## FACTORS AFFECTING HABITAT SELECTION AND POPULATION CHARACTERISTICS OF AMERICAN MARTEN (Martes americana atrata) IN NEWFOUNDLAND

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Thesis Advisor: Dr. Daniel J. Harrison

An Abstract of the Thesis Presented in Partial Fulfillment of the Requirement for the Degree of Doctor of Philosophy (in Wildlife Ecology) May, 2007

The Newfoundland marten (M*artes americana atrata*) is an endangered population of American marten (*M. a. americana*) endemic only to the island of Newfoundland. I documented home-range characteristics, habitat selection, survival rates, and causespecific mortality factors inside and outside a wildlife reserve, to provide insights into effects of anthropogenic influences (e.g., timber harvesting, snaring, and trapping) on marten populations. Median home-range areas of adult martens in Newfoundland (males = 27.6 km<sup>2</sup>, n = 43; females = 10.6 km<sup>2</sup>, n = 49) were disproportionately larger than those for a mainland marten population (males =  $3.3 \text{ km}^2$ , n = 135; females =  $2.4 \text{ km}^2$ , n = 91) in northcentral Maine. Allometric analyses revealed that home-range area of martens from Maine scaled approximately linearly with body weight whereas the relationship in Newfoundland was strikingly nonlinear, these differences being attributable to landscape configuration and prey abundance. Multi-scale habitat selection revealed that martens exhibited positive or neutral selection for a broad range of habitat types within their home ranges. Adult resident martens occupied home ranges that were not dominated by mature and overmature forest conditions. Selection for tall (> 12.5 m height) closed-canopied (> 50%) softwood stands, which based on previous work is required habitat for Newfoundland martens, was intermediate in relative preference, and comprised only 12.5% of home ranges. Age distributions were not different among martens with high, intermediate, and low amounts of mature and overmature forest in their home range. Further, survival of adult martens was not positively associated with increasing homerange availability of mature and overmature coniferous forest. I documented 52 mortalities during the study; human-caused mortality accounted for 45.3% of all mortalities and 71.9% of mortality outside the reserve. Models best characterizing survival of adults indicated a strong (positive) additive effect of increased habitat availability within the home range and increasing distance from roads where snowshoe hare (Lepus americanus) snaring and furbearer trapping of furbearers was legally permitted. Annual survival of adult martens (M = 112, F = 112) was 0.83 for both males and females. Survival of juvenile martens from October to April was 0.76 inside the reserve but only 0.51 in areas open to snaring and trapping. Marten populations outside the Pine Marten Study Area reserve are likely maintained by dispersal from the reserve or other untrapped refugia.

#### PREFACE

The Newfoundland marten (Martes americana atrata) is geographically-isolated and genetically-distinct (Kyle and Strobeck 2003) population of American marten (M. a. *americana*) endemic to the island of Newfoundland, where it is both federally and provincially listed as endangered (Forsey et al. 1995). The decline of the Newfoundland marten, both in numbers and distribution (Bergerud 1969, Snyder 1984, Snyder and Bissonette 1987, Thompson 1991, Forsey et al. 1995) began in the early 1900's and coincided with widespread declines of American marten and fisher (Martes pennanti) populations via overexploitation throughout North American (Aldous and Mendall 1941, Burt 1946, Yeager 1950, de Vos 1951, Quick 1956, Hagmeier 1956, Dodds and Martel 1971, Gibilisco 1994, Strickland and Douglas 1981, Krohn et al. 1994, Strickland 1994), as well as pine marten (*Martes martes*) and wolverine (*Gulo gulo*) populations in Scandinavia (Brainerd 1990, Landa et al. 1997, Helldin 2000). Thus, trapping in combination with habitat loss resulting from logging and fires has been postulated as the major factors contributing to the early decline of martens in Newfoundland (Thompson 1991, Forsey et al. 1995). Habitat loss via timber harvesting of mature (61-80- years old) and old-growth (> 80-years old) softwood forest has been frequently stated as the principle factor currently limiting recovery of the species (Bissonette et al. 1988, Thompson 1991, Forsey et al. 1995, Thompson and Curran 1995, Schneider 1997, Bissonette et al. 1997).

Ecological conditions for Newfoundland martens differ from other marten populations throughout North America. Newfoundland, like most islands, has fewer native species when compared to continental areas of similar size (MacArthur and Wilson

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1967, Simberloff 1974). For example, the composition of the terrestrial mammalian community is skewed, with a disproportionate number of predators and few prey species (Dodds 1983, Hearn et al. 2006). Historically, Newfoundland had only 14 species of native terrestrial mammals; at least 9 (64%) of which are considered by Dodds (1983) as distinct subspecies. Moreover, the island of Newfoundland has only 1 native microtine, the endemic Newfoundland meadow vole (*Microtus pennsylvanicus terraenovae*), reportedly the primary small mammal prey for Newfoundland martens (Bateman 1986, Tucker 1988, Drew 1995; but see Gosse and Hearn 2005). Over the last 150 years, however, an additional 11 species of terrestrial mammals have become established on the island of Newfoundland (Hearn et al. 2006), and 1 subspecies, the Newfoundland wolf (*Canis lupus beothucus*), is extinct (Allen and Barbour 1937). Furthermore, the landscape is inherently highly fragmented with numerous bogs, barrens, ponds, lakes, streams, and rock outcrops resulting in relatively small pockets of contiguous forest (Anonymous 2003).

Spatial distribution of martens in Newfoundland has been restricted for much of the previous three decades to the southwestern portion of Newfoundland within the Pine Marten Study Area (PMSA) - a 2,078 km<sup>2</sup> provincially designated wildlife reserve established in 1972 for the protection of the Newfoundland marten (Forsey et al. 1995). The PMSA is considered to contain the largest concentration of Newfoundland martens (Bissonette et al. 1989, Thompson 1991, Sturtevant et al. 1996), has been managed as a refuge from which martens can disperse to reoccupy surrounding areas of suitable habitat (Bissonette et al. 1988, Thompson 1991, Proulx et al. 1994); the PMSA is currently closed to all land-based snaring and trapping (Forsey et al. 1995). Previous research on

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Newfoundland martens has been concentrated within the PMSA (Snyder 1984, Snyder and Bissonette 1987, Tucker 1988, Bissonette et al. 1988, 1989, Fredrickson 1990, Drew 1995, Thompson 1991, Thompson and Curran 1995, Drew and Bissonette 1997) which coincidentally provides the greatest protection and the greatest concentration of oldgrowth forest remaining in western Newfoundland.

Despite decades of concern over the species' status and viability, fundamental information on the spatial ecology, habitat associations, and population dynamics of this endangered population was limited when this study began in 1995 (Schneider 1997). At that time, the available data suggested that: 1) home ranges of Newfoundland martens were particularly large (e.g., Bateman 1986 reported home-range areas of 27.5 km<sup>2</sup> for a single male and 17.7 km<sup>2</sup> for a single female on her study area in southwestern Newfoundland; Buskirk and McDonald 1989); 2) based on their provincial distribution, Newfoundland martens were more specific in their habitat associations than marten populations inhabiting mainland North America (Thompson 1991, Thompson and Curran 1995, Sturtevant and Bissonette 1997) and were hypothesized to be highly dependent on mature (61-80 year-old) and overmature (81+ years old) coniferous forests; and 3) this habitat restriction suggested that the Newfoundland marten was strongly tied to mature and overmature coniferous due to an obligate food dependency on the Newfoundland meadow vole (Thompson and Curran 1995, Sturtevant and Bissonette 1997).

To address the above knowledge gaps, this dissertation research focused on estimating the basic demographic and ecological attributes of marten populations in southwestern Newfoundland. My overarching goal was to better understand the mechanisms by which population growth was being constrained and spatial distribution

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restricted to areas of mature and overmature timber within the PMSA. Specifically, I documented baseline home-range characteristics from a sample of radio marked Newfoundland martens (Chapter 1) and compared these estimates of home range size to those reported from an intensively monitored (radiocollared) population of martens from northcentral Maine (Katnik 1992, Katnik et al. 1994, Chapin et al. 1997, Phillips 1994, Phillips et al. 1998, Payer 1999, Payer et al. 2004). The availability of the latter data provided a natural comparison of intraspecific variation in home-range area from the geographically closest study of American marten inhabiting a mainland setting. Subsequently, I used the spatial positioning of marten home-ranges on the landscape and the use of habitats (habitat-specific locations) within the home range to evaluate multiscale habitat selection by Newfoundland martens at the landscape (i.e., 2<sup>nd</sup>-order selection) and stand (i.e., 3<sup>rd</sup>-order selection) scale (Johnson 1980), respectively (Chapter 2). Finally, I documented cause-specific mortality factors and modeled survival of radiocollared martens inside and outside the PMSA reserve and modeled survival of adult and juvenile martens to evaluate competing hypotheses explaining survival of American marten, in particular martens in Newfoundland (Chapter 3).

The American marten is broadly distributed throughout North America; however, spatial requirements of martens are site-specific and highly variable, suggesting considerable regional differences in the availability of environmental resources. In Chapter 1, I compare spatial requirements (home-range area) of American martens in Newfoundland and Maine using allometric analyses to adjust for regional differences in body size. I characterized the availability of local environmental resources using indices of prey abundance and site-specific measures of spatial heterogeneity (i.e., habitat

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patchiness) using two metrics of landscape fragmentation. I also used allometric analyses to evaluate the hypothesized relationships between home-range area and body weight and to evaluate whether the large home-range requirements reported for Newfoundland martens can be explained as a result of larger body size, or is influenced by lower prey density, or inherent habitat fragmentation on the island.

Previous research on habitat associations of Newfoundland marten (Thompson and Curran 1995, Sturtevant and Bissonette 1997) speculated that habitat requirements of American martens developed throughout mainland North America may not apply to the local conditions of Newfoundland and that habitat management for this endangered population must recognize the constraints imposed by the limited prey resources. In Chapter 2, I evaluate multi-scale habitat selection by martens across a range of habitat types, including mature and overmature forests, extensive areas of softwood scrub forest, regenerating cuts, areas of insect-killed overmature coniferous forest, and precommercially thinned softwood stands. I tested the hypothesis that mature and overmature conifer stands were preferred by martens relative to other forest types occurring within their home range. I also evaluated 11 *a priori* predictions used to assess 7 questions about habitat preferences of Newfoundland marten. These questions were structured to evaluate the hypothesis that Newfoundland martens are more specialized for mature and overmature conifer-dominated forests than marten populations on the mainland.

Recently-logged forests have been postulated to be suboptimal habitat for martens and loss of mature and overmature timber has been associated with reduced survival, particularly in Newfoundland where marten are suggested to be more dependent on

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mature and overmature forests than mainland populations. However, martens are a highly-valued furbearer and overexploitation (trapping) has been implicated in the decline of marten populations throughout North American, particularly following the construction of logging roads associated with forest harvesting. In Chapter 3, I documented cause-specific mortality factors, and survival rates of 19 juveniles and 47 adults inside the PMSA and 25 juveniles and 56 adults outside the reserve. I used an information-theoretic approach to developed a suite of candidate models to assess how the survival of adult resident marten populations was influenced by variables indexing home-range habitat composition (i.e., % of recently logged forest, % suitable habitat, % mature and overmature forest), and risk to human-related mortality from roads (i.e., presence or absence of road from which snaring and trapping is legal within the home range, distance from the geometric center of the home range to the road). I also modeled survival of juvenile marten from October to April and developed a suite of candidate models to assess the timing and pattern of juvenile mortality. These analyses provided insight into the relative importance of habitat composition and human exploitation on the survival of martens inside and outside the PMSA and provided recommendations for managing recovery of this endangered population.

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# CHAPTER 1: ECOLOGICAL COMPARISONS OF HOME-RANGE CHARACTERISTICS OF AMERICAN MARTENS IN NEWFOUNDLAND AND MAINE: WHY ARE HOME RANGES OF NEWFOUNDLAND MARTENS SO LARGE?

