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The Influence of Landscape Structure on the Distribution of the North American Red Squirrel, *Tamiasciurus hudsonicus*, in a Heterogeneous Boreal Mosaic

by

Jason Thomas Fisher ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment

of the requirements for the degree of Master of Science

in Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall, 1999

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **The Influence of Landscape Structure on the Distribution of the North American Red Squirrel, *Tamiasciurus hudsonicus*, in a Heterogeneous Boreal Mosaic** submitted by Jason Thomas Fisher in partial fulfilment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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Date: August 11 1999

ABSTRACT

This study was conducted to determine whether naturally derived landscape structure could predict animal distribution. The presence / absence of the red squirrel, a conifer specialist, was censused in three areas in the mixed-wood boreal forest of northern Alberta: a Reference area, a Burned area, and a Managed Area. Landscape structure assessed at multiple spatial scales was a significant predictor of squirrel presence. The significant variables changed with spatial scale and between the Burned, Reference, and Managed areas. Landscape structure was still significant when local vegetation was accounted for; it significantly predicted squirrel presence at sites where conifer trees were abundant but did not where conifer was scarce. The results show that relationships between landscape structure and animal abundance can be dependent on scale of quantification, year, local vegetation, and area. Extrapolation of landscape effects from one area to another may not be possible without an understanding of the underlying mechanisms.

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Chapter One

The Rationale for Natural Landscape Research

1.0 INTRODUCTION

The patch has been the nucleus of ecological study. A patch - a relatively discrete, homogeneous unit of similar internal habitat and microclimatic attributes (Kotliar and Wiens, 1990) - has characteristics that influence population dynamics or individual behaviour, the net result of which are to impede or facilitate its occupation by an animal species. Typically patch characteristics are referred to by the nebulous epithet "habitat" (Southwood, 1977). As a dictate of rigorous scientific design, habitat is controlled for and then ignored in most ecological experiments. Those that deal with the explicit influence of habitat in maintaining animal populations have focused on patches with one or two disparate intrinsic characteristics and related these to organisms' survival, fecundity, or behaviour (see Wiens, 1976 for review). However, it is intuitively obvious that a patch must be influenced by its surroundings; it follows that population processes within that patch must also be impacted by these surroundings. The milieu in which a patch exists has been referred to as a landscape.

If the definition of habitat is vague then that of the landscape can only be described as amorphous. Urban et al. (1987) define a landscape as a "mosaic of heterogeneous land forms, vegetation types, and land uses". Turner (1989) designates a landscape as any spatially heterogeneous area typically several hectares to several square kilometres in size. Dunning et al. (1992) describe it as the mosaic of patches in which the focal patch of interest is ensconced. They acknowledge that the landscape is species-specific; that is, responses to landscape elements occur somewhere between an organisms' home range and its regional distribution. This organism-centric landscape is similar to the "ecological neighbourhood" of Addicott et al. (1987), the size of which is bounded by the spatial and temporal extent of a particular process. With the intent of simplicity, I will define a landscape as the area surrounding a focal patch, within a circular boundary of a given radius. The appropriate magnitude of that radius is a matter for debate, and will be discussed in Chapter Two.

A landscape can be quantified in terms of **composition** - the relative amounts of different patch types within its boundaries - and **configuration** or physiognomy - the physical placement of those patch types in space, relative to one another (Dunning et al., 1992). Taylor et al. (1993) have proposed a third measure, connectivity, to describe functional linkages within a landscape (see also Baudry and Merriam, 1988; Merriam, 1988, 1991). Connectivity is species-specific, and often process-specific, and is difficult to define without extensive empirical testing (*e.g.*, Pither and Taylor, 1998; Tiebout and Anderson, 1997) or using models of movement probabilities (Henein and Merriam, 1990; Henein et al., 1998). Composition and configuration remain the two most objective measures of landscape heterogeneity; together the two describe what is referred to herein as landscape structure.

Landscape structure has been shown to be a significant predictor of organisms' abundance and distribution. Most studies have been conducted in agricultural or other anthropogenically fragmented landscapes. The distance to nearest habitat patch, the presence of a suitable linear corridor (Merriam and Lanoue, 1990; Bennett et al., 1994; Andreassen et al., 1996; Schmiegelow et al., 1997), composition of the matrix (Åberg et al., 1995; Donovan et al., 1997; Fitzgibbon, 1997), can all contribute to spatial distribution of organisms. The mechanisms behind this influence are numerous. Isolation of habitat patches from others (by barriers or simple distance) can prevent recolonisation after local extinction (Kozakiewicz, 1993; Stouffer and Bierregaard, 1995; Fitzgibbon, 1997; Wiens et al., 1997; Henein and Merriam 1998). The presence of linear corridors may ameliorate this effect (Henderson et al., 1985; Henein and Merriam, 1990; Bennett et al., 1994; Schmiegelow et al., 1997). Linear corridors may also facilitate movement into sink habitat patches where death rate exceeds birth rate, and population growth is zero (Pulliam, 1988; Pulliam and Danielson, 1991; Danielson, 1991, 1992). These processes influence distribution by impeding or facilitating movement by individuals into patches; in other words; they act on the process of dispersal. Generally landscape configuration influences these processes, and does so at larger spatial scales.

Landscape composition may influence an organism's distribution through its differential response to the size, shape, or arrangement of different habitat patches. Intuitively, a patch's size will affect its use by an individual or population. This can lead to ephemeral extinction in small patches, as in the metapopulation model suggested by Levins (1970). Coupled with patch isolation, this can result in prolonged local extinction (Fahrig and Merriam, 1994). Patch shape can impede or facilitate movement of individuals in and out of the patch (Tamahazi, 1996; but see Harper et al., 1993). Shape also influences the perimeter-area ratio of the patch and hence the extent of edge effects

(Stamps et al., 1987), deleteriously impacting "interior" species and encouraging the introduction of other plant or animal species (Forman, 1997).

The arrangement of patches influences distribution through landscape complementation, landscape supplementation, and neighbourhood effects (Dunning et al., 1992). Complementation occurs when an organism uses several patch types for non-substitutable resources; supplementation occurs when the organism uses other patch types to supplement resources that are scarce in the focal patch. In either case, the juxtaposition of different patch types affects the abundance of organisms that can survive in the immediate area. Neighbourhood effects - the proximity of patches and permeability of interpatch boundaries - mediate these processes. Finally, what Dunning et al. (1992) termed "indirect landscape effects" - the response to landscape structure by predators, prey, competitors, mutualists, *etc.* - will also influence an organism's presence or absence within a patch. However, by considering landscape composition, one acknowledges that the effects of landscape structure are contextual, a crucial point that many studies have failed to consider.

The fundamental driver behind landscape structure is heterogeneity. Heterogeneity is perceived differently by different species, or even age/sex classes within a species (Kotliar and Wiens, 1990). Heterogeneity became a focus of interest in ecology under the pseudonym of fragmentation. Like "landscape", fragmentation has many descriptions, but is broadly considered as an "unnatural detaching or separation of expansive tracts [of habitat] into spatially separated fragments" (Harris and Silva-Lopez, 1992). Agriculture and forestry are two principal causes of fragmentation. Fragmentation can be intrusive, with small pockets of disturbance in an undisturbed matrix, or enveloping, with patches of natural habitat left in a matrix of anthropogenic patches (Harris and Silva-Lopez, 1992). The effects of fragmentation on animal populations are often considered to be synonymous with habitat loss, although Andren (1994; 1996) suggests true fragmentation effects occur when contiguity of natural landscape remnants is lost and patches become isolated; the detrimental effects on animal populations are greater than the effects of habitat loss alone. It should be noted in the preceding quotation that fragmentation is synonymous with unnatural, or anthropogenic, disturbance. As of the time of this writing few, if any, studies have addressed the effects of natural or non-anthropogenic heterogeneity on animal distribution; this will be addressed in Chapter Three.

Despite the growing awareness of the importance of landscape effects that has emerged in the last two decades, few could deny that habitat plays a vital role in determining the presence/absence or abundance of an organism. The plant (or animal) species composition within a patch comprises the food base for an organism; floristic structure provides nesting sites and shelter from predators (Southwood, 1977). By this token the ecological processes occurring within a given patch will be dictated by the habitat within it; an organism may forage in one patch type, den in another, disperse through yet another. As landscape effects are manifested by their influence on ecological processes (Wiens et al., 1993), it follows that landscape effects on animals within patches may vary with different local-scale vegetation. The relative effects of local habitat and landscape structure will be examined in Chapter Four.

Studies of the effects of landscape structure have used a wide range of taxa as study subjects, including birds (Wegner and Merriam, 1979; Donovan et al., 1997; Stouffer and Bierregaard, 1997; Schmiegelow et al., 1997); mammals (Kozakiewicz, 1993; Szacki et al., 1993), and invertebrates (Middleton and Merriam, 1983; Taylor and Merriam, 1996; Jonsen and Fahrig, 1997; Roland and Taylor, 1997; Wiens et al., 1997). In most cases the study organisms are ones that are known to rely on patches that comprise only a small part of the landscape; patches that are set into a less suitable (or completely unsuitable) matrix. Hence, the landscape is heterogeneous from the organism's perspective, and the researcher may use known habitat preferences to extrapolate the nature of that heterogeneity (Andren et al., 1997). In fragmented landscapes it is enough to choose a species that is affiliated with remnant native habitats and avoids novel patch types. To gauge the effects of landscape structure in a naturally heterogeneous area, I chose to study the North American red squirrel, *Tamiasciurus hudsonicus*.

T. hudsonicus is a conifer specialist. The seeds found in the cones of conifer trees such as *Abies*, *Picea*, and *Pinus* spp. are its primary food source (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; Riege, 1991). Although red squirrels also feed on mushrooms, berries, and nuts (Gurnell, 1983; Yahner, 1987), they rely on conifer cones for overwinter survival (Rusch and Reeder, 1978). Squirrels collect cones in the late summer/ early fall and cache them in middens (Hurly and Robertson, 1990; Dempsey and Keppie, 1993). Large middens contain the decomposed bracts of previous years' cones and provide a food-hoarding location as well as shelter for the squirrel. There may be several middens on a single squirrel territory.

Territories are relatively permanent entities (Rusch and Reeder, 1978) that are heavily defended (Stuart-Smith and Boutin, 1994). The territorial call, or rattle, denotes the squirrel's home turf and warns potential intruders of that area's occupation (Lair, 1990). The size of these territories varies with location and habitat type (Smith, 1968; Rusch and Reeder, 1978). There are no differences in territory size between males and females and no overlap exists (Smith, 1968). Males are permitted onto a female's territory only during a one-day oestrous, which is typically once a year (Lair, 1985). Breeding occurs in early March to mid June and litters are born between April and July (Larsen, 1993; Becker et al., 1998). Young typically must find their own territories, although some evidence of bequeathal or sharing exists (Price and Boutin, 1993). Squirrels without a permanent territory and thus a reliable source of overwintering food have a low probability of survival (Rusch and Reeder, 1978).

From these studies I postulate that red squirrels perceive mixed-wood boreal landscapes that contain a mix of conifer and other stand types as heterogeneous; that such a landscape is a mosaic of suitable patches embedded in a less suitable matrix. Based on this premise, the following chapters will address three questions:

1) What is the spatial scale at which we expect landscape structure to predict squirrel presence?

2) Does landscape structure derived from natural heterogeneity predict squirrel presence?

3) Does local vegetation influence the relationship between landscape structure and squirrel presence?

Conservation biology carries with it an undeniable urgency that has spawned a generation of fragmentation studies. The results of these studies have generated some intriguing theoretical ecological questions about organisms' response to the patterns of spatial heterogeneity in which they are immersed. This thesis will attempt to address some of these fundamental questions against the backdrop of the mixed-wood boreal forest of northern Alberta.

1.1 METHODS

1.1.1 Study Area

This study was conducted north of Lac La Biche, Alberta, on the Alberta-Pacific Forest Industries (AlPac) Forest Management Area (FMA). This area lays within the mixed-wood boreal forest, and is covered mainly by black spruce bogs (*Picea mariana*) in hygric areas; aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) mixed sparsely with white spruce (*Picea glauca*) in mesic areas; and jack pine (*Pinus banksiana*) in xeric areas (Strong and Leggat, 1992). The early 1990's heralded the cutting of aspen and some conifer stands in small cutblocks from some townships.

1.1.2 Sampling Design

Three areas had been selected by the Sustainable Forestry Management Interstand Dynamics Project, based on general landscape composition: a Managed, Burned, and Reference Area. The Managed Area had experienced some timber harvesting (ca. 9% of area). It encompassed townships T69 R13 W4 and T70 R13 W4; central coordinate was 55°5' W 112°15' N (Figure 1.1). The Burned Area was situated on townships T73 R11 W4, T73 R12 W4, T74 R11 W4, and T74 R12 W4, with central coordinate 55°30' W

112°0' N. The third area was not burned and had experienced very slight (ca.1%) timber harvesting activity; we termed this the Reference Area. It was located on T70 R13 W4, T71 R13 W4, T70 R14 W4, and T71 R14 W4, with a central coordinate of 55° W112°30' N (Figure 1.1). Within the Managed and Reference Areas a systematic sampling grid was installed, with points 1 km apart in a seven by nine pattern (Figure 1.1). These were called mega grids. Only upland sites were sampled, so points falling within a black spruce bog or other wetland were dropped and others added to the edges of the grid to compensate. There were a maximum of 64 sampling points in each of the Managed and Reference landscapes. Due to access problems a systematic design was impossible for the Burned landscape, so a stratified design was used that placed points at least 1 km apart, with points in each upland patch type. Twenty-eight sampling points were established there.

Within each of these mega grids, meso grids were installed (Figure 1.1). The position of the meso grid was chosen to encompass a representative sample of all landscape types. Points in meso grids were 250 m apart in the same pattern as mega grids, for a total of 64 points in each grid. Criteria for establishing points were the same as for mega grids. Two meso grids were established on each of the Managed and Reference grids; only one was established on the Burned grid. Landscape structure, squirrel presence, and local vegetation were assessed within these grid systems, and will be discussed in the subsequent chapters.

Figure 1.1: Location and design of the sampling system. The Reference mega and meso grids are shown. Circles indicate mega grid points, and squares represent meso grid points. Distance between mega grid points is 1 km; between meso grid points, 250 m.

1.2 LITERATURE CITED

Åberg, J., G. Jansson, J.E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia **103**: 265-269.

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

Andreassen, H.P., S. Halle, and R.A. Ims. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. Journal of Applied Ecology **33**: 63-70.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**: 355-366.

Andren, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos **76**: 235-242.

Andren, H, A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos **80**(1): 193-196.

Baudry, J., and G. Merriam. 1988. Connectivity and connectedness: Functional versus structural patterns in landscapes. In: Schreiber, K.-F. (ed.), Connectivity in landscape ecology. Proc.2nd International Association for Landscape Ecology. Munstersche Geogr. Arbeiten 29, pp 23-28.

Becker, C.D., S. Boutin, and K.W. Larsen. 1998. Constraints on first reproduction in North American red squirrels. Oikos **81**: 81-92.

Bennett, A., K. Henein, and G. Merriam. 1994. Corridor use and the elements of corridor quality - chipmunks and fencerows in a farmland mosaic. Biological Conservation **68**: 155-165.

Danielson, 1991. Communities in a landscape: The influence of habitat heterogeneity on the interactions between species. The American Naturalist **138**(5): 1105-1120.

Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evolutionary Ecology **6**: 399-411.

Dempsey, J.A., and D.M. Keppie. 1993. Foraging patterns of eastern red squirrels. Journal of Mammalogy **74**(4): 1007-1013.

Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**(7): 2064-2075.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**: 169-175.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**(1): 50-59.

Fitzgibbon, C.D. 1997. Small mammals in farm woodlots: the effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology **34**: 530-539.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review **13**(2/3/4): 133-148.

Harper, S.J., E.K. Bollinger, and G.W. Barrett. 1993. Effects of patch shape on populations dynamics of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy **74**(4): 1045-1055.

Harris, L., and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. Pp. 198-237 **In** Conservation Biology: The theory and practice of nature conservation, preservation, and management. P. Fiedler and S. Jain, Eds. Chapman and Hall, London.

Henderson, M.T., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biological Conservation **31**: 95-105.

Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology **4**: 157-170.

Hurly, T.A., and R.J. Robertson. 1990. Variation in the food hoarding behaviour of red squirrels. Behavioural Ecology and Sociobiology **26**: 91-97.

Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**(5): 763-779.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**: 253-260.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers - the effect on small mammal populations and communities. Acta Theriologica **38**(1): 1-30.

Lair, H. 1985. Mating seasons and fertility of red squirrels in southern Quebec. Canadian Journal of Zoology **63**: 2323-2327.

Lair, 1990. The calls of the red squirrel: a contextual analysis of function. Behaviour **115**: 254-282.

Larsen, K.W. 1993. Female reproductive success in the North American red squirrel, *Tamiasciurus hudsonicus*. Ph.D. Thesis, University of Alberta, Edmonton.

Levins, R. 1970. Extinction. Pp. 77-207 **In** Lectures on mathematics in the life sciences. Vol. 2. M. Gerstenhaber, ed. American Mathematical Society, Providence, RI.

Merriam, G. 1988. Landscape ecology: the ecology of heterogeneous systems. Pp. 43-50 **In** Landscape Ecology and Management. M. Moss, ed. Polyscience Publications Inc., Montreal.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. pp. 133-142 In Nature Conservation 2: The Role of Corridors. Edited by D.A. Saunders and R.J. Hobbs. Surrey Beatty and Sons Pty Ltd, Chipping Norton, NSW, Australia.

Merriam, G., and A. Lanoue. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. Landscape Ecology **4**(2/3): 123-131.

Middleton, J., and G. Merriam. 1983. Distribution of woodland species in farmland woods. Journal of Applied Ecology **20**: 625-644.

Pither, J., and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos **83**: 166-174.

Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. Behavioural Ecology **4**: 144-150.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist **132**(5): 652-661.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**: S5-S66.

Riege, D.A. 1991. Habitat specialization and social factors in distribution of red and grey squirrels. Journal of Mammalogy **72**(1): 152-162.

Roland, J., and P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature **386**: 710-713.
Rusch, D., and W. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Schmiegelow, F.K.A., C.G. Machtans, and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology **78**(6): 1914-1932.

