MULTI-SCALAR RESPONSES OF FOREST CARNIVORES TO HABITAT AND SPATIAL PATTERN: CASE STUDIES WITH CANADA LYNX AND AMERICAN MARTENS

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An Abstract of the Thesis Presented
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I examined responses of Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*) to habitat features at multiple spatial scales. At the stand-scale, lynx (n = 6) selected tall regenerating clearcuts (4.4-7.3 m, 11-26 years post-harvest) and established partially harvested stands (11-21 years post-harvest) and they selected against short regenerating clearcuts (3.4-4.3 m, 11-26 years), recent partially harvested stands (1-10 years), and mature stands (>40 years). The highest fractal dimension of foraging paths was in tall regenerating clearcuts and established partially harvested stands, which were stands that provided intermediate to high snowshoe hare (*Lepus americanus*) density, intermediate cover for hares, and intermediate levels of canopy closure and live-tree basal area. Movement paths of lynx had increasing fractal dimension at smaller scales and were straighter than they were at broader spatial scales, suggesting that lynx were trying to avoid switching from highly preferred to lesser preferred stands. Lynx maximized

time in areas with high-intermediate hare densities to facilitate increased capture success of snowshoe hares, supporting the hypothesis that lynx select for prey access over prey density.

I developed models incorporating landscape composition and configuration to predict occurrence of home ranges (n = 63) for American martens in Newfoundland and to evaluate the relative influences of habitat loss versus fragmentation on this endangered subspecies. Habitat loss was the primary determinant of occupancy of landscapes by martens. The probability of occupancy declined precipitously as the percent of suitable habitat fell below 60% of home-range sized landscapes; therefore, efforts to recover marten populations should focus on maintaining suitable habitat above 60%. I also compared threshold responses in occupancy of martens to the amount of suitable habitat in the landscape between two geographically isolated subspecies (*Martes americana americana* in Maine and *Martes americana atrata* in Newfoundland) that differed greatly in the amount of landscape-scale fragmentation and amount of suitable habitat. Drastic declines in occupancy occurred much sooner in Maine (70-80% suitable habitat) than in Newfoundland (30-40% suitable habitat), indicating that martens in Maine are more sensitive to landscape change, and the Newfoundland subspecies has evolved to be less responsive in its more inherently fragmented environment.

PREFACE

My Dissertation research involved comparing several common concepts in ecology between two carnivore species. The research included concepts of scale, spatial use of landscape features, movement patterns, and habitat selection at multiple spatial scales. Determining the appropriate scale to study a particular ecological problem has been recognized as increasingly important (Wiens 1989, Fahrig 1992, Bissonette et al. 1997), and pattern and scale have been considered a central problem in ecology (Levin 1992). To understand how and why species select particular habitat types or features within habitat types, we must first understand at what spatial scales the species views or perceives their habitat (Kotliar and Wiens 1990). However, species may respond strongly and simultaneously to habitat at different scales, and responses may be contradictory across scales (Bissonette et al. 1997). My dissertation research examined responses of Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*) to habitat features at several spatial scales. My overall goal was to understand how process and structure influence habitat choice at multiple spatial scales using the two carnivore species as case studies. Specifically, I evaluated habitat selection at the stand- (Chapter 1) and sub-stand scales (Chapter 2) for Canada lynx in northern Maine to understand how and why lynx perceive and utilize habitat heterogeneity within their home ranges. I also evaluated how martens in Newfoundland respond to habitat loss and fragmentation on a landscape-scale (Chapter 3), and compared threshold responses to habitat loss at the scale of the home range among two geographically isolated subspecies of marten in Maine and Newfoundland (Chapter 4).

American martens have large spatial requirements for their body size (Chapin et al. 1998, B. Hearn, unpublished report) and are sensitive to fragmentation (Bissonette et al. 1997, Chapin et al. 1998, Hargis et al. 1999). These specific habitat requirements of martens make them valuable as a coarse filter for evaluating broad-scale responses to pattern and processes within landscapes with different amounts of fragmentation. At the other end of the spatial scale spectrum, Canada lynx are food specialists that are predicted to respond to the fine-scale habitat responses associated with their primary prey, snowshoe hares (*Lepus americanus*). Although previous studies have documented stand-scale responses of lynx to specific habitat types, few studies had evaluated habitat selection for lynx at smaller spatial scales.

In Chapter 1, I compared three hypotheses related to habitat selection by Canada lynx during winter by evaluating stand-scale habitat selection, frequency of successful snowshoe hare kills, and tortuosity of foraging paths among 5 forest stand types. I evaluated whether lynx selected stands based on the highest densities of snowshoe hares (prey density hypothesis), based on areas where access to hares is enhanced by lower understory cover (prey access hypothesis), or based on areas with high thermal and escape cover for lynx (thermal and escape cover hypothesis). I also provided recommendations for provision of specific structural characteristics within managed forest stands.

In Chapter 2, I evaluated habitat selection by lynx at the sub-stand scale via analysis of movement patterns. I evaluated the prey density and prey access hypotheses by comparing foraging paths of lynx to determine if foraging effort was related to sub-stand scale structure of vegetation. I also evaluated at what spatial scales the movement paths of lynx responded to habitat by analyzing fractal dimension of movement paths across a range of spatial scales.

I developed predictive models of habitat occupancy for endangered Newfoundland martens in Chapter 3 and evaluated the relative influences of habitat loss versus habitat fragmentation on occupancy of landscapes by martens. I presented a model that predicts occupancy of landscapes by martens that can be used to predict how changes in habitat amount affect the probability of occupancy of landscapes by this endangered subspecies. Additionally, the model provides insights into the non-linear effects of habitat loss on species that are area-sensitive and exist in landscapes that are limited by the amount of suitable habitat.

In Chapter 4, I compared the responses of Newfoundland martens (*M. a. atrata*) and American martens in Maine (*M. a. americana*) to different amounts of suitable habitat, and identified threshold responses in occupancy. I compared empirical data from Newfoundland and Maine with theorized thresholds to fragmentation (Andrén 1994, Fahrig 1998, Angelstam et al. 2004) and to specific response curves hypothesized by previous researchers for martens in Utah and Maine (Bissonette et al. 1997). I evaluated whether martens experience linear declines, threshold responses, exponential declines, or curvilinear declines in occupancy based on the amount of suitable habitat within landscapes. These analyses provided insights into why threshold responses differ between the two sub-species and offered recommendations on the use of thresholds in habitat and landscape conservation.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

WINTER HABITAT SELECTION AND MOVEMENT PATHS BY CANADA LYNX IN MAINE

ABSTRACT

I studied winter habitat selection and compared frequency of successful snowshoe hare (*Lepus americanus*) kills and tortuosity of foraging paths among 5 forest stand-types to evaluate whether Canada lynx (*Lynx canadensis*) selected stands based on highest snowshoe hare densities (i.e., prey density hypothesis), based on areas where access to hares is enhanced by lower understory cover (i.e., prey access hypothesis), or based on areas with highest thermal and escape cover for lynx (i.e., thermal and escape cover hypothesis). I also estimated relative hare abundance based on track intersections and measured sub-stand scale structural characteristics in 5 stand-types and used an information-theoretic modeling approach to infer which characteristics in stands were associated with the highest densities of hares. Radiocollared adult lynx (3 F, 3 M) were snowtracked for 65.5 km during January - March, 2002 (2F, 1M) and 2003 (1F, 2M). At the stand-scale, lynx selected tall regenerating clearcuts (4.4-7.3 m, 11-26 years post-harvest) and established partially harvested stands (11-21 years post-harvest) and they selected against short regenerating clearcuts (3.4-4.3 m 11-26 years), recent partially harvested stands (1-10 years), and mature second-growth stands (>40 years, coniferous, deciduous, and mixed coniferous-deciduous). Density of snowshoe hares was positively associated with live stem cover units (SCU = 3 x coniferous saplings + deciduous saplings) and negatively associated with overstory canopy closure. Regenerating clearcuts (short and tall) supported the greatest relative density of hares based on having

the greatest SCU and the greatest index of hare abundance. Despite similar hare densities in tall and short regenerating clearcuts, taller clearcuts were in the self-thinning stage (i.e., 2.7X more dead saplings) and had 24% fewer conifer saplings and lower SCU, which likely enhanced the visibility and vulnerability of hares to lynx (i.e., support for the prey access hypothesis) and provided easier escape from fishers (*Martes pennanti*), who likely have a competitive advantage in stands with dense understories. Lynx killed a disproportionately greater numbers of hares in short and tall regenerating stands, despite that shorter stands had the highest cover value (i.e., SCU) for hares. This suggests a strong interaction between prey access and prey density in determining the foraging success of lynx. This interaction was apparent by the positive selection by lynx for established partial harvests, which had intermediate SCU and canopy closure, and intermediate hare densities; selection against recent partial cuts, which had the lowest hare densities and SCU; selection against mature stands, which had the highest canopy closure (negatively associated with hares) and low hare densities, and selection against short regenerating stands, which had high hare densities but the highest numbers of coniferous saplings and SCU. Correspondingly, the highest fractal dimension of foraging paths was in tall regenerating clearcuts and established partially harvested stands, suggesting that lynx were actively foraging in stands that provided intermediate to high hare density, intermediate cover for hares, and intermediate levels of canopy closure and live-tree basal area, but were exhibiting lower relative preference for stand-types with high densities of hares where coniferous saplings exceeded 14,000 stems/ha and SCU exceeded 50,000 stems/ha. Lynx also avoided stand-types with relatively lower prey density, with lower relative densities of conifer saplings (<5,000 stems/ha) and SCU

(<35,000 stems/ha), or stands with canopy closure >60%. In managed landscapes, high quality foraging habitat for lynx is provided by regenerating areas with few overstory trees dominated by a mixture of conifer and deciduous saplings that are in the stage of stem exclusion. In the Acadian forests of Maine, these stand conditions typically occur 10-30 years following partial or complete overstory removal.

INTRODUCTION

The Canada lynx (*Lynx canadensis*) is designated as federally threatened in the U.S. (USFS 2000) and is listed as provincially threatened (New Brunswick) or endangered (Nova Scotia) in some provinces of eastern Canada; however, little is known about habitat relationships of lynx in eastern North America (Aubry et al. 2000*b*, Ruggiero and McKelvey 2000, Ruggiero et al. 2000). Results of the few habitat studies conducted range-wide, primarily in the western United States and Canada (but see Parker et al. 1983, Hoving et al. 2004, 2005), have been extrapolated to areas with potentially unique ecologies (Buskirk et al. 2000), including differences in climate, prey abundance, predator-prey communities, tree species composition, and rates of forest succession. Because of these potential differences, region-specific data are needed to help elucidate habitat selection patterns of lynx in eastern North America.

Lynx are specialists on snowshoe hares (*Lepus americanus*) (Saunders 1963, Brand and Keith 1979), and habitat use by lynx is closely associated with density of hares (Koehler et al. 1979, Parker et al. 1983, Koehler 1990, O'Donoghue et al. 1998, Mowat et al. 2000). Within the mesic, mixed coniferous-deciduous Acadian forests of eastern North America (Seymour and Hunter 1992), silvicultural practices that create early-successional stages may increase densities of snowshoe hares (Monthey 1986, Fuller and

Harrison 2005, Homyack et al. 2006*a*) and associated foraging opportunities for lynx. Habitat choices by lynx may also be affected by factors other than high densities of snowshoe hares (Ruggiero et al. 2000), such as visibility and mobility needed to successfully capture hares (Parker et al. 1983, Murray and Boutin 1991, Murray et al. 1995, Mowat et al. 2000). Despite an apparent link between understory cover and hare density (Keith et al. 1984, Litvaitis et al. 1985*b*, Wirsing et al. 2002), it is unknown how the structure of vegetation affects the vulnerability of hares to be captured by lynx (Aubry et al. 2000*a*, Ruggiero et al. 2000). Habitat quality for lynx is likely determined by foraging success and prey accessibility rather than prey density (Parker et al. 1983, Murray et al. 1995).

I evaluated three competing hypotheses related to habitat selection by lynx during winter: 1) prey density hypothesis - lynx select areas with the greatest density of snowshoe hares; 2) prey access hypothesis - lynx select areas with intermediate densities of hares where lower stem cover enhances detection and pursuit of hares; and 3) thermal and escape cover hypothesis - lynx select areas with high thermal protection and escape cover from potential competitors (e.g., coyotes, *Canis latrans*; other lynx; fishers, *Martes pennanti,* and bobcats, *Lynx rufus*) provided by high canopy closure (thermal protection) of mature trees, which also provide vertical escape cover. To evaluate the three hypotheses, I modeled snowshoe hare density and vegetation relationships to provide an empirical framework for explaining which of the three hypotheses was most consistent with habitat selection by lynx. I then related stand-scale habitat selection by lynx during winter across 5 stand-types including short (3.4-4.3 m) and tall (4.4-7.3 m) regenerating (11-26 years post-harvest) clearcuts, recently (1-10 years) partially harvested stands

(PHS), longer-established (11-21 years post-harvest) PHS, mature forest (>40 years), and roads and their edges (30 m buffer) to the structural characteristics within each stand-type.

An understanding of variables that influence population density of snowshoe hares may facilitate inferences about which stand types are selected and avoided by lynx at the stand-scale. Thus, I evaluated which vegetation variables best described differences in hare abundance across the study area and compared the dominant structural characteristics within each stand-type to the variables most closely associated with high hare densities. I also calculated an index of relative hare abundance among stand types on the study area based on track intersections. Snowshoe hare kills and long beds were recorded to determine if stands that were selected for by lynx had disproportionate foraging success and resting sites. I also evaluated movement paths of lynx during winter to make inferences about foraging and travel patterns in habitat types selected for and against by lynx and hares.

Despite the apparent relationship of hare density with stem cover (Keith et al. 1984, Litvaitis et al. 1985*b*, Wirsing et al. 2002), others (Aubrey et al. 2000*a*, Buskirk et al. 2000, McKelvey et al. 2000*a*,*b*; Ruggiero and McKelvey 2000) have postulated that mature and overmature forests are important for lynx and hares (i.e., thermal and escape cover hypothesis). Thus, I also evaluated whether structural characteristics in mature stands coincided with high hare densities, patterns of stand-scale selection by lynx, higher foraging effort (i.e., more tortuous paths and more long beds/resting sites), and foraging success (kills per distance tracked).

The prey density hypothesis infers that lynx should select for areas that have the highest densities of snowshoe hares. The highest density of hares in Maine occurred in 16-yr-old regenerating clearcuts (1.64/ha), and densities were lower in mature coniferous stands (0.24/ha), mature mixed coniferous-deciduous stands (0.23/ha), mature deciduous stands (0.17/ha), and recent partially harvested mixedwood stands (0.17/ha) (Fuller and Harrison 2005). Snowshoe hares are associated with stands that have dense understories (Conroy et al. 1979, Orr and Dodds 1982, Wolfe et al. 1982, Keith et al. 1984, Litvaitis et al. 1985*b*, Wirsing et al. 2002) that provide hares cover from predation (Buehler and Keith 1982, Sievert and Keith 1985), thermal protection, and a source of browse (Litvaitis et al. 1985*b*). There was a strong relationship between hare density and stem cover units (3 x coniferous saplings + deciduous saplings) in eastern and western Maine and in Acadia National Park (Long 1995), suggesting that stem cover units (SCU) were an important determinant of hare density (Litvaitis et al. 1985*b*). The variable SCU adjusts for a difference in visual obstruction of softwood stems, thus, high values indicate greater thermal and predator escape cover for hares (Litvaitis et al. 1985*b*). Similar to snowshoe hares, lynx are also influenced by vegetation structure when selecting habitat; the most preferred vegetation types in the Yukon territory, Canada had high understory stem densities (Mowat and Slough 2003), which presumably supported high densities of snowshoe hares. If lynx select stands solely based on density of snowshoe hares, then I predicted that lynx would select for regenerating clearcuts with abundant coniferous understories and would exhibit lower relative preference for stands where hare density was low-intermediate, but where detectability of hares and lynx mobility would be enhanced by reduced numbers of woody stems.

Alternatively, the prey access hypothesis proposes that lynx would prefer stands where intermediate understory stem density provides lynx with greater visual detectability and enhanced pursuit of hares, and presumably, higher capture efficiency than in stands with optimal hare density and greater stem density. Hares use crypsis and escape through dense cover to avoid predators; therefore, dense understories provide hares with visual obstruction from predation, which has been documented to be positively associated with abundance of hares (Litvaitis et al. 1985*b*, Wirsing et al. 2002). Thus, I assumed that reduced understory density would be associated with lower hare densities. I evaluated this assumption by modeling vegetation variables associated with densities of hares and by calculating an index to relative hare abundance based on track intersections in snow.

Visual obstruction is particularly important for snowshoe hares to avoid predation because lynx hunt hares by stalking or ambushing (Murray et al. 1995, O'Donoghue et al. 1998*a*) and are thus adapted to visual foraging associated with their short-distance pounce and strike hunting technique (Kleiman and Eisenberg 1973). Hunting success by lynx in Nova Scotia was related more to cover that provided close encounters with hares than with density of hares (Parker et al. 1983). Lynx in the Yukon selected areas with the highest density of prey, but they used less dense cover than hares (O'Donoghue et al. 1998), which likely provided greater visibility and enhanced mobility when pursuing hares. Similarly, lynx in the Yukon were most successful in capturing prey in stands with low stem density and high visibility (Murray et al. 1995). Mowat et al. (2000) support these findings and suggest that some stands are too dense for lynx to be successful in capturing hares. The refugium of hares from predation that is provided by dense stands is evident during the lows in the snowshoe hare cycle when the few surviving individuals inhabit patches of dense vegetation (Wolff 1980). Despite the apparent protection provided to hares in stands with high woody stem densities, there is little empirical insight into how vegetation structure affects the vulnerability and accessibility of hares, and likewise, the mobility and visibility to hares by lynx (Aubry et al. 2000*a*, Ruggiero et al. 2000). I hypothesized that intermediate stem cover would place lynx at a selective advantage in foraging for snowshoe hares in areas with intermediate prey availability but relatively higher mobility and prey accessibility.

The thermal and escape cover hypothesis suggests that lynx would be associated with stands that have a closed overstory to provide thermal protection and mature trees to escape from potential predators at the expense of lower densities of snowshoe hares. Canopy closure and basal area are important thermal components for lynx because they intercept snow, moderate radiational heat loss, raise effective temperature by absorbing heat during the day, and reduce wind speed (Ozoga 1968, Kirchhoff and Schoen 1987, Pomeroy et al. 1998, Thompson and Fritzell 1988). Additionally, high basal area and the presence of mature trees provides vertical escape cover for lynx (e.g., from coyotes) and for kittens (e.g., from male lynx). Lynx experience infanticide by conspecifics (Elsey 1954, Nellis et al. 1972, Poole 1994, O'Donoghue et al. 1995, Slough and Mowat 1996, Apps 2000), so trees provided by increased basal areas could facilitate escape from coyotes and conspecifics.

Several authors have suggested that lynx require mature to over-mature coniferous forest (Aubry et al. 2000*a*, Buskirk et al. 2000, McKelvey et al. 2000*a*,*b*; Ruggiero and McKelvey 2000), particularly in the western United States. It is also suggested that old-growth coniferous forests provide temporally stable lynx habitat (Buskirk et al. 2000). Although mature stands have low densities of hares, they are proposed to be temporally stable for hares compared to regenerating clearcuts (Ruggiero et al. 2000). Buskirk et al. (2000) recognized that their hypothesis was based on weak evidence, and was largely derived from two hare studies (Lawrence 1955, Dolbeer and Clark 1975) conducted in the dry southern Rocky Mountains of Colorado where the shrub stage is absent from regenerating stands, from an unpublished study in Montana (Mills and Henderson, unpublished data), and from a Ph.D. dissertation in Wyoming (Beauvais 1997). Those authors suggest that lynx require mature forest despite the majority of evidence suggesting that the highest stand-scale densities of snowshoe hares are associated with shrub-sapling stages of regeneration (Conroy et al. 1979, Orr and Dodds 1982, Wolfe et al. 1982, Keith et al. 1984, Litvaitis et al. 1985*b*, Ferron et al. 1998, Hodges 2002*a,b*; Wirsing et al. 2002).

Mature conifer forests have also been postulated to provide denning habitat for lynx during summer (Koehler 1990, Squires and Laurion 2000), but this is again based on weak evidence from studies with small sample sizes (n = 4 and n = 1, respectively). Despite very limited empirical evidence in the western United States that mature and over-mature conifer forests are important for lynx, several studies have documented that lynx select against mature forests (Parker et al. 1983, Kesterson 1988, Mowat and Slough 2003). In Maine, mature coniferous forest was not associated with broad-scale occurrences of lynx, and mature deciduous forest was negatively associated with presence of lynx (Hoving et al. 2004), possibly because mature forest types in Maine have low densities of snowshoe hares (0.17-0.24 hares/ha) (Fuller and Harrison 2005).

Mature stands have high overhead canopy closure, and densities of snowshoe hare pellets were significantly lower in stands with 61-100% canopy closure than in stands with less canopy closure (Orr and Dodds 1982). Greater canopy closure in mature stands may be negatively associated with hare densities, particularly if understory stems are shaded out. Although the association of lynx with mature coniferous forests may be postulated as important in the western United States, there is no evidence for a positive association with mature forests in the eastern United States (Hoving et al. 2004) where forests are structurally more complex, mesic, and have younger age structures.

Further evidence to evaluate the three hypotheses related to habitat selection by lynx was obtained by quantifying characteristics of movement paths during winter. Animal movement patterns are influenced by the type and heterogeneity of habitat types (Crist et al. 1992, Wiens et al. 1995, Bascompte and Vilà 1997, Edwards et al. 2001, Phillips et al. 2004), and an analysis of path tortuosity in different habitat types can provide insights into habitat use patterns (Sugihara and May 1990, With 1994*a*, Bascompte and Vilà 1997). Straight line travel by lynx may indicate traveling, while more tortuous paths may indicate hunting or foraging behavior (Parker 1981, Arditi and Dacorogna 1988) and an attempt to maximize exposure and time investment in preferred foraging areas. Area-restricted foraging (Kareiva and Odell 1987, Haskell 1997) for snowshoe hares should increase foraging intensity and result in higher tortuosity of movement paths (Nams and Bourgeois 2004). I used tortuosity of paths as measured by fractal dimension (Mandlebrot 1967) to evaluate if lynx expend greater foraging effort in stands with vegetation supporting optimum hare densities (i.e., prey density hypothesis) or whether foraging effort was greater in stands with intermediate densities of hares and reduced stem cover (i.e., prey access hypothesis).

STUDY AREA

The lynx study area included parts of 9 townships in northwestern Maine, USA (T10 R10 WELS, T10 R11 WELS, T11 R10 WELS, T11 R11 WELS, T11 R12 WELS, T11 R13 WELS, T12 R11 WELS, T12 R12 WELS, T12 R13 WELS) with elevations 244-536 m. The townships were intensively managed for pulpwood and saw timber. Forestry activities included timber harvesting (clearcutting and partial harvesting), herbicide application to favor coniferous regeneration, and precommercial thinning to reduce competition among trees, increase rate of growth of crop trees, and to shorten harvest rotations. Partial harvesting, as defined by the Maine Forest Practices Act (12 MRSA Chapter 805, Subchapter III-A) of 1989 (Maine Forest Service 1990), is a timber harvest operation >2.02 ha in extent that results in a residual stand of trees ≥11.4 cm dbh with a residual basal area >6.9 m^2/ha, and includes shelterwood (harvest of mature trees in two or more stages creating an even-aged stand), selection harvests (harvest of mature trees individually or in small patches creating an uneven-aged stand), and overstory removal (a single entry where mature trees are removed to release natural advanced regeneration, stocked with at least 1,111 trees/ha). Clearcutting is defined by a complete overstory removal resulting in a residual basal area <6.9 m^2/ha (Maine Forest Service 1990).

Stand types on the study area (defined by the outer bounds of lynx home ranges) included (Table 1.1) mature (>40 years post-harvest) second-growth forest (10.6% mixed coniferous-deciduous, 26.9% deciduous, and 62.5% coniferous) with a regenerating understory, which represented 6.2% of the study area ($\overline{X}$ stand area = 8.96 ha);

Table 1.1. Description of stand types on the study area in northern Maine, including percent composition of the overstory or regenerating component of stands, percent of the study area that each stand type represents, and mean stand area.

Stand Type[a]	Composition (%)			% of Study Area	Mean Stand Area (ha)
	Mixed	Deciduous	Coniferous		
Mature	10.6	26.9	62.5	6.2	9.0
Regen Short	28.5	0.40	71.1	12.8	14.5
Regen Tall	57.7	22.0	20.3	15.9	13.0
PH Recent	18.4	73.8	7.8	7.6	17.6
PH Established	35.9	55.6	8.5	3.4	10.2

[a] Mature = >40 year old second-growth stands, Regen Short = 11-26 year old, 3.4-4.3 m regenerating clearcut, Regen Tall = 11-26 year old, 4.4-7.3 m regenerating clearcut, PH Recent = 1-10 year old partial harvest, PH Established = 11-21 year old partial harvest.

regenerating (11-26 years post-harvest) short (3.4 - 4.3 m tall) clearcuts (28.5% mixed coniferous-deciduous, 0.4% deciduous, 71.1% coniferous), which represented 12.8% of the study area ($\bar{X}$ stand area = 14.5 ha); tall (4.4-7.3 m tall) regenerating clearcuts (57.7% mixed coniferous-deciduous, 22.0% deciduous, 20.3% coniferous), which represented 15.9% of the study area ($\bar{X}$ stand area = 13.0 ha); recent (1-10 years) partially harvested (61.7% selection harvesting, 25.8% overstory removal, 12.5% shelterwood) stands (18.4% mixed coniferous-deciduous, 73.8% deciduous, 7.8% coniferous), which represented 7.6% of the study area ($\bar{X}$ stand area of 17.6 ha); and established (11-21 years) partially harvested (88.6% selection harvesting, 10.7% overstory removal, 0.7% shelterwood) stands (35.9% mixed coniferous-deciduous, 55.6% deciduous, 8.5% coniferous), which represented 3.4% of the study area ($\bar{X}$ stand area = 10.2 ha). The remaining 14.7% of the study area was composed of precommercially thinned stands (PCT), early successional (<10 years) clearcuts, older regenerating clearcuts (>7.3 m tall), non-forested areas, and water; areas in these land-cover categories were omitted from statistical analyses because they were considered non-habitat for lynx (water and non-forest), or because there was not enough of the type (<5% within home ranges) to statistically evaluate habitat selection (PCT, early successional clearcuts, older regenerating clearcuts). Many of the short- and tall-regenerating clearcuts received herbicide treatment (primarily glyphosate) 5-10 years post-harvest, which releases conifers from competition with deciduous trees and saplings (Newton et al. 1989, 1992) and often results in dense understories with high SCU.

Dominant species in second-growth deciduous stands included red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch

(*Betula papyifera*), and yellow birch (*B. alleghaniensis*). Second-growth coniferous forests were composed of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white pine (*Pinus strobus*). Forests regenerating from clearcutting were primarily composed of balsam fir, red spruce, red maple, paper birch, and raspberries (*Rubus* sp.).

The snowshoe hare study area was located in 2 townships in north-central Maine (T4 R11 WELS and T5 R11 WELS), approximately 50 km south of the lynx study area, but within the geographic distribution of lynx in Maine (Hoving et al. 2005). The area was managed for pulpwood and saw timber, and approximately 56% of the area was clearcut during 1974–1994. Dominant tree and shrub species were similar between the lynx and snowshoe hare study areas. The snowshoe hare study area was described in detail by Fuller and Harrison (2005).

METHODS

Overview

I evaluated whether structural differences between habitat types selected positively versus negatively by lynx were consistent with sub-stand scale habitat choices by snowshoe hares. I used previously published stand-specific density estimates for hares (Fuller et al. 2005) in the region and related them to stand types selected for and avoided by lynx. I also modeled sub-stand scale structural variables influencing hare density on a study area located to the south of the lynx study area, but within the geographic distribution of lynx in Maine (Hoving et al. 2005) and made comparisons to the structural attributes of stands selected for and avoided by lynx. Additionally, I obtained an index of relative abundance of hares on the lynx study area by calculating the density of hare intersections on random snowtrack transects within lynx home ranges. I evaluated stand-scale habitat selection by lynx during winter and then identified the structural characteristics within lynx home ranges that differentiated habitat types used greater than versus less than availability at the scale of the forest stand. The estimate of habitat use in the stand-scale analysis was obtained from snowtracking 6 radiocollared lynx during winter (percent of distance traveled by individual lynx in each habitat type) and the estimate of availability was obtained from defining home ranges based on radiotelemetry data (percent of each habitat type within the home range of an individual lynx). I also compared movement paths of lynx among habitat types previously documented to support different densities of hares. I used fractal dimension to evaluate the hypothesis that stands with high-intermediate densities of hares and understory vegetation would be associated with the highest values of fractal dimension (i.e., support for prey density or prey access hypothesis).

Snowshoe Hare Model

I developed a model to determine which within-stand structural variables best predicted stand-scale densities of snowshoe hares. Fecal pellet-counts provide a reliable index of over-winter abundance of snowshoe hares (Wolff 1980, Litvaitis et al. 1985*a*, Krebs et al. 1987, Murray et al. 2002, Homyack et al. 2006*b*, Mills et al. 2005). I censused hare pellets during 1996 and 1998 within 12 5-m x 30-cm transects on grids that were used to sample small mammals during a companion study (Fuller et al. 2004). Overstory types included regenerating clearcuts (11-20 years old; *n* = 7; 5 in 1996, 2 in 1998), second-growth mixed coniferous-deciduous (*n* = 7 grids; 3 in 1996, 4 in 1998) stands, second-growth mixed stands that were recently (3 – 6 years post harvest) partially harvested (*n* = 7; sampled in 1998), second-growth deciduous (*n* = 2; 1 in 1996, 1 in

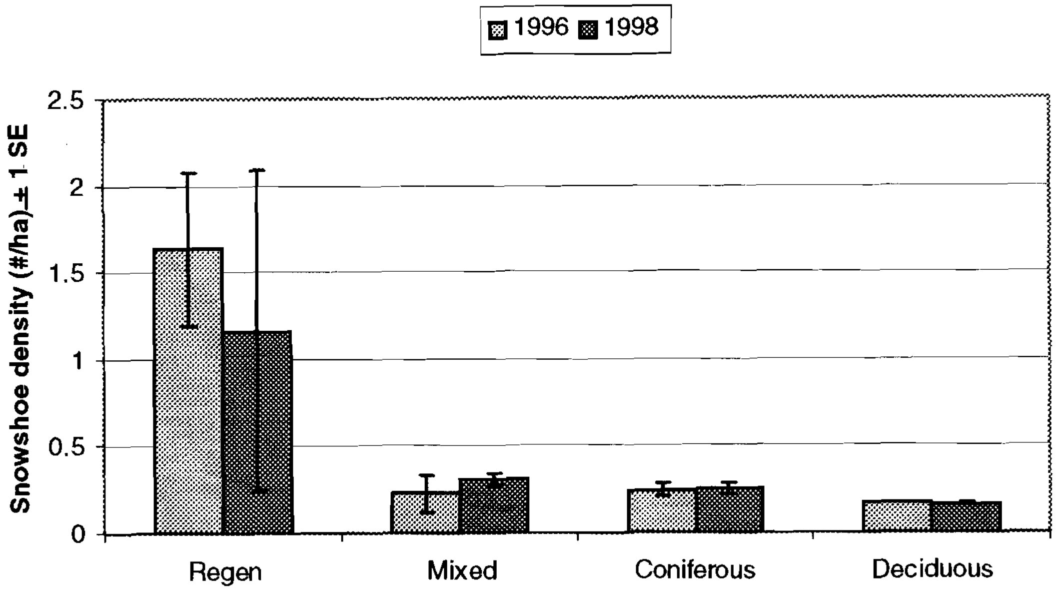

Figure 1.1. Temporal stability and relative density of snowshoe hares across stand-types (Regen = regenerating clearcut, 14-16 years old, n = 2; Mixed = second-growth, 80-140 years old coniferous-deciduous, n = 7; Coniferous = second-growth coniferous, n = 2; Deciduous = second-growth deciduous, n = 2) in north-central Maine, winters 1996 and 1998.

1998), and second-growth coniferous ($n = 2$; 1 in 1996, 1 in 1998) stands. Transects were cleared of all pellets during October of 1995 and 1997 and pellets deposited during winter and prior to emergence of deciduous leaves were counted during May of the following year. I used the regression formula of hare density/ha = (0.15979 + 0.0001 x pellet density/ha/month; $r^2 = 0.87$, $P < 0.001$) to transform over-winter pellet densities to over-winter hare densities (Homyack et al. 2006*b*). Stands were included from both winters (1996 and 1998) because snowshoe hare densities were stable during the 3-year period of the study (Figure 1.1).

Habitat variables were measured in 10 m x 2 m rectangular plots during summers 1995 and 1997. I measured density of coniferous and deciduous saplings (<7.6 cm dbh, >1.5 m height, alive), percent overhead canopy closure, and basal area of snags and live deciduous and coniferous trees. Understory lateral foliage density was estimated by recording visual obstruction for each 0.5 m zone (0-0.5, 0.5-1.0, 1.0-1.5, 1.5-2.0 m) on a 2.0 m cover pole as the percent of 0.1 m bands ≥25% obstructed by vegetation (Griffith and Youtie 1988). A detailed description of methods used to sample vegetation was described in Fuller et al. (2004). I averaged each habitat variable across 12 sampled plots to produce an average value for each stand. I screened for multicollinearity with a Pearson correlation matrix (r), and based on the recommendation by Burnham and Anderson (2002), retained all variables with $|r| \leq 0.95$. I used a squared transformation of canopy closure to meet parametric assumptions of normality (Zar 1999).

