37
at 2m above ground	0.62	0.01 **	0.22	0.37	0.30	0.22
Vegetation types						
tall trees (> 10m)	0.71	0 **	0.59	0.01 **	0.59	0.01 *
short trees (4 - 10m)	0.69	0 **	0.57	0.01 **	0.55	0.02 *
tall shrubs (1.5 - 4m)	0.54	0.02 *	0.50	0.03 *	0.51	0.03 *
short shrubs (< 1.5m)	0.20	0.43	0.25	0.33	0.24	0.35
tall vines (1.5 - 4m)	0.49	0.04 *	-0.13	0.6	0.09	0.71
short vines (< 1.5m)	0.17	0.51	-0.06	0.82	0.04	0.89
grass	-0.54	0.02 *	-0.35	0.15	-0.37	0.13
herbs	-0.42	0.08	-0.35	0.15	-0.37	0.13
Structural features						
litter cover	0.55	0.02 *	0.28	0.26	0.27	0.29
logs and rails	0.33	0.17	0.01	0.96	0.06	0.83
rocks	-0.05	0.85	-0.03	0.91	0.05	0.86
Linear continuity						
distance to nearest wood (log)	-0.13	0.62	-0.29	0.24	-0.22	0.38
path length between woods (log)	-0.05	0.85	-0.54	0.02 *	-0.40	0.10
% distance to nearest wood as gaps	-0.62	0.01 **	-0.58	0.01 **	-0.62	0.01 **
% distance between woods as gaps	-0.48	0.04 *	-0.69	0 **	-0.62	0.01 **
Floristic richness	0.54	0.02 *	0.45	0.06	0.41	0.09

Table 2.9

Stepwise multiple regression analysis for number of individual
chipmunks captured in fencerows versus fencerow attributes.
Entry level of significance = 0.05, retention level of significance = 0.05

Dependent variable	Variable retained	Parameter estimate	F	Prob > F	R²
Residents	Intercept	-0.2131	22.56	0.0011	0.75
	Tall trees	0.1779			
	Tall vines	0.0361			
Transients	Intercept	16.7101	11.89	0.0016	0.61
	log(% gaps between woods)	-2.3066			
	log(distance between woods)	-4.3055			
Total	Intercept	9.2865	10.2	0.0056	0.39
	log(% gaps between woods)	-4.8541			

Table 2.10a

Factors resulting from principal components analysis on fencerow attributes (loadings > 44 shown)

Factor 1 woody, complex (48% of variance)	Factor 2 shrubs, vines, no trees (15% of variance)	Factor 3 isolation (11% of variance)	Factor 4 herbs (6% of variance)
litter	93	83	84
tall shrubs	91	-64	57
floristic richness	90	63	50
grass (-)	-90	-56	
width at 1 metre	85	51	
width at 2 metres	83	-47	
(log) % gaps between woods	-83		
short trees	78		
(log) % gaps to nearest woods	-74		
short shrubs	68		
tall trees	62		
herbs (-)	-56		
tall vines	56		
logs	50		
		(log) distance between woods	herbs
		(log) distance to nearest woods	53
		rocks	

Table 2.10b

Correlation coefficients for the relationship between the use of fencerows by individual chipmunks and factors derived from principal components analysis on fencerow features

Factor	Residents	Transients	Total
1 woody, complex	0.67 **	0.48 *	0.49 *
2 shrubs and vines (no trees)	-0.16	-0.37	-0.29
3 isolation	0.08	-0.41	-0.26
4 herbs	-0.26	-0.11	-0.18

Table 2.11

Chi square test of independence of
landscape use and residency type
(trapping study - 1990)

residency type	landscape use			total
	woods only	fencerows only	woods & fencerows	
residents	36 (31.69)	12 (20.47)	20 (15.84)	68
temporary residents	12 (16.31)	19 (10.53)	4 (8.16)	35
Total	48	31	24	103

description	frequency		(O-E) ²	(O-E) ² / E
	observed	expected		
R, W	36	31.69	18.58	0.59
R, F	12	20.47	71.74	3.50
R, W+F	20	15.84	17.31	1.09
TR, W	12	16.31	18.58	1.14
TR, F	19	10.53	71.74	6.81
TR, W+F	4	8.16	17.31	2.12
			$\chi^2 =$	15.26

df = 2, $\chi^2_{\text{table}} = 5.99$

Table 2.12

Chi square test of independence of
landscape use and age class
(trapping study - 1989)

age class	landscape use			total
	woods only	fencerows only	woods & fencerows	
adults	15 (15.27)	9 (14.37)	20 (14.37)	44
young	19 (18.73)	23 (17.63)	12 (17.63)	54
Total	34	32	32	98

description	frequency		(O-E) ²	(O-E) ² / E
	observed	expected		
A, W	15	15.27	0.07	0.00
A, F	9	14.37	28.84	2.01
A, W+F	20	14.37	31.70	2.21
Y, W	19	18.73	0.07	0.00
Y, F	23	17.63	28.84	1.64
Y, W+F	12	17.63	31.70	1.80
			$\chi^2 =$	7.65

df = 2, $\chi^2_{\text{table}} = 5.99$

Table 2.13

Chi square test of independence of
landscape use and sex
(telemetry study)

sex	landscape use			total
	woods only	fencerows only	woods & fencerows	
males	3 (6)	0 (1)	17 (13)	20
females	9 (6)	2 (1)	9 (13)	20
Total	12	2	26	40

description	frequency		(O-E) ²	(O-E) ² / E
	observed	expected		
M, W	3	6	9.00	1.50
M, F	0	1	1.00	1.00
M, W+F	17	13	16.00	1.23
F, W	9	6	9.00	1.50
F, F	2	1	1.00	1.00
F, W+F	9	13	16.00	1.23

$$\chi^2 = \frac{7.46}{1}$$

$$df = 2, \chi^2_{table} = 5.99$$

Table 2.14

Seasonal trapping counts of chipmunks in 1989 and 1990
showing the use of woods and/or fencerows by individuals

	1989	1990
Spring		
woods only	16	29
fencerows only	10	13
woods & fencerows	8	3
Total	34	45
Summer		
woods only	25	44
fencerows only	38	28
woods & fencerows	23	12
Total	86	84
Fall		
woods only	40	29
fencerows only	12	20
woods & fencerows	5	11
Total	57	60

Table 2.15

Chi square test of independence of
landscape use and season
(trapping study - 1989)

season	landscape use			total
	woods only	fencerows only	woods & fencerows	
spring	16 (15.56)	10 (11.52)	8 (6.91)	34
summer	25 (39.36)	38 (29.15)	23 (17.49)	86
fall	40 (26.08)	12 (17.49)	5 (11.59)	57
Total	81	60	36	177

description	frequency		(O-E) ²	(O-E) ² / E
	observed	expected		
Sp, W	16	15.56	0.19	0.01
Sp, F	10	11.52	2.31	0.20
Sp, W+F	8	6.91	1.19	0.17
Su, W	25	39.36	206.21	5.24
Su, F	38	29.15	78.32	2.69
Su, W+F	23	17.49	30.36	1.74
F, W	40	26.08	193.77	7.43
F, F	12	19.32	53.58	2.77
F, W+F	5	11.59	43.43	3.75

$$\chi^2 = 24.00$$

$$df = 4, \chi^2_{table} = 9.49$$

Table 2.16a

Mean average distance moved between sightings for chipmunks in the radio-telemetry study by sex, age, and sex*age

	number of individuals	mean move (m)	std dev
SEX			
females	20	58.72	37.54
males	20	64.84	36.82
AGE			
adults	20	53.60	21.39
young	20	69.97	46.75
SEX*AGE			
fa	10	42.92	13.79
fy	10	74.52	47.22
ma	10	64.30	22.86
my	10	65.41	48.36

Table 2.16b

Analysis of variance of distance moved between sightings among radio-collared individuals. The response variable is (log) distance moved between sightings. A modified repeated measures design was used to correct for individual variation

Term	df	MS	F calculation	F	p(F)
SEX	1	1.282	MS(sex)/MS(indiv) =	0.09	0.7678
AGE	1	20.748	MS(age)/MS(indiv) =	1.43	0.2391
SEX*AGE	1	44.015	MS(s*a)/MS(indiv) =	3.04	0.0898
INDIVIDUAL	36	14.481	MS(ind)/MS(error) =	6.70	0.0001
ERROR	1680	2.161			

Table 2.17a

Mean longest single move for radio-collared chipmunks by sex and age

	number of individuals	mean longest single move (m)	max longest single move (m)	min longest single move (m)
SEX				
females	20	208.07 +/- 107.40	407.92	89.44
males	20	259.08 +/- 109.70	457.06	80.62
AGE				
adults	20	237.07 +/- 113.13	438.63	111.80
young	20	230.08 +/- 110.06	457.06	80.62

Table 2.17b

Analysis of variance of longest distance between sightings among individuals.
The response variable is (log) longest single move for each individual.

Term	Df	Sum of squares	Mean square	F value	p(F)
SEX	1	0.61	0.605	2.44	0.127
AGE	1	0.02	0.017	0.07	0.794
SEX*AGE	1	0.33	0.326	1.31	0.26
RESIDUALS	36	8.89	0.247		

Table 2.18a

Mean linear range length for radio-collared chipmunks by sex and age

	number of individuals	mean range length (m)	max range length(m)	min range length(m)
SEX				
females	20	257.69 +/- 139.91	566.04	92.20
males	20	360.00 +/- 200.87	902.50	94.34
AGE				
adults	20	311.75 +/- 178.10	837.38	111.80
young	20	305.94 +/- 183.57	902.50	92.20

Table 2.18b

**Analysis of variance of mean linear range length. The response variable is
(log) distance between 2 most distant sightings for each individual**

Term	Df	Sum of squares	Mean square	F value	p(F)
SEX	1	1.19	1.882	4.13	0.049
AGE	1	0.01	0.008	0.03	0.869
SEX*AGE	1	0.48	0.477	1.66	0.206
RESIDUALS	36	10.35	0.288		

Table 2.19a

Mean linear range length for radio-collared chipmunks by habitat use

habitat use	number of individuals	mean range length (m)	max range length(m)	min range length(m)
woods only	13	173.23 +/- 93.56	424.85	92.20
fencerows only	2	410.12 +/- 3.1	412.31	407.92
woods & fencerows	15	313.47 +/- 157.85	837.38	190.26
fencerows & woods	10	457.95 +/- 184.72	902.50	240.83

Table 2.19b

Analysis of variance of mean linear range length. The response variable is (log) distance between 2 most distant sightings for each individual

Term	Df	Sum of squares	Mean square	F value	p(F)
LANDUSE	3	6.46	2.153	13.94	0.0001
RESIDUALS	36	5.57	0.155		

Scheffe test of pairwise significance

alpha = 0.05, Df = 36, MSE = 0.15
critical value of F = 2.866

Significant pairs:

woods - fencerows
woods - woods and fencerows
woods - fencerows and woods

Table 2.20

Home ranges for chipmunks exclusively resident in woods
calculated by minimum area polygon method

individual	sex	age	sample	home range m ²	linear range m
1997	f	a	76	26050	208.09
1688	f	a	52	13350	178.89
1068	f	a	61	10550	128.06
1956	f	a	69	9500	136.01
9993	f	a	25	6500	111.80
178	f	a	26	3600	120.40
2084	f	y	44	15600	200.25
1968	f	y	35	13350	92.20
153	f	y	26	5900	116.42
2080	m	a	16	18200	424.85
1641	m	y	67	7500	161.55
1697	m	y	23	2350	94.87
mean home range =		11037.50 m ²			
standard deviation =		6749.25 m ²			

Table 2.21

Seasonal population sizes for chipmunks in 1989 and 1990
by age and sex

	spring		summer		fall	
	1989	1990	1989	1990	1989	1990
Adults						
male	17	20	12	11	3	6
female	16	10	12	12	10	5
total	33	30	24	23	13	11
Young						
male	0	9	25	17	12	7
female	0	6	18	18	15	7
total	0	15	43	35	27	14
Unknown						
male	0	0	11	13	14	19
female	1	0	8	13	3	16
total	1	0	19	26	17	35
Total	34	45	86	84	57	60

Figure 2.1. Study landscape in Manotick, Ontario showing trapping grids in woodlots (W1 to W4) and trap locations in fencerows (A to R). Double dotted lines represent a creek. Double solid lines represent a lane bordered on both sides by fencerows.

Figure 2.2: Frequency and per cent frequency of distances moved between sightings for radio-collared chipmunks in the agricultural landscape.

2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISION^{SM} RESOLUTION TARGETS

Chapter 3

The Simulation

*The land is one organism. Its parts, like our parts,
compete with each other and cooperate with each other.
The competitions are as much a part of the inner workings
as the cooperations.*

Aldo Leopold

INTRODUCTION

Conservation biologists urgently need to predict the effects of changes to landscape structure on representative species. However, empirical studies at large spatial and temporal scales in comparable landscapes with different sets of structural attributes are prohibitive for most researchers and decision makers (Turner 1989). Simulation modelling offers a method of exploring scenarios and predicting population responses based on a set of parameters that describe the demographics and behaviour of a species.

The use of models in ecology has been criticized on the grounds that they are simplistic, assumption-ridden, and yield contradictory results (Simberloff 1981). However, as Caswell (1988) has pointed out, many of these criticisms apply to empirical studies as well. Both empirical studies and models provide insight into complex relationships by focusing on a particular set of variables and ignoring others. Both require independent testing for validation, and neither routinely receive this during the original study, the task most often being left for others. Models should of course be built from a knowledge base assembled from empirical studies, and when this criterion is met, they serve a vital purpose in the study of ecological relationships. Models offer the advantage of removing time and space constraints from a study, and permit manipulation of independent variables without disrupting a natural system. They are especially useful in isolating interactions among variables in complex systems, and can be used for clarifying our assumptions about how a system works. For these reasons, I use a model to explore the effects of landscape spatial structure and connectivity on the size and persistence of chipmunk and white-footed mouse populations, using parameters derived from my field study,

John Wegner's work with *Peromyscus leucopus*, and other empirical studies reported in the literature.