Smith, C.C. 1968. The adaptive nature of social organization in the Genus of three (sic) squirrels *Tamiasciurus*. Ecological Monographs **38**(1): 31-63

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology **46**: 332-365.

Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. The American Naturalist **129**(4): 533-552.

Strong, W., and K.R. Leggat. 1992. Ecoregions of Alberta. Prepared for Alberta Forestry, Lands and Wildlife, Land Information Services Division, Resource Information Branch. Publication Number T:245.

Stouffer, P.C., and R.O. Bierregaard, Jr. 1995. Use of Amazonian forest fragments by understory (sic) insectivorous birds. Ecology **76**(8): 2429-2445.

Stuart-Smith, K., and S. Boutin. 1994. Costs of escalated territorial defence in red squirrels. Canadian Journal of Zoology **72**: 1162-1167.

Szacki, J., J. Babinska-Werka, and A. Liro. 1993. The influence of landscape spatial structure on small mammal movements. Acta Theriologica **38**(2): 113-123.

Tamahazi, T. 1996. Effects of patch shape on the number of organisms. Landscape Ecology **11**(5): 299-306.

Taylor, P.D., L. Fahrig, K. Henein., and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**: 571-573.

Taylor, P.D., and G. Merriam. 1996. Habitat fragmentation and parasitism of a forest damselfly. Landscape Ecology **11**(3): 181-189.

Tiebout, H.M., and R.A. Anderson. 1997. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. Conservation Biology **11**(3): 620-627.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**: 171-197.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. Bioscience **37**(2): 119-127.

Wegner, J.F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. Journal of Applied Ecology **16**: 349-357.

Wiens, J.A. 1976. Population responses to patchy environments. Annual Reviews in Ecology and Systematics **7**: 81-120.

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

Wiens, J.A., R.L. Schooley, and R.D. Weeks. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos **78**: 257-264.

Yahner, R.H. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*, in a marginal habitat in Pennsylvania. Canadian Field Naturalist **101**(4): 586-589.

Chapter Two

Using Foraging Range to Demarcate a Functional Landscape

2.0 INTRODUCTION

The cardinal consideration of any ecological study must be the identification of the spatial scale most appropriate to the pattern or process under investigation (Wiens, 1989). In landscape ecology, this translates into defining the patch and the landscape by some criteria pertinent to the organism under consideration, and describing a landscape relevant to the mechanisms by which landscape structure might influence distribution (Wiens et al., 1993). Recognizing that patches and landscapes are not fixed entities, Kotliar and Wiens (1990) proposed a theoretical model by which patchiness is arranged in a hierarchy. A given "patch" might have internal heterogeneity (*e.g.*, in floral species composition or physiognomy) but from the organisms' perspective during a given activity, this variance is averaged out so that it appears homogeneous. Patches aggregate to form larger functional units, which Addicott et al. (1987) dubbed "ecological neighbourhoods". Ecological neighbourhoods are defined by an ecological process, an appropriate time scale, and an organism's activity. Therefore, what constitutes an ecological neighbourhood or functional patch aggregate is not only species-specific, but will vary within a species depending on the process being considered.

An organism's response to its surroundings may actually occur at several different spatial scales (Morris, 1987, 1992; Urban et al., 1987). The smallest spatial scale at which a particular organism responds to patchiness is its "grain", while the largest scale that influences an organism is its "extent" (Kotliar and Wiens, 1990). Grain and extent are also process-specific, as suggested by ecological neighbourhoods. However the grain of study is often a matter of convenience for researchers, a launching point limited by the resolution of the data. It is assumed that below this grain, all things are equal. The extent, as suggested by the ecological neighbourhood (Addicott et al., 1987), will vary depending on the process under consideration; or alternatively, the dominant ecological process that is effecting the response to heterogeneity. To combine terminology, the grain can be considered the patch, and the extent is the landscape.

Defining landscape extent *a priori* is a dangerous business if done without proper consideration of the relevant spatial and time scales; this is analogous to conducting a population ecology study without first delineating the population. Following the example of ecological neighbourhoods, I define the landscape extent based on the spatial scale at which ecological processes occur to effect a response to landscape structure. This demarcation is based on the premise that there are two main mechanisms influencing patch occupancy by an organism: 1) it must get there, which is a dispersal phenomenon, and 2) it must survive there, which is related to foraging, among other things. Obviously there are many other factors involved, but I will limit my argument to these two for the sake of simplicity.

If an organism's distribution is dispersal-limited, aspects of the landscape beyond the patch should predict its presence. Landscape configuration, in terms of patch isolation (Fahrig and Merriam 1994), connectivity (Taylor et al., 1993; Pither and Taylor, 1998), and boundary permeability (Wiens et al., 1985) could play a role. So could composition, in that a proximal expanse of suitable habitat may act as a source for dispersers (Pulliam and Danielson, 1991; Danielson, 1991, 1992). In this scenario, landscape structure and a species' movement patterns interact to determine population distribution (Wiens et al., 1993). Alternatively, if an organism is forage-limited, one would expect a response to landscape structure at smaller, foraging scales. Landscape complementation or supplementation may facilitate occupation by an individual (Dunning et al., 1992). Patch size, shape and composition may constrain occupation (Harper et al., 1993; Tamahazi, 1996). In this case local-scale heterogeneity would drive distribution and larger-scale phenomena would be less important.

Red squirrels are not behaviourally restricted to conifer and can move through deciduous habitats (Rusch and Reeder, 1978; Yahner, 1987). Given that the red squirrel is dependent on conifer for overwinter survival (Gurnell 1987), and the areas in which I conducted this study are conifer-depauparate (ca. 20-30% of the area), I postulated that red squirrels are forage-, not dispersal-limited. I tested the predictions that 1) red squirrels are able to move through the matrix and thus are not dispersal-limited and 2) the response to landscape structure exists at small scales, the ecological neighbourhood of the foraging range. The aim of this chapter is to test the first prediction, and to provide an estimate of the foraging range of the red squirrel in the mixed-wood boreal ecosystem, as a prelude to the multiscalar landscape analysis in Chapter Three that tests the second prediction. The current chapter will also assess squirrels' use of the matrix (non-conifer) patches, a fundamental consideration when ascertaining whether larger-scale isolation could play a role in squirrel distribution.

The territory size of the red squirrel has been well studied in a variety of high-quality habitats, including white spruce in the Yukon (Price et al., 1986), lodgepole pine in Colorado (Gurnell, 1984), and jack pine in Alberta (Larsen, 1993). Rusch and Reeder (1978) examined territory size in conifer stands in the southern mixed-wood boreal forest of Alberta. However there is no documentation of foraging range size (which include important extraterritorial movements (Don. 1983)) in the marginal squirrel habitat of the mixed-wood boreal of north-central Alberta, where deciduous stands form the matrix and conifer is limiting.

To obtain an estimate of the foraging scale at which response to landscape structure was expected, I used radio telemetry to assess the size and content of the summer foraging range of red squirrels in the study area. This information will be used in subsequent chapters as a benchmark for assessing the appropriate extent of landscape analysis, a pivotal first step in evaluating the effects of landscape structure.

2.1 METHODS

2.1.1 Squirrel locations

To track squirrels within jack pine stands, grid points from within the Reference area were identified at which squirrel territorial calls had been recorded, and which had suitable access. Ten of these were selected randomly. For squirrels within spruce/deciduous/cut stands, the same protocol was followed on the Managed grid. Due to low capture success on these latter ten sites three extra sites were added, identified on the ground as containing spruce (adjacent to a deciduous stand or cutblock) and having a resident squirrel present.

Tomahawk live traps (Tomahawk Livetrap Co., Tomahawk, Wisconsin) were baited with ca. 5 g of peanut butter and located at middens, runways, and piles of stripped cones at each site; 4-6 traps were used per site. Seven squirrels were trapped in the Reference area, and nine were trapped in the managed area, for a total of 16 individuals (11 females, 5 males, all adults). Squirrels were handled in canvas and mesh bags. The mass and sex of each squirrel were recorded. Squirrels were fitted with radio transmitter collars (PD-2C; mass = 3.8 g; Holohil Systems, Woodlawn, Ontario) then released. From June - August (inclusive) 1997, radio telemetry (TR-2 receiver with RA-14 antenna; Telonics Canada, Winnipeg, Manitoba) was used to locate these individuals twice per day, morning and evening, for approximately two weeks, to yield 17-25 locations each. Telemetry was used to visually locate the individual. Its position was marked, and the angle and distance from a reference point with known Universal Transverse Mercator (UTM) coordinates were established.

2.1.2 Home range analysis

Angles and distances from a known central location (obtained using the Global Positioning System) were translated into UTM coordinates and entered into the Arc/Info geographic information system (GIS) (Esri Inc., California). The outermost points of each range were connected using a 100% minimum convex polygon to create a foraging range for each individual. Although exploration, breeding, or other activities may have been occurring during these movements, the polygons were termed "foraging ranges" as foraging is a daily activity known to have consistently occurred during the tracking period. The use of this term separates this range from home ranges, which typically encompass larger time-frames (*q.v.*).

Ranges were overlaid on digital Alberta Vegetation Index (AVI) forest inventory coverages reclassified to describe age and stand type (see Appendix 1 for reclassification protocols). The size of the range, and landscape composition and configuration within each, was quantified using FRAGSTATS (McGarigal and Marks, 1994). Tests for differences between mean range size by sex and by conifer content were performed using the non-parametric Rank Sum test (Ambrose and Ambrose, 1995) for low sample sizes and non-normal data.

2.2 RESULTS

2.2.1 Squirrel foraging range sizes

There was some variability in squirrel foraging range size, with the largest being 8.12 ha in size and the smallest 0.1 ha in size (Table 2.1). There was no difference between male (n=5) and female (n=11) foraging range sizes (Rank Sum test, $p>0.05$). The percent of conifer stands in the home range was defined by the landscape maps and included pure black spruce, white spruce, larch, and jack pine, as well mixed-deciduous stands in which conifer constituted the majority of trees within the stand. There was a difference in size between ranges with <90% conifer stands within them, (n=8) and >90% conifer stands (n=8), as defined by landscape maps (Rank Sum test, $p<0.05$; Table 2.2). Ranges with >90% conifer within their boundaries were smaller than those containing other elements, which included pure- and mixed-deciduous stands, and clearcuts.

2.2.2 Squirrel use of stand types

Squirrels were radio-located in black spruce, white spruce, jack pine, aspen / balsam poplar, and clearcuts. For those squirrels whose range included jack pine (n=7), an average of 86% +/- 14 (standard deviation) of the locations were within the jack pine, with the remainder falling in deciduous or deciduous/jack pine mix. Of the squirrels whose ranges included spruce, distribution of radio locations was quite variable. Two of the ranges did not include any conifer stands, as defined by the AVI maps. Ground-truthing revealed the presence of a few large cone-bearing white spruce trees within the deciduous patch. One range, the smallest, was entirely within old white spruce. Of those squirrels who used spruce next to deciduous patches (n=3), 37.33% +/- 32.5 locations fell within spruce: 62.67% +/- 32.5 fell within deciduous. Of those squirrels whose ranges bordered a clearcut (n=3), 70% +/- 22.9 fell within spruce; 23.33% +/- 16.07 fell within the cut. These results suggest that squirrels are not confined to conifer habitats and do make use of the matrix.

Table 2.1: Red squirrel foraging range statistics.

(n=16)	Foraging range size (ha)	% conifer within range
mean	1.7	61.48
std dev	2.03	42.50
median	0.95	84.88
maximum	8.12	100
minimum	0.1	0

Table 2.2: Relative sizes of squirrel foraging ranges (ha) with differing conifer content.

	<90% conifer	>90% conifer
n	8	8
mean area (ha)	1.92	1.48
std dev	1.19	2.69
median	1.565	0.635
maximum	4.41	8.12
minimum	0.92	0.1

2.3 DISCUSSION

2.3.1 Assessment of accuracy and the 100% minimum convex polygon

As squirrels were visually located, there is no error polygon associated with each observation, of the kind that should be presented with triangulation data (Harris et al., 1990). For each squirrel, the relationship between sample size (number of locations obtained) and the amount of area measured is not linear but does not display a perfect asymptote. This indicates that more locations per squirrel may have been required to obtain a more complete foraging range size. This was compensated for by using a relatively consistent number of points per individual (ca. 17-25) and employing a non-statistical home range estimator.

Statistical and non-statistical home-range estimators can be used to analyse radio location data (Harris et al., 1990). Statistical methods usually focus on the generation of probability ellipses (Dixon and Chapman, 1980). Methods such as these attempt to describe 'utilization distributions', or the distribution of an animal's position in space (Harris et al., 1990). The harmonic mean method, for example, is a statistical estimator that uses areal moments to calculate the most intensely used area, or 'centre of activity' as indicated by density of radio locations (Dixon and Chapman, 1980). Parametric methods such as these are susceptible to problems with autocorrelation of location data and sample size.

Non-parametric statistical estimators do not assume adherence to a theoretical distribution. Techniques include fixed and adaptive kernel methods (Worton, 1989) which delineate areas of intense usage, using a non-parametric smoothing function.

However, these methods are quite sensitive to both skewness of location data and to the type of smoothing parameters used. Harris et al. (1990) suggest that these methods are more reliable for examining relative range (habitat) use than total size.

The simplest non-statistical home range estimator is the minimum convex polygon (MCP) (Don, 1983). With the MCP a researcher can use either 100% of the points, as this study does, or restrict the number in such a way that outliers are omitted to provide a more conservative estimate of size. While considered a more robust estimator than statistical methods when number of fixes is small (Harris et al., 1990), it is still strongly affected by outliers and can include portions of habitat area beyond the main area of activity or that aren't visited by the individual. The MCP was deemed suitable for this study as it was not my intention to delineate core areas of habitat or determine the most parsimonious range or territory size; the goal of this study was to determine all movements by individuals, including all extra-territorial forays and movements off core areas. All of the points were used (100% MCP) rather than employing a restricted polygon, as longer movements within the foraging time frame were considered important indicators of the scale of squirrels' areal use.

2.3.2 Spatial scale of landscape analysis

A mean foraging range size of 1.7 ha corresponds to a circular landscape extent with a 73.6 m radius. The minimum and maximum-sized ranges correspond to 17.8 m and 160.8 m radii, respectively. Given the variation in foraging range size and the possibility that ranges are possibly underestimated, it is prudent to say that if squirrels are responding to landscape structure at the foraging scale, then landscape structural variables will become significant predictors of squirrel presence at the 50 m or 100 m scales of analysis, with less predictive power at the 250 m scale of analysis. If a stronger response occurs beyond these radii (250 m, 500 m or 1000 m) then other large-scale processes, processes, such as dispersal (natal or otherwise; Rusch and Reeder, 1978; Boutin et al., 1992; Larsen and Boutin, 1994) may be responsible.

2.3.3 Comparison to other systems

Don (1983) in his review of tree squirrel home range sizes from different studies and geographical areas reported an average size of approximately 1 ha. In white spruce forests in Kluane, YT, squirrel territory size was 0.2-0.5 ha (Price et al., 1986). In subalpine lodgepole pine in Colorado, Gurnell (1984) found an average home range size 0.56 ha with a much less variable range (0.28 - 0.80 ha; n=9) than found herein. He also noted extraterritorial forays in excess of 150 m, though did not quantify their total extent. In jack pine stands in Alberta, Larsen (1993) measured a mean territory size of 0.65 ha. Movements as far as 500 m off territories were also reported for adults (Larsen and Boutin, 1994). In the southern mixed-wood boreal of Alberta, Rusch and Reeder (1978) reported mean territory size of 0.24 ha +/- 0.03 (SE; n=6) in white spruce; 0.35 ha +/- 0.02 (n=11) in mixed spruce; and 0.66 ha +/- 0.17 (n=7) in jack pine. Mean movements of ca. 64 m in spruce, 110 m in jack pine, and 185 m in aspen were also observed (Rusch and Reeder, 1978). Variability in territory or home range size can be attributed to differences in food availability (Smith, 1968), with larger ranges found in mixed conifer/aspen habitats (Rusch and Reeder, 1978). However, ranges measured herein are larger and much more variable than those previously reported. This should be noted with caution, however, as problems with comparability arise that must be considered by those who seek to use published home ranges to quantify landscape extent. Utilization distributions, kernels, or even territories are not accurate gauges of the spatial scale of local (foraging) processes, nor of the influences of landscape structure upon them. In these cases use of the matrix by the study animal may be overlooked.

2.3.4 Territories and time frame

Squirrels defend traditional territories all year (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978). Despite the cost of territoriality (Stuart-Smith and Boutin, 1994) defence is zealous, as maintaining a territory is critical for overwinter survival (Rusch and Reeder, 1978; Gurnell, 1987; Larsen and Boutin, 1994).

Gurnell (1984) distinguishes between the territory and the home range, the former being nested within the latter. As a much frequented and defended area, a territory more closely approximates a high-density utilization distribution than a minimum convex polygon, which includes all locations (Harris et al., 1990). The ranges reported here are akin to the "domain" of Don (1983), which includes long-distance forays as well as intensely utilised areas. These are not often reported in the literature, making home-range comparison difficult. As an additional note, the time-frame in which my ranges and published territory sizes were measured, differ. Harris et al. (1990) emphasise that the time period during which tracking occurs can greatly influence the outcome of the observed home-range size. In this study locations were obtained only over a period of 2-3 weeks in June, July, and August. Therefore these ranges do not describe a complete (annual) home range size, nor demarcate territory boundaries; they do create an index of the spatial scale of summer land use by these small mammals, and determine the extent of movements between conifer and matrix habitats.

2.3.5 Matrix use by squirrels

From the data I can conclude that squirrels do make use of the deciduous / clearcut matrix, and are not confined to conifer habitats. Fisher and Merriam (*in press*) found that red squirrels in Ontario made use of an agricultural matrix when foraging, even when conifer habitats were within close proximity. In Alberta, Kemp and Keith (1970) suggested that deciduous habitats contained lightly defended seasonal territories that maintained juvenile populations until spruce territories became available. In the same area, Rusch and Reeder (1978) reported movements between spruce, jack pine, and aspen habitats that ranged between 1.1 and 5.3 km, coinciding with spring shuffle and fall dispersal. Yahner (1987) found red squirrels made use of marginal deciduous habitats in Pennsylvania where conifer is limiting. The matrix indisputably is used by red squirrels for movement and feeding.