I used an information-theoretic approach based on Kullback-Leibler (K-L) information to rank multiple *a priori* models. I computed AIC values and Akaike weights (w_i), and made inferences from these models following the methods of Burnham and Anderson (2002). I used AIC_c, the second-order AIC for small sample size, to compare 8 *a priori* models selected based on previously defined relationships between snowshoe hare density and vegetation variables that were biologically meaningful. I calculated AIC_c using the residual sum of squares from least-squares models (Burnham and Anderson 2002). I re-scaled AIC_c values relative to the best model, which received a ΔAIC_c value of zero. This model is considered the best model to approximate the data given the set of models considered. Values of ΔAIC_c from 0-2 are considered to have substantial support as being the K-L best model, values 4-7 have considerably less support, and values >10 have no support (Burnham and Anderson 2002). I evaluated ΔAIC_c and Akaike weights to select the most plausible model from the set of models considered. I also calculated the likelihood of the model [$\exp(-\frac{1}{2}\Delta_i)$] to determine the relative strength of evidence for each model. The model was developed for explaining habitat associations of snowshoe hares and was not developed for prediction, thus model averaging was not incorporated.

I developed a set of biological hypotheses based on within-stand variables known to influence snowshoe hare density and or risk of predation. I considered understory lateral foliage density, which is predicted to influence hare densities via lateral visibility to predators (Orr and Dodds 1982, Wolfe et al. 1982, Litvaitis et al. 1985*b*). Overhead canopy closure and basal area of trees and snags were included as variables for their potential to reduce understory density and for their effects on predation. I included the four single variable models (SCU, canopy closure [cc], basal area [BA], understory lateral foliage density [ULFD]), a global model, and 3 models with 2 variables (SCU + CC, CC + ULFD, ULFD + BA). Stem cover units and overhead canopy closure were included in a model because dense overhead cover is likely to reduce density and diversity of understory stems and, hence, density of hares. I included two models that described variables related to access to hares by avian and mammalian predation. Both models included understory lateral foliage density because of its potential association with access to hares and visibility of prey. Canopy closure was added to one model and basal area to the other to determine which was more important in combination with understory lateral foliage density.

Snowtracking

I chose 3 adult male and 3 adult female lynx with kittens out of a larger sample of 17 lynx. The lynx were chosen based on their proximity to each other, with the constraint that females produced kittens the previous spring. We followed 2 females and 1 male in 2002 and 1 female and 2 males in 2003. I was constrained to sample 3 lynx each year because of the short winter season (3 months), the maximum distance that lynx could be tracked in a day (two crews tracking 1 lynx for approximately 1 km each day), the goal of 10 km tracked per lynx, and the variable snow conditions. All tracking occurred <48 hours after snowfall, but typically <24 hours after snowfall (88% of sampling occurred <24 hours after snowfall). When snow conditions were favorable for tracking, 2 lynx were followed each day, with the goal of tracking each lynx for ≥1 km. We alternated the lynx that were tracked to ensure that each lynx was followed at least every other day when favorable snow conditions occurred.

We located radiocollared lynx, intersected their tracks, and back-tracked them on snow until the track was obscured by fresh snow or until the track was confused with tracks of other animals. We utilized continuous real-time GPS sampling (Trimble Pro

XR®) with sub-meter accuracy to map foraging paths of lynx. I calculated the distance tracked by converting observer-specific paces to meters. I spatially verified all prey kills and long beds (resting beds; defined as an area where a lynx bedded long enough for an ice crust to form; Parker 1981, O'Donoghue et al. 2001) that were encountered on the lynx track. I calculated the expected number of snowshoe hare kills and long beds in each habitat type (regenerating short and tall pooled; recent partial harvest, established partial harvest, mature, and road edge pooled) based on the total percent of the habitat type within home ranges, and tested whether the observed distribution fit the expected distribution using a X^2 test with Yate's correction for continuity (Zar 1999). Because hare densities in Maine have been previously documented to be greatest in regenerating clearcuts (Fuller and Harrison 2005, Homyack et al. 2006*a*), I evaluated whether lynx conformed to the prey density hypothesis and killed more hares and rested more frequently than expected in regenerating clearcut stands (short and tall pooled) than in all other stand types. I also indexed relative hare abundance by recording all snowshoe hare intersections on random transects that were surveyed within lynx home ranges and calculated an index of hare abundance in each stand type as the number of intersections of hare tracks per 100 m of transect. The index was adjusted for the number of 12-hour periods since last snowfall (Thompson et al. 1989), and did not include data >96 hrs after snowfall. I used a combination of density estimates for hares (Fuller and Harrison 2005) and the finer-scaled prey encounter index (track intersections by stand-type) to make inferences about whether lynx foraged disproportionately in areas with the highest hare density or prey encounter rate.

Landcover Database

Forest-type coverages to define areas used and available for lynx were based on stereoscopic interpretation of 1:15,840 color infrared aerial photographs obtained from Irving Woodlands, Clayton Lake Woodlands, and Seven Islands Land Company. Overstory types and snow-track data from lynx were incorporated in a geographic information system (ArcInfo 8.3, Environmental Systems Research Institute, Redlands, California). I defined habitat types that were biologically relevant to lynx and snowshoe hares based on previous associations and their relation to the prey density, prey access, and thermal and escape cover hypotheses and then combined landowner coverages.

Habitat types used in the analyses included short (3.4 - 4.3 m tall) and tall (4.4-7.3 m tall) regenerating (11-26 years since cutting) clearcuts, recent (1-10 years post-cut) and older established (11-21 years) partially harvested stands, mature (>40 years) second-growth stands (coniferous, deciduous, and mixed coniferous-deciduous), and road edge (30 m buffer on both sides of road). Road edge was defined as a transition zone between adjacent habitats (Murcia 1995) where vegetation structure is affected (Matlack 1994, Murcia 1995). Previous studies have quantified that edge effects persist up to 50 m from openings into the forest from the perspective of vertebrates and plants (Paton 1994, Murcia 1995) and 25-35 m for amphibians in Maine (DeMaynadier and Hunter 1998). Thus, I was conservative and set a 30 m buffer surrounding each side of roads to account for an edge effect. I included regenerating clearcuts of two different height classes (3.4 - 4.3 m and 4.4 - 7.3 m) because it is unknown if there is a height threshold to receive high use by snowshoe hares and because stands of the same age with more advanced development (i.e., taller trees) may undergo self-thinning sooner. It is known that regenerating clearcuts contain high densities of understory stems and high densities of snowshoe hares in Maine (Fuller and Harrison 2005), thus I included these types to evaluate the prey density and prey access hypotheses. I was also interested in young regenerating clearcuts with low regeneration (<3.4 m tall), but there wasn't enough of this type on the study area to statistically evaluate. I differentiated between recent and established partial harvests because recent partial harvests often support low densities of snowshoe hares in Maine (Fuller and Harrison 2005), but there was no information on hare densities or the use by lynx in established partial harvests within the Acadian forest when this study was initiated. I included mature second-growth stands to evaluate the thermal and escape cover hypothesis.

Habitat Selection

Habitat availability for lynx

Home ranges of lynx were estimated to provide third-order estimates of habitat availability (Johnson 1980) for analyzing stand-scale habitat selection by lynx during winter. Lynx were captured using foothold traps (Victor #3 soft catch traps, Woodstream Corp, Litiz, PA) or cage traps (model #50590, Safeguard Products, Inc., New Holland, PA) and were fitted with radio collars (SMRC-1, Lotek Wireless, Inc., Newmarket, ON, Canada). Lynx were immobilized with a 5:1 mixture of ketamine hydrochloride (100 mg/ml) and xylazine hydrochloride (100 mg/ml) administered intramuscularly with a syringe pole or dart gun. The locations of lynx were determined approximately every 3-4 days from fixed-wing aircraft (Piper Super Cub or Cessna 172) with 2 side-facing H-antennas mounted to the wing struts (Gilmer et al. 1981). The locations of lynx were recorded with a global positioning system (GPS) (GPS Map 195, Garmin International, Inc., Olathe, KS). Error associated with aerial telemetry was estimated at 44.3 m (SE = 5.5 m) based on the mean difference between actual and estimated locations for 22 transmitters. I calculated yearly (1 November – 31 October) 90% fixed kernel home ranges (Worton 1989) of adult lynx using the Animal Movements Extension (Hooge and Eichenlaub 2000) for ArcView (Environmental Systems Research Institute, Redlands, CA, USA). There was an insufficient number of relocations to calculate seasonal ranges; however, home ranges during winter have been documented to be larger than during summer (Bailey et al. 1986, Kesterson 1988, Squires and Laurion 2000), so the estimates of annual home range including both summer and winter seasons likely approximated winter home range size and incorporated winter availability (i.e., 97.3% of lynx foraging paths occurred within the annual home-range areas determined prior to snowtracking).

Selection analyses

I evaluated habitat selection at the scale of the forest stand by comparing the distance traveled by lynx in each overstory type (e.g., recent and established partial harvest, short and tall regenerating clearcuts, second-growth stands, and road edge) (Parker 1981, Murray et al. 1994) to the percent of those overstory types within the 90% fixed kernel home range of each lynx (estimated based on radiotelemetry data). Stand-scale habitat selection (third-order selection, *sensu* Johnson 1980) was evaluated for overstory types within home ranges using individual lynx as the sampling unit. I calculated log-ratio selection indices as *ln*(use/availability) (Aebischer et al. 1993) where use was defined as the proportional distance traveled by an individual lynx in a particular overstory type and availability was defined as the total percent of that overstory type within the home range. Differences in habitat selection were inferred by examination of non-overlapping standard errors around the mean log ratios (Gosselink et al. 2003). The natural log transforms the selection index so that it is centered on zero, which indicates use is in proportion to availability. Values greater than zero indicate use is greater than availability, and values less than zero indicate use is less than availability. Based on the small sample size (n = 3 of each sex), I was unable to statistically evaluate whether there was a difference in habitat selection between males and females, so I pooled data cross sexes. Mowat and Slough (2003) and Poole et al. (1996) reported that habitat selection did not differ between sexes in the Yukon (n = 45 F, 58 M) and Northwest Territories (n = 12 F, 15 M), respectively.

Stand-Scale Habitat Characteristics

To help explain the stand-scale habitat selection results by lynx and to evaluate the three competing hypotheses, vegetation was sampled within all overstory types while snowtracking and differences between habitat types that were selected for and avoided by lynx were evaluated. Additionally, habitat characteristics were measured (using a stratified random design) on transects that were placed within verified home ranges of lynx. The starting point and direction of each 1-km long transect was randomly chosen, with the constraints that the transect was completely inside the home range, and that all habitat types were proportionally sampled relative to the composition of habitat types within home ranges. Vegetation was measured in 6 m x 2 m plots spaced every 100 m. A total of 471 vegetation plots were sampled and the values were averaged across plots within stands: 125 plots in short regenerating clearcuts, representing 36 stands; 155 plots in tall regenerating clearcuts, representing 52 stands; 95 plots in recent partial harvests, representing 24 stands; 52 plots in established partial harvests, representing 15 stands, and 44 plots in mature second-growth stands, representing 23 stands. Canopy closure was measured at the center of the plot with a spherical densiometer (Lemmon 1956) and readings from the four cardinal compass directions were averaged. Basal area of live coniferous and deciduous trees (m^2/ha) was calculated with a 2-factor wedge prism (Avery and Burkhart 2002) and deciduous, coniferous, and dead saplings (<7.6 cm diameter, stems protruding through snow pack) were counted within the 12 m^2 plots. Further, I compared habitat variables selected for by lynx with the best explanatory variables from the models of snowshoe hare density to evaluate whether predator and prey were selecting for similar structural attributes within stands.

To determine if structural differences accounted for positive versus negative habitat selection by lynx at the stand-scale, I used a multivariate Hotelling's T^2 (Rencher 1995) to test for differences in stand-scale variables between treatments that represented different successional stages and were habitat types that were selected differently by lynx. Specifically, I compared regenerating short versus tall clearcuts to determine which structural variables created favorable conditions for lynx as clearcuts matured. I compared recent and established partially harvested stands to evaluate structural differences as partially harvested stands matured. I also compared differences between established partially harvested stands and mature second-growth stands to evaluate if the structure of older partially harvested stands converged towards the characteristics of mature stands. Normality of each variable was assessed with Lilliefor's test and homogeneity of error variances with Levene's test (Milliken and Johnson 1992). I transformed (Zar 1999) non-normal variables or those exhibiting heteroscedasticity to meet parametric assumptions. If the Hotelling's T^2 test suggested differences in habitat variables between habitat types, I used univariate *F*-tests with a Bonferroni-adjusted critical value of α/k (Rencher 1995) to determine which habitat variables differed significantly between habitat types selected for versus against by lynx.

Fractal Dimension

I used fractal dimensions to describe differences in movement paths (foraging versus travel) between habitat types that were selected for and avoided by lynx at the stand scale. Fractal dimension ranges from D = 1 when the path is a straight line to D = 2 when the path is so tortuous that it completely fills a plane. Fractal dimensions were calculated using a modification of the traditional divider method (Sugihara and May 1990) using the fractal mean estimator in the program FRACTAL 4.00 (V.O. Nams, Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). The measured length of a pathway decreases as the measurement scale increases according to the relationship:

$$L(\delta) = k\delta^{1-D}$$

where L is the length of the pathway, δ is the divider size that is used to measure the path, *k* is a positive constant, and D is the fractal dimension. The regression of log (total path length) versus log (divider size) results in a slope, which is subtracted from 1 to yield D. The specific value of fractal dimension has little biological meaning, but the relative fractal dimension gives insights into the time spent in a habitat type if it is calculated across the same range of spatial scales for all movement paths (Doeer and Doeer 2004). Relative D was calculated for each movement path by analyzing D over the same range of spatial scales (4 – 50 m). The minimum scale represented the lowest resolution of the data, which was a combination of the sampling precision of an observer on snowshoes (1 m) and the maximum distance between any two GPS points along the movement paths (4 m). The maximum scale was set by finding the distance that represented approximately 75% of all path lengths in each habitat type. I then used 1/3 that distance (With 1994*a*) to arrive at a maximum scale of 50 m. Minimum path length used in the analysis was 100 m. I estimated D at 50 spatial scales using dividers, with a minimum calculated as the lowest spatial scale divided by 1.25 to a maximum of the largest spatial scale times 1.25. The slope of the plot of log (total path length) vs. log (divider size) was calculated within each window of spatial scales, resulting in one overall estimate for D over the range of spatial scales considered. I analyzed the influence of sex, habitat type, and a sex-habitat interaction term on fractal dimension values with an Analysis of Variance (ANOVA) using a log (D-1) transformation. Habitat types used in the ANOVA were those types selected for by lynx at the stand-scale (tall regenerating clearcuts and established partially harvested stands pooled) and types selected against by lynx (short regenerating clearcuts and recent partially harvested stands pooled). I excluded mature stands from the analysis so the vegetation characteristics associated with mature stands would not confound the fractal dimension values (e.g., it would be difficult to interpret whether a high fractal dimension in mature stands was associated with hunting or an attempt by lynx to maximize time spent in a stand with higher thermal and escape cover), and instead chose to compare only among the harvested treatments.

RESULTS

Snowshoe Hare Model

Based on *a priori* knowledge of snowshoe hare habitat associations, I included 4 variables or combinations of variables to develop explanatory models of hare habitat-density relationships (Table 1.2). Correlation among variables was $<|0.83|$ (Table 1.3).

Table 1.2. Akaike's Information Criterion adjusted for small sample size (AIC_c) for the *a priori* set of candidate models considered to examine the influence of stem cover units (SCU), overhead canopy closure (CC), basal area (BA), and understory lateral foliage density (ULFD) on density of snowshoe hares in 25 stands during winters 1996 and 1998, north-central Maine.

Model[a]	Rank	K^b	Log $(L)^c$	AIC_c	ΔAIC_c	Model Likelihood	w_i^d
SCU + CC	1	4	5.544	-1.089	0	1.000	0.809
SCU	2	3	2.459	2.224	3.313	0.191	0.154
SCU + CC + BA + ULFD	3	6	5.767	5.133	6.222	0.045	0.036
CC + ULFD	4	4	-5.233	20.466	21.554	0	0
CC	5	3	-6.807	20.757	21.845	0	0
BA	6	3	-7.698	22.538	23.627	0	0
ULFD	7	3	-8.125	23.392	24.481	0	0
ULFD + BA	8	4	-7.088	24.176	25.265	0	0

[a] SCU = stem cover units (3*coniferous saplings +deciduous saplings), positive effect on density of snowshoe hares; CC = percent overhead canopy closure, negative effect; BA = basal area of snags and deciduous and coniferous trees, negative effect; ULFD = percent understory lateral foliage density, positive effect.

[b] K = number of estimable parameters.

[c] Log (L) = log-likelihood = $-n/2*\log(\hat{\sigma}^2)$ (Burnham and Anderson 2002).

[d] w_i = Akaike weight.

Table 1.3. Pearson correlation coefficients among 4 snowshoe hare habitat variables considered for inclusion in linear regression models for explaining density of snowshoe hares during winters 1996 and 1998 in north-central Maine.

	Canopy	Foliage density	SCU	Basal area
Canopy[a]	1.000			
Foliage density[b]	-0.305	1.000		
SCU[c]	-0.324	0.448	1.000	
Basal area[d]	0.828	-0.610	-0.267	1.00

[a] Canopy = percent overhead canopy closure.

[b] Foliage density = percent understory lateral foliage density.

[c] SCU = stem cover units (3*coniferous saplings + deciduous saplings).

[d] Basal area = basal area of snags + deciduous trees + coniferous trees.

The top ranked model was SCU (positive association) + overhead canopy closure (CC; negative association) ($\Delta AIC_c = 0.00$, likelihood = 1.00, adjusted $r^2 = 0.729$). The second ranked model was the single variable model SCU ($\Delta AIC_c = 3.31$, likelihood = 0.191, adjusted $r^2 = 0.654$), which also had substantial support as being a comparable model to the SCU + CC model (Table 1.2). The Akaike weight for the top ranked model (SCU + CC) indicates that the approximate probability that this model is the Kullback-Leibler best model is 81%. The combined Akaike weights for the top two models was 0.963 (Table1.2), suggesting that SCU and canopy closure are the 2 most important variables in explaining density of snowshoe hares across the 25 stands that were sampled. Variable importance was calculated by summing Akaike weights for all models containing a given predictor variable. The variable with the largest predictor weight is estimated to be the most important; SCU was greatest (1.0), followed by canopy closure (0.85), basal area (0.04), and understory lateral foliage density (0.04) (Table 1.2). The relationship between the variables and hare density was positive for SCU and understory lateral foliage density and was negative for canopy closure and basal area.

Stand-Scale Habitat Selection

Radiolocations totaling 592 were recorded and used to calculate home ranges for the 3 male and 3 female lynx ($\bar{x} = 99$, range = 85-113) included in the study. One lynx had 1% established partially harvested stands within the home range and no use, so the selection index for that lynx was not used when evaluating selection of that vegetation type. Stand-scale habitat selection by lynx was strongest for tall regenerating clearcuts and established partially harvested stands (Figure 1.2). Lynx selected against short

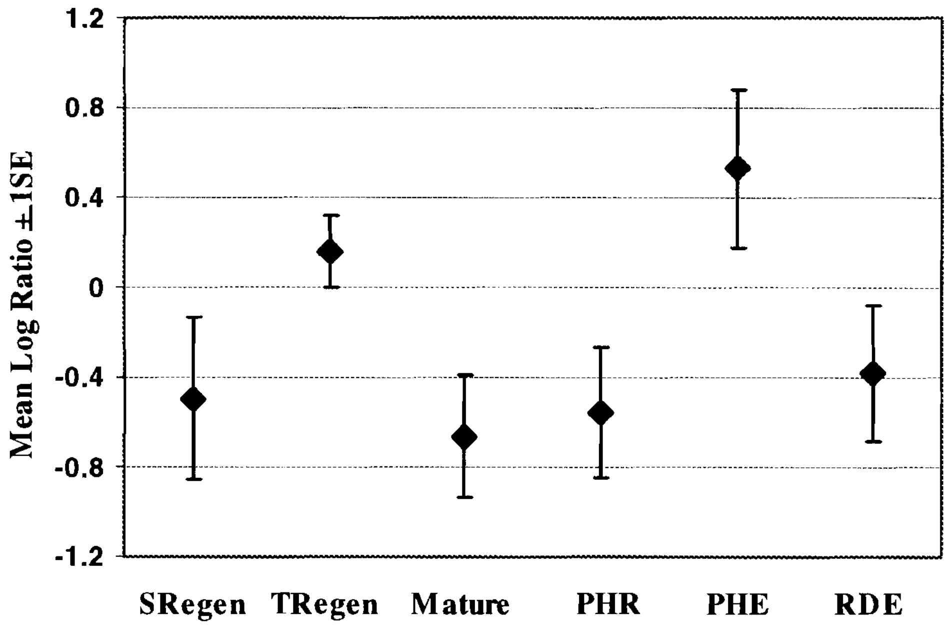

Figure 1.2. Mean (±SE) selection indices [ln(use/availability)] for 6 habitat types [SRegen = regenerating (11-26 year post-harvest) short (3.4-4.3 m tall) clearcut; TRegen = regenerating tall (4.4-7.3 m) clearcut; Mature = >40 year-old second-growth stands with a regenerating understory; PHR = recent partial harvest, 1-10 year post-harvest; PHE = established partial harvest,11-21 year post-harvest; RDE = road edge (30m buffer on both side of roads)], used to evaluate stand-scale habitat selection by Canada lynx in northern Maine, winters 2002-2003.

regenerating clearcuts and road edge and strongly selected against recent partially harvested and mature stands (Figure 1.2).

Snowtracking and Snowshoe Hare Kills

Radiocollared adult lynx were snowtracked during January – March 2002 (2F, 1M) and 2003 (1F, 2M) for 65.5 km (median = 10.77 km/lynx, range = 9.64 – 12.34), representing 74 individual snow-tracking days (median = 12 snowtracks/lynx, range = 11 – 14). All adult females were accompanied by kittens (1, 2, and 3 kittens) that remained with them during the January-March period when snowtracking occurred. We observed 16 snowshoe hare kills (12 by females, 4 by males); lynx killed 81% (13 of 16) of the hares in regenerating clearcuts (regenerating short, $n = 5$, regenerating tall, $n = 8$). The remaining (19%) of kills were observed in a recent (6 year-old) partially harvested stand ($n = 1$), in an established (12 year-old) partially harvested stand ($n = 1$), and in an early-successional (<3.4 m tall) clearcut ($n = 1$). There was a significant difference ($X^2 = 5.86$, $P = 0.02$, 1 *df*) between the frequency of kills in regenerating clearcuts (short and tall pooled) and all other types (recent and established partial harvest, mature, and road edge pooled) relative to the number of kills expected based on the percent of the vegetation-class within home ranges. Lynx killed more hares than expected in regenerating stands (tall and short), killed hares as expected in established partial harvests, and killed fewer hares than expected in recent partial harvests, mature second-growth stands, and road edge (Table 1.4). There were 34 long beds (23 M, 11 F) used by lynx. There was no difference ($X^2 = 0.80$, $P = 0.37$, 1 *df*) in the frequency of long beds between regenerating clearcuts (short and tall pooled) and all other types (recent and established partial harvest, mature, and road edge pooled). Most long beds were observed in tall, regenerating

Table 1.4. Observed and expected[a] number of long beds[b] and snowshoe hares killed by Canada lynx, and an index of snowshoe hare abundance[c] (SE) in northern Maine during winters 2002 and 2003.

	Snowshoe Hare Kills		Long Beds		Snowshoe Hare Abundance Index (#/100m)
Habitat Type[d]	# Observed	# Expected	# Observed	# Expected	
Short regenerating clearcut	5	3.2	6	6.8	4.96 (1.22)
Tall regenerating clearcut	8	4.0	11	8.6	5.06 (1.33)
Partial harvest recent	1	1.5	1	3.1	3.73 (1.37)
Partial harvest established	1	1.0	3	2.1	4.44 (1.47)
Mature	0	1.6	3	3.5	2.41 (1.01)
Road edge	0	1.8	2	3.8	
Other	1	2.9	8	6.1	
Regeneration pooled	13	7.2	17	15.4	
Non-clearcut pooled	2	5.9	9	12.5	

[a] Expected values were calculated by multiplying the total number observed by the percent of the habitat type within home ranges.

[b] Long bed = an area that a lynx rested long enough for an ice crust to form.

[c] Index of relative density of snowshoe hares based on the number of snowshoe hare intersections encountered on random transects within lynx home ranges.

[d] Habitat types: Short regenerating clearcut = 11-26 year old, 3.4-4.3 m regenerating clearcut, Tall regenerating clearcut = 11-26 year old, 4.4-7.3 m regenerating clearcut, Partial harvest recent = 1-10 year old, Partial harvest established = 11-21 year old, Mature = >40 year old second-growth stands with a regenerating understory, Road edge = 30 m on both side of roads, Other = all other types including pre-commercial thinning, older regenerating clearcuts (>7.3 m tall), and non-forest, Regenerating pooled = tall and short regenerating clearcuts pooled, Non-clearcut pooled = partial harvest recent, partial harvest established, mature second-growth, and road edge pooled.

clearcuts and established partial harvests, and fewer beds in short regenerating clearcuts, recent partially harvested stands, mature second-growth stands, and road edge (Table 1.4).

A relative index of snowshoe hare abundance was calculated on random transects by counting the number of hare intersections on 1,850 m surveyed in established partial harvests (8 stands), 7,187 m surveyed in tall regenerating clearcuts (23 stands), 6,406 m surveyed in short regenerating clearcuts (17 stands), 1,936 m surveyed in mature second-growth forest (12 stands), and 5,657 m surveyed in recent partially harvested stands (16 stands). The index of relative hare abundance was greatest in regenerating tall (5.06 tracks/100 m) and short (4.96 tracks/100 m) clearcuts and established partially harvested stands (4.44/100 m), and was relatively lower in recent partial harvests (3.73/100 m) and mature stands (2.41/100 m) (Table 1.4).

Stand-Scale Habitat Characteristics

I used Hotelling's multivariate T^2 tests to describe structural differences between treatments that differed in successional stage and use by lynx (regenerating short vs. tall clearcuts, established vs. recent partially harvested stands, and mature second-growth stands vs. established partially-harvested stands). Hotelling's multivariate T^2 test indicated that at least one of the structural variables differed between regenerating short and tall clearcuts (Wilk's $\lambda = 0.621$, $F = 10.03$, 5, 82 df, $P = 0.000$). Post-hoc univariate F-tests indicated that canopy closure ($P = 0.000$), density of deciduous saplings ($P = 0.002$), and density of dead saplings ($P = 0.000$) were greater (Bonferroni-adjusted $\alpha = 0.02$) in tall mid-succcessional clearcuts than in short regenerating clearcuts (Table 1.5). Structural variables also differed (Wilk's $\lambda = 0.677$, $F = 3.142$, 5, 33 df, $P = 0.020$)

Table 1.5. Mean values (SE) for 9 structural variables measured on random transects within 6 lynx home ranges across 5 habitat types, winters 2002-2003 in northern Maine.

	Habitat Type[a]				
	RegenShort	RegenTall	PHR	PHE	Mature
Canopy closure (%)	33 (3)	59 (3)	41 (3)	57 (6)	65 (5)
Coniferous basal area (m^2/ha)	7.3 (1.0)	10.3 (1.3)	3.7 (0.7)	9.0 (2.4)	18.5 (3.4)
Deciduous basal area (m^2/ha)	1.6 (0.5)	7.3 (1.0)	10.8 (1.2)	12.1 (2.0)	9.3 (1.9)
Snag basal area (m^2/ha)	1.4 (0.3)	1.6 (0.2)	2.6 (0.5)	2.0 (0.7)	3.5 (0.5)
Live-tree basal area (m^2/ha)	8.9 (1.1)	17.6 (1.4)	14.5 (1.1)	21.0 (2.5)	27.9 (2.6)
SCU[b]	52,249 (5,623)	48,054 (3,528)	33,253 (3,665)	39,674 (7,487)	44,984 (7,522)
Coniferous saplings[c]	14,304 (2,003)	10,923 (1,277)	4,476 (1,451)	7,676 (2,311)	11,084 (2,484)
Deciduous saplings[d]	9,335 (1,249)	15,283 (1,468)	19,825 (2,386)	16,646 (2,474)	11,733 (2,059)
Dead saplings[e]	1,613 (300)	4,324 (586)	1,799 (238)	4,237 (777)	3,783 (631)

[a] Habitat types: RegenShort = regenerating (11-26 year old) short (3.4-4.3 m tall) clearcut, RegenTall = regenerating (11-26 year old) tall (4.4-7.3 m) clearcut, PHR = recent (1-10 year old) partial harvest, PHE = established (11-21 year old) partial harvest, Mature = mature (>40 year old) second-growth stands with a regenerating understory.

[b] SCU = stem cover units (3*coniferous saplings + deciduous saplings), <7.6cm, protruding from snowpack.

[c] Coniferous saplings = <7.6 cm, protruding from snow pack.

[d] Deciduous saplings = <7.6 cm, protruding from snow pack.

[e] Dead saplings = <7.6 cm, protruding from snow pack.

between recent and established partially harvested stands. Established partially harvested stands had greater (Bonferroni-adjusted $\alpha = 0.02$) live-tree basal area ($P = 0.011$), density of dead saplings ($P = 0.001$), and canopy closure ($P = 0.018$) than recent partially harvested stands (Table 1.5). There was no significant difference (Wilk's $\lambda = 0.878$, $F = 0.888$, 5, 32 df, $P = 0.500$) in structural variables between established partially harvested stands and mature second-growth stands (Table 1.5).

Fractal Dimension

Fractal dimension was calculated for 122 path segments (n = 55 F, 67 M) in stand types that were selected positively (tall regenerating clearcuts and established partially harvested stands, n = 74) and negatively (short regenerating clearcuts and recent partially harvested stands, n = 48) by lynx at the stand-scale. Mean path length was 365 m. Fractal dimension ranged from 1.004 -1.402 (Table 1.6). The mean fractal dimension of paths was greater in habitat types that were selected positively ($\overline{X} = 1.11$, SE = 0.01) by lynx at the stand scale than those selected negatively ($\overline{X} = 1.07$, SE = 0.01) ($F = 2.74$, *df* = 1, 118, $P = 0.10$). Females had a greater mean fractal dimension ($\overline{X} = 1.13$, SE = 0.01) than males ($\overline{X} = 1.07$, SE = 0.01) ($F = 26.18$, *df* = 1, 118, $P = 0.00$). There was no interaction between sex and whether the habitat type was selected for or against at the stand-scale ($F = 0.00$, df = 1, 118, $P = 0.99$).

DISCUSSION

Snowshoe hares were positively associated with understory cover (stem cover units) and negatively associated with canopy closure. High values of SCU indicate greater thermal and predator escape cover for hares because the index adjusts for a difference in

Table 1.6. Fractal dimensions of movement paths of adult lynx in habitat types that were selected positively vs. negatively by lynx at the stand-scale in northwestern Maine, winters 2002-2003.

	Females					Males				
	n	$\bar{x}$	SE	Minimum	Maximum	n	$\bar{x}$	SE	Minimum	Maximum
Selected Positively[a]										
RegenTall	27	1.134	0.013	1.025	1.298	26	1.087	0.018	1.004	1.402
PHE	10	1.164	0.030	1.026	1.348	11	1.086	0.015	1.025	1.149
Selected Negatively[b]										
RegenShort	15	1.110	0.012	1.035	1.172	21	1.062	0.010	1.011	1.189
PHR	3	1.080	0.025	1.047	1.130	9	1.044	0.010	1.011	1.107
Pooled[c]										
For	37	1.142	0.013	1.025	1.348	37	1.087	0.013	1.004	1.402
Against	18	1.105	0.010	1.035	1.172	30	1.057	0.007	1.011	1.189

[a] Selected positively: habitat types selected for by lynx at the stand-scale during winter included RegenTall = regenerating (11-26 year old) tall (4.4-7.3 m) clearcut, and PHE = established (11-21 year) partial harvest.

[b] Selected negatively: habitat types selected negatively by lynx at the stand-scale during winter included RegenShort = regenerating (11-26 year old) short (3.4-4.3 m tall) clearcut, and PHR = recent (1-10 year) partial harvest.

[c] Pooled = habitat types that were selected positively (For = RegenTall, PHE) at the stand-scale by lynx during winter were pooled (For) and habitat types selected negatively (Against = RegenShort, PHRecent) by lynx during winter were pooled (Against).

visual obstruction of coniferous stems (Litvaitis et al. 1985*b*). Dense understories are important to hares because they are a refuge from predation by lynx that typically do not kill snowshoe hares in stands with the densest understories (Staples 1995). Additional evidence to suggest that understory cover is important to snowshoe hares was documented in precommercially thinned stands in Maine. Precommercially thinned regenerating clearcuts (treated with herbicide 0-4 years prior to thinning) were associated with reduced horizontal cover and structural diversity compared to unthinned stands (Homyack et al. 2004) and resulted in snowshoe hare densities <50% those observed in unthinned stands (Homyack et al. 2006*a*). The regenerating clearcuts (short and tall) that I sampled had high values of SCU and low canopy closure and thus ranked highest in relative density of hares. Recent partial harvests with low SCU and mature stands with high canopy closure ranked the lowest in relative density of hares. The index of hare abundance based on track intersections was also greatest in regenerating clearcuts and lowest in recent partial harvests and mature stands, corroborating results from the snowshoe hare model.

Lynx selected positively for stands (tall regenerating clearcuts and established partially harvested stands) that were associated with high to moderate densities (based on relative rank of hare densities using SCU and canopy closure from the snowshoe hare model, the index of hare abundance from snowtracking, and from previous densities calculated in Maine by Fuller and Harrison 2005) of snowshoe hares and exhibited negative selection for stands (mature second-growth and recent partially harvested stands) that were associated with the lowest densities of hares. One exception was that lynx selected against short regenerating clearcut stands that had high densities of hares.

The regenerating short and tall clearcuts were the same age (11-26 years old), but differed in maturity, as indexed by tree height. Lynx often forage in areas with the highest density of snowshoe hares (Ward and Krebs 1985, O'Donoghue et al. 1998, Aubry et al. 2000*a*, Mowat et al. 2000, O'Donoghue et al. 2001), and Krebs (1978) suggests that when prey are patchily distributed it is advantageous for predators to forage in areas that have the highest density of prey (i.e., prey density hypothesis). However, lynx were not always associated with stands with the highest density of hares, which suggests the importance of an interaction between prey density and prey access in determining foraging success and habitat selection by lynx. It is apparent that structural features contributing to cover for hares interact with densities of hares to determine the quality of foraging habitat for lynx.