The model is an individual-based, spatially explicit, stochastic simulation. This type of model is becoming more common for studying interactions of organisms with their environment (see Pulliam et al. 1992, Beier 1993, Fahrig in press), and is useful when interactions of individuals are local (Judson 1994). In my model, each animal is tracked separately, with its own probability of reproduction, mortality, and dispersal at each time step. Local as well as long distance moves affect survival; local encounters affect spacing; and reproductive activities (breeding, gestation, and maturation) are followed through time.

Making predictions about the persistence of species in fragmented landscapes requires consideration of the spatial structure of the landscape, individual demographics, and the behaviourally mediated interaction of the two through local movement and interpatch dynamics (Urban and Shugart 1986, Morrison et al. 1992). Temporal variation in availability of resources and of species requirements adds another important dimension to the spatial and behavioural factors (Addicott et al. 1987). All four factors were included in the design of the model.

Three important components of spatial structure were modelled: the amount of usable habitat in the landscape, the number of habitat patches, and the quality of connectivity allowing access to these patches for the target species. To compare species persistence for different amounts of habitat and numbers of patches, the outer dimensions of the model landscape are held constant. It should be noted that amount of habitat, patch size and interpatch distance cannot be varied independently when landscape area remains the same (Fahrig 1992, Harrison and Fahrig

1995). Therefore, I have not been able to control for interpatch distance in the simulations. However, data from the field studies suggest that long distance movement is possible at the scale of the simulated landscapes for both chipmunks and mice, so the effects of interpatch distance will be small in the simulation.

Species respond differently to changes in spatial structure, and therefore will fare differently in the same landscape. There is a vital link between the scale of fragmentation and the scale of movement (Lord and Norton 1990, Saunders 1990, Wiens 1995). The rate of change of dispersal must track the rate of change of the landscape for species' survival. For less mobile species unable to make the change, increased fragmentation means complete isolation and low probability of persistence. Soulé et al. (1988) found chaparral-requiring birds in urban habitats suffered high rates of extinction due to low vagility and high levels of fragmentation. For more mobile specialists, movement among habitat patches enables them to knit together enough traditional resources to persist. Studies of red squirrels in fragmented woodland in the Netherlands and Italy indicate that the animals use several patches to make up a home range provided there is adequate connectivity (Verboom and van Apeldoorn 1990, Celada et al. 1994). Finally, for generalists able not only to adjust their movement patterns but also their habitat requirements, adaptive behaviour that turns novel resources to their advantage ensures survival (Merriam 1988, Bright 1993). Laurance (1991) studied mammals in forest fragments in Australia and found that species that could move through modified habitats or could use new resources were more likely to remain stable or increase in the fragments compared with those adhering strictly to old behaviour patterns.

In this chapter, I describe the construction of experimental landscapes, and the design, parameterization, and implementation of a simulation model; I compare the specialist response (chipmunk results) with that of a generalist (white-footed mouse results) in selected similar landscapes; and I discuss the results and their implications in the context of current understanding of the effects of landscape fragmentation on the conservation of species in human-altered landscapes.

METHODS

DESIGN:

I simulated the population dynamics of chipmunks in 36 variants of a 200 ha landscape, and white-footed mice in a subset of 8, based on knowledge obtained in the field and studies from the literature, using an individual-based, spatially explicit model designed for the purpose. The landscapes reflected a range of habitat type, fragmentation and connectivity. For each landscape, four steps are required to obtain a measure of population success in that particular pattern (see figure 3.1):

- a) Landscape design - use of a GIS to prepare landscape grids identifying the spatial and functional parameters of the landscape.
- b) Routing - calculation of weighted routes for individual movement between all habitat patches based on quality of the route for the species and distance between the two patches.
- c) Demography and movement - simulation of population dynamics (initially 16 individuals) for 25 years based on demographic parameters, weighted routes, and landscape composition, configuration, and connectivity. One hundred trials (repetitions) are run within each simulation to obtain a statistical sample of results for each landscape variant.
- d) Results - calculation of response variables including mean number of years survived (out of 25), extinction rate, maximum population size in each trial, and mean coefficient of variation of the population size for the 100 trials.

I now present a more detailed description of each of these steps. Copies of all programs and a representative set of input and output files are included on disk.

A) Landscape design:

Landscapes for the simulations were designed using the GIS package EPPL7 (EPPL7, 1990). All landscapes contained 4096 cells (64 X 64 cells). Assuming each cell measures 22 X 22 m, the landscapes represent an area of approximately 200 ha. Landscape elements included woods, agricultural fields (corn, pasture and grain) and high and low quality fencerows. I varied the composition of the landscapes by setting the percentage of wooded habitat at 10, 30, or 50 per cent of the total area. This wooded habitat was divided evenly into 2, 4, or 8 patches within a landscape, giving 3 different configurations for each percentage of woods. For each of these 9 combinations there were 4 different levels of connectivity modelled, resulting in a total of 36 unique treatments of the same landscape (see figure 3.2). Connectivity was either high (all fencerows good quality), mixed (half fencerows high quality, half low quality), low (all fencerows low quality), or absent (no fencerows at all). Each level of quality was associated with a specific probability of mortality for individuals travelling through it.

Two files were produced by the GIS:

- i) a file with a unique identifier for each landscape element (i.e. each separate piece of the landscape). For example, all cells of the first woodlot might be assigned a 1, all cells of the second woodlot a 2, etc.
- ii) a file identifying the type of element (i.e. the cells of all woodlots from the previous file contain a 1 in this file, the cells of all corn fields contain a 2, etc.).

Two additional files were created based on these two GIS files:

- iii) a file containing XY coordinates for a central cell in each landscape element.
- iv) a file listing pairs of wooded patches that have direct connections (i.e. are connected by a single fencerow), and a code indicating the quality of these connections: 1 = high, 2 = low, 3 = mixed (for some 2-patch landscapes).

B) Routing:

The routing algorithm is part of a program called SETUP written in Turbo Pascal 6.0 (Borland 1990). This program converts the landscape files discussed above to the format expected by the model, creates a set of patch records, and calculates the routing information required to move animals around in the landscape. A copy of SETUP is on the disk.

The routing algorithm uses the file of direct connections and their ratings to calculate the most efficient route between all pairs of patches in the landscape. Ratings of indirect routes are based on the ratings of the incorporated direct routes plus the number of nodes (patches) between the target pair. Where the distance between the centres of the pair of patches exceeds 48 cells (1 km), the value of the rating is increased by one. Thus, short, direct, high quality routes have low ratings, and long, indirect, low quality routes have higher ratings. These new, comprehensive ratings are used in the movement routines of the population simulation model, where they help determine choice of destination and probability of survival during a long-distance move. For a more detailed description of this algorithm, see appendix I.

C) Demography and movement:

The simulation model was designed to follow a population in a specified landscape over 25 years. The program is called POPULATION, and was written in Turbo Pascal version 6.0 (Borland 1990). A general flowchart appears in figure 3.3 and a listing of the code may be found on the disk. POPULATION requires the following input:

The landscape grid from SETUP

The patch identification file from SETUP

The routing file from SETUP

A file containing the location in the landscape of each individual in the initial population

A set of parameters to control the demographics and movement probabilities of individuals

The program follows a population of females, individual by individual, weekly for 34 weeks plus an 18 week winter hiatus, for 25 years. Population size is reported yearly. One hundred repetitions (trials) are made for the same population and landscape, and each trial has a slightly different outcome because of the stochasticity of the demographics and movements. A different seed for the randomization function is chosen at the start of each set of 25 years to ensure variation among trials.

I limited the number of years in the simulation to 25 since this represents a practical projection period from a management perspective, given the present rate of change of landscapes. Twenty-five years was also sufficient time for the population in the highest quality landscape (50% habitat, 2 patches, high connectivity) to reach a size in all trials at which demographic stochasticity alone could not cause an extinction. Results for all other landscapes could then be

compared to this result. I did not analyse the model for steady states, since my goal was to assess the relative effects of landscape parameters and their interactions on species with generation times of a year or less over a period relevant to planners and conservationists, not to do dynamic systems analysis.

Three main procedures, MORTALITY, REPRODUCTION, and MOVEMENT, determine if individuals survive from the previous time period, mature, become pregnant or give birth (thereby adding new individuals to the population), or move within the landscape, either long or short distances. A more detailed description of these routines is given below, and flow diagrams are in figures 3.4 to 3.6. Finally, a file showing the size of the population at the end of each year for each of the 100 trials is produced and output at the end of the program.

Mortality:

The MORTALITY procedure is called first for each individual. Those surviving this 'first cut' every week may go on to reproduce or move in the landscape. Mortality rate varies depending on the age of the individual, the type of landscape element occupied, the population density within that element, and the season. There is no mortality in this procedure in the first week of the first year. It is assumed that members of the initial population are winter survivors. In the first week of subsequent years, an overwinter mortality rate is applied. This rate covers the 18 week period of inactivity in winter, and is therefore higher than the weekly rate used in the regular season. Mortality rates may be adjusted for age (young, adult, older adult), and location (poorer quality landscape elements may be assigned higher rates). The decision of whether or not the individual dies is based on the adjusted mortality rate and the value of a random number. The animal dies if the random number chosen is less than or equal to the

mortality rate. Animals that die are removed from the linked list of individuals, and from the landscape grid cell where they resided.

Mortality rates:

regular season calculation:

$$m = m_r * a_s * a_l$$

overwinter calculation:

$$m = m_o * a_s * a_l$$

high density calculation:

$$m = m_{cr} * a_s * a_l$$

$$m = m_{co} * a_s * a_l$$

where m = mortality rate, m_r = regular season mortality rate, m_o = overwinter mortality rate, m_{cr} = crowded seasonal mortality rate, m_{co} = crowded overwinter mortality rate, a_s = age adjustment, a_l = location adjustment.

Reproduction:

The REPRODUCTION procedure tracks the age and reproductive status of individuals, and applies breeding rates to adults in the appropriate weeks of the simulation. Breeding rates are adjusted for season and location. Litter size is randomly determined from a range of appropriate values, and infant survival rates determine how many new animals will be added to the population when the time required for pregnancy and nursing have elapsed. New young individuals being added to the population are initially assigned the same grid location as the mother. This is the only time more than one individual is allowed to occupy the same grid cell. These new individuals will be required to move and find their own home area in the movement routine. Finally, the reproduction routine keeps track of the age of young individuals to

determine when they become reproductive. New young are assigned the week in which they were born as an indicator. By comparing this to each current week, the age of maturity can be detected. Animals that have bred are flagged to prevent them from breeding again until the appropriate time has elapsed.

Reproduction rate:

$$r = r_w * a_i$$

where r = reproduction rate, r_w = reproduction for the current week, a_i = adjustment factor for the location of the animal.

Movement:

The MOVEMENT procedure follows reproduction, and determines if the individual will leave its current location and move to a new grid cell, either within the same immediate area (a local move) or to another patch (a distant move). Individuals that are pregnant or nursing do not move. Young individuals that were newly added in the previous routine always move, as explained above. Other adults and young move with some probability determined by their age, the season, and the population density of the landscape element where they are currently located.

When an individual is to move, there is some probability (p) that the move will be local, and a corresponding probability ($1-p$) that it will be distant. Separate subroutines, DISTANT_DISPERSAL and LOCAL_DISPERSAL, handle sections of the move depending on the choice made. The term 'dispersal' used in the simulation does not imply that these moves are irreversible. Individuals may move again in the next time period, as was observed in the empirical study.

1) DISTANT_DISPERSAL - moving to a distant location:

When the move is to be over a long distance, and the animal is currently located in a fencerow, the distant move is accomplished cell by cell over 45 cells. If the animal is currently in a patch, a table of all possible distant patches and the rating of the routes associated with them is constructed. The final destination is determined partly by chance and partly by the ratings of the routes.

Chipmunks in the field study demonstrated that animals discriminate among habitat types when moving in the landscape. Fencerows providing good cover of trees and tall shrubs were used more often for movement between wooded patches. In an earlier study, Merriam and Lanoue (1990) found that white-footed mice preferentially selected structurally complex fencerows over simpler ones for travel through farmland. This bias towards higher quality movement routes is built into the model.

Routes with lower ratings (higher quality routes) are favoured. There is a diminishing set of probabilities that permits the choice of lower quality routes should they exist in the table. When a destination has been chosen, the individual is moved to a central location in the new patch. A set of mortality rates associated with long distance moves is applied to these individuals, regardless of their point of departure. These probabilities are related to the ratings of the routes and may be adjusted for the age of the individual. Animals that die are removed from the population as in MORTALITY. The survivors are ready for the second stage of their journey: finding a vacant grid cell in the new patch. The algorithm for this is shared with the animals making a local move, and is described next.

2) LOCAL_DISPERSAL - moving within a patch:

Individuals enter this routine to move from their current grid location to another vacant one in the same patch. There is a probability of mortality associated with a local move as well. This is adjusted by age and applied at the beginning of the routine. Animals that die are removed from the population. Survivors are ready to move. There are three factors involved in a local move. They are i) direction of the move, ii) distance moved, and iii) finding a vacant location:

i) direction of move: Theoretically, there are nine possible directions in which to move from any grid cell. The initial direction is randomly chosen, and that direction, or its immediate neighbours on the compass points, are favoured for subsequent moves. For example, if the direction 'north' is chosen, possible moves are north-east, north, and north-west. Circular moves are not permitted.

ii) distance moved: An initial directional set of moves is made before the individual begins to search for a new cell.

iii) finding a vacant location: After the initial moves, each cell encountered is a potential home cell. A cell is acceptable if it is vacant and if some number of cells immediately adjacent to it are also vacant. For example, for chipmunks in woodland, there must be at least 1 empty cell between each inhabitant, since chipmunks are territorial within 15m of their burrow (Yahner 1978a). In high quality fencerows I set the minimum distance between occupants at 5 cells, based on field observations and the narrow width of these areas. If the cell is not acceptable, the animal moves to an adjacent cell. When a suitable cell is encountered, the individual becomes

established there. There is a maximum number of moves that can be made in search of an acceptable cell. If this is exceeded, the individual is removed from the population.