The data suggest that squirrels may be using landscape supplementation (Dunning et al., 1992) to provide a substitutable resource, especially in mixed spruce/deciduous/cut habitats. Berries, mushrooms, and hazelnuts can be found in deciduous stands and clearcuts (J. Fisher, unpubl. data). Alternative food sources such as these may be important components of a squirrel's diet (see Gurnell, 1983 for review). Since home ranges are smaller within contiguous conifer habitat than heterogeneous areas, it is possible that where conifer is limiting their seeds are used by squirrels mainly for overwinter survival, while summer forage is obtained from adjoining patch types.

Territorial rattles were often heard within both conifer and deciduous habitats, although were never noted in clearcuts, despite the extensive amount of time spent there. I would tentatively suggest that while deciduous habitat may be included within the boundaries of defended territories, clearcut movements represent extra-territorial forays for opportunistic foraging rather than a defended resource. However, much more research is needed to test such a hypothesis. The data do reveal that North American red squirrels enter the matrix quite readily, and are not behaviourally restricted from using the matrix. This suggests that dispersal or other movements are less likely to be impeded by lack of connectivity (Taylor et al., 1993) unlike Eurasian red squirrels (Verboom and van Apeldoorn 1990; Andren and Delin, 1994; van Apeldoorn et al., 1994; Celada et al., 1993; Wauters et al., 1994) and other habitat specialists in heterogeneous landscapes (Wegner and Merriam 1979; Henderson et al., 1985; Merriam et al., 1989; Fitzgibbon, 1993, 1997; but see Szacki et al., 1993; Wegner and Merriam, 1990).

2.4 CONCLUSIONS

In the mixed-wood boreal forest of northeast-central Alberta, 100% MCP's obtained for seventeen squirrels show that these organisms have highly variable foraging range sizes that exceed territorial estimates from other systems and studies. The mean ecological neighbourhood of foraging corresponds to an area 50 m to 100 m in radius. Squirrels travel through several patch types, suggesting that larger-scale effects stemming from lack of connectivity may be less relevant than local-scale phenomena.

2.5 LITERATURE CITED

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

Ambrose, H.W. III, and K.P. Ambrose. 1995. A Handbook of Biological Investigation. 5th Edition. Hunter Textbooks Inc., NC.

Andren, H., and A. Delin. 1994. Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. Oikos **70**: 43-48.

van Apeldoorn, R., C. Celada, and W. Nieuwenhuizen. 1994. Distribution and dynamics of the red squirrel (*Sciurus vulgaris L.*) in a landscape with fragmented habitat. Landscape Ecology **9**(3): 227-235.

Boutin, S., Z. Tooze and K. Price, 1992. Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*): the effect of local vacancies. Behavioural Ecology **4**(2): 151-155.

Celada, C., G. Bogliani, A. Gariboldi, and A. Maracci. 1993. Occupancy of isolated woodlots by the red squirrel *Sciurus vulgaris L.* in Italy. Biological Conservation **69**: 177-183.

Danielson, 1991. Communities in a landscape: The influence of habitat heterogeneity on the interactions between species. The American Naturalist **138**(5): 1105-1120.

Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evolutionary Ecology **6**: 399-411.

Dixon, K.R., and J.A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology **61**(5): 1040-1044.

Don, B.A.C. Home range characteristics and correlates in tree squirrels. Mammal Review **13** (2/3/4): 123-132.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**: 169-175.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**(1): 50-59.

Fitzgibbon, C.D. 1993. The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. Journal of Applied Ecology **30**: 736-

742.

Fitzgibbon, C.D. 1997. Small mammals in farm woodlots: the effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology **34**: 530-539.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review **13**(2/3/4): 133-148.

Gurnell, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole forest. Animal Behaviour **32**: 1119-1131.

Gurnell, J. 1987. The Natural History of Squirrels. Christopher Helm, London.

Harper, S.J., E.K. Bollinger, and G.W. Barrett. 1993. Effects of patch shape on populations dynamics of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy **74**(4): 1045-1055.

Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review **20**(2/3): 97-123.

Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**(5): 763-779.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**: 253-260.

Larsen, K.W. 1993. Female reproductive success in the North American red squirrel, *Tamiasciurus hudsonicus*. Ph.D. Thesis, University of Alberta, Edmonton.

Larsen, K.W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology **75**(1): 214-223.

Merriam, G., M. Kozakiewicz, E. Tsuchiya, and K. Hawley. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. Landscape Ecology **2**(4): 227-235.

McGarigal, K., and B.J. Marks. 1994. FRAGSTATS - Spatial Pattern Analysis Program for Quantifying Landscape Structure, Version 2.0. Oregon State University, Corvallis, OR.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology **68**(2):362-369.

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

Pither, J., and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos **83**: 166-174.

Price, K., K. Broughton, S. Boutin, and A.R.E. Sinclair. 1986. Territory size and ownership in red squirrels: response to removals. Canadian Journal of Zoology **64**: 1144-1147.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**: S5-S66.

Rusch, D., and W. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Smith, C.C. 1968. The adaptive nature of social organization in the Genus of three (sic) squirrels *Tamiasciurus*. Ecological Monographs **38**(1): 31-63

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology **46**: 332-365.

Stuart-Smith, K., and S. Boutin. 1994. Costs of escalated territorial defence in red squirrels. Canadian Journal of Zoology **72**: 1162-1167.

Szacki, J., J. Babinska-Werka, and A. Liro. 1993. The influence of landscape spatial structure on small mammal movements. Acta Theriologica **38**(2): 113-123.

Tamahazi, T. 1996. Effects of patch shape on the number of organisms. Landscape Ecology **11**(5): 299-306.

Taylor, P.D., L. Fahrig, K. Henein., and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**: 571-573.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. Bioscience **37**(2): 119-127.

Verboom, B., and R. van Apeldoorn. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. Landscape Ecology **4**(2/3): 171-176.

Wauters, L., P. Casale, and A. Dhondt. 1994. Space use and dispersal of red squirrels in fragmented habitats. Oikos **69**: 140-146.

Wegner, J.F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. Journal of Applied Ecology **16**: 349-357.

Wegner, J., and G. Merriam. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biological Conservation **54**: 263-267.

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

Wiens, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos **45**: 421-427.

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

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**(1): 164-168.

Yahner, R.H. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*, in a marginal habitat in Pennsylvania. Canadian Field Naturalist **101**(4): 586-589.

Chapter Three

Squirrel Response to Landscape Structure at Multiple Spatial Scales

3.0 INTRODUCTION

The relationship between landscape structure and animal abundance has been frequently demonstrated in agricultural and other anthropogenically modified landscapes. In these systems fragmentation is extensive; few small patches of native habitat remain; and organisms typically perceive considerable contrast between the native and novel habitat patches. Insects (Jonsen and Fahrig, 1997; Pither and Taylor, 1998), songbirds (Wegner and Merriam, 1979), tetraonids (Åberg et al., 1995), and small mammals (Wegner and Merriam, 1979; Henderson et al., 1985; Kozakiewicz, 1993; Bennett et al., 1994; Fitzgibbon, 1997; but see Wegner and Merriam 1990) have shown a response to fragmented landscape structure. The possible mechanisms driving this response vary, but in general an affinity for some aspect of the landscape - be it proximity of remnant patches (Åberg et al., 1995), corridors (Wegner and Merriam, 1979; Henderson et al., 1985; Merriam, 1988, 1991; Merriam and Lanoue, 1990; Fitzgibbon, 1997), edge (Donovan et al., 1997), diversity (Tapper and Barnes, 1986; Jonsen and Fahrig, 1997), or novel patches (Fisher and Merriam, *in press*) - coupled with a negative response to some other aspect, results in a net increase or decrease in abundance in comparison with a native system.

Although pervasive in modern landscapes, anthropogenic habitat fragmentation is not the sole form of heterogeneity. Natural processes also cause variation in landscape pattern (see Wiens, 1976; Urban et al., 1987 for reviews). In the Canadian mixed-wood boreal forest, for example, relatively small topographic differences can cause marked differences in the vegetation growing on a site. Fire, disease, pest outbreak, and windthrow all contribute to the creation of a diverse mosaic of plant and animal life (Hansson, 1992). While fragmentation has been the golden calf of landscape ecology for more than a decade, very few studies have explored the possibility that landscape structure might influence animal populations in naturally heterogeneous areas.

Natural landscapes are generally more complex than anthropogenic ones, lacking linear pattern and possessing higher fractal dimensions (Turner, 1989). Native patch types are generally contiguous except when rare in the landscape. Edges between native patches (inherent edges) are generally more gradual than their anthropogenic counterparts (induced edges; Voller, 1998), and are generally characterised by gradual ecotones rather than sharp edges (Hansson, 1994). Any existing anthropogenic fragmentation is intrusive rather than enveloping (Harris and Silva-Lopez, 1992). An example of such a landscape is the boreal mixed-wood forest of northern Alberta. In this region timber harvest for pulp has commenced within the last decade, creating small pockets of anthropogenic early-successional patches within the naturally heterogeneous matrix.

Like anthropogenic landscapes, perception of the degree of contrast between different patch types in natural landscapes is species-specific (Wiens, 1976; Kotliar and Wiens, 1990). By logical extension the influence of landscape structure on animal distribution is also species-specific, and depends on the organism's specialization to different patch types (Andren et al., 1997). A behaviourally flexible (Wegner and Merriam, 1990; Henein et al., 1998; Pither and Taylor, 1998) or 'mosaic species' (*sensu* Bright, 1993) would view the landscape as more homogeneous, or 'heterogeneously undivided' (Addicott et al., 1987) and would be able to use several patch types in the mosaic. Alternatively, a behaviourally inflexible or specialist species relies upon one or two specific patch types, rendering other patch types in the landscape marginal or even unusable habitat (Bright, 1993; Andren et al., 1997). For the latter species, if a required patch type was sparsely distributed within a matrix of less suitable habitat, a naturally heterogeneous landscape could parallel an anthropogenically fragmented one. I postulated that this was the case for North American red squirrels.

In the mixed-wood boreal forest of northern Alberta where this study was conducted, conifer is limited and occurs mainly in patches within the aspen matrix. This suggests that red squirrels, as conifer specialists (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; Riege, 1991), would perceive it as heterogeneous and would be susceptible to the effects of landscape structure. I censused red squirrels within three study areas, each with a different source of heterogeneity: a Managed area, a Burned area, and a Reference area. I tested the prediction that red squirrel presence or absence in these areas was related to the composition and configuration of the landscape, measured at a number of spatial scales.

The appropriate spatial scale at which to quantify a landscape has been a matter of some debate. An organism's response to heterogeneity can occur at several spatial scales (Wiens, 1976, 1989; Morris, 1987). If habitat selection (either behavioural or functional) is driving the response to landscape structure, then the integration of selection at several nested hierarchies of patchiness will produce non-random distribution patterns at a given scale (Kotliar and Wiens, 1990). For example, herbivores may respond to clumps of food plants within a stand, and stands within a landscape (Senft et al., 1987). Thus, response to landscape structure may occur at different grains, and different extents, and the relative importance of these will differ. When exploring the possible influence of landscape structure on organisms' distribution, it is critical to investigate that relationship in the context of an ecological process and the spatial scale at which it occurs.

In the absence of data to suggest which ecological process might be the most important in effecting the response to landscape heterogeneity, a prudent approach would be to examine the landscape at several different spatial scales (Wiens, 1989). In this chapter, I have quantified the landscape at five different extents and at two different grains. The five landscape extents were characterised by circular boundaries of different radii. The smallest radii (50 m and 100 m) correspond to the scale at which red squirrel foraging occurs (Chapter One); the largest radii purportedly correspond to the spatial scale at which longer-range movements, such as those undertaken during dispersal, occur. Regression analyses were performed to look for relationships between red squirrel presence and landscape structure as quantified at these different spatial scales. The grain of landscape analysis that yields significant predictors of squirrel presence should reveal the level of patchiness that squirrels respond to, whereas the spatial extent at which landscape structure becomes a significant predictor of squirrel presence should indicate the ecological process driving red squirrels' response to natural heterogeneity in this mixed-wood boreal system.

3.1 METHODS

3.1.1 Squirrel presence

Presence / absence data for red squirrels were obtained through call surveys. Points were visited 4 times over the summers of 1996 (managed grid only) and 1997 (all grids except one Managed meso grid). The occurrence of red squirrel territorial calls over a ten-minute period were noted at each visit; audible calls are assumed to originate from squirrels within 100 m of the point. Squirrels were termed "present" at a station where at least one call was heard and "absent" where they were not, within a given year, to yield a binary response variable.

3.1.2 Landscape classification

The study landscapes had been mapped using Alberta Vegetation Index (AVI) protocols and digitized using Arc/Info geographic information systems (GIS). These digital coverages, provided by Alberta-Pacific Forest Industries Ltd., describe canopy closure, dominant and subordinate stand types, and year of origin, for discrete stands termed polygons. Polygons in these coverages were reclassified to describe the landscape in two grains (*sensu* Kotliar and Wiens, 1990): FORCOV (forest cover) and UPLOW (upland / lowland). The UPLOW reclassification described each polygon as simply water, lowland (wetlands and bogs) or upland (mesic to xeric areas with no standing water). The FORCOV reclassification (Table 3.1) was based on dominant stand types to yield ten forest cover classes on the Managed and Reference grids. On the Burned grid the dominant tree species within the polygon was combined with burn information to categorize the polygon as burned lowland (burned SBLT or MARSH), designated BULOW, burned deciduous (BDEC), or burned pine (BPINE).

The landscape structure around each grid point was quantified using FRAGSTATS (McGarigal and Marks, 1994) at five spatial scales. To examine the effects of scale, landscape boundaries of 50 m, 100 m, 250 m, 500 m, and 1000-m radii were created around each mega grid point. Landscape structure was also analysed on the meso grids at 50 m, 100 m, and 250 m. Landscape configuration and compositional variables at each scale, around each point, were calculated for the FORCOV - reclassified coverages and the UPLOW - reclassified coverages.

Table 3.1: Reclassification protocol applied to Alberta Vegetation Index forest inventory maps to produce the landscape composition variables used in analysis. Variables printed in **bold** were transformed and included in regression analyses.

Variable	AVI Forest Cover Type	Relative Amount
A_OPEN	anthropogenic vegetated	
	anthropogenic non-vegetated	
CUT	cut	
DEC	trembling aspen	
	balsam poplar	
	birch	pure or mixed
MARSH	non-forest type	
M_DP	trembling aspen	
	birch	
	balsam poplar	70-80% or 20-30%
	and	
	jack pine	
	lodgepole pine	20-30% or 70-80%
M_DS	trembling aspen	
	birch	
	balsam poplar	70-80% or 20-30%
	and	
	white spruce	
	black spruce	
	larch	
	balsam fir	20-30% or 70-80%

Table 3.1 (cont.)

Variable	AVI Forest Cover Type	Relative Amount
PJ	jack pine	
	lodgepole pine	pure
	or	
	jack pine	
	lodgepole pine	70-80%
	and	
	larch	
	black spruce	
	white spruce	
	lodgepole pine	
	balsam fir	
	jack pine	20-30%
SBLT	black spruce or larch	pure
	or	
	black spruce	
	larch	70-80%
	and	
	jack pine	
	lodgepole pine	
	black spruce	
	white spruce	
	balsam fir	20-30%
	larch	
SW	white spruce	
	balsam fir	pure
	or	
	white spruce	70-80%
	balsam fir	
	and	
	larch	
	black spruce	
	lodgepole pine	20-30%
	jack pine	
	balsam fir	

3.1.3 Areal composition

In Arc/Info a buffer was created that extended approximately 1 km out from the outermost points on the Managed, Reference, and Burned Area mega and meso grids. The coverages were clipped, and these new digital coverages were imported into ArcView GIS (Esri Inc., California, USA). In ArcView the total areas in square metres of each FORCOV class type were calculated, to describe the overall composition of each study area.

3.1.4 Landscape composition

The different FORCOV classifications generated by our reclassification procedure are listed in Table 3.1. However, many of these occurred in small amounts within each radius landscape, leading to a Poisson distribution rather than a normal one. Variables were selected that did not have a large preponderance of zero values in the dataset; those that were included are printed in bold font in Table 3.1.

These variables were still not normally distributed at smaller scales (Kolmogorov-Smirnov test for normality; $p>0.05$; SPSS Inc., 1996) and so were transformed using the formula:

arcsin{square root(p)}

where p is the proportion of a given habitat type within the landscape at any given scale (Zar, 1996). All composition variables measured at all scales were transformed using this method. This resulted in variables not significantly different from a normal distribution (Kolmogorov-Smirnov test for normality; $p<0.05$; SPSS 1996), or variables that more closely approximated normality.

3.1.5 Landscape configuration: Heterogeneity

Although FRAGSTATS output includes many configuration variables, only a few were selected for analysis, based on limitations of our vector dataset and type of information that the variables provide (Table 3.2). These indices are highly correlated, and provide much the same information. To condense them into a single measure of landscape configuration, edge density (ED), largest patch index (LPI), mean patch size (MPS), mean shape index (MSI), patch density (PD), patch richness density (PRD), and Simon's evenness index (SIEI) were entered into a principle components analysis (PCA) using factor analysis by principle components in SPSS (SPSS Inc., 1996). The PCA was run for each scale, within each grid, within each area. This analysis incorporated information from each configuration variable into a single component that I termed heterogeneity (HET). Essentially, as HET increases, so does edge density, mean shape index, patch density, patch richness, and evenness; largest patch index and mean patch size decrease. This HET variable was used to represent landscape configuration in further analyses.

3.1.6 Statistical analysis

To look for differences in the explanatory power of landscape structure at different scales, logistic regression analyses (Hosmer and Lemeshow, 1989) were used to search for relationships between squirrel presence/absence and the landscape variables on the Managed, Burned, and Reference mega grids. A multiple logistic regression model (SPSS Inc., 1996) regressed squirrel presence against the composition variables listed in bold in Table 3.1 and HET, measured at each scale. Also included were the interaction terms between HET and those transformed composition variables that made up the largest portions of the landscape. I transformed variables for a better model fit although normal distribution of variables is not as necessary for logistic regression as it is for linear regression (Menard, 1995). A forward conditional selection procedure with a significance for inclusion criterion of p=0.05 was used (SPSS Inc., 1996) as this method reveals those predictor variables that explain the most variation in the response variable (Hosmer and Lemeshow, 1989; Menard, 1995).