I observed structural differences within stands that helped explain comparisons between similar treatments that were selected positively by lynx over types that were selected negatively. Although abundance of snowshoe hares was similar between regenerating short and tall clearcuts, tall regenerating clearcuts were selected positively by lynx and short regenerating clearcuts had negative selection indices. Tall regenerating clearcuts had greater tree height, canopy closure, 2.7X more dead saplings, 39% more deciduous saplings, 24% fewer conifer saplings, and lower SCU than short regenerating clearcuts. Consistent with research that concluded that lynx are typically associated with less dense stands than hares (O'Donoghue et al. 1998), greater densities of dead saplings and lower SCU indicate that the taller regenerating clearcuts were undergoing self-thinning, which likely increased the visibility and vulnerability of hares to lynx, supporting the prey access hypothesis. Stand composition between the two stand types likely affected visibility for lynx because short regenerating clearcuts were composed of 71% coniferous regeneration, which obstructs visibility to hares and tall clearcuts were composed of only 20% coniferous regeneration. Fisher were the primary predator of lynx on the study area (Vashon et al., unpublished report, Maine Department of Inland Fisheries and Wildlife) and the denser coniferous understory in short regenerating clearcuts may have influenced the negative selection by lynx for that stand type; lynx might have a difficult time escaping from fishers in stands with dense understories because of the shorter limbs and more elongated body of fishers. Because stand age *per se* is not as important as stand structure for snowshoe hares (Hodges 2000*a*), I speculate that structure in tall regenerating clearcuts is probably dictating the positive selection by lynx for this stand type over shorter regenerating clearcuts. Lynx may experience higher foraging success and may be less vulnerable to mortality from fishers in stands with lower understory structure than was typical in short regenerating conifer stands.

Prey access as measured by visibility and mobility is important for lynx because lynx hunt by stalking and rushing snowshoe hares and by ambushing (Murray et al. 1995, O'Donoghue et al. 1998). Thus, lower than optimal cover for hares may be more important than hare abundance in determining hunting success because lynx require a close approach to their prey (Parker et al. 1983); the greatest number of snowshoe hare kills in Nova Scotia occurred in regenerating clearcuts 22-28 years old, which also had the greatest abundance of hares (Parker 1981). Correspondingly, I observed disproportionately greater number of snowshoe hare kills (13 of 16) in regenerating clearcuts (short and tall), but of the kills that were documented in regenerating clearcuts, 8 of 13 occurred in the tall category. Lynx probably made most kills in tall regenerating clearcuts because they were associated with greater visibility associated with reduced understory structure resulting from self-thinning. Although lynx killed 5 hares in short regenerating clearcuts, 4 of the 5 kills occurred <60 m to the edge of a road and two of those kills were <4 m to the edge of the road. This suggests that lynx may opportunistically kill hares in short regenerating stands when they are traveling adjacent to the stand boundaries or along roads; however, lynx did not venture far into the densest regenerating stands in search of snowshoe hares.

Lynx selected stands with the highest relative densities of snowshoe hares and avoided areas with extremely high SCU; however, the disproportionately higher numbers of kills in both short and tall regenerating clearcuts suggests a strong interaction between prey density and prey access. Lynx also spent more time in tall regenerating clearcuts as evidenced by the greater number of long beds in those stands, which is associated with resting and eating after killing prey (Parker 1981), as well as a means of inactive hunting. The number of long beds in regenerating clearcuts pooled (short and tall) did not differ from those in all other stand types, however the number of beds in short regenerating stands was lower than expected and the number in tall regenerating clearcuts was greater than expected. This was consistent with results which indicated that lynx preferred taller regenerating clearcuts relative to the shorter stands. I speculate that when densities of hares are high (regenerating short and tall clearcuts), it is more energetically efficient for lynx to hunt in stands that afford greater visibility to hares (e.g., tall regenerating clearcuts).

Established partially harvested stands also provided lynx the opportunity to hunt in areas with intermediate density of hares and understory stems. Lynx killed the number of hares expected in established partial harvests and had more long beds than expected in these stands based on availability within home ranges. Older established partially harvested stands with 31% greater live-tree basal area, 28% greater canopy closure, 71% greater density of conifer saplings, and 2.3X greater density of dead saplings were selected positively by lynx, whereas more recent partial harvests were selected negatively. Recent partial timber harvesting reduces habitat quality for lynx as evidenced by their selection against these stands during winter, probably because of their low density of snowshoe hares. A reduction in understory stem density in recent (3-6 years post-harvest) partially harvested stands (52-59% basal area removal) was associated with the lowest winter density of snowshoe hares relative to regenerating clearcut-, mature coniferous-, mature deciduous-, and mature mixedwood-stands during a companion study in northcentral Maine (Fuller and Harrison 2005). Additionally, modeling work reported that recent partial harvesting was negatively associated with the landscape-scale presence of lynx (Hoving et al. 2004) and snowshoe hares (Hoving 2001) in Maine. Thus, I conclude that the reduced density of understory stems in recent partially harvested stands creates easy access to hares by lynx, but that the extremely low densities of hares in these stands make them unfavorable for lynx. This again suggests an interaction between density of snowshoe hares and access to hares.

Established partially harvested stands and mature second-growth stands with a regenerating understory had statistically similar structural characteristics, indicating that stand structure in older partial harvests was already approaching that found in mature stands. However, coniferous basal area in mature stands was more than twice that found in established partial harvests. Mature stands had the smallest patch size (9 ha) of all types that were sampled and 32% of these stands were <200 m wide. Additionally, 45% of mature stands were ≤60 m to the edge of a road or clearcut stand. The combination of small patch size and proximity to open areas suggests that these stands probably received substantial light penetration and wind throw, which partially explains the dense understory in these stands. Despite the statistical similarities in vegetation between established partial harvests and mature stands, there was greater selection for established partial harvests than for second-growth stands, and there was also greater relative density of hares in established partial harvests. I hypothesize that as partially harvested stands age they increase in stand structure to the point that they have intermediate densities of hares between regenerating clearcuts and mature second-growth stands. Intermediate densities of hares in combination with the high basal area (21 m^2/ha) and intermediate SCU (39,674/ha) in established partial harvests create good foraging opportunities for lynx, providing further evidence for the prey access hypothesis.

Mature second-growth stands and recent partial harvests had low densities of hares in this study and in northcentral Maine (Fuller and Harrison 2005), and probably accounted for the negative selection by lynx for these stand types. Elsewhere, mature forests are often used by lynx, but rarely receive positive selection (Mowat et al. 2000). In fact, many studies have reported negative selection for mature forests (Parker et al. 1983, Kesterson 1988, Mowat and Slough 2003). The thermal and escape cover hypothesis was not supported in mature second-growth stands despite high canopy closure (65%) and basal areas (27.9 m^2/ha) relative to other stands. Lynx have a competitive advantage over potential competitors (coyotes and bobcats) during winter because lynx are morphologically adapted to areas that have deep snow (Murray and Boutin 1991) related to their lower foot-loading and long limb lengths (Krohn et al. 2004). However, lynx may lose this relative advantage in mature stands that have shallower snow that is usually denser and harder (Peek 1986). Although mature stands provided large trees for vertical escape, they received lower relative selection by lynx because of the increased competition, risk of interaction with other species, and low prey availability. There were no snowshoe hare kills observed in mature stands and the thermal advantages provided by mature stands likely did not compensate for the low densities of hares in these stands. Thus, the assertion that lynx require mature to over-mature conifer forests (Aubry et al. 2000*a*, Buskirk et al. 2000, McKelvey et al. 2000*a*,*b*; Ruggiero and McKelvey 2000) is not consistent with the empirical data presented here.

Although there was not a sufficient amount of early (<10 year old) regenerating clearcut within lynx home ranges to statistically evaluate selection for this stand type, there was an apparent avoidance of these stands by lynx. There was 0.53 km of travel in early regenerating clearcuts during 65.5 km of snowtracking; however, 3.63 km of lynx tracks would have been expected based on availability. This apparent avoidance of early regenerating clearcuts is not surprising given their low densities of snowshoe hares (Ferron et al. 1998, de Bellefeuille et al. 2001). Lynx were negatively associated with recent (0-15 year old) clearcuts at the landscape scale in Maine, but were positively associated with older (15-25 years old) regenerating clearcuts (Hoving et al. 2004). Litvaitis et al. (1985*b*) suggested that hare densities may not reach their highest levels until 20-25 years after clearcutting, and in boreal forests it takes >10 years for clearcuts to begin to support hares (Dodds 1960, de Bellefeuille et al. 2001). Thus, clearcuts do not generally achieve the structure required by snowshoe hares and do not receive use by lynx until greater than 10 years post-harvest. This is consistent with my observations that lynx selected positively for >10 year-old clearcuts.

Lynx were documented traveling on roads (unplowed during winter), but roads and their associated edges were selected against at the stand scale. Contrary to my study, lynx followed road edges in Nova Scotia for "considerable" distances (Parker 1981) and road edge and roads <15 m wide were used in Washington (Koehler and Brittell 1990). Additionally, lynx in Washington did not cross roads greater than random expectation and there was no relationship between habitat selection and roads (McKelvey et al. 2000*b*). Lynx may have had lower relative selection for roads and their associated edges because roads may have increased interactions with generalist competitors such as coyotes and bobcats (Aubry et al. 2000*a*), or because they may have supported low densities of snowshoe hares relative to other stand types.

The highest fractal dimension of foraging paths occurred in the stand types that were selected for by lynx at the stand scale (tall regenerating clearcuts and established partially harvested stands), suggesting that lynx were actively foraging in stands that provided high hare density and intermediate cover for hares. A more tortuous path suggests that lynx invested more time hunting in these stand types (Dacorogna 1988, Parker 1981), but does not necessarily indicate greater prey abundance because it may be reflecting prey availability (Edwards et al. 2001) and accessibility. In tall regenerating clearcuts and established partial harvests where prey were likely abundant and easily accessible, lynx did not need to travel long distances to find hares, and therefore they maximized foraging efficiency by hunting within a restricted area (Tinbergen et al. 1967), which caused their movement pathways to be more tortuous. The harvested treatments that were selected against (short regenerating clearcuts and recent partial harvests) had straighter paths, suggesting that they provided less resistance to travel (With 1994*a*) and that lynx spent less time in these stands. Reduced directionality of movement in one area (high D) may be a result of a more heterogeneous and structurally complex stand (Wiens and Milne 1989, Crist et al. 1992, With 1994*b*), because of high prey density or availability (Edwards et al. 2001), or because the area provides refugia from predators (Phillips et al. 2004). Although the differences in fractal dimension that we observed appear to be small, fractal dimension is a scaling exponent, so small changes in D can indicate large differences in path structure (Wiens et al. 1993). For example, if two animals each traveled a net distance of 1 km and the difference in D of their movement paths was 0.10, the animal with the more tortuous path would have traveled a gross distance of twice as far, when measured at a scale of 1m (Nams and Bourgeois 2004). Because the highest fractal dimension was observed in tall regenerating clearcuts and established partially harvested stands, I suggest that lynx were actively foraging in stands that provided higher relative prey density and easier access and visibility to hares.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Lynx selected stands (tall regenerating clearcuts and established partial harvests) that had high to intermediate densities of hares and intermediate canopy closure (57-59%), live-tree basal area (18-21 m^2/ha), and stem cover units (40,000-48,000/ha) relative to all of the harvest treatments. These stand-types maintained a moderate level of protection provided by overhead canopy closure and basal area of live trees as well as intermediate understory density to create easier access to hares (prey access hypothesis). Lynx avoided habitats where relative prey density was low and with relatively low densities of conifer saplings (<5,000 stems/ha) and SCU (<35,000 stems/ha), dead saplings (<4,000/ha), or where canopy closure exceeded 60%. They also avoided areas with high densities of hares where coniferous saplings exceed 14,000 stems/ha and SCU exceeded 50,000 stems/ha, which seemed to create less favorable conditions for hunting hares. It is likely the interactions among density and availability of snowshoe hares, the vulnerability of hares, and the vulnerability of lynx to conspecific and interspecific predation that determines habitat decisions by lynx at the stand-scale during winter. This study provided little support for the thermal and escape cover hypothesis or previous speculation that lynx require mature and overmature forests. Further, limited support for the prey density hypothesis indicated that lynx may prefer stands with intermediate-high hare densities where hare vulnerability is compromised by suboptimal understory cover.

In managed landscapes, foraging habitat for lynx is provided by areas with few overstory trees dominated by a mixture of conifer and deciduous saplings that are in the stage of stem exclusion and self-thinning. In the Acadian forests of Maine, these stand conditions typically occur 20-35 years following partial or complete overstory removal. Although mature forests in Maine support low hare densities, were avoided by lynx, and contained less tortuous foraging paths of snowtracked lynx, there is little information on which to speculate the trajectory of lynx habitat quality from 25 years post-harvest (high quality) to poor quality (mature forest condition); this knowledge gap warrants further study.

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Chapter 2

DOES SUB-STAND SCALE HABITAT SELECTION INFLUENCE MOVEMENT PATTERNS OF CANADA LYNX DURING WINTER?

ABSTRACT

Others have hypothesized that the foraging behavior of Canada lynx (*Lynx canadensis*) maximizes their success in preying on snowshoe hares. I evaluated two hypotheses related to foraging behavior of lynx at the sub-stand scale using an information-theoretic modeling approach. The prey density hypothesis evaluated whether lynx expended greater foraging effort (i.e., more tortuous paths) in areas with the greatest density of snowshoe hares, and the prey access hypothesis evaluated whether lynx foraged in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promoted increased capture success of hares. Foraging effort was inferred to increase with fractal dimension of movement paths. I first analyzed whether fractal dimension (D) of males and females was constant with spatial scale by detecting breaks in D at a series of spatial scales. Piecewise regressions identified breaks in spatial scale at 50 m for males and 65 m for females, indicating domains of scale, or points where movement patterns changed quantitatively. Movement paths of males and females had increasing fractal dimension at smaller scales and were straighter than they were at broader spatial scales, suggesting that lynx were trying to maximize exposure to features that change at broader scales (>50 m). Lynx exhibited third-order habitat selection and avoided switching from stands with greater to stands with lesser foraging opportunity. I then evaluated the two hypotheses by testing multiple *a priori* regression models that related sub-stand scale habitat variables with the fractal dimension of movement paths as the response variable for males and females within domains of scale both above and below the break-point. Models for females at both small (0-65 m) and large (66-272 m) spatial scales identified snow depth (positive association) as the most important variable influencing the tortuosity of movement paths. Movement paths of female lynx were more tortuous in stands with greater snow depths, which were also stands that contained high densities of snowshoe hares. Models for males performed poorly, indicating that the structural variables measured were not the primary influences on the tortuosity of their movement paths. Logistic regression models indicated that lynx moved through areas with fewer stem cover units (3*coniferous saplings + deciduous saplings) and a greater percent of skid trails than what occurred randomly within home ranges, suggesting that lynx maximize time in areas with high-intermediate hare densities where understory cover is reduced to facilitate increased capture success of snowshoe hares (prey access hypothesis). It appears that that lynx are making their strongest foraging decisions when exhibiting second- and third-order resource selection, so focusing management activities to alter sub-stand scale structure may be less effective than efforts to create stand- and landscape-scale conditions that enhance foraging success of lynx.

INTRODUCTION

The foraging behavior of Canada lynx (*Lynx canadensis*) and their movement patterns are largely influenced by their strategies used to hunt snowshoe hares (*Lepus americanus*) (Parker 1981, Mowat et al. 2000). The movements of animals have implications for habitat selection, food search patterns, energy investments, and territorial and social behavior (Bascompte and Vilà 1997), and may be influenced by microhabitat selection (Nams 2005). The most traditional approach for understanding movements and habitat use by species is to evaluate time expenditure in different habitat types via radiotelemetry. Analyses of specific movement patterns of animals at scales finer than the stand or patch (i.e., fourth-order selection; Johnson 1980) are usually not conducted because of the difficulty in obtaining and analyzing the data (Koenig et al. 1996). Companion studies (Chapter 1) suggested that lynx make strong habitat selection decisions at the stand-scale (i.e., third-order selection; Johnson 1980) and maximize their time expenditure in habitat types with high-intermediate densities of snowshoe hares and intermediate levels of understory structure, which facilitates capture of hares. Thus, I predicted that the responses of lynx would be reflected in two scales of movement corresponding to the sub-stand (understory structure) and stand-scales (stand types associated with high-intermediate densities of hares).

I evaluated two competing hypotheses at the sub-stand scale: 1) Prey density hypothesis: lynx forage in areas with the greatest density of understory cover, which corresponds with the highest densities of snowshoe hares, and 2) Prey access hypothesis: lynx forage in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promote increased capture success of hares. To evaluate the two hypotheses, I selected *a priori* models associated with each hypothesis to determine which sub-stand scale habitat variables best predicted the tortuosity of movement paths. I evaluated how lynx responded to the structural features of their habitat at a range of spatial scales, assuming that foraging effort increased with tortuosity of movement paths; straight line travel by lynx may indicate traveling, while more tortuous paths may indicate hunting or foraging behavior (Parker 1981, Arditi and Dacorogna 1988).

Canada lynx are food specialists that are predicted to respond to the fine-scale habitat responses associated with their primary prey, snowshoe hares (Mowat and Slough 2003). Sub-stand scale habitat selection by snowshoe hares is well documented (e.g., Conroy et al. 1979, Orr and Dodds 1982, Wolfe et al. 1982, Keith et al. 1984, Litvaitis et al. 1985, Wirsing et al. 2002), but little is known about fine-scale habitat choices of lynx (Aubry et al. 2000). Vegetation and structural characteristics may influence habitat selection by lynx at the sub-stand scale and may be reflected in their movement patterns. At the stand scale, habitat selection by lynx is closely associated with habitats that contain high densities of snowshoe hares (Koehler and Aubry 1994, Aubry et al. 2000, Mowat et al. 2000, O'Donoghue et al. 2001). High densities of hares are associated with dense understories of saplings and shrub-sized woody vegetation (Conroy et al. 1979, Orr and Dodds 1982, Wolfe et al. 1982, Keith et al. 1984, Litvaitis et al. 1985, Wirsing et al. 2002), and Mowat and Slough (2003) reported that habitat quality for lynx is similarly dependent on density of understory woody vegetation. Because of the strong association between lynx and snowshoe hares, I was interested in investigating variables that were strongly associated with densities of snowshoe hares or with the access by lynx to hares.

Besides features related to understory and overstory density, snow may be important to lynx at the sub-stand scale. Lynx are morphologically adapted to areas that have deep snow (Murray and Boutin 1991), which provides lynx a competitive advantage over competitors such as bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), who have higher foot loading and shorter limb lengths (Krohn et al. 2004). Additionally, snow characteristics such as surface hardness and sinking depth are also important in determining the spatial distribution of lynx (Stenseth et al. 2004). Although large-scale distributions of lynx in eastern North America are associated with regions of high snowfall (Hoving et al. 2005), snow could also be important at finer scales when lynx are making stand- and substand-scale foraging decisions.

Determining how movement paths of lynx change with spatial scale in a heterogeneous environment can provide insight into the grain at which lynx perceive their environment. Movement paths can be evaluated at several spatial scales using fractal dimension (D). The fractal dimension is a number that explains the way in which the measured length between given points increases as scale decreases. Although it has been suggested that using fractal dimensions to describe movement paths is not appropriate if the paths do not display statistical self-similarity over many spatial scales (Turchin 1996), others suggest that this does not preclude their use (Mandelbrot 1977, Burrough 1981, Doeer and Doeer 2004). Part of the conflict arises from the definition of fractals. Mandelbrot (1983) asserts that objects do not have to be self-similar to be considered fractals. Self-similarity is defined as an object that appears invariant when expanded or contracted, such that a small part looks the same as the whole and vice versa. Dicke and Burrough (1988) suggest that exact geometric self-similarity is unlikely to be found because of the large variation found in natural phenomena. Despite the conflict, a test of self-similarity can be conducted to determine if fractal dimension changes with spatial scale.

Determining the spatial scales where fractal dimension changes can identify transition zones that indicate a change in process (Burrough 1981, Krummel et al. 1987, Kent and Wong 1982, Wiens 1989), which may be associated with different levels of habitat selection (e.g., sub-stand, stand, landscape scales). Mandelbrot (1977) called the breaks between spatial scales "transition zones" that identify different processes, and indicates that extrapolation between scales is no longer appropriate (Sugihara and May 1990). Indeed, the value of the fractal dimension is sometimes not as interesting as identification of the points where the scaling changes (Halley et al. 2004). If the processes that affect movement are the same at all scales, then a plot of scale vs. D should increase at a constant rate. However, if the value of D exhibits abrupt shifts between spatial scales, there is presumably also a shift in the underlying process that is responsible for the pattern (Krummell et al. 1987, Wiens 1989); therefore, the overall estimate of D is not a scale-independent measure of tortuosity. The abrupt shifts identify transition points between domains of scale (Wiens 1989), or the points where animal movement patterns change quantitatively (Sibly et al. 1990), indicating that processes and patterns are not constant (Wiens 1989, Nams 1996). It is important to identify if domains of scale exist because analysis of movement paths across all spatial scales would be misleading if different habitat selection processes are operating at multiple scales. I was interested in evaluating if domains of scales existed in the movement paths of lynx, and if the spatial scales where movement patterns change were associated with changes in levels of habitat selection from finer to broader-scale habitat decisions. This analysis would also identify the finest grain at which lynx respond to landscape heterogeneity.

STUDY AREA

The lynx study area included parts of 9 townships in northwestern Maine, USA (T10 R10 WELS, T10 R11 WELS, T11 R10 WELS, T11 R11 WELS, T11 R12 WELS, T11 R13 WELS, T12 R11 WELS, T12 R12 WELS, T12 R13 WELS) with elevations 244-536 m. Average snow depth measured during January – March was 45 cm in 2002 and 65 cm in 2003. The townships were intensively managed for pulpwood and saw timber. Forestry activities included timber harvesting (clearcutting and partial harvesting), herbicide application to promote coniferous regeneration, and precommercial thinning to reduce competition among regenerating saplings, to increase rate of growth of crop trees, and to shorten rotation length.

Dominant species in second-growth deciduous stands included red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch (*Betula papyifera*), and yellow birch (*B. alleghaniensis*). Second-growth coniferous forests were composed of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white pine (*Pinus strobus*). Forests regenerating from clearcutting were primarily composed of dense stands of balsam fir, red spruce, red maple, and paper birch saplings, interspersed with raspberry (*Rubus* sp.) thickets in areas with open overstories and soil disturbance from previous timber harvesting.

METHODS

Overview

To evaluate if pooling movement paths across sexes was appropriate, I analyzed fractal dimensions for males and females separately by plotting the mean and standard errors of D across a range of spatial scales. Next, I tested whether fractal dimension of males and females was constant with spatial scale by detecting breaks in D at a series of spatial scales. To evaluate the responses of males and females to vegetation structure at each domain of scale detected, I calculated an overall D in each domain of scale for each movement path. I then used the D values within each domain as the response variable and the sub-stand scale variables as predictor variables in *a priori* regression models used to evaluate whether movement paths were influenced by fine-grained habitat decisions; decisions were evaluated *vis a vis* their support for the competing prey density or prey access hypotheses. Those two hypotheses were further evaluated via sub-stand scale habitat models which compared vegetation structure along lynx movement paths versus random transects using logistic regression.

Snowtracking

I chose 3 adult male and 3 adult female lynx with kittens out of a larger sample of 17 lynx. The lynx were chosen based on their proximity to each other, with the constraint that females produced kittens the previous spring. We followed 2 females and 1 male in 2002 and 1 female and 2 males in 2003. We were constrained to sample 3 lynx each year because of the short winter season (3 months), the maximum distance that we could track lynx in a day (two crews tracking 1 lynx and measuring vegetation along paths for approximately 1 km each day), the goal of 10 km tracked per lynx, and the variable snow conditions. Methods for lynx capture, radiocollaring, radiotelemetry, and home range estimation are described in Chapter 1.

All tracking occurred <48 hours after snowfall, but typically <24 hours after snowfall (88% of paths were surveyed <24 hours after snowfall). When snow conditions were favorable for tracking, 2 lynx were followed each day, with the goal of tracking each lynx for ≥1 km. We alternated the lynx that were tracked to ensure that each lynx was followed at least every other day during periods of favorable snow conditions. We located radiocollared lynx, intersected their tracks, and back-tracked them until the track was obscured by fresh snow, until the track was confused with tracks of other animals, or until daylight was diminished. We utilized continuous real-time GPS sampling (Trimble Pro XR®) with sub-meter accuracy to track lynx and to record the foraging path. The foraging path was recorded directly over the snowtracks of the lynx, and a GPS point was recorded every 4 seconds and at every discernable turn. During all tracking technicians walked slowly to ensure that the GPS recorded the exact path shape and captured all deviations from a straight-line. The maximum straight-line distance between any 2 GPS points on the lynx foraging path was 4 m. All prey that intersected the lynx path and the distance that lynx followed the trails of snowshoe hares was also recorded.

Vegetation was sampled and prey intersections were recorded on random straight-line transects that were placed in a stratified random design within the 90% fixed kernel home ranges of our focal lynx (methods for determining home ranges are described in Chapter 1). The starting point and direction of each 1-km long transect was randomly chosen, with the constraints that the transect was completely inside the home range, and that all habitat types were proportionally sampled relative to the composition of habitat types within home ranges. The goal was to sample at least 10 random transects (10 km) per lynx. Random transects were sampled either when it was snowing too hard to track lynx, or when >48 hours had elapsed since the last snowfall.

Vegetation Sampling

Habitat variables included in sub-stand scale analyses provided a measure of the structure of the vegetation that has been documented or theorized to influence the local abundance of snowshoe hares and/or lynx. The variables that were measured were either related to the prey density or prey access hypotheses (Table 2.1). Variables associated with the prey density hypothesis were those that are known to influence densities of snowshoe hares, or provide an index to snowshoe hare abundance. Variables associated with the prey access hypothesis were those that influence a combination of prey density and access to hares by lynx. Stem cover units (SCU = 3*coniferous saplings + deciduous saplings) is a measure of understory structure that adjusts for a difference in visual obstruction of softwood stems, thus, high values indicate greater thermal and predator escape cover for hares (Litvaitis et al. 1985). Density of deciduous and coniferous saplings was measured to calculate SCU. Overhead canopy closure and SCU were measured because they were the two variables that best predicted densities of snowshoe hares in Maine (Chapter 1). Following trails of snowshoe hares has been documented as a hunting technique for lynx because of its potential to increase encounter rates (Brand et al. 1976, Keith et al. 1977); therefore, the total distance that lynx followed the trails of hares was recorded. I hypothesized that areas with deeper snow would create less favorable conditions for hunting, that skid trails would provide ease of travel to hunt hares, that lower values of SCU would increase visibility to hares and would provide easier travel through stands, and that a greater distance on the trails of snowshoe hares would increase the probability of encountering a hare.

Table 2.1. *A priori* models considered to evaluate the effect of sub-stand scale habitat variables[a] on movement patterns by Canada lynx.

Hypotheses	Models Considered
Prey Density[b]	SCU (+)
	CC (-), SCU (+)
	CC (-), SCU (+), SHI (+)
Prey Access[c]	SNOWR (-)
	SKID (+), SCU (-)
	SNOWR (-), SKID (+), SCU (-), HARETRAIL (+)
	SNOWR (-), SKID (+), SCU (-), HARETRAIL (+), BA (+)
Global Model	SNOWR, SKID, SCU, HARETRAIL, BA, CC, SHI

[a] SCU = stem cover units (3*coniferous saplings + deciduous saplings), saplings <7.6 cm dbh. CC = percent overhead canopy closure. SHI = number of snowshoe hare intersections/km adjusted for time since last snow. SNOWR = snow depth (cm) relative to depths recorded on random transects within home ranges of lynx, adjusted by two week averages, positive numbers indicate depth greater than on random transects, negative numbers indicate depth less than on random transects, and zero indicates the same snow depth. SKID = percent of the lynx movement path that was on skid trails. HARETRAIL = percent of the movement path of lynx where lynx followed snowshoe hare tracks. BA = live-tree basal area (m^2/ha).

[b] Prey density hypothesis = lynx forage in areas with the greatest density of understory cover, which corresponds with the highest densities of snowshoe hares.

[c] Prey access hypothesis = lynx forage in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promote increased capture success of hares.

Vegetation was measured in 6 m x 2 m plots spaced every 100 m along lynx paths and at 100 m intervals along randomly oriented 1 km transects placed within home ranges. Canopy closure was measured with a spherical densiometer (Lemmon 1956) and readings were averaged from the four cardinal compass directions. Basal area of live coniferous and deciduous trees (m^2/ha) was measured using a 2-factor wedge prism (Avery and Burkhart 2002). All deciduous and coniferous saplings (<7.6 cm diameter, stems protruding through snow pack) were measured, which were used in calculating stem cover units. Relative SCU (SCUR) was calculated as SCU on lynx transects – mean SCU within the regenerating clearcuts (11-26 years old) sampled along random transects. Regenerating clearcuts were considered to represent the locally optimal condition for hares because that stand-type was most consistently selected for by hares (Chapter 1), typically has the highest density of regenerating woody stems (Monthey 1986, Fuller and Harrison 2005, Homyack et al. 2006), and supports the highest densities of hares in Maine (Fuller and Harrison 2005, Homyack et al. 2006). Thus, positive values of SCUR indicated that lynx moved through areas with greater densities of SCU relative to the average observed within the locally optimal habitat for snowshoe hares. Correspondingly, negative numbers indicated that lynx moved through areas with lower densities of SCU relative to the best habitat for snowshoe hares. A snow depth measurement was also taken at the center of each plot and the relative snow depth (SNOWR) was also calculated by subtracting the snow depth measured on lynx paths from the average snow depth calculated on random transects during 2-week windows beginning January 10-23 and ending March 21-April 3. Positive SNOWR indicates that snow depth on lynx paths was greater than the average snow depth within home ranges of lynx and negative numbers indicate that snow depth was less than the average. The 2-week averages were calculated separately for lynx monitored in 2002 and 2003. The density of snowshoe hare intersections/km of lynx tracks (SHI) was calculated by dividing intersections by the number of 12-hour intervals since the last snowfall.

Fractal Dimension and Domains of Scale

I calculated fractal dimensions along continuous movement paths of lynx using a modification of the traditional divider method (Sugihara and May 1990) and using the fractal mean estimator in the program FRACTAL 4.00 (V.O. Nams, Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). The measured length of a pathway decreases as the measurement scale increases according to the relationship:

$$L(\delta) = k\delta^{1-D}$$

where L is the length of the pathway, δ is the divider size that is used to measure the path, *k* is a positive constant, and D is the fractal dimension. The regression of log (total path length) versus log (divider size) results in a slope, which is subtracted from 1 to yield D. Fractal dimension is estimated by measuring the length (L) of the pathway at various scales (δ). I estimated D at 50 spatial scales using dividers with a minimum calculated as the lowest spatial scale that could be measured (4 m) divided by 1.25 to a maximum of the largest spatial scale (272 m) times 1.25. At each spatial scale (divider size), the length of the path is estimated by walking the divider along the path. This is then conducted for larger and larger dividers. The slope of the plot of log (total path length) vs. log (divider size) was calculated within each of the 50 spatial scales, resulting in a line with slope 1-D, and one overall averaged estimate for D over the range of spatial scales considered. Fractal dimension is greatest when there is a large difference between the length calculated with small and large divider sizes, which results in a steeper slope on the plot.

To analyze patterns of scale variance, I evaluated plots of D versus spatial scale to detect changes in D with spatial scale to evaluate if movement patterns are influenced by heterogeneity within stands or within the landscape (With 1994, Bascompte and Vilà 1997). If lynx are responding to specific structural features within stands that occur at small spatial scales, you would expect to detect a change in D with spatial scale at smaller scales (fourth-order selection). If lynx are exhibiting third-order habitat selection and are using different cover types, you would expect a change in D with spatial scale at broader scales associated with moving between stand types that have better versus poorer foraging opportunities. If spatial structure within stands or landscapes is not influencing movement patterns, you would not expect to detect changes in D with spatial scale.

I analyzed males and females separately because females have greater fractal dimension values than males (Chapter 1, Figures 2.1 and 2.2). Patterns of fractal dimension with spatial scale were relatively consistent among individuals (Figure 2.2) and I was not interested in how fractal dimension varies by individual, but rather how D varies across spatial scales. Thus, I combined movement paths for all individuals of the same sex and calculated a mean D across the 3 males and the 3 females, separately, at each spatial scale. Minimum path length used in the analysis was 500 m. The minimum scale represented the lowest resolution of the data, which was a combination of the sampling precision of an observer on snowshoes (1 m) and the maximum distance between any two GPS points along the movement paths (4 m). To determine the

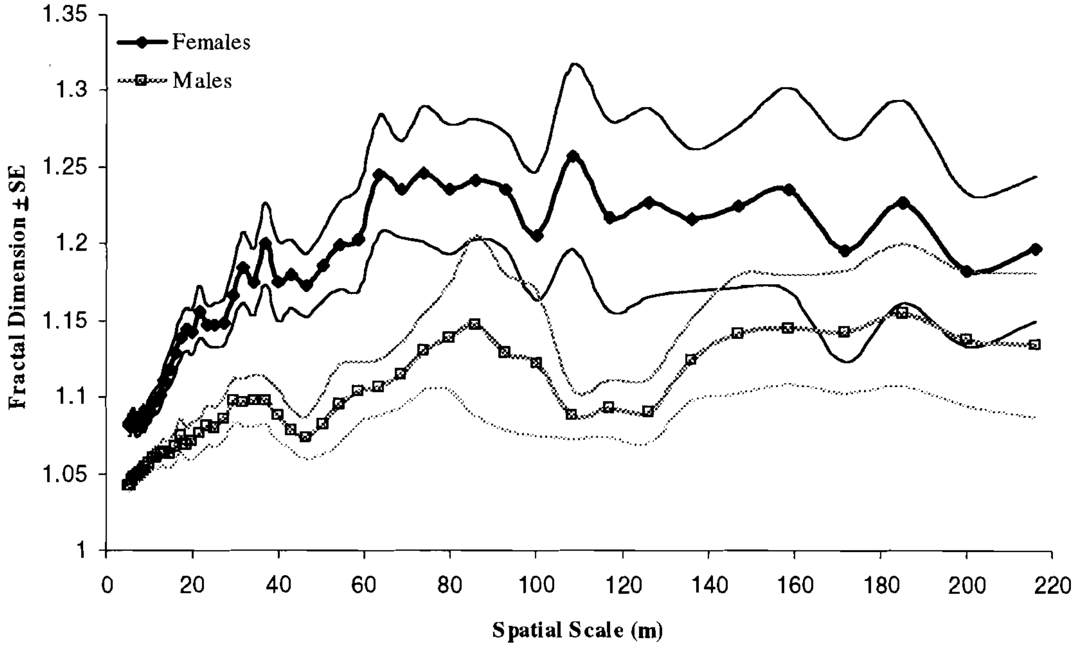


Figure 2.1. Fractal dimension (± SE) of movement paths during winter for female (n = 30 paths) and male (n = 30 paths) Canada lynx across a range of spatial scales.

