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INFLUENCES OF LANDSCAPE STRUCTURE ON SNOWSHOE HARE POPULATIONS IN FRAGMENTED FORESTS

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Chairperson: L. Scott Mills

For many wildlife species, fragmentation results in a mosaic of habitat types in which patches of preferred habitat are set amongst a matrix of less useful habitat types. Characteristics of the matrix surrounding patches of preferred habitat can affect the movement and dispersal of individuals, which affects population dynamics. For snowshoe hares (*Lepus americanus*) in the western United States, patches of densely forested, preferred habitat are often set amongst a matrix of more open-structured habitat types which vary in their usefulness. Although scientists have hypothesized for decades that snowshoe hare population dynamics are affected by the abundance of open-structured habitat in these heterogeneous forests, few studies have addressed whether and how matrix quality affects snowshoe hares. I addressed the extent to which relative snowshoe hare densities in patches of suitable habitat are affected by the surrounding forest matrix. Using fecal pellets to index hare density, I found that relative hare densities were negatively related to the amount of open-structured habitat types, and positively correlated with the amount of boreal forest within 300 m of a patch of dense forest. Although stand-level variables were stronger predictors, variation in matrix quality accounted for a substantial part of the variation in hare densities. I also explored how matrix quality affects the functional connectivity and spatial distribution of snowshoe hares across the landscape. Through radio-telemetry of hares in landscapes with varying matrix quality, I observed hares frequently using matrix habitats for inter-patch movements in landscapes dominated by high quality matrix habitat. However, in landscapes in which matrix quality was poor, snowshoe hares were less likely to make inter-patch movements, and they had more clumped distributions. Thus, matrix quality can affect snowshoe hare densities, movements, and spatial distribution. Because snowshoe hares are an important prey species for many forest carnivores, including the federally threatened lynx (*Lynx canadensis*), forest managers are interested in increasing snowshoe hare population densities. My results suggest that improving matrix quality— by decreasing the amount of open-structured forest and increasing the amount of boreal forest within 300 m of a patch of dense forest— could be beneficial for hare populations.

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Door/Open Heart approach to mentoring. Her positive encouragement and love of science have made dealing with reality a lot more bearable! I am also fortunate to have had the opportunity to work with Scott, whose Can-Do attitude will not let details get in the way of brilliant ideas. I thank him for consistently encouraging me to push my limits. I thank them both for their patience with me and my ‘donut’ drawings!

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INFLUENCES OF LANDSCAPE STRUCTURE ON SNOWSHOE HARE POPULATIONS IN FRAGMENTED FORESTS: AN INTRODUCTION

BACKGROUND

Habitat fragmentation, degradation, and loss pose significant threats to the structure and persistence of wildlife populations and communities (Saunders et al. 1991, Fahrig 2003). All of these processes effectively change the spatial structure of the landscape, creating patches of suitable habitat with altered connectivity to other suitable patches. A small local population isolated from other conspecific populations is prone to local extinction, but the species may have a chance of survival if the landscape structure allows for a network of habitat patches connected by dispersal (reviewed by Hanski 1998).

Metapopulation studies have contributed to our understanding of how patch size, proportion, and other spatial factors may influence survival, emigration, and immigration, but these studies generally assume a binomial landscape model, where patches of good habitat are set amongst a matrix of nonhabitat (Moilanen and Hanski 1998, Ricketts 2001). However, for many species, the matrix is not a homogenous entity, but a mosaic of habitat types of varying degrees of quality.

Characteristics of the landscape matrix have multiple effects on wildlife species. Matrix quality can affect the movement and dispersal of individuals, which in turn affects the colonization-extinction dynamics and densities of the population (Wiens 1997, Ricketts 2001, Brotons et al. 2003, Baum et al. 2004). Some matrix habitats may also provide alternative or supplemental resources for some species (Dunning et al. 1992, Norton et al. 2000) which may enhance population densities. In either case, a matrix of higher quality is expected to increase population densities and persistence within patches of preferred habitat (Estades 2001, Brotons et al. 2003).

In this study, I examine the effects of matrix quality on snowshoe hares (*Lepus americanus*) in a forest in which habitat degradation and habitat fragmentation have resulted in a mosaic of forest types which vary in their usefulness for snowshoe hares. Snowshoe hares are an important prey species for many forest carnivores, including the federally threatened Canada lynx (*Lynx canadensis*). Policy documents dictating the management protocols for forests in which lynx reside must incorporate an understanding of how to manage for snowshoe hare populations (Ruediger et al. 2000). To develop good policies, researchers need to investigate what level of snowshoe hare densities are needed for lynx persistence, how much habitat alteration can occur within lynx management units, and how fragmentation affects lynx and snowshoe hare populations (Ruggiero et al. 2000, Ruediger et al. 2000).

The Okanogan National Forest is an excellent system for researching such questions. The Okanogan has consistently supported lynx populations for decades (McKelvey et al. 2000), in both fragmented and continuous landscapes, thus creating a natural laboratory for comparative studies. The Okanogan Plateau, in which "The Meadows" study area is set (Figure A.1), is high-elevation habitat (>1460 m) comprised of extensive and homogenous lodgepole pine forest (*Pinus contorta*) with lesser components of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*; Brittell et al. 1989, Koehler 1990). Timber management and development have been minimal in this area, thus the most notable causes of fragmentation are natural fires and natural meadows. The vegetation type and contiguous, large-grained characteristics of the Okanogan Plateau resemble the boreal forests found in the northern parts of snowshoe hare and lynx range. Several studies on lynx and snowshoe hares have provided information on the habitat selection of lynx and the relative habitat use of hares in this area of contiguous boreal forest (Brittell et al. 1989, Koehler 1990a,b, McKelvey et al. 2000).

Although these studies provided important information on lynx and snowshoe hare habitat selection in WA, Geographic Information Systems (GIS) analyses indicate that there is a relatively small amount of such high-quality lynx and snowshoe hare habitat in the state. Most of the remaining habitat in WA occurs at lower elevations, has steeper slopes, and consists mostly of Douglas fir (*Pseudotsuga menziesii*)/Ponderosa pine (*Pinus* ponderosa) or Engelmann spruce/subalpine fir forests (Ruediger et al. 2000). Less than 20 km southwest of the Meadows area is an area more exemplary of the remaining habitat in the state of WA. The "Black Pine Basin" study area is more fragmented due to intermixed forest types, recent fires, and timber harvest activities.

In 2001-2004, extensive research on lynx was conducted in the Okanogan, with researchers studying habitat selection in the Meadows and Black Pine Basin study areas (von Kienast 2003 and Maletzke 2004, respectively). The two studies provided insight into both the similarities and differences in lynx habitat use in contiguous versus fragmented landscapes. My research was designed to complement these studies by examining snowshoe hare populations in areas of varying degrees of fragmentation. Because of the dependency of lynx on snowshoe hares, the most pertinent management-oriented questions at the time were related to identifying how landscape patterns affect snowshoe hare densities.

Landscape Ecology of Snowshoe Hares

In the northern parts of their range (e.g. Canada, Alaska) where boreal forest is relatively contiguous, snowshoe hare densities cycle regularly and reach peak densities of 4-6 hares/ha (reviewed in Hodges 2000a). In the southern parts of their range (e.g. northern United States) forests are more montane, with patches of dense boreal forest set amidst a matrix of drier, less suitable forest types that provide less of the dense understory that hares need. In addition, human disturbance in the southern ranges also contributes to a patchier distribution of suitable habitat. In these southern parts of their range, snowshoe hare populations do not seem to cycle as regularly, though fluctuations do occur (Hodges 2000b). Peak densities of hares in the southern parts of their range rarely reach the densities seen in northern latitudes.

Scientists have hypothesized for decades that habitat fragmentation in the southern ranges affects snowshoe hare population dynamics. The dominant paradigm explaining snowshoe hare population dynamics in the southern range of hares is that the fragmentation of landscapes is responsible for the lower hare densities and the previously hypothesized noncyclicity of hares in the southern regions (Keith 1993, Dolbeer and Clark 1975, Wolff 1980). Best articulated by Wolff (1980, 1981) the refugium model suggests that hares selectively use dense, safe patches of boreal-type forest. When population densities become too high, some individuals are forced into the matrix, which exposes them to greater predation mortality and suppresses densities in the refuge patches. In a fragmented forest in western Montana, Griffin (2003) showed snowshoe hares frequently used multiple forest stands for movement, foraging, and reproduction.

However, hares that spent more time in open-structured matrix habitats had lower survival, and these habitats represented population sinks.

STUDY OBJECTIVES

Although many have hypothesized that a greater abundance of open-structured habitat on the landscape negatively affects snowshoe hare populations, little published empirical data exists to support this hypothesis. Therefore my goal for this study was to examine how matrix quality, defined by the amount of open-structured habitat and boreal forest on the landscape, impacts snowshoe hare populations. I specifically focused on the impacts of matrix quality on snowshoe hare densities, as forest managers are concerned with providing high enough hare densities to support lynx populations.

Higher species densities within patches of preferred habitat have been correlated with higher matrix quality for some terrestrial species (Estades 2001, Brotons et al. 2003). On a coarse scale, I examined whether snowshoe hare densities in patches of dense forest differed between a more continuous landscape (The Meadows) and a fragmented landscape (Black Pine Basin; Appendix A). In Chapter II, I examined more closely whether the quality of matrix surrounding a patch of dense habitat affects the density of snowshoe hares within that patch. In addition, I identified the spatial scales at which matrix effects were strongest, and compared the relative influences of matrix quality on hare densities compared to the influences of stand-level variables.

To be able to fully interpret the relationship between matrix quality and population dynamics and develop informed management guidelines, it is important to understand the mechanisms by which the population is affected. The permeability of matrix habitats to animal movement can affect 'functional connectivity,' or the ability of individuals to cross a landscape (With et al. 1999, Ricketts 2001, Goodwin and Fahrig 2002), which can then affect population dynamics (Moilanen and Hanski 1998; Pither and Taylor 1998). Additionally, some matrix types may provide alternative habitats or supplemental resources for individuals (Dunning et al. 1992, Norton et al. 2000). Landscapes dominated by these matrix types may influence population dynamics by increasing the carrying capacity of patches of preferred habitat and by affecting the distribution of individuals across the landscape (Brotons et al. 2003). In Chapter III, I examine snowshoe hare movements and habitat use in landscapes of varying matrix quality to determine if matrix quality affects functional connectivity or the availability of supplemental resources for snowshoe hares.

Results from this study will be applicable at many levels. I provide information on relative densities of snowshoe hares within the Okanogan National Forest, which can be used for comparisons with lynx habitat use data, and as a baseline for future studies. More broadly, forest managers in fragmented forests of the western United States will benefit from better understanding of the factors that influence snowshoe hare densities. Specifically, I show that landscape pattern is indeed an important factor that should be considered, I offer general suggestions for matrix improvement, and I discuss the possible consequences if matrix quality decreases. Finally, my data contribute more broadly to the world of landscape ecology. Most studies examining the effects of matrix quality have been conducted on insects (Wiens et al. 1997, Ricketts 2001, Baum et al. 2004), amphibians (Stevens et al. 2004), birds (Norton et al. 2000, Brotons et al. 2003), and small mammals (Mabry and Barrett 2002, Selonen and Hanski 2003, Cook et al. 2004), which are all species that operate at scales small enough to be manipulated experimentally. Very few studies have been conducted with larger mammals. My results confirm that the effects of matrix on hare densities and the mechanisms by which matrix affects snowshoe hare populations are comparable to patterns seen in smaller animals.

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CHAPTER II:
MULTI-SCALE FACTORS INFLUENCING SNOWSHOE HARE DENSITIES IN FRAGMENTED FORESTS

ABSTRACT

Habitat needs of snowshoe hares (*Lepus americanus*) have been examined extensively at scales as large as forest stands, but few data exist to suggest how larger-scaled landscape composition affects hare populations. I explored how snowshoe hare densities in patches of suitable habitat are affected by the surrounding forest matrix, using fecal pellets to index hare density. Models that included a combination of landscape- and stand-level variables performed substantially better than single-scale models. Stand-level variables, especially sapling and medium-sized tree density, were the best univariate predictors of snowshoe hare pellet density, but pellet densities were also positively associated with the amount of boreal forest at 300 m, and negatively correlated with the amount of open-structured forest at 300 m. These results reinforce the importance of stand-level vegetative factors, yet add an understanding of the extent to which the matrix affects snowshoe hare densities. When forest managers wish to increase snowshoe hare densities, they should consider softening the matrix by creating more boreal forest and less open-structured habitat.

INTRODUCTION

Although local scale characteristics of habitat patches that influence suitability for a species are often known, less is usually known about the importance of spatial relationships between such patches. Metapopulation studies have contributed to our understanding of how patch size, isolation, and other spatial factors may influence survival, emigration, and immigration, but these studies generally assume a binomial landscape model, where patches of good habitat are set amongst a matrix of nonhabitat (Moilanen and Hanski 1998, Ricketts 2001). However, for many species, the matrix is not a homogenous entity, but a mosaic of habitat types of varying degrees of quality.

Characteristics of the landscape matrix have multiple effects on wildlife species. Matrix quality affects the movement and dispersal of individuals, which in turn affects the colonization-extinction dynamics and densities of the population (Wiens 1997, Ricketts 2001, Brotons et al. 2003, Baum et al. 2004). Some matrix habitats may also provide alternative or supplemental resources for some species (Dunning et al. 1992, Norton et al. 2000), which may enhance population densities. In either case, a matrix of higher quality is expected to increase population densities within patches of preferred habitat (Estades 2001, Brotons et al. 2003).

For snowshoe hares, as for many forest-dwelling species, some matrix habitat types offer less resistance to movement than others, or provide alternative or supplemental resources. Forest stands with dense understory vegetation support the highest densities of hares (reviewed in Hodges 2000b) and may act as population sources (Griffin 2003). These patches of dense, preferred habitat are often surrounded by other matrix habitat types that are less dense, such as open-structured south-facing forest stands or thinned stands. While these stands are used more than the highly open matrix habitats (e.g. clearcuts, meadows) and can support moderate hare densities (Thompson et al. 1989, Koehler 1990a,b), they may be population sinks (Griffin 2003). Little is known about how the composition of matrix habitats affects snowshoe hare population dynamics.

Differences in animal densities can exist between patches with similar characteristics that are imbedded in different matrices (Gustafson and Gardner 1996, Vandermeer and Carvajal 2001). Such a pattern is evident in fragmented forests in Montana, where differences on the magnitude of two to three times as many hares per hectare have been documented in patches of habitat with similar stand-level attributes (Griffin 2003, Mills and Hodges, unpublished data), suggesting that landscape-level factors may be influencing densities. In fact, scientists have hypothesized for decades that snowshoe hare densities may be affected by landscape design (Leopold 1933, Dolbeer and Clark 1975, Wolff 1980, Hodges 2000b). The Refugium model, best articulated by Wolff (1980), suggests that hare populations in high quality "refuge" patches grow to carrying capacity, at which point some individuals are forced to disperse into the less desirable matrix habitats where they face low chances of survival as a result of poorer food quality (Hik 1995) or predation by facultative predators (Wolff 1980, 1981). Wirsing et al. (2002) alternatively proposed that refuge patches create concentrated pockets of hares that become disproportionately preyed upon by facultative predators, which thus reduces snowshoe hare densities. Both models suggest an inverse relationship between hare density in dense patches of forest and the amount of non-suitable matrix habitat on the landscape, yet little published data exists to support or refute this assumption.

Understanding local and landscape processes that drive snowshoe hare dynamics is important because hares are an important food source for many forest carnivores, including the federally threatened Canada lynx (*Lynx canadensis*). Forest management strategies in potential lynx habitat must include guidelines for maintaining or improving hare densities (Ruediger et al. 2000).

In this study I used a multi-scale approach to evaluate the influence of stand- and landscape-level factors on snowshoe hare densities within patches of preferred habitat (i.e. densely forested stands) in northern Washington. Based on previous habitat studies on snowshoe hares (reviewed by Hodges 2000a,b), I predicted a positive correlation between snowshoe hare density and understory cover, as well as positive relationships between snowshoe hare densities and canopy cover, stand size, and stand vegetation type. At the landscape scale, I predicted a negative relationship between snowshoe hare densities and the amount of open-structured forest, and a positive relationship between hare densities and the amount of boreal forest in the landscape. The primary objectives of the study were to determine which, if any, landscape-level factors are important determinants of snowshoe hare density, and to evaluate the extent to which forest managers should consider matrix quality in regards to snowshoe hare populations.