## ABSTRACT

The American marten (*Martes americana*) is a forest-dependent carnivore broadly distributed from the spruce-fir forests of northern New Mexico to the northern limit of trees in arctic Alaska and Canada, and from the southern Sierra Nevadas of California to the island of Newfoundland. Spatial requirements of martens are site-specific and highly variable, suggesting considerable regional differences in the availability of environmental resources. I documented home-range characteristics of (*M. a. atrata*), a genetically distinct and endangered population of martens endemic to the island of Newfoundland, Canada, from a sample of 157 radiocollared individuals. Subsequently, I used allometric analyses to compare my estimates of home-range area of the larger-bodied Newfoundland marten to published estimates of home-range area from an intensively monitored population of smaller-bodied martens in northcentral Maine, USA. I compared availability of environmental resources for marten populations in Newfoundland and Maine using two indices of small mammal prey abundance and two site-specific measures of habitat patchiness: the percent of the home-range in suitable habitat, and the percent of the home range composed of the single largest patch of habitat. Median annual home-range areas (95% minimum convex polygon) of adult resident martens in Newfoundland averaged 27.6 km<sup>2</sup> for males (n = 43) and 10.6 km<sup>2</sup> for females (n = 49), and were disproportionately larger than median home-range areas reported for

martens in Maine (males =  $3.3 \text{ km}^2$ , n = 135; females =  $2.4 \text{ km}^2$ , n = 91). Home range area (HR) of martens from Maine scaled approximately linearly (slope = 0.914) with body weight (BW) as HR =  $0.73BW^{0.914}$  (r<sup>2</sup> = 0.148). By comparison, the home-rangebody-size relationship for martens in Newfoundland was nonlinear (slope = 1.545; HR = 0.04BW<sup>1.545</sup>; r<sup>2</sup> = 0.412). Home-range areas of martens in Maine and Newfoundland were approximately 2.5 times, and 8-12 times larger, respectively, than predicted for terrestrial carnivores. Indices of small mammal prey abundance were 3 - 5 times higher for martens in Maine. Additionally, home ranges of marten in Maine were typically dominated by a single large patch of suitable habitat, whereas home ranges of Newfoundland martens were more fragmented. Mean percent suitable habitat within marten home ranges in Maine was 70-77% with 75-80% of the range being comprised of a single large patch of suitable habitat. In contrast, martens in Newfoundland occupied home ranges comprising only 46-47% suitable habitat and the largest patch typically comprised only 31-35% of the range. Natural resource managers should consider the unique ecological (prey availability) and environmental (high natural fragmentation) factors that have shaped the large spatial requirements of martens in Newfoundland when formulating habitat conservation planning for this endangered population.

## **INTRODUCTION**

Ecologists have long sought to understand how species distribute themselves in space and time and optimize their use of environmental resources (Buskirk 2004). Distribution of a population is generally believed to reflect the spatial and temporal distribution of one or more limiting resources on the landscape in some hierarchical fashion (Powell 2000, McLoughlin and Ferguson 2000, Mitchell and Powell 2004).

Thus, understanding the spatial structure of a population (i.e., where, when and why individuals are present in some locations and absent in others) provides insights into population characteristics and ecological and evolutionary processes such as resource distribution (Mitchell and Powell 2004, Johnson et al. 2000, 2001), scale-dependent habitat associations (Johnson 1980, Schaefer and Messier 1995, Kie et al. 2002, Weir and Harestad 2003, McLoughlin et al. 2004), population density (Fuller et al. 2001), and social organization and mating systems (Powell 1994, Powell 2000, Johnson et al. 2001, Revilla 2003). Further, knowledge of how individuals in a population use space is fundamental for the development of spatially explicit models to predict species occurrence or habitat occupancy (e.g., Mladdenoff et al. 1995, Hoving et al. 2004, Hoving et al. 2005). The need to understand a population's spatiotemporal characteristics is further heightened when designing conservation strategies (e.g., carrying capacities for reserves or recovery areas; Schwartz 1999, Herfindal et al. 2005) or modelling population viability across landscapes (e.g., Schneider and Yodiz 1994, Schneider 1997, Akcakaya et al. 2004, Lindsey et al. 2004).

Home range (Burt 1943) is a concept that has been widely used to describe the spatial arrangement of individuals, particularly territorial mammals (Fuller et al. 2001, Olson and Lindzey 2002, Grigione et al 2002, Atwood and Weeks 2003, Fuller and Harrison 2005, Herfindal et al. 2005), over some specified time (e.g., season, year). Conceptually, the term territory is typically used to describe a home range that is actively "defended" wherein territorial residents retain exclusive use of the resources within the occupied area (Maher and Lott 1995); martens exhibit intrasexual territoriality (Powell 1994, Katnik et al. 1994). An animal's home-range area is presumably determined by its

energetic requirements (McNab 1963, Nunn and Barton 2000), although factors such as climate (Lindstedt et al.1986), food availability (McNab 1963, Harestad and Bunnell 1979, Lindstedt et al. 1986, Gompper and Gittleman 1991), resource patchiness (McLoughlin and Ferguson 2000, Kie et al. 2002, Anderson et al. 2005), social system (Nunn and Barton 2000), and density of conspecifics (Rogers 1977, Wolf and Schauber 1996) also influence home-range area.

## Variation In Spatial Requirements

Space use by animals is strongly tied to body size because larger animals require more resource, and thus larger areas to secure these resources (McNab 1963, Harestad and Bunnell 1979, Mace and Harvey 1983, Nunn and Barton 2000, Jetz et al. 2004). McNab (1963) was the first to study the relationship between home-range size and body size for 26 species of mammals, which were divided by trophic level into two groups: hunters (species that "hunt" for their food, e.g., insectivores, and carnivores); and croppers (i.e., species that browse or graze for their food). McNab (1963) concluded that home-range size in mammals increased according to Kleiber's law, which states that an animal's size-dependent basal metabolic rate (BMR) scales nonlinearly with body mass raised to the power of 0.75 (i.e.,  $BMR = aM^{0.75}$ , where M is body mass and a is the allometric coefficient, and 0.75 is the scaling exponent b; Kleiber 1975). McNab (1963) also noted that the allometric coefficient (y-intercept) was higher for "hunters" than "croppers" presumably because of lower food density for hunters. Subsequent analyses of interspecific variation in home-range size-body-size relationships (e.g., Schoener 1968, Harestad and Bunnell 1979, Lindstedt et al. 1986) did not support McNab's conclusion of a simple metabolic (0.75) scaling exponent (b), reporting that the slope of

the relationship ranged from linear (1.0) to strongly nonlinear (1.4) depending on trophic level. Collectively, these papers suggest that home-range area can not be fully explained as a simple consequence of per capita energetic needs and further suggested that larger than predicted scaling exponents (i.e., Home range = a\*body weight<sup>>0.75</sup>) was a result of reduced production of energy per unit of habitat with increasing body mass. For example, Lindstedt et al. (1986) reported that home-range areas scale linearly to body mass across a wide variation of mean body sizes among species of terrestrial mammalian carnivores as  $A_{hr} = 170M^{1.03}$ , where  $A_{hr}$  is home-range area, in hectares and M is body mass, in grams.

Generally, previous studies of allometric relationships have relied on interspecific comparisons because the range in body size within a single taxa (or species) is typically too small to provide enough variation in body size or home-range area (or other lifehistory traits) to capture sufficient variation for quantitative analysis (Shine et al. 1998). However, interspecific comparisons (e.g., McNab 1963, Schoener 1968, Harestad and Bunnell 1979, Damuth 1981, Lindstedt et al. 1986, Reiss 1988, Swihart et al. 1988, Gompper and Gittleman 1991, Perry and Garland 2002) are confounded by numerous methodological and biological factors, including: 1) differences in home-range estimation methods (e.g., direct observation, capture-recapture, home-range estimation models; 2) intersexual and interregional differences in body size within species (i.e., sexual dimorphism, clinal variation); phylogenetic nonindependence (i.e., data from closely related species sharing similar life-history traits and history are not independent); 3) imperfect accounting of important local environmental and ecological factors (e.g., intraand inter-specific diet, trophic level, conspecific density, predation risk, % home-range with exclusive use, resident status); and 4) differences in landscape characteristics (e.g., natural or anthropogenic fragmentation, landscape productivity, habitat composition and relative habitat preference). Collectively, these differences introduce confounding factors affecting relationships across species (interspecific variation) and between populations (intraspecific variation) within a species (Nunn and Barton 2000, Kelt and Van Vuren 2001, Grigione et al. 2002, Anderson et al. 2005); these shortcomings greatly limit the inferential value of such studies (Shine et al. 1998). As pointed out by McLoughlin and Ferguson (2000), home-range size is a highly integrative ecological expression of a species' environment, operating in a hierarchical structure, and patterns may differ, and explanations for underlying mechanisms diverge, from level to level (e.g., across species, between populations within a species, between sexes within a population).

Interspecific analyses of the allometric associations between body size and spatial requirements also ignore intraspecific variation in life history or morphology that has been shaped by evolutionary history and local environmental selection pressures. Further, intraspecific variation is understated during interspecific analyses by the lumping of individuals (and/or populations) from vastly different geographical or ecological areas, in order to secure a single value to describe a species (Gompper and Gittleman 1991). Yet variation in home-range size can be substantial within and across populations. For example, summer ranges of elk (*Cervus elaphus*) in North America reported by Anderson et al. (2005) varied 6 fold in size, home-range size of Eurasian lynx (*Lynx lynx*) reported by Herfindal et al. (2005) varied by a factor of 10 between different study areas in Europe, and home-range size of polar bears (*Ursus maritimus*) reported by Ferguson et al. (1999) varied 10 fold between populations, over 500 fold between individuals, and

were substantially larger than that predicted based on Lindstedt et al.'s (1986) interspecific allometric regression of mammalian carnivores in terrestrial environments (i.e.,  $A_{hr} = 170 M^{1.03}$ ).

More recent studies of variation in life-history traits, including home-range size, have focused on explaining intraspecific variation (e.g., Shine et al. 1998, McLoughlin et al. 2000, Kie et al. 2002, Grigone et al. 2005, Herfindal et al. 2005). At the population level, habitat productivity (i.e., variation in food abundance and distribution) appears to have the greatest influence on home-range size. Inverse relationships between home-range size (or density) and food availability, or surrogate measures of habitat productivity (e.g., environmental productivity and seasonality; McLoughlin et al. 2000, Herfindal et al. 2005), have been noted for a variety of species, including voles (*Microtus townsendii*; Taitt 1981), red squirrels (*Sciurus vulgaris*; Wauters and Dhondt 1992), black bears (*Ursus americanus*; Powell et al. 1997), brown bears (*U. arctos*; McLoughlin et al. 1999), and Eurasian lynx (*Lynx lynx*; Herfindal et al. 2005). Additionally, Carbone and Gittleman (2002) reported that across 25 species of carnivores, population density, a correlate of home-range size, (Damuth 1981), is positively correlated with prey biomass.

Spatial heterogeneity and physical structure of the environment have also been suggested as important factors shaping spatial requirements of local populations. For example, Kie et al. (2002) reported that 57% of the variation in home-range size of mule deer (*Odocoileus hemionus*), which varied markedly across 5 diverse study sites in California, was explained by a suite of landscape metrics indexing habitat heterogeneity. Further, landscapes that are highly fragmented, either through natural or anthropogenic processes, typically have smaller patch sizes, higher ratios of edge to interior habitat,
increased isolation of patches, and higher variation in the degree of connectivity of patches (Saunders et al. 1991), factors inherently related to resource distribution (e.g., Gehring and Swihart 2004).

## **Spatial Requirements of American Marten**

The American marten (*Martes americana*) is a forest-dependent carnivore broadly distributed from the spruce-fir forests of northern New Mexico to the northern limit of trees in arctic Alaska and Canada, and from the southern Sierra Nevadas of California to the island of Newfoundland (Buskirk and Ruggiero 1997). In most parts of its North American range, marten populations are stable or increasing (Strickland and Douglas 1987) and are managed as a valued furbearer (Strickland and Douglas 1987, Buskirk and Ruggiero 1997). Martens are sexually dimorphic (i.e., males are 20-40% larger, Strickland and Douglas 1987) and are intrasexually territorial (i.e., defend exclusive within-sex home ranges; Powell 1994, Katnik et al. 1994). Further, spatial requirements of martens are disproportionately large per unit body weight, and approximately 3-4 times larger than predicted for a 0.5-1.5 kg terrestrial carnivore (Buskirk and McDonald 1989, Buskirk and Zielinski 1997). Published estimates of individual area requirements for American martens are site-specific and highly variable (Bateman 1986, Lindstedt et al. 1986, Martin 1987, Thompson and Colgan 1987, Buskirk and MacDonald 1989, Slough 1989, Katnik et al. 1994, O'Doherty et al. 1997, Potvin and Breton 1997, Phillips et al. 1998, Smith and Schaefer 2002, Fuller and Harrison 2005, Gosse et al. 2005) which suggest that martens encounter considerable regional differences in the availability of environmental resources (McLoughlin and Ferguson 2000, Nunn and Barton 2000, Mitchell and Powell 2004).