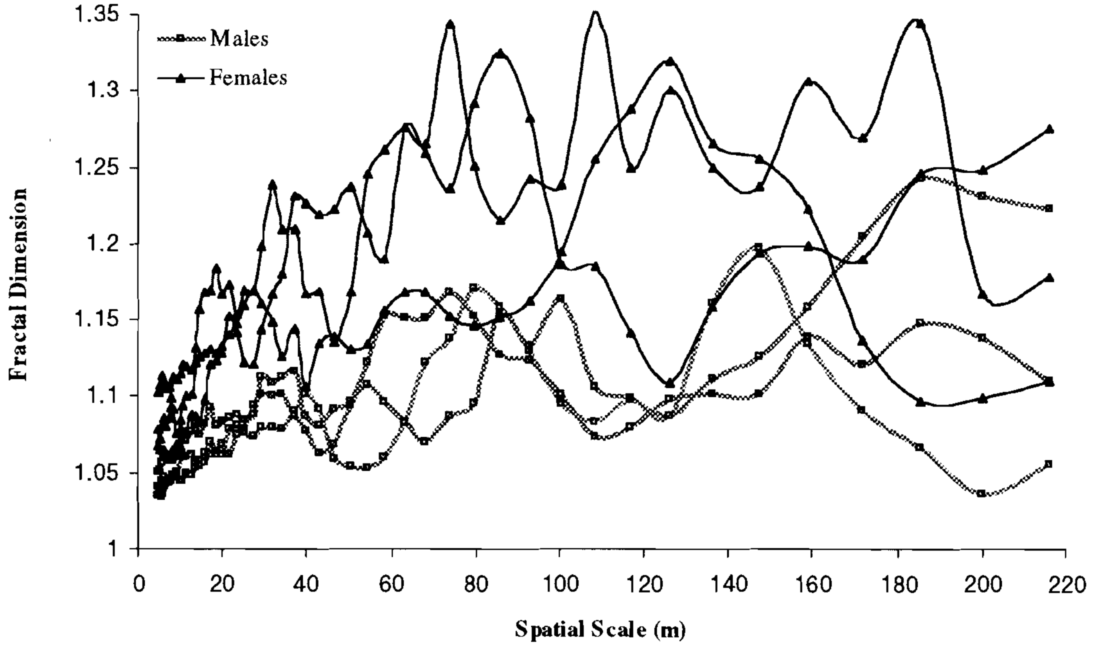


Figure 2.2. Individual variation in fractal dimension of movement paths during winter for 3 male and 3 female Canada lynx in northern Maine, 2002-2003.

maximum spatial scale, I calculated the 25th percentile of the distribution of path lengths for males (850 m, n = 30) and females (816 m, n = 30) as this represented a natural break in the data and allowed inclusion of the majority of lynx movement paths. I used the lower of the two distributions (816 m) and divided by three because three points are needed in regression (With 1994). Thus, the maximum spatial scale was 272 m. If fractal dimension consistently and uniformly increases or decreases with spatial scale, the graph of fractal dimension versus spatial scale will be linear. I used piecewise regression (Neter et al. 1996) to fit two lines to different portions of the data, with a break point that resulted in the best fit for both lines. I chose to fit two lines because I was interested in determining if lynx respond to spatial structure of vegetation at small scales within stands (fourth-order habitat selection) or within larger scales of moving between different stand types (third-order habitat selection). I had no *a priori* reasons to suggest that lynx would respond to >2 spatial scales that could be described within the 4 m-272 m resolution of my data.

Because the standard error on fractal dimension was low at small spatial scales and increased at larger spatial scales, I examined the trend to determine if the variability in fractal dimension was dependent on sample size at each spatial scale. If the variability of D is dependent on sample size at each spatial scale, the larger variation at larger spatial scales could just be a function of a smaller sample size at larger spatial scales and not a true biological response. Thus, I calculated the coefficient of variation at each spatial scale to determine if variability in D increases with increasing spatial scale regardless of mean D values (Doeer and Doeer 2004).

Sub-Stand Scale Habitat Selection Models

Movement models

I used an information theoretic approach based on Kullback-Leibler (K-L) information to rank 7 *a priori* models related to the prey density and prey access hypotheses. The response variable in all models was the fractal dimension of movement paths, using the individual movement path of males (n = 30) and females (n = 30) separately as the unit of replication. I evaluated D within the range of scales identified on either side of the breakpoint in the regression of D vs. scale and considered those to refer to different movement decisions made by lynx at two statistically distinct scales. I then used the D of each foraging path of lynx within each respective scale and coupled it with the explanatory variables that measured prey density, snow, and vegetation structure and modeled their relationships using logistic regression to identify which models best described differences in D at each of the 2 scales considered. All variables were examined for pairwise correlation and were retained if $r < |0.95|$ (Burnham and Anderson 2002).

I computed AIC values and Akaike weights (w_i), and made inferences from these models following the guidelines of Burnham and Anderson (2002). I used AIC_c, the second-order AIC for small sample size, calculated using the residual sum of squares from least-squares models (Burnham and Anderson 2002). I re-scaled AIC_c values relative to the best model, which received a ΔAIC_c value of zero. This model is considered the best model to approximate the data given the set of models considered. Values of ΔAIC_c from 0-2 are considered to have substantial support as being the K-L best model, values 4-7 have considerably less support, and values >10 have no support

(Burnham and Anderson 2002). I evaluated ΔAIC and Akaike weights to select the most plausible model from the set of models considered. The likelihood of the model [$\exp(-\frac{1}{2}\Delta_i)$] was also calculated to determine the relative strength of evidence for each model.

Models related to the prey density hypothesis included variables known to influence densities of snowshoe hares. Variables in models included stem cover units (SCU), canopy closure (CC), and the number of snowshoe hare intersections on lynx movement paths (Table 2.1). Density of snowshoe hares in Maine was best described by a model including SCU and CC (Chapter 1), thus I also included that model to determine if lynx movements responded to areas with the highest density of hares. Models related to prey access included variables that would positively influence the ability of lynx to move through stands and would enhance visibility and ease of pursuit by lynx. Variables included snow depth relative to the average snow depth within the study area (SNOWR), the percent of the movement path that was on skid trails (SKID), stem cover units, the distance that lynx followed the trails of snowshoe hares (ONSH), and live-tree basal area (BA) (Table 2.1).

Lynx vs. random models

I also used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative support for sub-stand scale habitat selection models related to the prey density and prey access hypotheses by comparing variables on lynx movement paths with those surveyed along random straight-line transects within the home ranges of lynx. If lynx do not exhibit sub-stand scale habitat selection, I would expect that the models comparing lynx versus random transects would perform poorly. However, if lynx select sub-stand scale structure to maximize either prey access or prey density, I would expect that there would be a difference between variables measured on lynx movement paths and on random transects.

I evaluated the same models that were used in the sub-stand scale fractal dimension analyses, with three exceptions. I was unable to use a variable related to snow because in the other models I calculated the difference between snow depths on lynx and random transects. I also could not measure the percent of the transect on the paths of snowshoe hares (ONSH) or the number of snowshoe hare intersections (SHI) because too much time had elapsed since last snowfall on random transects for those measures to be meaningful. Thus, I evaluated two models related to prey density that included variables SCU and CC, two models related to prey access that included variables SKID, SCU, and BA, and a global model (Table 2.1).

RESULTS

Snowtracking

Radiocollared adult lynx (3 F, 3 M) were snowtracked for 65.50 km (median = 10.77 km/lynx, range = 9.64 – 12.34) during January - March, 2002 and 2003; 74 individual movement paths (median = 12 snowtracks/lynx, range = 11 - 14) were tracked. Sixty (30 M, 30 F) movement paths were >500 m in length (i.e., complete length, median F = 1,050 m, range = 526 – 1673 m; median M = 1,159 m, range = 611 – 2,878 m). The remaining 14 movement paths were not used in analyses. All adult females were accompanied by kittens (1, 2, and 3 kittens) that remained with them throughout the January – March period when snowtracking occurred.

Vegetation Sampling

Vegetation plots (n = 641) were sampled along the 60 complete lynx paths and the values were averaged across plots within transects (mean = 10.7 plots/transect, SD = 3.6). I sampled 684 vegetation plots along 64 random transects (mean = 10.7 plots/transect, SD = 1.5) within lynx home ranges. The random transects were sampled in a stratified-random fashion to ensure that each habitat type was sampled in proportion to the availability within home ranges of lynx. For example, the mean percent availability of short regenerating clearcuts within home ranges was 20%, which corresponded closely with the 21% of random vegetation plots that were sampled in that vegetation class. Tall regenerating clearcuts represented 24% of the home range composition, and 21% of vegetation plots were sampled in that class. Recent partial harvests composed 10% of home ranges and 14% of the random vegetation plots were in that class. Established partial harvests represented 6% of home ranges and 9% of random vegetation plots were sampled in established partial harvests. Finally, mature second-growth stands represented 10% of home range composition and 9% of vegetation plots were sampled in that class.

Snow depth measured along the movement paths of lynx was less than the average snow depth within the home ranges for both males and females (Table 2.2). Males and females also selected stands that had a lower mean density of stem cover units than observed in the habitat type that supported the greatest density of hares (Table 2.2). Stem cover units on movement paths of males were 60% less than those observed on random transects, and SCU along paths of females were 47% of SCU on random transects (Table 2.2). Females moved through areas with greater live-tree basal areas and canopy closure

Table 2.2. Mean (SE) values of sub-stand scale habitat variables measured on lynx movement paths and on random straight-line transects that were sampled within the home ranges of lynx. Variables were used in models to explain movement patterns of Canada lynx.

	Females	Males	Random
SNOWR[a]	-2.58 (2.19)	-3.91 (2.48)	
Basal area (m^2/ha)	15.36 (1.35)	10.80 (1.20)	15.70 (0.81)
Canopy closure (%)	46.85 (2.69)	33.19 (2.92)	46.87 (2.12)
Stem cover units/ha[b]	23,733 (3,068)	17,712 (1,710)	44,885 (2,690)
Stem cover units relative[c]	-27,550 (3,068)	-33,571 (1,710)	
SKID (%)[d]	14.17 (2.12)	20.74 (3.24)	9.10 (0.97)
HARETRAIL (%)[e]	9.75 (1.66)	9.65 (2.32)	

[a] SNOWR = snow depth (cm) relative to depths recorded on random transects within home ranges of lynx, adjusted by two week averages, positive numbers indicate depth greater than on random transects, negative numbers indicate depth less than on random transects, and zero indicates the same snow depth.

[b] Stem cover units/ha = 3*coniferous saplings + deciduous saplings (<7.6 cm dbh).

[c] Stem Cover Units Relative = difference in SCU on lynx movement paths relative to the best cover for snowshoe hares in mid-successional regenerating clearcuts.

[d] SKID = percent of lynx movement path that was on skid trails.

[e] HARETRAIL = percent of lynx movement path where lynx followed snowshoe hare tracks.

than males, but there was not a large difference between those variables between lynx movement paths and random transects (Table 2.2). Twenty-one percent of movement paths of male lynx occurred on skid trails, while 14% of movement paths of females occurred on skid trails. Both sexes traveled a greater percentage of their paths on skid trails relative to the occurrence of skid trails on random transects (9%). Approximately 10% of the movement paths of both males and females followed the trails of snowshoe hares (Table 2.2).

Fractal Dimension and Domains of Scale

A piecewise regression model with two line segments (Females $r^2 = 0.94$, Males $r^2 = 0.83$) had a better fit to the data than a single linear regression model (Females $r^2 = 0.50$, Males $r^2 = 0.71$) (Table 2.3). Females had a transition point at a larger spatial scale than males; the break-point for females was at 65 m (Figure 2.3) and the break-point for males was at 50 m (Figure 2.3). The piecewise regression model for females was: $D = 1.08 + 0.003 * X_{i1} + -0.0003(X_{i1} - 65.14)X_{i2}$, where X_{i1} = spatial scale and $X_{i2} = 1$ if $X_{i1} > 65.14$ and otherwise $X_{i2} = 0$. The piecewise regression model for males was: $D = 1.04 + 0.001 * X_{i1} + 0.0002(X_{i1} - 49.48)X_{i2}$, where X_{i1} = spatial scale and $X_{i2} = 1$ if $X_{i1} > 49.48$ and otherwise $X_{i2} = 0$.

The standard error around the mean fractal D was small at the smallest spatial scales, indicating that movement was similar among individuals (Figure 2.1). Movement paths were straighter (i.e., D was lower) at the smaller range of spatial scales than at larger scales for both males and females (Figure 2.1). At finer scales the D of the 3 females was always higher than for the 3 males ($\bar{x}$: F = 1.14, M = 1.08) (Figures 2.1, 2.2). At larger scales, females exhibited a tendency for greater D, although 1 female and 1 male

Table 2.3. Akaike's Information Criterion (AIC_c)[a] to examine the influence of a linear regression model vs. a one break-point piecewise regression model on the fractal dimensions of foraging paths of lynx during winters 2002 and 2003, northwestern Maine.

Model	K[b]	Log (L)[c]	AIC_c	ΔAIC_c	Model Likelihood	w_i[d]
Females						
One-Break	5	212.33	-413.31	0	1.00	1.00
Linear	3	104.11	-201.69	211.61	0.00	0.00
Males						
One-Break	5	215.16	-419.96	0	1.00	1.00
Linear	3	145.44	-284.36	134.60	0.00	0.00

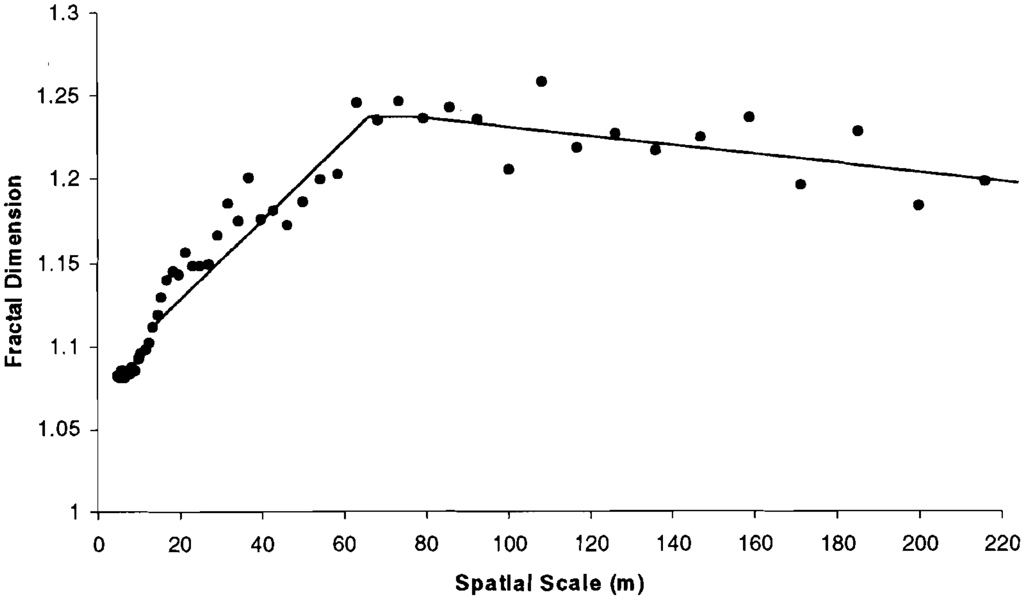
[a] Akaike's Information Criterion adjusted for small sample size.

[b] K = number of estimable parameters.

[c] Log (L) = log-likelihood = $-n/2*\log(\hat{\sigma}^2)$, $\hat{\sigma} = RSS/n$ (Burnham and Anderson 2002).

[d] w_i = Akaike weight.

a) Females



b) Males

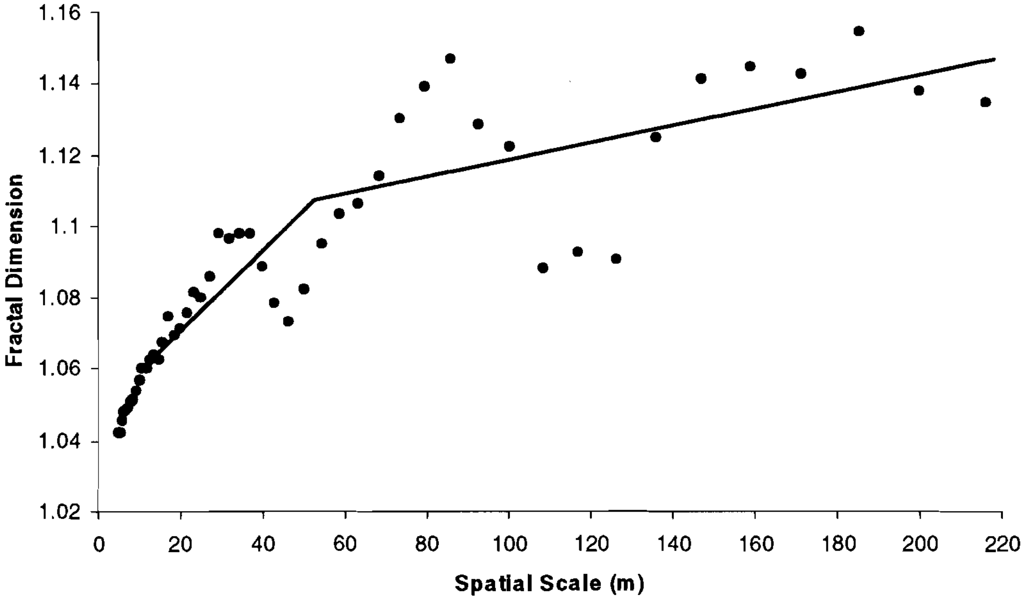


Figure 2.3. Piecewise regression models of fractal dimension across a range of spatial scales for 3 female a) and 3 male b) lynx in northern Maine, 2002-2003. Note the breaks in spatial scale at 65 m and 50 m for females and males, respectively.

exhibited substantial overlap in path tortuosity (mean F = 1.33, M = 1.22) and larger variation in D was observed across both sexes (Figures 2.1, 2.2). The increase in variability of fractal dimension with spatial scale was not due to a reduction in sample size because the coefficient of variation did not increase at the larger spatial scales. The coefficient of variation fluctuated, but was relatively consistent in males and females across spatial scales ranging from 4-272 m (Figure 2.4).

Sub-Stand Scale Habitat Selection Models

Movement models

There was low correlation between all of the variables that were included in models ($r < |0.70|$) (Tables 2.4 and 2.5). The top-ranked model for explaining increasing levels of fractal dimension for female lynx at the scale of 4-65 m was related to prey access and included snow depth relative to random (positive association) ($\Delta AIC_c = 0.00$, likelihood = 1.00, $w_i = 0.87$, r^2 adjusted = 0.18) as the sole explanatory variable (Table 2.6). At larger spatial scales (66-272 m), there were two comparable models ($\Delta AIC_c < 2$) for females which included the seven variable global model ($\Delta AIC_c = 0.00$, likelihood = 1.00, $w_i = 0.45$, r^2 adjusted = 0.46) and the five variable model snow depth relative to random (SNOWR) (+ association), skid trails (SKID) (+), SCU (+), percent of path on the trail of snowshoe hares (HARETRAIL) (+), and basal area (+) ($\Delta AIC_c = 1.95$, likelihood = 0.38, $w_i = 0.17$, r^2 adjusted = 0.31, Table 2.6). I calculated variable importance by summing Akaike weights for all models containing a given predictor variable. The variable with the largest predictor weight is estimated to be the most important. Relative variable importance of SNOWR was greatest at both larger (0.87) and smaller (0.89) spatial scales.

Table 2.4. Pearson correlation coefficients among 7 variables[a] considered for inclusion in linear regression models for explaining fractal dimension of movement paths of female lynx during winters 2002 and 2003, northwestern Maine.

	SNOWR	BA	CC	SCU	SKID	HARETRAIL	SHI
SNOWR	1.00						
BA	-0.56	1.00					
CC	-0.31	0.70	1.00				
SCU	0.37	-0.25	0.06	1.00			
SKID	0.27	-0.29	-0.36	0.21	1.00		
HARETRAIL	-0.13	0.08	0.21	0.10	0.03	1.00	
SHI	-0.07	-0.09	0.23	0.08	0.03	0.30	1.00

[a] SNOWR = snow depth (cm) relative to depths recorded on random transects within home ranges of lynx, adjusted by two week averages, positive numbers indicate depth greater than on random transects, negative numbers indicate depth less than on random transects, and zero indicates the same snow depth. BA = live-tree basal area (m^2/ha). CC = percent overhead canopy closure. SCU = stem cover units (3*coniferous saplings + deciduous saplings), saplings < 7.6 cm dbh. SKID = percent of the lynx movement path that was on skid trails. HARETRAIL = percent of the movement path of lynx where lynx followed snowshoe hare tracks. SHI = number of snowshoe hare intersections/km, adjusted for time since last snow.

Table 2.5. Pearson correlation coefficients among 7 variables[a] considered for inclusion in linear regression models for explaining fractal dimension of movement paths of male lynx during winters 2002 and 2003, northwestern Maine.

	SNOWR	BA	CC	SCU	SKID	HARETRAIL	SHI
SNOWR	1.00						
BA	0.08	1.00					
CC	0.16	0.86	1.00				
SCU	0.33	0.08	0.06	1.00			
SKID	0.30	-0.33	-0.35	0.23	1.00		
HARETRAIL	-0.01	-0.18	-0.16	-0.40	-0.09	1.00	
SHI	0.03	0.03	0.10	-0.09	-0.16	0.50	1.00

[a] SNOWR = snow depth (cm) relative to depths recorded on random transects within home ranges of lynx, adjusted by two week averages, positive numbers indicate depth greater than on random transects, negative numbers indicate depth less than on random transects, and zero indicates the same snow depth. BA = live-tree basal area (m^2/ha). CC = percent overhead canopy closure. SCU = stem cover units (3*coniferous saplings + deciduous saplings), saplings < 7.6 cm dbh. SKID = percent of the lynx movement path that was on skid trails. HARETRAIL = percent of the movement path of lynx where lynx followed snowshoe hare tracks. SHI = number of snowshoe hare intersections/km, adjusted for time since last snow.

Table 2.6. Akaike's Information Criterion (AIC_c)[a] for the *a priori* set of candidate models related to prey density or prey access. Models were structured to evaluate which sub-stand scale habitat variables[b] influenced the fractal dimension of movement paths of female Canada lynx during winters 2002 and 2003, northwestern Maine.

Model	Rank	K[c]	Log (L)[d]	AIC_c	ΔAIC_c	Model Likelihood	w_i[e]
Spatial Scales = 4-65 m							
Prey Density[f]							
SCU	2	3	48.22	-89.51	5.44	0.07	0.06
SCU, CC	4	4	48.38	-87.16	7.79	0.02	0.02
SCU, CC, SHI	6	5	49.10	-85.70	9.25	0.00	0.01
Prey Access[g]							
SNOWR	1	3	50.94	-94.95	0.00	1.00	0.87
SCUR, SKID	3	4	48.66	-87.71	7.24	0.03	0.02
SCU, SKID, SNOWR, HARETRAIL	5	6	51.25	-86.85	8.10	0.02	0.02
SCU, SKID, SNOWR, ONSH, BA	8	7	51.32	-83.55	11.40	0.00	0.00
Global Model[h]	7	9	56.25	-94.50	9.45	0.01	0.01
Spatial Scales = 66-272 m							
Prey Density[f]							
SCU	6	3	28.80	-51.59	2.31	0.31	0.09
SCU, CC	7	4	28.80	-49.60	4.99	0.08	0.03
SCU, CC, SHI	8	5	29.85	-47.71	5.78	0.06	0.02
Prey Access[g]							
SnowR	4	3	29.37	-52.74	1.16	0.56	0.17
SCU, SKID	5	4	30.18	-52.35	2.24	0.33	0.10
SCU, SKID, SNOWR, HARETRAIL	3	6	34.23	-56.45	0.18	0.91	0.28
SCU, SKID, SNOWR, HARETRAIL, BA	2	7	36.04	-53.08	0.00	1.00	0.31
Global Model[h]	1	9	40.97	-54.93	0.00	1.00	0.45

[a] Akaike's Information Criterion adjusted for small sample size. [b] See Table 2.1 for a description of variables. [c] K = number of estimable parameters. [d] Log (L) = log-likelihood $= -n/2 * \log(\hat{\sigma}^2), \hat{\sigma} = RSS/n$ (Burnham and Anderson 2002). [e] w_i = Akaike weight. [f] Prey density hypothesis = lynx forage in areas with the greatest density of understory cover, which corresponds with the highest densities of snowshoe hares. [g] Prey access hypothesis = lynx forage in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promote increased capture success of hares. [h] Global Model = SCU, SKID, SNOWR, HARETRAIL, BA, CC, SHI.

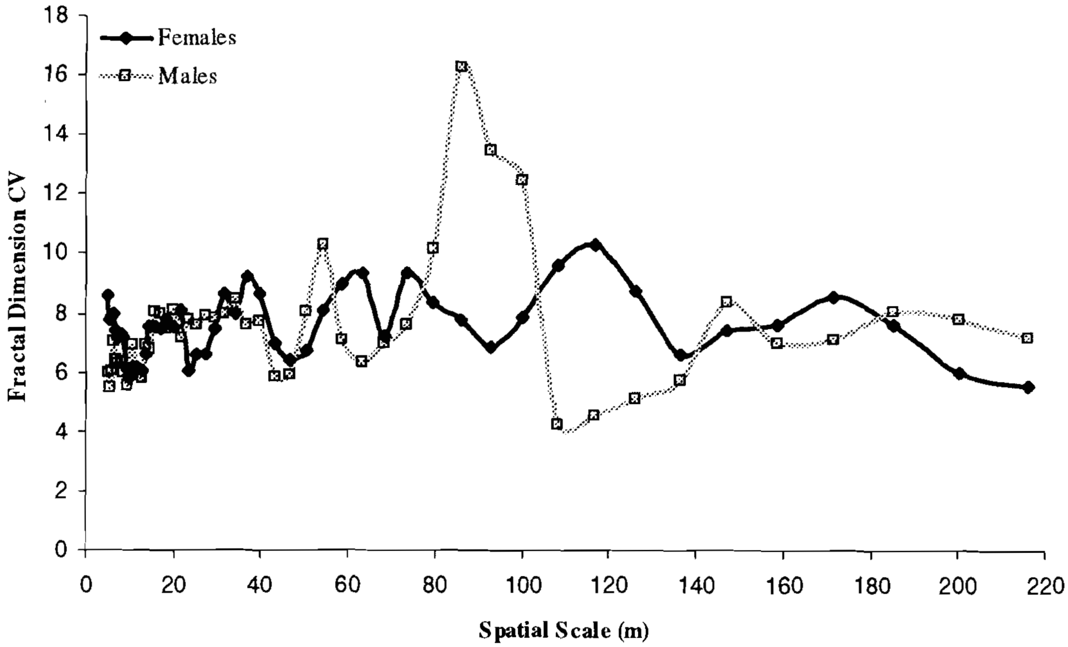


Figure 2.4. Coefficients of variation in fractal dimension of movement paths during winter at each spatial scale for male (n = 30 paths) and female (n = 30 paths) lynx in northern Maine, 2002-2003.

For males at the scales of 4-50 m and 51-272 m the global model had a poor fit to the data (adjusted $r^2 = 0.04$ and 0.00, respectively), therefore I did not test any of the reduced models relating to the prey density or prey access hypotheses using AIC.

Lynx vs. random models

The top model that best differentiated between variables on lynx movement paths and random straight-line transects was related to prey access and included variables SKID (positive association) and SCU (negative association) ($\Delta AIC_c = 0.00$, likelihood = 1.00, $w_i = 0.51$, McFadden's Rho-Squared = 0.38, Table 2.7). The other competitive model was also related to prey access and included variables SKID (+), SCU (-), and BA (-) ($\Delta AIC_c = 0.92$, likelihood = 0.63, $w_i = 0.32$, McFadden's Rho-Squared = 0.39, Table 2.7). The two models related to prey density both had ΔAIC_c values >9 (Table 2.7).

DISCUSSION

Fractal Dimension and Domains of Scale

Fractal dimension was not a scale-independent measure of movement paths in lynx because fractal dimension was not constant with spatial scale, indicating that there was a change in process (Burrough 1981, Krummel et al. 1987, Kent and Wong 1982, Wiens 1989) at approximately 50 m for males and 65 m for females. Fractal dimension within each domain of scale was homogeneous, but became heterogeneous between domains (Palmer 1988), indicating where the movement pattern changed quantitatively (Sibly et al. 1990). Domains of scale in hierarchical systems are indicated by an increase in variance as the transition between domains is approached (O'Neill et al. 1986), and this was apparent in the data as variance increased at approximately the scale where I identified the transition (Figures 2.1, 2.4). Fractal dimension increased with spatial scale

Table 2.7. Akaike's Information Criterion (AIC_c)[a] for the *a priori* set of logistic regression models related to prey density and prey access. Models were structured to evaluate which sub-stand scale habitat variables[b] best differentiated between areas used by Canada lynx and random straight-line transects (availability) within the home ranges of lynx, winters 2002 and 2003, northwestern Maine.

Model	Rank	K[c]	Log (L)[d]	AIC_c	ΔAIC_c	Model Likelihood	w_i[e]
Prey Density[f]							
SCU	5	2	-58.80	121.70	9.61	0.01	0.00
SCU, CC	4	3	-57.92	122.03	9.94	0.01	0.00
Prey Access[g]							
SCU, SKID	1	3	-52.95	112.09	0.00	1.00	0.51
SCU, SKID, BA	2	4	-52.34	113.01	0.92	0.63	0.32
Global Model[h]	3	5	-51.91	114.33	2.24	0.33	0.17

[a] Akaike's Information Criterion adjusted for small sample size.

[b] See Table 2.1 for a description of variables.

[c] K = number of estimable parameters.

[d] Log (L) = maximized log-likelihood.

[e] w_i = Akaike weight.

[f] Prey density hypothesis = lynx forage in areas with the greatest density of understory cover, which corresponds with the highest densities of snowshoe hares.

[g] Prey access hypothesis = lynx forage in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promote increased capture success of hares.

[h] Global Model = SCU, SKID, BA, CC.

for males and females both up to and after the break in spatial scale as identified by piecewise regressions (Figures 2.3, 2.4). Fractal dimension increases with spatial scale as the search pattern approaches a random walk (Mandelbrot 1983, Katz and George 1985, Nams 1996), and the movement patterns became more tortuous with spatial scale. Overall, both males and females exhibited more tortuous paths at broader spatial scales, presumably to avoid traversing from preferred to avoided stand types; this behavior was not a response to select for specific within-stand structural attributes. Lynx exhibited more tortuous paths at scales >50-65 m, which I inferred to result from efforts to concentrate their foraging in stands with intermediate to high densities of SCU and hares and to minimize transitions to lower-quality stands (Chapter 1). Companion studies utilizing the same 6 lynx, but evaluating stand-scale (third-order, *sensu* Johnson 1980) habitat selection indicated strong relative preferences by lynx for stands with intermediate-high densities of SCU and snowshoe hares, which were found in tall regenerating clearcuts (4.4-7.3 m, 11-26 years post-harvest) and established (11-21 years post-harvest) partial harvests (Chapter 1). Therefore, the greater tortuosity of movement paths at broader spatial scales may be indicative of lynx trying to maximize their investment in stand types that create increased prey access and which are characterized by intermediate-high hare density and stem densities that are lower than optimal for hares to escape predators.

It was not surprising that movement paths were straighter for both males and females at smaller spatial scales. At the smallest spatial scales lynx are moving in a straight line between strides; thus, I conclude that lynx were not making fine-grained decisions at a resolution below the average characteristics of a stand. When making stand-scale habitat decisions, lynx appear to consider both the density and access to prey and make tradeoffs which maximize their overall foraging efficiency. Strong third-order habitat selection by lynx (Chapter 1) likely placed female lynx in areas with favorable hare densities and structural conditions for successful prey capture, which precluded the need for strong fourth-order selection.

The transition between domains in movement paths was at a larger spatial scale for females, but the difference between 50 m for males and 65 m for females is probably not biologically significant. However, the greater overall fractal dimension values for females versus males suggests that that females may encounter greater landscape complexity within their home ranges (Westcott and Graham 2000), or they may invest greater foraging effort per linear distance traveled than males because females must encounter more prey to successfully meet energy demands of themselves and their kittens, which accompanied them on 100% of the movement paths. Males are not responsible for foraging success of kittens and may be balancing foraging and breeding opportunities (Sandell 1989) during the winter period; motivations unrelated to foraging may explain the more directed movement paths of males. Although the differences in fractal dimensions between males and females appear to be small, fractal dimension is a scaling exponent, so small changes in D can indicate large differences in path structure (Wiens et al. 1993). For example, if two animals each traveled a net distance of 1 km and the difference in D of their movement paths was 0.10, the animal with the more tortuous path would have traveled a gross distance of twice as far, when measured at a scale of 1m (Nams and Bourgeois 2004).

Movement Models

Path tortuosity for females at the scales of 4-65 m was related to snow depth. The prey access model related to snow depth predicted that lynx would gain easier access to hares in areas with shallower snow depths and that this increased movement related to hunting would be reflected in a more tortuous path. However, females had more tortuous paths where there was greater snow depth relative to the snow depth on the study area. This suggests that female lynx are maximizing their exposure to habitats with structural components associated with high hare density (i.e., low canopy closure; Chapter 1) and minimizing exposure to stands with high snow interception (high basal areas and canopy closure) and poor structural conditions for hares (mature stand types). Snow depth can increase by 30-60% as coniferous cover decreases (Murray et al. 1994) because dense canopy intercepts snow and reduces snow depths (Kirchoff and Schoen 1987, Wambolt and McNeal 1987, Armleder et al. 1994). Thus, at smaller spatial scales, female lynx are foraging in stand types that have deep snow, which are associated with stands characterized by open canopies, high SCU, and high densities of hares (Chapter 1). This may also provide female lynx with foraging advantages over potential competitors (e.g., fishers, coyotes, bobcats, red foxes) for hares who have either shorter limbs and/or higher foot loading on snow (Krohn et al. 2004).