METHODS

Study Area and Vegetation Classification

The field research was conducted in May-Aug of 2003-04 in the Okanogan National Forest in north-central Washington (48°N, 120°W), specifically concentrated in a 211 km^2 study area that was delineated for a lynx habitat use study in 2002-2004 (Figure 2.1; Maletzke 2004). Elevations in the study area range from 643 m to 2134 m. For site selection and spatial analyses, I used Geographic information system (GIS) coverages developed by Maletzke (2004). Coverages were created by digitizing stand boundaries from orthophotos, then populating each stand with information regarding the vegetation type and canopy and understory cover; coverages had an overall accuracy of 77%.

Maletzke (2004) identified four main vegetation types in the study area: Boreal Forest, Dry Forest, Recent Burns, and Natural Openings. Boreal Forest stands were characterized by subalpine fir (*Abies lasciocarpa*) and Englemann spruce (*Picea enlemanii*) as the dominant canopy species, with Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and whitebark pine (*Pinus albicaulis*) occasionally interspersed. Boreal Forest covered 52% of the study area, mostly on north-facing slopes and steeper drainage bottoms. Dry Forest stands were comprised of Douglas fir and ponderosa pine (*Pinus ponderosa*) as the dominant canopy species. Dry Forest covered 37% of the study area, dominating lower elevations (<1066 m) and found at higher elevations on south-facing slopes and in wide drainage bottoms. Recent Burns covered 6% of the study area and were characterized as areas affected by wildfires in the last 10 years that had sparse sapling regeneration (<10% understory cover). Natural openings such as meadows and rocky slopes covered 5% of the study area.

Canopy cover and understory cover were both classified by Maletzke (2004) in 4 classes: 0-10%, 11-39%, 40-69%, and 70-100%. From these data I identified 'Open-structured' stands, or those in which canopy cover and understory cover were both ≤10%. These stands encompassed 28% of the study area, and represented all natural openings, recent burns, and recent timber harvests, which are not considered snowshoe hare habitat (reviewed in Hodges 2000a,b).

The study area contains a mosaic of patch types, resulting from the varied topography, natural and prescribed fires, and microclimates, and anthropogenic alterations such as roads, timber harvests, and thinning projects. Patch sizes for the 984 stands ranged from 1-1190 ha. Large patches of homogenous vegetation were rare, as the median stand size was 10 ha and the mean was 21 ha (SE=1.5). In general, the patchiness within this study area is exemplary of most of the lynx habitat found in the state of Washington (G. Koehler and R. Naney, personal communication).

Site Selection

I selected focal stands that, based on stand-level characteristics, could potentially support high snowshoe hare densities. I began by using the GIS data to identify all stands within the study area with canopy cover >40% or understory cover >40% (n=356). I randomly selected 78 stands that ranged from 3.4 to >190 ha (median=22.5 ha, mean=31.5 ha) for examination. For any stands >20 ha, I selected a 20 ha portion from the middle of the stand.

Snowshoe Hare Abundance Indices

Abundance and density of snowshoe hares are best estimated with mark-recapture approaches. Mills et al. (2005) compared estimated hare densities to predicted hare densities based on pellet density regression equations and concluded that pellets may be useful for qualitatively ranking relative hare density across large spatial scales.

I conducted fecal pellet surveys in the 78 focal stands by counting the number of pellets within 50 randomly placed "Krebs plots" (3.05 m x 5.08 cm; Krebs et al. 2001, Hodges and Mills in review). For regression analyses, I used log-transformed mean pellets per stand as the dependent variable. To convert mean pellet counts to snowshoe hare density estimates, I used the equation developed by Krebs et al. (2001):

$$\text{Hare density (hares/ha)} = 1.567 * e^{(-1.203+(0.889*\ln(\text{mean pellets/stand})))} \qquad \text{[Equation 1]}$$

This equation, developed in the Yukon, performed as well at identifying relative hare density as did locally-derived regression equations in Montana (Mills et al. 2005).

Stand-level Variables

Within each focal stand I collected data on multiple physical and vegetative characteristics (Table 2.1). I classified the dominant vegetation type as "Dry Forest," in which the canopy was composed of >75% Douglas fir and/or ponderosa pine, or as "Boreal Forest," in which canopy species were a mix of Engelmann spruce, subalpine fir, and <50% Douglas fir. I used GIS data to quantify geographical characteristics of each stand, including stand size, the length of the perimeter of the area surveyed, and the ratio of perimeter to stand area.

In each stand I sampled 10 randomly placed 5 m radius plots. At each plot center I recorded slope and aspect, and estimated canopy cover in 10% increments using a relascope. To estimate understory cover I used a 2 m x 0.5 m cover board viewed at 5 m from plot center and estimated the percentage of the board obstructed by vegetation. To account for the high variation in understory cover, I recorded the average horizontal cover at true north, 120°, and 240°. To determine tree densities, I counted all trees and shrubs standing >1 m tall within the 5 m plot, and converted to trees/ha. Size classes were: saplings (0 - 10.2 cm); medium trees (10.3 - 27.9 cm); or large trees (>27.9 cm). I averaged all variables for the 10 plots to obtain values for each stand.

Landscape Scale Selection

When the appropriate landscape scale at which animals relate to their environment is unknown, exploring multiple scales can be an effective technique (Naugle et al. 1999, Fuehlendorf et al. 2002, Martin and McComb 2003). I selected three landscape scales for study: Perimeter, 300 m, and 600 m. The Perimeter scale examined the stands immediately adjacent to the focal stand, or the habitats available to a hare should it decide to leave the focal patch. The 300 m scale represented habitats available to hares on a daily basis, as 300 m is approximately the diameter of an average hare's home range (Hodges 1999, de Bellefuille et a. 2001, Griffin 2003), and is within the maximum distance hares will move in an hour (Chapter 3). The 600 m scale represented habitats available to a dispersing hare (Gillis and Krebs 1999, Griffin 2003).

Landscape-level Variables

At the landscape scale I quantified the amount of Boreal Forest, Dry Forest, Natural Openings, Recent Burns, and Open-structured habitat within each scale using GIS data (Table 2.1). For the perimeter scale, I quantified the percentage of the perimeter that was bordered by each stand type. I drew buffers at 300 m and 600 m around the perimeter of each focal stand, and calculated the proportion of the buffer area characterized by each variable.

a priori Model Selection and Evaluation

Because I wanted to evaluate the relative importance of landcape-level attributes, I examined models that included stand-level variables, landscape-level variables, or a combination of stand- and landscape-level variables. Stand-level variables included understory cover, canopy cover, stand size, and vegetation type, or attributes that often correlate with snowshoe hare density (reviewed in Hodges 2000a,b). Landscape-level variables included Open Forest and Boreal Forest at all three scales. I considered models at each scale separately, and also combined the stand-scale variables with variables from each of the three landscape scales. The global model included stand-level and landscape-level variables from all three scales.

Because the number of stands surveyed was small relative to the number of parameters in most models (i.e. n/K<40), I used Akaike's Information Criterion corrected for small sample size (AIC_c) for model selection (Burnham and Anderson 2002). I calculated Akaike weights (w_i) to determine the weight of evidence in favor of each model.

Univariate and *Post hoc* Model Evaluation

Results from *a priori* model evaluation showed that the global model, which contained spatially autocorrelated variables (e.g. boreal forest at the three landscape scales), best fit the data. This model contained 10 variables, was biologically difficult to interpret, and had poor fit (R^2=0.46). In situations in which the global model has relatively poor fit, Burnham and Anderson (2002) suggest that further consideration of the data may be warranted. Therefore, I performed *post hoc* data explorations to identify other stand- or landscape-scale variables that were better predictors of hare density. I performed univariate regressions of all stand and landscape variables against log-transformed pellet density (Table 2.3). Several of the stand-level variables I used in the *a priori* models (e.g. stand area and canopy cover) were poor predictors of pellet density, and were highly correlated with one another (Table 2.4). Two variables not included in the *a priori* models, sapling and medium-sized tree density, were the strongest stand-level variables. The *post hoc* models followed the same form as the *a priori* models. However, I replaced the original stand-level variables with tree density variables, as those were more predictive, and although they were correlated they were not redundant.

RESULTS

Mean pellet density across 78 surveyed stands was 2.15 pellets/plot/stand (SE=0.24), with a range of 0.04 to 13.8 pellets/plot/stand (Figure 2.2). Using Equation 1 to estimate hare density from mean pellets, I observed a mean of 0.89 hares/ha (SE=0.09), and hare density estimates ranged from 0.03 to 4.85 hares/ha.

Two stands had extraordinarily high pellet densities (6.7 and 13.8 pellets/plot). These stands are unrepresentative of the stands surveyed, as they are remnant patches of habitat within a 1200 ha area that burned in 1994. Although these two stands had similar stand-level characteristics as others surveyed (6.5 ha and 9.0 ha, boreal forest, dense understory and canopy), they were very different at the landscape scales than the rest of the sample population. The matrix surrounding these two stands was much more open than any of the other stands surveyed, with >94% Recent Burn at the 300 m scale and >85% Recent Burn at the 600 m scale. I believe that the high degree of isolation of these two stands in a recently fragmented landscape may have caused a crowding effect leading to higher densities (Darveau et al. 1995, Hagan et al. 1996). Thus, I treated these two stands as outliers and removed them from analyses. Doing so did not change the relative ranking of *a priori* or *post hoc* models, but it improved model fit for models including landscape variables by as much as 10%. Upon removal of the two outliers, the mean pellet density per stand was 1.93 (SE=0.19) pellets/plot, or 0.82 (SE=0.07) hares/ha.

a priori Model Evaluation

The global model, which contained variables from all four spatial scales, was the best model considered, with an AIC_c value >5 points separating it from the next best model (Table 2.1). The Akaike weight of 0.84 indicated substantially more support for this model than for the other competing models. Even though the global model contained 10 variables, it explained less than half of the variation in the data (R^2=0.46). In addition, the global model is difficult to interpret biologically, as several variables are spatially nested (e.g. boreal forest at 300 m and 600 m). Therefore, I explored the data further to develop a more explanatory model that contained fewer variables and had clearer biological interpretation.

Stand-scale Variables: Relationships with Pellet Density

Results from univariate regressions showed that snowshoe hare pellet density exhibited significant positive correlations with understory cover (Table 2.2; $R^2=0.14$, $p<0.01$), sapling density ($R^2=0.24$, $p<0.01$), and medium tree density ($R^2=0.22$, $p<0.01$). Boreal Forest stands had significantly higher pellet densities than did dry forest stands (2.14 vs. 0.94 pellets/plot, $F_{1,74}= 6.27$, $p=0.01$).

Landscape-scale Variables: Relationships with Pellet Density

No perimeter-scale variables explained a significant amount of the variation in pellet densities. Dry forest was the only perimeter-scale variable that correlated with pellet density (Table 2.2; $R^2=0.05$, $p=0.06$). Several variables were significant predictors of pellet densities at the 300 m scale. Boreal forest was significantly positively correlated with pellet density ($R^2=0.18$, $p<0.01$). Conversely, dry forest exhibited a strong negative correlation ($R^2=0.17$, $p<0.01$). The amount of open forest was negatively correlated, although this relationship was not statistically significant ($R^2=0.04$, $p=0.07$). At the 600 m scale, the amount of boreal forest was a significant predictor, and it had a positive correlation with pellet densities ($R^2=0.08$, $p=0.01$). The amount of dry forest within 600 m of the focal stand was also significantly negatively related to pellet density ($R^2=0.05$, $p=0.05$).

Multi-scale *post hoc* models

The best model in the *post hoc* analysis included variables at the stand and 300 m scales (Table 2.5). This model was clearly the best, with more than five AIC_c values separating it from the second best model and with an Akaike weight of 0.90. The model showed a positive correlation between pellet density and sapling and medium-sized tree density and boreal forest at the 300 m scale, and a negative correlation with open forest at 300 m. This multi-scale model was 5.5 AIC_c values higher than the best single-scale model, which included sapling density and medium-sized tree density. The nested structure of these two models shows that the addition of the landscape variables increased model fit by 10.0% (R^2=0.42 vs. 0.32).

DISCUSSION

Matrix Effects

My results confirm the prediction that stands of suitable hare habitat support higher estimated hare densities when surrounded by a higher quality matrix. Although many researchers have hypothesized that snowshoe hare densities are suppressed in areas in which fragmentation causes an abundance of open-structured habitat in the matrix (Dolbeer and Clark 1975, Woolf 1980, Hodges 2000b), this study is among the first to articulate the extent to which matrix characteristics affect snowshoe hare densities. Matrix quality is an important factor that should be considered when studying snowshoe hare population dynamics and when managing for snowshoe hare densities.

Both stand- and landscape-level characteristics are important determinants of snowshoe hare densities. This claim is supported by the fact the *post hoc* model containing both stand and landscape variables at the 300 m scale performed far better than any other models explaining snowshoe hare pellet densities. Stand-level variables were retained in all of the top models, and the model containing only stand-level variables explained 32% of the variation in pellet densities. However, the addition of landscape-level variables at the 300 m scale substantially improved model fit, and explained an extra 10% of the variation in pellet densities. This amount of explanatory power for landscape variables is consistent with two other studies that have used multi-scale models to evaluate snowshoe hare densities in Montana (Shick 2003) and northeastern Washington (Thomas et al. 1997).

The relative influence of matrix quality on snowshoe hare densities may reflect the amount the matrix is used. Radio-telemetry studies on snowshoe hares have shown that their day-to-day activities of eating, resting, and rearing young occur at relatively small scales, within core areas generally <10 ha (Ferron and Ouellett 1992, Hodges 1999, Griffin 2003). Additonally, hares rarely travel >200 m away from their core area in a night and use open-structured matrix habitats approximately 25% of the time or less, preferring to spend the majority of their daily lives in the densest of habitat types (Chapter 3). Dispersal and mate-finding movements occur at larger scales than daily activities (hundreds to thousands of meters; Gillis and Krebs 1999, Griffin 2003), and necessitate the use of matrix habitats in heterogeneous landscapes, but these movements occur less frequently than daily movements.

Matrix quality may affect snowshoe hare densities by a number of mechanisms. Research on other vertebrate populations have shown that matrix quality can affect functional connectivity, or ability of animals to move across the landscape (With et al. 1999, Ricketts 2001, Goodwin and Fahrig 2002), the abundance of supplemental or alternative resources (Dunning et al. 1992, Norton et al. 2000), and the spatial structuring of populations, all of which can have effects on population densities. This study documents an effect of matrix quality on hare densities, but does not address the mechanisms by which matrix quality does so (but see Chapter 3).

Multi-scale Habitat Associations

At the stand scale, the density of saplings and medium-sized trees were the best predictors of snowshoe hare density. Many other studies have shown understory cover to be the best stand-level variable (reviewed in Hodges 2000a,b). A possible explanation for this disparity is that I surveyed stands throughout the growing season (early May-early September), during which time foliage from deciduous species (*Alnus spp.* and *Salix spp.*) changed understory cover dramatically; stem densities were constant through time and were also less subjective to measure in the field. Using sapling and medium-sized tree density as the stand-level variables instead considerably improved the fit and clarity of *post hoc* models.

Other stand-level variables that have been correlated with snowshoe hare density and habitat use in other studies were not important in this study area. I included canopy cover in the *a priori* models because other studies have shown a relationship between canopy cover and understory cover, and thus hare density (Orr and Dodds 1982, Parker et al. 1983, Rogowitz 1988). However, I did not find such a relationship. In my study area the densest understory and sapling densities were found in stands in which canopy closure was moderate (30-50%) and Engelmann spruce and subalpine fir dominated the canopy. These species have tapered crowns, which provides gaps in the canopy that promote the growth of saplings in the understory.

I also did not find a relationship between patch size and snowshoe hare pellet density, despite such findings from other studies on snowshoe hares (Keith et al. 1993, Thomas et al. 1997), other leporid species (Barbour and Litvaitis 1993, Forys and

Humphrey 1996), and other wildlife species (reviewed in Connor et al. 2000). Brotons et al. (2003) suggest that for high quality matrices, patch size may not be as important to density as it is in low quality matrices. In an area where patches of dense forest were surrounded by very poor quality matrix (i.e. recently burned forest with little regeneration), I observed nearly twice the pellet density in a 9.5 ha patch of dense forest as I did in a nearby 6.5 ha stand, despite the fact that the smaller stand had higher stem densities. This observation is weak evidence, though, and the overall lack of correlation between hare density and patch size in the rest of the study area suggests that hares in this landscape existed in moderate to good matrix quality.