Dispersal rates are affected by age, season, current location of the individual, and local population density. Probability of a long distance versus a local move is affected by age.

Dispersal rates:

$$d = d_y * a_s * a_l * c$$

$$d = d_a * a_s * a_l * c$$

$$D = D_{ny} \text{ or } D_y \text{ or } D_a$$

where d = dispersal rate (probability of moving), d_y = probability of moving for young, d_a = probability of moving for adults, a_s = adjustment for season, a_l = adjustment for location, c = adjustment for high population density, D = distant dispersal rate, D_{ny} = probability of distant dispersal for new young, D_y = probability of distant dispersal for young, D_a = probability of distant dispersal for adults.

Dispersal mortality rates:

$$m_{dd} = m_r * a_a$$

$$m_{dl} = m_l * a_a$$

where m_{dd} = mortality rate for distant dispersal, m_{dl} = mortality rate for local dispersal, m_r = probability of mortality for route rating, m_l = probability of mortality for local move, a_a = adjustment for age.

D) Results:

A separate program called SUMMARY converts the output from the simulation model to a SAS compatible format, and calculates summary statistics from the 25 year X 100 trial file of population sizes produced by the model for a particular landscape. These include:

- i) extinction rate: the number of trials out of 100 in which a population fell to zero. This is a measure of persistence of a population in a particular landscape beyond 25 years.
- ii) mean years of survival: the number of years survived (out of 25) in each trial, averaged over 100 trials. This provides a measure of length of persistence in the landscape.
- iii) global maximum population size: the largest population recorded for a landscape anywhere within the 25 years X 100 trials. This provides an upper limit to the size of population a landscape will support.
- iv) mean local maximum population size: the average over 100 trials of the largest population size recorded for each trial.
- v) pre-extinction maximum population size: maximum population size reached before an extinction. This was calculated to determine population levels where the risk of extinction remained present.
- vi) coefficient of variation of population sizes: This is calculated from the average (over 100 trials) of the mean population sizes and variance calculated for each trial. Population sizes of zero are not included in the calculation of the mean for a particular trial after the first occurrence. The coefficient of variation provides a relative measure of the amount of variability of a population in a particular landscape (Pimm 1991).

A copy of SUMMARY is on the disk.

PARAMETERS:

Parameter values common to both chipmunk and mouse simulations include grid size (64 X 64 cells), number of weeks (34), number of years (25), and number of trials (100). Demographic parameters have been tailored to the individual species, and the values used are shown in table 3.1. I have chosen the value of these parameters based on my chipmunk field data, the chipmunk literature, John Wegner's white-footed mouse field data, and the white-footed mouse literature.

All simulations began with 16 individuals in the population, evenly distributed among habitat patches. This number was chosen as a result of preliminary runs made using the landscape with 30% wooded habitat, 4 patches and high connectivity (the landscape that corresponds most closely to the study landscape), as I did not want the size of the initial population to constrain the outcome of the simulations. I varied the starting numbers from 8 to 24 individuals. At 8 individuals, the extinction rate was 35%. However, it fell sharply as additional individuals were added. At an initial population size of 16 individuals, the extinction rate in the test landscape was zero. Trials beginning with more than 16 individuals showed little additional improvement in population sizes achieved. Therefore all runs began with 16 individuals, evenly divided among habitat patches (woods for chipmunks, woods and corn for mice) but distributed randomly within them.

A) CHIPMUNKS:**Reproduction:**

In the spring of 1989, 15 of 18 females present in my mark-recapture study site were pregnant or lactating, a reproduction rate of 83%. Nine of 10 females were reproductive in the spring of 1990, a rate of 90%. This gives a mean reproduction rate of 86%. These rates are consistent with the range of rates found in studies by Pidduck and Falls (1973) (mean of 80%) and White and Svendsen (1990) (90%). In the model, I have used a probability of pregnancy of 0.4 per week for the 4 spring breeding weeks, which is an overall rate of 86%.

There is a different rate for animals breeding in summer that have not bred in spring. In the summer of 1989 there were 6 females that had not been pregnant that spring. Of these, 4 subsequently bred (a rate of 66%). In 1990 there were 5 that failed to reproduce in spring and 2 of these individuals became pregnant in the summer (a rate of 40%). The mean summer reproduction rate was thus 53%. Pidduck and Falls (1973) reported rates of 0, 14, and 100% over the summer (a mean of 47%), suggesting high levels of variation associated with summer breeding. Environmental factors such as weather and food supply as well as survival of summer born females from the previous year are likely important. I have used a summer breeding probability of 0.20 per week for 4 weeks for individuals that did not breed in spring, which is an overall rate of 50% for the summer period.

Females sometimes breed twice in the same year (Yerger 1955, Smith and Smith 1972). In 1989, 5 individuals that had bred in spring were recaptured in the summer, and two of these

were pregnant (40%). There were 7 surviving previous breeders captured in summer 1990, and one of these was pregnant (15%). This gives an average summer rate for repeat breeding of 28%. However, this estimate may be low because there were several summer breeders that were not captured in the spring, so I have used a rate of 34% which represents a weekly probability of breeding of 0.10.

An adjustment factor was applied to the basic rate to reflect differences in the probability of successfully raising a litter in different types of habitat. I used a lower reproduction rate for chipmunks in fencerows because fewer females raised families in that habitat. Reproduction probabilities were halved in fencerows of high quality and animals did not breed at all while in low quality fencerows.

In the chipmunk simulation, females born in the spring are eligible to breed the following spring, and females born in summer are eligible to breed the following summer. Pregnant females remain in the same cell for 10 weeks (4 weeks gestation, 5 to 6 weeks of lactation and mothering (Burt, 1940, Pidduck and Falls 1973, Yahner 1978b)). After 10 weeks the new young are added to the mother's cell, and they subsequently disperse, because mothers become intolerant of their young a few days after they emerge from the natal burrow (Roberts and Snyder 1971).

To determine litter size, I looked at the number of adult females trapped between early May and early July in 1990. I found that of 10 individuals, 9 were in reproductive condition. Forty-four young were identified before mid July. This gives a surviving litter size of 4.9 animals. Smith and Smith (1972) suggest that litter sizes in Canada range from 1 to 9, and they reported means of 4.9 ± 0.2 in their study based on uterine scars. Other researchers agree that

litters are commonly 4 or 5 individuals (Yerger 1955, Seidel 1961). Pidduck and Falls (1973) reported a mean of 2.8, 4.9, and 5.3 emergent young from their study. These values suggest that some infant mortality may occur prior to emergence, but that it is quite low. For the model, litter size was drawn from a range of 1 to 5 pups (females only) using the Turbo Pascal random number function. I applied a 90% probability of survival to spring born infants. For summer births, the same range of litter size was used (Pidduck and Falls 1973), but I applied a survival rate of 50%, since Yerger (1955) found only 18% of summer born individuals were recaptured the following spring.

Chipmunks are coded by age as follows:

- 1 = new young. Individuals retain this status between the time they are added to their mother's cell and their dispersal to a cell of their own.
- 2 = young. This is the status individuals receive after successfully dispersing from their natal cell.
- 3 = adult. Animals mature in the week of their birth the following year. Animals with this status are 1 year old.
- 4 = adult. These adults are 2 years old.
- 5 and up = old adults. These individuals are over 2 years old. The probability of mortality increases by a factor of three.

Mortality:

I used a weekly probability of mortality for each chipmunk of 0.02. Over 33 weeks (between April and November) this amounts to a survival rate of 54%. This rate is consistent

with results of Tryon and Snyder (1973) who reported a survival rate of .66 for 6 months, which gives a weekly probability of survival of 0.98.

When patches become crowded, good burrows are hard to get and food may be insufficient to support the population. I have increased the mortality probability to 0.15 per week in crowded patches. Patches are considered crowded when:

$$(\text{number of cells in patch} / \text{number of cells occupied}) < 7.$$

Fencerows are not included in this calculation.

Mortality rate is also adjusted for location. The base mortality rate is multiplied by a factor of 2 in low quality fencerows, and by a factor of 1.1 in high quality fencerows. Therefore mortality in low quality fencerows > mortality in high quality fencerows > mortality in woods.

I used trapping data to estimate the overwinter mortality rate for the chipmunk population. I identified 61 individual chipmunks present between August 28 and September 28, 1989. Thirty-eight of these animals were recaptured in 1990, beginning in early May. This gives a mortality rate of 38% over 30 weeks (18 winter weeks plus 8 additional weeks in the fall and 4 in the spring), which translates to a weekly probability of mortality of about 0.02 for this period. This is similar to the weekly mortality rate of 0.02 that I have used for the 34 week regular season, and may not be unreasonable since risk of predation is lower while animals are below ground and may offset increased risks due to extreme temperatures, flooding, and food

limitations. I have used a mortality rate of 25% for the 18 week inactive period, which represents a weekly probability of mortality of 0.018, and results in a 30 week rate of 38%..

In patches where crowding occurs, overwinter mortality rises to 50% over the 18 weeks, since more animals are assumed to be using inferior burrows.

Movement:

Probability:

Chipmunks in the telemetry study moved around a great deal, but 50% of these moves were less than 40 m and few involved permanent shifts in home area. Nevertheless, longer moves do take place: 45% of all moves were over 200 m, and 14% of individuals made moves greater than 340 m. These longer moves are important for recolonizing local extinctions (Henderson et al. 1985) and providing gene flow in the landscape (Slatkin 1985, White and Svendsen 1990). I wanted to simulate the ability of chipmunks to move in the landscape without recording every short exploratory move, since this would have taken a prohibitive amount of time to run, and would not have served a useful purpose. I will refer to these longer moves as dispersal, although they are not necessarily permanent (i.e. the individuals may move again the following week).

I calculated the proportion of individuals in the 1989 and 1990 weekly populations that were transients, and found they made up 6% of the weekly population over the summer. Transients are so classed because they were caught only once; the failure to recapture these

individuals may be due either to mortality or dispersal. Since the mortality probability is .04 per week, I used a probability of dispersal of .02 per week for adults.

Yahner (1978a) found that young chipmunks shifted burrow systems twice as frequently as adults. Young individuals have an enforced shift in the model in the week they are added to the population. I set the probability of subsequent dispersal for young chipmunks to .03 per week.

Table 3.2a shows the adjustment factors applied to the basic probabilities of dispersal for adults and for young based on home location and season. These factors were determined from seasonal use of landscape elements (table 2.14) and age-specific uses of the landscape obtained from the field data (tables 2.12, 2.15). For example, I reduced the dispersal rate for adults located in woods in spring and fall, but increased it for young in woods in summer. I doubled the probability of dispersal in the fall for both adults and young if they were located in a high quality fencerow, and I increased dispersal probability 10 times more likely for animals located in low quality fencerows. In addition, when the home patch was crowded, the probability of dispersal increased five-fold.

Once an individual has been selected to disperse, the move may be local (a cell by cell move) or distant (a direct transfer to another patch to which a route exists). I needed to estimate the proportion of each type of move. Yahner (1978a) measured how far chipmunks moved when establishing a new home area in a 5 ha woodlot. He found an average shift of 40 m with a maximum shift of 125 m. Since movements in my study are larger than those reported in previous work, I chose 80 m as the minimum distance of a local home range shift.

I used both trapping and telemetry data to estimate the threshold for distant dispersal. First, I looked at real distances and exchanges between patches. Woodlots in the study landscape are 360 m to 1500 m. apart. Three of 257 individuals in the trapping study were captured in more than one woodlot, and one of these moves covered a round trip distance of 1600 m. One of 40 individuals in the telemetry study also used two woodlots, moving a distance of 840 m in a single day. In a previous study in the same landscape, a male chipmunk moved back and forth between two of the woodlots several times, a distance of 320 m each way (K. Stuart-Smith and G. Merriam, unpublished data). Henderson et al. (1985) recorded 6 animals moving between woodlots over a distance of 0.5 km or more. Four of these animals were young of the year, and 2 were older individuals.

Since distances between patches in the model landscapes range from 88 m to 1360 m, the above moves confirm that chipmunks were capable of covering these distances. I chose 180 m as the threshold for long distance moves. A move of 180 m every day for 7 days would enable the traveller to make all but one of the trips between patches in the model in the simulation time step. Since 7% of moves in the telemetry study exceeded 180 m, the outstanding trip is also possible.

I then ran a frequency distribution on all moves over 80 m. for adults and young. For adults, 20% of these moves were greater than 180 m. I therefore set the adult probability of local dispersal in the model to 80% and the probability of distant dispersal to 20%. For young animals, 40% of moves over 80 m were greater than 180 m, so I set the probability of a young animal dispersing locally to 60%, and of dispersing between patches to 40%.

Mortality:

A set of mortality rates were applied within the dispersal routines to simulate increased risk associated with moves into new territory. Clarke et al. (1993) showed that chipmunks in unfamiliar territory took longer to find shelter under threatening conditions than did chipmunks in their home area. I used 0.02 for a local move, and a set of increasing rates for decreasing quality of routes for long distance moves, ranging from 0.03 for the highest quality route to 0.50 for the lowest quality one. Animals that moved long distance and failed to find a vacant cell in the new patch suffered 100% mortality.

In landscapes with isolated patches, no distant dispersal takes place. Ten per cent of animals that become distant dispersers are returned to their original patch as local dispersers. The other 90% disappear from the population.

Length of moves:

Local dispersers move a random number of cells (LocalMoves) in a random direction before beginning to search for a vacant cell. This can result in moves out of the home patch into the fencerows, or out of fencerows into a new patch. I set the maximum number of pre-moves at 12.