At broader spatial scales, lynx appear to be making tradeoffs among foraging in areas with high densities of hares while also favoring conditions that increase foraging success (prey access hypothesis). At the larger spatial scales (66-272 m) for females, tortuous paths were associated with deeper snow, greater use of skid trails, greater density of stem cover units, greater distances following the trails of snowshoe hares, and less live-tree basal area. Relative variable importance of snow depth (0.92) was also the greatest at broader spatial scales. At the stand-scale, lynx select for tall mid-successional regenerating clearcuts and old partially harvested stands (Chapter 1), which also had deep snow and may indicate that stands with greater snow depths have greater tortuosity because of their link to stand-scale habitat selection.

Lynx also exhibited greater path tortuosity in areas with a greater density of SCU and less live-tree basal area than occurred on random transects; this reflected habitat selection at the stand-scale because stands with these characteristics have the greatest densities of hares (Chapter 1). Additionally, walking in the trails of snowshoe hares has potential to increase encounter rates (Brand et al. 1976, Keith et al. 1977), and approximately 10% of the movement paths of female lynx followed the trails of hares; this behavior likely contributed to the higher tortuosity of their movement paths in areas with habitat characteristics favoring intermediate-high hare densities. Correspondingly, the percent of lynx tracks that were on trails of snowshoe hares ranged from approximately 10-25% in the Yukon (O'Donoghue et al. 2001).

Movement paths of female lynx were also associated with increased use of skid trails, which facilitates movement through stands and creates good viewing opportunities for hares, which is important given the stalking and ambushing hunting behavior exhibited by lynx (Murray et al. 1995, O'Donoghue et al. 1998). The combined weight of evidence of the top two models at this larger spatial scale was only 0.59, suggesting that either there are other variables that influence path tortuosity at these scales, or that path tortuosity by lynx responds at larger spatial scales than what was measured.

For males, the global model at both spatial scales did a poor job of explaining the tortuosity of movement paths. It appears that the movement paths of males were not strongly influenced by sub-stand scale features within the home range, but that they were making strong third-order habitat decisions (Chapter 1).

Lynx vs. Random Models

Although the sub-stand scale models that were evaluated related to movement paths of lynx did not have consistently strong support, lynx did appear to be selecting specific features within stands as evidenced by the comparison of structural features on lynx movement paths versus random transects. Although fourth-order habitat variables did not greatly influence the tortuosity of movement paths, they did influence where lynx moved within stands. Similar to the movement models, the logistic regression model also identified prey access as more important than prey density in determining areas used by lynx. Lynx selected areas that had lower density of stem cover units relative to what occurred within the home range and also traveled on skid trails more than what occurred on random transects within the home range. Habitat choices by lynx are associated with the visibility and mobility needed to successfully capture hares (Parker et al. 1983, Murray and Boutin 1991, Murray et al. 1995, Mowat et al. 2000), since it is more energetically efficient for lynx to hunt in stands that afford greater visibility to hares. For example, lynx in the Yukon were most successful in capturing prey in stands with low stem density and high visibility (Murray et al. 1995). Lynx on my study area selected areas that had lower stem densities relative to random straight-line transects, lower SCU relative to the locally optimal conditions for hares, and also used more skid trails. All of those conditions likely provided greater visibility and mobility when hunting hares.

CONCLUSIONS

There are some potential ecological factors that may have hampered the ability to detect consistent and significant habitat patterns at the sub-stand scale. First, it may have been related to the use of the tortuosity of movement patterns as the response variable. Movement paths of lynx were not strongly influenced by the vegetational, snow, and prey density variables that were measured at scales of 4-272 m. It is possible that lynx were making decisions at the sub-stand scale, but that these decisions did not strongly influence the tortuosity of their paths. For example, stem cover units measured on lynx movement paths were 61% less for males and 47% less for females compared with stem cover units on random transects within the home ranges of lynx. So, although lynx may have been selecting specific structural features within their home ranges, they were not related to *how* lynx moved through the stands. This was likely because their decisions were largely driven by stronger third-order habitat selection (Chapter 1).

More importantly, the large home range size of lynx may influence their perceptive scale. For example, smaller species of grasshoppers had more tortuous paths than larger species, suggesting that smaller species interacted with patch structure at a finer scale than larger species (With 1994). Lynx may select specific features within stands, but because of their large stride length and large home ranges they perceive structure at a coarse resolution, and this difference is not apparent in their movement patterns. Based on their mobility and large home range areas, habitat selection by lynx appears coarse-grained. Lynx in eastern North America exhibit strong patterns of first-order (Hoving et al. 2005) and second-order (Hoving et al. 2004) habitat selection. Additionally, lynx show strong habitat selection at the third-order by selecting for stand types within home ranges that enhance foraging opportunities (Chapter 1, Poole et al. 1996). Lynx in this study exhibited strong third-order selection (Chapter 1) for stands with intermediate-high densities of hares and SCU, which provided both prey encounters and mobility to pursue hares. Because habitat selection is not independent across scales, lynx may have no reason to alter their sub-stand scale movements (i.e., to exhibit fourth-order selection), other than to avoid crossing from stands with high to low foraging success. This likely explains the switch to less directed (i.e., more tortuous) foraging paths at scales of 65-272 m (females) and 50-272 m (males) compared to finer scales.

It is important to recognize that habitat selection (including selection of microhabitats) is a multi-level hierarchical process, both in space and time (Johnson 1980, Kotliar and Wiens 1990, Orians and Wittenberger 1991). Individuals first select a geographical range (first-order), they position their home range on the landscape (second-order), they select for different stand types within the home range (third-order), and then make subsequent decisions about the finer-grained habitat components related to different structural features within the home range (fourth-order). Thus, patterns of habitat selection at larger scales may differ from patterns of habitat selection at smaller scales (Johnson 1980, Wiens et al. 1987, Wiens 1989, Orians and Wittenberger 1991, Schaefer and Messier 1995). Only at finer scales can the foraging decisions of species determine habitat selection patterns. The lack of strong support for the models related to foraging over two ranges of spatial scales associated with fourth-order habitat selection may indicate that the most important habitat selection decisions are made by lynx at broader spatial scales (i.e., third-order, Chapter 1, Poole et al. 1996; second-order, Hoving et al. 2004; first-order, Hoving et al. 2005).

MANAGEMENT IMPLICATIONS

Intensive management for lynx via manipulation of within-stand structure may be ineffective and unwarranted based on evidence of coarser-grained patterns of resource selection. Habitat management for lynx should be focused at the scales where the strongest habitat selection is observed, which corresponds to the stand (third-order) and landscape scales (second-order). At the second-order (*sensu* Johnson 1980), lynx in Maine occurred in landscapes with a lot of regenerating forest and very little recent partial harvest and mature forest (Hoving et al. 2004). Similarly, at the third-order (*sensu* Johnson 1980), lynx in Maine selected tall regenerating clearcuts and older partial harvests and selected against mature forests and recent partial harvests (Chapter 1).

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Chapter 3

PREDICTIVE MODELS OF HABITAT OCCUPANCY FOR ENDANGERED NEWFOUNDLAND MARTENS: EFFECTS OF HABITAT LOSS VERSUS FRAGMENTATION

ABSTRACT

The relative influences of habitat loss and fragmentation on population processes is a contentious issue in conservation biology. Newfoundland marten (*Martes americana atrata*) are a genetically distinct, endangered subspecies of mustelid that are endemic to the island of Newfoundland. Members of the genus *Martes* have large area requirements per unit body weight, have been documented to be sensitive to fragmentation, and to respond to landscape pattern at scales larger than individual home ranges. I developed models incorporating landscape composition and configuration to predict occurrence of home ranges (n = 63, representing 54 individuals) for adult martens and to evaluate the relative influences of habitat loss versus fragmentation on this habitat-limited subspecies. Simulated home ranges (n = 29) were generated in areas that were surveyed, but were unoccupied by resident martens, incorporating the size, shape, and range overlap observed in occupied ranges. I used an information-theoretic approach to rank 9 logistic regression models, including 3 variables representing landscape composition (percent of the home range in suitable habitat, largest patch index, radius of gyration) and 5 variables representing landscape configuration (mean patch size, patch size coefficient of variation, mean nearest neighbor, mean nearest neighbor coefficient of variation, CLUMPY). I defined a statistically based and biologically relevant categorization of suitable versus unsuitable habitat (suitable = coniferous stands $\geq$6.6 m tall, canopy closure >50%;

coniferous stands ≥12.6 m tall, ≤50% canopy closure; insect killed conifer stands, <25% canopy closure; and precommercially thinned conifer stands, 20-30 years old, >50% canopy closure) to create a binary landscape. The top-ranked model included a single variable describing the extent of habitat loss (PHR: percent of the home range in suitable habitat) and correctly predicted 72% of the verification data and 77% of the validation data (n = 21 occupied and 10 unoccupied ranges). Model sensitivity was 94% for the verification data and 95% for the validation data, indicating that the model was reliable for predicting home range occupancy. Models that incorporated landscape fragmentation did not perform better than the PHR-only model, suggesting that landscape composition is the primary determinant of occupancy of landscapes by martens in Newfoundland. Of the 84 occupied home ranges, 82% had ≥35% suitable habitat in their home range, 50% had ≥45% suitable habitat, and 15% had ≥60% suitable habitat. In contrast, of the 39 unoccupied home ranges, 49% had ≥35% suitable habitat, 31% had ≥45% suitable habitat, and only 5% had ≥60% suitable habitat. The probability of occupancy by martens began to decline faster as the percent of suitable habitat fell below 60% of home-range sized landscapes, thus, efforts to recover marten populations should focus on maintaining suitable habitat above 60% of landscapes. This model can be used to predict how changes in habitat currency affect the probability of occupancy of landscapes by this endangered subspecies of marten, and to provide insights into the non-linear effects of habitat loss on wide-ranging, area sensitive species in landscapes with limited suitable habitat resulting from natural and anthropogenic processes.

INTRODUCTION

Conservation biologists are often faced with a shortage of information on the potential distribution of species over large areas (Hairston 1949, Andrewartha and Birch 1954, Scott et al. 2002), particularly for endangered species. Predictive habitat modeling can provide spatially explicit information on the distribution of species and can be used to identify and prioritize areas of potential habitat that have important conservation value (Ball et al. 2005), to identify areas for potential species reintroductions (Yanez and Floater 2000), to identify areas that have a high risk of species extinction (Araujo and Williams 2000), or to predict the effects of management practices on featured species (Dettmers and Bart 1999). Additionally, predictive models that incorporate landscape metrics can be used to evaluate the relative effects of habitat loss and fragmentation on occupancy of landscapes by species (Trzcinski et al. 1999, Reunanen et al. 2002).

Predictive habitat models are especially important to the Newfoundland marten (*Martes americana atrata*), an endangered, genetically distinct subspecies (Kyle and Strobeck 2003) of mustelid that is endemic to the island of Newfoundland, Canada. They have been listed by the Committee on the Status of Endangered Species in Canada (COSEWIC 2001) and are estimated to number less than 300 individuals (Forsey et al. 1995). Limiting factors associated with declines in marten populations are thought to be associated with direct mortalities associated with non-target capture in furbearer traps and snares set for snowshoe hares and loss of late successional forests (Bissonette et al. 1989, Thompson 1991, Buskirk 1992). Although most management efforts for martens in Newfoundland have been directed at the scale of the forest stand, recently published data from Maine (Chapin et al. 1997), Utah (Hargis and Bissonette 1997), and Quebec (Potvin et al. 2000) indicate that martens may be extremely sensitive to landscape-scale fragmentation. Fragmentation may be even more relevant to conservation of martens in Newfoundland, which maintain home-range areas that are up to 8X larger than those observed for martens in Maine (Gosse et al. 2005, B. Hearn, unpublished data) and up to 5.5X times larger than the mean value reported for North America (Powell 1994). Because of the large area requirements of martens in Newfoundland, and for their unwillingness to cross large gaps of unsuitable habitat (Drew 1995), they are considered a species that is hypothesized to be strongly affected by forest fragmentation (Dale et al. 1994). Across the species geographic range, martens are reluctant to venture into areas with low overhead canopy cover and few trees (Spencer et al. 1983, Thompson and Harestad 1994, Drew 1995, Hargis and Bissonette 1997, Potvin et al. 2000, Payer and Harrison 2003, 2004). Therefore, the highly fragmented nature of western Newfoundland, which is bisected by large unforested bogs and barrens, and which is extensively logged using overstory removal techniques, presents difficult conservation challenges for an endangered subspecies which is wide-ranging, forest dependent, and fragmentation sensitive.

Habitat loss and fragmentation are important issues in conservation biology, and are often considered the primary threats to biological diversity (Wilcox and Murphy 1985, Fahrig 1997, With 1997). Habitat loss can include reduction in habitat area, habitat fragmentation, deterioration of habitat within patches, and deterioration between patches (matrix) (Sih et al. 2000). Habitat loss and fragmentation can lead to reductions in population size, increased isolation of populations, and decreased colonization (Lawton 1995), which can in turn increase the probability of extinction by demographic, environmental, or genetic stochasticity (Andrén 1994, Burkey 1995, Fahrig 1997). These responses are especially critical for endangered species, which already occur at low densities and are thus at increased risk of local extinction (Gaston 1994).

Conservation efforts that have not considered the size, shape, or distribution of habitat patches across a landscape have faced criticism (Pulliam et al. 1992, Dunning et al. 1995, Wahlberg et al. 1996, Huxel and Hastings 1999). Habitat fragmentation has three separate components: reduction of suitable habitat, reduction in patch size, and increasing isolation of the remaining patches (Andrén 1994). Spatial patchiness can be quantified by composition (patch types and abundance) and configuration (shape and juxtaposition). While some studies have concluded that habitat arrangement or configuration is the most important determinant of population response (Hiebler 2000), others suggest that the dominant factor in determining species persistence is the total amount of suitable habitat (McIntyre and Wiens 1999, Trzcinski et al. 1999, Fahrig 1997, 2002; Flather and Bevers 2002). Andrén (1994) analyzed data from modeling and empirical studies and concluded that habitat fragmentation is a function of habitat loss up until the landscape has 30% suitable habitat remaining. When the landscape is reduced below 30% suitable habitat, the size of patches and their isolation compound the effects of habitat loss, resulting in a reduction in population size that is greater than expected from habitat loss alone (Andrén 1994). Further, the effects of habitat fragmentation can compound the effects of pure habitat loss (Bender et al. 1998), and the effects of fragmentation on population persistence can be dramatic when landscapes are limited by the amount of suitable habitat (McLellan et al. 1986, Andrén 1994, Fahrig 1997, 1998). Because of the fragmented landscape in Newfoundland, any additional habitat loss or fragmentation may not be additive to what occurs naturally. Determining the role of habitat loss, fragmentation, and the interaction between loss and fragmentation are central to species conservation and can be used to help focus conservation and management efforts of endangered Newfoundland martens.

Habitat fragmentation is especially critical for larger-bodied vertebrates because they often have large individual territories (Lindstedt et al. 1986) and low intrinsic rates of increase (Blueweiss et al. 1978), which makes them more sensitive to fragmentation. Additionally, martens in particular have large area requirements per unit body weight (Snyder and Bissonette 1987, Chapin et al. 1998) and have been documented to respond to landscape pattern at scales larger than individual home ranges (Bissonette et al. 1989, Chapin et al. 1997, Hargis et al. 1999). However, martens are intrasexually territorial (Katnik et al. 1994) and may not be able to expand their ranges into new areas following habitat loss or fragmentation. These specific habitat requirements of martens make them a good coarse filter species to use in evaluating the effects of habitat loss and fragmentation on how species respond to pattern and process on the landscape.

Very few studies of habitat fragmentation effects exist for wide-ranging vertebrates, and studies that have simultaneously evaluated loss versus fragmentation are restricted primarily to invertebrates, small rodents, and birds (Andrén 1994, Jansson and Angelstam 1999, Villard et al. 1999, Cooper and Walters 2002, Reunanen et al. 2002, Schmiegelo and Mönkkönen 2002, Radford and Bennett 2004, Radford et al. 2005, Suorsa et al. 2005). However, wide-ranging quadrapeds, which have been little studied, may be more sensitive due to their large area requirements and their inability to focus their activities in a few high quality patches via second-order habitat selection (Johnson 1980) when habitats become severely fragmented. Thus, the objectives of this study were to develop predictive models to evaluate the relative performance and weight of evidence for loss versus fragmentation as dominant predictors of landscape-scale occupancy by martens in Newfoundland. This is especially critical where spatial requirements are the largest recorded for the species and where landscapes are naturally fragmented with additional fragmentation from human-induced habitat alteration via clearcut logging. I predicted that natural landscapes for martens would approach or exceed fragmentation thresholds previously defined, and that the importance of fragmentation relative to loss would be greater for martens in Newfoundland than for the less area-sensitive species studied previously.

STUDY AREA

The study area (Figure 3.1) was approximately 1,900 km^2 in southwestern Newfoundland. The western portion (40%) of the area (centered on Little Grand Lake) was composed of a provincially designated wildlife reserve (Pine Marten Study Area: PMSA). The PMSA includes a wildlife reserve, a public reserve, and a provisional ecological reserve. The provisional ecological reserve does not allow snaring, trapping, forest harvesting, development, or road building; the public reserve does not allow forest harvesting, trapping, or snaring, but does allow limited development with permits; the wildlife reserve does not allow snaring/trapping, but does allow limited development and timber harvesting via a permit process. Past timber harvesting occurred on the western portion of the PMSA where Snyder and Bissonette (1987) documented avoidance of recent clearcuts by martens. Topography on the study area was rugged and averaged 352 m in the PMSA (range = 0-715 m) and 373 m (range = 122-621 m) in the eastern portion

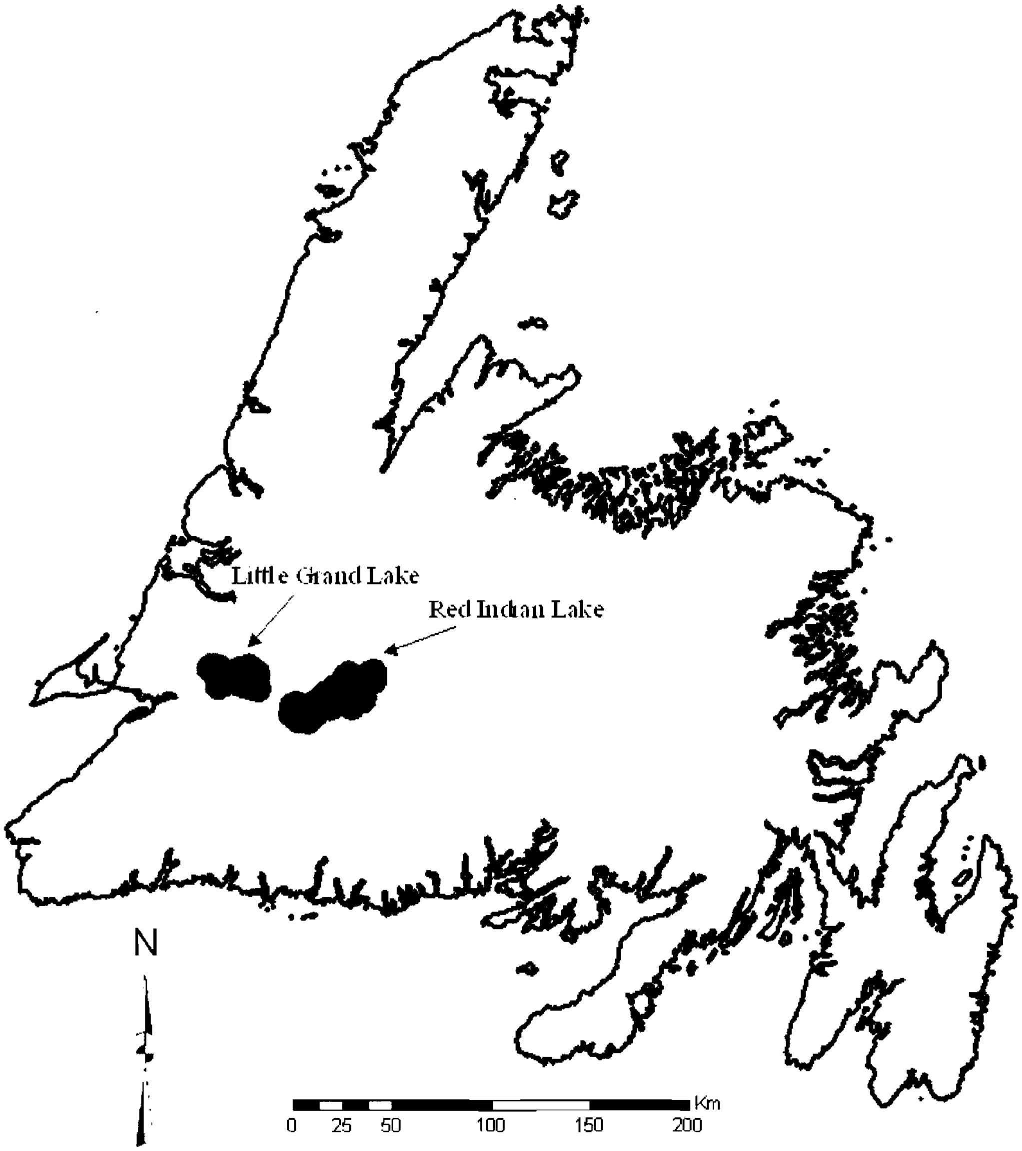

Figure 3.1. Map of study areas centered on Little Grand Lake and Red Indian Lake, Newfoundland, Canada.

(60%) of the study area that was outside of the PMSA. The eastern portion of the study area (centered on Red Indian Lake, Figure 3.1) was characterized by a higher density of logging roads and trails and more human alteration of the landscape via clearcut logging. Snaring for snowshoe hare, furbearer trapping, and timber harvesting was permitted within the eastern portion of the study area.

The overall composition of the study area included 35% coniferous stands, 21% unforested bogs and barrens, 15% water, 11% regenerating and recently cut stands, 9% unmerchantable softwood stands, 6% other (roads, forest clearings, and small stands of deciduous and mixed coniferous-deciduous forest), and 3% insect and wind disturbed areas (Table 3.1). The study area included large patches of old-growth (81+) balsam fir (*Abies balsamea*) with some white pine (*Pinus strobus*), black spruce (*Picea mariana*), eastern larch (*Larix laricina*), and white birch (*Betula papyrifera*). Hemlock looper *(Lambdina fiscellaria)* and spruce budworm *(Choristoneura fumiferana)* infestations in the mid 1980's defoliated patches of old-growth forest as large as 143 ha, which created various stages of regeneration with a significant volume of standing snags and coarse woody debris.

METHODS

Overview

I used an information-theoretic approach (Burnham and Anderson 2002) to develop and evaluate a suite of *a priori* models constructed to evaluate the relative importance of landscape composition versus landscape configuration in determining occupancy versus non-occupancy by resident, adult martens. Predictive models were developed, verified,

Table 3.1. Description of vegetation classes and the percent of the study area in each class, western Newfoundland, Canada.

Vegetation Class	Code	Description	% of Area
Bog/Barren	Bog	Open, generally treeless bogs; rock and soil barrens	20.8
Recent Cuts	Cuts	Recent (≤ 5 years) cuts	3.6
Scrub	Scrub	Unmerchantable softwood, ≤ 6.5 m	8.8
Regenerating Forest	Regen	Conifer regeneration, ≤ 6.5m height, ≥ 75% canopy closure	4.0
Precommercially Thinned Stands	PCT	7-17 years post-thinning, >50% canopy closure, 20-30 year old conifer stands; typical density of 1,500 stems/ha	3.9
Medium Open Softwood	MOS	Medium height (6.6-12.5m tall) conifer stands, ≤50% canopy closure	13.0
Medium Closed Softwood	MCS	Medium height (6.6-12.5m tall) conifer stands, >50% canopy closure	3.9
Tall Open Softwood	TOS	Tall (≥ 12.6m) conifer stands, ≤50% canopy closure	6.5
Tall Closed Softwood	TCS	Tall (≥ 12.6m) conifer stands, >50% canopy closure	11.2
Insect-killed Stands	IK	Insect-killed conifer stands, primarily ≥12.6 m tall, <25% canopy closure, dense understory	2.6
Other	n/a	Hardwood, mixedwood, stand remnants, cleared land, transmission lines, roads.	6.3
Water	n/a	Lakes, ponds, rivers, streams	15.4

and validated using reserved data to predict occupancy rates of martens in landscapes with varying composition and configuration. Models were developed to assist in quantifying the effects of human-induced landscape change on occupancy of this endangered mammal in a naturally fragmented environment. I defined portions of the landscape that were occupied by martens (i.e., second-order habitat occupancy, Johnson 1980) and areas that were surveyed, available to martens, and were unoccupied. This was accomplished by intensively trapping across a range of landscape conditions and defining home range areas of radiocollared martens. Areas occupied by resident martens, but where data were insufficient to estimate home range areas were approximated using a regression model and were excluded from the unoccupied portion of the landscape and were omitted from analyses involving calculation of landscape metrics. Metrics defining landscape composition and configuration were calculated within occupied marten ranges and within landscapes of similar size and shape that were simulated within unoccupied areas.

Trapping and Home Range

Marten trapping was conducted during June 1995-1997 and traps were located every 1-2 km along roads, snowmobile trails, and shorelines to maximize the likelihood that all potential marten territories would include ≥1 trap (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report). Traps were also placed within home ranges of martens whose transmitter batteries were scheduled to expire soon so that their radiocollar could be replaced. Traps were open for a minimum of 7 days to ensure that all resident martens in an area had the opportunity to be captured. Martens were immobilized with an intramuscular injection of ketamine hydrochloride (10-15 mg/kg body weight), were weighed, sexed, ear-tagged or marked with passive integrated transponder tags, and were fitted with radiocollars (Lotek®, Newmarket, Ontario or Holohil Systems®, Toronto, Ontario). A first premolar was extracted for aging using cementum annuli (Strickland et al. 1982).

Martens were located every 7-10 days using fixed-wing aircraft (Cessna 185) with strut-mounted 2-element H-antennas or using helicopters (Bell 206 B or Aerospatial A-star) with one front-mounted and two side-mounted 2-element H-antennas. Locations were recorded using a differently corrected GPS while hovering at low altitude (≤10 m above forest canopy). Only adult resident animals (≥12 months old, ≥10 radiolocations collected over 90 days) were used to define portions of the landscapes occupied. Based on area-observation curves, Hearn et al. (unpublished report) determined that 19 was the minimum number of radiolocations required to obtain a stable home range estimate. Yearly 95% minimum convex polygon home ranges (Mohr 1947) were estimated from 1 May – 30 April. I avoided use of probabilistic home range methods (Boulanger and White 1990) because they greatly overinflated home range estimates (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report); likely causes were the failure of probabilistic models to account for territoriality and lack of a central "core" tendency of individual locations within areas occupied by martens. I obtained fewer than 19 radiolocations for some adult resident martens who occupied space on the landscape; therefore, I estimated their home range indirectly and excluded that portion of the landscape from the area deemed unoccupied by martens. For those individuals (n = 24; 13M, 11F, 22% of adult, resident marten monitored), I estimated home range size and placement using 10-18 radiolocations by increasing the MCP home range (calculated using 100% of available locations) on all boundaries until the area equaled that estimated by a regression using the minimum distance between consecutive independent radiolocations (MINDIST) (Harrison and Gilbert 1985, Phillips et al. 1998). The index MINDIST was a reliable predictor of home range area for 30 martens with >30 radiolocations on the study area (95% MCP = 0.013[MINDIST] - 13.785, $r^2 = 0.79$) (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report). Space occupied by martens whose home ranges were estimated using MINDIST were excluded from the unoccupied portion of the landscape, but were omitted from the sample of occupied ranges for the purposes of estimating metrics to describe habitat composition and configuration. Thus, those areas were excluded from the occupied sample of marten ranges during subsequent modeling. Previous studies of habitat selection by martens have indicated no significant differences in preferences between sexes (Chapin et al. 1997, Payer 1999); thus, I pooled information across males and females for modeling purposes to maximize the available sample size of occupied ranges.

The study area boundary was defined as the effective trapping capture-area. I determined if males were likely to be trapped anywhere within their home range by comparing the number of successful trap locations inside versus outside of 50% adaptive kernel core areas with >30 radiolocations (n = 22) using a sign test (Conover 1999). There was no difference in trap vulnerability inside versus outside of 50% core home ranges of males ($P = 0.80$, n = 22). This analysis implies that there was the ability to capture a male anywhere within their home range because there were captures inside and outside of their core area. I created a boundary around all buffered (diameter = 6.36 km) trap locations based on the average male 95% MCP home range size ($\bar{x}$ = 30.71, n = 40), assuming a circular home-range shape. I then created year-specific areas that defined occupied and potential, unoccupied home ranges within this boundary.

Forest Inventory

I created a habitat map of the study area using the Provincial forest inventory, interpreted from 1:12,500 stereoscopic, black and white aerial photography taken in 1986 with a minimum mapping unit of 0.3 ha (S. Payne, Newfoundland Forest Service, personal communication). The forest inventory was partitioned according to dominant overstory cover, height class, and crown closure. To adjust for differences in stand height between 1986 and the beginning of the study (1995), I increased height by 2.9 m (1 height class) for all stands occupying sites with a site quality index of medium or better based on local growth and yield equations (Anonymous 1991). Year-specific inventories were created for each year of the study by incorporating forest harvesting, road construction, silvicultural activities, and insect disturbances. The final inventory included 11 vegetation types (Table 3.1) representing mature forest characteristics, harvesting activities, regenerating forests, unmerchantable stands, bogs and barrens, and water.

Simulating Unoccupied Home Ranges

I simulated home ranges within areas that were surveyed, available to martens, but were unoccupied to evaluate the differences in landscape composition and configuration between areas that were occupied and unoccupied by martens. I simulated potential home ranges for males and females separately (to account for intersexual differences in home-range areas [B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report] and differences in extent of intra-sexual overlap of home ranges between males and females) within areas that were unoccupied by resident martens. This process was conducted with year-specific landscapes that reflected the most current harvesting practices and disturbances. Unoccupied home ranges were simulated within the unoccupied areas by incorporating the mean sex-specific home-range area (M = 31.7 km^2, F = 12.8 km^2) and intrasexual territorial overlap (F = 12%, M = 25%) observed within used areas. The simulated home ranges were then extracted from the study area to comprise a sample of landscapes that were unoccupied by martens. Each time that an unoccupied home range was removed from the available landscape, a new available landscape was created for the next simulated range. I used 5 different shapes of unoccupied home ranges (4 orientations of an ellipsoid polygon and a circle) that approximated the sex-specific average size of a marten home range on the study area. At each iteration, the simulated home range shape with the largest available area of land within its boundaries was selected, with the constraint that each simulated range must have at least one trap site within its boundary to ensure that it had the opportunity to be classified as occupied if an adult marten resided there. This iterative process continued until no additional unoccupied home ranges could be positioned on the landscape.

Defining Habitat Currency

Landscape composition and configuration are most easily quantified using metrics based on binary classifications to define suitable and unsuitable habitat patches. Thus, I defined the best statistical and biological breakpoint for defining suitable versus unsuitable habitat in a boolean fashion by collapsing the 11 vegetation types (Table 3.1, excluding water and other) into the most parsimonious groupings to define suitable and unsuitable "currencies". I used stand-scale habitat selection results (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report) from companion studies and a subsequent Kolmogorov-Smirnov test (Zar 1999) to maximize the difference between the amount of suitable and unsuitable habitats between occupied and unoccupied landscapes. Based on third-order (Johnson 1980) habitat selection by 58 adult martens representing 92 marten-years on the study site, (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report) reported that insect-killed stands (IK) were selected for and medium height (6.6-12.5 m tall) open canopy (≤50% canopy closure) softwood stands (MOS), Scrub (unmerchantable softwood stands ≤6.5 m tall), and bog/barren (bogs, rock and soil barrens) were selected against by martens. Regenerating (conifer regeneration, ≤6.5 m height, ≥75% canopy closure) clearcuts (REGEN), tall (≥12.6 m tall) closed canopy (>50% canopy closure) softwood stands (TCS), tall open canopy softwood stands (TOS), medium height closed canopy softwood stands (MCS), pre-commercially thinned (PCT) stands (7-17 years post-thinning, >50% canopy closure, 20-30 year conifer stands), and recent (≤5 years) clearcuts (CUT) were used in proportion to availability. All types that were used greater than or in equal proportion to availability were considered as suitable habitat. For ambiguous types (i.e., recent cuts), they were evaluated alternatively as suitable and unsuitable habitat and the classification with the greatest *KS* value was chosen. I tested 2 suitable habitat groupings: 1) PCT + MCS + TOS + TCS + REGEN + IK 2) PCT + MCS + TOS + TCS + REGEN + IK + CUT and 2 unsuitable habitat groupings: 1) Bog + Scrub + MOS 2) Bog + Scrub + MOS + CUT.

Landscape Metrics

Many landscape metrics are not necessarily relevant to species or ecological processes (Hulshoff 1995, Tischendorf 2001, Li and Wu 2004), so I chose metrics based on previous studies of responses of martens to landscape pattern (Chapin et al. 1998, Hargis et al. 1997, Hepinstall and Harrison, University of Maine, unpublished data), ecological relevance (Li and Wu 2004), general knowledge of marten habitat selection and behavior, and metric behavior (Tischendorf 2001, Hargis et al. 1999, Saura and Martínez-Millán 2001, Neel et al. 2004). Landscape metrics (Table 3.2) were generated using FRAGSTATS version 3.3 (McGarigal and Marks 1995. The "landscape" was considered an individual marten home range. I only calculated metrics associated with suitable habitat because in the binary landscapes, metrics associated with suitable habitat are highly correlated with those associated with unsuitable habitat. I chose metrics as outlined above and then structured a strategic set of *a priori* models in an information-theoretic framework that would allow an evaluation of the relative influence of habitat loss, fragmentation, and the combined effects of loss and fragmentation in determining the observed patterns of landscape occupancy by martens. I used Pearson product-moment correlation coefficients to examine the correlation among landscape metrics for occupied and unoccupied home ranges separately, and did not include variables in the same model if the correlation was $>|0.95|$ (Burnham and Anderson 2002).