At the landscape scale, the most explanatory landscape variables were those that measured the amount of boreal forest (or conversely, dry forest) and the amount of open-structured forest. The mechanisms by which these factors affect snowshoe hare densities are unknown. Boreal forest (i.e. subalpine fir/Engelmann spruce forest) usually supports greater sapling densities and low-hanging branches that provide lateral cover (Agee 2000) than the drier forest types. Thus boreal forest stands in general may improve matrix quality by providing supplemental or alternative habitats and easier habitats to move through. Boreal forest is not beneficial, however, if disturbance events decrease the structural density and turn it into Open-structured habitat. Open-structured forest presumably presents the greatest resistance to inter-patch movement by snowshoe hares of any matrix habitat type (Wirsing et al. 2002, Griffin 2003), although this hypothesis has not been formally tested. Food and shelter resources in open-structured habitats are low, especially in winter when ground-level vegetation is covered with snow, making these habitats unlikely to provide supplemental resources for hares.

My results suggest that matrix quality should be considered at the 300 m scale. I found strong relationships between pellet densities and variables at all three landscape scales, and other studies have shown relationships between snowshoe hare pellet densities and landscape variables at 100 m, 600 m, and 1000 m (Thomas et al. 1997, Shick 2993). However, the model evaluation process showed that the 300 m scale was the most appropriate scale that I considered. The 300 m scale is tied to hare movement information, as it is approximately the diameter of an average home range (Hodges 1999, de Bellefuille et al. 2001, Griffin 2003) and the larger distances a hare moves in an hour (Chapter Three). Thus the 300 m scale represents the habitat available to hares on a daily basis. Additional studies should explore the 300 m scale with other scales, and also examine the mechanisms by which matrix quality at the 300 m scale affects snowshoe hare densities.

Model Scope and Accuracy

The stands I surveyed represented possible snowshoe hare habitat, but were not representative of the full spectrum of habitat types on the landscape in which I worked. I did not survey recent cuts, burns, natural openings, or obviously thin dry forest that would generally not be considered good snowshoe hare habitat. Thus the accuracy of my models should be evaluated in terms of their ability to predict pellet abundance in the patches of moderately to very dense forest.

The best-fitting *post hoc* model is limited in its ability to accurately predict snowshoe hare density. The top model was able to explain 40% of the variation in the pellet density data, and the global model (which contained 4 additional parameters), explained just 51% of the variation. There are several possible sources of error that could have resulted in the high amount of residual variation. Inaccuracies in GIS data, the omission of other important variables or spatial scales, and observation error could all explain some amount of residual variation. However, the largest source of error probably comes from the discrepancies inherent in using pellets as an index of snowshoe hare density, where both defecation and decomposition may differ across habitat types. Mills et al. (2005) found the discrepancy between pellet index and mark-recapture estimates of hare densities varied across hare densities. Between 0.6 and 1.6 mean pellets/plot (0.3-0.7 hares/ha), Mills et al. (2005) recommend mark-recapture estimation as opposed to pellet counts to distinguish between relatively subtle differences in hare abundance. When I removed all stands that had estimated densities within this range (n= 26) and then re-fit the data using the variables from the best overall model, the fit improved remarkably (R^2= 0.57 vs. 0.40) despite the substantially lowered sample size; thus, the models do better when predicting very low or very high hare densities.

The models should be used cautiously in terms of predictive purposes, as they have not been cross-validated in other study areas and thus their robustness is not known. For example, to support similar hare densities, Griffin (2003) and Shick (2003) found a need for much higher sapling densities in the Seeley Lake area of Montana than I found in northern Washington. Another caution is in interpreting my finding that medium-sized trees were positively correlated with hare densities. In my study area, most medium-sized trees were spruces and firs, which generally have low-hanging branches that can provide understory cover for hares. Shick (2003) found the opposite relationship between medium-sized tree density and pellet densities in forests dominated by lodgepole pine, which typically has substantial crown lift and therefore would not provide horizontal cover or browse for hares. Therefore, in interpreting the results from this and other similar studies, it is important to remember that for individual variables, the scope of inference is limited to particular study areas rather than broadly applicable.

To strengthen the models, plus our overall understanding of the effects of matrix quality, I encourage a meta-analysis across multiple fragmented forests in the southwestern part of snowshoe hare range (i.e. Cascades, Rockies, and associated mountain ranges of WA, MT, ID, WY, CO, etc.). Refinement of GIS coverages to include consistent data on structural composition of forest stands across the intermountain west is necessary for such an analysis to be possible. I also encourage additional research into the mechanisms by which landscape structure affects snowshoe hare populations.

MANAGEMENT IMPLICATIONS

Some of my results can provide such suggestions for my particular study area, and general concepts can be applied elsewhere. However, several aspects of this study highlight the difficulty in providing such information across a large region, and stress the importance of local knowledge of a system.

Stand-level factors are the most important factors influencing snowshoe hare densities, and it should not be assumed that just concentrating on matrix quality will suffice. The relationship between vegetative density and hare density is indisputable across the range of snowshoe hares, despite substantial variation in the vegetation measurement schemes used. At the stand scale, management activities that decrease vegetation structure from 0-3 m above ground-level should be conducted with caution, as hare densities are tied to vegetation density.

Beyond the stand scale, managers should think about trying to improve matrix quality. From this study, I would recommend trying to maintain as much boreal (spruce-fir) forest as possible, and selecting against projects that create large expanses of open habitat. These recommendations echo those in the Lynx Conservation Assessment and Strategy (LCAS; Ruediger et al. 2000), which require that no more than 30% of the area within a lynx analysis unit (LAU; ~6,500-10,000 ha) can be unsuitable lynx habitat (i.e. open, or unsuitable snowshoe hare habitat). The LCAS guidelines do not address the spatial juxtaposition of habitats, but I recommend that management strategies consider the size and shape of human-caused disturbances, such as harvests and thinning units. Matrix quality may be decreased by creating large blocks of disturbance areas that increase the amount of open habitat. Instead, small patches of open habitat set amongst dense forest patches may allow for greater landscape connectivity between patches, not only for hares but also for lynx. If matrix quality is relatively good, and hares are more likely to use the matrix, then increasing matrix quality may also provide for more foraging opportunities for predators. Poor matrix quality may create remnant patches with very high hare densities, as I observed for the two patches of habitat that were set within a recent large-scale fire (e.g. the outlier stands in this study). Such a landscape design results in a high variance in hare densities at a larger landscape scale, whereas increasing matrix quality likely decreases the landscape-wide variance in hare density and increases overall abundance.

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Table 2.1. Description of local and landscape variables used to explain snowshoe hare pellet densities from 76 stands in northern Washington. Acronyms in text are shown in parentheses.

Stand-level variables quantified within focal stands
Stand size (AREA)
Canopy cover (CAN)
Understory cover (UND)
Sapling density (SAPS)
Medium-sized tree density (MED)
Large tree density (LRG)
Vegetation type (VEG)
Slope (SLOPE)
Aspect (ASP)
Perimeter (PER)
Edge:Area ratio (EA)
Landscape attributes quantified around the Perimeter and within 300 m and 600 m buffers
Boreal forest (BOR)
Dry forest (DRY)
Recently burned (BURN)
Natural openings (NATOP)
Open-structured habitat (OPEN)

Table 2.2. *A priori* models developed to explain snowshoe hare pellet data from 76 stands in northern Washington. Stand-level variables included: UND, CAN, AREA, VEG; landscape-level variables at each scale included: BOR and OPEN (Table 1). Values reported represent number of model parameters (K), AIC_c scores, AIC_c differences (Δ_i), Akaike weights, and model fit (R^2).

Model	K	AIC_c	Δ_i	w_i	R^2
global (stand + perimeter + 300 m + 600 m)	12	3.66	0.00	0.42	0.43
stand	6	4.30	0.63	0.30	0.30
stand + 300 m	8	5.67	2.00	0.15	0.32
stand + perimeter	8	7.22	3.56	0.07	0.31
stand + 600 m	8	8.73	5.06	0.03	0.19
300 m	4	9.79	6.13	0.01	0.09
600 m	4	18.96	15.29	<0.01	0.09
perimeter	4	24.96	21.29	<0.01	0.01

Table 2.3. Relationships between stand- and landscape- level variables and snowshoe hare pellet data from 76 stands in northern Washington, listed from the strongest to weakest predictors of pellet density. Values represent univariate model fit (R^2), p-value, and standardized coefficients.

Scale	**Variable**	**R^2**	**p**	**Coeff**
Stand-level	SAPS[a]	0.24	<0.01	0.49
	MED[a]	0.22	<0.01	0.47
	VEG[b]	0.21	<0.01	0.45
	HOR[b]	0.14	<0.01	0.37
	PER	0.03	0.12	-0.18
	CAN	0.03	0.13	0.18
	EA	0.02	0.27	-0.13
	ASP	<0.01	0.62	-0.06
	AREA[b]	<0.01	0.79	-0.03
	LRG	<0.01	0.94	-0.01
	SLOPE	<0.01	0.94	0.01
Perimeter	OPEN[a,b]	0.05	0.06	0.22
	BURN	0.02	0.28	0.13
	BOR[a,b]	0.01	0.40	-0.10
	NATOP	0.01	0.50	-0.08
300 m	BOR[a,b]	0.18	<0.01	0.43
	DRY	0.17	<0.01	-0.39
	OPEN[a,b]	0.04	0.07	0.21
	BURN	0.02	0.24	-0.14
	NATOP	<0.01	0.80	0.03
600 m	BOR[a,b]	0.08	0.01	0.29
	DRY	0.05	0.05	-0.22
	OPEN[a,b]	0.01	0.43	0.09
	BURN	0.01	0.47	-0.08
	NATOP	<0.01	0.58	-0.07

[a] variable used in *post hoc* models

[b] variable used in *a priori* models

Table 2.4. Spearman rank correlations between variables considered for post-hoc models to explain log-transformed snowshoe hare pellet densities (Pellets) in northern Washington. Abbreviations for variables are from Table 1, with scale indicated in parentheses. Underlined variables were significant at $p<0.05$.

	Pel	VEG	UND	SAPS	MED	BOR (per)	OPEN (per)	BOR (300)	OPEN (300)	BOR (600)
VEG	0.37									
UND	0.34	0.30								
SAP	0.55	0.29	0.30							
MED	0.54	0.34	0.28	0.54						
BOR (per)	-0.03	-0.25	-0.01	-0.01	-0.17					
OPEN (per)	0.12	0.22	0.33	0.22	0.03	0.07				
BOR (300)	0.29	0.47	0.08	0.13	0.44	-0.66	-0.04			
OPEN (300)	-0.01	0.16	0.15	0.06	0.01	0.10	0.59	-0.11		
BOR (600)	0.22	0.42	0.10	0.13	0.32	-0.44	0.08	0.82	-0.15	
OPEN (600)	0.10	0.17	0.11	0.11	0.09	-0.21	0.13	0.15	0.06	0.19

Table 2.5. *Post hoc* models describing snowshoe hare pellet density data from 76 forest stands in northern Washington. Values reported represent number of model parameters (K), AIC_c scores and differences (Δ_i), Akaike weights, and model fit (R^2) for the 8 *post-hoc* models. Variables included sapling and medium-sized tree density at the stand scale; boreal forest and open forest around the perimeter; boreal forest, open forest, and degree of heterogeneity at 300 m and 600 m.

Model	K	AICc	Δ_i	w_i	R^2
stand + 300 m	6	-8.72	0.00	0.90	0.42
Stand	4	-3.21	5.52	0.06	0.32
stand + 600 m	6	-1.86	6.87	0.03	0.35
global (stand + perimeter + 300 m + 600 m)	10	0.02	8.74	0.01	0.32
stand + perimeter	6	1.32	10.05	0.01	0.51
300 m	4	9.79	18.52	<0.01	0.18
600 m	4	18.96	27.68	<0.01	0.09
Perimeter	4	24.96	33.68	<0.01	0.01

Figure 2.1. Forest stands surveyed (n=78) for snowshoe hare abundance in the Okanogan National Forest in northern Washington, 2003-2004.

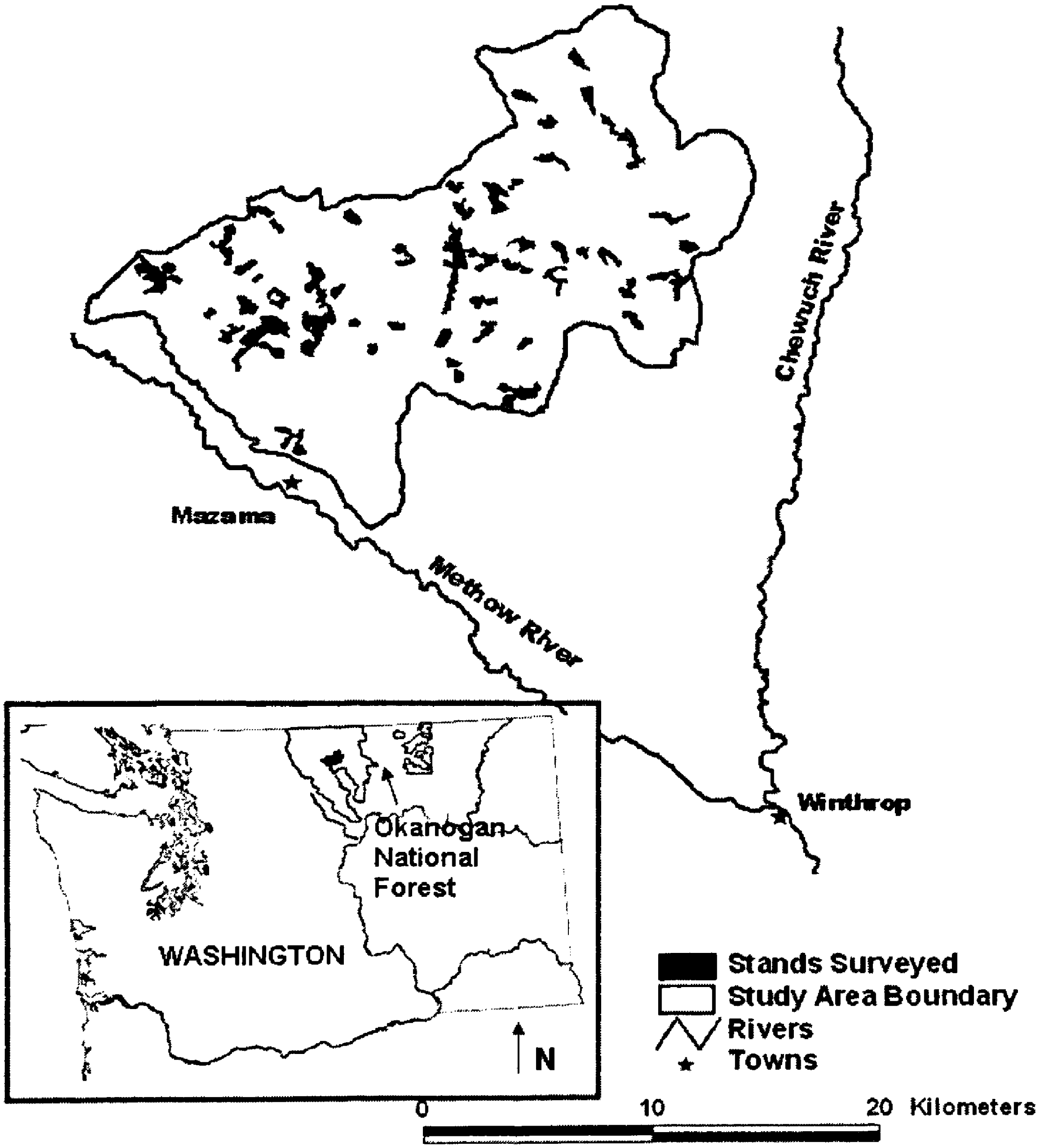
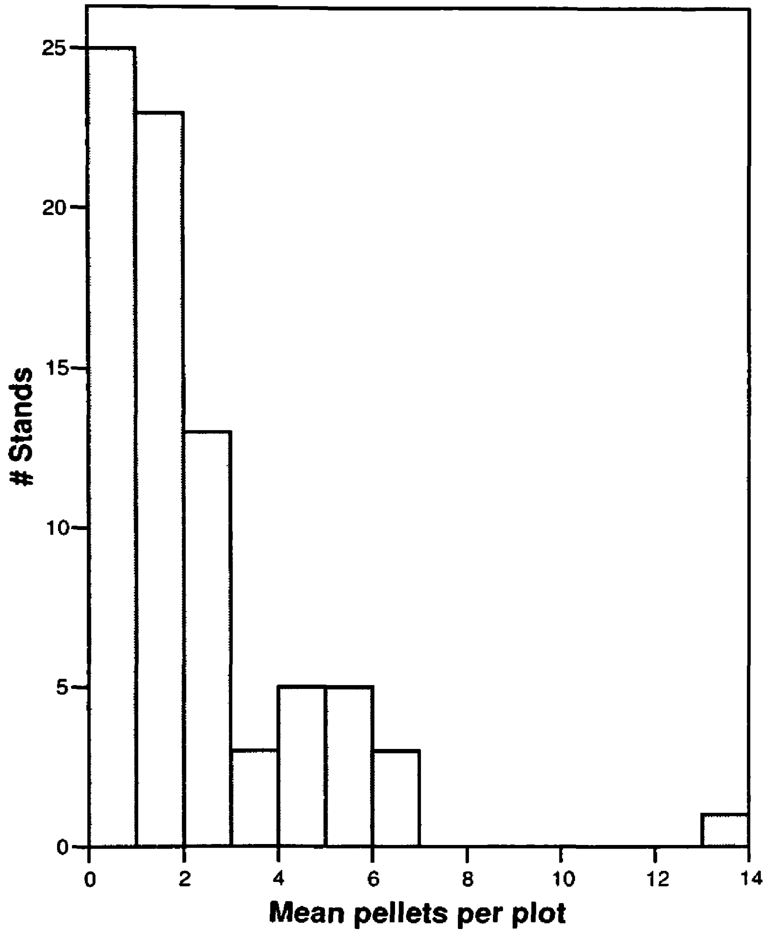


Figure 2.2. Mean number of snowshoe hare pellets from 50 plots within each of 78 stands surveyed in the Okanogan National Forest, WA, 2003-2004.