Distant dispersers that start their moves in a fencerow move 45 cells before beginning to look for a vacant cell. This is to ensure a long-distance move in all landscapes.

To prevent chipmunks from wandering forever in the local patch in search of a vacant cell, I assigned a limit of 50 moves (not including the 45 moves above). The animal then becomes a frustrated disperser with a mortality rate of 100%.

Spacing:

Each chipmunk in the simulated landscape must have at least one vacant cell between it and a neighbouring animal. This gives a minimum distance between burrows of 44 m. This is consistent with White and Svendsen's (1992) estimate of 40 m. The spacing between individuals in fencerows was set at 5 cells in high quality fencerows and 7 cells in low quality fencerows.

B) MICE:

Reproduction:

Breeding in white-footed mice is bimodal, with peaks in spring and fall, and a hiatus over midsummer (Sheppe 1965, Rintaama et al. 1975, Cornish and Bradshaw 1978, Wolff 1985, Morris 1986). The lull in breeding falls in July in the Ottawa area (Wegner unpublished). Wolff (1985) and Cornish and Bradshaw (1978) report breeding beginning in late March and peaking in April and May, with a second peak in September and October. I have set a higher probability of reproduction (0.30) for weeks 1 to 10 (late March through May) and 22 to 27 (late August to early October), and a lower one (0.20) for weeks 11 to 14 (June) and weeks 19 to 21 (early August). There is no breeding in July. Nest box data (Wegner unpublished) suggest that natality is highest in woods and cornfields, the relationship between natality and habitat type being: natality in woods = cornfield > grainfield > fencerow > pasture. Morris (1991) also found

a higher success rate for litters in woods than in fencerows. I therefore adjusted the basic probability by a factor based on the individual's location. The rate was not adjusted for woods or cornfields, it was reduced by 25% for grainfields and by 50% for high quality fencerows. Mice did not breed in low quality fencerows or pasture. Harland et al. (1979) reported a reproduction rate of 66% over the breeding season at this latitude. My basic rate is 75%, but the true rate may be somewhat lower depending on the location of the animals at the time of breeding.

Unlike chipmunks, most adult mice breed at least twice during the season. Pregnancy lasts for 3 weeks, mothers nurse their pups for another 3 weeks, and the young are weaned in the 7th week (Millar et al. 1979). They separate from their mother the following week (Nicholson 1941) and disperse up to 1 km from the natal site (Stickel and Warbach 1960). In week 11 they become reproductive (Millar et al. 1979).

In the simulation, pregnant females remain in the same cell over the 6 week period, and the new young are added to their mother's cell in week 7. The young all disperse the following week and find their own home cells. They attain adult status 7 weeks later. Mice in their third year are considered old. Although the OLD parameter is set to 5, the same value as for chipmunks, the mice are old a year earlier because they mature in their year of birth while chipmunks mature in the following year. Although turnover is very high among mice in the agricultural landscape (Wegner and Merriam 1990), much of this can be attributed to the highly mobile nature of these individuals. Therefore I have assumed that some individuals may survive for 2 years.

There is general agreement that average litter size approaches 5 at this latitude (Coventry 1937, Millar et al. 1979, Millar 1984, Morris 1986, Wegner unpublished). Therefore litter size was randomly selected from a range of 1 to 5 (females only) using the Turbo Pascal random function. There are two levels of infant survival, a slightly higher one for spring and summer litters, and a lower one for fall litters. Harland et al. (1979) found 69% to 88% of nestlings entered the population. Wegner (unpublished) found 90 individuals weaned out of a possible 115 from the nestbox study, which is a 78% survival rate over the season. I used a survival probability of 0.9 for spring and summer infants and 0.8 for fall infants. Since some additional mortality occurs in the model as a result of the obligatory initial dispersal event, this slightly higher infant survival rate is likely justified.

Mortality:

Reports of adult survival during the breeding season are quite consistent. A literature survey by Millar (1984) yielded an average two week survival rate of 0.81. This represents a weekly survival rate of 0.91. Adler and Tamarin (1984) found an average weekly survival rate of 0.96 and Wolff (1985) observed a range from 0.87 to 0.95 per week. Since Krohne et al. (1984) suggest that up to 15% of disappearances are due to dispersal rather than death, I chose a slightly higher rate of 97% survival, which gives a basic probability of mortality for adults of 0.03 per week. Mortality increases to .10 in crowded patches.

Adjustments to the basic mortality rate are made for age and location as they were for chipmunks. The average rate of survival for young white-footed mice is reported to be less than that for adults (Adler and Tamarin 1984, Millar 1984). I have increased the probability of

mortality for young mice by a factor of 2 to 0.06 per week. Old individuals have a chance of dying that is three times the basic adult rate. Individuals in grain fields in the fall are considered at higher risk because of increased exposure to predators after harvest. Mice in low quality fencerows are also considered more vulnerable. Mortality rate is doubled in these areas. For high quality fencerows the basic rate is increased by a factor of 1.1 resulting in a rate of 0.033.

Overwinter mortality is higher for white-footed mice than chipmunks. Snyder (1955) and Harland et al. (1979) found overwinter mortality rates in woodland of 0.88 and 0.87 respectively (Millar 1984). Wegner (unpublished) estimated minimum number of individuals known alive in Ontario farmland in November 1987 and in March and April 1988, prior to spring births. The size of his spring population was only 30% of the fall one. However some imbalance in dispersal into and out of the population may be imbedded in these results. A 15% reduction in the mortality rate due to dispersal is not unreasonable according to Krohne et al. (1984). Lackey et al. (1985) even suggest that overwinter mortality may sometimes be lower than mortality during the regular season. I set the overwinter mortality rate at 0.60 for 18 weeks, which is a weekly probability of mortality of 0.06.

Movement:

Probability:

Mice in the agricultural landscape move frequently and cover large distances. Wegner and Merriam (1990) rarely captured the same individual more than 2 or 3 times, and reported an average turnover rate of 75%. By comparison, mean turnover rate of chipmunks in my study was 53%, so I set the weekly probability of dispersal for mice at 1% higher than the rate for

chipmunks. This gave adult mice a dispersal probability of 0.03 per week. Most studies agree that young mice have a higher rate of dispersal than adults (Madison 1977, Fairbairn 1978, Krohne and Miner 1985, Adler and Tamarin 1985), so I set the probability for young individuals to 0.04 per week.

The high turnover rate also suggests a higher proportion of long distance to local moves, with young individuals again having larger ranges than adults (Wegner unpublished). I set the ratio of long distance to local dispersal to 30:70 for adult mice and 40:60 for young mice. New young were less likely to be transient than the other groups (Madison 1977), so I set their ratio at 20:80. Krohne et al. (1984) found no correlation between density and dispersal, so the adjustment to the basic dispersal rate for crowded locations was not used for mice.

Table 3.2b shows the adjustment factors applied to the basic probabilities of dispersal for adult and young mice based on season and home location. I determined these factors from the probabilities for dispersal for adults and young in different seasons observed by Krohne and Miner (1985) and turnover levels in a farm landscape (Wegner unpublished) in different seasons.

Mortality:

Krohne and Burgin (1987) reported a higher mortality rate during dispersal events than in their home area for white-footed mice. I have used the same dispersal mortality rates and rules for behaviour in isolated patches for the mice as for the chipmunks.

Length of moves:

Average moves for mice in the agricultural landscape were smaller than those that I found for chipmunks (Wegner unpublished). Therefore I reduced the local pre-moves ceiling to 6 for the mice. They moved a random number of cells from 1 to 6 in the simulation before searching for a vacant cell.

Pre-moves for long distance dispersal originating in fencerows remain at 45 cells (representing a distance of 990 m), and the limit to the number of moves made in the search for a vacant location remains at 50 cells (1100 m).

Spacing:

Female *Peromyscus leucopus* are territorial during the breeding season (Burt 1940, Nicholson 1941). I have set the number of cells required between individuals in woods, corn, and grainfields to 1, a minimum distance of 44 m between nests. Female home range sizes are estimated to be from 0.1 to 0.5 ha. The mean home range estimated by Wegner from nestbox data in this agricultural landscape was 0.45 ha. Assuming a circular range, the diameter would be 76 m. It is unlikely that a female is aggressively territorial over the whole area, so my parameter is approximately half the diameter of the largest reported area. The spacing between individuals in fencerows was set at 3 cells for high quality fencerows and at 5 cells in low quality ones.

RUNS:**A) Chipmunks:**

I made 36 runs using chipmunk parameters in the basic model to determine the effect of different levels of wooded habitat, fragmentation, and connectivity on the persistence and potential size of a chipmunk population in a landscape of fixed dimensions. The proportion of wooded habitat in the landscape was set at 10% or 30% or 50%. Each of these habitat levels was combined with 3 levels of fragmentation, i.e. the wooded habitat was divided into 2, 4, or 8 patches. Four different levels of connectivity for chipmunks were applied to each of these nine arrangements. Connectivity was either high (all fencerows good chipmunk habitat), low (all fencerows marginal chipmunk habitat), intermediate (a mixture of high and low quality fencerows), or absent (no usable margins around or between fields). I ran 100 trials for each landscape.

Persistence for each trial was measured as:

- 1) the presence or absence of an extinction by year 25
- 2) the number of years survived out of 25.

Large populations are buffered against stochastic reductions that occur as a result of environmental fluctuations (eg. harsh winters, variable food supply). Therefore, the size of population that a landscape can support is a factor in the population's potential to persist, so I also measured:

3) the maximum size (local maximum) reached by the population during each trial.

Summary statistics calculated for populations in each of the 36 landscapes include extinction rate (number of extinctions out of 100 trials), mean years survived, mean local maximum population size, global maximum population size (the largest local maximum of the 100 trials), and maximum population size reached before an extinction, if applicable.

The amount of variability between years has a relationship with population persistence. Large fluctuations may put a population at risk even at moderate population sizes (Pimm et al. 1988). I measured the variation from year to year (from year 1 to the year of extinction, or year 25, whichever came first) and calculated a coefficient of variation from trial population means and variances for each landscape for comparative purposes.

B) Mice:

I set up the model with mouse parameters and made 8 runs for the mice in 8 of the same landscapes described above. I chose the landscapes with 30% habitat, 4 patches, and the landscapes with 10% habitat, 8 patches for each level of connectivity. I chose these landscapes since the former matched the field study area, a moderately fragmented site with a moderate amount of wooded habitat, and the latter had the least amount of wooded habitat at the highest level of fragmentation. Since the mice were capable of using all habitat types except pasture, these landscapes each provided over 75% mouse habitat, with movement between woods and cropfields mostly unrestricted. Therefore it was not necessary to repeat all 36 runs. The 8 combinations provided an adequate comparison of mouse and chipmunk populations under

average and low levels of remaining woodland and habitat integrity. I measured the same response variables for the mice as for the chipmunks.

A few minor changes were made to the basic model to account for differences in the reproductive patterns of the mice.

I also made a similar set of runs with mouse parameters, but with the specialist behaviour mode characteristic of chipmunk use of the landscape. That is, the mice were restricted to woods and fencerows. Mice are known to survive in landscapes that support chipmunks but where mice do not use cropfields as habitat (Iverson et al. 1967). These runs were a way of validating the model for mice by confirming their persistence even when their behaviour mode was not adapted to landscape change.

All runs were made on an IBM type 486 computer with a math co-processor. Simulations for chipmunks took from 5 minutes to 3 hours to run depending on the landscape pattern. Simulations in higher quality landscapes that supported larger populations took longer to run than simulations in lower quality landscapes where populations incurred frequent extinctions.

STATISTICAL ANALYSIS:

I used the statistical package SAS (SAS Institute 1990) for all statistical tests. I conducted three-way Model I analyses of variance for 3 population response variables: numbers of extinctions (EXT), years of survival (SURV), and maximum population size (MAXPOP). The independent variables (landscape factors) were: amount of wooded habitat (HAB), number of

patches i.e. degree of fragmentation (PATCH), and level of connectivity (CONN). All interactions were included in the models. The SAS procedure GLM (general linear models) was used for all tests. I tested the following models:

- 1) EXT = HAB, PATCH, CONN, 2 and 3-way interaction terms.
- 2) SURV = HAB, PATCH, CONN, 2 and 3-way interaction terms.
- 3) MAXPOP = HAB, PATCH, CONN, 2 and 3-way interaction terms.

The assumptions of the ANOVA were met for all analyses. A Scheffé multiple comparison test was performed on all significant main source independent variables to determine which components of these terms differed significantly from one another.

A second set of AVOVAs was run for each level of each independent variable to test for thresholds in interaction effects that cannot be extracted from the 3-way ANOVA. Scheffé tests were run on significant main source factors.

I ran a regression analysis of extinction rate on the coefficient of variation of the population size over 25 years to determine if variation within a population could be used to predict probability of extinction.

The confidence level was set at 95% for all tests.

SENSITIVITY ANALYSIS:

I ran a sensitivity analysis (Jorgensen 1986) to determine the relative sensitivity of the model to changes in the base values of the following demographic variables:

- 1)   **Reproduction (ReproWkHi, ReproWkLo)**
- 2)   **Mortality (SeasonalMortality, BaseWinterMortality)**
- 3)   **Dispersal (DisProbA, DisProbY)**
- 4)   **Dispersal mortality (LocalDispMort, DistDispMort1, DistDispMort2, DistDispMort3, DistDispMort4)**
- 5)   **Litter size.**

I varied the parameter values by 25% above and below the values used in the model, and calculated a measure of sensitivity S for each parameter, using the mean local maximum population size as a response variable. Mean local maximum population size is linearly related to the persistence factors (extinction rate and mean length of survival), so it is a good indicator of the effects of the parameter changes on the population.

$$(\log)\text{EXT} = 4.64 - 1.90(\log)\text{LOCMAX} \quad (R^2 = 0.91, p < 0.0001)$$

$$(\log)\text{SURV} = -1.83 + 3.17(\log)\text{LOCMAX} - 0.77(\log)\text{LOCMAX}^2 \quad (R^2 = 0.93, p < 0.0001)$$

Sensitivity is calculated as:

$$S = (P_1 + P_2) / P_1$$

where P_1 = original mean local maximum, P_2 = mean local maximum after parameter change.