Metrics related to habitat loss included percent of the home range composed of suitable habitat (PHR), largest patch index (LPI), and radius of gyration (GYRATE). The PHR is the most direct measure of the quantity of suitable habitat in marten home ranges without respect to configuration and is easily extracted from GIS databases without need

Table 3.2. Variables representing habitat loss and configuration included in logistic regression models to predict home range occupancy by martens in Newfoundland, Canada during 1995-1997.

Code	Description	Relevant Measurement (McGarigal and Marks 1995)
PHR	Percent of the home range in suitable habitat	Percent of home range in suitable habitat
LPI	Largest patch index	Largest patch of suitable habitat in home range
MPS	Mean patch size	Mean size of largest patch in home range
PSCV	Patch size coefficient of variation	Variability in patch sizes within home range
GYRATE	Radius of gyration	Mean distance between each cell in a patch of suitable habitat and the patch centroid
MNN	Mean nearest neighbor	Shortest distance between patches of suitable habitat
MNNCV	Mean nearest neighbor coefficient of variation	Variability in the shortest distance between patches of suitable habitat
CLUMPY	Clumpy	Comparison of observed proportion of like cell adjacencies of suitable habitat with the proportion expected under a spatially random distribution

Table 3.2. Continued.

Code	Description	Relevant Measurement (McGarigal and Marks 1995)
MPS*PD	Mean patch size * patch density	Interaction between average patch size in home range and density of patches in home range
MPS*PSCV	Mean patch size * patch size coefficient of variation	Interaction between average patch size in home range and variability in patch sizes in home range
MNN*MNNCV	Mean nearest neighbor * nearest neighbor coefficient of variation	Interaction between shortest distance between patches of suitable habitat in home range and variability in those distances

for fragmentation software. The LPI is the percent of the home range that is comprised by the largest patch of suitable habitat (McGarigal and Marks 1995), and can be used as an index of area requirements. I used this metric because the largest, continuous forest patch averaged >75% of marten home ranges in Maine (Chapin et al. 1998). GYRATE is calculated as the mean distance between each cell in a patch of suitable habitat and the patch centroid, and is a measure of cluster size used in percolation theory (Stauffer and Aharony 1991). The metric can be described as the distance that an individual that is placed and moves randomly can traverse and remain within a single patch of suitable habitat (Keitt et al. 1997).

Metrics related to habitat fragmentation included CLUMPY, mean patch size (MPS), patch size coefficient of variation (PSCV), mean nearest neighbor (MNN), and mean nearest neighbor coefficient of variation (MNNCV). CLUMPY measures how aggregated suitable habitat is by comparing the observed proportion of like cell adjacencies of suitable habitat with the proportion expected under a spatially random distribution (McGarigal and Marks 1995). Mean patch size and patch size coefficient of variation (relative variability in patch sizes) were included because small patches relative to home range size are predicted to receive less use based on observations that used patches were 18X the size of unused patches by martens in Maine (Chapin et al. 1998). Mean nearest neighbor is a measure of patch isolation, reflecting how spatially accessible habitat is to dispersing individuals by measuring the shortest distance between patches of suitable habitat. Landscapes with MNN between non-forest patches <100 m were considered unsuitable for martens in Utah (Hargis et al. 1999) and used patches were closer to other large patches than were unused patches for martens in Maine (Chapin et al. 1998).

I used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative support for potential relationships between home range occupancy and measures of habitat composition and configuration using logistic regression. I included each variable describing habitat loss (PHR, LPI, GYRATE) as a single variable model to determine which loss variable best differentiated between occupied and unoccupied home ranges. However, when combining habitat loss and fragmentation metrics in the same model, I chose to use PHR because of its simplicity and previous association with occupancy by martens in Maine (Hepinstall and Harrison 2003). I did not test metrics related to fragmentation alone because either the behavior of the metric requires an additional metric for interpretation, or because a second-order metric increases the interpretation of a first-order metric (McGarigal and Marks 1995). CLUMPY behaved poorly at low values of aggregation because the metric was similar at both high and low values of percent area, but the metric was good across intermediate to high values of aggregation across a range of percent area (Neel et al. 2004); therefore, I included a model of CLUMPY and PHR to facilitate understanding of differences between occupied and unoccupied ranges when fragmentation occurred at intermediate to high levels. Mean patch size is not appropriate as a single model because it is not informative about the distribution of patches, thus I included a model of MPS*PSCV to evaluate the size and variability in patch sizes. I also included this model with PHR to determine if the percent of suitable habitat improves the fragmentation only model. Mean nearest neighbor metrics were tested with PHR because in simulations MNN was only sensitive at low values of percent area and high values of aggregation, and had low variability across much of the aggregation by area gradient (Neel et al. 2004). I also included a global model with PHR + MPS*PSCV + MPS*PD + MNN*MNNCV + CLUMPY. The global model included what I felt would be the most sensitive metric related to habitat loss (PHR), models of patch size, variability, and density, the interaction of mean nearest neighbor and the variability in nearest distances, and CLUMPY. I chose to include MNN*MNNCV and did not include MNN or MNNCV in the global model because of their redundancy.

I judged the relative support for each model using Akaike's Information Criterion (AIC) adjusted for small sample size (AIC_c), where the model with the smallest AIC_c value (or within <2 of the model with the smallest AIC_c) and the largest AIC_c weight (ωAIC_c = the weight of evidence of each model where the sum of all model weights = 1) was judged as the most parsimonious fit to the data (Burnham and Anderson 2002). Differences between the AIC_c value for the best model and values from other models (ΔAIC_c) were used to evaluate the relative plausibility of competing models. I considered all models with $\Delta AIC_c \leq 2$ of the best model. To establish further evidence for the importance of each independent variable, relative importance was estimated by adding all w_i values for all models containing the variable (Burnham and Anderson 2002). Parameter estimates were generated by averaging over models within 2 AIC_c units of the best model (± unconditional standard error).

Model Evaluation

The most robust approach for evaluating predictive capabilities of models is to incorporate independent data (Fielding and Bell 1997, Manel et al. 1999, Pearce and Ferrier 2000), but for an endangered species with low prevalence, the data were not available. Since it was not possible to validate the models on a data set from a different location, the predictive ability of the models was tested using 2-fold partitioning (Smith 1994) by dividing the data in two different sets by randomly assigning 75% of the data to a calibration data set and 25% of the data to an evaluation data set. The calibration data set was used to develop the model and was subsequently tested on the evaluation data set (Fielding and Bell 1997).

To facilitate comparison with other studies, I also differentiated a predicted presence from a predicted absence with the commonly used 0.5 probability threshold (Fielding and Bell 1997). Because this approach requires an arbitrary critical threshold probability (P_{crit}) to classify species as present or absent from model prediction, the threshold chosen will influence the outcome of the model (Hosmer and Lemeshow 1989, Fielding and Bell 1997). Thus, I used a range of criteria in assessing model performance, including sensitivity, specificity, CCR, and a threshold independent metric that assesses performance across a range of probability thresholds using receiver operating characteristic (ROC) curves (Hanley and McNeil 1982, Zweig and Campbell 1993, Fielding and Bell 1997, Pearce and Ferrier 2000). A ROC curve provides an unbiased measure of accuracy (Fielding and Bell 1997) by plotting the sensitivity (true positive fraction) on the y-axis and 1-specificity (false positive fraction) on the x-axis for a range of decision thresholds from 0-1 at intervals of 0.005 (Murtaugh 1996). Each point on the curve represents a sensitivity/false positive pair that corresponds to a particular decision threshold and the resulting curve is called the ROC curve. The proportion of the area under the curve (AUC) is a single measure of accuracy with values between 0.5 and 1.0. I calculated AUC using the program ROC/AUC (Bonn and Schröder 2001). Perfect discrimination between presence and absence (AUC = 1.0) results in a plot that passes through the upper left corner, where the true positive fraction equals one (sensitivity = 100%) and the false positive fraction equals zero. A model with no discrimination ability (AUC = 0.5) would result in a 45 degree diagonal line from the lower left corner to the upper right corner of the plot. Areas under the curve >0.9 indicate very good discrimination, areas from 0.7-0.9 indicate satisfactory discrimination, and areas 0.5-0.7 indicate poor discrimination (Swets 1988). The ROC/AUC can be interpreted as the probability that a model will correctly distinguish between occupied and unoccupied ranges; if you select an occupied and unoccupied range at random, the ROC estimates the probability that the model will predict a higher probability of occurrence for the occupied home range than for the unoccupied home range (Hanley and McNeil 1982).

Two disadvantages of ROC plots are that the decision threshold is not displayed on the plot even though that threshold is used to generate the plot, and area is an imperfect measure of performance because two ROC plots can have similar areas, but can differ in shape (Zweig and Campbell 1993). Thus, I also present a graph displaying sensitivity, specificity, and CCR at each decision threshold. I also calculated P_{fair} (Schröder & Richter 1999), which minimizes the difference between sensitivity and specificity (Capen et al. 1986) and the optimized correct classification rate (P_{opt}, Zweig and Campbell 1993, Schröder and Richter 1999/2000), which maximizes the percentage of true absences and presences that are correctly identified.

I mapped the extent of suitable habitat across the study area for male and female martens separately to quantify the amount of habitat with a probability of occupancy ≥90% (corresponds to 60% suitable habitat within the home range), which corresponded with the range of habitat conditions before occupancy by martens declined rapidly. I mapped suitable habitat using the top-ranked logistic regression model of PHR (percent of suitable habitat within the home range).

RESULTS

Defining Habitat Currency

All suitable habitat groupings were significantly different ($P \leq 0.02$) between occupied and unoccupied home ranges. The best separation between occupied and simulated unoccupied home ranges (largest *KS* value) was provided by the suitable habitat type grouping IK + PCT + MCS + TOS + TCS + Regen ($KS = 0.38$, Table 3.3). Both of the suitable and unsuitable habitat groupings were significantly different ($P \leq 0.02$) between occupied and unoccupied home ranges (Table 3.3). The largest *KS* value was the same ($KS = 0.38$, $P = 0.00$) for the top suitable and top unsuitable group, indicating that these groups were nearly mirror images of each other. Thus, I chose the suitable grouping as the measure of currency to facilitate comparisons with other studies (e.g., Trzcinski et al. 1999, Reunanen et al. 2002, Hepinstall and Harrison 2003) that evaluated declines in species occupancy using the percent of suitable habitat on the landscape as the independent variable.

Table 3.3. Comparison of habitat currency using a boolean classification of suitable or unsuitable vegetation classes. A Kolmogorov-Smirnov test (*KS*) was used to maximize the difference in the percent of vegetation types in suitable or unsuitable groupings between occupied and simulated unoccupied home ranges of martens in western Newfoundland, Canada, 1995-1997.

Vegetation Types[a] in Grouping	*KS* Value	*P*-Value
Suitable		
IK + PCT + MCS + TOS + TCS + Regen	0.38	0.00
IK + PCT + MCS + TOS + TCS + Regen + CUT	0.30	0.02
Unsuitable		
Bog + Scrub + MOS	0.30	0.02
Bog + Scrub + MOS + Cut	0.38	0.00

[a] See table 3.1 for a description of vegetation type codes.

Marten home ranges averaged 47% of suitable habitat (range = 24-78%). Based on 84 occupied home ranges, 82% were composed of ≥35% suitable habitat, 50% of ≥45% suitable habitat, and 15% of ≥60% suitable habitat (Figure 3.2). Of 39 unoccupied home ranges, 49% were composed of ≥35% suitable habitat, 31% of ≥45% suitable habitat, and only 5% contained ≥60% suitable habitat (Figure 3.2).

Model

I used actual home ranges based on 84 adult marten-years (40M, 44F) representing 54 individual animals (29M, 25F) to delineate occupied landscapes and also modeled 39 potential (21M, 18F), but unoccupied landscapes based on simulated home-ranges in portions of the study area where adult martens were not documented to reside during 1995-1997. The logistic regression model was built using 92 landscapes (63 occupied, 29 unoccupied) and the model was verified using 31 randomly selected landscapes (21 occupied, 10 unoccupied) that were withheld from the model-build data set.

The best model was the single variable model PHR (standardized coefficient = 3.01). The sum of model weights for PHR equaled 0.93, indicating strong support for this variable as the dominant metric influencing probability of landscape occupancy by martens. A subset of 5 models (of 9 candidate models; Table 3.4) had $\Delta AIC_c \leq 2$ relative to the top model that best predicted occupancy by martens; 4 candidate models were inferior ($\Delta AIC_c = 3.34\text{-}10.60$) to the top-ranked model. The 5 most parsimonious models all included the variable PHR (Table 3.4). Although the other 4 best models that included PHR and a variable describing landscape composition were close in terms of ΔAIC_c, the standardized coefficients did not provide strong support that landscape configuration metrics were related to probability of occupancy (MNN*NNCV $\beta = -0.88$,

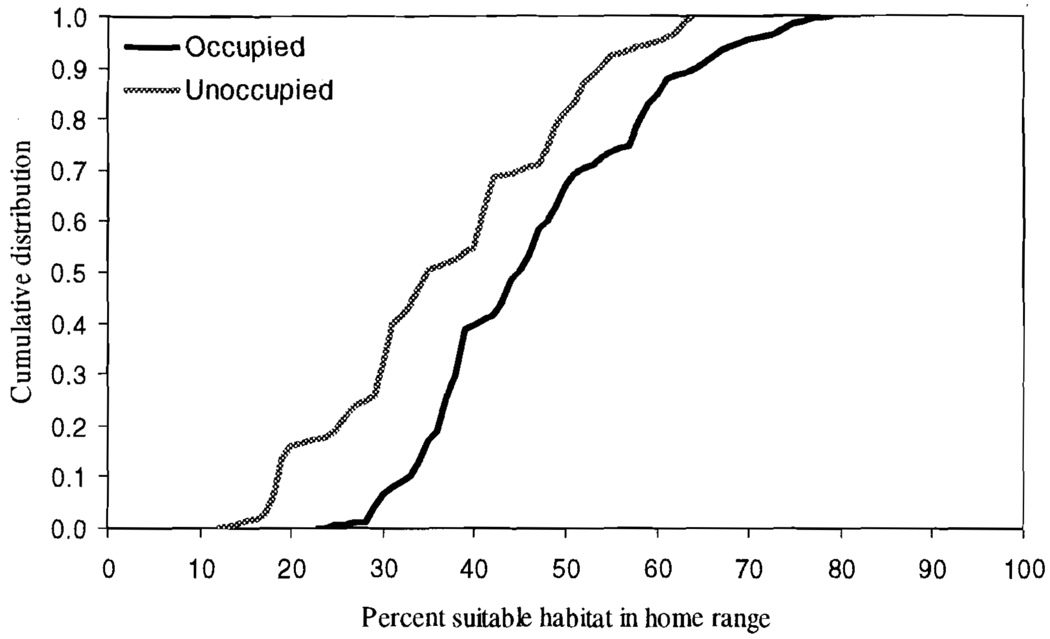

Figure 3.2. Cumulative distribution of the percent of the home range in suitable habitat for martens in western Newfoundland, Canada, 1995-1997. Occupied home ranges are depicted by the solid black line, whereas simulated home-range-sized areas that were not occupied (i.e., unused landscapes) are depicted by the hatched gray line.

Table 3.4. Akaike's Information Criterion (AIC_c)[a] for the *a priori* set of candidate models used to examine the influence of variables describing habitat loss and habitat fragmentation on home range occupancy by Newfoundland martens, western Newfoundland, Canada, 1995-1997.

Model[b]	Rank	K[c]	Log (L)[d]	AIC_c	ΔAIC_c	Model Likelihood	w_i[e]
PHR	1	2	-50.50	105.14	0.00	1.00	0.35
PHR, MPS*PSCV	2	3	-50.14	106.55	1.40	0.50	0.17
PHR, CLUMPY	3	3	-50.41	107.10	1.96	0.38	0.13
PHR, MNN*MNNCV	4	3	-50.43	107.13	1.99	0.37	0.13
PHR, MNN	5	3	-50.44	107.14	2.00	0.37	0.13
LPI	6	2	-52.17	108.48	3.34	0.19	0.07
PHR, MPS*PSCV, MNN*MNNCV, CLUMPY	7	5	-50.10	110.90	5.75	0.06	0.02
Gyrate	8	2	-55.52	115.18	10.04	0.01	0.00
MPS*PSCV	9	2	-55.80	115.74	10.60	0.00	0.00

[a] Akaike's Information Criterion adjusted for small sample size.
[b] See table 3.2 for a description of variables.
[c] K = number of estimable parameters.
[d] Log (L) = log-likelihood.
[e] w_i = Akaike weight.

MNN $\beta = -0.37$, MPS*PSCV $\beta = -0.88$, CLUMPY $\beta = -0.44$). Additionally, the 95% confidence interval on the odds ratio for MNN*MNNCV, MNN, MPS*PSCV, and CLUMPY all included 1, suggesting that those variables were ineffective as predictors (Hosmer and Lemeshow 1989). The second-ranked model included PHR and MPS*PSCV (Table 3.4); MPS*PSCV was highly correlated with PHR (r = 0.63, 0.61) and LPI (r = 0.89, 0.72) in actual and simulated ranges, respectively, suggesting that MPS*PSCV may be measuring habitat loss as much as it is measuring fragmentation. The third, fourth, and fifth best models that had $\Delta AIC_c \leq 2$ relative to the top ranked model included fragmentation variables (CLUMPY, MNN*MNNCV, MNN) (Table 3.4). Those models had lower correlation ($r \leq |0.50|$) with loss metrics in both occupied and unoccupied landscapes (Table 3.5), but added very little additional evidence that habitat fragmentation is an important variable influencing home range occupancy by martens.

The model averaged parameter estimate and the unconditional SE for PHR indicated that the proportion of suitable habitat in a home range increased as occupancy increased (PHR = 0.073, SE = 0.024). The model averaged equation for predicting the probability of home range occupancy by martens was:

$$p(O) = \frac{e^{-2.147+0.073(PHR)}}{1+e^{-2.147+0.073(PHR)}}$$

The model averaged equation predicts a 50% probability of occupancy when the percent of suitable habitat in the home range is 30% (Figure 3.3). The probability of occupancy increases to 80% when 49% of the home range is in suitable habitat, and reaches a 90% probability at 60% suitable habitat within the home range (Figure 3.3). The probability of occupancy curve declines more rapidly when suitable habitat in the landscape is below 60% (Figure 3.3).

Table 3.5. Pearson correlation coefficients between variables[a] representing habitat loss and habitat fragmentation calculated on a) simulated unoccupied (n = 29) home ranges, and b) actual marten home ranges (n = 63) home ranges, 1995-1997, western Newfoundland, Canada.

a)

	PHR	LPI	MPS	PSCV	GYRATE	MNN	MNNCV	CLUMPY	MPS*PD	MPS*PSCV	MNN*MNNCV
PHR	1.00										
LPI	0.86	1.00									
MPS	0.56	0.80	1.00								
PSCV	0.29	0.26	-0.011	1.00							
GYRATE	0.69	0.88	0.88	0.25	1.00						
MNN	-0.47	-0.22	0.10	-0.41	-0.04	1.00					
MNNCV	-0.43	-0.12	0.12	-0.29	0.06	0.85	1.00				
CLUMPY	0.11	0.32	0.62	-0.48	0.50	0.53	0.49	1.00			
MPS*PD	1.00	0.86	0.56	0.29	0.69	-0.47	-0.43	0.11	1.00		
MPS*PSCV	0.63	0.89	0.96	0.11	0.95	0.01	0.11	0.50	0.63	1.00	
MNN*MNNCV	-0.45	-0.19	0.05	-0.32	-0.04	0.97	0.92	0.47	-0.45	0.00	1.00

[a] See table 3.2 for a description of variables.

Table 3.5. Continued.

b)

	PHR	LPI	MPS	PSCV	GYRATE	MNN	MNNCV	CLUMPY	MPS*PD	MPS*PSCV	MNN*MNNCV
PHR	1.00										
LPI	0.92	1.00									
MPS	0.68	0.64	1.00								
PSCV	-0.16	-0.05	-0.47	1.00							
GYRATE	0.28	0.43	0.35	0.38	1.00						
MNN	-0.33	-0.37	0.04	-0.31	-0.24	1.00					
MNNCV	-0.31	-0.31	-0.26	-0.04	-0.07	0.60	1.00				
CLUMPY	-0.18	-0.25	0.24	-0.51	-0.09	0.55	0.30	1.00			
MPS*PD	1.00	0.92	0.68	-0.16	0.28	-0.33	-0.31	-0.18	1.00		
MPS*PSCV	0.61	0.72	0.68	0.11	0.84	-0.27	-0.22	-0.10	0.61	1.00	
MNN*MNNCV	-0.29	-0.30	-0.13	-0.15	-0.12	0.80	0.94	0.42	-0.29	-0.21	1.00

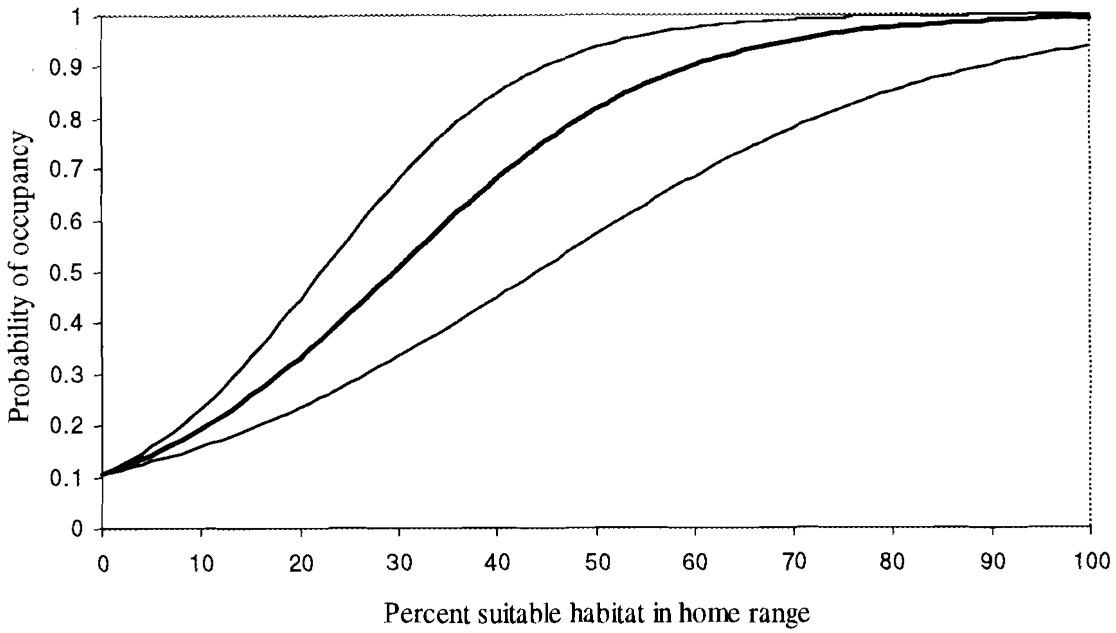

Figure 3.3. Relationship between probability of landscape occupancy by martens in western Newfoundland (1995-1997) and the proportion of suitable habitat within home ranges using a model averaged parameter estimate and unconditional standard error (± SE) on the model averaged estimate based on logistic regression analyses.

I mapped the extent of suitable habitat for males and females in 1996 using the top-ranked logistic regression model (PHR). The total study area size was 1,796 km^2 in 1996, and suitable habitat with a probability of occurrence (POC) $\geq$90% (corresponded to 60% PHR within home ranges, the value before which occupancy by martens declines most rapidly) represented only 145 km^2 for males (Figure 3.4) and 188 km^2 for females (Figure 3.5). The largest contiguous patch of suitable habitat with POC $\geq$90% was 120 ha for females and 72 ha for males (excludes water bodies).

The best model (PHR) correctly predicted (based on a cutoff probability of 0.5) 72% of the verification data and 77% of the validation data. The model sensitivity was 94% for the verification data and 95% for the validation data, indicating that the model did an excellent job of correctly predicting home range occupancy. The model specificity was 24% for the verification data and 40% for the validation data. The AUC from the ROC plot (Figure 3.6) was 0.71 (SE = 0.06), indicating that 71% of the time a random selection from the occupied home ranges will have a greater percent of suitable habitat than a random selection from the unoccupied home ranges. The classification threshold where sensitivity, specificity, and CCR were equal (P_{fair}) was 0.69 (Figure 3.7). The optimized correct classification rate (P_{opt}), which maximizes sensitivity and specificity, was at a classification threshold of 0.57; at this classification threshold, sensitivity was 89%, specificity was 48%, and the overall correct classification rate was 76% (Figure 3.7).

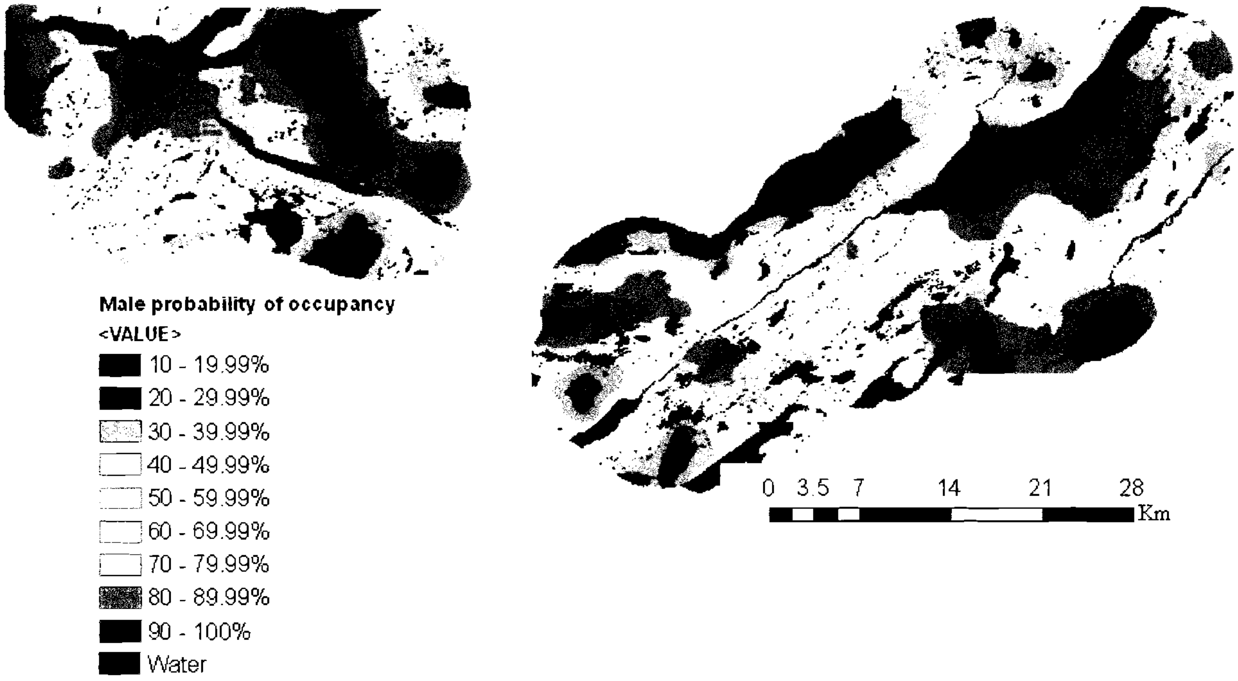

Figure 3.4. Predicted probability of occupancy across the study area based on the top-ranked logistic regression model (i.e., a one-variable model including the percent of the home range in suitable habitat) for male martens in western Newfoundland, Canada, 1996.

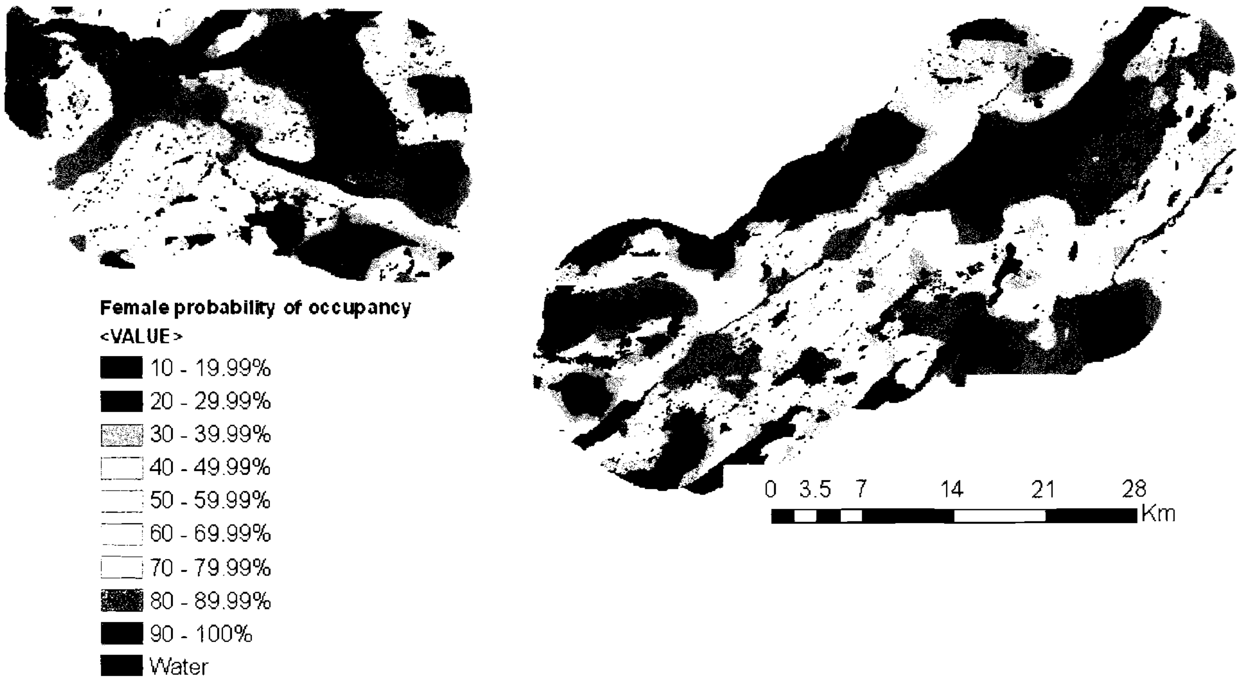

Figure 3.5. Predicted probability of occupancy across the study area based on the top-ranked logistic regression model (i.e., a one-variable model including the percent of the home range in suitable habitat) for female martens in western Newfoundland, Canada, 1996.

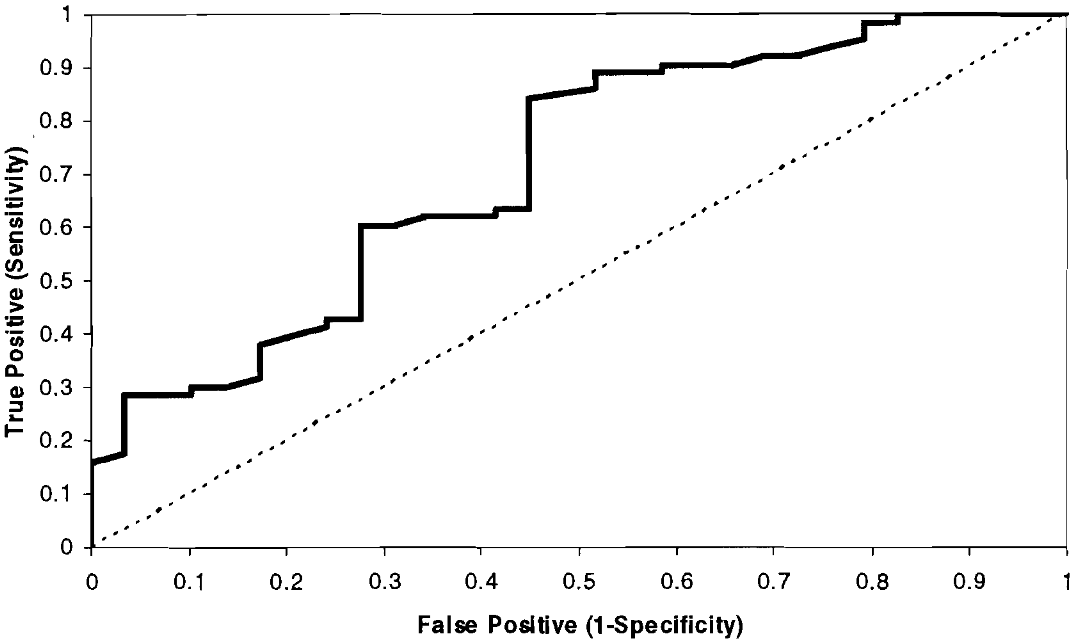

Figure 3.6. Receiver operating characteristic (ROC) curve to assess the discriminative ability of a logistic regression model developed to predict probability of occupancy by martens based on the percent of a home-range sized landscape in suitable habitat. The ROC plots the true positive rate (sensitivity) versus the false positive rate (1-specificity) for all possible threshold probabilities.