Chapter III:
EFFECTS OF LANDSCAPE STRUCTURE ON SNOWSHOE HARE MOVEMENT AND HABITAT USE

ABSTRACT

In spite of the importance assumed for inter-patch dynamics for wildlife species in fragmented systems, we know very little about the real nature of how individuals respond to characteristics of the matrix. Matrix quality can increase population densities by influencing movement characteristics and by influencing resource availability. Forest fragmentation in the western United States results in a heterogeneous mosaic of land cover types, in which patches of preferred habitat are set amongst a matrix of less-suitable habitat types. Scientists have hypothesized for decades that snowshoe hare populations are affected by forest fragmentation, especially by the abundance of presumably poor matrix habitats. In this study I proposed two hypotheses for how matrix quality affects snowshoe hare populations: by influencing movement characteristics, and by influencing resource availability. To test for support for either of these hypotheses, I followed radio-collared snowshoe hares in their travels through landscapes with varying degrees of matrix quality. I found that functional connectivity was highest for snowshoe hares in landscapes with the highest matrix quality and the highest proportion of suitable habitat patches (Continuous), and was lowest for hares in landscapes in which suitable habitat was sparse and surrounded by poor quality matrix habitats (Isolated). Snowshoe hares in Continuous landscapes used matrix habitats most frequently, had the highest propensity for using multiple stands, and were most evenly distributed across the landscape. Results from this study suggest that matrix quality affects both the functional connectivity and the availability of supplemental resources, both of which could affect snowshoe hare densities in heterogeneous forests.

INTRODUCTION

Spatially explicit population models can be used to predict population dynamics given potential changes in landscape structure, and thus can be important tools for developing land management strategies (Hanski and Gilpin 1997, Fall and Fall 2001). Such models typically assume a binomial landscape in which patches of preferred habitat are set amongst a matrix of non-habitat (Hanksi 1998), in which individuals may disperse through the matrix at specified rates and probabilities, but are not allowed to use the matrix for other purposes. In many terrestrial systems, however, patches of preferred habitat are surrounded by a complex mosaic of other habitat types that vary in their permeability and resource availability (Wiens et al. 1997, Ricketts 2001). Because in reality animals may use matrix habitats for more than inter-patch movement, population models that assume a homogenous non-habitat matrix may dramatically oversimplify population dynamics (see review by Turchin 1991). In spite of the huge importance assigned to inter-patch dynamics in fragmented systems, we know very little about how different species respond to different matrix characteristics (Wiens 1997). Therefore studies that address how matrix characteristics affect wildlife species are needed for understanding population dynamics in fragmented systems and to improve the abilities of spatially explicit population models to guide natural resource managers in making land-use decisions.

Recent research has documented substantial effects of matrix quality on population persistence (Moilanen and Hanski 1998, Fahrig 2001, Vandermeer and Carvajal 2001) and on the density of species within patches of preferred habitat (Brotons et al. 2003). For individuals that simply use the matrix for inter-patch movement, the permeability of the matrix can affect population dynamics (Moilanen and Hanski 1998; Pither and Taylor 1998) by affecting 'functional connectivity,' or the ability of individuals to cross a landscape (With et al. 1999, Ricketts 2001, Goodwin and Fahrig 2002). For animals that use the matrix for more intensive purposes than just inter-patch movement, some matrix types may provide alternative habitats (Norton et al. 2000) or supplemental resources (Dunning et al. 1992). Landscapes dominated by these matrix types may influence population dynamics by increasing the carrying capacity of patches of preferred habitat and by affecting the distribution of individuals across the landscape (Brotons et al. 2003). At the highest levels of intensity, animals may use matrix habitats for mating and reproduction, though matrix habitats may be population sinks (e.g. Griffin 2003).

The forests of the western United States are heavily fragmented by fire, timber harvest, roads, and development. The increasing fragmentation is thought to affect many wildlife species, including the federally threatened Canada lynx (*Lynx canadensis*; Buskirk et al. 2000). Because snowshoe hares (*Lepus americanus*) are the primary prey species for lynx, management strategies for lynx call for managing forests to obtain high snowshoe hare densities (Reudiger et al. 2000). Understanding the effects of fragmentation on snowshoe hares and the causes of those effects is therefore important for guiding forest management strategies in much of the western United States.

For snowshoe hares in the heterogeneous landscapes of the western United States, matrix composition and inter-patch movements are thought to be fundamental drivers of population dynamics (Dolbeer and Clark 1975, Wolff 1980, Sievert and Keith 1985). Hare densities, population growth, survival, and population growth are highest in densely forested stands (Wolff 1980; Orr and Dodds 1982; Parker 1984, 1986; Thompson et al. 1989; Hik 1994). Because snowshoe hares rely upon understory structure for forage and protection from predators, densely forested stands with thick understory components are the preferred habitat type for hares. In fragmented forests, patches of preferred habitat are set amongst mosaic of other habitat types. Hare densities, survival, and use are lowest in open-structured habitats, such as recent clear cuts, natural meadows, and recently burned forests (O'Donoghue 1983, Sievert and Keith 1985, Hik 1994, Ferron et al. 1998). Therefore open-structured matrix habitats are considered poor habitat for snowshoe hares. Moderately dense forest stands are used more than open-structured stands and may support moderate hare densities (Thompson et al. 1989, Koehler 1990a,b). However, these stands may be population sinks (Griffin 2003), thus moderately dense stands (e.g. south-facing forest stands or recently thinned stands) are considered intermediate matrix habitats. Landscapes in which hares reside vary in their spatial structure, from those in which preferred habitat is abundant and surrounded by intermediate matrix habitats, to those in which preferred habitat is scarce and set amongst a matrix of poor habitat types.

Snowshoe hare densities in patches of preferred habitat can be affected by the quality of the matrix surrounding such patches (Chapter 2), with lower densities where preferred habitat is set amongst a matrix of more open-structured habitats. In addition to affecting hare densities, the matrix may also have other effects on snowshoe hare populations. In this chapter I investigate the relationships between matrix quality and (1) the functional connectivity of hares in the landscape, and (2) the spatial distribution of hares across the landscape, as evidenced by habitat use. I used three different landscape types for comparison. ‘Continuous’ landscapes had a high proportion of preferred habitat patches, and these were set amongst a matrix that contained relatively little open-structured habitat. ‘Isolated’ landscapes had a small proportion of preferred habitat set amongst a matrix of mostly open-structured habitat. ‘Moderate’ landscapes had more of a balance between habitat types in the matrix.

Functional connectivity refers to the ability of an individual to cross a landscape (With et al. 1999, Goodwin and Fahrig 2002). Functional connectivity relies on the interaction of two components: patch boundary permeability (i.e. hard or soft edges; Stamps et al. 1987, Wiens et al. 1997, Schtickzelle and Baguette 2004), and matrix viscosity, or the degree to which a given component of the landscape allows the crossing of individuals (With 1994, Wiens et al. 1997). I examined patch boundary permeability by quantifying how readily hares use multiple habitat patches. I also compared movement rates and nightly displacement for hares in the different landscapes. If functional connectivity was related to the amount of poor matrix habitat, I would expect to see a lower propensity to use multiple stands for hares in the Isolated landscapes, and I would expect to see differences in movements between the three landscape types.

I also compared the habitat use of hares in the different landscapes. In patchy landscapes, habitat use can affect the spatial distribution of individuals. In the Isolated landscapes in which matrix quality was poor, I expected hares to use the isolated patches of preferred habitat proportionately more than did hares in the Continuous landscapes in which the matrix could provide supplemental or alternative resources.

METHODS

Study Area

Field research was conducted in the Okanogan National Forest in north-central Washington (48°N, 120°W) in May thru September of 2003 and 2004, and also in December 2003 and January 2004. Two main vegetation types occur within the study area. Dry montane forest stands containing Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) dominate the lower elevations (<1066 m), and are also found at higher elevations on south-facing slopes and in wide drainage bottoms. Moist boreal forest stands, containing a mix of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and Douglas fir, exist mostly on north-facing slopes and steeper drainage bottoms. Natural meadows and rocky slopes, natural and prescribed fires, and timber harvest units create a mosaic of different habitat types in the area. Elevations in the area ranged from 643-2134 m.

Site Selection and Mapping

I used geographic information system (GIS) coverages for the study area that were created by Maletzke (2004) from digitized aerial photographs and ground-truthed data. I used the GIS to identify three habitat types in terms of their relative habitat quality for snowshoe hares: preferred, intermediate, and poor habitat. Preferred habitat had ≥40% understory cover, and represented habitat types in which snowshoe hares have the highest densities and the highest survival rates (reviewed in Hodges 2000b, Griffin 2003). Intermediate habitats were stands in the matrix with a moderate understory cover, 11-39%; lower understory resulted from natural characteristics of the stand (e.g. south-facing Douglas fir stand) or from timber harvests or pre-commercial thinning. Such stands can support moderate hare densities, but may be sink habitats (Griffin 2003). Poor habitat stands had ≤10% understory cover, and consisted of subalpine meadows and recent burns or timber harvests with little regeneration. Such stands usually support no hares or very low densities and are thought to present the greatest predation risk to hares (Litvaitis et al. 1985a, Ferron and Ouellet 1992, deBellefuille et al. 2001).

From within the set of suitable habitat stands, I selected nine focal stands for intensive study. Focal stands had similar stand-level characteristics: high sapling density (>2200 trees/ha), dense understory cover (>40%), and closed canopy cover (>30%), as described in Chapter 2. Additionally, stands were 6.5 to 18.0 ha, large enough to encompass a hare's home range (Hodges 1999, de Bellefuille et al. 2001, Griffin 2003), but small enough for a hare to be able to leave in an hour or less (maximum distance to edge= 240 m).

Each focal stand was set within one of three different landscape types— Continuous, Moderate, or Isolated— referring to the amount of poor quality matrix within 300 m of the patch. I used the GIS data to quantify the amount of poor habitat within a 300 m buffer around the perimeter of the each focal patch. I chose the 300 m scale because that is the diameter of an average home range for hares in patchy landscapes (8 ha; deBellefuille et al. 2001, Griffin 2003). Continuous, Moderate, and Isolated landscapes had <25%, 40-60%, and >90% poor habitat within 300 m of the focal stand. Focal stands were all of the preferred habitat type, but matrix habitats surrounding the focal stand were a mix of other suitable stands as well as both intermediate and poor habitat types (Figure 3.1). By selecting focal stands that had similar within-stand characteristics but were surrounded by different matrix habitat types, I avoided the confounding effect of stand quality and matrix quality (Haynes and Cronin 2004).

Hare Location Data

I trapped snowshoe hares only within the nine focal stands. By doing so, I assumed that hares used the focal stand at least part of the time, and that all stands within 300 m of the focal stand were available for their use. I placed 40-50 live traps (7x7x20" single-door traps, Tomahawk Live Trap Co., Tomahawk, WI) baited with alfalfa in sheltered locations (e.g. under branches, near hare travel routes) throughout each stand. Trapping lasted three to eight nights, until at least four adult hares had been trapped. Each hare was sexed and given a monel eartag (No. 3, National Band and Tag Co., Newport, Kentucky). Adults weighing at least 900 g were fitted with 35 g radio-collars equipped with a mortality sensor (Advanced Telemetry Systems, Isanti, MN).

I used handheld receivers and H-antennae (Telonics, Mesa, AZ) to locate radio-collared hares. I used a walk-in method in which hares were approached directly until they were located visually, or until a strong signal could be heard using the receiver without the cable or antenna. Field tests indicated that this method was accurate to within 15 m (Griffin 2003, Walker unpublished data). I visually located hares 25% of the time, and thus was able to record exact locations. I recorded the time and the location using a hand-held GPS unit and noted habitat type for comparison with GIS data if a hare was near a stand edge.

Because snowshoe hares are more active at night and during crepuscular hours than during the day (Keith 1964, Foresman and Pearson 1999) and more active under the new moon than the full moon (Griffin 2003), I located hares between dusk and dawn (approximately 1900 and 0800 in summer, 1600 and 0800 in winter), avoiding the 2-3 days on either side of the full moon. I attempted to locate each hare on an hourly basis for six hours each tracking session. Because of the difficulty in obtaining locations exactly on the hour, I allowed any locations obtained between 45 and 90 minutes apart to be considered a "move" (mean= 61 minutes between locations, SE=0.3, n=643). I attempted to obtain six sampling sessions per hare within a three-week time frame. I was not always able to complete all six sessions or obtain six locations per session per hare (Table 3.2) because of issues including hare mortalities, weather, or a hare stopped being active in a given session.

Movement Characteristics

I spatially linked all hare locations to GIS layers in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA 2002). I calculated each hare's *Propensity to use multiple stands* by dividing the number of tracking sessions that a hare used multiple stands by the total number of tracking sessions. *Propensity* was not affected by number of tracking sessions (data not shown).

The straight-line distance between successive points was considered a step, and successive steps formed a movement path for each individual. I calculated all step lengths, and standardized distances to a 60-min period to calculate an hourly rate, or *Movement Rate.* For each hare I calculated distance moved within a tracking session, and standardized the distance to a 5-hour period to get *Total Distance* for each session for each hare. *Net Displacement* is the straight-line distance between start and end points for a tracking session, standardized to a 5-hour period.

Habitat Use

I calculated the proportion of locations in the focal stand, *In Focal*, for each hare. A hare in the focal stand was necessarily in preferred habitat, but a hare in preferred habitat was not necessarily in the focal stand because some matrix stands were of the preferred habitat type. Thus I calculated *In Non-Preferred Matrix* as the proportion of locations per hare that were in either the intermediate or poor matrix habitat types, but not in preferred habitat types.

Data Analysis

My goal was to compare movement rates between landscape types. So although individual hares were my sampling unit, my unit of comparison was the landscape type.

Thus my sample sizes were 3, 4, and 2 for Continuous, Moderate, and Isolated landscapes, respectively. Because of low sample sizes, finding statistically significant differences between landscape types would be difficult, and may miss important biological trends. Therefore, I do not report statistics for the variables measured (though they can be found in Appendix E).

RESULTS

I obtained 821 hourly locations for 30 hares (16 females, 14 males), along 143 movement paths. I sampled 3 moderate sites and 1 continuous site in summer 2003, 2 isolated and 1 continuous site in winter 2004, and 1 moderate and 1 continuous site in summer 2004. I found no differences between season or sex for any of the variables, thus data were pooled for analyses.

Movement Characteristics

Most hares used multiple stands. The average numbers of stands used in Continuous, Moderate, and Isolated stands were 2.5, 2.7 and 2.1, respectively. Only one hare (in an Isolated landscape) never used multiple stands. The majority of hares used two or three stands (53.3% and 36.7%), and one hare used six different stands.

The *Propensity to use multiple stands* was highest for hares in Continuous landscapes and lowest for hares in Isolated landscapes (Figure 3.2). Hares in Continuous landscapes used multiple stands an average of 62% of track-nights, whereas hares in Moderate and Isolated used multiple stands 48% and 37% of nights, respectively.

Because of low sample sizes, I was unable to analyze movement characteristics by habitat type, thus I compared mean movement characteristics between landscape types. *Movement Rates* were similar among landscape types (Figure 3.3), and ranged between 1 and 346 m/hr, with an overall mean of 53 m/hr (SE=2, n=643). *Net Displacement* was also comparable between landscape types (Figure 3.3), ranging from 5 to 737 m in five hours, with an overall mean of 113 m (SE=9, n=143). *Total Distances* were also similar among landscape types (Figure 3.3), with distances moved in five hours ranging from 55 to 863 m, and an overall mean of 259 m (SE=12, n=143).