#### Newfoundland Marten

The Newfoundland marten (*M. a. atrata*) is a geographically-isolated and genetically-distinct (Kyle and Strobeck 2003) population of the American marten, endemic to the island of Newfoundland (hereafter NF), where it is both federally and provincially listed as endangered (Forsey et al. 1995). Since the early 1900's, the NF marten has declined both in numbers and distribution (Bergerud 1969, Snyder 1984, Snyder and Bissonette 1987, Thompson 1991, Forsey et al. 1995). Overexploitation (trapping) in combination with habitat loss resulting from logging and fires have been suggested as the major factors contributing to the decline of these martens (Thompson 1991, Forsey et al. 1995). Habitat loss via timber harvesting of mature and old-growth (> 80-years old) softwood forest has been considered the principle factor currently limiting recovery of this population (Bissonette et al. 1988, Thompson 1991, Forsey et al. 1995). Thompson and Curran 1995, Schneider 1997, Bissonette et al. 1997).

Ecological conditions for NF martens differ from many other marten populations throughout their North American range. Newfoundland, like most islands, has fewer native species when compared to continental areas of similar size (MacArthur and Wilson 1967, Simberloff 1974). Additionally, the composition of the terrestrial mammalian community is skewed, with a disproportionate number of predators and few prey species (Dodds 1983, Hearn et al. 2006). Historically, NF had only 14 species of native terrestrial mammals; at least 9 (64%) of which are considered distinct subspecies (Dodds 1983). Moreover, the island of NF has only 1 native microtine, the NF meadow vole (*Microtus pennsylvanicus terraenovae*), reportedly the primary small mammal prey for NF martens (Bateman 1986, Tucker 1988, Drew 1995; but see Gosse and Hearn 2005).

Over the last 140 years, however, an additional 11 species of terrestrial mammals have become established on the island of NF (Hearn et al. 2006) and 1 subspecies, the NF wolf (*Canis lupus beothucus*), is extinct (Allen and Barbour 1937). Furthermore, the landscape is inherently highly fragmented with numerous bogs, barrens, ponds, lakes, streams, and rock outcrops resulting in relatively small and dispersed patches of forest (Anonymous 2003).

Spatial distribution of martens in NF has been restricted for much of the previous three decades to the southwestern portion of NF within the Pine Marten Study Area (PMSA) - a provincially designated wildlife reserve established in 1972 for the protection of the NF marten (Forsey et al. 1995). The PMSA is considered to contain the largest concentration of NF martens (Bissonette et al. 1989, Thompson 1991, Sturtevant et al. 1996), has been managed as a refuge from which martens can disperse to reoccupy surrounding areas of suitable habitat (Bissonette et al. 1988, Thompson 1991, Proulx et al. 1994), is closed to all land-based snaring and trapping (Forsey et al. 1995), and contains the largest concentration of old-growth forests remaining in western NF. Previous research on NF martens has been concentrated within the PMSA (Snyder 1984, Snyder and Bissonette 1987, Tucker 1988, Bissonette et al. 1988, 1989, Fredrickson 1990, Drew 1995, Thompson 1991, Thompson and Curran 1995, Drew and Bissonette 1997).

Despite decades of concern over the species' status and viability, fundamental information on the ecology and spatial requirements of martens in NF is limited (Schneider 1997). Available data suggest, however, that home ranges of NF martens are particularly large (Buskirk and McDonald 1989). Bateman (1986) reported exceptionally

large home-range areas of 27.5 km<sup>2</sup> for a single male and 17.7 km<sup>2</sup> for a single female, on her study area in southwestern Newfoundland. More recently, Gosse et al. (2005) reported mean home-range sizes of 29.5 km<sup>2</sup> (n = 15) and 15.2 km<sup>2</sup> (f: n = 24) for males and females, respectively, for a recently-introduced population of martens in eastern NF centered on Terra Nova National Park. This latter population was established in the early 1980's using animals obtained from southwestern NF, and persisted at extremely low densities until the late 1990's when the population was supplemented using additional translocated animals (Gosse et al. 2005).

## Maine Marten

American marten populations in Maine (hereafter ME) were also severely overexploited during the first decades of the 1900's (Aldous and Mendall 1941, Coulter 1959) and a trapping moratorium was enforced from 1937 to 1972 (Hodgman et al. 1994). Since 1986, annual harvests of martens in ME have averaged 3,603 individuals (Maine Department Inland Fisheries and Wildlife, unpublished data), suggesting that the population has recovered from historical overharvesting. This recovery was drastically different from the experience in Newfoundland where martens continued to decline after fur trapping seasons were closed in 1934. Both the evolutionary history and the ecological setting for martens in ME is very different from that in NF with respect to the structure of the terrestrial mammalian community (e.g., competitors and predators) and prey availability. Martens in ME typically occupy less fragmented landscapes (Fuller 2006) with higher diversity of potential prey and competitors and predators (Table 1.1). Coincidentally, martens in ME have evolved to be approximately 40% smaller in body mass than martens in NF (Buskirk and McDonald 1989: Table 1) and sex-specific home-

Common Name	Scientific name	ME	NF
Prev			
Masked Shrew	Sorex cincereus	Х	$\mathbf{X}^1$
Water Shrew	Sorex palustris	X	
Smoky Shrew	Sorex fumeus	Х	
Long-tailed Shrew	Sorex dispar	Х	
Thompson's Pygmy Shrew	Sorex hoyi	Х	
Northern Short-tailed Shrew	Blarina brevicauda	Х	
Star-nosed Mole	Condylura cristata	Х	
Southern Red-backed Vole	Clethrionomys gapperi	Х	$\mathbf{X}^1$
Meadow Vole	Microtus pennsylvanicus	Х	Х
Woodland Vole	Microtus pinetorum	Х	
Southern Bog Lemming	Synaptomys cooperi	Х	
Northen Bog Lemming	Synaptomys borealis	Х	
Deer Mouse	Peromyscus maniculatus	Х	$\mathbf{X}^1$
White-footed Mouse	Peromyscus leucopus	Х	
Meadow Jumping Mouse	Zapus hudsonius	Х	
Woodland Jumping Mouse	Napaeozapus insignis	Х	
Eastern Chipmunk	Tamias striatus	Х	$\mathbf{X}^1$
Red Squirrel	Tamiasciurus hudsonicus	Х	$\mathbf{X}^1$
Northern Flying Squirrel	Glaucomys sabrinus	Х	
Snowshoe Hare	Lepus americanus	Х	$\mathbf{X}^1$
Arctic hare	Lepus arcticus		Х
<b>Competitors / Predators</b>			
Short-tailed weasel	Mustela erminea	Х	Х
Long-tailed weasel	Mustela freneta	Х	
Mink	Mustela vison	Х	$\mathbf{X}^1$
Fisher	Martes pennanti	Х	
Lynx	Lynx canadensis	Х	Х
Bobcat	Lynx rufus	Х	
Red Fox	Vulpes vulpes	Х	Х
Eastern Coyote	Canis latrans	Х	$\mathbf{X}^1$
Black Bear	Ursus americanus	Х	Х

Table 1.1. Potential prey, competitor and predator species of martens in Maine (ME; *Martes americana americana*) and Newfoundland (NF; *Martes americana atrata*).

1 Non-native species; intentionally or accidentally introduced (Dodds 1983, Hearn et al. 2006.

range sizes for ME martens (Steventon and Major 1982, Katnik 1992, Phillips et al. 1998, Payer 1999) are among the smallest reported for the species (Strickland and Douglas 1987, Buskirk and McDonald 1989, Powell 1994).

# A Comparative Analysis

In a previous analysis of intraspecific variation in spatial requirements of American marten from nine different geographical locations, Buskirk and McDonald (1989) found no relationship between home-range area and latitude (Powell 1994), which was used as a surrogate index of prey availability. Subsequently, Powell (1994) concluded while Buskirk and McDonald's failure to document patterns between latitude and home-range area probably resulted from a lack of specific information on site-specific (local) prey resources and to inconsistencies in methods for calculating home-range size, (e.g., minimum convex polygon estimator). Thus, I conducted a comparative study of homerange and body-size relationships among martens in NF and ME where identical methods for calculating home-range areas were used, and where information on relative differences in landscape configuration and prey populations were available.

The specific objectives of the present chapter were twofold: first, to document baseline spatial requirements (i.e., home-range size, variation by sex, season and year, and home-range fidelity) of NF martens from a relatively large sample of radio-marked individuals from the core of their current distribution in southwestern Newfoundland. To accomplish this, I evaluated two home-range models (i.e., MCP and AK) commonly used to estimate home-range characteristics of American martens to discern which estimator was most appropriate to describe home-range areas of martens in Newfoundland. In particular, I evaluated Powell's (1994:110) earlier conclusion that the use of the

minimum convex polygon method produces inflated estimates of spatial requirements for marten. Secondly, I used allometric analyses to compare my estimates of home-range area of the larger-bodied NF marten to those from an intensively monitored population of small-bodied martens in northcentral ME (Katnik 1992, Katnik et al. 1994, Chapin et al. 1997, Phillips 1994, Phillips et al. 1998, Payer 1999, Payer et al. 2004). The availability of the latter data, which used identical methods for determining home-range areas and with large sample sizes (i.e., number of radiocollared individuals), provided a comparison of intraspecific variation and allometric relationship in home-range area from the geographically closest study of American marten in a mainland setting. Specifically, I used this approach to evaluate the following questions: Do the relationships between home-range area and body weight vary by sex within and between the ME and NF populations?; Is the relationship between home- range area and body weight consistent between ME and NF (i.e., do the two regressions of home-range area and body weight have the same scaling exponents (b) and y-intercepts?; and finally, does the slope of the regressions suggest that home-range requirements scale according to simple metabolic requirements (i.e., scaling factor exponent  $\approx 0.75$ ), which would suggest that the larger home-range requirements of NF martens are likely a simple result of larger body size (i.e., not related to lower prey density or habitat fragmentation).

### STUDY AREAS

### Newfoundland

The 1,900 km<sup>2</sup> study area was located in southwestern NF (Figure 1.1) and incorporated 55% of the 2,078-km<sup>2</sup> PMSA. The boundary was defined as the effective trapping area and was determined by creating a 6.26-km buffer around all locations



Figure 1.1 Map of the study area in Newfoundland and Maine. The Pine Marten Study area (PMSA) is a provincially designated wildlife reserve created in 1972 for the protection of the remaining core population of martens.

(buffer = diameter of the mean 95% minimum convex polygon mean; *results herein*) where traps were placed to capture resident martens (Fuller 2006).

Balsam fir (*Abies balsamea*) was the predominant tree species occurring on the study area and was occasionally intermixed with white pine (*Pinus strobus*), eastern larch (*Larix laricina*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*), the latter becoming more common on the eastern extreme of the study area. The fir-dominated forests in this region of boreal forest are atypical in that natural disturbance is primarily caused by insect infestations and not fire (Bakuzis and Hansen 1965, Thompson et al. 2003). Hemlock looper (*Lambdina fiscelaria*) and spruce budworm (*Choristoneura fumiferana*) infestations occurred on the study area during the mid-1980's and resulted in a mosaic of insect-killed softwood stands; median patch size = 2.85 ha, range 0.60 - 200 ha). These insect-killed stands are currently in various stages of decline and regeneration and typically have little to no crown closure, an abundance of snags in various stages of decay, advanced coniferous regeneration on richer sites, and substantial volumes of coarse woody debris.

Forest harvesting, primarily for coniferous pulpwood production, has been ongoing on the study area for much of the last century and occurred during the study period with 11.0% of the area in recent ( $\leq$  5 years) cuts. Intensive forest silviculture began in the late 1970's, and has focused almost exclusively on precommercial thinning of 13-15 year-old coniferous stands; 3.4% of the study area was composed of 20- to 30-year-old stands that had been precommercially thinned to an average of 1,500 stems per ha. Old-growth ( $\geq$ 81 years-old) conifer forest, postulated by previous researchers as a requirement for NF

martens (Bissonette et al. 1988, Thompson 1991, Thompson and Curran 1995, Bissonette et al. 1997, Sturtevant and Bissonette 1997), comprised 17.3% of the study area.

Stands were concentrated on the eastern and western thirds of the study area; the area is bisected naturally by a higher-elevation plateau (18% of total study area) that is dominated by large lakes, coniferous scrub vegetation ( $\leq 6.5$  m forest on low productivity sites), bogs, and soil and rock barrens - habitat types with low relative preference or avoided by NF martens (Chapter 2). Consequently, this plateau likely supported few resident martens, and previously had been considered a barrier to dispersal and genetic exchange between local marten subpopulations in southwestern and southcentral NF (J. Brazil, Department of Environment and Conservation, Wildlife Division, personal communication). Accordingly, I considered this portion of the study area to be unsuitable habitat for resident martens and restricted my trapping efforts to the eastern and western portions of my study area. Approximately one half (58%) of the area (excluding the higher-elevation plateau) was forested and the remaining landcover was composed of bogs and barrens (21%), water (15%) or various other (e.g., roads, disturbed areas, small unclassified areas) landcover types (6%).