Regressions were carried out for variables measured at each scale separately. For the 1000 m-scale analysis adjacent points were dropped systematically to prevent overlap and maintain independence between landscapes.

To augment the number of areas investigated, regressions were also performed on data from the Managed, Burned, and Reference meso grids. Adjacent points were dropped systematically at the 250-m analysis on the meso grids to maintain statistical independence. As the scale range was limited on these grids, and the number of data points included in analysis differed from the mega grids, this analysis was conducted only to determine if the landscape variables predicting squirrel presence were the same as on the mega grid systems, not for scalar comparison.

Table 3.2: FRAGSTATS landscape configuration variables chosen for use in analysis. The relationship between each variable to the PCA component HET (heterogeneity) is shown. An increase in HET within a landscape indicates more edge, no large contiguous patches, small mean patch size, complex-shaped patches, a high density of patches and different patch types, and high landscape diversity.

Variable acronym	Variable name	Description	Contribution to HET
ED	edge density	A measure of total edge between all patch types in the landscape, per unit area.	+
LPI	largest patch index	The percentage of total landscape area comprised by the largest patch.	-
MPS	mean patch size	The average patch size of all patch types in the landscape.	-
MSI	mean shape index	Compares the shape of a patch to a circular standard; averages across all patches in the landscape.	+
PD	patch density	The number of patches of all landscape types, per unit area.	+
PRD	patch richness density	The number of patch types present, per unit area.	+
SIEI	Simon's Evenness Index	The observed patch diversity, divided by total possible diversity, while controlling for patch richness.	+

Multiple stepwise logistic regression analyses were repeated for variables measured at each scale, at each Area, and within each year, separately. These analyses were expected to reveal the important predictors of squirrel presence at each scale. The spatial scale at which the regression model has the greatest deviance explained (predictive power), as measured by the Nagelkerke R^2 (Nagelkerke, 1991) should indicate the spatial scale at which squirrels respond to landscape structure.

3.2 RESULTS

3.2.1 The upland / lowland grain

The percent of upland in the study area did not predict squirrel presence at any scale in any area; nor did FRAGSTATS configuration variables derived from these reclassified landscapes. The remainder of the analyses focused on the forest cover (FORCOV) reclassification.

3.2.2 Forest cover: Composition of the study areas

Figure 3.1 depicts the composition of the Managed Area. DEC dominates the landscape, covering 43% of the area. SBLT constitutes the next largest area at 21%. PJ (7%) and SW (2%) comprise the remaining conifer element. MDS and MDP cover only 1% and 2% of the landscape, respectively. Only 9% of the landscape has been harvested for timber (CUT); another 2% has been cleared for roads, pipelines, and agriculture (A-OPEN).

Figure 3.2 portrays the composition of the Burned Area. It is dominated by BULOW, which covers 34% of the area. Unburned SBLT covers 10%; burned and unburned pine cover 11% and 2%, respectively. Unburned DEC comprises 12% and burned DEC another 7%. Salvage logging has occurred on 2% of the landscape.

Like the Managed Area, the Reference Area is dominated by DEC (40%) (Figure 3.3). SBLT (22%) and PJ (18%) make up the majority of conifer. MDP (3%) and MDS (1%) is limited, as is SW (2%). Two percent of the area has been cut and another 1% cleared for roads and pipelines.

Figure 3.1: Landscape composition of the Managed Grid.

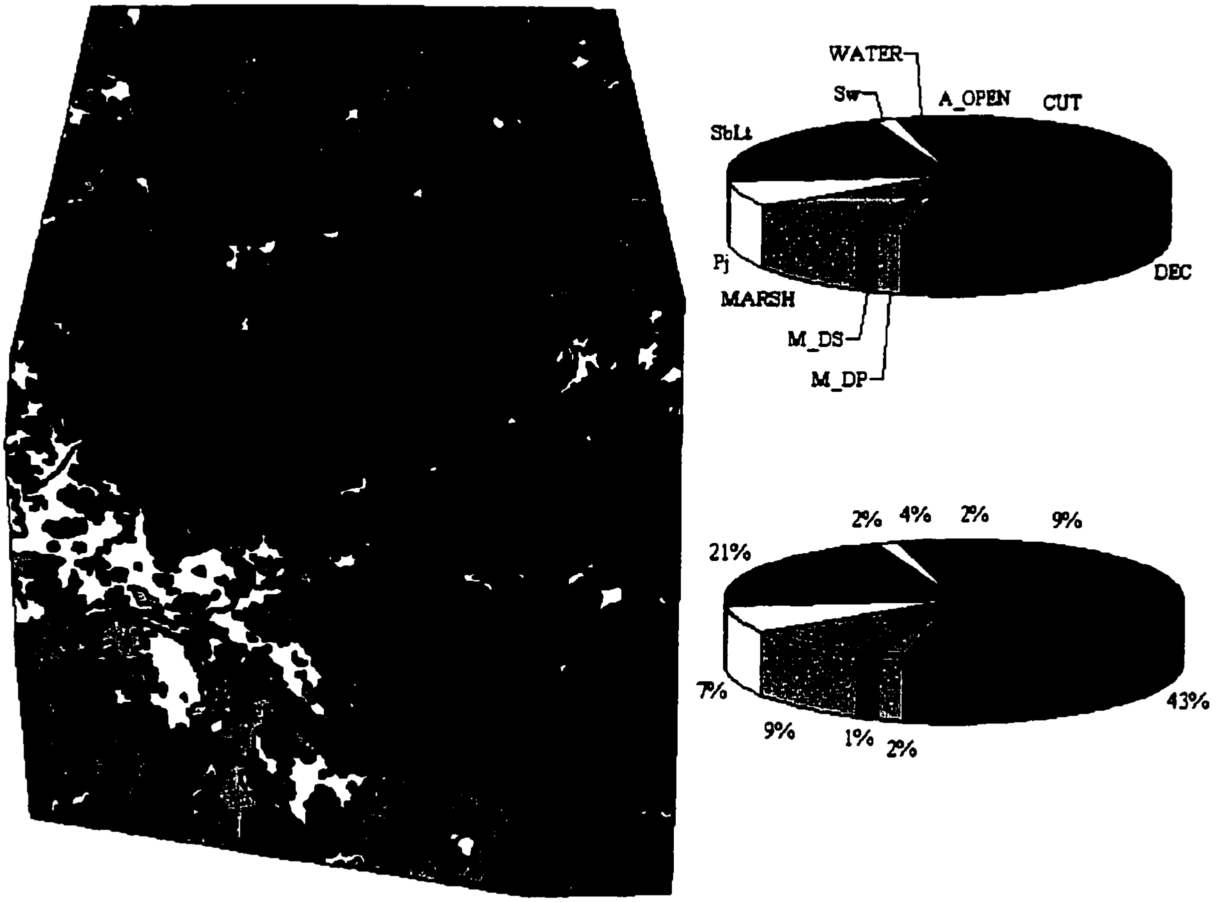


Figure 3.2: Landscape composition of the Burned Grid.

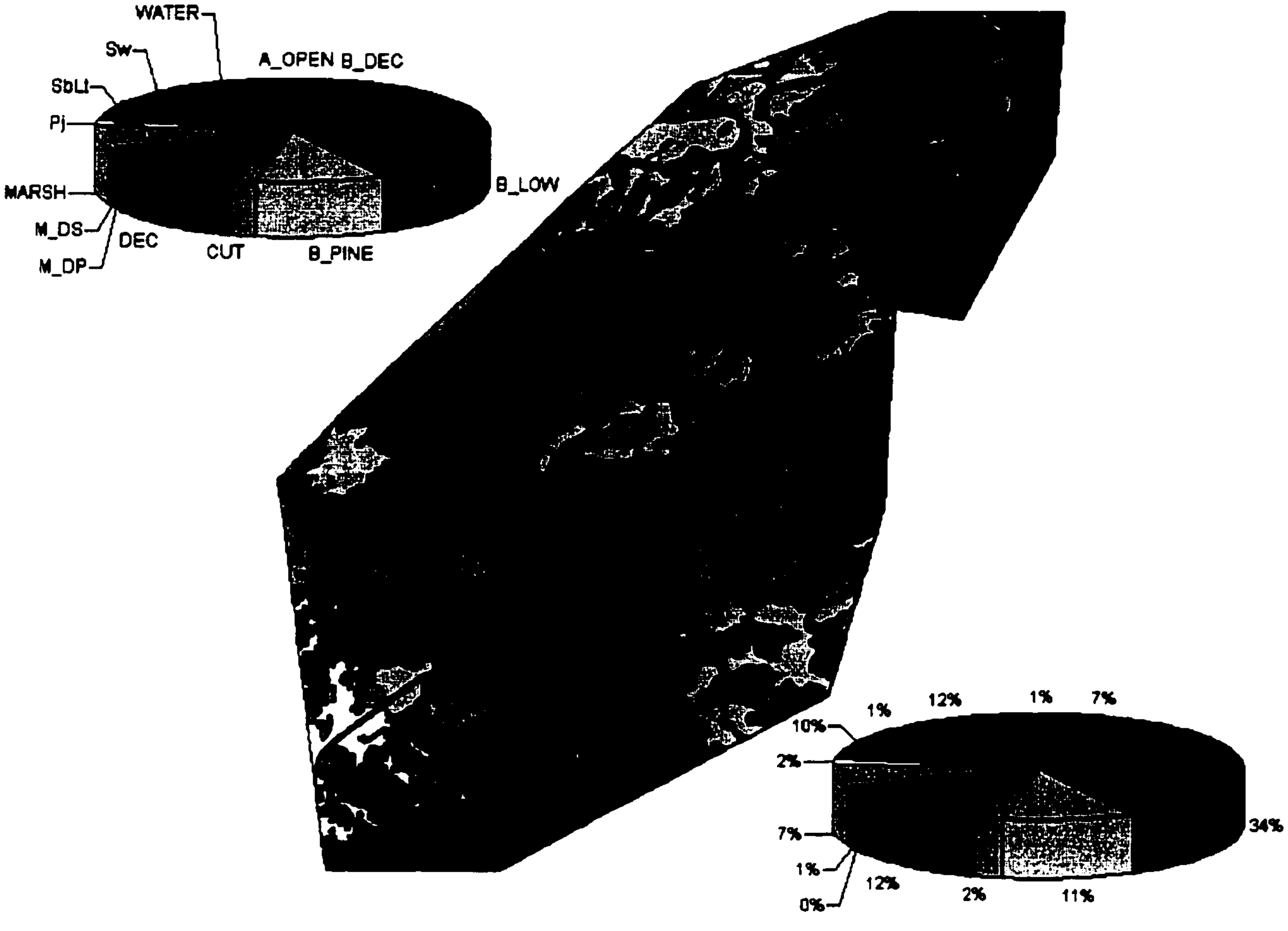
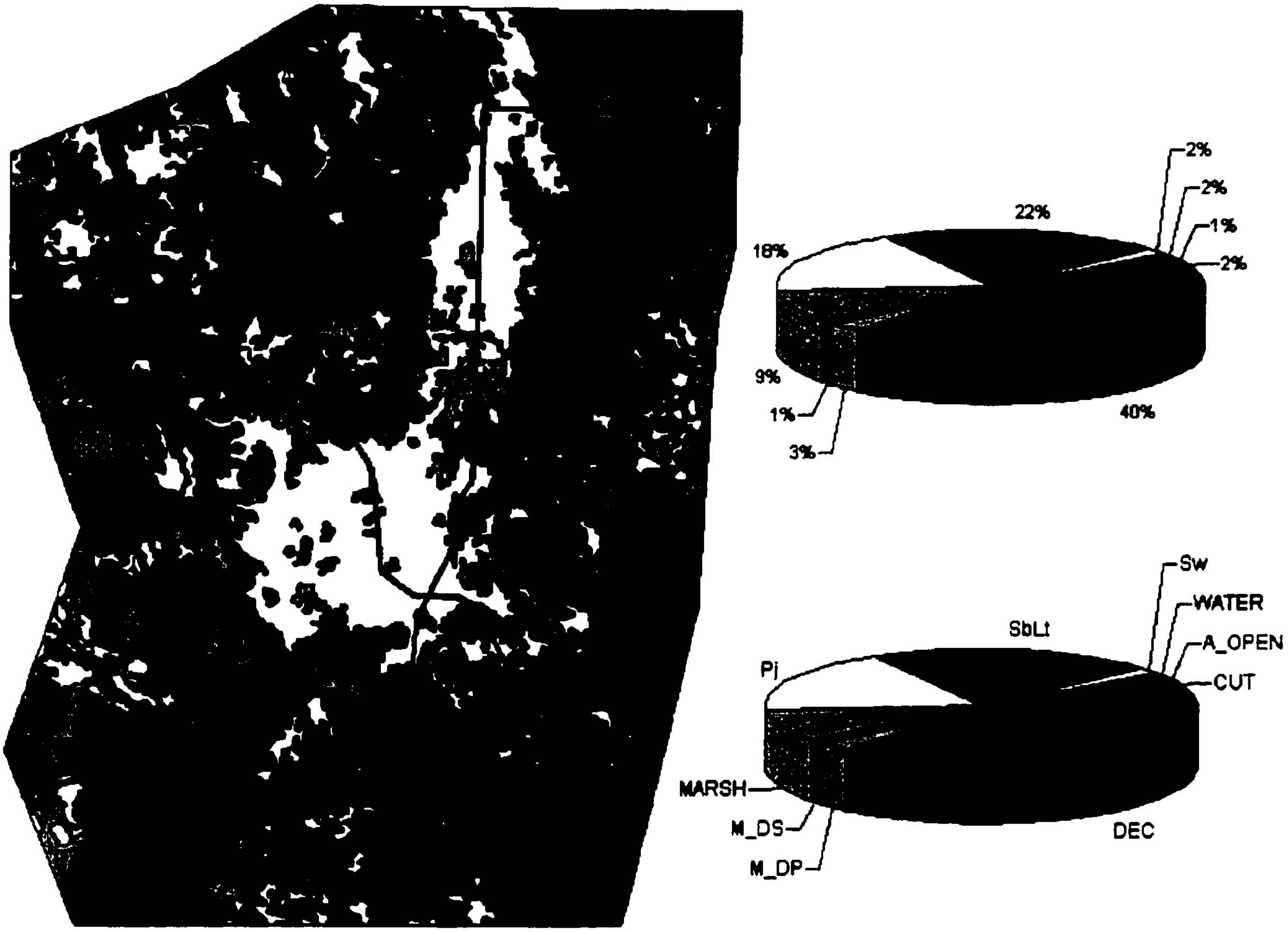


Figure 3.3: Landscape Composition of the Reference Grid.



3.2.3 Goodness of fit of the logistic model

The -2 log likelihood (-2LL) computed in logistic regression approximates a χ^2 distribution and allows one to test if the model is significantly different from a logistic function (Menard, 1995). Appendix 1 lists the -2LL's of each of the models and the p-value associated with it (Zar, 1996). At every scale on the mega grids, the models created do not deviate significantly from a logistic function. They do, however, deviate slightly on the Managed meso grids at 50 m and 100 m (1996), and on the Reference meso grids at 50 m. In these cases the -2LL values of the models are very close to the χ^2 values associated with $\alpha = 0.05$. Therefore the logistic function is the best one to describe the relationship between the landscape variables and squirrel presence / absence.

3.2.4 Landscape structure and squirrel presence

The predictive power of the regression models (as measured by the Nagelkerke R^2) changed with spatial scale, but did not do so consistently across grids. Different landscape variables significantly predicted squirrel presence in each grid, and at each scale within a grid. The attained statistical significance, the percentage of correctly classified cases, and the number of cases from all models are listed in Appendix 2.

On the Managed Area mega grid in 1996, the predictive power of landscape structure peaked at 100 m but was roughly similar across all scales except 1000 m, where no variables predicted squirrel presence (Figure 3.4a). Heterogeneity and jack pine were significant at 50 m; deciduous and black spruce, or interactions, were significant at larger scales. On the Managed meso grid in 1996 deviance explained peaked at 250 m, with deciduous and heterogeneity as significant predictors at different scales (Figure 3.5a).

In 1997 on the Managed Area mega grid, R^2 decreased from 50 m to 250 m, then increased from 250 m to 1000 m (Figure 3.4b). At 50 m to 250 m, conifer composition variables were significant. At 500 m and 1000 m, interaction terms between conifer composition and heterogeneity were also significant; interestingly, there is a negative relationship between heterogeneous black spruce and larch, and squirrel presence at the 500-m scale, unlike the positive relationships observed at other scales. On the Managed meso grid in 1997 only HET was significant, explaining a low amount of deviance (R^2 <0.2) at 50 m and 100 m (Figure 3.5b). No variables were significant at 250 m.

On the Reference Area mega grid, predictive power was greatest at the 250-m scale (Figure 3.6a). Deciduous was a significant negative predictor of squirrel presence along with marsh, at 50 m. Conifer composition variables were significant at the 100 m and 250 m scales. Deciduous was the only significant (negative) variable at 500 m; nothing was significant at 1000 m. On the Reference meso grid, deciduous negatively predicted squirrel presence at 50m, while white spruce and jack pine predicted squirrel presence at 100 m, with greater deviance explained (Figure 3.6b). Nothing was significant at the 250-m scale.

On the Burned Area mega grid, predictive power was highest at 50 m, with no significant models at 250 m and 500 m (Figure 3.7a). Mixed deciduous-pine and the heterogeneity-deciduous interaction were significant at the 50-m scale; the latter negatively predicted squirrel presence. Deciduous was a positive predictor at 100 m, unlike the other Areas. On the Burned meso grid predictive power is also greater at 100 m, but different variables are significant at each scale (Figure 3.7b).

Figure 3.4: The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables. The significant variables ($p<0.05$) included using a forward selection procedure are listed on top of the deviance bars in the order in which they entered the model.