Habitat Use

Hares in all landscape types spent a disproportionately greater amount of time in dense forest than in more open habitat types. Of the 821 total locations obtained for hares, 71.0% were in patches of dense forest (focal stands and preferred matrix habitats), 25.7% in intermediate matrix habitat, and 3.3% in poor matrix habitat. Five of the 30 hares were located in poor matrix habitats at least once—four hares in the Isolated landscape, and one in a Moderate landscape.

The proportion of locations *In Focal* stands was highest for hares in Isolated landscapes (Figure 3.4), indicating that activity was restricted to focal patches more than it was for hares in Moderate and Continuous landscapes. In Moderate and Continuous landscapes, which had a higher proportion of intermediate habitat, the proportion of locations *In Non-Preferred Matrix* were only slightly higher than in Isolated landscapes (Figure 3.4).

DISCUSSION

My results show that landscape structure may affect snowshoe hare populations to some degree, by affecting the functional connectivity and spatial structuring of populations. Hares preferentially used patches of forest with dense understory structure, but they were fairly adept at moving through matrix habitats, even when matrix quality was poor.

My data were not conclusive as to whether landscapes with an abundance of open-structured habitat in the matrix had lower functional connectivity than did landscapes with fairly continuous dense forest. Because of low sample sizes and the nested nature of the data, my power to detect statistically significant differences between landscape types was low. Although some of the data showed trends, I am unable to draw many definite conclusions, and thus must discuss multiple possible alternatives.

Functional connectivity may have been lowest for hares in Isolated landscapes. One of the two components of functional connectivity, patch boundary permeability, may have been lower for hares in Isolated landscapes than for hares in Moderate and Continuous landscapes, as evidenced by the lower propensity to use multiple stands and the higher proportion of locations within the focal patch. If hares are less likely to cross patch boundaries and to move between patches, then the overall connectivity of the population may be decreased. However, because hares in Isolated landscapes still used multiple stands an average of 37% of nights, there may be more functional connectivity than would be expected based on the structure of the landscape.

The other component of functional connectivity, matrix viscosity, did not seem to be affected by landscape type, as I did not observe any differences between landscape type and movement rates or distances traveled by hares. Because I was not able to separate movements by habitat type, I am unable to quantify viscosity by habitat type. Anecdotally, hares' movement rates and displacements varied within dense forest stands, but were often slow and tortuous. In contrast, hares that moved through open-structured habitat did so very rapidly, moving 90, 310, and 400 m in less than an hour. Individuals in the Isolated landscapes almost always crossed the open matrix in less than an hour, moving quickly and in a straight line across the open areas. Such movements that are straight and fast are characteristic of animals moving through landscapes while dispersing, while searching for food or mates, or moving through an area of actual or perceived risk (Zollner and Lima 1999).

Hares' habitat use affected their spatial distribution across the landscape. My results suggested that snowshoe hares in areas with a higher quality matrix (e.g. Continuous landscapes) were located more frequently outside of the focal stand and in matrix habitats, whereas hares in poorer quality matrix areas (e.g. Isolated landscapes) were restricted to patches of suitable habitat.

By affecting population connectivity and the availability of resources, landscape structure may influence snowshoe hare populations. In the Isolated landscapes, the matrix was used mostly for movement, and hares spent very little time in the poor habitats. Hares avoided using the poor matrix, perhaps because of lack of food or because of the threat (actual or perceived) of predation. In any case, the effect was that the distribution of snowshoe hares across the landscape was much more clumped in the Isolated landscapes than in the Moderate or Continuous landscapes. The clumped distribution of hares and the use of matrix for quick inter-patch movements shows that Isolated landscapes resemble the landscapes of patchy population models. In such landscapes, the distance between patches and the size of patches are important factors determining population persistence (Hanski 1998) and population densities (Brotons et al. 2003). Small isolated patches, such as those in the Isolated landscapes, may be more susceptible to local extinction, which in turn can negatively affect the dynamics of the entire population (reviewed by Hanski 1998). Conversely, hares in the Moderate and Continuous landscapes were more evenly distributed across patches, and were using the matrix for more than inter-patch travel. The population dynamics in landscapes with higher quality matrices may be less affected by the explicit spatial patterning of habitat patches, such that the overall abundance of suitable habitat is most important. For example, in simulations examining the effects of matrix quality, Fahrig (2001) suggested that up to 58% less habitat could be required for population persistence if matrix is converted from poor to high quality.

Impacts of Landscape Structure on Population Dynamics

Matrix quality not only affects the spatial distribution of snowshoe hares across the landscape, but it also affects the overall abundance of hares on the landscape. Although estimated snowshoe hare densities were highest in patches of suitable habitat in the Isolated landscapes (Table 3.1), hares were relatively restricted to patches of suitable habitat. However, if we were to find an average density for the entire Isolated landscape (i.e. the focal patch plus all habitats encompassed in the 300 m buffer), we would see that <10% of the landscape was a habitat type able to support high snowshoe hare densities, while the remaining habitat was poor and supported no to very low number of hares at any point. Thus the average landscape density of hares would be low. In comparison, focal patches in the Continuous landscapes had moderately high hare densities (Table 3.1), plus hare densities were presumably comparable in the surrounding matrix. Thus the average landscape density would be as high if not higher than in the Isolated landscapes.

Showing that snowshoe hares use landscapes differently based on matrix quality contradicts one of the dominant paradigms found in the snowshoe hare literature. The Refugium model, best articulated by Wolff (1981), argues that snowshoe hares in fragmented forests are restricted to patches of preferred habitat ('refugia') until densities become too high, at which point hares are forced into the matrix where they starve or are preyed upon. This model views the matrix as an inhospitable area, with landscape structure resembling those assumed by classic metapopulation models. My data suggest, however, that the Refugium model is inconsistent with the population structure seen in moderately fragmented landscapes, in which hares frequently use the matrix. Even in the Isolated landscapes, hares successfully crossed through poor quality matrix on multiple occasions, displaying higher population connectivity than the Refugium model suggests (Dolbeer and Clark 1975, Wolff 1981).

Future Directions

Additional research studying hourly movements in landscapes of varying matrix quality would be beneficial to increase our power to detect differences in movement and habitat use. I would also encourage using experimental studies to quantify movement abilities in different matrix habitat types (e.g. Stevens et al. 2004). Once these data are obtained, researchers may develop complex, spatially explicit models for snowshoe hares in fragmented landscapes, similar to efforts by Gustafson and Gardner (1996), Moilanen and Hanski (1998), and Schultz and Crone (2001). Such models should include data on the movement capabilities and vital rates for hares in various landscape types, and could be used to examine the effects of major and minor landscape alterations on snowshoe hare population dynamics. To further our development of such models, I recommend investigations into the effects of matrix quality, especially examining larger spatial scales than I studied. I showed that hares are able to cross poor quality matrix at distances that are commonly traveled within an hour. I expect, though, that as the distance between habitat patches increases, functional connectivity will decrease, and that the effects on connectivity would be larger in areas of poorer quality matrix habitat. Further examinations along this line would not only strengthen parameter estimates for movement capabilities of hares, but would also help in identifying thresholds of landscape connectivity beyond which population density and persistence would be severely impacted.

MANAGEMENT IMPLICATIONS

Increasing matrix quality for snowshoe hares should be a goal for forest managers in the western United States who strive to increase snowshoe hare densities and persistence for the benefit of carnivores, including lynx, goshawks (*Accipiter gentilis*), and others. The greater dispersion of hares across the landscape, as seen in landscapes with higher quality matrices, may benefit carnivore populations. If prey are relatively evenly distributed across the landscape, forest carnivores that rely on hare populations would presumably have smaller home ranges (Koehler 1990; Mills and Knowlton 1991) and need to expend less energy on hunting. Although Wirsing et al. (2002) suggested that a clumped distribution of hares may allow predators to disproportionately hunt patches of preferred habitat, I contend that a patchy distribution of prey is not an suitable situation for sustaining carnivore populations. From the carnivores' perspective, landscapes in which prey are more evenly distributed may be preferable to landscapes in which prey distributions are clumped.

If landscapes are moderately to highly continuous (e.g. <40-60% open-structured habitat), hares can use high quality matrix habitats for movement and resource acquisition, decreasing the concern over patch isolation and habitat connectivity. Thus increasing matrix quality may also decrease the necessity for developing habitat corridors, stepping stones, and other structures designed to increase habitat connectivity (Mabry and Barrett 2002, Baum et al. 2004). Developing forest management strategies for increasing matrix habitat allows for flexibility and forest planning.

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Table 3.1. Characteristics of within-stand and matrix variables for nine sites in which snowshoe hare movement and habitat use were studied in northern Washington. Values represent means and standard errors (in parentheses) for the 3 Continuous, 4 Moderate, and 2 Isolated matrix areas. Values for all variables were calculated using the methods described in Chapter 2.

Matrix Type	**Continuous**	**Moderate**	**Isolated**
Hare Density (hares/ha)[a]	1.9 (0.1)	0.9 (0.1)	3.7 (1.2)
Stand Area (ha)	13.7 (3.0)	14.4 (3.2)	8.0 (1.5)
Canopy Cover (%)	37.5 (5.9)	35.4 (2.0)	30.0 (10.0)
Understory Cover (%)	43.2 (4.3)	45.7 (3.5)	36.8 (0.2)
Sapling Density (0-4" dbh trees/ha)	3221 (1051)	2499 (709)	3183 (560)
Open-structured Habitat w/in 300 m (%)	16.8 (4.3)	47.2 (3.1)	97.8 (1.0)
Stands w/in 300 m	10.7 (0.9)	12.5 (2.2)	5.0 (1.0)

[a] estimated from pellet counts

Table 3.2. Sample sizes for snowshoe hares tracked on an hourly basis in three different landscape types. Within each landscape type were multiple sites, with multiple hares in each site. Each hare was tracked for 1-6 nights, with 3-6 locations obtained each night per hare.

LandscapeType	Site Identification Number	# Hares	# Sessions	# Locations
Continuous	10	3	14	84
	216	4	20	115
	396	4	16	96
Moderate	292	3	9	48
	371	2	21	103
	598	2	8	39
	643	3	17	94
Isolated	12	4	22	128
	19	4	18	114
Total	**9**	**30**	**143**	**821**

Figure 3.1. Characteristics of the matrix within 300 m of focal stands in which snowshoe hares were captured. Stands were classified by matrix type: Continuous (n=3), Moderate (n=4), or Isolated (n=2), referring to the amount of open-structured habitat surrounding them. Bars represent the average amount of each habitat type within 300 m of the focal stand, with 95% CI. Preferred, intermediate, and poor habitats had ≥40%, 11-39%, and ≤10% understory cover, respectively.

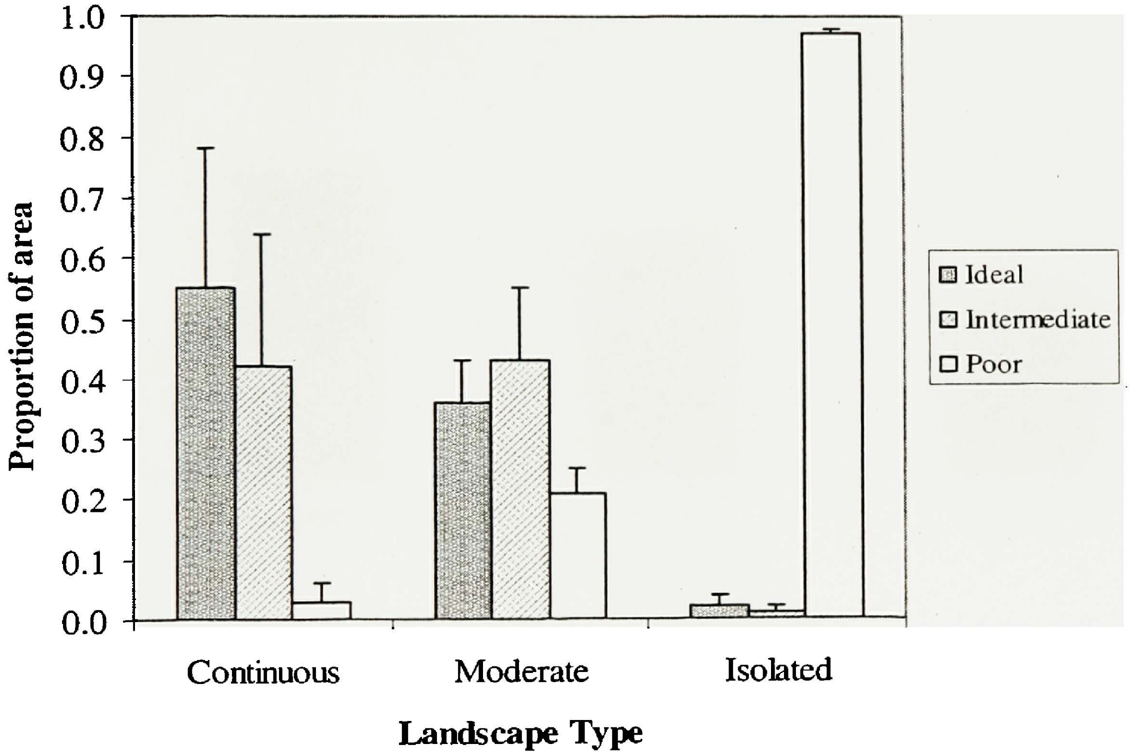


Figure 3.2. Propensity for snowshoe hares to use multiple stands in northern Washington, or the proportion of tracking nights that each hare used multiple stands. Bars represent untransformed means and 95% confidence limits for hares in the three landscape types.

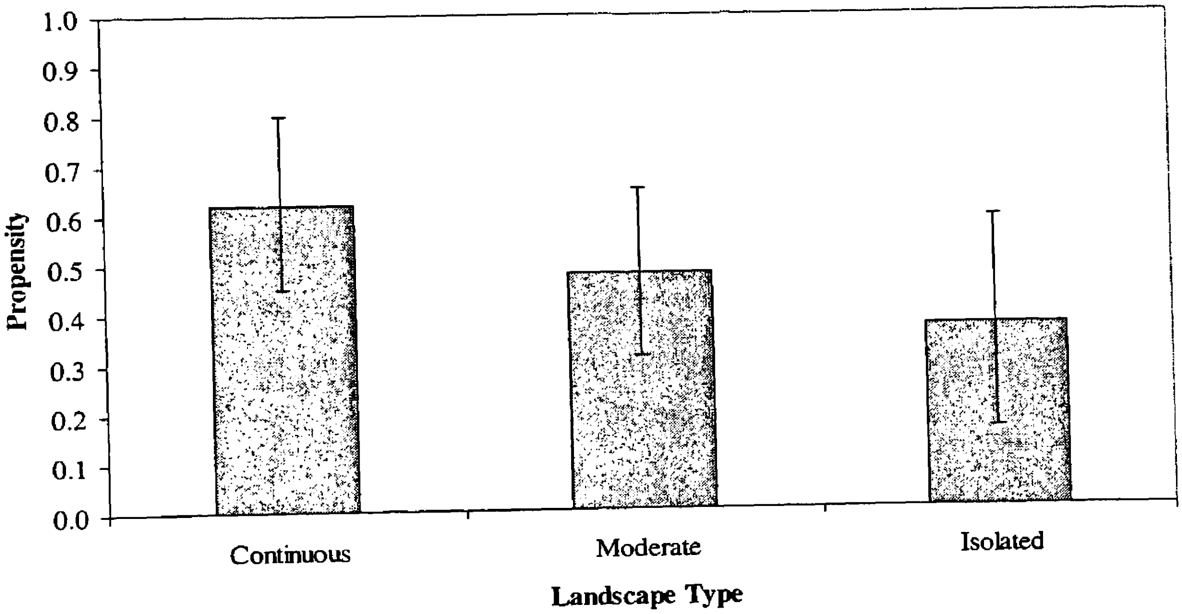


Figure 3.3. Movement characteristics for snowshoe hares in each of three landscape types in northern Washington. Values represent means and 95% confidence intervals for hourly movement rate, total distance in five hours, and net displacement.