## Maine

Descriptions of the ME study area are provided in detail in Katnik (1992), Chapin et al. (1997), Phillips (1994), Phillips et al. (1998), and Payer (1999). Briefly, marten studies were conducted on a 180-km<sup>2</sup> study area in northcentral ME which included an area of forest reserve and adjacent industrially-managed forestland (Payer 1999; Figure 1.1). The region was within the Acadian forest zone, which comprises the ecological

transition between the eastern boreal forest and the temperate deciduous forest (Seymour and Hunter 1992).

The 50-km<sup>2</sup> forest reserve was dominated by 70- 100-year-old stands (73.4% of the area), consisting of 51.4% deciduous (> 75% deciduous species), 16.9% coniferous (> 75% coniferous) and 31.7% mixed (25-75% coniferous species) stands. The dominant coniferous species were red spruce (*Picea rubens*) and balsam fir (Phillips 1994, Payer 1999). The 130-km<sup>2</sup> commercial forest area was contiguous and west of the reserve; forests on the commercial forest areas were managed for pulpwood and sawtimber production. Approximately 50% of the commercial forest portion of the study area was harvested between 1974 and 1994, primarily by clearcutting (Fuller and Harrison 2005). Many of the young and immature stands resulting from natural regeneration of clearcuts were silviculturally treated with herbicides (e.g., glyphosate) 3-5 years after harvesting to promote coniferous species. These regenerating stands included balsam fir, red spruce, red maple (Acer rubrum), white birch, and pin cherry (Prunus pensylvanica). Mature coniferous stands were dominated by red spruce, balsam fir, and scattered white pine. Black spruce, northern white cedar (*Thuja occidentalis*), and eastern larch dominated in forested wetlands (Payer 1999). Sugar maple (Acer saccharum), red maple, yellow birch (Betula alleghaniensis), white birch, and American beech (Fagus grandifolia) were common in mature deciduous forests.

# **METHODS**

### **Trapping and Radiotelemetry**

### **Newfoundland**

I trapped martens for a 2- to 4-week period each summer (June – August) and each autumn (typically late September – early October), 1995 - 2000. I used collapsible Tomahawk ® live traps (18 x 18 x 48 cm) using a variety of baits, including sardines, beaver (*Castor canadensis*) meat, or a mixture of rolled oats, peanut butter, raspberry jam and fish oil; trapping sites were also scented using an assortment of commercial trapping lures. Traps were placed inside plywood shelters, sheep's wool was placed in the back for nesting material, and then the trap was covered with bark and moss to provide thermal protection. Traps were usually checked once per day but were sometimes checked twice or more daily depending on trap location, weather, and season.

Traps were located every 1-2 km along roads and snowmobile trails or along the shoreline of lakes and were spaced to maximize the likelihood that all potential marten territories would include at least 1 trap. During winter, I used snowmobiles to improve my trapping coverage in an attempt to capture all resident marten. Trap placement on the study area was, however, influenced by road and trail access. All trapping locations were permanently marked and subsequently mapped using Global Positioning System (GPS) technology and post-differential correction to 2 m accuracy (TRIMBLE ®). Subsequently, traps were also strategically placed within home-range centers of radio-collared martens to recapture individuals when their radio collars were approaching or had exceeded their operational life.

At first capture, martens were transferred to a handling cone, and immobilized with an intramuscular injection of ketamine hydrochloride at the dosage of 10-15 mg / kg of body weight (Schemnitz 1994). Martens were sexed, weighed, ear-tagged (Monel No. 1; National Band and Tag Co., Newport, KY), measured and examined using standardized field procedures (Snyder and Bissonette 1987, Hodgman et al. 1994, Katnik et al. 1994, Bull et al. 1996, Chapin et al. 1997). A first premolar (PM<sub>1</sub>) was removed from each marten for aging using cementum analysis (Matson's Laboratory, Milltown, MT). Whenever possible, a PM<sub>4</sub> tooth was extracted from animals that died during the study to confirm initial aging.

Initially (June - October 1995), martens were fitted with radio collars (Lotek ®, Newmarket, Ontario, ca. 28 grams) that had an expected operational life of 7-9 months. After October 1995, a new radio collar was designed for the study which had an expected operational life of 13 months and which incorporated a mortality sensor (12-hour delay; Lotek Engineering ®, Newmarket, Ontario, ca. 34 g or Holohil Systems ®, Toronto, Ontario, ca. 36 g). Collars weights represented a maximum of 2.9% and 4.7% of the mean body weight of male and female marten, respectively.

All females captured each summer (May and August) were assessed for evidence of lactation or suckling (e.g., nipples enlarged, elongated, or crusted; milk expressed; obvious hair loss around the teat). Ear tagging was discontinued in 1997 when I started marking captured martens with passive integrated transponder (PIT) tags for individual identification (York and Fuller 1997). Martens recaptured within each trapping session were identified via their ear tags or scanned for PIT tags and released without further handling.

Radio-collared martens were located every 7-10 days (n = 5,086) primarily using either an amphibious fixed-wing airplane (Cessna 185) or helicopter (Bell 206 B or Aerospatial A-star). Fixed-wing aircraft were equipped with two strut-mounted 2element H antennas. I typically flew at low altitude (< 200m AGL) and plotted the position of all radio-collared martens using on-board navigational equipment (i.e., either GPS or Loran C instruments). Helicopters were equipped with either a single frontmounted, 2-element H antenna or a 3-antennae configuration utilizing one front-mounted and two side-mounted 2-element H antennas. After May 1997, I plotted all marten locations using a differentially-corrected GPS while hovering at low altitude ( $\leq$  10 m above the forest canopy), often resulting in a visual observation of the collared marten. Aerial telemetry resulted in 88% of locations, far more than trapping (7%) and ground telemetry (5%).

# <u>Maine</u>

Martens were livetrapped in ME using standard field procedures comparable to those described above for NF marten (Katnik 1992, Chapin et al. 1997, Phillips 1994, Phillips et al. 1998, and Payer 1999). Telemetry locations were obtained from aircraft and by triangulation from fixed receiving locations positioned along the road system on the study area.

### **Home-Range Models and Asymptotes**

Many statistical home-range estimators (Mohr 1947, Jennrich and Turner 1969, Dixon and Chapman 1980, Worton 1989), each with various underlying assumptions (Kernohan et al. 2001), which may produce dissimilar results (Boulanger and White 1990, Powell 2000, Kernohan et al. 2001), have been proposed. Two alternative home-

range models that have been widely used to calculate home-range areas of many species are the minimum convex polygon (MCP) estimator (Mohr 1947) and the adaptive-kernel (AK) estimator (Worton 1989). The MCP model is computationally simple, is not constrained by any underlying statistical distribution (Powell 2000), and has been used extensively to estimate spatial distribution of American martens (Buskrirk and McDonald 1989, Thompson and Colgan 1987, Katnik et al. 1994, O'Doherty et al 1997, Phillips et al. 1998, Smith and Schaefer et al. 2002, Poole et al. 2004, Fuller and Harrison 2005, Gosse et al. 2005). Although widely used (Seaman et al. 1999), the MCP model has been criticized (e.g., Worton 1987, White and Garrott 1990, Powell 2000) as a less precise estimator of an individual's use of space in comparison to adaptive kernel-based estimators (Worton 1989, Seaman and Powell 1996, Powell 2000, Kernohan et al. 2001). However, the AK model overestimates home-range area when numbers of relocations are limited (O'Doherty et al. 1997, Seaman et al. 1999) prompting Garton et al. (2001) to suggest that up to 200 locations per animal might be required when using AK estimators a sampling intensity that would be difficult to achieve in most telemetry studies using VHF transmitters, or in studies where body size prohibits the use of larger transmitters (i.e., larger batteries and longer operational life). Further, large numbers of relocations that meet assumptions of spatial independence are required for reliably estimating homerange area with probabilistic methods (e.g., AK method). In fact, Hemson et al. (2005) recently questioned the reliability and application of the AK method and concluded that its use is of particular concern when sample sizes are large (i.e.,  $\geq 100$  locations per animal) and range-use patterns (by individual animals) are not uniform (e.g., intensive use of core areas or site fidelity). Thus, while the development of home-range estimation

models is ongoing (Kernohan et al. 2001), there is no consensus on which home-range estimators perform best under varying patterns of animal-range use (Hemson et al. 2005).

## **Newfoundland**

Home ranges were estimated for all resident martens using the Animal Movement extension (Hooge et al. 1999) for ArcView ® 3.2 with Spatial Analyst (Environmental Systems Research Institute, Redlands, California). I classified a marten as resident if it met the following criteria:  $1 \ge 12$  months old;  $2 \ge 10$  locations collected over  $\ge 90$  days with locations  $\ge 24$  hours apart; and (3) mean minimum distance moved between consecutive locations (MINDIST; Harrison and Gilbert 1985) was  $\le$  mean + 3 SD MINDIST for all marten, stratified by sex; residency criteria was based on Phillips et al. (1998). I defined the biological year as 1 May – 30 April and pooled data to produce individual marten- and year-specific databases.

Locations were pooled within the biological year; therefore, I originally tested for seasonal shifts in home range. For each animal, the year-specific location data were sorted chronologically and plotted, with summer (1 May-1 September) locations highlighted to visually assess their dispersion in relation to all locations for that year. Secondly, I plotted the individual movement path of each animal to further assess if seasonal shifts in home-range position were evident. If either approach suggested that an animal had made a seasonal shift (i.e., distinct seasonal ranges), no annual home range was calculated for that marten for that year.

I calculated marten home ranges for a sample of 20 NF martens using 2 alternative home-range models, MCP and AK, to evaluate which model best described spatial distribution, as suggested by Harris et al. (1990), and evaluated the effect of increasing

sample size on the performance of the two home-range estimators by plotting the relative increase in home-range area as a function of the numbers of relocations available per animal (Swihart and Slade 1985). Hypothetically, home-range area estimates reach an asymptote as sample size increases (Stickel 1954, Harris et al. 1990, but see Gautestad and Mysterud 1995). Therefore, to determine the relationship between the number of locations available per animal and the estimate of home-range size, I constructed 95% MCP area-observation curves (Laundre and Keller 1984, Harris et al. 1990) for a sample of 43 martens using the bootstrapping function in Animal Movement; each animal had a minimum of 30 locations (mean = 36.9; range 30 - 45). The bootstrapping algorithm samples the relocation database of each animal with replacement, drawing a number of random samples (iterations) of relocations (e.g., 5, 6, 7, 8...n relocations where n = maximum number of relocations available for each particular animal) to estimate the mean + 95% confidence limits of home-range area. I set the minimum number of relocations at 5, the sampling interval (step) at 1 and used 100 iterations. To allow for the variation in home-range area between sexes and across animals, I averaged the 43 individual area-observation curves by converting the absolute estimate of home-range area  $(km^2)$  into the % of home-range area achieved after 5, 6, 7, 8...n locations.

# <u>Maine</u>

Home ranges for adult ( $\geq 1$  yr) resident martens in NF followed the original residency criteria developed for marten studies in ME (i.e., Katnik et al. 1994, Phillips et al. 1998, and Payer et al. 2004); generally, residents were defined as marten  $\geq 1$  year old, relocated  $\geq 10$  times, with mean distance travelled between consecutive relocations ( $\geq 12$ hours apart; MINDIST; Davis et al. 1948, Harrison and Gilbert 1985) < mean + 3 SD

MINDIST for all marten, stratified by sex. Similarly, home ranges were calculated only for martens with sufficient numbers of locations to meet asymptotic home-range requirements (Laundre and Keller 1984, Harris et al. 1990). Subsequently, home ranges of adult resident martens were calculated using 95% MCP methods. Detailed descriptions of methods used to calculate home-ranges are provided by Katnik et al. (1994), Phillips et al. (1998), and Payer et al. (2004).