I used the landscape with 30% habitat, 4 patches and high connectivity for the sensitivity runs.

RESULTS

A) CHIPMUNKS:

Persistence:

Extinction rates in the simulations covered the whole range from 0 to 100%, and mean years of survival ranged from a high of 25 (survival in all trials) to a low of 8.8 (figures 3.7, 3.8). The fewest extinctions occurred in highly connected landscapes with 30% or more wooded habitat. Landscapes with only 10% wooded habitat, 4 or 8 patches, and no connectivity had extinction rates of 100%. Survival was correspondingly greatest in highly connected landscapes with at least 30% wooded habitat and shortest in landscapes with only 10% wooded habitat, 4 or 8 patches, and no connectivity.

For both measures of persistence, the levels of fragmentation (number of patches) and connectivity are most critical at 10% wooded habitat; amount of fragmentation becomes less important in landscapes with higher percentages of wooded habitat. In landscapes with over 30% wooded habitat, a mix of high and low quality connections was as effective as having exclusively high quality routes. Population persistence was very low in all landscapes without connectivity.

I used an analysis of variance to test whether extinction and years of survival were dependent on the habitat factors and their interactions (tables 3.3, 3.4). The three landscape factors, both two-way interactions, and the three-way interaction were all highly significant ($p < 0.0001$) for both number of extinctions and years of survival. The model explained 62% of

the variation in extinction and 61% of the variation in length of survival. Residuals from the ANOVA were homoscedastic and normally distributed. When survival was the dependent variable, 84% of the variation explained by the model was due to connectivity, 7% was due to % habitat, and 3% to fragmentation, with the remaining 6% due to the interaction terms. When extinction was the dependent variable, 80% of the variance explained by the model was due to connectivity, 10% to habitat, 3% to fragmentation, and 7% to the interaction terms.

I conducted *a posteriori* tests on the main effects of the independent variables using a Scheffé test at a 95% level of confidence to identify significant differences in means within each class of independent variable. There was a significantly longer survival time and lower extinction rate for landscapes with 30% or more wooded habitat than for landscapes with only 10% wooded habitat. Landscapes with 2 patches had significantly lower numbers of extinctions and longer survival times than landscapes with 4 patches, which in turn provided for significantly greater population persistence than landscapes with 8 patches. Both measures of population persistence were significantly different at each level of connectivity.

The interactions are critical to understanding the effects of the landscape patterns on the population. I examined the two-way interactions by holding each individual factor constant and running a two-way analysis of variance on the remaining factors. Results were revealing in terms of critical levels of composition, configuration and connectivity. When wooded habitat levels are held constant, it becomes clear that the less wooded habitat available, the more sensitive the population is to fragmentation and lower quality connectivity. The results of these analyses are summarized in tables 3.5 and 3.6.

1) the interaction between % wooded habitat and fragmentation:

At 10% wooded habitat, the number of patches making up the habitat was always important. There was a significantly higher number of extinctions and shorter survival time in 8 patch landscapes than in landscapes with 4 or fewer patches, and in 4 patch landscapes than in 2 patch ones.

At 30% wooded habitat, 2 patch landscapes had significantly longer survival times than 8 patch landscapes. There was no significant difference in length of survival between 2 and 4 patch landscapes or between 4 and 8 patch landscapes. Extinction rates were significantly lower for both 2 and 4 patch landscapes than for 8 patch landscapes.

At 50% wooded habitat, only 2 and 8 patch landscapes had extinction rates and survival times significantly differed from each other.

2) the interaction of % wooded habitat and connectivity:

The more habitat that remained in the landscape the less impact a few lower quality connections had on the persistence of the population. There were no significant differences in number of extinctions or survival time between high quality or mixed (intermediate) quality connections for 50% or 30% wooded habitat. Only at 10% habitat did extinctions and survival time differ significantly between high and mixed levels of quality of connections. Landscapes with uniformly low quality routes always had significantly higher numbers of extinctions and lower survival time than those with some or all high quality connections. Landscapes with no connections had extinction rates above 90% and mean survival times less than 13 years. They

were always very significantly lower than landscapes with some connectivity, regardless of % wooded habitat.

3) the interaction of fragmentation and connectivity:

Regardless of the number of patches into which the wooded habitat was divided, there were always significantly more extinctions, and fewer years of survival for populations in landscapes with no connectivity. Landscapes with low quality connectivity were significantly better than those with none, but significantly worse than those with either mixed or high quality for both measures of population persistence at all levels of fragmentation.

At higher levels of connectivity, there were differences in the effects of level of fragmentation on number of years survived and numbers of extinctions. Two and 4 patch landscapes had significantly lower extinction rates and longer survival than 8 patch landscapes when connectivity was high or mixed.

4) The three-way interaction:

This relationship was examined by holding % wooded habitat, level of fragmentation, or connectivity constant in turn and looking at the two-way interaction terms for the remaining independent variables. The two-way interaction term between number of patches and connectivity level was significant for both years of survival and rate of extinction for all levels of wooded habitat, and the two-way interaction between % wooded habitat and level of connectivity was also significant for both measures of persistence at all levels of fragmentation. When levels of connectivity were held constant, the two-way interaction between % wooded habitat and fragmentation was significant for years survived at all connectivity classes. These two-way

interactions were also significant for number of extinctions for the classes high, mixed and low, but for the class with no connectivity, the two-way interaction between % habitat and fragmentation did not contribute significantly to the determination of numbers of extinctions. This suggests the effect of habitat amount on persistence does not depend significantly on the level of fragmentation when patches are isolated.

Population size:

The largest population size achieved in any trial was 261 individuals. This occurred in the landscape with 50% habitat, 2 patches and high connectivity. Mean maximum population sizes for the 36 landscapes ranged from 244.51 ± 22.36 in that landscape to 17.63 ± 2.87 in the landscape with 10% habitat, 4 patches and no connectivity. Figure 3.9 shows the (global) maximum population sizes and figure 3.10 shows the mean maximum population sizes in landscapes with 50%, 30% and 10% wooded habitat at 2, 4, and 8 patches for high, intermediate, low, and no connectivity. Chipmunk populations were proportionally larger in landscapes with more wooded habitat, little fragmentation, and higher quality connectivity. At 10% wooded habitat, no population reached 80 individuals regardless of level of connectivity. Mean local population sizes were significantly larger at high and mixed levels of connectivity than at low or no connectivity at 30% and 50% wooded habitat.

I ran an analysis of variance on the effects of the independent variables and their interactions on local maximum population size for all trials (table 3.7). The ANOVA was highly significant ($R^2 = 0.91$, $p < 0.0001$). All three main effects and all interactions contributed significantly to the model. A Scheffé test showed significant differences in local maximum

populations among all habitat, fragmentation, and connectivity levels. Connectivity explained 47% of the variation in population size, amount of wooded habitat explained 29% and the interaction between habitat amount and connectivity explained 21%. Level of fragmentation explained only 2% of the total variation. When landscapes with no connectivity were excluded from the test, habitat amount explained 50% of the variation in population size, connectivity explained 31% and level of fragmentation 2%.

I also ran an analysis of variance on the effects of the independent variables and the two-way interaction terms on global maximum population sizes for the 36 landscapes (table 3.8). The overall ANOVA was highly significant ($R^2 = 0.99$, $p < 0.0001$). All three main effects and 2 interaction terms HAB*CONN and PATCH*CONN contributed significantly to the variance in global maximum population size. HAB*PATCH was not significant. Amount of wooded habitat was the most important factor to global maximum population size, contributing 44% of the model explanation. Connectivity explained 36%, and the interaction between % habitat and connectivity explained 15%. A Scheffé test showed that global maximum population sizes were significantly different at each habitat level. Larger maxima occurred in landscapes with greater proportions of wooded habitat. Two patch landscapes supported significantly larger populations than 4 or 8 patch landscapes, and those with high or mixed connectivity had significantly larger global maximums than those with low connectivity. Populations in landscapes with no connectivity had significantly lower global maximums than all others. The size a population may attain is a reflection of landscape pattern.

I regressed mean coefficient of variation on extinction rate for each landscape to find out whether extinction rate increased with increasing variability (figure 3.11). There was a

significant linear relationship (model = $244.13 \text{ CV} - 94.43$, $R^2=0.74$, $df=1$, $p<0.0001$). Generally, the higher the coefficient of variation, the higher the rate of extinction. This was especially marked in landscapes with only 10% wooded habitat. Populations with high levels of variability from year to year were at increased risk of extinction, and this was related to landscape quality.

Although generally, small populations were prone to extinction and large ones were not, some populations persisted to year 25 without achieving population sizes over 20, and several went extinct even after growing to more than 50 individuals. Figure 3.12 shows the percent of total extinctions occurring at various local maximum population sizes. Seventy-three per cent of all extinctions occurred in populations that had not grown past 30 individuals. However, one population that had reached 65 individuals subsequently suffered an extinction. Populations that grew beyond 65 chipmunks always persisted to year 25.

B) MICE:

Figures 3.13 to 3.15 contrast extinction rates, mean years of survival, and mean maximum population sizes for chipmunks with generalist mice (current behaviour mode in farm landscapes in this area), and specialist mice (behaviour mode for mice studied in wooded habitat in regions further south).

I ran analyses of variance to test whether years of survival, extinctions, and maximum population size differed significantly for the species (generalist mice, chipmunks, specialist mice), the landscape (30% wooded habitat and 4 patches or 10% wooded habitat and 8 patches), and the

level of connectivity (high, mixed, or low quality, or no connections) (tables 3.9, 3.10, 3.11). All 3 models were highly significant ($p < 0.0001$) and included all main effects and interaction terms ($p < 0.0001$). The model for years of survival explained 71% of the variance in the data, the model for number of extinctions explained 75%, and the model for maximum population size explained 99%. The species explained the largest proportion of the variance in each model (32% of variance for years survived, 38% of variance for number of extinctions, 74% of variance for maximum population size). A Scheffé test on the main effects showed generalist mice had significantly longer survival times, lower rates of extinction, and larger mean maximum population sizes than chipmunks or specialist mice. These relationships held in both landscapes, which also differed significantly from each other.

Generalist behaviour:

Generalist mouse populations were highly successful in all simulations. Connectivity is defined in terms of chipmunks in these landscapes, and therefore does not represent connectivity for these mice, which is in fact high in all cases, since the mice travel across corn and grain fields as well as fencerows. Generalist mouse populations in landscapes with 30% wooded habitat divided into 4 patches persisted to year 25 in all trials, and those in the landscapes with 10% wooded habitat in 8 patches did so in all but one trial. Mean maximum population size was 376.25 ± 11.73 in 30% wooded habitat 4 patch landscapes and 244.00 ± 20.26 in 10% habitat 8 patch landscapes. This difference in population size between the two landscapes was significant ($t = 11.30$, $df = 6$, $p < 0.0001$), however it is due to the increased proportion of pasture land in the landscape with only 10% wooded habitat rather than decreased woodland *per se*.

Specialist behaviour:

When mice were restricted to specialist behaviour in the simulation (use of woods and fencerows but not cropfields) they had mean persistence times ranging from 25 years in the landscape with 30% wooded habitat, 4 patches and high connectivity, to 6.23 years in the landscape with 10% wooded habitat, 8 patches and no connectivity. Extinction rates ranged from 0 to 100%. Despite similar demographic parameters, specialist mice were significantly less successful than generalist mice in all landscapes.

MODEL SENSITIVITY:

All parameters had higher sensitivity ratings when changed in the direction favouring lower mean maximum population sizes than in the direction favouring higher ones (table 3.12). The model was most sensitive to an increase in the seasonal mortality rate. Increasing the overwinter mortality rate, or decreasing litter size or rate of reproduction also had strong effects. Changes to dispersal rates or mortality rates during dispersal affected only the proportion of the population dispersing, and had a much smaller impact on mean maximum local population size. This suggests that a rise in mortality rate in fragmented landscapes, as could happen with the introduction of domestic predators or the encouragement of edge species, has the potential to seriously affect small mammal populations, especially in northern areas where there is a long non-reproductive period with sustained mortality.

SUMMARY:

- 1) Chipmunk population persistence was very low in all landscapes without connectivity. (Over 90% extinction rate, less than 13 years survived).
- 2) All factors and all interactions contributed significantly to chipmunk persistence, but not equally. Connectivity explained over 79% of the variance in persistence explained by the models. Presence/absence of connectivity contributed heavily to this. When landscapes with no connectivity were excluded from the analyses, level of connectivity (high, mixed or low) contributed 42% of the models' explanation and % wooded habitat contributed 27% to length of survival and 36% to rate of extinction. The level of fragmentation contributed a relatively small amount (3 to 11%) regardless of connectivity levels included.
- 3) Population sizes were higher for chipmunks in landscapes with more wooded habitat and better connectivity. Fragmentation levels contributed very little to explanations of variation in maximum population size attained in a landscape. Habitat amount explained 44% of the variance in global maximum population size, connectivity explained 36% and fragmentation only 1%.
- 4) The less habitat available, the more sensitive the chipmunk population was to the presence of some lower quality connections and to the level of fragmentation.
- 5) Chipmunk populations with high relative levels of variation (CV) from year to year were at greater risk of extinction, and this relationship was stronger at low quantities of habitat (10%).

6) One chipmunk population suffered extinction after reaching 65 individuals. However, 73% of extinctions occurred in populations that had not exceeded 30 individuals (45% of maximum size at which population was vulnerable), and some persisted with only 20 individuals. This suggests that it is difficult to predict the fate of small populations.