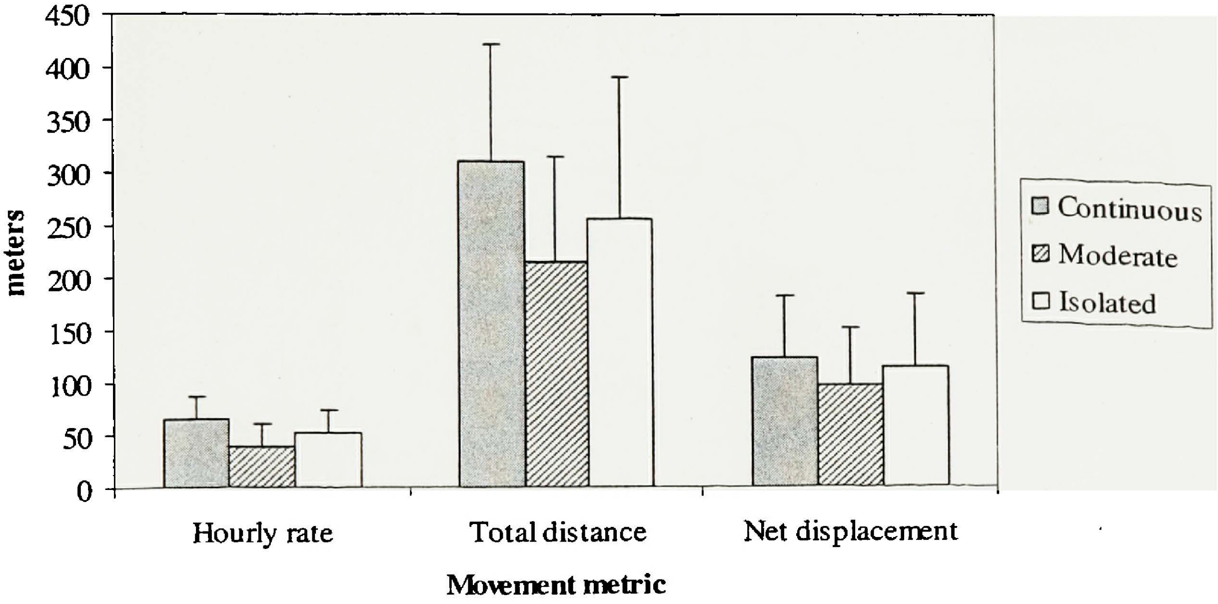


Figure 3.4. Proportion of hare locations observed in the focal patch and in different matrix habitat types. Bars represent means and 95% confidence limits for hares in each landscape type.

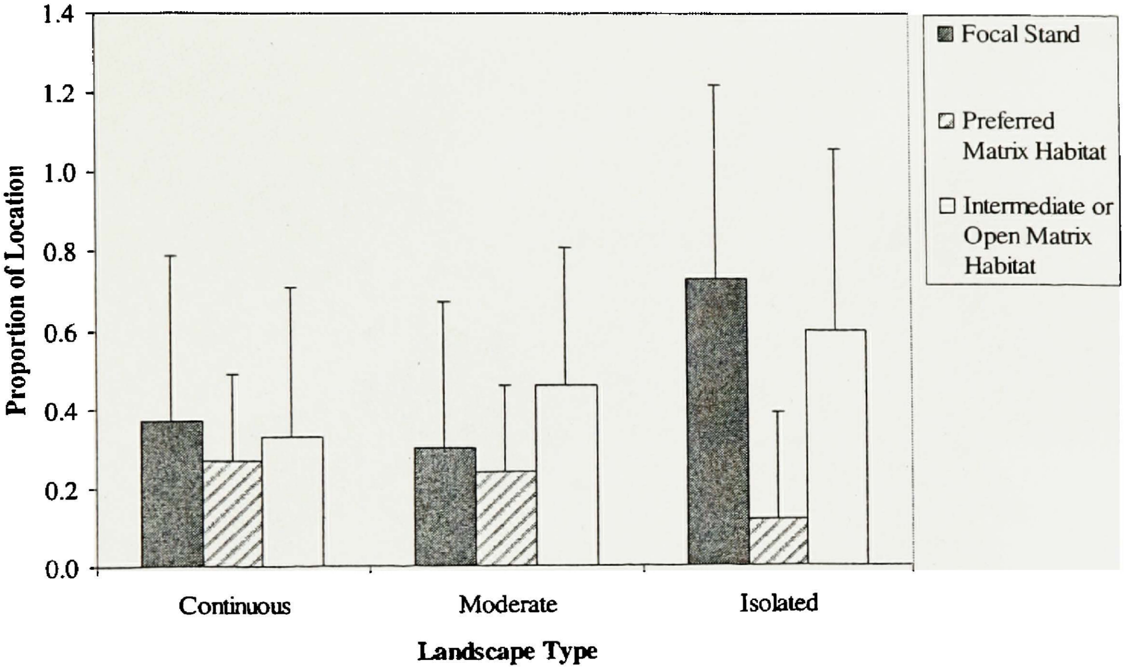
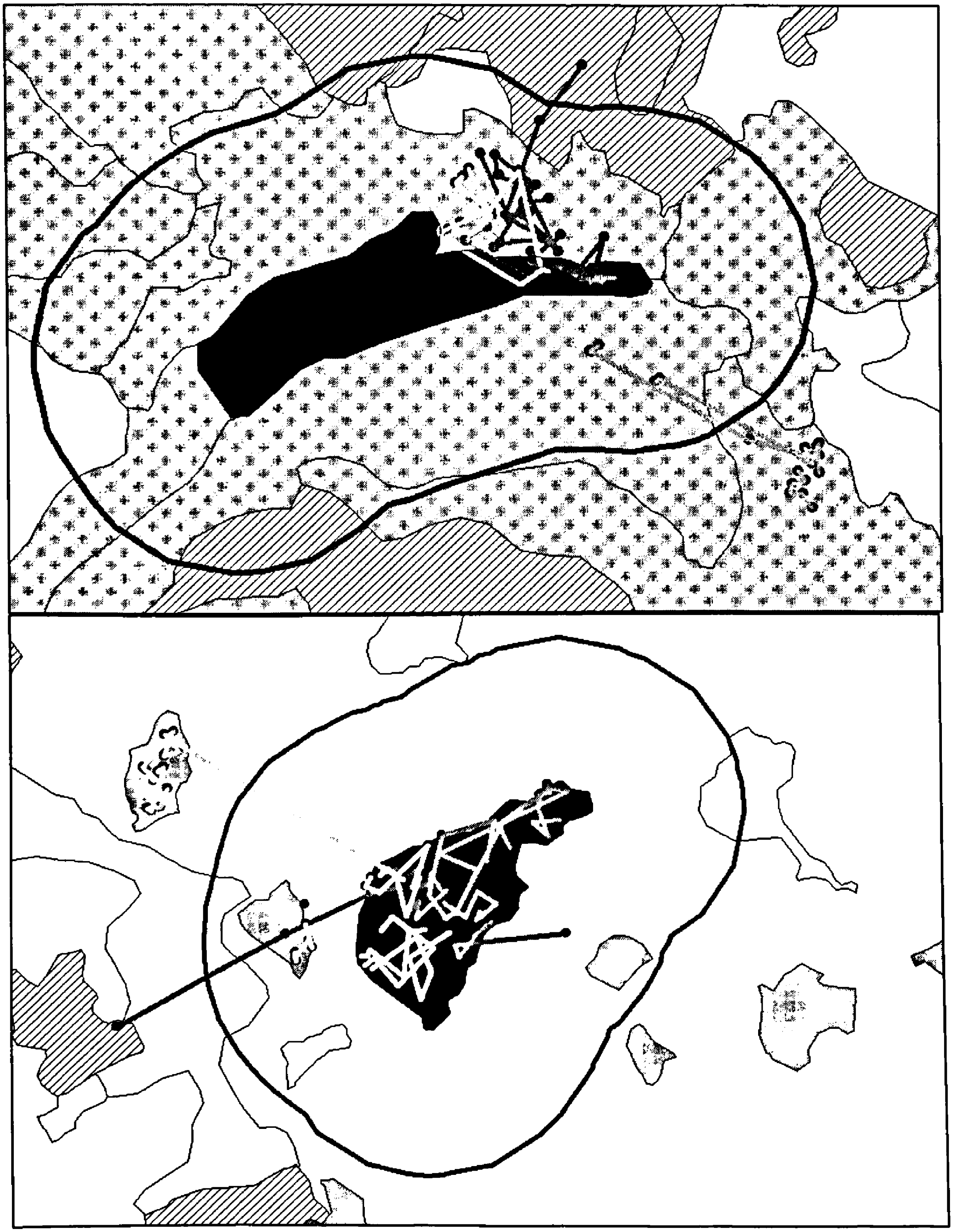


Figure 3.5. Examples of snowshoe hare distribution and movement paths in a Continuous (top) and an Isolated (bottom) landscape. Dots represent hare locations, and lines connecting dots represent hourly movement paths. Black patches are the focal stands; dark gray patches are preferred habitat in the matrix; light gray slashes represent intermediate matrix; and white shows poor quality matrix. The dark lines around focal stands show the 300 m buffer.



APPENDIX A.

COMPARISON OF RELATIVE SNOWSHOE HARE DENSITIES BETWEEN TWO STUDY AREAS IN NORTHERN WASHINGTON

INTRODUCTION

Two separate areas in northern Washington have been the focus of intensive lynx (*Lynx canadensis*) habitat use studies. "The Meadows", characterized by extensive and homogenous forest upon a high plateau, is considered to be the best lynx habitat in the state of Washington (G. Koehler, R. Naney, personal communication). Boreal forest dominates, and fragmentation is due primarily to wildfires and natural meadows. Although this study area offers consistently good lynx habitat (Brittell et al. 1989, Koehler 1990, von Kienast 2003), Geographic Information Systems (GIS) analyses indicate that there is a relatively small amount of such high-quality habitat in the state. Most of the remaining lynx habitat in Washington is characterized by patches of boreal forest that are interspersed amongst a matrix of drier forest types, resulting in greater fragmentation (Ruediger et al. 2000). The "Black Pine Basin" study area is more representative of the lynx habitat in the rest of the state. The area is more fragmented due to intermixed forest types, recent fires, and timber harvest activities. Recent research in these two areas has compared winter habitat use of lynx, with the goal of identifying similarities and/or differences that will help better guide lynx management strategies in continuous versus fragmented habitats (von Kienast 2003, Maletzke 2004).

Because lynx depend greatly on snowshoe hares (*Lepus americanus*) for food, lynx habitat suitability and management strategies are strongly tied to snowshoe hare habitat (Mowat et al. 2000, Ruggiero et al. 2000). Across their extensive range, snowshoe hare densities are most strongly correlated with understory cover—stands with shrubs, high tree densities, or substantial lateral cover by tree branches are more heavily used by hares (Dolbeer and Clark 1975, Wolfe et al. 1982, Litvaitis et al. 1985, Koehler 1990, Thomas et al. 1997). Plant species composition is less correlated with snowshoe hare habitat use and population density than is understory structure (Ferron and Ouellet 1992, Thomas et al. 1997, Shick 2003).

In addition to stand-level characteristics, landscape patterns may also affect snowshoe hare densities. In the northern parts of their range where high quality hare habitat is more contiguous, snowshoe hare populations reach peak densities higher than densities typically reported in the southern ranges where habitat is more fragmented (Hodges et al. 2000a,b). Additionally, in fragmented forests in Montana, differences on the magnitude of two to three times as many hares per hectare have been documented in patches of habitat with similar stand-level attributes (Griffin et al. 2003, Mills and Hodges, unpublished data), suggesting that landscape-level factors may be influencing hare densities. Researchers have hypothesized for decades that differences in landscape patterns may be responsible for differences in snowshoe hare densities and population dynamics, and that densities and population cycles in the southern forests are suppressed by fragmentation (Dolbeer and Clark 1975, Woolf et al. 1980, Wirsing et al. 2002). However little data has been published to support this hypothesis (but see Thomas et al. 1997, Griffin 2003, Shick 2003).

In this study, I compared relative snowshoe hare densities in patches of potential hare habitat (identified by stand-level characteristics) between a highly fragmented area (Black Pine Basin) and a relatively contiguous area (The Meadows). My specific goals were to (1) compare means and variances in snowshoe hare density, as indexed by pellet counts, between the two areas to test the prediction that relative densities are lower in fragmented areas, and (2) provide information on relative snowshoe hare densities in both areas that will aid in the interpretation of lynx habitat use studies.

METHODS

Study Areas

The Meadows (49°N, 120°W), is high-elevation habitat (>1460 m) comprised of extensive and homogenous lodgepole pine (*Pinus contorta)* forest with lesser components of Engelmann spruce (*Picea engelmannii)* and subalpine fir (*Abies lasiocarpa*), most of which is at or near the climax seral stage (Brittell et al. 1989; Koehler 1990). Natural meadows, recent burns, and other non-habitats for hares constitute <20% of the 200 km^2 area. In the Black Pine Basin study area (48°N, 120°W), open-structured non-habitat, or land with <10% canopy or understory cover, encompasses 28% of 212 km^2 area. The remaining habitats are boreal forest stands (characterized by subalpine fir (*Abies lasciocarpa*) and Englemann spruce (*Picea enlemanii*) as the dominant canopy species, with Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and whitebark pine (*Pinus albicaulis*) occasionally interspersed) or dry forest stands (comprised of Douglas fir and ponderosa pine (*Pinus ponderosa*) as the dominant canopy species). Elevations in the study area range from 643 m to 2134 m.

Site Selection

I selected focal stands that, based on stand-level characteristics, could potentially support high snowshoe hare densities. In Black Pine Basin I used GIS data (Maletzke 2004) to select 78 stands with canopy cover >40% or understory cover >40%. In The Meadows such GIS coverages were not available, so I used ortho-photographs to select

26 sites that had dense canopy cover. For any stands >20 ha, I selected a 20 ha portion from the middle of the stand.

Snowshoe Hare Abundance Estimates

Although abundance and density of snowshoe hares are best estimated with mark-recapture approaches, Mills et al. (2005) found for hares in Montana a reliable concordance between estimated mark-recapture density and predicted density using fecal pellet counts coupled with the equation developed by Krebs et al. (2001) in the Yukon. Mills et al. (2005) suggested that for western U.S., where hare densities are often sparse, pellets may be used to identify relative hare density across space, reserving mark-recapture for questions where absolute density is of interest.

I conducted fecal pellet surveys in Black Pine Basin in 23 stands in 2003 and 55 stands in 2004. Twenty-six stands in The Meadows were surveyed in 2004. Within each stand I counted the number of pellets within 50 randomly placed "Krebs plots" (3.05 m x 5.08 cm; Krebs et al. 2001, Hodges and Mills in review). For purposes of better biological interpretation, I converted mean pellet counts to snowshoe hare density estimates, using the equation developed by Krebs et al. (2001):

$$\text{Hare density (hares/ha)} = 1.567 * e^{(-1.203+(0.889*\ln(\text{mean pellets/stand})))} \qquad \text{[Equation 1]}$$

Data Analysis

To meet assumptions of normality, I used the log-transformed mean number of pellets from each stand as the dependent variable for all analyses. Because variance was not homogeneous between study areas (see Results), I used the Mann-Whitney test to compare mean pellet counts.

RESULTS

Means, medians, and ranges for pellet counts per stand and estimated snowshoe hare densities (calculated using Equation 1) are shown in Table 1. Snowshoe hare pellet densities were significantly higher in The Meadows than Black Pine Basin (p=0.01; Figure 2). The variance was also significantly higher in The Meadows than in Black Pine Basin (Levene statistic= 4.95, df=1,102, p=0.03). The Meadows had a higher proportion of higher density stands than did Black Pine Basin (Figure 3). I did not observe spatial correlation of higher density stands, as no one drainage or ridge had a disproportionate number of higher or lower density stands relative to the other areas (Figures 4 and 5).

DISCUSSION

In both areas, patches of densely vegetated stands varied dramatically in their relative snowshoe hare densities. However, average densities were higher in the continuous Meadows area than in the fragmented Black Pine Basin, perhaps supporting the prediction that landscape structure affects snowshoe hare densities.

Differences in relative densities could be attributable to a number of factors besides landscape structure, including differences in predator densities, microclimates, and vegetation composition. Unfortunately, GIS data for the Meadows study area is not detailed enough to quantify matrix characteristics surrounding the surveyed patches. Such analyses for now are restricted to the Black Pine Basin area. Because only two landscapes were compared, other factors cannot be ruled out, and sample sizes within the study areas were low, especially in the Meadows, I advise caution in interpreting these results as proof that fragmentation suppresses snowshoe hare densities. However, the differences between relative densities in these two study areas is compelling enough to warrant further investigation into the question of whether landscape patterns affect snowshoe hare densities.

Average snowshoe hare densities were higher in the Meadows than in Black Pine Basin, and were more consistently high, as evidenced by the higher proportion of stands in which estimated densities were >1.0 hares/ha. Although the variance in pellet counts was higher for the Meadows than for Black Pine Basin, the range of values was smaller for the Meadows than for Black Pine Basin. I suspect that the higher variance in the Meadows is more a reflection of sample size than an ecological trend. Also, snowshoe hare densities were indexed using pellet counts, which allow us to make comparisons between stands and between study areas. If actual densities are of concern, however, mark-recapture studies should be conducted to obtain density estimates.