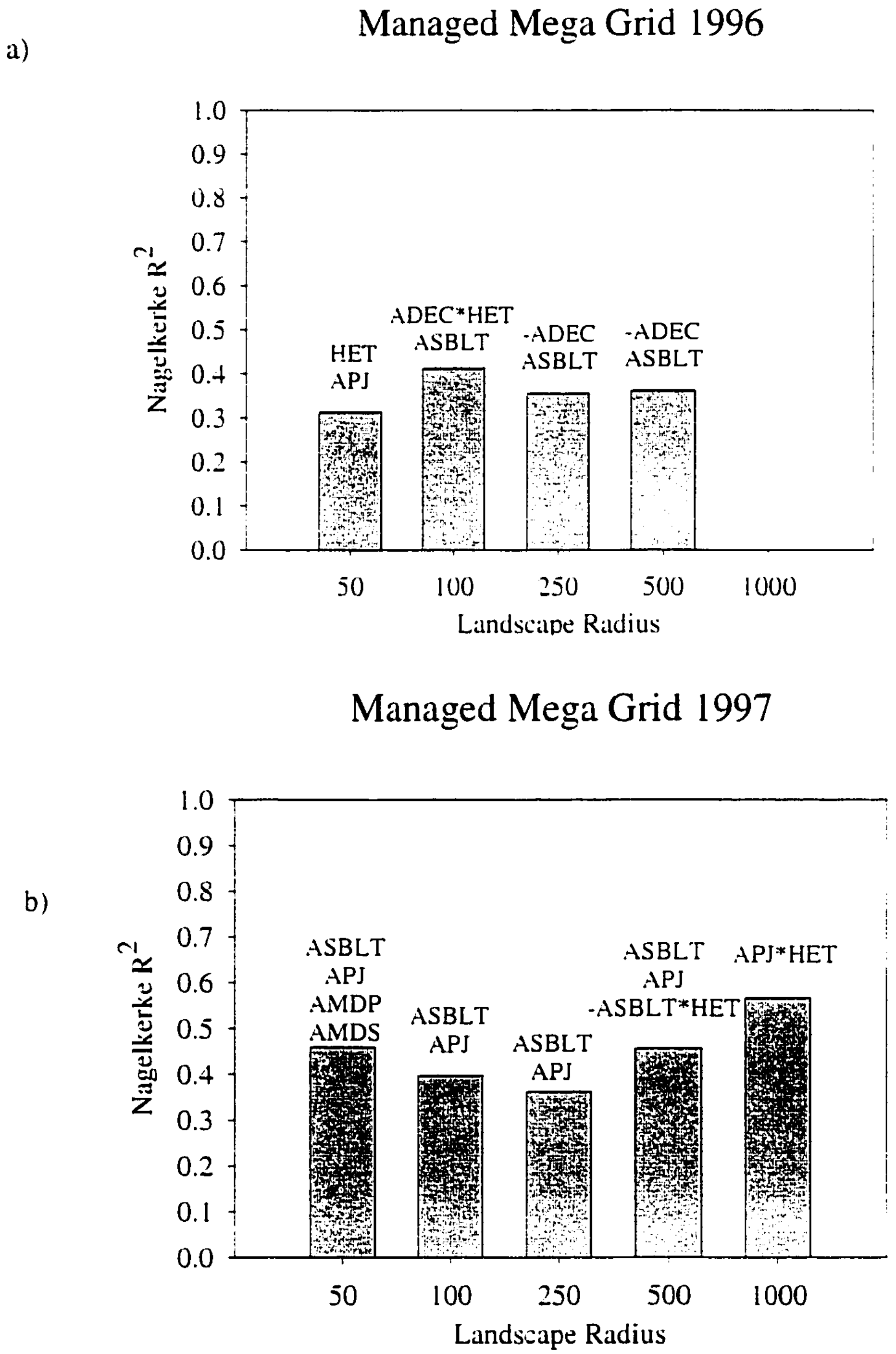
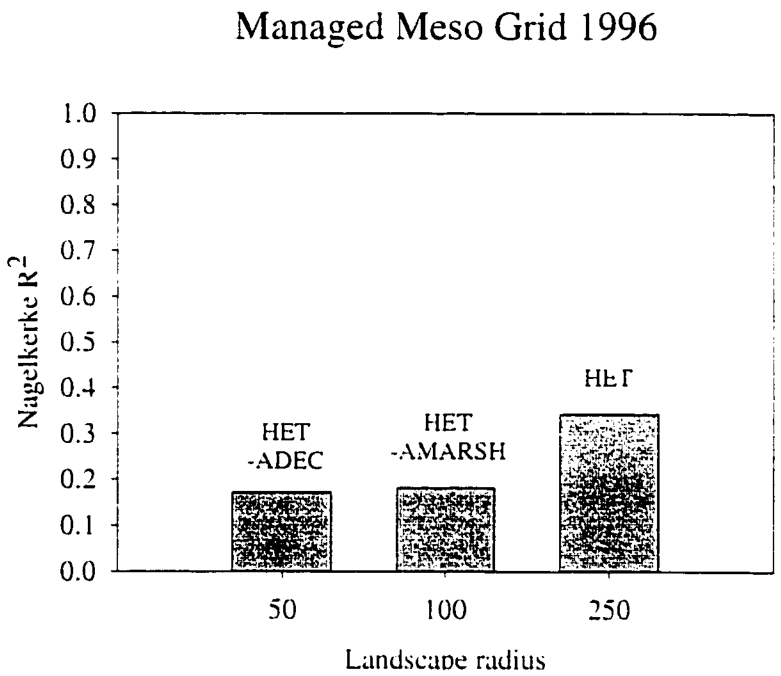


Figure 3.5: The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables. The significant variables (p<0.05) included using a forward selection procedure are listed on top of the deviance bars in the order in which they entered the model.

a)



b)

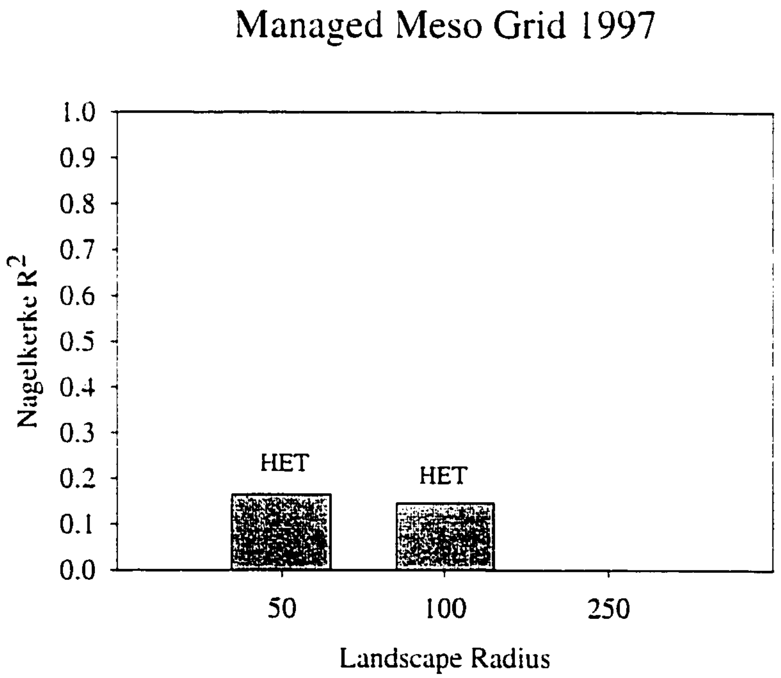


Figure 3.6: The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables. The significant variables ($p<0.05$) included using a forward selection procedure are listed on top of the deviance bars in the order in which they entered the model.

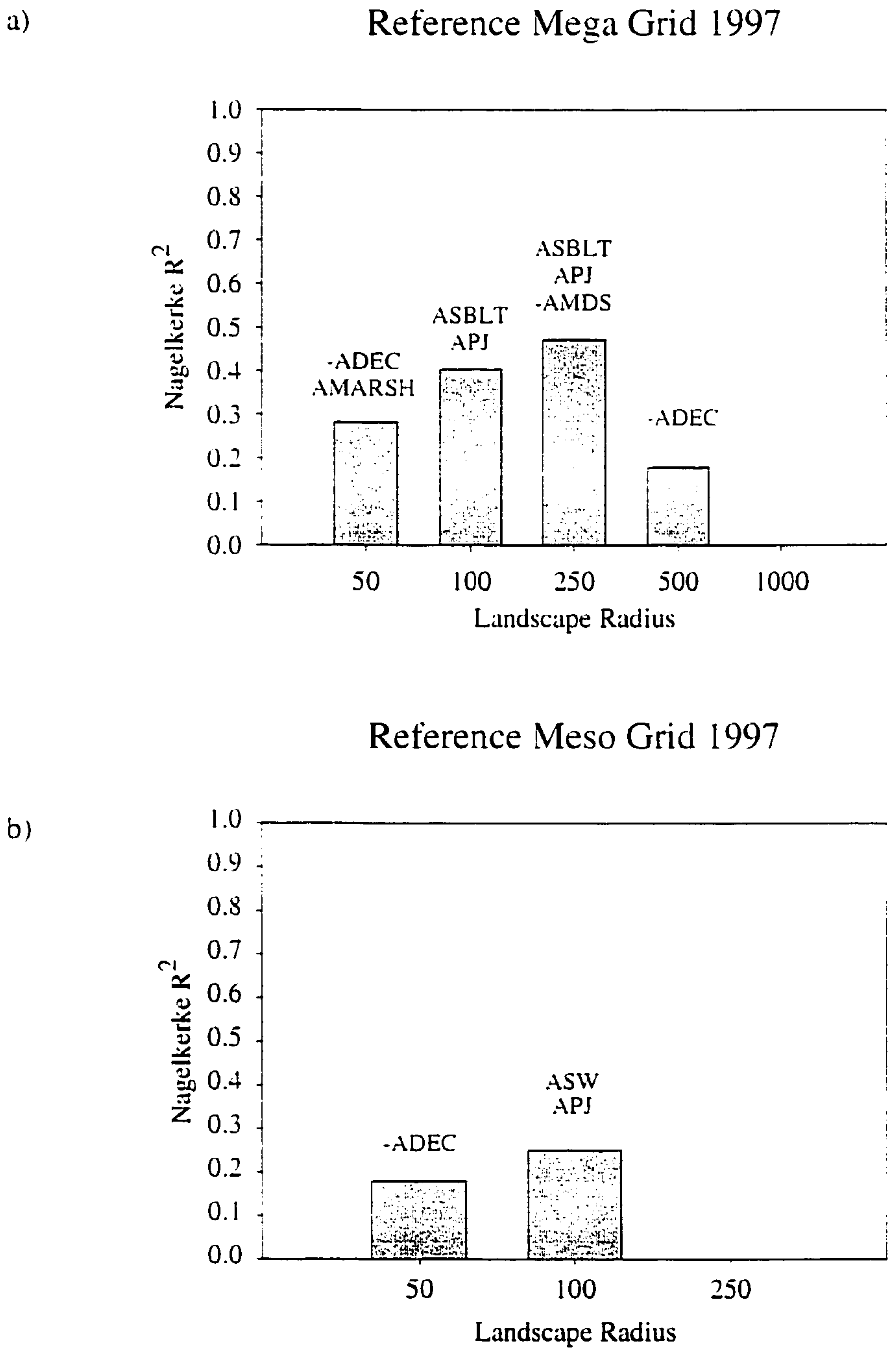
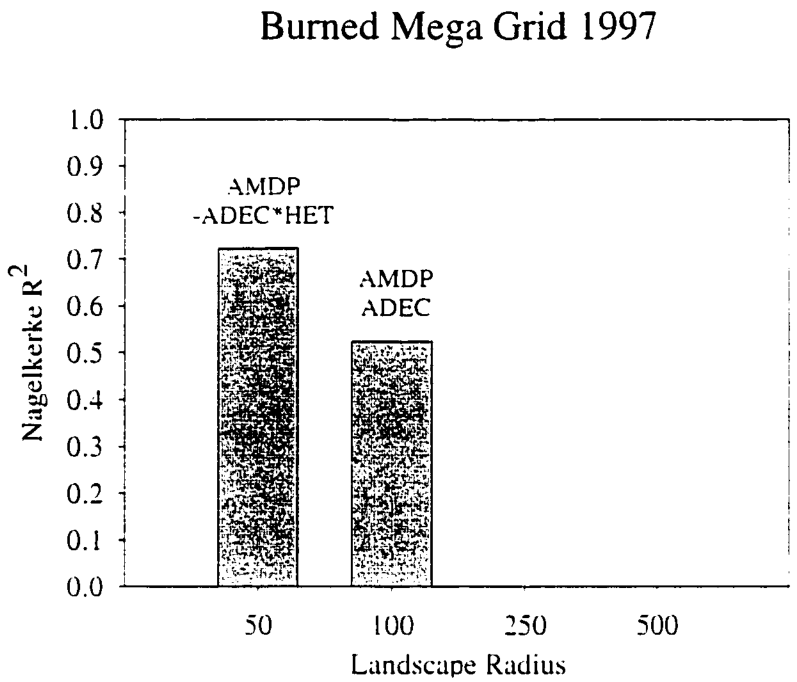
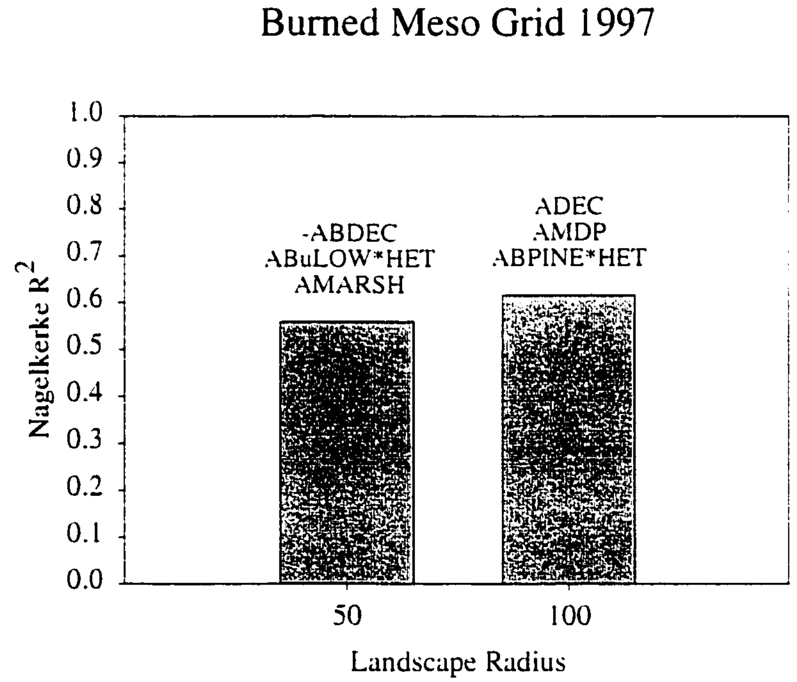


Figure 3.7: The deviance explained by multiple logistic regression models in which squirrel presence was regressed against landscape structural variables. The significant variables ($p<0.05$) included using a forward selection procedure are listed on top of the deviance bars in the order in which they entered the model.

a)



b)



3.3 DISCUSSION

3.3.1 The explanatory spatial scale

The reclassification of forest cover types into upland or lowland proved too coarse a grain to predict squirrel presence. The data suggest that squirrels are responding to patchiness that occurs at a finer resolution. Although this conclusion is intuitively obvious from the known habitat preferences of red squirrels (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978), this exercise serves to demonstrate the importance of determining the appropriate grain of analysis before searching for organisms' response to landscape structure.

At the forest cover (FORCOV) grain, no one landscape extent consistently predicted squirrel presence on any of the mega grids. On the Managed Area, more of the deviance was explained at the 50 m scale than the 100 m or 250 m scales, as hypothesised. However the difference between scales was marginal; deviance explained actually peaked at the 500 m and 1000 m scales. On the Burned mega grid, deviance explained peaked at 50 m, with nothing significant at scales beyond 100 m. On the Reference mega grid the 250 m scale best predicted squirrel presence, although there were significant models at all scales. Clearly, a single spatial scale at which landscape structure affects squirrels' distribution is not discernible using this approach.

Response to patchiness at multiple landscape extents (hereafter synonymous with spatial scale) has been observed in a host of other cross-scalar studies (see Wiens, 1989 for review). In a study very similar to this one, Mönkkönen et al. (1997) found that the probability of patch occupation by flying squirrels in Finland was related to landscape structure quantified at several different landscape radii, including the presumed home range radius of an individual and the 'local range' radius of several individuals, but not at the population scale. Tree frog occupation of ponds in the Netherlands was found to be related to landscape elements at several concentric landscape extents, as well as local factors (Vos and Stumpel, 1995). Rukke and Midtgaard (1998) found that response of fungivorous beetles to spatial structure measured at local (basidiocarp) and larger (forest island) scales but not intermediate ones. Colony performance of forest tent caterpillars in Alberta (Rothman and Roland, 1998), as well as rates of parasitoid infection (Roland and Taylor, 1997) were also predicted by fragmented forest structure at several concentric spatial scales.

The scales of foraging range and dispersal might be the two most likely to influence patterns of animal distribution (Morris, 1992), but no evidence of a strong response to either was found in this study. Kotliar and Wiens (1990) suggest that since heterogeneity occurs over a range of scales of patchiness, then response to that patchiness also has an integrated multidimensional property. For example, red squirrels may be responding to aggregations of cones within a tree, trees within stand, stands within a stand aggregate, and aggregates within a landscape. The influence of several different patch levels in the hierarchy interact to effect the response observed at any given spatial scale (Urban et al., 1987; Wiens et al., 1993). Therefore the 'ecological neighbourhood' (Addicott et al., 1987) may be delimited by the spatial and temporal scale associated with one particular ecological process, but it is likely that several processes operating concurrently ultimately influence the probability of patch occupation by red squirrels. The relative importance of each process might be context-specific. My data suggest that the scale at which response is most prominent (highest deviance explained) varies with areal composition. This is also true of the landscape structural variables themselves.

3.3.2 Explanatory variables differ between areas and scales

Naturally derived heterogeneity, as quantified by landscape composition and configuration, did predict red squirrel presence in all three study areas. The important variables selected by the regression procedure changed with landscape radius. Heterogeneity (HET) was often included as a positive significant predictor of squirrel presence on the Managed and Reference grids (1997). Heterogeneity alone was significant on the Managed meso grid; positive interactions with conifer composition were found on the Managed mega grid and both Burned grids. This interaction suggests that when the relative amount of conifer was low, heterogeneity was important in predicting squirrel presence. Small patches of conifer with larger amounts of edge habitat, juxtaposed with other marginal habitat types (deciduous), had higher probability of occupation. Where the relative amount of conifer in the landscape increased, the importance of heterogeneity decreased; probability of occupation was higher in contiguous conifer tracts than in fragmented (naturally or otherwise) patches. A contradiction occurred at the 500 m scale on the Managed mega grid (1997), where heterogeneous conifer negatively predicted squirrel presence once contiguous conifer entered the model. In contrast, heterogeneity did not predict squirrel presence at any scale on the Reference mega or meso grids. This area is characterised by large contiguous tracts of conifer (Figure 3.3), which may explain why heterogeneity failed to predict (positively or negatively) squirrel presence.