### Home-range Area & Fidelity

Sex-specific differences in home-range area have been well documented in American martens (Buskirk and McDonald 1989, O'Doherty et al. 1997, Payer 1999, Smith and Schaefer 2002, Gosse et al. 2005). Additionally, martens may expand their home ranges during years of reduced prey availability (Thompson and Colgan 1987; but see Payer 1999:111). Accordingly, I tested for sex-specific and year-specific differences in home-range area for martens in NF using a 2-factor analysis of variance (ANOVA). I assessed the appropriateness of the ANOVA using a Kolmogorov-Smirnov 1-sample test using normal distribution, and tested for homogeneity of variance using a Brown-Forsythe test (i.e., Modified Levene test, Kutner et al. 2005). Home-range areas were not multivariate normal, (P < 0.000) and could not be normalized using data transformations. Subsequently, home-range area was ordered, ranked, and analyzed using ANOVA on ranks. I restricted my analysis of year, sex, and year-sex interaction in the full model to the 1995-1997 period when data were most abundant.

Data were too limited to conduct meaningful tests for the effect of age (yearling versus adult) or reproductive status (lactating versus nonlactating) on home-range size for NF martens. However, Chapin et al. (1997), Phillips et al. (1998), and Payer (1999) all

reported no difference in home-range area between yearling and adult ( $\geq 2$  yr) martens in ME. Similarly, Payer (1999) reported that martens in Maine displayed no differences in home-range area between nonbreeding yearling versus lactating adult female martens, or in home-range for either male or female martens despite a 3-fold (67%) decline in small mammal populations between years.

Based on my asymptotic area-observation curves observed for martens in NF and my subsequent criterion for determining the minimum number of locations required to accurately calculate home ranges (*results herein*), I had insufficient data to estimate seasonal home ranges, or to test for seasonal differences in home-range area using direct estimates of home-range area. However, home-range area and minimum distance travelled between consecutive independent relocations (MINDIST; Davis et al. 1948, Harrison and Gilbert 1985) are highly correlated, and have been used as an index for evaluating seasonal differences in home-range area for martens (Katnik et al. 1994, Phillips et al. 1998, Payer 1999). Likewise, MINDIST and home-range area were strongly correlated for martens in NF (Pearson's r = 0.89, n = 41 ranges, P < 0.000; Figure 1.2) indicating that MINDIST was a reasonable surrogate for home-range area. Thus, I calculated seasonal MINDIST values for summer and winter for each animal for which I had sufficient locations to calculate an annual home range, but restricted my analysis to animals for which I had  $\geq 8$  locations in each season. Thereafter, I conducted a sex-specific paired *t*-test to examine if there was evidence that martens adjust their home-range areas seasonally. I blocked on the individual year-specific home range as the unit of sampling replication and conducted a paired analysis to control for individual



Figure 1.2. Regression of home-range area (km<sup>2</sup>; 95% minimum convex polygon) and minimum distance travelled between consecutive independent relocations (MINDIST; Davis et al. 1948, Harrison and Gilbert 1985) for 41 home ranges of adult ( $\geq$  1 yr) resident martens in southwestern Newfoundland, 1995-1999; minimum of 31 locations per annual home range.

variation in home-range size. I defined summer as the snow-free period (i.e., 1 May – 30 November) and winter as 1 December – 30 April.

Martens are intrasexually territorial (Katnik et al. 1994, Powell 1994) and display fidelity to home-range location (Phillips et al. 1998, Payer et al. 2004). Consequently, I considered the individual year-specific home range as the unit of replication for the analysis (i.e., locational data were not pooled within individuals across years). As a result, radio-monitored animals that survived  $\geq 2$  years sometimes contributed data for 2 or more home ranges. This approach increased my sample size, hence statistical power, while concurrently avoiding the underrepresentation of high quality portions of the study area that received repeated use by surviving resident animals throughout the study.

Finally, I estimated annual home-range fidelity for all adult (> 1yr), resident martens that were monitored for  $\geq$  2 consecutive years. My measure of fidelity was the percent overlap of the 95% MCP home ranges between consecutive years (O'Doherty et al. 1997, Phillips et al. 1998, Payer et al. 2004). Again, I obtained too few locations to compare home-range areas and home-range fidelity between seasons.

## Allometric Home-range Analyses

Allometric home-range analyses typically begin by logarithm transformations of home-range area and body mass to yield a straight-line relationship appropriate for linear statistical models (Peters 1986, Nunn and Barton 2000). After logarithmic transformation, the expected relationship between home-range area (*HRA*) and body weight (*BW*) is:

$$Log(HRA) = Log(a) + b*Log(BW)$$

where Log *a* is the allometric coefficient (i.e., y-intercept) and *b* is the slope of the equation describing the linear relationship (McNab 1963, Peters 1986). Thus, allometric analyses allow us to examine whether home-range sizes (or other ecological traits) scale proportionately to body size and allow examination of factors (e.g., intersexual and interregional differences) influencing home-range area by controlling for body size. Accordingly, I used multiple linear regressions to contrast the log-transformed relationship between home-range area and body mass. For NF marten, I used home-range estimates (*calculated herein*) and body weights and compared these to published data on home-range area (i.e., Katnik 1992, Phillips 1994, and Payer 1999) and unpublished records of individual weights at the time of capture for the sample of martens in ME (D. Harrison, University of Maine, unpublished data). I included sex, source area, and all 2- and 3-way interaction terms in the full regression model.

## Site-specific Resource Availability

Intraspecific variation in home-range requirements has been commonly attributed to variation in prey density and environmental productivity (Harestad and Bunnell 1979, Nilsen et al. 2005, *see review in* McLoughlin and Ferguson 2000). However, site-specific (or home-range specific) estimates of prey productivity and its spatial distribution are difficult to quantify, typically resulting in the use of surrogates of habitat "quality" (e.g., trophic level, diet, latitude, seasonality, climate, spatial heterogeneity, remotely-sensed indices to photosynthetically active radiation absorbed by vegetation; Harestad and Bunnell 1979, Buskirk and McDonald 1979, Gompper and Gittleman, McLoughlin et al. 2000, Kie et al. 2002, Smith and Schaefer 2002, Anderson et al. 2005, Nilsen et al. 2005).

Accordingly, I indexed habitat "quality" for marten populations in ME and NF using estimates of prey abundance and landscape heterogeneity. I indexed local prey abundance with data on relative abundance of small mammals (i.e., captures per 100 snap-trap nights) in mature coniferous stands in both ME (Monthey and Soutiere 1985) and NF (B. J. Hearn, unpublished data). Site-specific measures of the spatial distribution of resources was indexed using measures of landscape (i.e., home-range) "patchiness" (McGarigal and Marks 1995) as indexed by the spatial arrangement of habitat patches inside all of the marten home ranges documented in the NF and ME studies. I used two landscape metrics, the percent of home range in suitable habitat (PHR) and largest patch of suitable habitat in the home range (LPI) to index fragmentation and dispersion of resources (Chapin et al. 1998, Chapter 2). Suitable habitat for NF martens was determined from a multi-scale (i.e., landscape- and stand-scale) assessment of habitat use by radiocollared marten (Chapter 2) and was defined as: 1) insect-killed conifer stands, primarily  $\geq 12.6$  m tall, < 25% canopy closure with a dense understory; 2) 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; 3) medium height (6.6-12.5m tall) closed (> 50% canopy closure) conifer stands; 4) tall ( $\geq$  12.6m) open-canopy ( $\leq$  50% canopy closure) conifer stands; 5) tall closed-canopy conifer stands, and 5) conifer regeneration  $\leq 6.5$  m high with  $\geq 75\%$  canopy closure (Chapter 2, Fuller 2006). Suitable habitat for martens in ME was similarly determined from a multi-scale habitat assessment from radiocollared martens (Payer 1999, Hepinstall and Harrison, University of Maine, unpublished report) and 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.

# RESULTS

## **Trapping and Radiotelemetry**

I captured 159 individual martens (Appendix) during 494 captures between June 1995 and August 2000, including 93 adults ( $\geq 1$  yr) and 54 juveniles (< 1 yr); ages were not obtained for 12 animals. Of the 93 confirmed adults, 58 individuals (30 males; 28 females) were monitored for a sufficient period to meet my residency and asymptotic home-range criteria, from which I produced 92 year-specific home ranges (43 and 49 year-specific male and female home ranges, respectively; Table 1.2). Data were sufficient for only 1 year-specific home range for 32 of the 58 individual marten; however, 20 martens provided annual home ranges for 2 years, 5 for 3 years, and 1 marten provided estimates for each of the 5 years of the study. Ages based on cementum annuli were available for 56 of my 58 individuals; minimum age for the remaining 2 animals was  $\geq 1$  and  $\geq 2$  years old. Median age of animals occupying year-specific home ranges was  $\geq 3.0$  years (n = 92; range = 1 - 8 years of age). I obtained a total of 2,881 locations (separated by > 24 hours) for these 58 individual marten. Mean number of locations per annual home range was 31.3 (range 19 - 54).

### **Home-range Models and Asymptotes**

For my data, the AK model provided home-range estimates that were 1.4 and 1.7 times larger than MCP estimates at the 75% and 95% probability (kernel-based) / data utilization (MCP-based) levels, respectively (Figure 1.3). Furthermore, Figure 1.4 displays the relative increase in home-range area for the 95% AK versus the 95% MCP

Table 1.2. Numbers of year-specific home ranges of 58 adult ( $\geq 1$  yr), resident Newfoundland martens (30 males, 28 females), southwestern Newfoundland, 1995 -1999.

Year	Males	Females	Totals
1995	11	8	19
1996	18	19	37
1997	11	17	28
1998	1	5	6
1999	2	0	2
Totals	43	49	92



Figure 1.3. Average relative increase in home-range area using adaptive kernel (AK) versus minimum convex polygon (MCP) home-range estimator for 20 adult ( $\geq$  1 year) resident martens at 75%, 80%, 85%, 90% and 95% probability (AK) or data utilization (MCP) levels. On average, AK home-range estimates were 1.4 and 1.7 times larger than MCP estimates of home-range area at 75% and 95% levels, respectively.



Figure 1.4. Relative ratio of home-range size using the 95% adaptive kernel (AK) versus the 95% minimum convex polygon home-range estimator as the number of relocations available increases from a sample of 20 adult ( $\geq 1$  year) resident marten home ranges.

method as numbers of relocations available per animal increased; range 18 - 48 locations per animal. The trend line (3-point running average) indicated that even for animals with  $\geq$  40 locations per year, the AK home-range estimate was still 50% larger than the MCP estimate. Thus, similar to O'Doherty et al. (1997), I concluded that the MCP model was a more appropriate model of home range for species like martens that display sharply defined territorial boundaries (Katnik et al. 1994). On average, 80%, 90%, and 95% of the maximum 95% MCP home-range area was defined after 19, 25, and 31 locations, respectively (Figure 1.5). I subsequently used only martens with  $\geq$  19 locations per year when calculating a MCP home-range area.

# **Home-range** Area

There were no differences in home-range area between years (P > 0.80) or interaction between year and sex (P > 0.26); therefore, data were pooled across all years (1995-1999) and differences in home-range area between sexes were analyzed using Mann-Whitney U tests. Median home-range area for male martens was 27.6 km<sup>2</sup> (SE = 2.2, n = 43) which was significantly larger (U = 233, P < 0.001) than the median homerange area of females (10.6 km<sup>2</sup>, n = 49, Table 1.3). Regardless of sex, adult resident martens displayed considerable variation in home-range area, ranging from 5.6 – 67.0 km<sup>2</sup> for males and from 3.1- 27.4 km<sup>2</sup> for females (Table 1.3). By comparison, homerange area of martens in ME were nearly an order of magnitude smaller; median homerange area was 3.3 km<sup>2</sup> (n = 135, range 0.7-11.0 km<sup>2</sup>) for males and 2.4 km<sup>2</sup> (n = 91, range 0.5-9.8 km<sup>2</sup>) for females (Table 1.4).

After screening individual year-specific home ranges for  $\geq 8$  seasonal locations, I calculated MINDIST values for 61 year-specific home ranges (28 male and 33 females;



Figure 1.5. Averaged area-observation curve for 43 adult ( $\geq 1$  year) resident marten home ranges. Approximately 80%, 90%, and 95% of the maximum home-range area (area estimated using all locations) is achieved after 19, 25, and 31 locations, respectively; error bars indicate  $\pm 2$  standard errors around the mean. All animals had a minimum of 30 locations (mean = 37; range 30-45 locations); number of animals with > 30 locations indicated above error bars.

Table 1.3. Annual home-range area (95% minimum convex polygon) by sex and mean minimum distance traveled between consecutive locations (MINDIST; Davis et al. 1948) by sex and season for adult ( $\geq$  1 year), resident marten, southwestern Newfoundland, 1995-1999.