For lynx and other forest carnivores, the Meadows may offer better habitat in terms of prey availability than does the Black Pine Basin area. Any given patch of dense boreal forest in the Meadows is more likely to have a greater density of snowshoe hares. Additionally, dense boreal forest is much more abundant in the Meadows than in Black Pine Basin, most likely resulting in a landscape-wide higher snowshoe hare abundance. Because of the relative homogeneity of prey abundance in the Meadows, I predict that lynx in the Meadows have smaller home ranges than lynx in the more heterogeneous Black Pine Basin (Koehler 1990, Mills and Knowlton 1991, Marzluff et al. 1997, Relyea et al. 2000, Kie et al. 2002). Because animals' movement paths are generally straighter and faster (i.e. less tortuous) when moving through habitats in which resource availability is low (Pastor et al. 1997, Wiens et al. 1997, Zollner and Lima 1999), I also predict that lynx trails in the Meadows are more tortuous on average. I recommend future research to test these predictions to gain a better understanding of the connection between prey availability and lynx behavior.

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Table A.1. Mean fecal pellets per stand and estimated snowshoe hare densities[a] for patches of snowshoe hare habitat in a contiguous landscape (The Meadows, n=26 stands) and a fragmented landscape (Black Pine Basin, n=78) in northern Washington.

	Mean Pellets Per Stand		Estimated Snowshoe Hare Density[a]	
	Meadows	Black Pine Basin	Meadows	Black Pine Basin
Minimum	0.5	0.04	0.3	0.03
Maximum	7.2	13.8	4.9	2.7
Median	2.4	1.6	1.0	0.7
Mean	2.8	2.1	1.2	0.9
SE of mean	0.3	0.2	0.1	0.1

[a] estimated using Equation 1, based on pellet counts

Figure A.1. Map of Black Pine Basin Study area (blue outline) and The Meadows study area (black outline), in the Okanogan National Forest and Loomis State Forest, Washington. Blue shades show Lodgepole pine and Engelmann spruce/subalpine fir forest types, red shades represent the lower elevation, dry Douglas-fir/ponderosa pine forest types. The black shadings show recent wildfires (<15 years). The white line represents the 1525 m elevation contour. Map was created by Maletzke (2004).

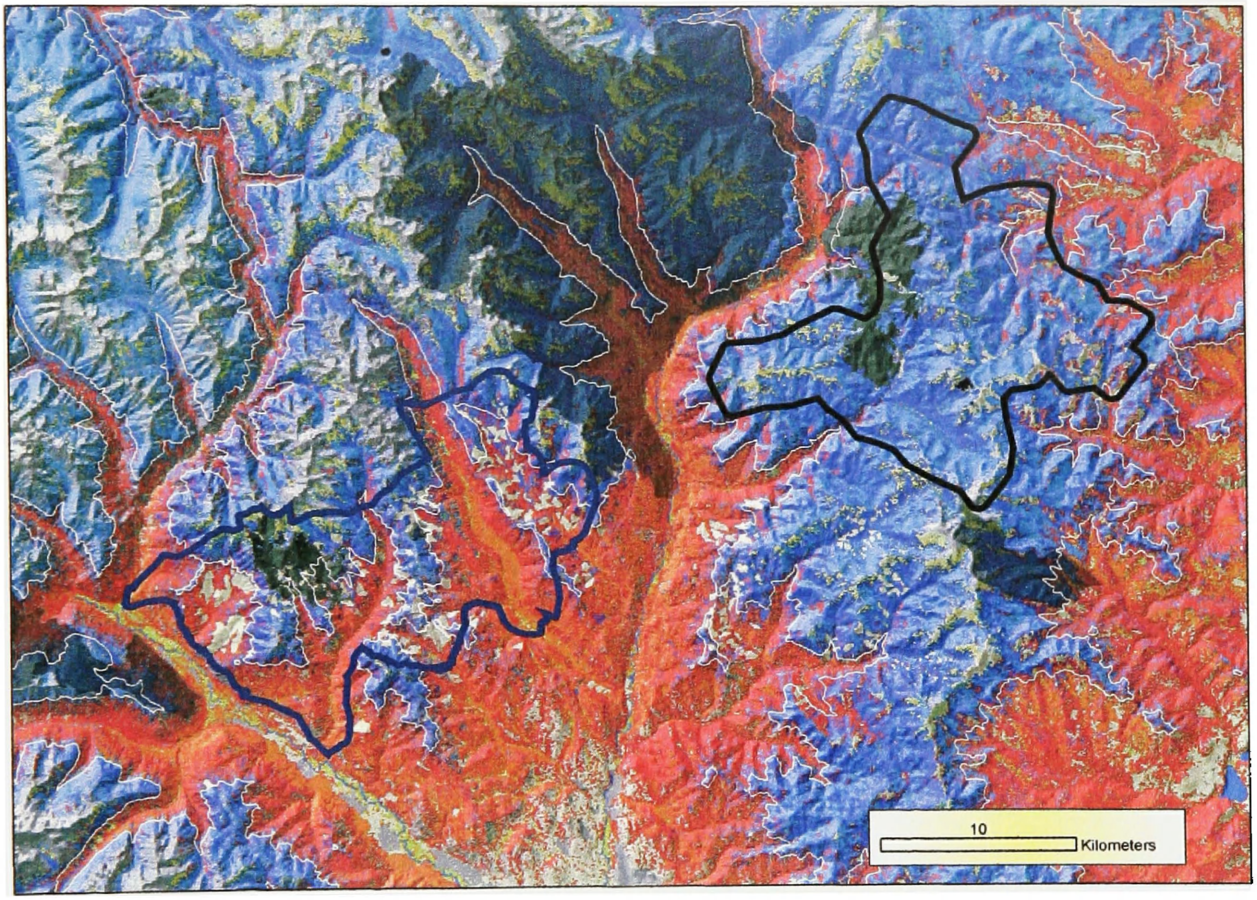


Figure A.2. Average number of pellets in 50 'Krebs plots' patches of potential snowshoe hare habitat in a fragmented (Black Pine Basin) versus a continuous landscape (Meadows) in northern Washington. Squares show the log-transformed mean pellets per plot with 95% confidence limits.

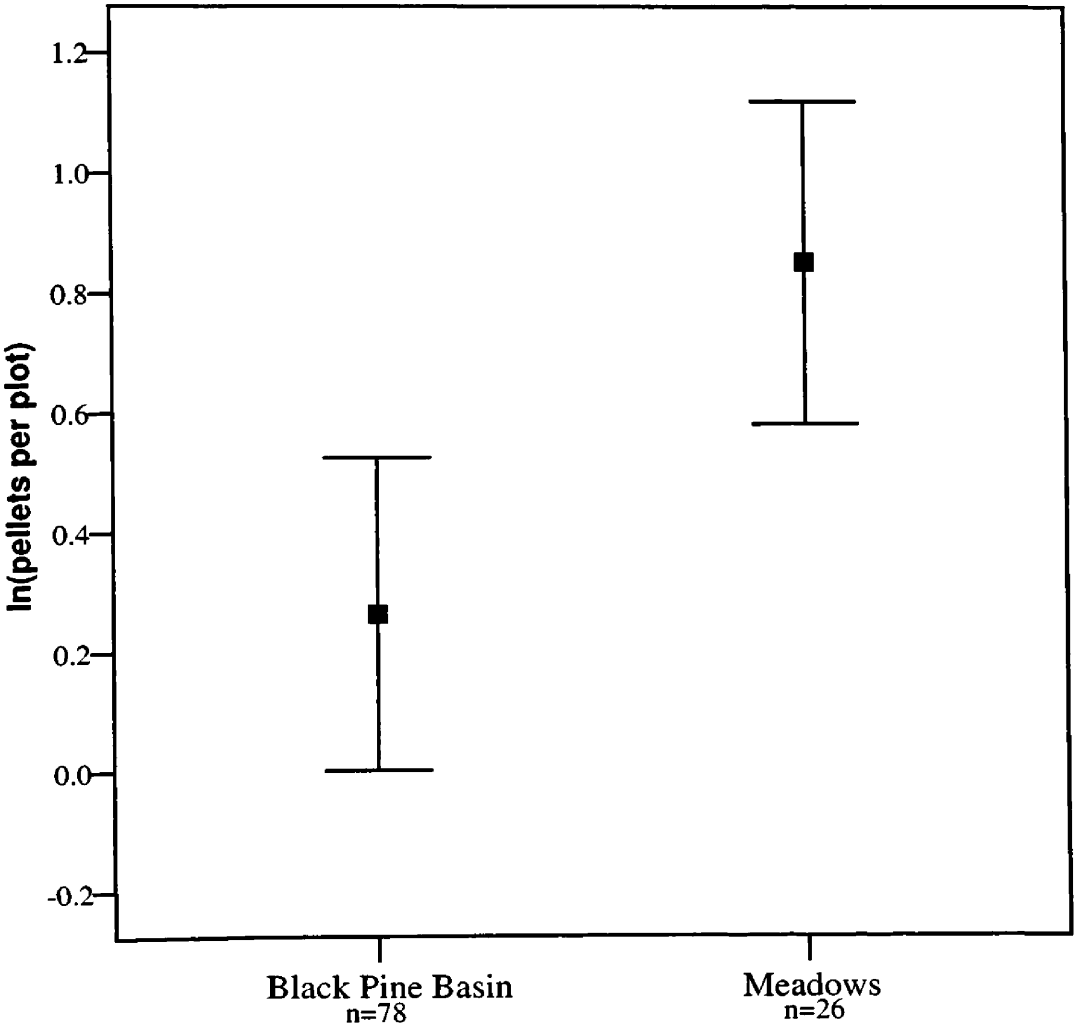


Figure A.3. Proportion of densely forested stands with Low (0-0.5), Medium (0.5-1.0), High (1.0-2.5), or Extra High (>2.5) snowshoe hare densities in a continuous (Meadows, n=26) and a fragmented (Black Pine Basin, n=78) landscape in northern Washington. Densities were indexed using fecal pellet counts.

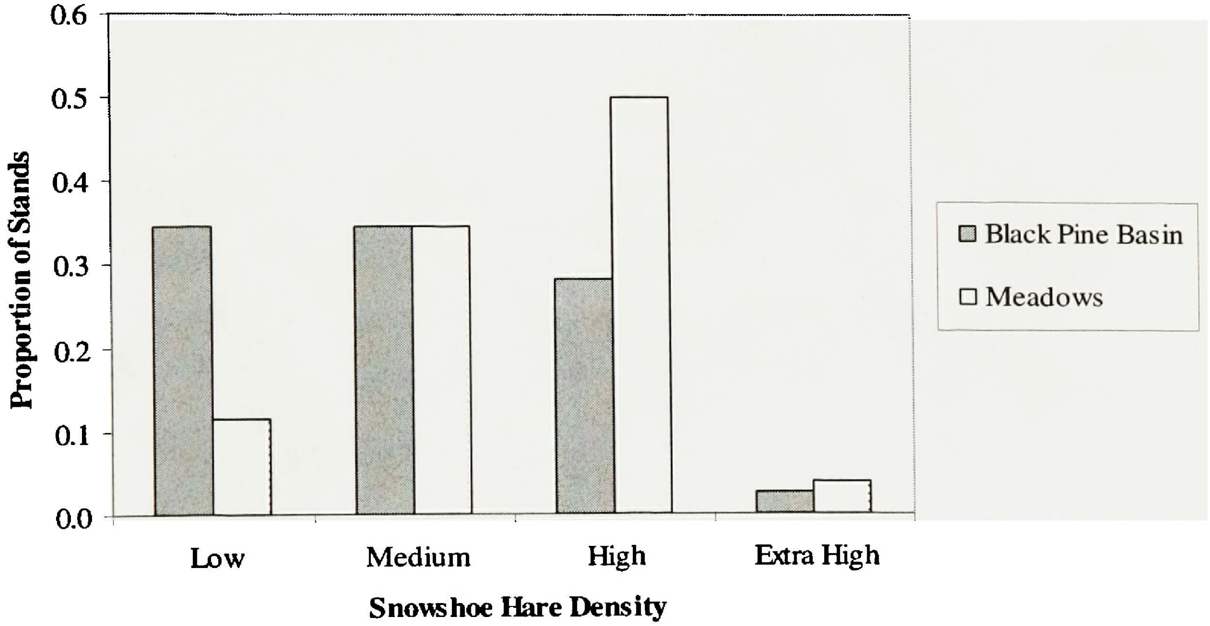


Figure A.4. Snowshoe hare densities, indexed by fecal pellet counts, for 78 stands of dense forest in the Black Pine Basin study area of northern Washington in 2003-2004.

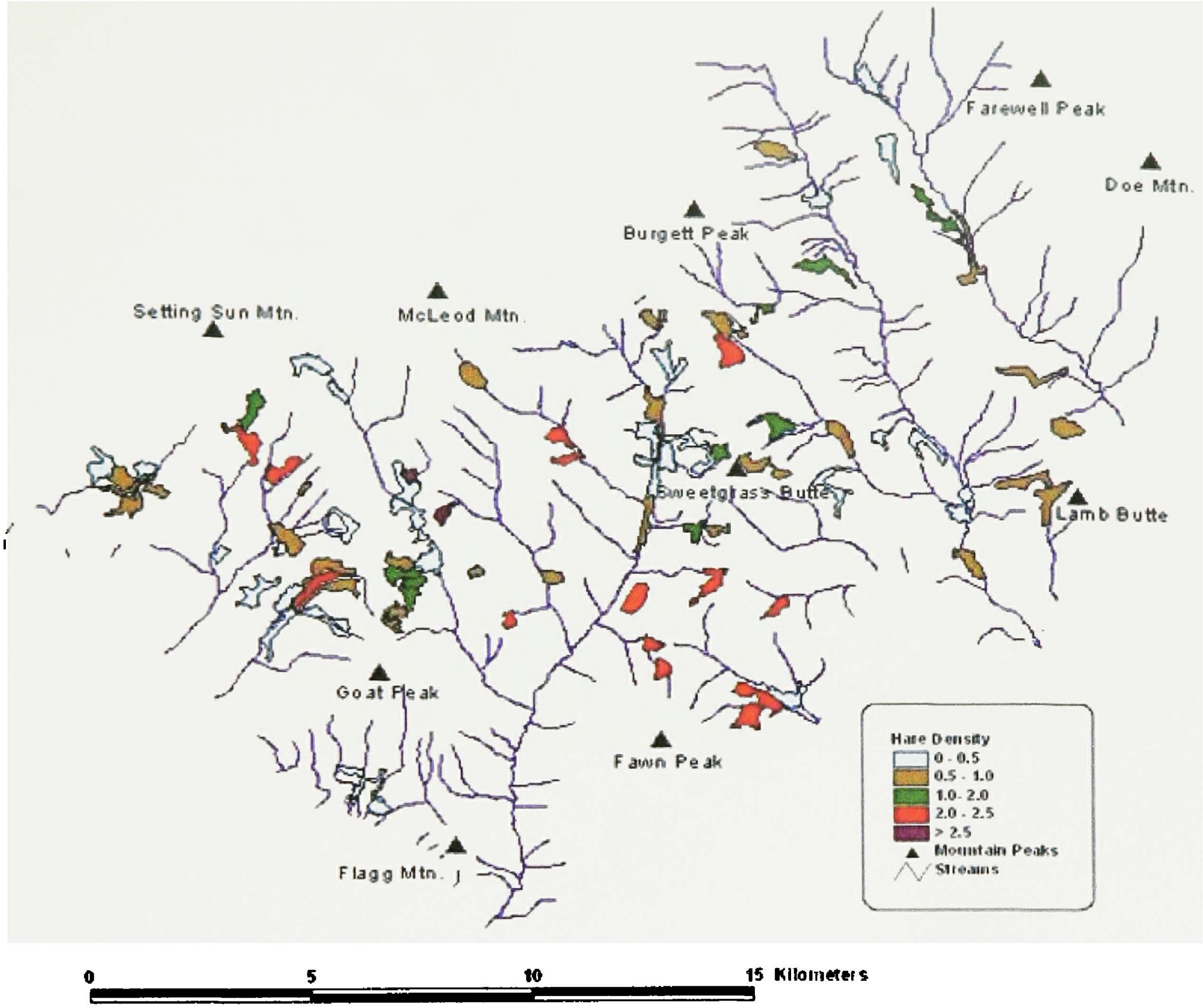
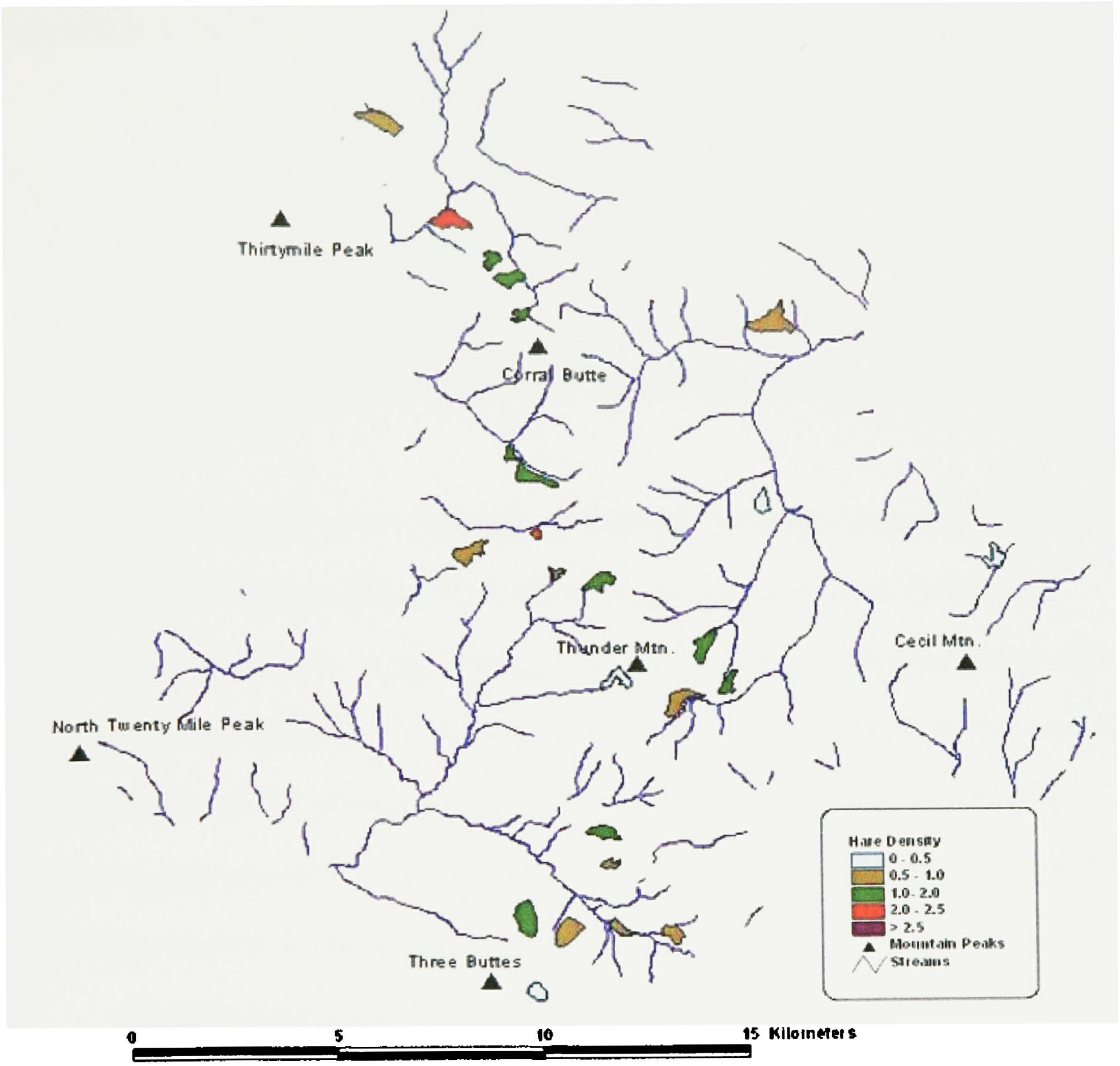