7) White-footed mice with generalist behaviour did well in all the landscapes, and suffered only 1 extinction in 800 trials. Since these mice were not restricted to woodlots and fencerows the landscapes were all highly connected for them and provided over 78% usable habitat. Generalist mice were significantly more successful than chipmunks or specialist mice in all landscapes.

8) The model was most sensitive to increased mortality over the 34 weeks from early spring to late fall.

DISCUSSION

The chipmunk simulations support the suggestion that connectivity has the greatest influence on population persistence of the three landscape features investigated (composition, configuration, and connectivity). Model population sizes were very low and there were many extinctions in landscapes with barriers to movement, modelled as lack of connections between patches.

Constraining dispersal among habitat areas has been shown empirically to depress populations (Pettersen 1985, Soulé et al. 1988, Saunders 1990, Celada 1994). When landscapes are fragmented, the ability to move among patches is vital at several scales. At a local scale, the seasonal use of several patches for complementation and supplementation of resources may be the key to survival (Dunning et al. 1992, Taylor et al. 1993). For example, Carnaby's cockatoo used different patches for nesting than for foraging (Saunders and Ingram 1987). Rajska-Jurgiel (1992) studied two woodland rodents inhabiting forest fragments in an agricultural landscape in Poland. She found that the rodents moved among woodlots and used the whole area as patchy habitat. Many chipmunks in my field study moved back and forth between woodlots and fencerows daily, and altered their landscape use seasonally. At a larger scale, theory predicts that the inability to disperse successfully can lead to permanent local, and ultimately regional, extinctions (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988, Henein and Merriam 1990), and, where isolation is extreme, a loss of genetic diversity associated with genetic drift (Slatkin 1985).

When the simulation landscapes were connected, whether with high quality routes (implying high survival for individuals moving through them), lower quality routes, or a mix of the two types, persistence was enhanced. Burkey (1988) also found that including "migration" in his model of fragmented reserves significantly lowered extinction rates.

The contribution of habitat area to the explanation of variation in population size and persistence rose markedly in connected landscapes. It would seem intuitive that landscapes with larger amounts of remaining habitat would support larger, more persistent populations (Verboom et al. 1991). All else being equal, this is true, but all else is seldom equal in nature. The simulations show this prediction to be too simplistic when other landscape features vary, because there are important interactions among habitat amount, fragmentation, and connectivity. For example, the model landscape with 10% habitat, 2 patches and high connectivity actually had a significantly lower extinction rate and supported a slightly larger population than did the landscape with 50% habitat, 8 patches and low connectivity. By this I do not mean to recommend habitat decimation, but to point out that habitat area is not everything in conservation; connectivity and patchiness may also play important roles.

Generally, the less habitat available, the more sensitive the population was to fragmentation (smaller, more numerous patches) and to the presence of some lower quality connections. This is consistent with the findings of Andrén (1994), who used a percolation model and literature studies of birds and mammals in landscapes with different amounts of remaining original habitat to examine the relationship between habitat amount and fragmentation in predicting population size. He concluded that if the amount of habitat in an area was high, the

effects of habitat loss on a species were due to the reduction in habitat. However, if original habitat amount was low, then patch area and isolation effects were most critical.

The model results allow the conclusion that the level of fragmentation in the landscape, as defined here, contributes a relatively small proportion of the explanation of variance in persistence and population size. However, there are several reasons why this should not be interpreted as an invitation to carve up landscapes. First, the definition of the term fragmentation is not always clear. In this study, fragmentation does not involve loss of habitat, but for many real life situations, fragmentation occurs through the removal of habitat for anthropogenic use, and the result includes reduced habitat availability and increased isolation (lower connectivity) (Wilcox and Murphy 1985). This suggests that the SLOSS debate (the relative merits of single large versus several small patches) may have focused on the wrong factors. When fragmentation includes habitat loss and reduced connectivity, effects can not be attributed solely to patchiness, so assuming a minimal impact on populations from fragmentation would be a serious error. Second, even when habitat amount is held constant, as in the model, fragmentation effects are reduced by high levels of connectivity, since individuals can move among patches, and locally between patches and connecting elements, with low risk. When breeding can also occur in some of these connections, the landscapes are functionally less fragmented than might be expected from the number of patches alone. Finally, factors not included in the model may become important when habitat is fragmented. For example, the perimeter to area ratio increases as patch size is reduced resulting in edge effects to which some species are sensitive (Laurance and Yensen 1991). Therefore, although my results suggest that the primary focus of landscape managers should be on enhancing connectivity and retaining as much natural habitat as possible, minimizing fragmentation is also desirable, and may be critical when connectivity is low.

Highly variable populations (identified as having high mean coefficients of variation over 25 years) were at greater risk of extinction than more stable populations. The relationship between coefficient of variation and risk of extinction has also been shown by Karr (1982) and by Pimm et al. (1988). The simulation results suggest that risk of extinction will be greater in landscapes where the amount of habitat is small, since these landscapes support fewer animals and extinctions may occur at lower levels of variation.

The populations in the highest quality landscape (50% habitat, 2 patches, high quality connectivity) grew, on average, to 244 individuals. No extinctions occurred in this landscape. Most extinctions in other landscapes occurred at landscape population levels of less than 30 individuals. However, one population went extinct even after reaching 65 chipmunks. Therefore some risk of extinction remained in the simulation until a population of 66 individuals was attained. The risk was higher in lower quality landscapes (i.e. those with low % habitat, low connectivity, and more patches).

Using an analytical island model with demographic stochasticity, Richter-Dyn and Goel (1972) predicted a high risk of extinction for a population of less than 20 breeding individuals, and persistence for thousands of years for populations above that size. Quinn and Hastings (1987) borrowed from reliability theory to model the effects of habitat subdivision on population persistence when environmental stochasticity was non-synchronous. They concluded that many patches with few individuals were most effective. However, Gilpin (1987) argued that these approaches were unrealistic in most cases since movement into and out of patches was not included in the models, and small populations affected by demographic or environmental

stochasticity could thus not be rescued by immigration from other sources, as commonly occurs in terrestrial systems (Brown and Kodrick-Brown 1977).

My simulation, which includes demographic stochasticity and dispersal, produced results that support Gilpin's concerns. All landscapes in my simulations began with 16 breeding females, and only 24% of simulations in connected landscapes resulted in an extinction. In simulations without connectivity, however, the percentage of extinctions was 96%, closer to Richter-Dyn and Goel's result. Quinn and Hastings (1987) further suggested that extinction probability decreases only slowly with increased population size, but I found an exponential decline in extinction rate in populations exceeding 30 individuals. My results support the view that risk of extinction in small populations can be reduced by the presence of connectivity (Pettersen 1985, Soulé et al. 1988, Saunders 1990).

As predicted, there was a marked difference in population size and persistence between generalist mice and chipmunks in the 8 selected landscapes. Chipmunk populations had at least some risk of extinction in all but the very highest quality landscapes. Connections between habitat patches in the form of wooded fencerows were very important for chipmunks, and loss of these landscape features, or reduction in their quality had a detrimental effect on persistence and population size and variability. Chipmunk populations were very sensitive to depressed demographic parameters in the model (i.e. increased mortality and reduced reproduction) suggesting that landscape changes that raised levels of predation or degraded nesting or overwintering sites would have a negative effect on survival.

There is little to be said about the generalist mice *vis à vis* the individual simulation landscapes. Because of their adaptive behavioural response, their populations prospered in all of the patterns since the only areas unacceptable for movement or habitat were pasture fields, which made up a very small proportion of the total area. In effect, all 8 landscapes were highly connected for these mice and contained over 75% usable habitat. However, comparisons of generalist mice with both chipmunks and specialist mice are informative.

Although the runs for specialist mice were initially made for validation purposes, they allowed me to isolate the behavioural differences in use of the landscape while holding demographic parameters constant. The success of generalist mice compared to specialist mice coupled with the relative lack of sensitivity of the model to increases in reproduction parameters suggests that changes in demographics may be less effective than shifts in land use patterns for increasing population persistence in rapidly changing landscapes. Traditional r- and K-selection (Pianka 1970) may thus be bypassed by changes in habitat use.

The contrast between the success of the chipmunk and generalist mouse populations in the same landscapes illustrates the importance of viewing landscapes from a species perspective, and of determining the likely behavioural response of a species before predicting how it will be affected by landscape change. The chipmunk remains a specialist, apparently little affected by the presence of novel resources such as grains and corn in its domain, still using the landscape in a relatively coarse grained, selective manner (*sensu* Kotliar and Wiens 1990). In contrast, the behaviourally flexible mouse, having become a generalist in this region, now uses most areas of the landscape as habitat, and moves through the mosaic almost unimpeded. A similar dichotomy of responses to woodland fragmentation has been noted for the Florida panther, a species

requiring wooded corridors between patches, and the Florida black bear, a species that can move through open country (Harris and Gallagher 1989, Maehr 1990, Beier 1995).

The simulation model provides potentially useful information for decision making at the landscape scale. It directs data collection towards those demographic and behavioural parameters important for locating species on the gradient of behavioural flexibility; it reveals interactions among composition, configuration, connectivity, and the behavioural mode of species; it predicts short-term variability and long term persistence of populations in a particular landscape. Its results support Laurance's (1991) prediction that species able to travel through or alter their traditional behaviour to use resources in modified habitat such as the farmland matrix will be more likely to remain stable or increase in numbers in fragmented areas.

To extend this study to species other than chipmunks and mice, data will be needed on the vagility of target species, the sorts of habitat moved through and chosen for nesting sites and refuges, and predisposition for making use of non-traditional resources in the landscape. This information can help position species on the gradient of behavioural adaptability. Demographic parameters will also be needed. The sensitivity of chipmunk and mouse populations to survival rates, both seasonal and over winter, and reproductive rates suggests that populations in which these rates fluctuate widely will be more variable in size from year to year. The simulation suggests that high short-term variability places populations at risk in fragmented landscapes and is a predictor of extinction probability. Empirical studies will be needed to monitor population levels, measure distances moved in heterogeneous landscapes, and quantify habitat use.

Since connectivity has been identified as a major factor in survival in landscape mosaics, it is vital to determine what constitutes connectivity for each species, and to take steps to ensure that their ability to access all vital landscape elements is maintained by landscape management when fragmentation occurs. For some species, this will require the presence of areas between patches offering specific types of cover, such as the fencerows preferred by the chipmunks. But for others, it could be an absence of barriers such as roads (Kozakiewicz and Jurasinska 1989, Merriam et al. 1989, Fahrig et al. in press), or a critical distance between habitat fragments (Fahrig and Paloheimo 1988), or the seasonal presence of breeding ponds (Gill 1978). Field work will be needed to determine limiters of connectivity for species. The model predicts that failing to address this component of landscape structure can have a significant impact on population survival, even when relatively large amounts of habitat remain.

Insight provided by the model into the relationship between population size and persistence and landscape structure and connectivity is necessary but not sufficient. For each species there will be unique considerations important in decision making at the landscape level. For example, some species sensitive to parasitism or predation from edge species may require large areas of breeding habitat that are well buffered from the matrix (Gates and Gysel 1978, Brittingham and Temple 1983, Small and Hunter 1988), in which case the assumption of equal probability of reproduction and mortality in all patch sizes would not be valid. Some species require a minimum size of population for breeding to occur (Pettersen 1985). When habitat is ephemeral and generation times are short, patch duration and location may be more important than patch size (Fahrig 1992). Since these phenomena did not affect mice or chipmunks, the model does not address them. However, the simulation provides a starting point for predicting survival for a varied set of landscape characteristics and behavioural responses.

Wiens et al. (1993) have called for the use of experimental model systems (EMS) to facilitate investigation of the effects of landscape fragmentation on large, wide-ranging species that are difficult to study in the field. I offer my study as an experimental model system for behaviourally flexible and behaviourally inflexible species. EMS involves the study of empirically tractable species operating at a small scale. The relationship of such species to a landscape, or set of landscapes, is observed and some general conclusions are drawn regarding responses to fragmentation that can be extended to other experimentally less tractable species with similar behaviour modes. This approach appears promising for developing a set of responses that can be matched to species operating at large spatial scales. Thus vole behaviour may predict responses of capercaillie to fragmentation (Ims et al. 1993), and chipmunk and mouse behaviour in this study may simulate the response of panthers and black bears in Florida (Maehr 1990). In an era of rapid anthropogenic change, a system of classification that groups species by their responses to fragmentation and ecosystem change, and positions the groups on a gradient of behavioural adaptability to human activity, could be of more practical use to planners and conservationists than taxonomic, evolutionary, and ecological classification systems that have been used to group species historically.