The relative importance of contiguous versus patchy coniferous merits further investigation. A source-sink dynamic may be operating (Pulliam, 1988; Danielson, 1992), wherein small sink patches of conifer set into a deciduous matrix can support individuals that 'overflow' from larger contiguous source patches, but where mortality exceeds natality. This is suggested by the habitat-specific demographic data of Kemp and Keith (1970) and Rusch and Reeder (1978). Such overflow systems can be important in maintaining a population of territorial animals where juveniles may have to wait until a territory suitable for reproduction becomes available (*i.e.*, ideal pre-emptive distribution; Pulliam and Danielson, 1991). This supposition is supported by the negative influence of heterogeneity at larger scales, which would be expected to effectively 'draw' individuals away from a site rather than contribute to occupation probability. A more involved investigation is required to test this hypothesis however; this study provides information on patch occupancy, but habitat- and landscape-specific demographic rates are needed to provide more insight into the mechanisms behind the distribution patterns observed.

In terms of landscape composition, the amount of conifer (black spruce, white spruce, jack pine, and mixed conifer/aspen) was positively, and the amount of deciduous negatively, related to squirrel presence on the Managed and Reference Grids. This occurred at the local scale and at larger scales. The relative importance of each patch type in the model changed with scale and with grid. The importance of conifer in general was obviously expected, as squirrels rely on conifer for overwinter survival (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; Riege, 1991). It is interesting to note that the presence of conifer beyond the patch - at radii of 500 m and 1000 m - also predicted squirrel presence, often with variables dissimilar from those that at smaller scales. This suggests that there is a cross-scalar association between different patch types within the mosaic. Depending on local frequency, some patch types (*e.g.* black spruce) may be important for squirrel presence locally, in conjunction with other patch types (*e.g.* jack pine) within the larger landscape. A similar situation was discovered by Mönkkönen et al. (1997); they found that although open habitats negatively predicted flying squirrel presence at larger scales, at the scale of individual movement the presence of open habitats positively predicted squirrel presence. Local-scale heterogeneity favoured squirrel presence through the juxtaposition of patch types and the presence of edge, although at larger scales open habitats simply represented non-preferred habitat. A cross-scalar patch-type interaction, or a shift in the direction of a relationship with scale, has rarely been considered and has significant implications for ecologists and those seeking to manage wildlife habitat.

Also of vital importance is the idea that the context in which the landscape is situated is a critical component of the overall effect of landscape structure. On the Burned grid, for example, the amount of deciduous cover positively predicted squirrel presence (mega and meso grids) contrary to results from the Managed and Reference areas and known red squirrel habitat preferences. In the Burned area where little mast remains, a few mature conifer trees located in stands classified by AVI maps as unburned deciduous are possibly important habitat for the population. Context-dependency was noted by Andren (1994, 1996, 1999) who suggested that in areas where large tracts of contiguous suitable habitat are present, landscape composition would be the driving influence of animal distribution. In areas where suitable habitat is rare, then configuration is more important. Investigation of the importance of landscape context in mediating response to landscape structure has been addressed in few studies and mainly as a peripheral issue (*e.g.*, Åberg et al., 1995; Delattre et al., 1996; Donovan et al., 1997; Hansson, 1998). The problem becomes especially complex when one considers that the response to landscape structure differs not only across space, but across time as well.

3.3.3 Differences between years

The differences between regression models drawn from 1996 and 1997 data are marked, despite the fact that from one year to the next, only the amount harvested (and conversely the amount of deciduous habitat) changed slightly. Nonetheless the relative predictive power of each scale changed between years; in 1996 landscape structure at 1000 m radius failed entirely to predict squirrel presence, but in 1997 most of the deviance was explained at this scale. The interaction between heterogeneity and deciduous was important at the small scales in 1996; in 1997 the heterogeneity - jack pine interaction was significant at large scales. These results indicate a large amount of temporal variability in squirrels' response to landscape structure in this system.

Patchy distributions of organisms are often speculated to be the product of fitness differentials among patch types; a tacit assumption of this is that there is no temporal relaxation of selection pressure to occupy prime habitat (Wiens, 1976). This assumption is often violated in heterogeneous habitats throughout the year. Population dynamics are often adapted to the degree of temporal variability in a system, especially in systems where natural disturbance is frequent (Wiens, 1976) such as the boreal forest (Hansson, 1992). Red squirrels may be especially prone to temporal fluctuations in habitat quality, as the cone crop produced by conifers (white spruce and black spruce, but not necessarily jack pine) varies dramatically over time, and red squirrel survival, immigration, and hence density are known to fluctuate in response to cone crops (Wheatley, 1999). Habitat-dependent variability in demography and density would have a significant effect on a source-sink dynamic if it were operating in this system, and would account for the striking change in the relative effects of landscape structure over time. This temporal variability should be alarming to most landscape ecologists, as many studies are conducted within the space of only one year. The next generation of landscape ecology studies should focus on the causes of this temporal variation, as this may shed light on the all-to-often ignored mechanisms behind organisms' response to landscape structure.

3.3.4 Management implications

This study was mandated under the Sustainable Forestry Management Network of Centres of Excellence to determine the importance of landscape structure in determining animal abundance in the hopes of creating management plans that would minimise the impact of timber harvesting on wildlife. The percent of the landscape cut (CUT) was not a significant predictor of squirrel presence in the Managed Area. This may be because only 9% of the landscape was harvested (Figure 3.1). The radio tracking data (Chapter One) show that squirrels are found in the cutblocks and are not behaviourally restricted from travelling or foraging in them. Extrapolation of these results to landscapes with more extensive modification is not possible: even extrapolation between similar naturally heterogeneous areas is untenable. Given the high degree of variability in the patterns detected it is impossible to create a universal harvest management plan. For example, one may conjecture that where black spruce is scarce in the landscape removal of the aspen habitat may exaggerate effects of isolation (see Andren 1994), although there may be little impact in areas where spruce patches are contiguous. A better understanding of the mechanisms driving distribution, rather than pattern-seeking, is required before sound management recommendations can be made. These may have to be made on a case-by-case basis; as it stands no single variable or spatial scale has been shown to be consistently important. The only sound conclusion is that landscape structure does influence the distribution of red squirrels in this area and that planning should occur on the landscape level, as red squirrels are influenced by large-scale landscape structure.

3.4 CONCLUSIONS

Natural (non-anthropogenic) landscape composition and configuration did predict squirrel presence, explaining up to 70% of the deviance in the squirrel dataset, indicating that response to landscape structure is not an artefact of anthropogenic fragmentation, but is a naturally occurring phenomenon. The scale at which this response occurred varied with landscape context, with different scales dominating on the Burned, Managed, and Reference grids. It also varied between years on the Managed grid. There is no evidence to suggest that response to landscape structure is associated mainly with local-scale processes such as foraging or alternatively with larger-scale processes such as dispersal. It is possible that a variety of processes interact to generate the observed distribution pattern of red squirrels.

The variables that predicted squirrel presence varied with spatial scale and landscape context. They also changed between years within the Managed grid. In general, increased heterogeneity and conifer was positively associated with squirrel presence, while contiguous deciduous forest predicted squirrel absence. The shift in relative importance of landscape variables may be a function of the fluctuations of resource use by squirrels in response to habitat quality (cone crop). A shift in emphasis from pattern-seeking to hypothesis testing is required to establish the mechanisms causing the multi-faceted response to heterogeneity observed in this study.

3.5 LITERATURE CITED

Åberg, J., G. Jansson, J.E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia **103**: 265-269.

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

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**: 355-366.

Andren, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. Oikos **76**: 235-242.

Andren, H. 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. Oikos **84**(2): 306-308.

Andren, H, A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos **80**(1): 193-196.

Bright, P.W. 1993. Habitat fragmentation - problems and predictions for British mammals. Mammal Review **23**(3/4): 101-111.

Danielson, 1991. Communities in a landscape: The influence of habitat heterogeneity on the interactions between species. The American Naturalist **138**(5): 1105-1120.

Danielson, B.J. 1992. Habitat selection. interspecific interactions and landscape composition. Evolutionary Ecology **6**: 399-411.

Delattre, P., P. Giraudoux, J. Baudry, J.P. Quéré, and E. Fichet. 1996. Effect of landscape structure on Common Vole (*Microtus arvalis*) distribution and abundance at several spatial scales. Landscape Ecology **11**(5): 279-288.

Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**(7): 2064-2075.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**: 169-175.

Fisher, J.T., and G. Merriam. In press. Resource patch array use by two squirrel species in an agricultural mosaic. Landscape Ecology.

Fitzgibbon, C.D. 1997. Small mammals in farm woodlots: the effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology **34**: 530-539.

Hansson, L. 1992. Landscape ecology of boreal forests. Trends in Ecology and Evolution **7**(9): 299-232.

Hansson, L. 1994. Vertebrate distributions relative to clearcut edges in a boreal forest landscape. Landscape Ecology **9**(2): 105-115.

Harris, L., and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. Pp. 198-237 **In** Conservation Biology: The theory and practice of nature conservation, preservation, and management. P. Fiedler and S. Jain, Eds. Chapman and Hall, London.

Henderson, M.T., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biological Conservation **31**: 95-105.

Hosmer, D.W. Jr., and S. Lemeshow. 1989. Applied Logistic Regression. Wiley, New York.

Jonsen, I.D., and L. Fahrig. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology **12**: 185-197.

Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**(5): 763-779.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**: 253-260.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers - the effect on small mammal populations and communities. Acta Theriologica **38**(1): 1-30.

McGarigal, K., and B.J. Marks. 1994. FRAGSTATS - Spatial Pattern Analysis Program for Quantifying Landscape Structure. Version 2.0. Oregon State University, Corvallis, OR.

Menard, S.W. 1995. Applied Logistic Regression Analysis. Sage Publications, Thousand Oaks, California, USA.

Merriam, G. 1988. Landscape ecology: the ecology of heterogeneous systems. Pp. 43-50 **In** Landscape Ecology and Management. M. Moss, ed. Polyscience Publications Inc., Montreal.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. pp. 133-142 In Nature Conservation 2: The Role of Corridors. Edited by D.A. Saunders and R.J. Hobbs. Surrey Beatty and Sons Pty Ltd, Chipping Norton, NSW, Australia.

Merriam, G., and A. Lanoue. 1990. Corridor use by small mammals: field measurement for three experimental types of Peromyscus leucopus. Landscape Ecology **4**(2/3): 123-131.

Middleton, J., and G. Merriam. 1983. Distribution of woodland species in farmland woods. Journal of Applied Ecology **20**: 625-644.

Mönkkönen, M., P. Reunanen, A. Nikula, J. Inkeröinen, and J. Forsman. 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. Ecography **20**: 634-642.

Morris, D.W. 1987. Ecological scale and habitat use. Ecology **68**(2):362-369.

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

Nagelkerke, R.J.D. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**: 691-692.

Pither, J., and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos **83**: 166-174.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**: S5-S66.

Riege, D.A. 1991. Habitat specialization and social factors in distribution of red and grey squirrels. Journal of Mammalogy **72**(1): 152-162.

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

Rothman, L.D., and J. Roland. 1998. Forest fragmentation and colony performance of forest tent caterpillar. Ecography **21**: 383-391.

Rukke, B.A., and F. Midtgaard. 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest landscape. Ecography **21**: 561-572.

Rusch, D., and W. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience **37**(11): 789-799.

Smith, C.C. 1968. The adaptive nature of social organization in the Genus of three (sic) squirrels *Tamiasciurus*. Ecological Monographs **38**(1): 31-63

SPSS Inc. 1996. SPSS Version 7.5. Chicago, IL.

Strong, W., and K.R. Leggat. 1992. Ecoregions of Alberta. Prepared for Alberta Forestry, Lands and Wildlife, Land Information Services Division, Resource Information Branch. Publication Number T:245.

Tapper., S.C., and R.F.W. Barnes. 1986. Influence of farming practice on the ecology of the brown hare *(Lepus europaeus)*. Journal of Applied Ecology **23**: 39-52.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics **20**: 171-197.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. Bioscience **37**(2): 119-127.

Voller, J. 1998. Managing for edge effects. pp. 215-233 ***In*** Conservation Biology: Principles for Forested Landscapes. J. Voller and S. Harrison, Eds. BC Ministry of Forests, UBC Press, Vancouver, BC.

Vos, C.C., and A.H.P. Stumpel. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology **11**(4): 203-214.

Wegner, J.F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. Journal of Applied Ecology **16**: 349-357.

Wegner, J., and G. Merriam. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. Biological Conservation **54**: 263-267.

Wheatley, M.T. 1999. Does Density Reflect Habitat Quality for Red Squirrels During a Spruce Cone Failure? M.Sc. Thesis, University of Alberta, Edmonton, AB.

Wiens, J.A. 1976. Population responses to patchy environments. Annual Reviews in Ecology and Systematics **7**: 81-120.

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

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

Zar, J.H. 1996. Biostatistical Analysis. Third Edition. Prentice Hall, New Jersey.

Chapter Four

The Influence of Local Vegetation on Squirrel Response to Landscape Structure

4.0 INTRODUCTION

Context sets the stage for any ecological process. The search for general laws or a unifying theory in ecology has only substantiated the importance of variability in defining system function (Allen and Hoekstra, 1992; Lawton, 1999). In an (ironic) attempt to organise and classify ecological inconsistencies, hierarchy theory was implemented. Implicit in hierarchy theory is the notion that scale, both spatial and temporal, is variable, and that patch characteristics change depending on the way in which they are viewed (Allen and Starr, 1982; Allen and Wyleto, 1983). Traditionally patches are considered internally homogeneous, as they have been in this study. Grain, the lowest level of resolution, has been set as the forest stand type as defined by Alberta Vegetation Index (AVI) data. However, *a priori* assumptions of grain ignore the fact that internal heterogeneity within a patch does exist (Kotliar and Wiens, 1990). While apparently internally homogenous at some scale of analysis, reducing the scale (increasing resolution) of analysis of the patch reveals internal heterogeneity (Wiens, 1989). This heterogeneity may exhibit either random or clumped dispersion, low or high contrast. Elements with high contrast and aggregation form patches within the context of the larger patch. This hierarchy of patchiness progresses as one decreases scale. Alternatively, the areas we have defined as patches can aggregate to form patches on a larger scale (Wiens, 1989; Kotliar and Wiens, 1990).

Because processes at any scale are aggregates of those occurring at several lower levels in the hierarchy (Pickett et al., 1989; Senft et al., 1987), a correlation between some independent variables measured at a pre-defined grain, and the response variable, cannot always be detected even if a relationship does exist. In the sense that response to landscape structure may change as the observer changes extent (Chapter Three), response to structure may also change as one changes grain. Simply stated, the internal composition of a patch may alter the detectability of landscape effects operating on organisms within it. In this chapter I endeavour to answer the question: Does the apparent relationship between landscape structure and red squirrel presence change when the effects of local vegetation within the patch have been accounted for?

As previously reported, the North American red squirrel is a conifer specialist, relying on *Abies*, *Pinus*, and *Picea* seeds to overwinter (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; Riege, 1991). It also feeds on mushrooms, berries, nuts, and other ephemeral foods opportunistically (Gurnell, 1983; Yahner, 1987). Therefore, one may expect that in the summer months (May-August), squirrels may be found in association with a variety of vegetation types. They probably do not establish territories in non-conifer habitats (Smith, 1968; Kemp and Keith, 1970), but do use them to feed. Juveniles disperse through them in search of an empty territory. Squirrels' use of the landscape, and hence the effects of structure, may vary depending on the context in which a squirrel is found.

The Alberta Vegetation Index (AVI) data from which the landscape structure data originate are derived from air photo interpretation. Forested stands are classified by species, age of origin, and canopy closure. Although ground-truthed for consistency, fine-scale detail is missed or averaged away in such a coarse-scale analysis. In this study (and many, perhaps all, others) a patch as defined by the caveat of internal homogeneity is not always a patch in the truest sense. Internal heterogeneity - local vegetation - may guide processes that confound (or exaggerate) our ability to detect the effects of landscape structure.

Other researchers investigating landscape effects have included in their analysis variables describing local vegetation, and these variables are often the ones that explain the most deviance in the response variables, with landscape structure explaining some additional deviance after the fact (Verboom and van Apeldoorn, 1990; Fitzgibbon, 1993; van Apeldoorn et al., 1994; Vos and Stumpel, 1995; McGarigal and McComb, 1995; but see Celada et al., 1994, where vegetation was not significant). To determine if red squirrels in the mixed-wood boreal show a similar relative response to vegetation and landscape structure, the regression models of Chapter Three have been modified to include internal patch characteristics; that is, a variable describing the number of conifer trees within plots at a site. I predict that 1) the number of conifer trees at a site will be a significant predictor of squirrel presence and that 2) landscape structure will be a significant predictor of presence after tree number has been accounted for. Given the disparity of the responses to landscape structure displayed in Chapter Three, I also predict that 3) the relative influence of vegetation and landscape structure will differ between the Managed, Burned, and Reference mega grids.

Most landscape studies of this nature have chosen study sites *a priori* based on known habitat preferences of the animal and thus have a low range of variation in their patch characteristic (vegetation) datasets (*e.g.* Mönkönnen et al., 1997; Fisher and Merriam, *in press*). No studies were uncovered that have addressed the possibility that response to landscape may actually differ depending on the local habitat: that is, organisms in patches with one set of vegetational characteristics may have a different relationship with landscape structure than those in patches with a different set of characteristics. In terms of hierarchy theory, selection occurring at lower hierarchical levels may alter the effects of selection observed at higher levels.

To address this question, I divided the red squirrel data into two subsets: sites with conifer trees present, and sites at which conifer trees were scarce. I then repeated the landscape analysis as previously described on each subset separately, to determine if the relationship between landscape structure and squirrel presence changed with local vegetation. Disparity between the two analyses would suggest that different mechanisms operate within each subset of patch types. Pattern-seeking at different extents has revealed varying influence of landscape structure at each: by the same token pattern-seeking at different grains may begin to reveal potential mechanisms that generate the observed patterns of animal distribution.