Median Home-range Area (km <sup>2</sup> )		MINDIST (m)				
Sex	Area	n <sup>a</sup>	Range	Summer	Winter	n <sup>b</sup>
Male	27.6	43	5.6 - 67.0	3,276 (20.1) <sup>c</sup>	3,611 (12.1)	28
Female	10.6	49	3.1 – 27.4	2,247 (17.6)	2,360 (11.5)	33

<sup>a</sup> n = 92 year specific home ranges for 58 individual marten; 30 males and 28 females with  $\geq$  19 locations collected over  $\geq$  90 days.

<sup>b</sup> n = 61 year-specific measures of MINDIST for 43 (21 male; 22 female) individual marten.

<sup>c</sup> Average number of locations per season; MINDIST calculated only for animals with  $\geq 8$  locations available for each season.

Table 1.4. Median home-range area (km<sup>2</sup>; 95% minimum convex polygon) for adult ( $\geq$  1 yr) resident martens, northcentral Maine, reported for 1989-1992 by Katnik (1992: Appendix C), 1990-1993 by Phillips (1994: Appendix A), and for 1994-1998 by Payer (1999: Appendix A).

	Males			Females		
Source	Area	n <sup>a</sup>	Range	Area	n	Range
Katnik (1992)	5.5	14	1.4-11.0	2.1	14	1.2-9.8
Phillips (1994)	2.2	25	0.9-10.9	2.1	17	0.8-4.4
Payer (1999)	3.3	96	0.7-8.6	2.4	60	0.5-5.4
Pooled	3.3	135	0.7-11.0	2.4	91	0.5-9.8

<sup>a</sup> Number of individual martens with  $\geq$  19 independent locations collected over  $\geq$  90 days.

Table 1.3) of NF martens. Mean number of relocations for summer and winter, respectively, was 20.1 and 12.1 for males and 17.6 and 11.5 for females. MINDIST did not differ between summer and winter for either males (3,276 m versus 3,611 m, t = 1.336, df = 27, P = 0.19) or females (2,247 m versus 2,360 m, t = 0.875, df = 32, P = 0.39), suggesting that home-range area of martens in NF did not differ seasonally. Annual MINDIST values (calculated across seasons) averaged 3,397m and 2,301m for males and females, respectively.

### **Home-range Fidelity**

I calculated home-range fidelity, as defined by the percent of year <sup>(x)</sup> home range overlapping the home range of year <sup>(x-1)</sup>, for 24 individual adult resident NF martens (15 females and 9 males) of which 19 were monitored for 2 years, 4 for 3 years, and 1 for 5 years. There was no difference in home-range fidelity between female (mean = 73.6%; n = 18; range 22.6 - 99.4) and male marten (mean = 62.6%; n = 13; range 5.6 - 97.1) (Mann-Whitney, U = 141, P = 0.34); fidelity, pooled across sex, was 69.2%

### Allometric Home-range Analyses

The ratio of mean body weight for martens from NF and ME averaged 1.49 and 1.58, for females and males, respectively (Table 1.5). However, home-ranges of NF martens were disproportionately larger, with female and male home-ranges being 4.5 and 8.2 times larger, respectively, in NF. I analyzed home range versus body weight relationships for 311 marten using allometric analysis; n = 86 (40 males: 46 females) from NF and n = 225 (134 males: 91 female) from ME (Table 1.4). There were no significant 3-way or 2-way interactions between variables ( $P \ge 0.58$ ) and all interaction terms were dropped from the model. Furthermore, sex was not a significant factor (P =

	Source	Males	Females	Male / Female
	Source			Ratio
Body Mass (g)	NF	1275 (40)	772 (46)	1.65
	Maine	808 (134)	518 (91)	1.56
	Ratio <sup>a</sup>	1.58	1.49	
Median Home-range	NF	27.6 (43)	10.6 (49)	2.60
Area (km <sup>2</sup> )	Maine	3.3 (135)	2.4 (91)	1.41
	Ratio	8.19	4.51	
PHR <sup>b</sup>	NF	45.6 (40)	47.4 (44)	0.96
	Maine	70.25 (80)	77.16 (70)	0.91
	Ratio	0.65	0.61	
Largest Patch	NF	31.3 (40)	34.30 (44)	0.95
Index <sup>c</sup>	Maine	75.0 (13)	80.0 (14)	0.91
	Ratio	0.42	0.43	
Small Mammal Prev	NF	1.35 (4981)		
Index <sup>d</sup>	Maine	4.14 (8490)		
	Ratio	0.33		
Voles + Mice Prev	NF	0 72 (4981)		
Index	Maine	3 60 (8490)		
	Ratio	0.20		

Table 1.5. Mean body weight, home-range statistics, prey indices, and relative ratios for male and female marten in Maine versus Newfoundland; sample sizes in parentheses.

<sup>a</sup> Ratio of NF to Maine.

<sup>b</sup> Percent of home range in suitable habitat.

<sup>c</sup> Percent of home range represented by largest patch; data from Maine = Chapin et al. 1998.

<sup>d</sup> Snap-trap captures per 100 trap nights in mature softwood stands. Data sources: Maine = Monthey and Soutiere (1985; Table 1); NF = B. J. Hearn, unpublished data.

0.370) in explaining the home-range size variation and was similarly dropped from the model.

The home-range versus body-weight relationship across both sexes was significantly different between NF and ME (Figure 1.6a); y-intercept (P < 0.001, slope P = 0.09). Home-range area (HR) of martens from ME scaled approximately linearly (slope = 0.914, 95% CI = 0.62-1.20) with body weight (BW) as HR =  $0.73BW^{0.914}$  (r<sup>2</sup> = 0.148). By comparison, the home-range – body-size relationship for NF martens was noticeably nonlinear (slope = 1.545, 95% CI = 1.14 - 1.95; Figure 1.6b). For NF martens, home range scaled exponentially with body weight as HR =  $0.04BW^{1.545}$  (r<sup>2</sup> = 0.412, P < 0.000). Home-range areas of martens in ME and NF (calculated from telemetry) were approximately 2.5 times, and 8-12 times larger, respectively, than predicted by Lindstedt et al. (1986) using a generalized (interspecific) allometric equation for home-range size in terrestrial carnivores (i.e., HRA =  $170M^{1.03}$ , where HRA is in hectares and mass in kilograms).

### Site-specific Resource Availability

There were also significant differences in my measures of habitat "quality" between ME versus NF. Relative indices to small mammal prey availability were 3 times higher for marten populations in ME, and 5 times higher when calculated on captures of larger-bodied mice and voles (i.e., excluding soricids, Table 1.5). Further, marten home ranges in ME were more homogeneous with respect to the dispersion of habitat patches as indexed by my measures of spatial heterogeneity. Typically, home ranges of marten in ME were characterized by a single large patch of suitable habitat whereas home ranges of NF marten were more highly fragmented. Mean percent suitable habitat within marten



Figure 1.6. Regression of log-transformed relationships of body-weight and home-range area for American martens in Newfoundland (n = 86; open circles) versus Maine (n = 225; black triangles) (**a**); and untransformed relationship showing nonlinear nature of Newfoundland relationship (**b**).

home ranges in ME was 70-77%, with 75-80% of the home ranges being comprised of a single large patch of suitable habitat (Table 1.5). In contrast, NF martens occupied home ranges that were composed of an average of only 46-47% suitable habitat (range 23.6%-78.3%, Fuller 2006). Further, suitable habitat patches within home ranges of NF marten were more widely dispersed relative to marten home ranges in ME; the largest patch index averaged  $\leq$  33% (range 6.0-76.8%) of the home ranges of martens in NF (Table 1.5).

## DISCUSSION

Adult resident martens in NF occupied home ranges that were disproportionately larger than those previously reported for other populations of American martens (Thompson and Colgan 1987, Buskirk and MacDonald 1989, Katnik et al. 1994, Latour et al. 1994, Potvin and Breton1997, O'Dohery et al. 1997, Phillips et al. 1998, Payer 1999, Poole et al. 2004, Fuller and Harrison 2005). My estimates (median home-range area) of 27.6 km<sup>2</sup> (males) and 10.6 km<sup>2</sup> (females) are significantly larger than the mean home-range sizes of 8.1 km<sup>2</sup> (males) and 2.3 km<sup>2</sup> (female) reported for American martens throughout its range, as summarized by Powell (1994; Table 6.2). These estimates of home-range area are among the largest home ranges yet reported for adult resident American martens and very similar to the 25.4 km<sup>2</sup> (male) and 15.0 km<sup>2</sup> (female) estimates recently reported by Gosse et al. (2005) for adult martens in a translocated population in eastern NF.

Variation in the estimates of home-range area in American martens (Buskirk and McDonald 1989) has been attributed to lack of consistency in methods, and in particular, to the use of the minimum convex polygon method; MCP allegedly incorporates
significant areas inside home-range boundaries that are not actually used (Powell 1994). While accurate measurement of home-range boundaries using any method is problematic (White and Garrott 1990, Gautestad and Mysterud 1993, Powell 2000, Kernohan et al. 2001), my estimates of home-range area were not inflated by the use of the MCP model. To the contrary, my AK estimates of home-range area were much larger than my MCP estimates (i.e.,  $\approx$  70% larger at the 95% probability level; Figure 1.2) which are similar to results presented by O'Doherty et al. (1997). Contrary to suggestions made by Powell (1994, 2000), my AK home ranges incorporated large areas outside the territorial boundaries that were never used by resident marten. Use of the AK model appears to be biologically inappropriate to quantify home ranges for territorial species such as marten (Katnik et al. 1994, Powell 1994, Payer et al. 2004) that have sharply-defined home-range boundaries and lack a central "core" tendency.

Martens have a high mass-specific surface area (Brown and Lasiewski 1972, Iverson 1972), minimal body fat reserves (Buskirk 1983, Buskirk and Harlow 1989), a relatively short and poorly insulated pelage relative to other northern mammals (Scholander et al. 1950, Brown and Lasiewski 1972), remain active throughout the winter (Taylor and Buskirk 1994), and appear maladapted for northern temperate environments. Consequently, martens might be expected to reduce their exposure to lower temperatures hence energetic costs by decreasing their spatial requirements in winter. Nevertheless, I did not observe seasonal differences in home-range area (as indexed by MINDIST) indicating that martens in NF did not respond to changes in environmental conditions, resource availability, or energetic demands, in winter, by reducing the area of their home ranges. This is consistent with Gosse et al. (2005) who also reported no seasonal

differences in MINDIST values for martens in eastern Newfoundland. Both O'Doherty et al. (1997) and Phillips (1994) also observed no seasonal changes in home-range area for martens in southern Wyoming, and northcentral Maine, respectively. By comparison, Payer (1999) reported that overall MINDIST values were smaller during the winter (leafoff) season for both males and females in northcentral Maine. In contrast, Fuller and Harrison (2005) reported that martens with partially harvested stands in their home ranges (i.e.,  $\geq 10\%$ ) used areas almost twice as large during the winter (i.e., leaf-off) season as did martens with no partial harvesting.

These findings do not preclude the possibility that martens in NF respond to changing seasonal conditions (within fixed home-range boundaries) through behavioural adjustment. Thompson and Colgan (1987, 1994) reported that martens in Ontario were less active, less territorial, and primarily diurnal in winter to reduce energetic costs. Conversely, Zielinski et al. (1983) reported that martens inhabiting their study area in California (with relatively mild winters) exhibited a significant increase in nocturnal activity in winter, supposedly to synchronize their activity with that of their primary prey. By comparison, Drew and Bissonette (1997) reported that martens in NF inhabiting a portion of the PMSA which was primarily mature forest with few snowshoe hares did not synchronize their activity patterns in winter to those of the primary prey (*Microtus pennsylvanicus*) and speculated that this nocturnal activity pattern may reduce potentially fatal encounters with red foxes (*Vulpes vulpes*). Red fox caused the only known natural mortality during their study and was the most significant natural mortality factor for martens during this study ( $\geq 56.3\%$  of predator mortalities; n = 16; Chapter 3).

Zielinski et al. (1983) also suggested that martens compensate for reduced foraging time in winter by improving their foraging efficiency through hunting and eating larger prey. There is evidence that the latter behavioural switch occurs seasonally in NF marten. Frequency of occurrence of snowshoe hares in the diet increased 10-fold from 2.8% in summer to 28% in winter (Gosse and Hearn 2005). Based on calculations presented by Cumberland et al. (2001) snowshoe hares likely accounted for the bulk of the caloric intake in winter for NF marten; large prey, such as hares, are more easily digested and have a higher metabolizable energy per unit volume than mice and voles (Zielinski 1986, Cumberland et al. 2001). Fuller and Harrison (2005) reported over a 4-fold increase in frequency of occurrence of snowshoe hare in the diet of martens between summer (6.9%) and winter (29.3%), and similarly concluded that snowshoe hares likely provided the bulk of the caloric intake in winter for martens in northcentral Maine. Similarly, Bull (2000) also noted an increase in larger prey (i.e., squirrels, woodrats, and lagomorphs) during winter for martens in northceatern Oregon.