Table 3.1
Parameters for the simulation model

Parameters	Description	Chipmunks	Mice
Reproduction			
ReproWkHi	reproduction rate for prime weeks	0.40	0.30
ReproWkLo	reproduction rate for secondary weeks	0.20	0.20
ReproTwice	reproduction rate for a second pregnancy per year	0.10	
LocReproAdjWoods	adjustment to repro rate for resident of woods	1.00	1.00
LocReproAdjCorn	adjustment to repro rate for resident of cornfield		1.00
LocReproAdjPasture	adjustment to repro rate for resident of pasture		
LocReproAdjGrain	adjustment to repro rate for resident of grainfield		0.75
LocReproAdjHQF	adjustment to repro rate for res. of high quality fencerow	0.50	0.50
LocReproAdjLQF	adjustment to repro rate for res. of low quality fencerow	0.00	0.00
MaxBabies	limit of litter size	5	5
InfantSurvivalEarly	survival rate for infants born early in the season	0.90	0.90
InfantSurvivalLate	survival rate for infants born late in the season	0.50	0.80
WeanTime	no. of weeks after breeding that new young are added	10	7
Old	age at which mortality rate is increased due to old age	5	5
Mortality			
SeasonalMortality	regular weekly mortality rate	0.02	0.03
CrowdedSeasonalMortality	mortality rate in crowded locations	0.15	0.10
BaseWinterMortality	overwinter mortality rate	0.25	0.60
CrowdedWinterMortality	overwinter mortality rate in crowded locations	0.50	0.60
AgeMortAdjAdult	adjustment to mortality rate for adults	1.00	1.00
AgeMortAdjYoung	adjustment to mortality rate for young	1.00	2.00
AgeMortAdjOld	adjustment to mortality rate for old adults	3.00	3.00
LocMortAdjWoods	adjustment to mortality rate for individuals in woods	1.00	1.00
LocMortAdjCorn	adjustment to mortality rate for individuals in cornfields		1.00
LocMortAdjPasture	adjustment to mortality rate for individuals in pasture		0.00
LocMortAdjGrain	adjustment to mortality rate for individuals in grainfields		1.00
LocMortAdjGrainFall	adjustment to mortality rate for individuals in grainfields in fall		2.00
LocMortAdjHQF	adjustment to mortality rate for individuals in high quality fencerows	1.10	1.10
LocMortAdjLQF	adjustment to mortality rate for individuals in low quality fencerows	2.00	2.00

Table 3.1 (continued)
Parameters for the simulation model

Parameters	Description	Chipmunks	Mice
Movement			
<i>Probability</i>			
DisProbY	probability of movement for young	0.03	0.04
DisProbA	probability of movement for adults	0.02	0.03
DisProbYLocal	probability that moves for young are local	0.60	0.60
DisProbYDistant	probability that moves for young are distant	0.40	0.40
DisProbALocal	probability that moves for adults are local	0.80	0.70
DisProbADistant	probability that moves for adults are distant	0.20	0.30
DisProbNYLocal	probability that moves for new young are local	0.80	0.80
DisProbNYDistant	probability that moves for new young are distant	0.20	0.20
DispAdjCrowd	adjustment to prob. of movement for crowded locations	5.00	1.00
Mortality			
LocalDispMort	mortality rate for local movement	0.02	0.02
DistDispMort1	mortality rate for long distance move by highest quality route	0.03	0.03
DistDispMort2	mortality rate for long distance move by high-interm route	0.10	0.10
DistDispMort3	mortality rate for long distance move by low-interm route	0.30	0.30
DistDispMort4	mortality rate for long distance move by lowest quality route	0.50	0.50
DispMortAdjNY	adjustment to dispersal mortality for new young	1.50	1.50
FrustrDispMort	mortality rate for individuals that do not find a spot	1.00	1.00
LostDispersalLimit	control for loss of long distance movers from isolated patches	1	1
<i>Length of moves</i>			
MaxMoves	limit of numbers of local moves without finding an empty cell	50	50
FencerowMoves	number of pre-moves in fencerows for long distance dispersal	45	45
LocalMoves	limit for number of pre-moves in patch for local move	12	6
Spacing			
Woodspace	number of cells required between individuals in woods	1	1
Cornspace	number of cells required between individuals in cornfields	1	1
Pasturespace	number of cells required between individuals in pasture		
Grainspace	number of cells required between individuals in grainfields		1
HQFspace	number of cells req'd between individuals in high quality fencerows	5	3
LQFspace	number of cells req'd between individuals in low quality fencerows	7	5

Table 3.2a**Seasonal patch-specific dispersal adjustment factors for chipmunks**

	woods	corn	pasture	grain	HQF	LQF
Adults						
spring	0.5	0.0	0.0	0.0	1.0	10.0
summer	1.0	0.0	0.0	0.0	1.0	10.0
fall	0.5	0.0	0.0	0.0	2.0	10.0
Young						
spring	1.0	0.0	0.0	0.0	1.0	10.0
summer	2.0	0.0	0.0	0.0	1.0	10.0
fall	1.0	0.0	0.0	0.0	2.0	10.0

Table 3.2b**Seasonal patch-specific dispersal adjustment factors for mice**

	woods	corn	pasture	grain	HQF	LQF
Adults						
spring	0.1	0.1	0.0	0.1	1.0	10.0
summer	1.0	1.0	0.0	1.0	1.0	10.0
fall	0.1	0.1	0.0	10.0	2.0	10.0
Young						
spring	0.1	2.0	0.0	1.0	1.0	10.0
summer	1.0	1.0	0.0	1.0	1.0	10.0
fall	1.0	1.0	0.0	10.0	2.0	10.0

Table 3.3

Analysis of variance of years of survival of a chipmunk population
in landscapes with 50%, 30% or 10% wooded habitat, 2, 4 or 8 patches,
and high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
HAB	2	8457.76	4228.88	199.27	0.0001
PAT	2	3135.70	1567.85	73.88	0.0001
CONN	3	97200.44	32400.15	1526.77	0.0001
HAB*PAT	4	1709.59	427.40	20.14	0.0001
HAB*CONN	6	1670.80	278.47	13.12	0.0001
PAT*CONN	6	2729.15	454.86	21.43	0.0001
HAB*PAT*CONN	12	955.18	79.60	3.75	0.0001
Error	3564	75633.06	21.22		

$R^2 = 0.61$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
HAB	50	20.73	1200	a
	30	20.44	1200	a
	10	17.34	1200	b
PAT	2	20.63	1200	a
	4	19.55	1200	b
	8	18.35	1200	c
CONN	high	24.27	900	a
	mixed	23.34	900	b
	low	19.33	900	c
	none	11.10	900	d

Table 3.4

Analysis of variance of extinction of a chipmunk population in
landscapes with 50%, 30% or 10% wooded habitat, 2, 4 or 8 patches,
and high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
HAB	2	55.91	27.96	296.86	0.0001
PAT	2	14.19	7.09	75.32	0.0001
CONN	3	432.41	144.14	1530.57	0.0001
HAB*PAT	4	4.91	1.23	13.03	0.0001
HAB*CONN	6	18.48	3.08	32.70	0.0001
PAT*CONN	6	12.95	2.16	22.92	0.0001
HAB*PAT*CONN	12	4.82	0.40	4.27	0.0001
Error	3564	335.63	0.09		

$R^2 = 0.62$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
HAB	50	0.32	1200	a
	30	0.35	1200	a
	10	0.60	1200	b
PAT	2	0.35	1200	a
	4	0.42	1200	b
	8	0.50	1200	c
CONN	high	0.07	900	a
	mixed	0.18	900	b
	low	0.48	900	c
	none	0.97	900	d

Table 3.5

Summary of results of 2-way analyses of variance of years of survival of chipmunk populations in landscapes of each habitat, fragmentation and connectivity level.
ns = not significant; ** = significant at $p < 0.01$;

Fixed % wooded habitat	# patches		connectivity		2-way interaction
	relationship	significance	relationship	significance	
50	2 > 8	**	h, m > l > n	**	**
30	2 > 8	**	h, m > l > n	**	**
10	2 > 4 > 8	**	h > m > l > n	**	**

Fixed number of patches	% wooded habitat		connectivity		2-way interaction
	relationship	significance	relationship	significance	
2	50, 30 > 10	**	h > m > l > n	**	**
4	50, 30 > 10	**	h, m > l > n	**	**
8	50, 30 > 10	**	h > m > l > n	**	**

Fixed connectivity level	% wooded habitat		# patches		2-way interaction
	relationship	significance	relationship	significance	
high	50, 30 > 10	**	2, 4 > 8	**	**
mixed	50, 30 > 10	**	2, 4 > 8	**	**
low	50, 30 > 10	**	2 > 4 > 8	**	**
none	50, 30 > 10	**	2, 4, 8	ns	**

Table 3.6

Summary of results of 2-way analyses of variance of extinctions of chipmunk populations in landscapes of each habitat, fragmentation and connectivity level.

ns = not significant; ** = significant at $p < 0.01$;

Fixed % wooded habitat	# patches		connectivity		2-way interaction
	relationship	significance	relationship	significance	
50	2 < 8	**	h, m < l < n	**	**
30	2, 4 < 8	**	h, m < l < n	**	**
10	2 < 4 < 8	**	h < m < l < n	**	**

Fixed number of patches	% wooded habitat		connectivity		2-way interaction
	relationship	significance	relationship	significance	
2	50, 30 < 10	**	h < m < l < n	**	**
4	50, 30 < 10	**	h < m < l < n	**	**
8	50, 30 < 10	**	h < m < l < n	**	**

Fixed connectivity level	% wooded habitat		# patches		2-way interaction
	relationship	significance	relationship	significance	
high	50, 30 < 10	**	2, 4 < 8	**	**
mixed	50, 30 < 10	**	2, 4 < 8	**	**
low	50, 30 < 10	**	2 < 4 < 8	**	**
none	50, 30 < 10	**	2, 4, 8	ns	ns

Table 3.7

Analysis of variance of local maximum population size for chipmunks in
landscapes with 50%, 30% or 10% wooded habitat, 2, 4 or 8 patches,
and high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
HAB	2	5552005.70	2776002.85	5624.81	0.0001
PAT	2	287158.01	143579.00	290.92	0.0001
CONN	3	8775237.98	2925079.33	5926.87	0.0001
HAB*PAT	4	54490.04	13622.51	27.60	0.0001
HAB*CONN	6	3924455.62	654075.94	1325.30	0.0001
PAT*CONN	6	169546.37	28257.73	57.26	0.0001
HAB*PAT*CONN	12	59213.35	4934.45	10.00	0.0001
Error	3564	1758936.00	493.00		

$R^2 = 0.91$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
HAB	50	130.61	1200	a
	30	85.11	1200	b
	10	34.46	1200	c
PAT	2	94.19	1200	a
	4	83.67	1200	b
	8	72.32	1200	c
CONN	high	139.10	900	a
	mixed	124.62	900	b
	low	46.11	900	c
	none	23.75	900	d

Table 3.8

Analysis of variance of global maximum population size for chipmunks in landscapes with 50%, 30% or 10% wooded habitat, 2, 4 or 8 patches, and high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
HAB	2	94050.17	47025.08	249.83	0.0001
PAT	2	3095.17	1547.58	8.22	0.0056
CONN	3	77600.11	25866.70	137.42	0.0001
HAB*PAT	4	879.67	219.92	1.17	0.3727
HAB*CONN	6	32885.39	5480.90	29.12	0.0001
PAT*CONN	6	3901.72	650.29	3.45	0.0331
Error	3564	2258.78	188.23		

$R^2 = 0.99$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
HAB	50	175.92	12	a
	30	115.83	12	b
	10	50.75	12	c
PAT	2	127.00	12	a
	4	110.08	12	b
	8	105.42	12	b
CONN	high	159.11	9	a
	mixed	150.56	9	a
	low	104.89	9	b
	none	42.11	9	c

Table 3.9

Analysis of variance of years of survival of populations of generalist mice, chipmunks, and specialist mice in landscapes with 30% wooded habitat and 4 patches, and 10% wooded habitat and 8 patches, at high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
SPP	2	30218.42	15109.21	942.86	0.0001
LANDSCP	1	17756.16	17756.16	1108.04	0.0001
CONN	3	20528.25	6842.75	427.01	0.0001
SPP*LANDSCP	2	11686.22	5843.11	364.63	0.0001
SPP*CONN	6	11392.12	1898.69	118.48	0.0001
LANDSCP*CONN	3	1367.19	455.73	28.44	0.0001
SPP*LANDSCP*CONN	6	884.74	147.46	9.20	0.0001
Error	2376	38075.06	16.02		

$R^2 = 0.71$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
SPP	g. mice	24.97	800	a
	chips	17.68	800	b
	s. mice	17.23	800	b
LANDSCP	30-4	22.68	1200	a
	10-8	17.24	1200	b
CONN	high	23.07	600	a
	mixed	22.06	600	b
	low	19.18	600	c
	none	15.54	600	d

Table 3.10

Analysis of variance of years of extinctions of populations of generalist mice, chipmunks, and specialist mice in landscapes with 30% wooded habitat and 4 patches, and 10% wooded habitat and 8 patches, at high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
SPP	2	158.45	79.22	1338.95	0.0001
LANDSCP	1	75.26	75.26	1271.92	0.0001
CONN	3	70.97	23.66	399.81	0.0001
SPP*LANDSCP	2	43.10	21.55	364.23	0.0001
SPP*CONN	6	41.25	6.88	116.19	0.0001
LANDSCP*CONN	3	17.27	5.76	97.31	0.0001
SPP*LANDSCP*CONN	6	9.08	1.51	25.59	0.0001
Error	2376	555.99	0.06		

$R^2 = 0.75$

Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05

Variable	Level	Mean	N	Grouping
SPP	g. mice	0.001	800	a
	chips	0.541	800	b
	s. mice	0.551	800	b
LANDSCP	30-4	0.19	1200	a
	10-8	0.54	1200	b
CONN	high	0.17	600	a
	mixed	0.26	600	b
	low	0.40	600	c
	none	0.63	600	d

Table 3.11

Analysis of variance of maximum size of populations of generalist mice, chipmunks, and specialist mice in landscapes with 30% wooded habitat and 4 patches, and 10% wooded habitat and 8 patches, at high, mixed, low, or no connectivity

Source	degrees of freedom	Type III sum of squares	Mean square	F value	Pr > F
SPP	2	22154537	11077269	77759	0.0001
LNDSCP	1	5319004	5319004	37338	0.0001
CONN	3	580176	193392	1358	0.0001
SPP*LNDSCP	2	554100	277050	1945	0.0001
SPP*CONN	6	780948	130158	914	0.0001
LNDSCP*CONN	3	389812	129937	912	0.0001
SPP*LNDSCP*CONN	6	242998	40500	284	0.0001
Error	2376	338474	143		

$R^2 = 0.99$

**Scheffé Test of significance within main source variables:
Means with same grouping letter are not significantly different at p 0.05**

Variable	Level	Mean	N	Grouping
SPP	g. mice	281.69	800	a
	chips	106.79	800	b
	s. mice	57.87	800	c
LANDSCP	30-4	195.86	1200	a
	10-8	101.71	1200	b
CONN	high	167.27	600	a
	mixed	160.47	600	b
	low	137.78	600	c
	none	129.61	600	d

Table 3.12

Sensitivity of the model to parameters used in the chipmunk simulations

Parameter name	P1	M1		P2	M2	$\Delta P/P$	$\Delta M/M$	S
reproduction	.40 / .20	130.57	decrease increase	.30 / .15 .50 / .25	65.21 142.18	0.25 0.25	0.50 0.09	2.00 0.36
litter size	5	130.57	decrease increase	4 6	44.61 149.46	0.25 0.25	0.66 0.14	2.64 0.56
seasonal mortality	0.02	130.57	decrease increase	0.015 0.025	159.23 35.82	0.25 0.25	0.22 0.73	0.88 2.92
overwinter mortality	0.25	130.57	decrease increase	0.1875 0.3125	146.53 59.70	0.25 0.25	0.12 0.54	0.48 2.16
dispersal	.03 / .02	130.57	decrease increase	.0225/.015 .0375/.025	127.96 118.39	0.25 0.25	0.02 0.15	0.08 0.60
dispersal mortality	(.02/.03/ .10/.30/.50)	130.57	decrease increase	(.015/.0225/ .075/.225/.375) (.025/.0375/ .125/.375/.625)	138.72 109.00	0.25 0.25	0.06 0.16	0.24 0.64

P1 = original value of parameter

P2 = altered parameter value

$\Delta P / P$ = change in parameter

S = sensitivity (calculated as change in popn size / change in parameter)

M1 = original mean local maximum population size

M2 = altered mean local maximum population size

$\Delta M / M$ = change in population size

Figure 3.1: General systems flowchart

Figure 3.2: 36 arrangements of a landscape used in the simulations for mice and chipmunks.