4.1 METHODS

4.1.1 Vegetation Sampling

The vegetation at each grid point was assayed in the summers of 1996 and 1997. Three 10-m by 20-m plots were surveyed at each site: one at the point and two at randomly selected bisected cardinal directions. The latter two were placed 65 m out from the point and it was therefore assumed that vegetation surveyed would be representative of an 85-m radius around each point. The species and number of conifer trees (*Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Abies balsamea*, and *Larix laricina*), was recorded and averaged across plots to obtain a single abundance value per species per point. These abundance values were summed across species to yield the variable SUMCON. The squirrel presence / absence dataset was collected as described in Chapter Three. To ascertain the relative importance of landscape structure and local (within-patch) vegetation, two approaches were employed.

4.1.2 Building a forced logistic model

In the first approach, a multiple logistic regression model was built in blocks (SPSS Inc., 1996). In the first block, squirrel presence was regressed against SUMCON using a standard 'enter' model (SPSS Inc., 1996). In the second block, all of the landscape structural variables used in Chapter 3 were included in a multiple 'forward conditional' logistic regression procedure with an inclusion criterion of $p = 0.05$. This model thus tested for a relationship between squirrel presence and SUMCON; if significant, it retained this model with its explained deviance and searched for landscape variables that might explain further deviance in the 1997 squirrel dataset. This analysis was repeated for the Managed, Reference, and Burned Mega grids at each scale.

4.1.3 Splitting the squirrel dataset

Each site was designated 'conifer-abundant' or 'conifer-poor based on the average number of trees per point. Those sites with 2 or less conifer trees per point were considered 'conifer-poor'. Those with more than 2 were denoted 'conifer-abundant'. The squirrel dataset was then divided into subsets based on each site's conifer designation. This division is somewhat arbitrary but was designed to split the dataset into roughly equal parts. Given our vegetation sampling design, zero conifer found within plots at a site does not necessarily imply that conifer are completely absent from that site, so splitting the set using zero conifer per plot would also be somewhat arbitrary.

Data from the Managed and Reference areas were used, as the Burned area had a low number of squirrel presences that did not lend itself to dataset division. Only variables measured at the four lowest scales were used, due to low sample size at the subsampled 1000-m scale. Analysing each subset separately, squirrel presence was regressed against landscape structural variables using a multiple 'forward conditional' logistic regression analysis (SPSS Inc., 1996), using the same variables and inclusion criteria outlined in Chapter Three. This analysis was expected to show difference response to landscape structure by red squirrels living in conifer-poor and conifer-abundant habitats.

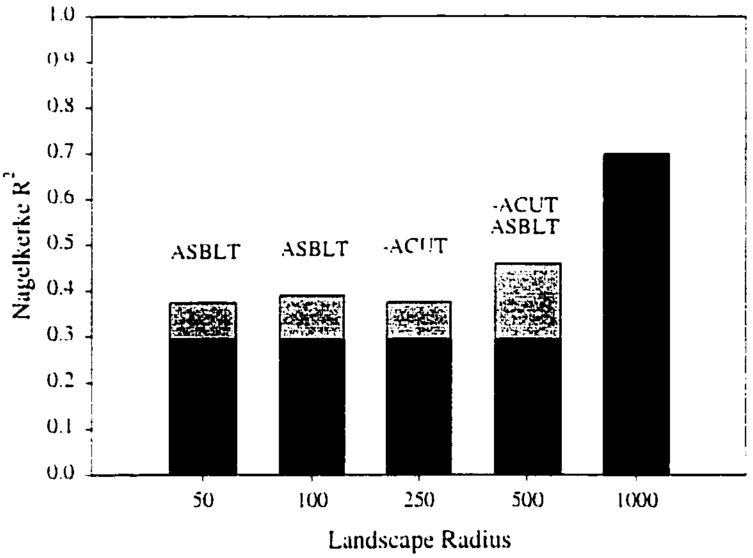
4.2 RESULTS

4.2.1 The forced model

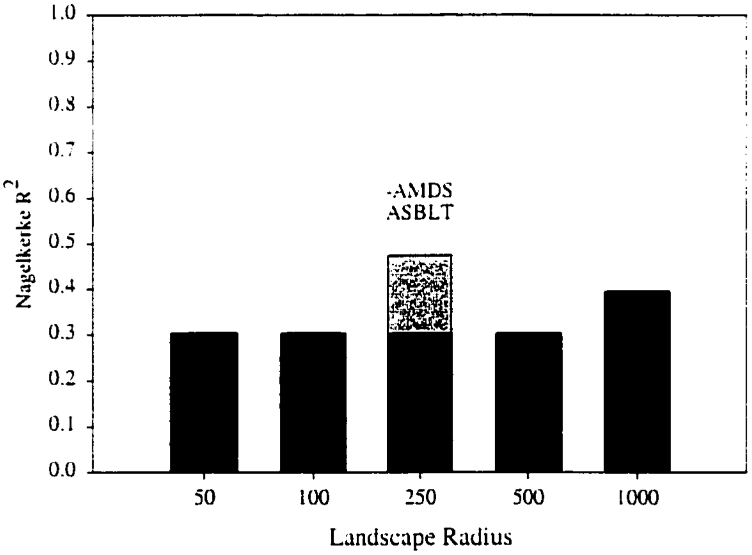
The SUMCON variable, representing the average number of conifer trees per point summed across all conifer species, significantly predicted red squirrel presence on the Managed mega grid (n= 58) (Figure 4.1a; see also Appendix 3). The R^2 of these regressions was 0.295.

Figure 4.1: The relative effects of local vegetation and landscape structure. The deviance explained in squirrel presence by the number of conifers at a site is presented in black bars. Further deviance explained by landscape structure at each extent is illustrated in grey bars. The significant variables in the final model, and direction of the relationship, are listed on top of the deviance bars.

a) Managed Mega Grid 1997



b) Reference Mega Grid 1997



The 1000-m radius, which had a lower n (16) because adjacent points were dropped, had a higher R^2 (0.699). After local conifer was accounted for, landscape structure explained further deviance at all scales except the 1000-m radius. The amount of black spruce / larch explained *ca.* 10% of the deviance at 50 m and 100 m. There was a negative relationship with the amount of cut area at 250 m and 500 m. The most variation explained by landscape occurred at 500 m, with black spruce positively and cutblocks negatively predicting squirrel presence. SUMCON failed to predict squirrel presence on the meso grids.

On the Reference mega grid, SUMCON also significantly predicted squirrel presence at all scales (Figure 4.1b). The deviance explained for the 50 - 500 m scales ($R^2 = 0.303$; $n = 63$) was similar to that for the Managed grid at these scales, but was less than the Managed at the 1000 m scale ($R^2 = 0.394$; $n = 18$). Interestingly, once local conifer trees were accounted for, further deviance was explained by landscape structure only at the 250-m scale. Black spruce / larch positively, and mixed deciduous spruce negatively, predicted squirrel presence.

On the Burned area the relationship between SUMCON and squirrel presence was not significant at the $p = 0.05$ level. Further analysis of the block of landscape variables was therefore not pursued.

4.2.2 The split squirrel dataset

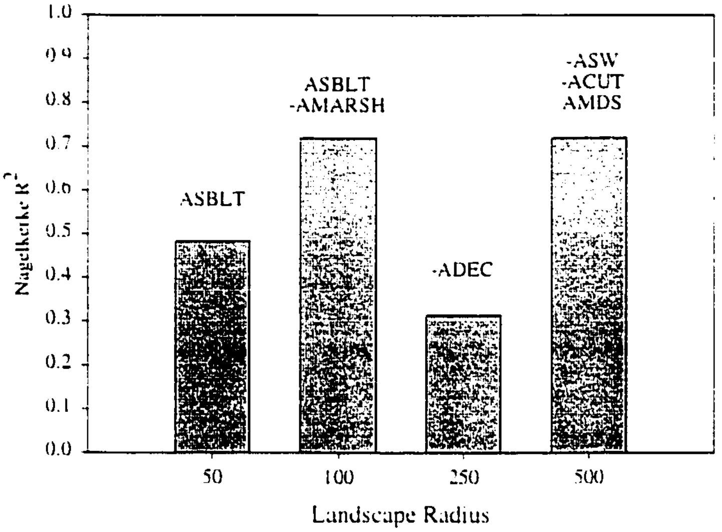
Within the Managed Area, landscape structure failed to predict squirrel presence at the sites designated conifer-poor. At the conifer-abundant sites the deviance explained by landscape structure again varied with scale, peaking at 100 m and again at 500 m at *ca.*

70% explained (Figure 4.2a; see also Appendix 4). Black spruce positively predicted presence at the smaller scales. CUT was again a negative predictor at 500 m, but interestingly so was white spruce. At all scales only composition was significant; configuration or interactions failed to enter the model.

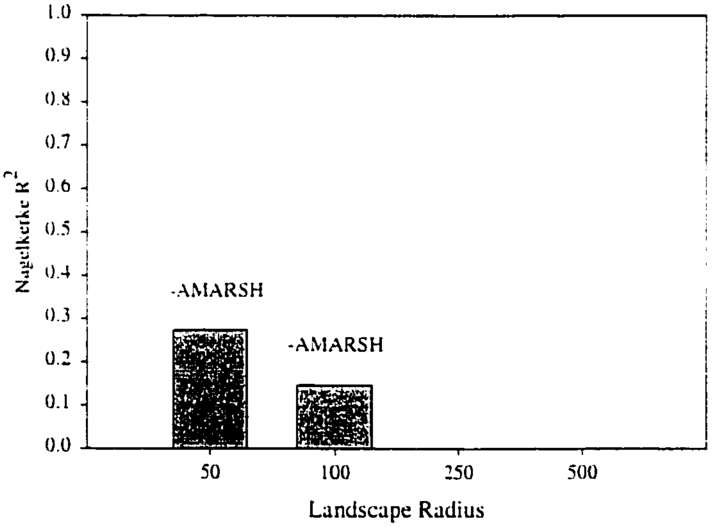
On the Reference area, landscape structure was not significant at the conifer-poor sites except at 250 m (-ASBLT*HET; R^2 = .260; n = 26). At the conifer-abundant sites landscape structure predicted squirrel presence at the 50 and 100 m scales but not at larger scales (Figure 4.2b). R^2 at each scale was low (0.146 to 0.274), peaking at the 50 m scale. MARSH negatively predicted presence at 50 and 100 m. Heterogeneous black spruce negatively predicted presence at the 250-m scale. There were no positive significant predictors of squirrel presence on the Reference grid.

Figure 4.2: The influence of landscape structure at conifer-abundant sites. The deviance explained in squirrel presence by landscape structure at each extent is illustrated in grey bars. The significant variables in the final model, and direction of the relationship, are listed on top of the deviance bars.

a) Managed Mega Grid 1997 (conifer-abundant sites)



b) Reference Mega Grid 1997 (conifer-abundant sites)



4.3 DISCUSSION

4.3.1 The relative importance of habitat beyond the focal patch

As one might expect from known habitat preferences of red squirrels, the number of conifers at a site positively predicted squirrel presence on the Managed and Reference mega grids with a relatively high amount deviance explained, but did not on the Burned grid. This emphasises the importance of context when seeking relationships between animal abundance and habitat use. As well, including local vegetation in the model changed the patterns seen in Chapter Three (compare Figures 4.1a and 3.4b; 4.1b and 3.6a).

In the Burned area, many live conifers that were recorded were jack pine seedlings re-establishing themselves from serotinous cones after the forest fire in 1989 and were not yet mature mast-bearing trees capable of supplying cones to squirrels. In the other areas, mature mast-bearing conifers were common and therefore strongly associated with squirrel presence. As landscape was a significant predictor on the Burned grid (Figure 3.7), it appears that the proximity to stands skipped by fire (*i.e.*, unburned deciduous) was more important to site occupation than the local presence of conifer. On the Managed grid, once local vegetation was accounted for the proximity of black spruce in the immediate and larger landscapes, and the absence of cutblocks in the larger landscapes, were significant predictors. On the Reference grid vegetation was of sole importance at all scales except at 250 m, where the absence of heterogeneous black spruce patches was important. The unique patterns observed between the three grids show that the relative effects of vegetation and landscape are context-dependent, similar to the strictly landscape effects in Chapter Three. Because no replication of Areas was possible I cannot conclude what caused the disparity in response between the three Areas, but tentatively attribute it to differences in areal composition. The relative importance of dominant stand types (spruce, pine, and aspen) for squirrels is possibly different in each area.

On the Managed Grid, the importance of black spruce at the smaller radii, which are within the summer foraging range of the red squirrel (Chapter One), suggest that landscape supplementation is occurring (Dunning et al., 1992). With high squirrel densities the relative amount of conifer within each territory in black spruce patches may be limited. If so, squirrels in these nearby stands may have travelled to the focal sites to obtain substitutable resources, as suggested by larger foraging ranges in conifer-limited areas (Chapter One). On the Reference grid where jack pine is more dominant and stands are larger and more contiguous, supplementation may not have been necessary.

The importance of black spruce at larger radii on the Managed Grid suggests a source-sink population dynamic (Pulliam, 1988; Pulliam and Danielson, 1991) as in Chapter Three. For a patch to be colonised it is important to have conifer present (for overwinter survival), but proximity to large amounts of black spruce is also consequential as a source for dispersers. The source-sink hypothesis, unlike the supplementation hypothesis, implies that the individuals recorded at a site are permanent residents and not ephemeral occupants. A study that tracks the movement, mortality, and fecundity of individuals at different sites is required to test these two hypotheses.

The negative influence of cutblocks on squirrel distribution in the Managed Area is interesting, as only 9% of the area has been harvested for timber (Fig 3.1). As red squirrel individuals do use cutblocks (Chapter One), and behaviour and survival are apparently are not greatly affected by anthropogenic edges (Elizabeth Anderson, unpubl. data), this raises some interesting ecological questions. Are squirrels attracted away from conifer trees to summer forage at cutblocks, a scenario predicted by landscape supplementation (Dunning et al., 1992)? Or are more indirect processes (Dunning et al., 1992) operating, such as increased pressure from predators attracted to these open high-diversity areas (Andren et al., 1985; Hansson, 1989, 1994) ? If this is true, why are the effects seen only at the larger scales, rather than the smaller ones? A rigorous test for these mechanisms would illuminate the large void in our knowledge of spatial dynamics in naturally heterogeneous systems. While extensively pontificated (Levin, 1970; Pulliam, 1988), there is little empirical evidence for the existence of supplementation, source-sink dynamics, or related processes. Whatever the mechanism, it can be concluded that in this heterogeneous area landscape structure does influence the probability of patch occupation by red squirrels, over and above the influences of local vegetation, and that this relationship is context-dependent.

Similar results have been shown for other species in other systems. Vos and Stumpel (1995) found tree frog occupation of ponds was predicted by distance to the nearest occupied pond once the chemical conditions with the pond were accounted for. Verboom and van Apeldoorn (1990) and van Apeldoorn et al. (1994) showed that the proximity to large "source" stands, and hedgerow connections to them, predicted occupation of woodlots by Eurasian red squirrels once conifer within the patch had entered the model, and that this relationship changed over time. The latter authors proposed that this relationship was due to a source-sink model: that small woodlots were occupied by excess individuals from larger stands in years when those stands reached maximum capacity. Fitzgibbon (1993) found similar results for grey squirrels. In contrast Celada et al. (1994) found that local vegetation characteristics were not significant; only patch area predicted squirrel presence in one study area, while proximity to source areas predicted presence in another study area. They also invoked the source-sink model to explain these distribution patterns, although conceded that landscape supplementation may also be occurring among several small patches.

My results support the classic tenets of landscape ecology - that landscape elements beyond the local patch are significant influences on the distribution of organisms. While many authors have indirectly acknowledged the importance of internal patch heterogeneity in mediating the response to landscape structure, the nature of these effects has been largely ignored in favour of the search for broad-scale patterns. This dereliction may lead to misleading results. Combining sites of differing quality causes one to overlook the possibility that individuals living within different patch types may respond to landscape structure differently. This is a fundamental assumption of source-sink dynamics and related mechanisms such as ideal pre-emptive distribution but is never explicitly addressed.

4.3.2 Two different responses to landscape structure

The relationship between landscape structure and squirrel presence was markedly different between the conifer-poor and conifer-abundant sites. There was a single scale on the Reference grid where landscape was a significant predictor in the conifer-poor subset.

In the conifer-abundant sites on the Managed Grid, the deviance explained by landscape was generally higher than the same regression performed on the entire set of grid points (Figure 3.4b), although this was not true of the Reference grid (Figure 3.6a). Statistically, this disparity in response indicates that combining the two site types into a single analysis increases random error among experimental units, reducing the sensitivity of the statistical test (Hurlbert, 1984), thereby obscuring the detection of existing patterns. Ecologically, the striking contrast between the two conifer designations indicates that there are (at least) two different processes at work affecting squirrel presence in this system. On those sites where one would assume the probability of squirrel survival is high - the conifer-abundant sites - black spruce positively predicted squirrel presence. Deciduous, white spruce, cutblocks (Managed Area), marsh, and heterogeneous black spruce (Reference Area) negatively predicted it. This suggests that patch occupation at these sites areas is affected by proximity to other patch types in the landscape, possibly as sources of dispersing individuals or sources of competitors and predators at the larger scales, and juxtaposed patch types at smaller scales (Dunning et al., 1992). In contrast, at the conifer-poor sites where one would expect survival to be low, landscape structure is apparently not important. There are a several possible explanations for this disparity.

This survey was conducted in the late spring and early summer of 1997, a time when young squirrels are dispersing to find their own territories (Kemp and Keith, 1970). It is possible that the individuals surveyed in the conifer-poor sites were summer transients without a defended winter food supply (conifer cones) searching for a territory. Although Larsen and Boutin (1995) found that adult squirrels don't redistribute to better vacant territories within jack pine, data from Klenner (1990) and Wheatley (1999) suggests that this might occur in habitats where territory quality (food availability) is more highly contrasted. The lack of landscape effects found here indicates that the location of these individuals is not influenced by proximity to preferred conifer habitat as one might expect. Factors not measured here may contribute to an ephemeral distribution, or it may in fact be random. Although other studies (*e.g.* Smith, 1968; Kemp and Keith, 1970) have established the existence of individuals without territories (that may acquire one later on) no studies have examined the processes driving their distribution in a heterogeneous mosaic. If these are individuals without territories waiting to acquire one, and are as important to population dynamics as Pulliam (1988) and Pulliam and Danielson (1991) suggest, then this segment of the population and the effects of habitat and landscape structure upon its distribution merit further investigation.