Martens may restrict their use of space in winter to a narrower range of habitats (Buskirk and Ruggiero 1994). For example, Payer (1999) noted reduced spatial requirements (MINDIST) in winter for martens in ME and attributed this reduction to restricted habitat preferences for areas with complex near-ground structure as a means to reduce energetics costs. Further, Campbell (1979), Soutiere (1979), and Steventon and Major (1982) all report seasonal changes in habitat selection patterns by martens with increased use of conifer stands in winter. However, despite seasonal changes in prey utilization patterns, martens in NF did not change their habitat selection patterns between summer and winter (Chapter 2) which suggests that changes in spatial-use patterns

occurred temporally or at a finer spatial scale than that of the home range or individual patch type.

O'Doherty et al. (1997) using bootstrapping procedures to estimate the expected variance in home-range overlap, considered > 65% home-range overlap between home-range polygons from successive periods to be indicative of high fidelity. Therefore, the high overlap of annual home ranges (fidelity) documented during this study (mean = 69.2%) suggests that the spatial distribution of martens on my study areas was relatively stable between years. My results are similar to those reported for the much higher density marten populations in northcentral Maine (i.e., observed mean seasonal fidelity of 67.4%; Payer et al. 2004).

Carpenter and MacMillen (1976) developed theoretical cost-benefit models that predicted that territoriality would only occur at intermediate levels of local resource (food) abundance, with territoriality being cost-prohibitive at either high or low levels of resource availability. Accordingly, Powell (1994) predicted that martens would become transient during periods of resource scarcity. Intraspecific variation in home-range area is generally inversely related to food abundance (see review by McLoughlin and Ferguson 2000), thus the large spatial requirements of NF martens imply that resource availability is minimal relative to mainland populations (Buskirk and McDonald 1989, Powell 1994). Further, direct indices to resource availability (prey availability) and dispersion (habitat fragmentation) in NF (Table 1.4) as measures of spatial variation in critical resources (Kie et al. 2002, Nilsen et al. 2005, Atwood 2006) were significantly lower for martens in NF relative to marten populations in ME. Nonetheless, resource availability for NF martens was sufficient to maintain high fidelity and territorial

behavior (Carpenter and MacMillen 1976) even in a highly fragmented environment with limited and dispersed resources (Powell 2000, Powell 2004). This finding is consistent with Payer et al. (2004) who similarly reported high fidelity to home-ranges across a wide range of resource conditions.

#### **Home-range Comparisons**

Powell (1994) summarized the structure and spacing in Martes populations and noted two generalizations. First, male home ranges are larger than females. Secondly, home range area is correlated with body size; however, home ranges of males tend to be larger than those of females by a factor greater than expected from metabolic requirements (McNab 1963). As evidence, Powell referred to Buskirk and McDonald's analysis of variability in home-range area of American martens wherein males averaged 1.5 times heavier than females, whereas home ranges averaged 1.9 times larger. Thus, Powell concluded that mass-specific metabolic requirements do not appear to explain intersexual variation in home-range size. Further, Powell (1979, 1994) hypothesized that home-range area is driven by energetic requirements for female mustelids whereas homerange area is driven in males to maximize their reproductive success by encountering as many mates in their range as possible (see also Erlinge and Sandell 1986, Lindstedt et al. 1986, Johnson et al. 2000). To the contrary, Katnik et al (1994), in a previous study of spatial relationships of martens in ME, concluded that territory size in males was not influenced by access to females (i.e., area of male ranges was not a function of the number of overlapping female ranges), and further, that male territories were not larger than those of females relative to differences in body size.

Consistent with previous studies, (summarized in Buskirk and MacDonald 1989, Table 1; Powell 1994, Table 6.2) home ranges of male martens were larger than females both in NF and ME (Table 1.5). Further, consistent with conclusions of Katnik et al. (1994), male to female body-mass ratios and male to female home-range-area ratios for martens in ME were virtually identical ( $\approx 1.5$ ), suggesting that in this region, home-range area for both males and females can be explained by mass-specific energetic needs and the relative density of local resources (McNab 1963, Harestad and Bunnell 1979, Mace and Harvey 1983, Haskell et al. 2002). By comparison, the male to female home-rangearea ratio of martens in NF (2.41; Table 1.4) was appreciably higher than the 1.65 ratio of male to female body mass. This is not surprising, however, given the differences in allometric scaling exponent describing home-range area and body size for ME (linear) and NF (exponential; Figure 1.6b). Because home-range area is a square of a linear measurement (Bowman et al. 2002), taking the square root of home-range area creates a linear index to home-range area and scales it linearly with body weight (e.g., MINDIST is a linear measure of home-range area, Figure 1.2). Accordingly, the ratio of the average of the square roots of male (5.25; n = 43) and female (3.24; n = 49) home-ranges for martens in NF is 1.61, approximately equal to the ratio of male to female body weight (1.65), and similar to the ratio of male and female home-range area for martens in ME (1.41). Similarly, the male to female ratio of annual MINDIST values for martens in NF, a linear measure of spatial requirements, is also 1.48 (Table 1.3). While home-range sizes of martens are very different between ME and NF, and larger than expected based on simple metabolic energy requirements (b  $\approx 0.75$ , McNab 1963), or allometric equations for terrestrial carnivores developed from broad interspecific analyses

(Lindstedt et al. 1986), it appears that intersexual differences in home-range area within each region is primarily energetically driven, reflecting per capita energetic needs relative to local resource availability (McNab 1963, Kleiber 1975, Haskell et al. 2002). This finding is consistent with my result that sex was not a significant factor (P = 0.370) in explaining home-range area and body size relationships in the regression model. Further, this finding is in agreement with previous studies that reported no sexual differences in metabolic requirements of martens (Worthen and Kilgore 1981, Buskirk et al. 1988) and other mustelids (Moors 1977, Casey and Casey 1979, Powell 1979b).

I found a significant relationship between home-range area and body size for American marten in NF and ME, in agreement with previous allometric analyses (McNab 1963, Harestad and Bunnell 1979, Lindstedt et al. 1986, and others – see Introduction); however, the allometric form of this relationship varied between NF and ME. For a given body size and hence metabolic (food) requirement, the spatial requirements for Newfoundland marten were 3-5 times higher than for martens in Maine. For example, the predicted home-range area of a 600g female marten is 2.5  $\text{km}^2$  in ME and 8.2  $\text{km}^2$  in NF (Figure 1.6b), an indication of the relative size of the area presumably needed to meet metabolic needs and a reflection of the local prey availability. Similarly, the nonlinear slope of the NF home-range-size – body-size relationship indicates that as body size increases in NF marten, spatial requirements scale (increase) at a rate greater than 1:1. Thus, in Newfoundland's naturally fragmented environment, larger martens require disproportionately larger areas (more food) relative to martens in ME and must access larger areas at the cost of incorporating more patches of unsuitable habitat in their home range. Consequently, martens in ME can meet energetic requirements by centering their

home ranges on a single patch of suitable habitat, whereas martens in NF must acquire their energy requirements across dispersed patches and must incorporate a higher proportion of unsuitable habitat into their home ranges. This causes metabolic-adjusted home-range area to be larger in NF and puts even greater energetic constraints on the largest males which experience nonlinear increases in home-range area as body weight increases.

Home range is a highly integrative concept that collectively expresses the influence of many intrinsic and extrinsic factors such as: social organization (Damuth 1981, Johnson et al. 2001, Revilla 2003); sex (Powell 1979a, Erlinge and Sandell 1986); climate and environmental seasonality (Lindstedt et al. 1986, Ferguson et al. 1999, Nilsen et al. 2005); landscape heterogeneity (Kie et al. 2002, Atwood 2006); and diet and prey availability (Harestad and Bunnell 1979, Lindstedt et al. 1986, Zabel et al. 1995, Grigone et al. 2002). Further, these factors operate in a nested hierarchical structure operating at different spatial and temporal scales (McLoughlin and Ferguson 2000). Consequently, mounting evidence suggests that past attempts to explain use of space by animals (e.g., McNab 1963, Harestad and Bunnell 1979, Lindstedt et al. 1986, Reiss 1988) were incomplete in their assessment of factors affecting home-range area and were confounded by various factors inherent in interspecific analyses (Kelt and Van Vuren 1999, 2001, Haskell et al. 2002, Jetz et al. 2004). This study suggests an interaction between homerange area, body size, prey availability, and habitat heterogeneity that have important implications for conservation of endangered NF marten.

More recent attempts to model the scaling of animal space use suggest that there may be no universal scaling exponent, and that home-range area is an interaction between

an organism's physiological rates (Kleiber 1979), the structure of the local environment, and resource distribution operating in a hierarchical structure (Haskell et al. 2002, Jetz et al. 2004). At the macro level variation in home-range area is strongly driven by body size, that is, larger animals need more resources. At lower levels, allometric relationships developed from interspecific analyses of body size explain far less of the observed variation in spatial requirements, and are confounded by ecological and environmental factors that can be highly site-specific. However, linear (ME) versus nonlinear (NF)) scaling exponents aid in understanding of landscape heterogeneity as an additional spatial and energetic constraint for recovery of wide-ranging species in fragmented environments.

Kelt and Van Vuren (2001) recently describe a theoretical model of the relationship between home-range area and body size as an oblong polygonal constraint space; the relationship constrained at the lower and upper minimum and maximum by the energetic requirements of the individual and the biophysical characteristics (limitations) of the local environment. Kelt and Van Vuren's analysis, like most previous analyses of homerange area and body size (e.g., McNab1969, Harestad and Bunnell 1979, Lindstedt et al. 1989) was broadly interspecific and based on home-range data for 279 individual species from various trophic groups ranging in mass from 10 to  $10^7$  grams). Thus, a portion of their polygonal constraint space model is always defined by intraspecific variability in home-range area and body size within the species (intraspecific). Thus, the extreme variation in home-range area displayed by martens in ME and NF (i.e.,  $0.5 - 67.0 \text{ km}^2$ ; Table 1.3 and Table 1.4) defines a large portion of the overall polygonal constraint space for small-bodied (0.5-1.5 kg) terrestrial carnivores, and specifically for American

martens. Further, given that my estimates of home-range area for martens in NF are close to the maximum reported for American martens, my data likely defines the upper maximum of the polygonal constraint space for American marten and exemplifies the unique spatial, energetic, and habitat constraints of the endangered NF marten.

Future analyses attempting to explain site-specific differences in home-range characteristics of American martens (e.g., Buskirk and McDonald 1989, Smith and Schaefer 2003) will require additional data, currently unavailable, to better quantify resource distribution and dispersion (e.g., relative habitat selection indices and habitatspecific prey indices), measures of intra- and inter-sexual home-range overlap, and estimates of the exclusivity of resources within individual home-range boundaries (Jetz et al. 2004). Without site-specific estimates for these parameters, future intraspecific analyses of factors affecting home-range size variation in American martens (e.g., Buskirk and McDonald 1989, Smith and Schaefer 2002) will likely only confirm wellestablished general patterns of increasing home-range size with increasing body size (e.g., McNab 1963, Harestad and Bunnell 1979).

### **CONSERVATION IMPLICATIONS**

Spatial requirements and life-history traits of NF martens have been shaped by its uniquely structured biophysical environment. Martens in NF have disproportionately large home ranges and large body sizes relative to marten populations at similar latitudes elsewhere throughout the species' North American range (see reviews in Buskirk and McDonald 1989, Powell 1994). These unique site-specific factors include a depauperate prey base and distinctive assemblage of competitors and predators, all interacting in a highly naturally-fragmented forested environment. Home-range sizes of NF martens

(i.e., males =  $27.6 \text{ km}^2$ , n = 43, females =  $10.6 \text{ km}^2$ , n = 49) are the largest yet recorded for the species, are 3-5 times larger than those of a mainland population of martens in northcentral Maine at a similar latitude (even after allometric adjustment), and 8-12 times larger than predicted (i.e., Lindstedt et al. 1986) for a terrestrial mammalian carnivore of such body size.