Landscapes may have 50%, 30% or 10% wooded habitat. Within each of these composition types, the wooded habitat may be divided into 2, 4, or 8 patches. Within each of these combinations of composition and configuration, the wooded patches may be connected with high quality fencerows, low quality fencerows, a mix of high and low quality fencerows, or may be unconnected.

50% habitat

30% habitat

10% habitat

2 patches

4 patches

8 patches

high

mixed

low

none

Figure 3.3: Main flowchart for the simulation model. Expanded logic for the mortality, reproduction and movement routines appear in Figures 3.4 to 3.6.

n INDIVIDUALS
34 WEEKS
25 YEARS

Figure 3.4: Mortality routine of the simulation model. Probabilistic events based on parameters estimated from field studies are shown in bold.

Figure 3.5: Reproduction routine of the simulation model. Probabilistic events based on parameters estimated from field studies are shown in bold.

Figure 3.6: Movement routine of the simulation model. Probabilistic events based on parameters estimated from field studies are shown in bold.

Figure 3.7: Extinction rates for a chipmunk population in landscapes of different composition, configuration, and connectivity.

Figure 3.8: Mean years of survival for a chipmunk population in landscapes of different composition, configuration, and connectivity.

Figure 3.9: Global maximum population size for a chipmunk population in landscapes of different composition, configuration, and connectivity.

10% wooded habitat

30% wooded habitat

50% wooded habitat

Figure 3.10: Mean local maximum population size for a chipmunk population in landscapes of different composition, configuration, and connectivity.

Figure 3.11: Relationship between mean coefficient of variation of a chipmunk population in 36 different landscape arrangements and rate of extinction. ■ = 50% habitat, ▨ = 30% wooded habitat, □ = 10% wooded habitat.

Figure 3.12: Frequency (%) of total chipmunk population extinctions occurring after reaching various population levels.

Figure 3.13: Extinction rates for populations of chipmunks, white-footed mice behaving as generalists, and white-footed mice behaving as specialists in 8 different landscape arrangements. Landscapes have 30% habitat divided into 4 patches or 10% habitat divided into 8 patches. All levels of connectivity are represented.

10% wooded habitat in 8 patches

30 % wooded habitat in 4 patches

Figure 3.14: Mean years of survival for populations of chipmunks, white-footed mice behaving as generalists, and white-footed mice behaving as specialists in 8 different landscape arrangements. Landscapes have 30% habitat divided into 4 patches or 10% habitat divided into 8 patches. All levels of connectivity are represented.

3

OF/DE

3

PM-1 3 1/2" x 4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISION^{SM} RESOLUTION TARGETS

10% wooded habitat in 8 patches

30% habitat in 4 patches

Figure 3.15: Global maximum population size for populations of chipmunks, white-footed mice behaving as generalists, and white-footed mice behaving as specialists in 8 different landscape arrangements. Landscapes have 30% habitat divided into 4 patches or 10% habitat divided into 8 patches. All levels of connectivity are represented.

10% wooded habitat in 8 patches

30% wooded habitat in 4 patches

Chapter 4

Ethical and Policy Implications: Beyond Chipmunks and Mice

The important thing is to pursue our experiment hopefully, in the expectation of finding every element of harmony we can in the relationship between ourselves and the rest of nature, rediscovering old harmonies and perhaps finding some new ones too.

William Jordan III

Changes to the land:

Once, not very long ago, some settlers cut some farms out of the wilderness to make their living in a new land. A few towns sprang up, supported by produce from the nearby farms and energy from the surrounding forests - relatively self sustaining communities. These patches of human habitation were small compared to the vastness of the wild matrix. Nobody worried about loss of habitat, resource depletion, isolation or extinction of wild populations. The settlers felt threatened by a sinister wilderness rather than threatening to it.

However, as increasing amounts of land were cleared and more urbanization took place, the overall landscape became gradually more heterogeneous, and the wild parts became more fragmented. The effects of these changes were negligible at first. Plenty of land still existed for all and wild species could easily avoid human encounters. But gradually humans took more and more land, and one day a threshold was crossed; the landscape matrix was now human altered land, and the patches were remnants of the wild.

This is the way the world ends

Not with a bang but a whimper. (T.S. Eliot)

Human pressure on the land relentlessly continues to fragment the landscape, resulting in ever increased scales of heterogeneity, shrinking amounts of natural habitat, and more isolated populations.

Responses:

When change is slow, over evolutionary time, species have time to adapt genetically. Large populations may be fine-tuned through natural selection. However, rapid changes on a human time-scale cannot be countered by evolutionary mechanisms. Only species with inherent behavioural flexibility have a chance of coping with the altered resource base remaining.

Species unable to cope suffer local or regional extinctions. These species are most likely to be inflexible in their use of resources. They possess low mobility relative to their level of isolation, leading to few exchanges of individuals with other areas within the fragmented landscape. They have small populations with high levels of variance and are therefore vulnerable to stochastic events that precipitate extinction.

The first and most basic response to fragmentation that a species can make to improve probability of survival is to increase the extent of individual movement. Mobility is essential for persistence in human-altered landscapes. When resources become scattered in space, and animals are no longer able to make a living within the confines of a single patch, they must construct a larger neighbourhood from a set of smaller patches. They need to move through the matrix to do this. Movement may also be required for finding mates, and for locating and taking advantage of temporally changing resources. Since a degree of heterogeneity existed even in wilderness, many species were already somewhat mobile, albeit at a smaller scale. By extending this pre-existing behaviour, persistence becomes possible in the fragmented landscape, even for specialist species like chipmunks that are behaviourally inflexible in terms of resource requirements, provided travel among patches can occur. Connectivity is crucial to these species.

Some species demonstrate an additional and higher level of behavioural flexibility by changing their resource base as well as their inclination to move through novel patches in the matrix. These behaviourally flexible species, exemplified by the mice in this study, have responded as generalists. However, these are generalists by necessity rather than tradition. Some of these behaviourally flexible species have become very successful in urban areas as well as rural ones. In the extreme, raccoons and herring gulls have reached the status of pest species by taking advantage of the abundance of novel resources available in garbage disposal areas. These species are in fact encouraged by anthropogenic change.

Making predictions:

Faced with these varied responses to loss of habitat and fragmentation, it can be difficult for researchers and planners to predict the reaction of species to landscape changes. While field work is important for obtaining basic information about species numbers and habitat preferences, it is sometimes difficult to do for highly mobile species. Smaller scale experimental model systems that reveal basic responses to landscape alteration can be supplemented by computer simulations to explore the effects of different landscape patterns and the interactions of landscape elements on populations. For example, this study found the importance of the level of connectivity and the number of habitat patches to the vulnerability of a chipmunk population to extinction increased in landscapes with less than 30% habitat. The same inference could be drawn for other specialist species threatened with extinction by loss of habitat, a situation all too prevalent because of population and economic pressure. Over time, a system of classification could be developed to help identify requirements for persistence based on responses to habitat alteration.

Responsibility:

Awareness of any problem is the first step to solving it. There is a growing awareness that something is not right with our relationship to the natural world. Forests are disappearing at an alarming rate, erosion is destroying arable lands, and fisheries are collapsing, devastating entire cultures. Everyone is affected. It is time to change our philosophy from one that promotes taking from the land to one that focuses on sharing it with our fellow inhabitants. As philosopher Thomas Birch (Grumbine 1992) writes,

the fundamental human relationship with nature...is participatory, cooperative, and complementary rather than conflictive.

There is a need for land stewardship in public policy and in private management. By this I mean accepting responsibility for other forms of life besides our own. There is a need to integrate wild areas into our human landuse patterns, recognizing the importance of connectedness in the landscape for other species.

Research and management:

Maintenance of natural systems within a human-populated landscape requires an understanding of the processes necessary for sustaining native wildlife populations. This means matching resources and resource distribution within the landscape with the requirements and movement capabilities of the species. The landscape must be viewed from a species perspective. It is important to focus on a large enough area to sustain a demographic unit. To accomplish

this, researchers will need to learn about the scale of movement of the species, the resource patches it uses, the area required to support a demographic unit, the type of landscape elements used for local movements and dispersal, and which elements create barriers, or are otherwise avoided.

In addition, at local grassroots levels, maintenance of windbreaks and fencerows along the margins of agricultural fields, riparian vegetation along streams, small woodlots and rural forest fragments, ravines, urban corridors and natural parkland could all contribute to continuity of wild habitat within the anthropogenic matrix. Not only would this be beneficial to wild species, it would allow urban humans to experience, locally, a sense of connectedness to the global system that sustains them and of which they are a part. It is not enough to set aside wilderness parks in remote areas. Parks are important, but they offer a false sense of having painlessly solved the problems of endangered species and spaces with one stroke of a pen. Habitat loss, fragmentation and disconnectedness are all around us, reducing biodiversity and quality of life. We all bear a responsibility for caring for our wild neighbours by providing for connectedness in our common landscapes at local and regional levels. Results from studies like this may help to provide direction for planners, conservationists, and all who work to maintain the integrity of natural systems in human-dominated landscapes.

Appendix

I: Routing algorithms:

1) A file containing the direct routes between patches in the landscape must be created by the user. There is one entry per route (first patch identification number, second patch identification number, rating of route).

Direct route ratings are:

- 1 = high quality route;
- 2 = low quality route;
- 3 = intermediate quality route (for 2 patch landscapes only).

2) **SETUP** program: This program reads the file of direct routes described above, and converts the low quality ratings to 4.

Converted route ratings are:

- 1 = high quality route;
- 3 = intermediate quality route (for 2 patch landscapes only).
- 4 = low quality route;

From the initial file of converted direct routes and their ratings, the program builds the best route (lowest rating) between all possible patch combinations. Composite ratings are calculated by adding up ratings of direct links contained in the route and adding 1 for each node (patch) through which the route passes.

For example:

Direct routes exist between patch A and patch B, between patch B and patch C.

These routes each have a rating of 1 (they are high quality). The route from A to C is via B.

Therefore the rating for that pathway is $1_{A,B} + 1_{B,C} + 1_{\text{node B}} = 3$.

If the origin and destination patches are more than 49 cells apart, the composite rating is increased by 1 to reflect the increased risk to the dispersing animal due to distance.

The ratings are then consolidated to produce 4 categories of routes that will be used to determine frequency of use and probability of mortality during dispersal.

1	no change	(mortality rate = .03)
2,3	becomes 2	(mortality rate = .10)
4,5	becomes 3	(mortality rate = .30)
6 or more	becomes 4	(mortality rate = .50)

The complete set of routes and their new ratings is written to a file for use in the simulation (POPULATION).

3) POPULATION program.

The routes created by SETUP are read and the ratings are stored in a direct access array for fast lookup. When distant dispersal occurs, a table of all possible destinations from the patch of origin for which a route exists is assembled. From this table, a route will be chosen. For example, in the landscape below, there are 3 destinations from patch A, and the ratings are:

A to B rating 1
 A to C rating 3
 A to D rating 4

First, a table entry is randomly selected (R_i). This will be where table look-up begins. Then a number N between 0 and 15 is chosen randomly, and the following rule is applied:

if $N < 1$ look for a route with a rating of 4
 if $N < 3$ look for a route with a rating of 3
 if $N < 7$ look for a route with a rating of 2
 else look for a route with a rating of 1

The table is searched completely starting at R_i for a route with the appropriate rating. If a match is found, that route is chosen, and a probability of mortality during the dispersal event related to that rating is applied. If no match is found, the next highest rating is searched for (i.e. if the random number is 0, a route with a rating of 4 is the first choice. If that does not exist, one with a rating of 3 is the next choice, and so on. Sometimes, with higher N , no match will be found at the higher levels. In that case, the route at R_i is chosen, regardless of rating.

This method gives the following probabilities of choosing routes with various ratings given that all exist for the patch of origin, and given that N is 0:

rating 1 = 53.3%
 rating 2 = 26.7%
 rating 3 = 13.3%

rating 4 = 6.7%

When the choice of routes is limited to fewer rating types, these probabilities change. For example, when only type 1 and type 3 routes are present, there is a 26.7% chance of choosing type 3 and a 73.3% chance of choosing a type 1. A route with a higher rating always has a better chance of being used, but is never the exclusive choice.

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