Nonetheless I can safely conclude that there is an interaction between local vegetation and landscape structure and their influence on red squirrel distribution. The data strongly suggest that the response to landscape structure is local habitat-dependent. The processes operating on individuals at one site may be quite different from those operating at another, resulting in different probabilities of occupation and hence disparate patterns of abundance.

4.4 CONCLUSIONS

Local habitat accounted for some deviance in squirrel presence on the Managed and Reference areas but not the Burned area. Landscape structure accounted for further deviance on the Managed Grid at several scales but only one on the Reference Grid.

Different variables were important at each. When sites were separated into conifer-poor and conifer-rich categories different responses to structure were observed at each. The results are important in that 1) landscape structural effects are not restricted to anthropogenically fragmented landscapes; 2) context-dependency indicates landscape studies limited to one area cannot be extrapolated to another; 3) combining sites of differing quality in these studies may obscure detection of existing patterns; and 4) the interaction between local vegetation and landscape structure supports the idea that different mechanisms effect the response to landscape structure in different patch types.

4.5 LITERATURE CITED

Allen, T.F.H., and T.W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York.

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: Perspectives for Ecological Complexity. The University of Chicago Press, Chicago.

Allen, T.F.H., and E.P. Wyleto. 1983. A hierarchical model for the complexity of plant communities. Journal of Theoretical Biology **101**: 529-540.

Andren, H., P. Angelstam, E. Lindström, and P. Widén. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. Oikos **45**(2): 273-277.

van Apeldoorn, R., C. Celada, and W. Nieuwenhuizen. 1994. Distribution and dynamics of the red squirrel (*Sciurus vulgaris L.*) in a landscape with fragmented habitat. Landscape Ecology **9**(3): 227-235.

Celada, C., G. Bogliani, A. Gariboldi, and A. Maracci. 1994. Occupancy of isolated woodlots by the red squirrel *Sciurus vulgaris L.* in Italy. Biological Conservation **69**: 177-183.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**: 169-175.

Fisher, J.T., and G. Merriam. In press. Resource patch array use by two squirrel species in an agricultural mosaic. Landscape Ecology.

Fitzgibbon, C.D. 1993. The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. Journal of Applied Ecology **30**: 736-742.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Review **13**(2/3/4): 133-148.

Hansson, L. 1989. Predation in heterogeneous landscapes: how to evaluate total impact? Oikos **54**(1): 117-119.

Hansson, L. 1994. Vertebrate distributions relative to clearcut edges in a boreal forest landscape. Landscape Ecology **9**(2): 105-115.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**(2): 187-211.

Kemp, G.A., and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**(5): 763-779.

Klenner, W. 1990. The effect of food abundance and territorial behaviour on population dynamics of the red squirrel. Ph.D. Thesis. University of British Columbia, Vancouver, BC.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**: 253-260.

Larsen, K.W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology **75**(1): 214-223.

Larsen, K.W., and S. Boutin. 1995. Exploring territory quality in the North American red squirrel through removal experiments. Canadian Journal of Zoology **73**: 1115-1122.

Lawton, J. 1999. Are there general laws in ecology? Oikos **84**: 177-192.

Levins, R. 1970. Extinction. Pp. 77-207 **In** <u>Lectures on mathematics in the life sciences</u>. Vol. 2. M. Gerstenhaber, ed. American Mathematical Society, Providence, RI.

McGarigal, K., and W. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs **65**(3): 235-260.

Mönkkönen, M., P. Reunanen, A. Nikula, J. Inkeröinen, and J. Forsman. 1997. Landscape characteristics associated with the occurrence of the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. Ecography **20**: 634-642.

Pickett, S.T.A., J. Kolasa, J.J. Armesto, and S.L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos **54**: 129-136.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist **132**(5): 652-661.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**: S5-S66.

Riege, D.A. 1991. Habitat specialization and social factors in distribution of red and grey squirrels. Journal of Mammalogy **72**(1): 152-162.

Rusch, D., and W. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**(11): 789-799.

Smith, C.C. 1968. The adaptive nature of social organization in the Genus of three (sic) squirrels *Tamiasciurus*. Ecological Monographs **38**(1): 31-63

SPSS Inc. 1996. SPSS Version 7.5. Chicago, IL.

Verboom, B., and R. van Apeldoorn. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. Landscape Ecology **4**(2/3): 171-176.

Vos, C.C., and A.H.P. Stumpel. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology **11**(4): 203-214.

Wheatley, M.T. 1999. Does Density Reflect Habitat Quality for Red Squirrels During a Spruce Cone Failure? M.Sc. Thesis, University of Alberta, Edmonton, AB.

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

Yahner, R.H. 1987. Feeding site use by red squirrels, *Tamiasciurus hudsonicus*, in a marginal habitat in Pennsylvania. Canadian Field Naturalist **101**(4): 586-589.

Chapter 5

The Protean Nature of Landscape Effects

5.0 CONCLUSIONS

The earliest landscape ecology research revealed that the observed influences of structure on animal distribution were species-dependent (see for example Wegner and Merriam, 1979; Middleton and Merriam, 1983). This specificity is often attributed to behavioural differences, degree of specialization, or varying levels of adaptive flexibility (Bright, 1993; Andren, 1994; Andren et al., 1997; Henein et al., 1998). As well, differences in body size influence how heterogeneity is perceived, with larger vagile organisms perceiving more a fine-grain mosaic than smaller less vagile ones. More technically, the response to heterogeneity differs depending on how many hierarchical levels of heterogeneity between the organism's grain and extent are perceived (Kotliar and Wiens, 1990) and the spatial and time scale of the process that is effecting that response to heterogeneity for an organism (Addicott et al., 1987).

Landscape structural effects have been demonstrated almost exclusively in anthropogenically fragmented landscapes. This thesis has revealed that landscape structural effects are not limited to these areas but also exist in naturally heterogeneous landscapes with minimal anthropogenic impact. More importantly, it also reveals that the relationship between landscape structure and red squirrel distribution is dependent on a number of factors beyond species-specificity.

Time-dependent: The relationship between squirrel presence and landscape structure changed between the summers of 1996 and 1997 on the Managed area. As a prescriptive conclusion, landscape ecology studies should be conducted over a number of years in order to compensate for temporal variability in the system. This may be especially important in 'ephemeral' landscapes such as agricultural environments where matrix patch types (crops) change between years or even seasons (Szacki et al., 1993), or in boreal forests where fluctuations in patch characteristics may profoundly influence dynamics within them (Hansson, 1992). The obvious theoretical conclusion is that the mechanism driving the response to heterogeneity may change between years. In the case of red squirrels, the amount of forage and hence quality of a patch (a stand of some tree species) may change with time (Wheatley, 1999), thus changing the relative importance of landscape composition and configuration and hence squirrel distribution patterns. Detecting temporal variability may be as important as spatial variability in constructing plausible hypothesis regarding distribution patterns.

Scale-dependent: The response of red squirrel presence to landscape structure occurred at a number of different spatial extents, including small scales corresponding to the summer foraging range (Chapter One) and to larger scales. It also changed depending on the scale of squirrel sampling, *i.e.*, between the mega grids and the meso grids within the same area (Chapter Three). This suggests that more than one mechanism was responsible for the observed pattern in distribution. The response to heterogeneity at small scales, squirrels' use of several different patch types, and the existence of larger ranges where conifer is limiting, all suggest that landscape supplementation (Dunning et al., 1992) may be occurring. The response to structure at larger scales indicates that processes encompassing larger areas, such as dispersal, are involved. The positive relationship with large homogeneous black spruce tracts, and negative association with marginal deciduous stands and cutblocks, suggest that a source-sink dynamic (Pulliam, 1988; Pulliam and Danielson, 1991) exists that (in part) causes the observed pattern of distribution. I can conclude that the variables that predict squirrel distribution change depending on the scale of landscape quantification. This conclusion is not really innovative (see Wiens, 1989). However what is provocative is that the relative importance of each scale changes between areas or contexts.

Context-dependent: The deviance explained at each scale was different between the Burned, Managed, and Reference areas. The landscape variables that significantly predicted squirrel presence also varied between the three areas. These inconsistencies strongly suggest that different mechanisms drive the response to heterogeneity in different areas. Smaller-scale mechanisms such as complementation may be more important in some areas while larger-scale processes such as source-sink dynamics may dominate in others. The net result of a particular mechanism may also differ; in burned areas tracts of unburned deciduous may be important as 'sources' whereas on the Managed and Burned areas these were most likely sinks. The mechanisms effecting the response to heterogeneity can only be hypothesised at this time, but the finding that landscape effects differ by area is a critical one. Few studies have analysed several different areas independently, and combining points in different areas into a single analysis could yield spurious results (Hurlbert, 1984). To extrapolate specific landscape effects from one area to another would be erroneous.

While this pattern-seeking approach has revealed that there are different responses in the different areas, why this is so is completely open to debate. The areas have different compositions, and hence different ranges of variability in the independent dataset, so statistically it is expected that dissimilar variables would become important within each. Statistical reasons aside, the ecological importance of patch types may change between areas. For example heterogeneity (HET) may be beneficial for squirrels in one area, at one scale, but detrimental in another area or at another scale. To claim that deciduous is a vital landscape element for squirrels based a study conducted on the Burned area, even with a fair sample size (30-50 points), would be spurious if applied to the Managed or Reference areas. Instead of yielding many answers, this thesis instead poses a crucial question: Under what circumstances are certain landscape structures important elements of animal occupation? I can conclude that these effects are context-specific, but the nature of that specificity remains the salient ecological issue.

Local habitat-dependent: The relative influence of landscape structure is also local-habitat-dependent. The number of conifer trees at a site is an important predictor of squirrel presence in the non-burned areas, but landscape structure still explains more deviance once this has been accounted for. How it does so differs between landscape extents and areas. More interestingly, the importance of landscape structure shifts from being insignificant in conifer-poor patches, to highly significant in conifer-abundant patches. Pooling these patch types into a single analysis obscures the detection of processes driving distribution. While conifer-abundant sites may be subject to source-sink dynamics (Pulliam, 1988; Pulliam and Danielson, 1991), neighbourhood or indirect effects (Dunning et al., 1992), a metapopulation model (Levins, 1970) or any other number of processes that are heavily influenced by landscape structure, conifer-poor sites appear unaffected by any of these. These results beg the same question proposed in the last paragraph, but framed in a slightly different context: Under what circumstances are certain landscape structures important elements of animal occupation within a specific habitat type?

That landscape structure plays a role in influencing animal distribution is incontrovertible. Although landscape ecology is firmly entrenched in conservation-oriented studies of anthropogenic systems (see for example Forman, 1997) we now know that the influence of structure is a naturally occurring phenomenon in heterogeneous areas. We also know that the nature of these effects are not easily extrapolated from one year, habitat type, or area, to the next. The search for processes to explain these inconsistencies will require a marriage of landscape ecology and population ecology - a demographic study that explicitly considers landscape structure as a treatment effect. As scientists we can then gain insights into the diversity of processes that shape the observed patterns. As managers we can then make predictions about the effects of landscape alteration (e.g. timber harvest) on animal populations. If nothing else, we will be one step closer to understanding the protean nature of ecological systems, and the role of stochasticity in shaping those patterns we thought to be concrete.

5.1 LITERATURE CITED

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

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**: 355-366.

Andren, H, A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos **80**(1): 193-196.

Bright, P.W. 1993. Habitat fragmentation - problems and predictions for British mammals. Mammal Review **23**(3/4): 101-111.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**: 169-175.

Forman, R.T.T. 1997. Land Mosaics: The ecology of landscapes and regions. Cambridge University Press, UK.

Hansson, L. 1992. Landscape ecology of boreal forests. Trends in Ecology and Evolution 7(9): 299-232.

Henein, K., J. Wegner, and G. Merriam. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos **81**: 168-186.

Kotliar, N.B., and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**: 253-260.

Levins, R. 1970. Extinction. Pp. 77-207 **In** Lectures on mathematics in the life sciences. Vol. 2. M. Gerstenhaber, ed. American Mathematical Society, Providence, RI.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist **132**(5): 652-661.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**: S5-S66.

Szacki, J., J. Babinska-Werka, and A. Liro. 1993. The influence of landscape spatial structure on small mammal movements. Acta Theriologica **38**(2): 113-123.

Wegner, J.F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. Journal of Applied Ecology **16**: 349-357.

Wheatley, M.T. 1999. Does Density Reflect Habitat Quality for Red Squirrels During a Spruce Cone Failure? M.Sc. Thesis, University of Alberta, Edmonton, AB.

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

Appendix 1: The fit of the logistic regression model. -2 log likelihood values of the significant multiple logistic regression models obtained at each spatial scale, grid, and area are tested for significant deviation from a χ^2 distribution given the number of samples in each regression (n) and the number of parameters in the regression model (pr). The degrees of freedom equals n-pr. The $\alpha = 0.05$.

Area	Grid	Scale	n - pr	-2LL	different from χ^2
Managed (1996)	mega	50	64 - 3	69.546	no
		100	64 - 3	63.168	no
		250	64 - 3	66.942	no
		500	64 - 3	66.5	no
	meso	50	127 - 3	157.375	yes
		100	127 - 3	156.269	yes
		250	34 - 2	36.942	no
Managed (1997)	mega	50	58 - 5	55.354	no
		100	58 - 3	59.341	no
		250	58 - 3	61.489	no
		500	58 - 4	55.608	no
		1000	16 - 2	12.586	no
	meso	50	64 - 2	75.365	no
		100	64 - 2	76.394	no
Burned	mega	50	29 - 3	6.73	no
		100	29 - 3	10.776	no
	meso	50	57 - 4	47.938	no
		100	57 - 4	43.591	no
Reference	mega	50	63 - 3	72.347	no
		100	63 - 3	64.589	no
		250	63 - 4	59.762	no
		500	63 - 2	78.263	no
	meso	50	127 - 2	157.110	yes
		100	127 - 3	149.072	no

Appendix 2: Output of logistic regression models. Squirrel presence was regressed against landscape composition and configuration variables; the significant variables selected by the forward selection procedure, the p value, and fit of the final model are listed for each landscape scale at each grid.

a) Managed Mega Grid 1996

scale	significant variables	p(model)	N	Nagelkerke R^2	overall %correct
50	APJ HET	0.0002	64	0.313	67.19
100	ASBLT ADEC*HET	0.0000	64	0.412	73.44
250	-ADEC ASBLT	0.0001	64	0.355	71.88
500	-ADEC ASBLT	0.0000	64	0.362	70.31
1000	none		16		

b) Managed Mega Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	AMDP AMDS APJ ASBLT	0.0001	58	0.460	74.14
100	APJ ASBLT	0.0000	58	0.397	72.41
250	APJ ASBLT	0.0001	58	0.362	72.41
500	APJ ASBLT -ASBLT*HET	0.0000	58	0.456	72.41
1000	APJ*HET	0.0034	16	0.566	81.25

c) Managed Meso Grid 1996

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-ADEC HET	0.0002	127	0.171	67.72
100	HET -AMARSH	0.0001	127	0.181	64.57
250	HET	0.0015	34	0.342	73.53

d) Managed Meso Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	HET	0.0041	64	0.165	68.75
100	HET	0.0073	64	0.146	68.75
250	none		18		

e) Reference Mega Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-ADEC MARSH	0.0006	63	0.282	66.67
100	APJ ASBLT	0.0000	63	0.404	69.84
250	ASBLT -AMDS APJ	0.0000	63	0.472	76.19
500	-ADEC	0.0026	63	0.179	69.84
1000	none		18		

f) Reference Meso Grid 1997

Scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-ADEC	0.0000	127	0.179	66.93
100	APJ ASW	0.0000	127	0.250	71.65
250	none		32		

g) Burned Mega Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-ADEC*HET AMDP	0.0019	29	0.724	93.10
100	ADEC AMDP	0.0142	29	0.524	89.66
250	none		29		
500	none		29		

h) Burned Meso Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-ABDEC AMARSH ABuLOW*HET	0.0000	57	0.559	80.70
100	ADEC AMDP ABPINE*HET	0.0000	57	0.616	84.21

Appendix 3: Output of logistic regression models that include local vegetation. Squirrel presence was regressed against number of conifer trees at a site; then landscape composition and configuration variables were allowed to enter the model. The significant landscape variables selected by the forward selection procedure, the p value, and fit of the final model are listed for each landscape scale at each grid.

a) Managed Mega Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	overall %correct
50	CON_TREES ASBLT	0.0001	58	0.374	70.69
100	CON_TREES ASBLT	0.0000	58	0.390	70.69
250	CON_TREES -ACUT	0.0001	58	0.375	72.41
500	CON_TREES -ACUT ASBLT	0.0000	58	0.459	77.59
1000	CON_TREES	0.0007	16	0.699	87.50

b) Reference Mega Grid 1997

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	CON_TREES	0.0001	63	0.303	65.08
100	CON_TREES	0.0001	63	0.303	65.08
250	CON_TREES -AMDS ASBLT	0.0000	63	0.474	73.02
500	CON_TREES	0.0001	63	0.303	65.08
1000	CON_TREES	0.0123	18	0.394	77.78

Appendix 4: Output of logistic regression models using conifer-abundant sites. Squirrel presence was regressed against landscape composition and configuration variables. The significant landscape variables selected by the forward selection procedure, the p value, and fit of the final model are listed for each landscape scale at each grid.

a) Managed Mega Grid 1997 (Conifer-abundant)

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	ASBLT	0.0014	25	0.484	72.00
100	ASBLT -AMARSH	0.0002	25	0.719	84.00
250	-ADEC	0.0132	25	0.314	72.00
500	-ASW -ACUT AMDS	0.0006	25	0.720	92.00

b) Reference Mega Grid 1997 (Conifer-abundant)

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	-AMARSH	0.0049	37	0.274	78.38
100	-AMARSH	0.0449	37	0.146	75.68
250	none		37		
500	none		37		

c) Reference Mega Grid 1997 (Conifer-poor)

scale	significant variables	p(model)	N	Nagelkerke R^2	%correct
50	none		26		
100	none		26		
250	-ASBLT*HET	0.260	26	0.0317	84.62
500	none		26		