Figure A.5. Snowshoe hare densities, indexed by fecal pellet counts, for 26 stands of dense forest in the Meadows study area of northern Washington in 2004.



APPENDIX B:
COMPARISON OF STAND- AND LANDSCAPE-LEVEL VARIABLES FOR STANDS WITH LOW, MEDIUM, AND HIGH SNOWSHOE HARE DENSITIES

For the purposes of comparing my data with other studies, I conducted further data explorations than were reported in Chapter 2. In this appendix, I report on the differences in magnitude of certain stand- and landscape- level variables between stands with varying levels of snowshoe hare density. I also show the relationships between pellet densities and landscape-scale variables that were not included in the modeling process.

I compared differences in stand and landscape variables among stands with differing levels of hare density. To develop density categories, I converted pellet densities to hare densities using Equation 1 (Chapter 2), then divided stands into three categories of hare density: Low (0-0.5 hares/ha), Medium (0.51-1.0 hares/ha), and High (>1 hare/ha). Density estimates were only used for categorization; I still used log-transformed pellet counts as the dependent value. I used analysis of variance (ANOVA) and Tukey's post-hoc test to compare means between groups.

Comparisons between stands with low, medium, and high snowshoe hare densities show that four stand variables differed significantly between one or more groups (Table I). Understory cover was 45% denser in high hare stands than in low hare stands (32.8% vs. 22.5% cover; $p=0.005$, $F_{1,47}=8.83$). Stands with high hare density had more than twice as many saplings as did stands with low hare densities (2784 vs. 1039 saplings/ha; $p<0.001$, $F_{1,47}=17.67$). Density of medium-sized trees was twice as high (712 vs. 356 trees/ha) in high hare stands than in low hare stands ($p<0.001$, $F_{1,47}=17.89$). Stands with high snowshoe hare densities had about 20% more boreal forest at the 300 m scale than did stands with low hare densities (p<0.01, f=5.34, df=2,73). I did not find significant differences between density categories for any other stand- or landscape-scale variables. These results do not differ from those reported in Chapter 2, but rather show the magnitude of variables needed to produce particular hare densities.

Table B.1. Mean values (and SE) for stand- and landscape-scale variables for three levels of snowshoe hare density (indexed by pellet counts) from 76 stands in the Okanogan National Forest. Hare density levels are: Low (0.0-0.5 hares/ha), Medium (0.5-1.0 hares/ha), and High (>1.0 hares/ha).

Scale	**Variable**	**Low Hare Density**	**Medium Hare Density**	**High Hare Density**
Stand	Stand size	16.0 (1.1)	16.2 (1.0)	15.1 (1.3)
	Canopy cover	32.4 (2.1)	39.3 (3.0)	37.6 (2.8)
	Horizontal cover	22.5 (1.8)[a]	27.3 (1.6)	32.8 (3.2)[c]
	Sapling density	1039 (210)[a]	1555 (227)[a]	2784.4 (381.8)[b,c]
	Medium-sized tree density	356 (39)[a]	526 (38)[a]	712 (80)[b,c]
Perimeter	Open Forest	23.2 (6.9)	17.3 (5.5)	24.2 (7)
	Boreal Forest	21.5 (6.5)	26.7 (6.3)	10.4 (5.3)
300 m	Open Forest	34.5 (4.7)	34.0 (5.5)	37.8 (6.0)
	Boreal Forest	50.4 (7.2)[a]	62.7 (5.6)	78.8 (4.2)[c]
600 m	Open Forest	33.5 (4.4)	29.6 (2.8)	37.9 (5.0)
	Boreal Forest	52.8 (6.6)	54.4 (5.9)	71.9 (3.6)

[a] Significantly different from High Density stands

[b] Significantly different from Medium Density stands

[c] Significantly different from Low Density stands

APPENDIX C.
GUIDE TO DATA FILES PERTINENT TO THESIS RESEARCH

The purpose of this appendix is to provide a guide to data files used in the research for this thesis. A compact disc of all files will be given to Dr. Mills and Dr. Hodges. Data files may be available for reference for future research in the Okanogan National Forest, or for snowshoe hare research in other areas. Any parties wishing to use any of the files should contact Dr. Mill, Dr. Hodges, or the author for permission.

Data files on the cd are organized as follows:

- GIS FILES
  - Black Pine Basin GIS Data (NAD1927, UTM Zone11)
    - Features
      (shapefiles of roads, peaks, etc.)
    - Maletzke BPB Coverages
      (vegetation, elevation, slope coverages developed by Ben Maletzke)
    - MrSIDS
      (digital orthophotos of the study area)
    - Study Area Polygons
      (shapefile of stand delineations)
    - Study Sites
      (shapefiles of stands used for pellet surveys and for telemetry studies)
  - Meadows GIS Data (NAD1927, UTM Zone10)
    - Features
      (shapefiles files of roads, peaks, etc)
    - K2d_01
      (study area boundaries used by von Kienast)
    - MrSIDS
      (digital orthophotos of the study area)
    - All_Meadows_Pellet_Stands.shp
      (shapefile of all stands surveyed by Walker 2004)

- TELEMETRY AND TRAPPING DATA
  - All Hourly Tracking.xls
    (location and habitat data from all hares used in radio telemetry study; UTM locations for BPB are in Zone 11, Zone 10 for Meadows hares)
  - Telemetry Stand Characteristics.xls
    (vegetation and landscape data for 9 stands used for telemetry study)
  - All Hares Trapped.xls
    (locations and information on all hares trapped, including whether or not DNA samples were taken)
  - Mark-Recapture Data 2003.xls
    (data from 4 sites at which 9-ha grids were trapped in summer 2003)

- PELLET STAND DATA
    - Pellet Model Data.xls
      (pellet counts, density estimates, stand- and landscape-level data for all stands surveyed)
    - Raw Pellet Data.xls
      (raw data from all pellet stands; includes UTM locations for 50 random pellet plots within each stand)
    - All_Veg_Data
      (raw stand-level vegetation data for all stands in BPB and Meadows)

APPENDIX D:
EFFECTS OF CHANGING STAND- AND LANDSCAPE-LEVEL VARIABLES

To evaluate how changes in habitat variables would affect snowshoe hare densities, I conducted a simulation exercise to examine the effect sizes of each of the stand-and landscape-level variables on snowshoe hare pellet densities. I wanted to evaluate how changes in each variable would affect snowshoe hare densities. The best fitting model from Chapter II explains pellet density in terms of stand-level variables (e.g. sapling and medium-sized tree density) and landscape-level variables (e.g. boreal forest and closed-structured forest within 300 m; Equation D.1).

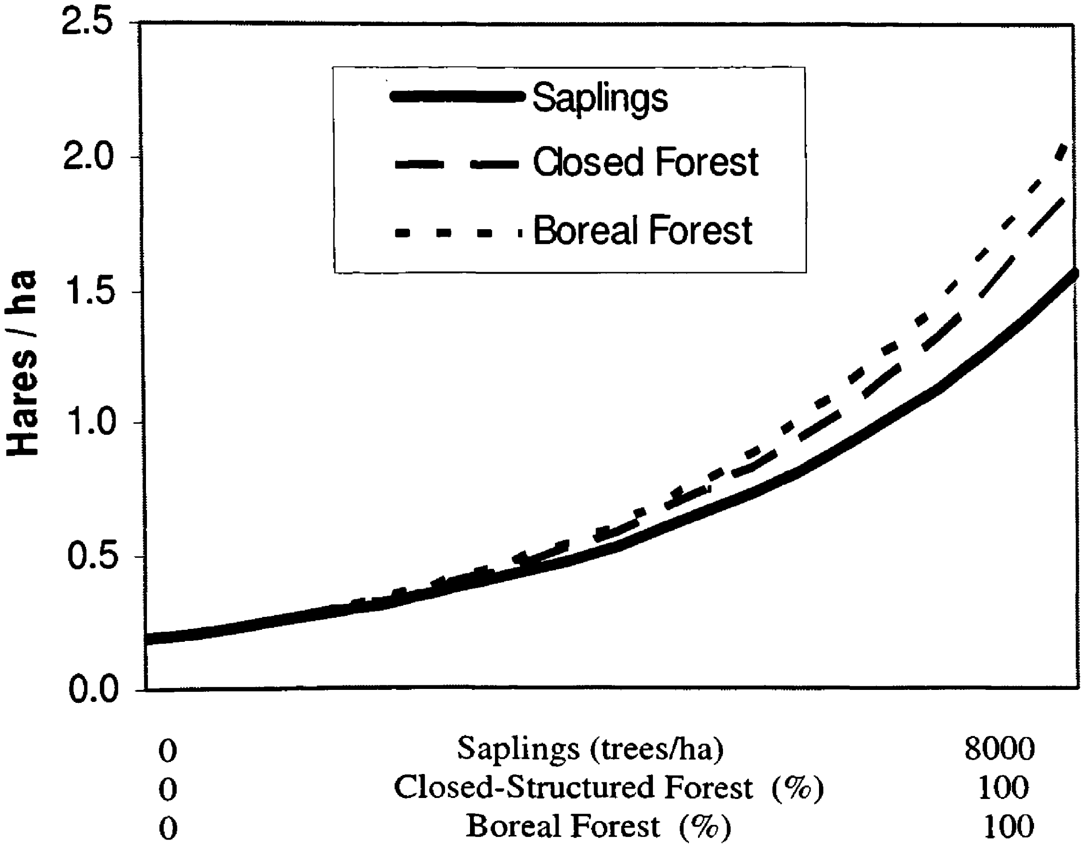
$$\ln(\text{pellets}) = -1.405 + 0.0003(\text{sapling density}) + 0.0007(\text{medium tree density}) + 0.0113\,(\text{boreal forest}) + 0.0021(\text{closed-structured forest}) \qquad \text{[Equation D.1]}$$

To evaluate the effect of changing sapling density, I kept all other variables constant (medium trees= 500 trees/ha, boreal forest= 0%, closed-structured forest= 0%), but let sapling density change from 0-8000 trees/ha. I then let the amount of closed-structured forest (the opposite of open-structured forest; e.g. stands with >10% understory and overstory structure) change from 0 to 100% of the area within 300 m of the focal stand. Finally I allowed the amount of boreal forest to change from 0 to 100% of the 300 m buffer.

I used the Krebs equation (Equation 2.1) to convert pellet densities to snowshoe hare densities, and evaluated the effect of changing sapling densities on snowshoe hare densities. While sapling density was responsible for the largest changes in snowshoe hare density, increasing closed-structured forest and boreal forest also improved hare density by as much as 0.5 hares/ha (Figure D.1).

The results from this simulation exercise show that improving landscape-level variables can improve snowshoe hare densities, especially in stands with high sapling densities. The effects of improving matrix quality can be especially important for increasing hare densities in patches of dense forest.

Figure D.1. Changes in snowshoe hare densities in response to changes in stand- and landscape-level variables. Variables changed were sapling density within in the focal stand, and closed-structured forest and boreal forest within 300 m of the focal stand.



APPENDIX E:
STATISTICAL ANALYSES OF HARE MOVEMENT DATA

Because my sample sizes were very low for comparing movement and habitat use across landscape types, I did not report statistical results in Chapter 3. However, I did perform statistical tests on the data, and I present those results here. Some of the data follow predicted trends, but sample sizes are too low to determine if statistically or biologically important differences truly exist.

To meet assumptions of normality, I used an arcsine transformation on all proportional variables (e.g. Propensity, In Focal) and a natural log transformation on linear variables (e.g. rate and distances). I compared differences in variables between landscape types using a mixed model (PROC MIXED) in SAS 9.0 (SAS Institute, Cary, NC, 2002), in which site was nested within landscape type, and hare was nested within site for habitat use and propensity, and session was additionally tested within hare for movement characteristics.

None of the variables were significantly different. I observed high amounts of variation between hares within each landscape and between sites within each landscape.

Table E.1. Mean (transformed) values for habitat use and movement characteristics of snowshoe hares in three different landscape types (Continuous, Moderate, and Isolated). Values in bold represent means, with 95% confidence limits in parentheses).

	Continuous		**Moderate**		**Isolated**		**$F_{2,6}$**	**p**
In Focal	**0.55**	(0.19-0.91)	**0.38**	(0.04-0.72)	**0.84**	(0.40-1.29)	2.58	0.21
In Non-Preferred Matrix	**0.41**	(0.18-0.63)	**0.41**	(0.18-0.64)	**0.27**	(0.01-0.55)	0.43	0.61
Propensity to use multiple stands	**0.77**	(0.64-0.90)	**0.68**	(0.55-0.81)	**0.56**	(0,41-0.72)	2.96	0.12
Total displacement	**0.37**	(0.17-0.57)	**0.48**	(0.27-0.68)	**0.48**	(0.24-0.72)	1.52	0.6
Net displacement	**0.59**	(0.30-0.89)	**0.79**	(0.49-1.10)	**0.74**	(0.38-1.10)	0.58	0.55
Movemement rate	**0.67**	(0,51-0.83)	**0.68**	(0.54-0.83)	**0.82**	(0.64-1.01)	3.14	0.31