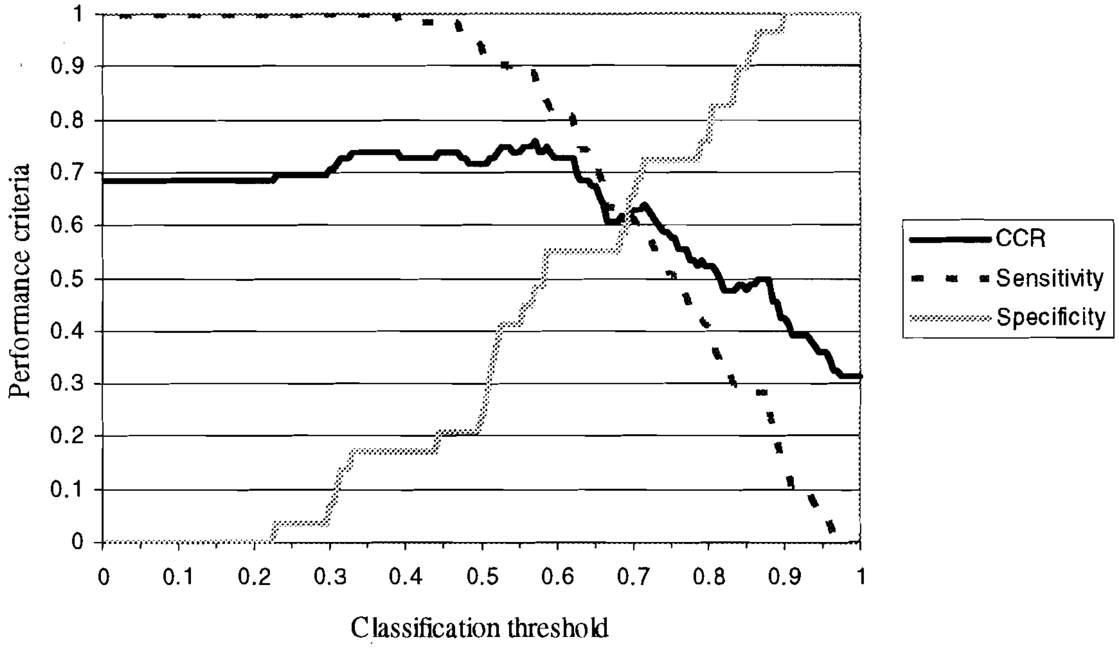

Figure 3.7. Performance criteria (correct classification rate, sensitivity, or specificity) at different classification thresholds (i.e., different probability of occupancy rates generated from logistic regression models, used to make binary predictions as to whether an area will be occupied or unoccupied by martens) developed from a logistic regression model predicting home range occupancy by martens based on percent of the home range in suitable habitat, western Newfoundland, Canada, 1995-1997.

DISCUSSION

Habitat Loss versus Fragmentation

The logistic regression habitat model successfully predicted the probability of landscape occupancy by Newfoundland martens. The results suggest that habitat loss is the most important determinate of species persistence for this endangered subspecies. The top ranked model was the single variable model PHR (percent of the home range in suitable habitat). Indeed, the proportion of the class of interest is often the dominant metric describing spatial pattern (O'Neill et al. 1988, Gustafson and Parker 1992), indicating that the predominant effect of habitat loss is describing patterns of home range occupancy. Competing models that included a variable measuring fragmentation had low correlation with loss metrics, but added very little additional evidence that habitat fragmentation had an additive affect on second-order (Johnson 1980) habitat occupancy by Newfoundland martens.

Contrary to this study, previous studies have suggested that martens are sensitive to both landscape composition and configuration (Bissonette et al. 1997, Chapin et al. 1998, Hargis et al. 1999, Hepinstall and Harrison 2003), but these studies were conducted in areas with much less natural fragmentation and a greater percent of the landscape in suitable habitat. Correspondingly, neutral landscape models have predicted that landscape function is influenced more by the abundance of habitat than by fragmentation, especially when habitat is sparse (With et al. 1997, McIntyre and Wiens 1999). These results are consistent with neutral model predictions; habitat composition is more important than habitat configuration on this landscape with a small percentage of suitable habitat. Additionally, Andrén (1994) concluded that individuals respond to habitat loss when the landscape has >30% suitable habitat remaining, but will respond to fragmentation when suitable habitat drops below 30% of the landscape. The landscape contained 32% suitable habitat and the average amount of suitable habitat within home ranges (47%) was substantially greater than the threshold when Andrén (1994) predicted increasing effects of fragmentation. This suggests that martens were exhibiting second-order habitat selection (*sensu* Johnson 1980). By selectively positioning their ranges in areas with >30% suitable habitat, martens may be able to reach all stands of suitable habitat within their home range, and the landscape may thus be viewed as functionally continuous even though suitable habitat is divided into fragments. I caution that this study area approached the threshold (30%) predicted for adverse fragmentation effects by Andrén (1994) and that management practices which increase habitat fragmentation and decrease PHR to <30% could lead to catastrophic, non-linear declines in rates of habitat occupancy by martens.

I hypothesize that because the distinct subspecies of Newfoundland marten evolved in a naturally fragmented landscape, that they are not as sensitive to habitat fragmentation as they are to habitat amount. Further, the larger body size and disproportionately larger home range sizes observed for Newfoundland martens compared to mainland populations (Gosse et al. 2005, B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report) may result from the low representation of suitable habitat in the inherently fragmented landscapes of Newfoundland. The large home range requirements of martens in Newfoundland greatly affected the extent and distribution of suitable habitat across the landscape. The extent of suitable habitat with a probability of occurrence ≥90% represented only 10% of the landscape for females and 8% of the landscape for males. Larger home range requirements in wide-ranging species affects habitat loss responses and may partially explain why Newfoundland martens occur at low densities and tolerate a greater percentage of unsuitable habitat within their home ranges than populations of *M. americana* in the contiguous portion of their North American range.

Evaluating how individuals respond to habitat loss and fragmentation can provide a guideline for scaling individual-level responses to patterns that occur at larger scales on the landscape or that operate at the population level (Wiens et al. 1985). Thus, these results have implications for conservation of mobile, area-sensitive species that require a minimum percentage of suitable habitat within their home range. For example, the model can be used to evaluate the influences of proposed forest harvesting scenarios on landscape-level habitat occupancy by Newfoundland martens and other species that are limited by amount of suitable habitat; however, these models should not be applied where suitable habitat is below 30% because habitat fragmentation effects might result in catastrophic declines in probability of occupancy (Andrén 1994). By providing what constitutes suitable habitat for martens, habitat suitability maps can be used to facilitate management for the protection of critical habitat and can be used in conservation and recovery planning (Manel et al. 1999, Pearce and Ferrier 2001). Such maps can be used to develop recovery strategies to provide and maintain suitable habitat at desired levels in spatially-explicit forest planning applications.

Model Predictions and Reliability

Model predictions will only be reliable with data of sufficient quality and quantity (Stockwell and Peterson 2002). The presence data were reliable and accurate, but the absence records may have occasionally contained an actual presence. The trapping coverage was limited to roads and access via water bodies, so there is potential that an area identified as unoccupied may have occasionally contained a marten. Modeling results suggest that habitat generalists can be modeled less accurately than habitat specialists, and wide-ranging generalist species are even more sensitive to absence data (Brotons et al. 2004). Marten in Newfoundland appear to be more characteristic of habitat generalists than martens studied elsewhere (B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report); therefore, undetected presences of martens likely reduced the model specificity more than the sensitivity. Managers attempting to apply this model should recognize that it is more reliable at predicting presence than absence which is desirable when attempting to predict effects of landscape change or to identify areas of particular recovery potential for an endangered species.

Deciding on the ability of a model to correctly predict presence and absence is largely dependent on the conservation implications of the model (Fielding and Bell 1997), and the overall discriminatory properties of a model may be different from decision rules used in applying the model to real-world scenarios (Hanley and McNeil 1982). The model had very high rates of sensitivity, but because the model was poor at exact estimation because of low discrimination capacity, it would not be useful to identify areas predicted to be occupied from areas predicted to be unoccupied (Pearce and Ferrier 2000). However, failing to correctly predict that a marten does not occur should be regarded as having a smaller cost relative to the cost of failing to predict that a marten does occur. For an endangered species, overestimating areas with high probability of occupancy is preferable to underestimating their existence. For example, if the model is to be used to identify suitable habitat for the endangered Newfoundland marten, the omission of sites where martens are present may be more of a concern than the mistaken inclusion of potentially suitable, but unoccupied sites. Thus, maximizing sensitivity at the cost of some specificity is preferable, and the model exhibits high (>80%) sensitivity at classification thresholds of <62% (i.e., predicted probability of occurrence used to classify occupancy versus non-occupancy in a binary decision-making framework). If the model is to be used to identify potential sites to re-introduce martens (only the best habitat), a relatively high threshold probability would result in sites with a high predicted probability of occurrence. If the model is to be used to identify areas where threats may affect martens, a precautionary approach would warrant a lower decision threshold to identify all potentially suitable areas for martens and the model would predict more area as potentially occupied. Use of the graph depicting performance criteria at each probability threshold (Figure 3.7) is an important tool for management and can be used to evaluate trade-offs associated with sensitivity, specificity, and overall correct classification rates. Deciding on a threshold probability is an important consideration that must weigh the relative costs associated with errors of omission versus commission in a particular conservation setting.

Conservation Implications

This study highlights 3 general principles that are important in habitat conservation. First, maximizing the total amount of suitable habitat is the most important goal in maintaining persistence of Newfoundland martens, as well as biodiversity in general (Fahrig 1997). The probability of occupancy by martens begins to decline more rapidly and in a non-linear fashion as suitable habitat in the landscape falls below 60% (Figure 3.2). At 60% suitable habitat, there is a 90% probability of occupancy by martens, but a reduction to 40% suitable habitat reduces the probability of occupancy to only 68%. The reduction in the cumulative occupancy curve does not appear to be a one-for-one loss as suitable habitat declines below 60%, indicating a qualitative threshold amount of suitable habitat required before occupancy drops precipitously. This suggests that Newfoundland martens may modify their behavior to partially compensate for unsuitable habitat up to approximately 40% unsuitable habitat in their home range, but that effects of habitat loss may accelerate declines in occupancy when the available landscape exceeds 40% unsuitable habitat. These results correspond to percolation theory (Gardner and O'Neill 1991), which predicts that habitat fragmentation occurs when unsuitable habitat reaches 41%.

Second, simply planning the spatial arrangement of habitat (Kareiva and Wennergren 1995, Hill and Caswell 1999, Huxel and Hastings 1999) will not mitigate the risk of extinction posed by the effects of habitat loss (Fahrig 1997, 1998), and such approaches are inappropriate for conservation (Trzcinski et al. 1999). Thus, the exact spatial configuration and proximity of suitable habitat patches is less important than maintaining an adequate quantity of suitable habitat for Newfoundland martens. However, as the percent of suitable habitat in the landscape declines, the effects of fragmentation and spatial arrangement could become increasingly important to conservation of this species.

Third, patterns of patch occupancy must be considered in a landscape context. Although the percent of suitable habitat within a landscape is the most important predictor of occupancy, the distribution of blocks of suitable habitat must be arranged such that they encompass at least 60% of home-range sized landscapes to avoid the risk of non-linear declines in occupancy when the amount of suitable habitat in the home range declines below 60%. Thus, management activities (e.g., timber harvesting) in areas targeted for recovery of Newfoundland marten should be planned such that either harvests are aggregated to influence the fewest number of potential home ranges, or they should be distributed so that home-range sized landscapes do not drop below 60% of suitable habitat.

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Chapter 4

OCCURRENCE THRESHOLDS FOR TWO ISOLATED SUBSPECIES OF WIDE-RANGING FOREST CARNIVORE: MARTENS IN MAINE AND NEWFOUNDLAND

ABSTRACT

I examined the response to habitat loss for two subspecies of American marten (*Martes americana*) in Maine (*M. a. americana*) and Newfoundland (*M. a. atrata*) that evolved in landscapes with differing composition and configuration of suitable habitat to evaluate threshold responses in second-order habitat occupancy. I identified threshold zones as areas with non-linear and drastic declines in occupancy, calculated as the difference between the slopes of occupied and unoccupied cumulative distribution functions of the amount of suitable habitat within home-range-sized landscapes. I compared my empirical data on threshold responses of martens to theory and to responses hypothesized for martens in the literature. I evaluated whether the shape of the occupancy curves best represented a) linear declines, b) exponential declines, or c) curvilinear declines and compared my observed threshold values to those reported in the literature. Martens in Maine and Newfoundland exhibited responses to habitat loss, but the shape of the decline curves and actual threshold zones differed between subspecies and did not approximate the responses predicted by threshold theory or by hypothesized responses for martens. The greatest declines in occupancy occurred much sooner in Maine (70-80% suitable habitat) than in Newfoundland (30-40% suitable habitat), indicating that *M. a. americana* were more sensitive to landscape change than *M. a. atrata*. The occupancy curve for *M. a. americana* was best represented by an exponential

decline and *M. a. atrata* was best represented by a curvilinear decline. I suggest that the differences in responses to changes in amount of suitable habitat between the two subspecies of marten can be explained by differences in landscape composition and configuration, community structure, and ecological traits. I hypothesize that Newfoundland martens were not as sensitive to landscape change because that subspecies evolved in a naturally fragmented landscape where their larger body size and home ranges relative to martens in Maine allowed them to include more unsuitable habitat. Lower diversity and density of potential prey species in Newfoundland necessitated traversing a wider range of habitat conditions relative to martens in Maine. Further, the lack of fishers (*Martes pennanti*) in Newfoundland allowed increased use of open areas by martens without the need for vertical cover to escape predation from the larger congeneric competitor (i.e., ecological release). The different responses that I observed by the same species in different geographic areas suggest that threshold responses are not an inherent species-specific trait. This exemplifies the need to understand the specific responses in second-order habitat occupancy of populations that have evolved in different types of landscapes with different competitors and cautions against the assumption that a particular response curve is an inherent trait of a species. Finally, these results indicate the insufficiency of assuming that animals exhibit theoretical or hypothetical responses to landscape change and that wildlife community and landscape processes interact to determine the different responses of isolated populations to local conditions.

INRODUCTION

Threshold responses of species to habitat amount have been cited as one of the major problems facing conservation biologists (Pulliam and Dunning 1997, With and King 1999) because of the difficulty in predicting the outcome of habitat loss or fragmentation until the threshold is exceeded (With and King 1999). A threshold is an abrupt, non-linear decline in occupancy across a narrow range of habitat loss (With and King 1999), which can lead to nonlinear population declines that may be catastrophic (Lande 1987). Thresholds have also been defined by the amount of habitat at which there is a shift from habitat loss effects to effects of habitat fragmentation (Andrén 1994, 1996; Flather and Bevers 2002, Fahrig 2001), resulting in declines in population persistence (Fahrig 2001). It is important to identify thresholds of habitat amount before declines in populations become severe due to habitat loss (Fahrig 2001) because future management options become limited and policy decisions must be weighted (Groffman et al. 2006). Early identification of thresholds facilitates conservation planning for habitat protection and allows management plans to be implemented before irreversible change has occurred.

Most of the empirical research on thresholds has been conducted on birds (Jansson and Angelstam 1999, Carlson 2000, Radford and Bennett 2004, Drinnan 2005, Guénette and M-A. Villard 2005, Lindenmayer et al. 2005, Radford and Bennett 2004, Radford et al. 2005, Suorsa et al. 2005), amphibians (Homan et al. 2004, Drinnan 2005), plants (Drinnan 2005), marsupials (van der Ree et al. 2003), and reptiles (Lindenmayer et al. 2005). To my knowledge, there is no study that has attempted to identify habitat amount thresholds for mammalian carnivores using empirical data. Mammalian carnivores have many traits that make them especially susceptible to landscape change, including large home range sizes, low reproductive output, relatively low population densities, and long dispersal distances (Sunquist and Sunquist 2001). These traits make mammalian carnivores especially at risk, since habitat loss and fragmentation are the two mechanisms that have the greatest influence on increasing a species' risk of extinction (Kareiva and Wennergren 1995, Wilcove et al. 1998).

American marten (*Martes americana*) has been identified as a mammalian carnivore that is sensitive to habitat loss and fragmentation (Bissonette et al. 1997, Chapin et al. 1998, Hargis et al. 1999). Indirect evidence from recently published field studies in Utah (Hargis and Bissonette 1997, Hargis et al. 1999), Maine (Chapin et al. 1998), and Quebec (Potvin et al. 2000) suggests that martens seldom occupy landscapes with greater than 25-40% of the forest in openings or early seral stages. With up to 30% of the landscape in unsuitable habitat (e.g., openings), martens can traverse the landscape without crossing large gaps and thus perceive the landscape as connected (Hargis et al. 1999, Chapin et al. 1998). Although studies on three different populations of martens have identified a similar range in tolerance for unsuitable habitat within landscapes, it is unknown whether this represents a threshold response.

Andrén (1994) reviewed studies documenting birds and mammals in habitat patches within landscapes with different proportions of suitable habitat and concluded that there appeared to be a threshold of 10-30% suitable habitat in a landscape. Above that threshold habitat fragmentation is represented as pure habitat loss and below the threshold population declines are due to isolation effects. Consistent with Andrén's (1994) review, forest and woodland birds and mammals (and 1 insect) had an average landscape-scale threshold of 19% with a range of 10-50% (Angelstam et al. 2004).

Fahrig (1998) also identified a fragmentation threshold at approximately 20% in her simulation study. Of the three studies reviewed above that identified fragmentation thresholds, very little of the data were from area-sensitive mammal species. Only 34% of the studies reviewed by Andrén (1994) included mammals, but they were predominately small in size (e.g., *Clethtrionomys, Microtus, Tamias, Sciurus, Ochontonta*). The review by Angelstam et al. (2004) included only 3 mammal species, and the study by Fahrig (1998) was a simulation model based on hypothetical species. It appears that in general, species respond to habitat loss up until approximately 70% of suitable habitat is removed, and further loss is represented as habitat fragmentation; however, there is very little empirical evidence for threshold effects on mammals.

Thresholds have been examined by simulating landscape patterns using neutral landscape models (Gardner et al. 1987). Models derived from percolation theory (Orbach 1986, Stauffer and Aharony 1991) have been used to describe a rapid change in the size, number, and shape of habitat patches around a critical probability (proportion of suitable habitat) where the largest patch of suitable habitat percolates, or spans from one edge of the map to another (Stauffer and Aharony 1991, Gardner and O'Neill 1991). The point of percolation (0.59) indicates a sudden change in landscape connectivity, where below the percolation threshold there no longer exists a continuous patch across the landscape (Gardner and O'Neill 1991, Gustafson and Parker 1992). Theoretical threshold values are dependent on the dispersal abilities of species (Keitt et al. 1997), and will vary depending on the perceptual range (Lima and Zollner 1996) of the species. These models are useful for predicting the amount of habitat loss required to induce a fragmentation threshold (Gardner et al. 1987, With and Crist 1995, Fahrig 1997, 1998, 2001, 2002, With and King 1997), and have value when used as a null model to compare to empirical data on real landscapes (With and King 1997).

Many recent studies have evaluated threshold effects, however, increased rigor and improved quantitative methods are needed (Toms and Lesperance 2003, Guénette and Villard 2004, Huggett 2005). Many studies report thresholds in habitat amount or patch size solely through visual identification of areas of rapid decline (e.g., Jansson and Angelstam 1999, Carlson 2000, Schneider 2001, van der Ree et al. 2003, Radford and Bennett 2004, Drinnan 2005, Suorsa et al. 2005), which is not suitable for quantifying thresholds (Toms and Lesperance 2003). Thresholds often are difficult or impossible to detect because of limited data on the responses of species to habitat loss and fragmentation (Huggett 2005) and due to the inherent variability in ecological studies (Lindenmayer et al. 2005). Further, because ecological responses seldom are represented by abrupt thresholds (Villard et al. 1999), perhaps a more important concept is to define the zone of greatest non-linear decline in occupancy of landscapes. Angelstam et al. (2003) suggested that, instead of identifying an exact habitat threshold value, non-linear relationships should be classified as having 3 intervals with a range of values that define insufficient, uncertain, and clearly sufficient amounts of habitat. Describing responses to habitat loss and fragmentation via statistical approaches that identify thresholds or zones of non-linear decline using empirical data will be valuable for species conservation.

I compared thresholds in occupancy of landscapes by two subspecies of American marten (*Martes a. americana* in Maine and *M. a. atrata* in Newfoundland) to determine if they exhibited differences in their response to habitat loss. I compared my empirical data to hypothesized relationships of martens to habitat loss and fragmentation based on prior theoretical and empirical work in Maine and Utah. Although martens in Maine and Utah were hypothesized to have the same maximum value for unsuitable habitat (25-30%), the form and shape of the response curve to reach that point was hypothesized to differ among the 2 areas (Figure 4.1), suggesting that different processes may be driving the response (Bissonette et al. 1997). In Maine, a curvilinear response (Figure 4.1) was hypothesized to result from low levels of fragmentation creating increased access to alternate foods (e.g., fruits), which may have benefited martens, but once a threshold amount of unsuitable habitat was reached, the population declined exponentially (Bissonette et al. 1997). In contrast, the hypothesized occupancy curve for martens in Utah declined immediately and exponentially as soon as any forest was altered (Figure 4.1). As additional mature forest was removed in Utah, Bissonette et al. (1997) theorized that patches exhibited increased edge and area effects, which might lead to an increased exponential decline. If martens responded to habitat loss alone, there should be a linear relationship between occupancy and percent of suitable habitat removed (Andrén 1999, Figure 4.1). The traditional threshold model described by Andrén (1996), Fahrig (1998, 2001), and Angelstam et al. (1994) is characterized by linear decline up to the threshold, at which point declines become non-linear. If fragmentation leads to habitat loss, there should be a point where occupancy by martens should decline at a higher rate than expected, given the proportion of lost habitat. The actual shape of these threshold response curves can differ, with the threshold values ranging from approximately 19-30% (Figure 4.1). I evaluated whether the shape of the occupancy curves for martens in

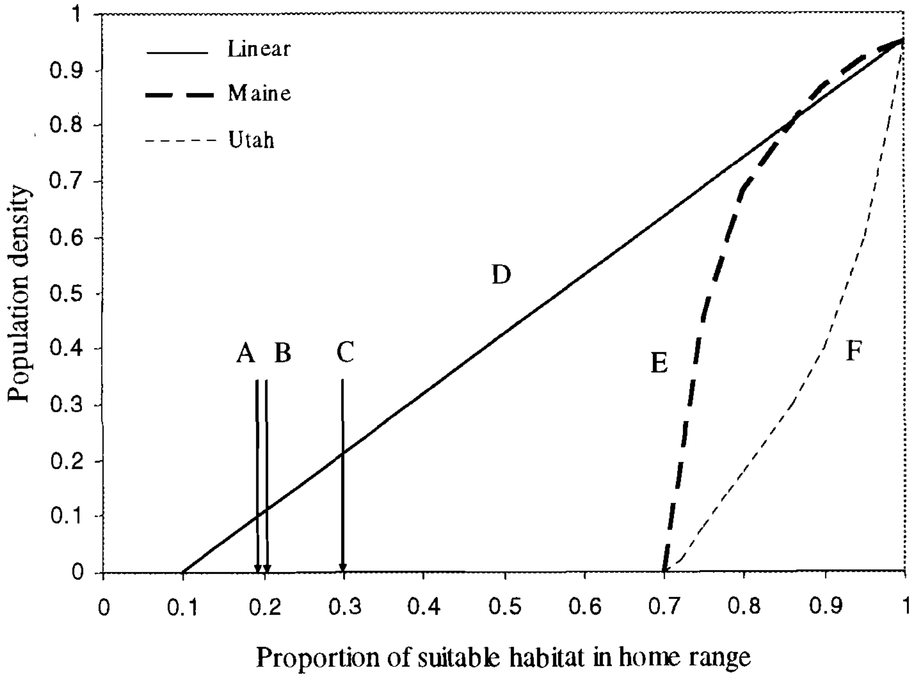

Figure 4.1. Hypothesized and theorized responses of American martens to habitat loss. Arrow A represents the threshold value of 19% (range = 10-50%) hypothesized by Angelstam et al. (2004). Arrow B represents the threshold value of 20% hypothesized by Fahrig (1998). Arrow C represents the threshold value of 30% (range = 10-30%) hypothesized by Andrén (1994). Curve D represents a linear response. Curve E represents a curvilinear response hypothesized for martens in Maine (Bissonette et al. 1997). Curve F represents an exponential decline as hypothesized for martens in Utah (Bissonette et al. 1997).

Maine and Newfoundland represented a) curvilinear declines, b) exponential declines, or c) linear declines, and compared observed threshold responses to those hypothesized in the literature.

Thresholds depend on the landscape context in which habitat patches are embedded, and may differ between landscapes or geographical regions (Andrén 1996, Mönkkönen and Reunanen 1999), the spatial scale at which the organism uses the landscape (O'Neill et al. 1988, Pearson et al. 1996, Mönkkönen and Reunanen 1999), or the habitat specificity of the species (With and Crist 1995). Further, body size is an important determinant of landscape perception in mammals, with larger mammals perceiving a more homogenous landscape (Lidicker and Koenig 1996) composed of fewer isolated patches (Addicott et al. 1987, Gehring and Swihart 2003). I predicted that martens in Maine and the genetically distinct subspecies in Newfoundland (Kyle and Strobeck 2003) would respond at different threshold values to loss of habitat. I hypothesized that martens in Newfoundland would respond at a lower threshold (higher threshold for habitat fragmentation) than martens in Maine because of their large home range size compared to martens in Maine (martens in Newfoundland have home ranges that are 8x larger for males and 5x larger for females than martens in Maine) and because Newfoundland martens evolved in naturally fragmented landscapes (Table 4.1).

Mönkkönen and Reunanen (1999) and Fahrig (2001) suggested that the actual value and slope of the threshold response is species specific and is based on habitat composition and matrix quality of the landscape, reproductive potential, dispersal ability, and territory size. Mönkkönen and Reunanen (1999) suggested that life histories of species may differ among geographical locations, causing different responses to

Table 4.1. Percent of the landscape composed of unsuitable habitat[a], potential mammalian competitors and predators, body size, and home range size comparisons of martens in Maine (*M. a. americana*) and Newfoundland (*M. a. atrata*).

	Unsuitable Habitat	Potential Mammalian Competitors	Potential Mammalian Predators	Body Size[b] (g)		Home Range[c] (km^2)	
				M	F	M	F
M. a. atrata	68%	*Canis latrans* *Lynx canadensis* *Mustela vison* *M. erminea* *Ursus americanus* *Vulpes vulpes*	*Canis latrans* *Vulpes vulpes*	1275	772	30.8	12.8
M. a. americana	49%	*Canis latrans* *Lynx canadensis* *Lynx rufus* *Martes pennanti* *Mustela erminea* *Mustela freneta* *Ursus americanus* *Vulpes vulpes*	*Canis latrans* *Martes pennanti*	808	517	3.83	2.47

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[a] Unsuitable habitat for *M. a. atrata* = medium height (6.6-12.5 m tall) open canopy (≤50% canopy closure) softwood stands, scrub (unmerchantable softwood stands ≤6.5 m tall), bogs, rock and soil barrens, recent (≤5 year-old) clearcuts, and open water. Unsuitable habitat for *M. a. americana* = stands with trees ≤6 m tall and ≤40% canopy closure, and open water.

[b] Sample sizes: Newfoundland (n = 40 M, 46 F), Maine (n = 134 M, 91 F).

[c] Sample sizes: Newfoundland (n = 43 M, 49 F), Maine (n = 135 M, 91 F).

landscape change. However, if threshold responses are species specific, I hypothesized that threshold responses are an inherent property of the species and will not vary across the geographic range of the species. If threshold responses do vary among populations of the same species that occupy different landscapes, thresholds may not be an inherent property, but rather a response of populations to landscape composition and configuration as well as community composition. I evaluated if threshold responses existed for *M. a. americana* and *M. a. atrata* and compared the shapes of the response curves to determine if thresholds are an inherent species-specific reaction to habitat loss.

STUDY AREAS

The 1,900 km^2 study area in Newfoundland (Figure 4.2) was composed of regenerating and recently cut coniferous, insect damaged, mature deciduous, and mature coniferous stands. The area included stands of old-growth (81+) balsam fir (*Abies balsamea*) with some white pine (*Pinus strobus*), black spruce (*Picea mariana*), eastern larch (*Larix laricina*), and white birch (*Betula papyrifera*). The western portion of the study area (40%) was part of a large (2,100 km^2) reserve (i.e., pine marten study area, PMSA) established for the protection of this provincially and federally endangered subspecies. Topography on the study area was rugged and averaged 352 m in the PMSA (range = 0-715 m) and 373 m (range = 122-621 m) in the eastern portion (60%) of the study area that was outside of the PMSA. Hemlock looper *(Lambdina fiscelaria)* and spruce budworm *(Choristoneura fumiferana)* infestations in the mid 1980's defoliated areas as large as 143 ha, which created various stages of regeneration with a significant volume of standing snags and coarse woody debris. The composition of the study area was 35% coniferous stands, 21% unforested bogs and barrens, 15% water, 11%

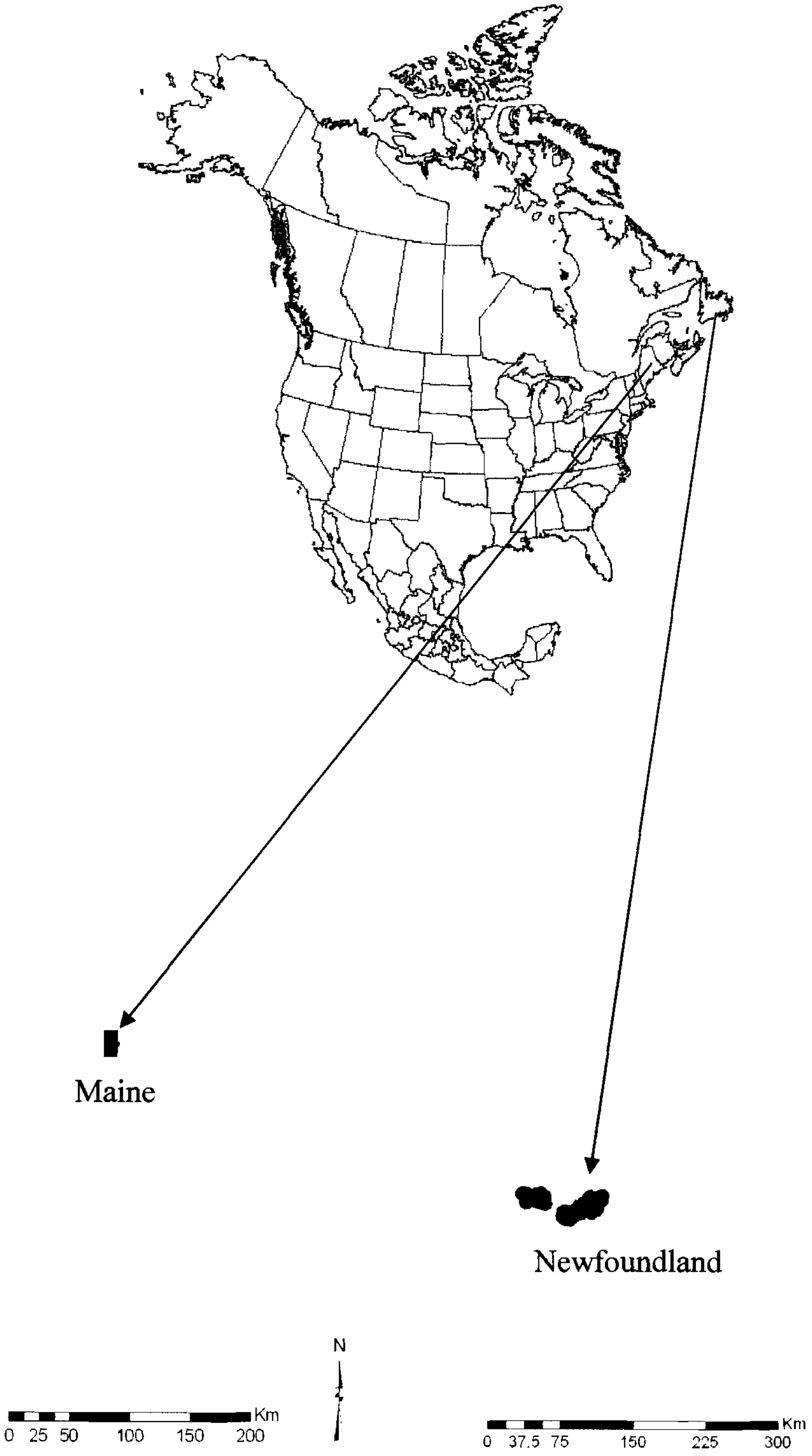


Figure 4.2. Location of study areas (in black) in Maine and Newfoundland.

regenerating and recently cut stands, 9% unmerchantable softwood stands, 6% other (roads, forest clearings, and small stands of deciduous and mixed coniferous-deciduous forest), and 3% insect and wind disturbed stands.

The Maine study area (Figure 4.2) included 219 km^2 in two townships (T5 R11 and T4 R11 WELS), north-central Maine. The townships were managed for pulpwood and sawtimber and were comprised of 40% mature forest (coniferous, deciduous, and mixed coniferous-deciduous), 53% recently harvested and regenerating stands, 4% ponds and lakes, 3% forested and unforested wetlands, and <1% natural and man-made clearings. Common overstory species in the study area included balsam fir, red spruce (*P. rubens*), white pine, red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), white birch, and yellow birch (*B. alleghaniensis*).

METHODS

I used home ranges of martens acquired during long-term studies in western Newfoundland and north-central Maine. Marten home ranges in Newfoundland represented 84 (40 M, 44 F) adults (> 1 year) representing 54 individuals (24 M, 25 F) captured and radio-tracked during 1995-1997. In Maine, home ranges were derived from 150 adult martens (80M, 70 F) representing 112 individuals (58 M, 54F) during 1994-1998 (Katnik 1994, Phillips 1994, Payer 1999). I simulated home ranges in areas that were unoccupied by martens using the same methods in both areas according to methods described in Chapter 3 and by Hepinstall and Harrison (Univ. of Maine, unpublished report). I defined portions of the landscape that were unoccupied by martens (i.e., second-order habitat occupancy, Johnson 1980) and simulated ranges within this area by incorporating the mean sex-specific home-range area (M = 31.7 km^2, F = 12.8 km^2) and intrasexual territorial overlap (F = 12%, M = 25%) observed within used (i.e., occupied) areas. I simulated 39 potential (21M, 18F), but unoccupied home ranges in Newfoundland and 139 potential (103F, 36M), but unoccupied home ranges in Maine.

Suitable habitat for martens in Newfoundland was defined as insect-killed conifer stands, primarily ≥12.6 m tall, <25% canopy closure with a dense understory; precommercially thinned (7-17 years post-thinning) 20-30 year old conifer stands with >50% canopy closure and typical density of 1,500 stems/ha; medium height (6.6-12.5m tall) closed (>50% canopy closure) conifer stands; tall (≥12.6m) open canopy (≤50% canopy closure) conifer stands; tall closed-canopy conifer stands; and conifer regeneration, ≤6.5m height with ≥75% canopy closure (Chapter 3, B. Hearn et al., Natural Resources Canada, Canadian Forest Service, unpublished report). Suitable habitat for martens in Maine was defined as areas with trees >6m tall and with >40% canopy closure and included mature forest, immature closed canopy forest, and partially harvested stands (Payer 1999, Hepinstall and Harrison, Univ. of Maine, unpublished report).

The availability of suitable habitat is an important consideration when evaluating occupancy (Dunning et al. 1992, Andrén 1994); therefore, I compared the difference between the amount of suitable habitat in occupied and unoccupied (i.e., simulated) home ranges using cumulative distribution functions (cdf). The cdf is the probability that occupancy of landscapes by martens takes on a value ≤*X*% of suitable habitat within the home range. To identify the zone of greatest decline in occupancy (i.e., occurrence threshold), I calculated the difference in slope between the percent suitable habitat within home-range sized landscapes of occupied and unoccupied cdf's in increments of 10%

habitat loss. Positive values indicated that the decline in occupancy was greater for occupied than for unoccupied areas, whereas, negative values indicated that the decline in occupancy was greater for unoccupied areas. I use the term occurrence threshold (Guénette and Villard 2004) instead of ecological threshold, fragmentation threshold, extinction threshold, or critical threshold to define the value below which occurrence of martens is unlikely.

I compared my empirical occupancy curves for martens to occupancy curves that were hypothesized from the literature on martens (Bissonette et al. 1997, Figure 4.1). I compared hypothesized distributions approximating a linear relationship, an exponential decline to approximate the hypothesized responses of martens to habitat loss and fragmentation in Utah (Bissonette et al. 1997), a curvilinear response to approximate the hypothesized responses of martens to habitat loss and fragmentation in Maine (Bissonette et al. 1997), and also evaluated several threshold values (19%, 20%, 30%) predicted from the literature (Andrén 1994, Fahrig 1998, Angelstam et al. 2004).

I used an incomplete beta function (cumulative distribution function of beta distribution) to estimate the shapes of the occupancy curves for my empirical data. The mean and sample variance of my empirical data was used to estimate the two shape parameters (*a* and *b*) of the beta distribution for percent of the home range in suitable habitat for martens in Maine and Newfoundland separately:

$$\hat{a} = \hat{\mu}_Y \left[\frac{(\hat{\mu}_Y)(1-\hat{\mu}_Y)}{\hat{\sigma}_Y{}^2} - 1 \right] \quad \hat{b} = (1-\hat{\mu}_Y)\left[\frac{(\hat{\mu}_Y)(1-\hat{\mu}_Y)}{\hat{\sigma}_Y{}^2} - 1 \right]$$

I tested how well my empirical data fit the beta distribution with a one-sample Kolmogorov-Smirnov test (Conover 1999). I used beta distributions to provide a distribution that could be used in the future to compare to other *Martes* populations.

I examined the probability density function of the cumulative beta distribution (first derivative of the beta cdf) of the Maine and Newfoundland estimated beta distributions to examine the shape of the density function and to determine where the greatest decline in occupancy occurred irrespective of habitat availability.

I created 95% confidence bands on the empirical cdf using the 0.95 quantile of the two-sided Kolmogorov Test Statistic (Conover 1999). To test whether my empirical data fit either the Maine or Utah hypothesized distributions, I evaluated their potential to intersect the 95% confidence interval on the empirical cdf distribution. The confidence band around the empirical distribution will only permit certain shaped cdf's, so I visually identified which hypothesized distributions would potentially fit within the 95% confidence band for the empirical distributions observed in Maine and Newfoundland.

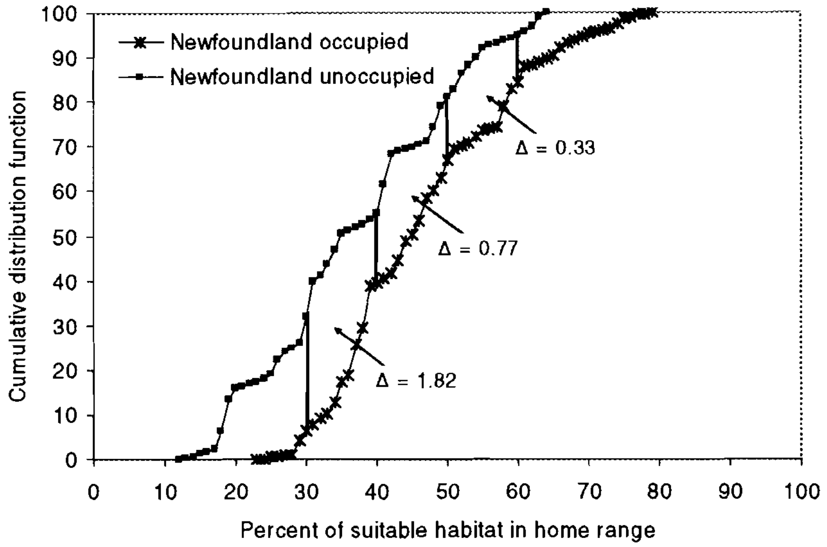
To determine if source-sink dynamics were operating in Maine or Newfoundland, I evaluated the age distribution of martens by comparing the proportion of one-year-olds (non-breeding yearlings) and animals ≥2 years-old (breeding age) (Strickland et al. 1982) above and below the hypothesized percolation threshold (Gardner and O'Neill 1991, Stauffer and Aharony 1991) of suitable habitat (0.59) with a *G*-test. Specifically, I evaluated whether younger animals disproportionately occupied areas with percentage of suitable habitat beyond the point where matrix fracture typically occurs (Gardner and O'Neill 1991). I also compared the number of martens above and below the value of suitable habitat where the confidence interval on the occupancy curves for Maine and Newfoundland intersect (0.38). My sample size was too small to statistically evaluate the 0.38 threshold in Maine because a very small proportion of martens had <38% suitable habitat, so I report the percentages only.

RESULTS

The maximum amount of suitable habitat observed within a Newfoundland marten's home range was 78% (Figure 4.3), whereas martens in Maine occupied home ranges composed of up to 100% suitable habitat. Fifty-two percent of martens in Maine had at least 78% suitable habitat in their home range (Figure 4.3). The suitable habitat comprised a mean of 73% of occupied home ranges in Maine and 47% of home ranges in Newfoundland. The minimum amount of suitable habitat within home ranges was 13% in Maine and 24% in Newfoundland (Figure 4.3). However, simulated home ranges in unoccupied areas contained as little as 0.8% suitable habitat in Maine and 13% for martens in Newfoundland (Figure 4.3), suggesting that martens in both areas appeared to be exhibiting second-order habitat selection by selecting home ranges that were composed of a disproportionate amount of suitable habitat relative to areas that they chose not to occupy.

The occupancy curve for martens in Maine best approximated exponential loss; probability of home range occupancy declined as soon as the percent of suitable habitat was reduced below 100% (Figure 4.3). The decline was initially steep and the probability of occupancy dropped below 50% when the percent of suitable habitat declined to <76%. The occupancy curve became less steep as the percent of suitable habitat in the home range declined below 59% (i.e., landscape percolation). The occupancy curve for martens in Newfoundland initially declined at a slower rate than martens in Maine, but declines became steeper (i.e., greater slope) than in Maine when <40% suitable habitat occurred in the landscape (Figure 4.3).

a)



b)

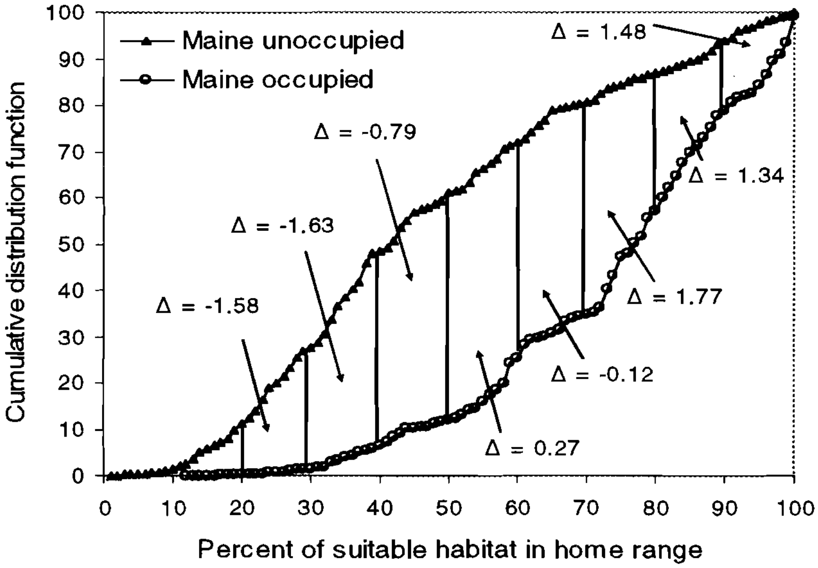


Figure 4.3. Cumulative distribution functions (cdf) of the percent of suitable habitat within home-range-sized landscapes for American martens in a) Newfoundland and b) Maine. Data represent 150 and 84 home ranges for resident martens >1 year of age (occupied) and 139 and 39 potential, but unoccupied home ranges (unoccupied) in Newfoundland and Maine, respectively. Delta values represent the difference in the slopes of the cdf between home-range-sized areas occupied and unoccupied (i.e., simulated) by martens for each decile of habitat loss.

The greatest difference between the slopes of the cumulative distribution functions of the percent suitable habitat for areas that were occupied and unoccupied by martens in Maine occurred at 70-80% suitable habitat, while the greatest difference in cdf's in Newfoundland occurred at 30-40% suitable habitat (Figure 4.3). In Maine, 57% of all martens occupied areas with ≤80% suitable habitat; however, only 35% of ranges were composed of ≤70% (Figure 4.3). In Newfoundland, 39% of all martens occupied areas with ≤40% suitable habitat, but only 6.5% of marten occupied home ranges composed of ≤30% suitable habitat (Figure 4.3). The difference between the cdf's for occupied versus unoccupied home ranges was similar in Newfoundland (Δ slope = 1.82) and Maine (Δ slope = 1.77, Figure 4.3). The rate of decline in occupied areas at the region of steepest slope was steeper in Newfoundland (Δ slope = 3.50 at 30-40% suitable habitat) than in Maine (Δ slope = 2.42 at 70-80% suitable habitat) indicating that martens in Maine exhibit declines in occupancy sooner than in Newfoundland, but that declines are more drastic in Newfoundland once suitable habitat is reduced below 30%.

The 95% confidence band on the cdf included both the empirical cdf and the beta distribution (Maine $a = 3.11$, $b = 1.24$; Newfoundland $a = 6.89$, $b = 7.91$) within its bounds (Figure 4.4), so I was confident that it approximated the 95% confidence interval of my data. The 95% confidence bands on the occupancy curves for Maine and Newfoundland converged at 38% suitable habitat. Although the shape of the response curves differed at higher values of suitable habitat (i.e., martens in Newfoundland were less affected by habitat loss), probability of occupancy declined to <30% in both areas when suitable habitat composed <38% of the landscape (Figure 4.4).

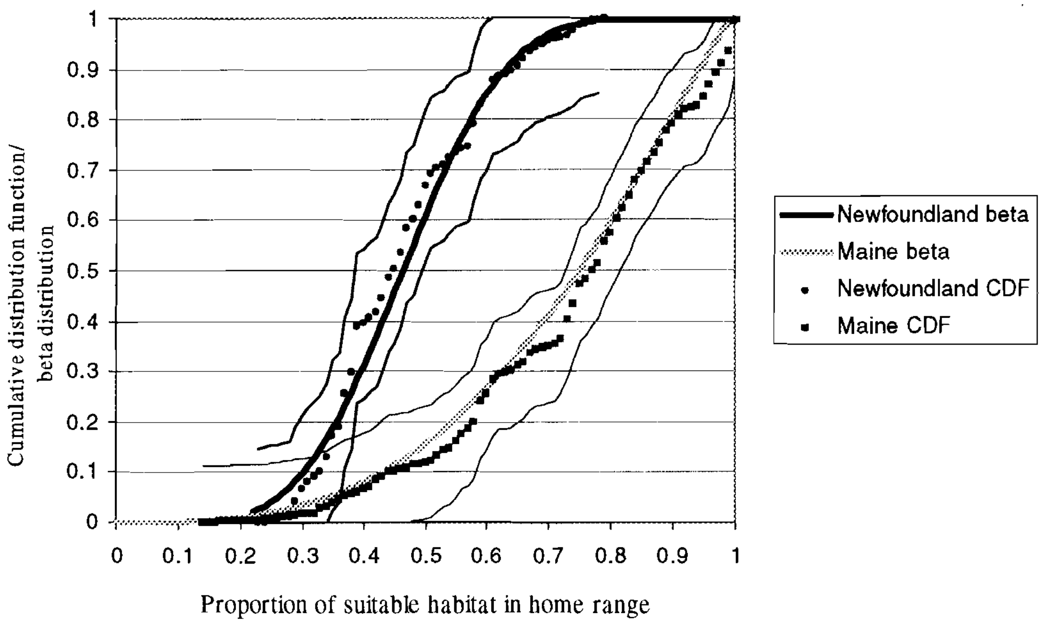


Figure 4.4. Comparison of actual cumulative distribution functions (cdf) and beta distributions depicting the proportion of suitable habitat within home-range sized landscapes for two subspecies of American martens in Maine and Newfoundland. The 95% confidence band on the cdf is represented by thin lines.

The Newfoundland data approximated a beta distribution ($KS = 0.114$, $P = 0.22$) and captured 97.1% of the probability in the range of the data (Figure 4.4). The Maine data also fit the beta distribution ($KS = 0.063$, $P = 0.59$) and captured 99.8% of the probability (Figure 4.4). The beta distribution that was estimated from the cumulative distribution function based on empirical data from Maine had the greatest decline in occupancy at 89% suitable habitat (Figure 4.5). In contrast, the beta distribution of empirical data from Newfoundland experienced the greatest decline in occupancy at 45% suitable habitat (Figure 4.5). The shape of these two density functions was very different, with a steeper shape in Newfoundland that was more normally distributed, while the density function in Maine was skewed to the right (Figure 4.5).

The rate of decline, inflection points, and shapes of the response curves differed greatly between the two subspecies. The occupancy curves for Maine and Newfoundland captured the processes (i.e., shape of response curve) that were predicted to occur according to hypothesized responses, but the threshold values differed from predictions (Figure 4.5). The model that hypothesized linear declines in probability of occupancy with decline in proportion of suitable habitat had the poorest fit with the empirical and beta distributions for both subspecies of martens (Figure 4.5). The threshold models predicted thresholds at approximately 19-30% (Andrén 1994, Fahrig 1998, Angelstam et al. 2004), which was much lower than the actual values that I observed for both *M. a. americana* (70-80%) and *M. a. atrata* (30-40%). These findings suggest that martens are more sensitive to habitat loss than the species (predominately birds) studied previously (Andrén 1994, Angelstam et al. 2004).

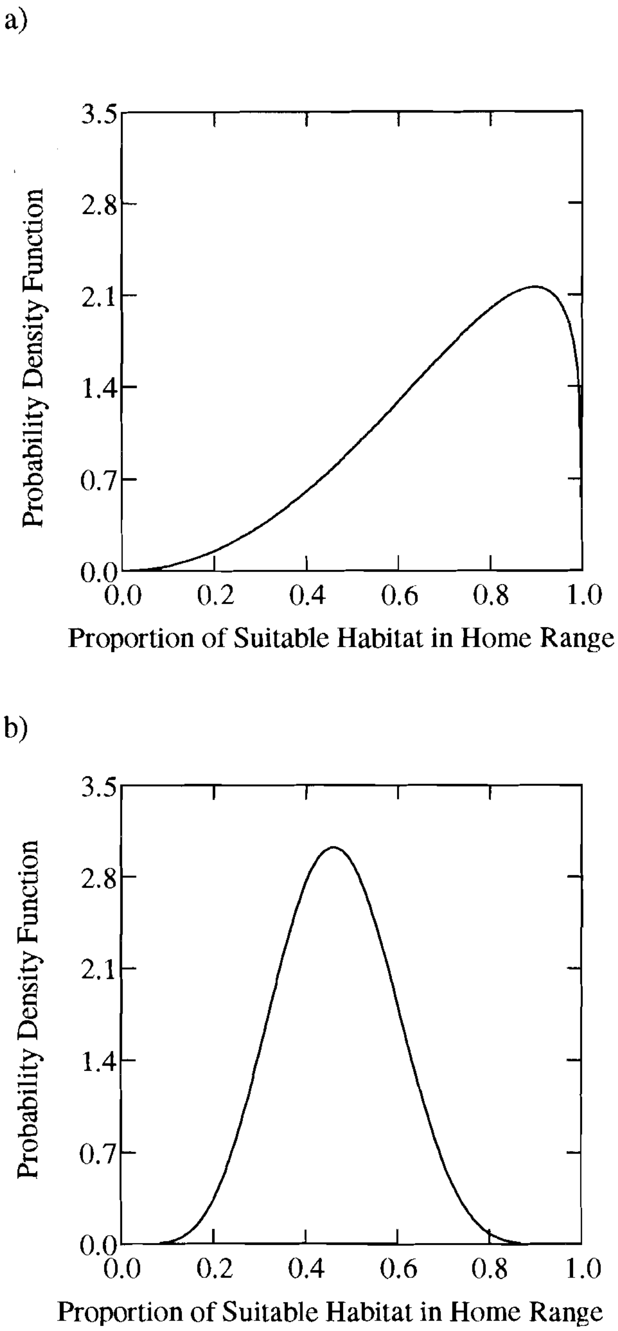


Figure 4.5. Probability density function (pdf) of the cumulative beta distribution (first derivative of the cumulative beta distribution) of American martens in a) Maine and b) Newfoundland. The pdf describes the region of habitat loss with the greatest inflection in probability of home-range-scale occupancy by martens (Maine = 0.89, Newfoundland = 0.45).

The Maine data most closely represented the exponential decline hypothesized to exist in Utah; however, the hypothesized decline was steeper than empirically documented. Martens in Maine were less responsive to habitat loss than predicted for martens in Utah, resulting in a threshold at lower values of habitat loss. The Utah model captured the process of nonlinear decline observed in Maine as soon as habitat in a landscape becomes unsuitable, but the rate of loss was overestimated by the Utah model. Empirical data from Maine suggests a more gradual decline that is less steep than that hypothesized for Utah. The Maine hypothesized model did not fit the empirical Maine data or the linear loss model.

The Newfoundland empirical data was best approximated by the Maine hypothesized curvilinear relationship (Figure 4.5). The Maine hypothesized relationship declined gradually at low levels of habitat alteration, and once a threshold level was reached, the decline became exponential. However, the empirical Newfoundland data declined faster at low levels of habitat loss than the Maine hypothesized distribution, and experienced a non-linear decline throughout the entire curve. The Maine hypothesized distribution had poorer concordance with the actual data for Newfoundland martens at lower levels of habitat loss; the hypothesized threshold response declined at a faster rate than the empirical data. The Newfoundland empirical data had poor concordance with the hypothesized Utah curve or the linear loss model.

Martens in Maine that occupied landscapes at or below levels (<0.59 proportion of suitable habitat) where fragmentation is hypothesized to be an important factor in causing declines in occupancy (i.e., below landscape percolation) were younger (n = 35, 60% were 1 year-old, 40% were ≥2 years-old) than martens that occupied landscapes above percolation (n = 108, 58% were ≥2 years-old, 42% were 1 year-old; $G^2 = 3.52$, $P = 0.06$). There was no difference in the proportion of yearling martens in Newfoundland above or below the percolation threshold of 0.59 ($G^2 = 3.84$, $P = 0.27$). There was also no difference in the age of martens in Newfoundland above or below 38% suitable habitat, which represented the point where the confidence intervals on the occupancy curves for Maine and Newfoundland intersected ($G^2 = 3.84$, $P = 0.59$). All 8 individuals in Maine that occupied landscapes with <38% suitable habitat were either 1 year-old (n = 5) or 2-years old (n = 3), and of the 135 individuals that occupied landscapes with ≥38% suitable habitat, 45% were 1 year-old, and 55% were ≥2 years old.

DISCUSSION

This study demonstrated the existence of zones in habitat amount where there was a rapid decline in occupancy by martens. Newfoundland martens exhibited a true threshold response, while martens in Maine did not exhibit a threshold response because declines in occupancy occurred immediately. The probability of home range occupancy for both *M. a. americana* in Maine and *M. a. atrata* in Newfoundland exhibited a non-linear decline as the amount of suitable habitat within home-range sized landscapes decreased. Thus, below the zones identified, martens are at increased risk of dramatic declines in occupancy as habitat is converted from suitable to unsuitable condition. Further, martens may have dramatically different probabilities of occurrence in landscapes with slight differences in composition of suitable versus unsuitable habitat. Landscape connectivity for a species has been reported to depend on dispersal ability (Keitt et al. 1997), habitat specificity, and the abundance and spatial arrangement of suitable habitat (With and Crist 1995). The shapes of the decline curves in occupancy in both areas differed from each other, indicating that thresholds are not an inherent species-specific trait, but that evolution of morphology and behavior in these isolated populations occurred in response to inherent differences in landscape composition and configuration, abundance and availability of prey, and potential predators and competitors.

Martens in Maine were more sensitive to landscape change than were martens in Newfoundland, as evidenced by the zone of greatest declines in occupancy occurring much sooner for *M. a. americana* (70-80% suitable habitat) than the threshold zone identified for *M. a. atrata* (30-40% suitable habitat). The probability density function of the empirical beta cumulative distribution functions that describe the shape of the decline curve irrespective of habitat availability also indicated an earlier response for *M. a. americana* (89%) compared to *M. a. atrata* (45%). The occupancy zone declines (Maine) and thresholds (Newfoundland) identified for martens occurred sooner than the 10-30% suitable habitat remaining reported in previous studies (Andrén 1994, Angelstam et al. 2004), suggesting that martens may be more sensitive to landscape change than the majority of bird and mammals species studied previously. Additionally, percolation theory suggests that occupancy should decline with increasing loss of mature forest until approximately 59% remains, and it is at this point that matrix fracture occurs (Gardner and O'Neill 1991). *M. a. americana* experienced declines in occupancy sooner than percolation theory predicted, whereas *M. a. atrata* were not as sensitive to landscape change and responded at values below predicted by percolation theory. My results indicate that it is inappropriate to assume that populations exhibit theoretical or hypothetical responses to habitat loss, and that the interaction of wildlife communities and local landscape processes must be considered.

Although the zone of greatest decline in occupancy differed from threshold values predicted in other studies, occupancy curves for both subspecies captured the process (i.e., shape of the response curve) that were predicted to occur according to hypothesized responses. The overall response of martens in Maine was best represented by an exponential decline, similar to the catastrophic response hypothesized for *M. a. americana* in Utah (Bissonette et al. 1997), but the observed declines were less steep than predicted. Martens in Maine exhibited steep, non-linear declines in occupancy from the beginning, which accelerated and peaked at 20-30% unsuitable habitat in the landscape. In contrast, *M. a. atrata* in Newfoundland exhibited responses that were best approximated by a curvilinear relationship similar to the response hypothesized for *M. a. americana* in Maine (Bissonette et al. 1997). This model predicts that occupancy declines gradually at low levels of habitat loss, but once a threshold level is reached, declines become exponential. The responses of the two subspecies differed from each other, suggesting that different landscape and community processes have caused divergence of their response to habitat loss and fragmentation.

Newfoundland martens evolved in a landscape inherently fragmented by bogs and barrens and adaptations of Newfoundland martens (larger body size, more generalist habitat use) have been selected for relative to *M. a. americana* in Maine, which evolved in landscapes with less inherent fragmentation. The maximum amount of suitable habitat in any home range in Newfoundland was 78%, whereas martens in Maine included up to 100% suitable habitat in their home ranges. This difference is a function of smaller home range sizes, smaller body sizes, and a higher landscape availability of suitable habitat for *M. a. americana* in Maine (Table 4.1). As indicated by exponential declines in occupancy at low-intermediate levels of habitat loss (Figure 4.4), martens in Maine were initially more sensitive to landscape change. Newfoundland martens responded later, but declines in occupancy were steeper after a threshold of 30% unsuitable habitat than were observed for *M. a. americana.* The confidence interval on the occupancy curves overlapped and both subspecies responded similarly after suitable habitat amount was reduced to <38% of the landscape. Fewer than 7% of *M. a. americana* and <30% *M. a. atrata* occupied home ranges with <38% suitable habitat. My results suggest that landscape composition and configuration in different landscapes can partially explain the different responses that I observed to tolerances for unsuitable habitat by the 2 different subspecies.

The larger body size of *M. a. atrata* compared to *M. a. americana* (Table 4.1) may have caused this subspecies to view the landscape at broader spatial scales, resulting in a lower threshold for habitat amount. Thresholds are a result of species' interactions with landscape structure (With and Crist 1995). That interaction is largely influenced by the species' perceptual range (Lima and Zollner 1996), which increases with body size (Zollner 2000). This causes animals with larger body sizes to perceive landscapes at broader scales (Wiens 1996, Wiens et al. 2002). Thus, thresholds in habitat amount are relevant only at scales within which species perceive the landscape (Wiens et al. 1997), and the scale at which species respond to spatial heterogeneity influences the value of the threshold (O'Neill et al. 1988). Differential responses of carnivores to fragmentation is partially explained by body size (Crooks 2002), and body mass is highly correlated with home range size in mammals (Lindstedt et al. 1986, Crooks 2002). The large body size, larger home ranges, and increased perceptual range likely caused the initially lower response to heterogeneity on the landscape for *M. a. atrata*.

The large home range size of martens in Newfoundland and their reduced sensitivity to habitat loss may be partially explained by the low diversity and abundance of potential prey (Lindstedt et al. 1986, Thompson and Colgan 1987). Availability of food is the most important factor affecting home range size in carnivores (Lindstedt et al. 1986, McLoughlin and Ferguson 2000). There are very few small mammal species available to martens in Newfoundland (8), and on my study area martens only consumed 5 of the species available (Gosse and Hearn 2006). Meadow voles (*Microtus pennsylvanicus*) were the most common food item (Gosse and Hearn 2006) and the meadow vole is the only small mammal prey in Newfoundland that occurs in forested areas that are also used by martens (Thompson and Curran 1995, Sturtevant and Bissonette 1997). Martens in Newfoundland may include a greater percent of unsuitable habitat within their home ranges and are less sensitive to habitat loss and fragmentation than martens in Maine because the abundance and distribution of prey is limited, which necessitates that *M. a. atrata* include a greater diversity of habitat conditions.

Interspecific relationships, particularly competition, will also influence thresholds (Tilman 1994, Kareiva and Wennergren 1995, Debinski and Holt 2000). Predation risk can be particularly costly depending on how able the species is to traverse unsuitable habitat. Martens in Newfoundland can traverse unsuitable habitat with minimal risk of predation due to the absence of fishers (*Martes pennanti*). Martens in Newfoundland are permitted an expanded use of resources because ecological release (Schoener 1986) has reduced interspecific competition from predators (Table 4.1). Intraguild predation is common in carnivores (Palomares and Caro 1999), and fishers are the primary source of mortality for martens in Maine (Hodgman et al. 1994, Payer 1999). Martens in Maine use vertical escape routes to avoid predation from fishers (Hodgman et al. 1997), while martens in Newfoundland have less reliance on large trees as vertical escape routes because fishers are absent. Fishers kill martens outright, but they also may induce character displacement in martens by altering the habitat selection of martens to avoid fishers to reduce the risk of fatal encounters (Mills and Gorman 1997). This interspecific avoidance has potential to increase the energetic costs associated with hunting and may place *M. a. americana* at a disadvantage by being more sensitive to landscape change associated with traversing the matrix of unsuitable habitat to avoid fishers. Fishers are specialists on snowshoe hares (Arthur et al. 1989, Martin 1994), and hares are most strongly associated with areas with regenerating understories (Conroy et al. 1979, Orr and Dodds 1982, Wolfe et al. 1982, Litvaitis et al. 1985). Thus, Newfoundland martens expand their range of suitable habitats to include regenerating clearcuts, presumably to enhance access to hares without the risk of predation by fishers in areas lacking vertical escape cover (i.e., larger trees). Beyond the zone of greatest decline in occupancy in Maine (70-80% suitable habitat), martens have to increase travel costs or reduce foraging success, which affects energetics and may therefore restrict *M. a. americana* to landscapes with a greater proportion of suitable habitat relative to *M. a. atrata*.

Martens in Maine may exist in a source-sink dynamic where dispersal from source populations is important for survival. Martens in Maine exhibited steep, non-linear declines that peaked at 70-80% suitable habitat in the landscape. Beyond 30% unsuitable habitat the rate of decline in occupancy slowed as source-sink dynamics began operating and a predominantly yearling population occupied sub-optimal landscapes where the probability of occupancy by adult (>2 year) animals was reduced. Some individuals may persist in sub-optimal habitat, but sink habitats maintain populations below replacement levels (Pulliam 1988). Although individuals in sink habitat contribute to population persistence at the landscape scale via emigration from source areas, recruitment of young is insufficient to compensate for adult and juvenile mortality, and these individuals would eventually decline without continued immigration (Pulliam 1988). Individuals should select home ranges where their survival and reproductive success is high (Fretwell and Lucas 1970), and areas with high proportions of suitable habitat in Maine were occupied by older martens. Home ranges with a low proportion of suitable habitat may be functioning as "ecological traps" where individuals survive, but have lower reproduction or higher mortality than in other habitat types (Pulliam and Danielson 1991). Recognition of potential source-sink dynamics is important in a conservation perspective because declines in occupancy below matrix fracture (0.59 suitable habitat) may be even more severe if individuals below this value are only maintained via emigration from source areas.

CONCLUSIONS

This new statistical approach for estimating beta distributions from cumulative distribution functions of occupancy by species can be used to compare the responses of species, subspecies, or populations to differences in landscape processes and community structure. The curves describing changes in occupancy in response to amount of suitable habitat are important in understanding the effects of habitat loss and responses to matrix fracture (i.e., landscape percolation). Further, comparisons of cumulative distribution functions between occupied and unoccupied home-range sized landscapes are useful for understanding second-order habitat selection and for interpreting how changes in the composition of suitable habitat influences distribution and abundances of animals in changing landscapes.

Threshold responses are a powerful conservation tool that enables managers to predict the effects of human-induced changes in the landscape (e.g., alternative forest harvest scenarios) on the probability of landscape occupancy by featured species and allows management plans to be focused to help prioritize conservation actions. Identification of thresholds and specific habitat requirements is important for conservation planning, particularly for species that are declining in areas where habitat is being modified (Luck 2002), which is occurring for the endangered Newfoundland marten.

Despite the usefulness of the threshold concept, I feel that there are important limitations for conservation that must be acknowledged. There are potential problems with identifying point thresholds, such as misuse of the point threshold as a target that allows land managers to alter habitat up to that point instead of maintaining suitable habitat above the threshold limit (Huggett 2005, Lindenmayer and Luck 2005). The threshold level is the point where rapid changes in occupancy occurs, and therefore it is important not to use the threshold as a minimum goal for management (Radford et al. 2005), but to maintain landscapes well above the threshold level of habitat amount because individuals will be lost long before the threshold is reached (Mönkkönen and Reunanen 1999). Therefore, rather than a point threshold (e.g., With and King 1999, Fahrig 2001, 2002), I used the idea of a zone threshold (Reunanen et al. 2004), where instead of identifying the point where the rate of change in habitat amount is accelerated, I identified the zone with the most rapid decline in occupancy, which is similar to Angelstam et al.'s (2004) approach of identifying "zones of risk and uncertainty." Although zones of the greatest non-linear declines in occupancy by species may not always represent true thresholds, it is important not to discount the importance of these zones for use in conservation planning by maintaining suitable habitat above the zone identified.

It is also important to realize that species may not respond to fragmentation immediately, but extinctions in populations could occur generations after fragmentation, representing an "extinction debt" (Tilman et al. 1994). Management actions that are focused below the threshold may create opportunities for landscapes to shift to conditions that are characteristic of landscapes above the threshold. However, conservation planning should realize the importance of maintaining intact areas that are above threshold levels. Finally, thresholds will vary across species and landscapes (Andrén 1996, Mönkkönen and Reuannen 1999), and the same species may vary their response to habitat loss and fragmentation between geographic regions depending on landscape characteristics (Cardillo et al. 1999) and community structure. It is important to examine the effects of habitat loss and fragmentation within a biogeographical context (Swihart et al. 2003); thus, management decisions based on thresholds identified from one region may not be applicable in other regions where thresholds have not been identified.

The different responses that I observed by *M. a. americana* and *M. a. atrata* in different geographic areas suggest that threshold responses are not an inherent species-specific trait. This demonstrates the need to understand the specific responses in habitat occupancy of populations that have evolved in landscapes with different composition and configuration of suitable habitat and wildlife communities (i.e., competitors), and cautions against the assumption that a particular response curve is an inherent trait of a species. Finally, it is inappropriate to assume that species exhibit theoretical or hypothetical responses to landscape change because it is the interaction between community and landscape processes that determine the different responses of isolated populations to local conditions.

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Angela Kate Fuller was born in Concord, New Hampshire on August 6, 1970. She was raised in Colchester, Vermont and graduated from Colchester High School in 1988. She attended the The University of Maine at Machias and graduated in 1996, *summa cum laude*, with a Bachelor's degree in Environmental Studies, a minor in Biology, and a self-designed concentration in Wildlife Biology. Her senior project involved developing a play-back technique for surveying owls in Maine.

Angela received her Master's degree from the Department of Wildlife Ecology at The University of Maine in 1999. Her thesis was titled, "Influence of Partial Timber Harvesting on American Marten and Their Primary Prey in Northcentral Maine". She received the Department's Outstanding Graduate Student Award in April 1999 and the George F. Dow and Fred Griffee Graduate Student Research Award in December, 1999. Angela published two chapters of her Masters research in *The Journal of Wildlife Management* and in *Forest Ecology and Management.*

Angela entered the Doctoral program in Wildlife Ecology at The University of Maine in 2001. During her Doctoral program she co-edited a book titled, "*Martens and Fishers in Human-Altered Environments: an International Perspective*". She also authored a paper on her lynx research that was published in *The Northeastern Naturalist* and co-authored a paper on graduate education in the United States that was published in *Frontiers in Ecology and the Environment.* Angela is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from The University of Maine in May, 2006.