Consequently, natural resource managers must recognize these unique ecological and environmental factors when formulating conservations actions for this endemic, endangered population. Given the large spatial requirements demonstrated by martens in NF, and because martens are intrasexually territorial (Katnik et al. 1994, Powell 1994), marten densities in NF are inherently low. Thus, conservation of habitat for viable populations of NF martens will involve large areas, and planning for future habitat supply must be conducted at the appropriate spatial and temporal scale to protect, and ultimately recover, the species by the provision of refugia. Further, the forest environment in Newfoundland is naturally fragmented and suitable patches of habitat for NF martens are widely dispersed (e.g., > 50% of the home ranges of adult resident martens reported on herein were comprised of <50% suitable habitat; Chapter 2). Furthermore, prey resources for martens in Newfoundland are limited relative to mainland populations. Thus, in landscapes where forest harvesting will be a prevailing activity, habitat planning must recognize that forest harvesting may potentially fragment habitat further by subdividing environmental resources over larger areas. The cumulative effects of the natural landscape heterogeneity, in combination with increased (anthropogenic) fragmentation via forest harvesting, needs to be considered when evaluating effects of proposed logging activities on Newfoundland martens. In this regard, newly developed spatial planning

tools that can predict the probability of occupancy by NF martens for current (and proposed future) landscapes (Fuller 2006), developed from the empirical results of this study (i.e., home-range composition and landscape configuration), should be used to inform forest-harvesting planning processes both spatially and temporally.

Overexploitation of martens at the turn of the century was the likely cause of the historical decline of marten populations throughout North America (Aldous and Mendall 1941, Burt 1946, Yeager 1950, de Vos 1951, Quick 1956, Hagmeier 1956, Dodds and Martel 1971, Gibilisco 1994, Strickland and Douglas 1981, Strickland 1994) including NF (Thompson 1991, Forsey et al. 1995, Chapter 3). Further, I present evidence in Chapter 3 that incidental mortality of martens in traps and snares is currently limiting recovery of the species in NF. Martens are easily trapped (Strickland and Douglas 1987) and are highly susceptible to overharvesting (Hodgman et al. 1994). Given that higher movement rates (thus trap encounter rates) have been associated with increased vulnerability to human-related mortality for martens (Strickland and Douglas 1987, Powell 1994) the large spatial requirements and movement rates (MINDIST) of NF marten likely increase their relative vulnerable to incidental mortality. Therefore, mortality could exceed sustainable levels even when snaring and trapping pressure is light. Accordingly, a landscape-scale view will be required when setting harvesting regulations to protect and recover NF martens.

Finally, an earlier attempt to model population viability of NF martens did not have the data necessary to explicitly model spatial requirements, relying instead on a review of spatial requirements and habitat requirements from studies of marten populations inhabiting areas of mainland North American (Schneider 1997). This earlier model used

an optimum territory size of 4 km<sup>2</sup>, but incorporated viable territories as small as 1 km<sup>2</sup>.

Thus, my results emphasize the need for site-specific research to provide scientific data

for informed decision making, particularly for area-sensitive species at risk.

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# CHAPTER 2: MULTI-SCALE HABITAT SELECTION BY THE ENDANGERED NEWFOUNDLAND MARTEN: A GENERALIST IN REFUGIUM ABSTRACT

The Newfoundland marten (Martes americana atrata) is a genetically distinct, endangered population of American marten endemic to the island of Newfoundland. Past studies have suggested that Newfoundland martens are currently limited by habitat availability and constrained to areas of overmature (> 80-years old) coniferous forest. I studied the habitat ecology of the remaining core population of Newfoundland marten and evaluated multi-scale habitat selection across landscapes comprising a range of habitat types. I tested the hypothesis that mature (61-80-years old) and overmature conifer stands were preferred by martens relative to other forest types occurring within their home range and compared the age structure and daily survival of resident martens with different amounts of mature and overmature forests in their home ranges. Additionally, I evaluated 11 *a priori* predictions to assess habitat preferences of Newfoundland martens. Between June 1995 and August 2000, I trapped 168 juvenile and adult martens and monitored habitat use by radiotelemetry. My inferences were based on 2,861 locations for 58 adult ( $\geq$  1 yr) resident martens for which I calculated 92 year-specific home ranges. I identified 10 habitat classes, ranging from bog and barren, recent ( $\leq$  5-years old) cutovers, and regenerating ( $\leq$  6.5 m) forest, to tall ( $\geq$  12.6 m) overmature forest, and insect-killed stands, and evaluated whether use was proportional to availability on the landscape and within each individual's home range. Further, I tested the hypothesis that martens showed higher preference for mature and overmature stands relative to regenerating, recently cut, and insect-killed stands. At both the

landscape- and stand-scales, martens utilized a broad range of habitat types within their home ranges, including recent cuts, regenerating forest < 6.5 m, precommercially thinned stands, and medium height (6.6-12.5 m) softwood stands, as well as mature (61-80-years old) and overmature forest. Martens occupied home ranges that were not dominated by mature and overmature forest conditions; median availability of mature and overmature forest within the individual home range was only 30.03% (range 10.7-75.6%). Tall closed softwood stands, which based on previous work represent "preferred" marten habitat, were intermediate in relative preference to other vegetation classes at the landscape scale (i.e., 2<sup>nd</sup>-order selection), and comprised only 12.5% of home ranges of adult resident martens. Age distributions were not different among martens with high, intermediate, and low amounts of mature and overmature forest in their home range. Further, martens occupying home ranges dominated by mature and overmature forests did not exhibit higher survival rates. Past studies of habitat selection by Newfoundland martens that concluded Newfoundland martens were more dependent on old-growth coniferous forests than populations inhabiting mainland North America were not supported by my results. Habitat selection by martens in Newfoundland is more generalized and complex than previously understood, and current habitat interpretations used in Newfoundland are overly conservative. Further, high levels of inherent landscape fragmentation, in combination with the absence of many predators and competitors (i.e., ecological release), may have caused the Newfoundland marten to evolve as a more generalized predator than mainland martens.

## **INTRODUCTION**

American marten (Martes americana) have been described as forest dependent, and as a habitat specialist for late successional, conifer-dominated forest (Koehler and Hornocker 1977, Meslow et al. 1981, Allen 1982, Hargis and McCullough 1984, Buskirk 1992, Buskirk and Powell 1994, Buskirk and Ruggerio 1994). Thompson and Harestad (1994) summarized hypotheses to explain associations of martens with forests characterized by large diameter trees, closed canopy, and considerable within-stand coarse woody debris: 1) martens require overhead canopy for security or avoidance of terrestrial and avian predation (Herman and Fuller 1974, Pulliainen 1981, Hargis and McCullough 1984); 2) martens require structurally-complex forests with abundant coarse woody debris and large diameter trees to provide suitable winter resting sites, maternal dens, and subnivean access to small mammal prey in winter (Bergerud 1969, Steventon and Major 1982, Wynne and Sherburne 1984, Thompson 1986, Sherburne and Bissonette 1994, Corn and Raphael 1992); and 3) martens are more successful in accessing prey in older, structurally-complex forests and not necessarily where prey are most abundant (Thompson 1986, Thompson and Colgan 1987).

More recent evidence from across the geographic range of the marten, suggests that habitat associations may be more variable than previously understood (Bowman and Robitaille 1997, Chapin et al. 1997, Payer 1999, Payer and Harrison 2000, Potvin et al. 2000, Payer and Harrison 2003, Poole et al. 2004, Mowat 2006), and that forest structure may be a more important determinant of marten habitat than forest species composition or forest age (Chapin et al. 1997, Porter et al. 2005). At the stand scale, martens are better defined as structural obligates, requiring complex horizontal and vertical structure

(Payer and Harrison 2000, 2003); these structural requirements are likely provided by a variety of forest types throughout the range of the species.

In the transitional Acadian forests of northeastern North America (Seymour and Hunter 1992), martens utilize a wide range of forest types, including mixed coniferousdeciduous and deciduous-dominated stands (Katnik 1992, Chapin et al. 1997, Payer 1999, Fuller and Harrison 2005), as well as open-canopy stands regenerating following insect defoliation (Chapin et al. 1997, Payer and Harrison 2000, 2003). Suitable habitat for martens was described by these studies as well-stocked stands with trees > 9 m with canopy closure > 30% and a minimum basal area of 18  $m^2$ /ha (Payer and Harrison 2003, Fuller and Harrison 2005). Similarly, martens inhabiting second-growth boreal forests in western Quebec preferred deciduous and mixed deciduous forests > 30-years and showed no selection (i.e., proportional use) of coniferous habitats, including, overmature (> 80 years), mature (61-80-years old), immature (30-60-years old), and recent (<4 years) clearcuts with dense regeneration (Potvin et al. 2000). More recently, Poole et al. (2004) reported on a moderate-density population of martens in the Pacific Northwest that made extensive use of 30- to 40-year-old deciduous-dominated stands. Furthermore, fitness of this population, as indexed by small home ranges, multi-year residency by adults ( $\geq 1$  yr), and high survival rates, suggested that second-growth forests on previous agricultural land had sufficient structure, overhead cover, and prey to maintain a long-term resident population. Collectively, these more recent studies indicate that marten habitat associations are likely broader and more complex than previously understood; and that habitat quality for martens does not necessarily equate with the extent and degree of maturity of conifer-dominated stands.

The Newfoundland marten is a genetically distinct population (*M. a. atrata*) of the American marten found endemic to the island of Newfoundland (Kyle and Strobeck 2003). Since the early 1900's the population has declined both in numbers and distribution (Bergerud 1969, Snyder 1984, Snyder and Bissonette 1987, Thompson 1991, Forsey et al. 1995). In 1986, the Newfoundland marten was listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Threatened (Forsey et al. 1995); COSEWIC uplisted the species to Endangered in 1996. Even though excessive trapping, in combination with habitat loss due to fire and logging, had been suggested as the major factors contributing to the early (1900's) decline of martens in Newfoundland (Thompson 1991, Forsey et al. 1995), habitat loss via timber harvesting of mature and old-growth (> 80-years old) softwood forest has been widely stated to be the principle factor currently limiting recovery of the Newfoundland marten (Bissonette et al. 1988, Thompson 1991, Forsey et al. 1995, Thompson and Curran 1995, Schneider 1997, Bissonette et al. 1997, Thompson et al. 2003).

Despite the precarious status of the *M. a. atrata*, few inferences can be drawn from the limited data on marten-habitat associations in Newfoundland (Schneider 1997). Available data are based on snow tracking of unmarked individuals (Snyder and Bissonette 1987), in an area of old-growth conifers and recent clearcuts, or are inferred from few (n = 6) radio-marked individuals in a small study area dominated by overmature conifer stands (Drew 1995). Habitat associations inferred from intensively monitoring few individuals in areas dominated by habitat types perceived to be preferred, may be biased (Thomas and Taylor 1990). Thus, previous work does not allow inferences regarding the range of environmental conditions suitable for occupancy by

Newfoundland martens across multiple spatial scales (Johnson 1980), or about the relative performance (e.g., residency status, age structure, age-specific fecundity and survival) of martens inhabiting areas with different availabilities of overmature conifer stands (Hobbs and Hanley 1990). Regardless of these limitations, reports from the 1970's to 1990 (e.g., Snyder and Hancock 1985, Bissonette et al. 1988) stressed the association of *M. a. atrata* with old-growth conifer forests, and protection and recovery efforts focused on stand-scale protection of older forests (i.e., 80+ year-old softwood-dominated forest; Thompson 1991, Forsey et al. 1995, Schneider 1997, Sturtevant and Bissonette 1997).

Ecological conditions for Newfoundland martens differ from other marten populations throughout the North American range. Newfoundland, like most islands (MacArthur and Wilson 1967, Simberloff 1974), has fewer native species when compared to continental areas of similar size. Moreover, the composition of the terrestrial mammalian community is highly skewed, with a disproportionate number of predators and few prey species (Dodds 1983). Historically, Newfoundland had only 14 species of native terrestrial mammals; at least 9 (64%) are classified as distinct subspecies. Over the last 140 years, however, an additional 11 species of terrestrial mammals have been either intentionally or accidentally introduced (Dodds 1983, Hearn et al. 2006) and 1 species, the Newfoundland wolf (*Canis lupus beothucus*) has been extirpated (Allen and Barbour 1937). Furthermore, the island of Newfoundland has only 1 native microtine, the Newfoundland meadow vole (*Microtus pennsylvanicus terraenovae*) which was historically thought to be the primary small mammal prey for Newfoundland martens (Bateman 1986, Tucker 1988, Drew 1995, Thompson and Curran

1995, Sturtevant and Bissonette 1997). However, recent food habits data from Newfoundland (Gosse and Hearn 2005) suggest that marten diets may include a greater representation of other prey species (i.e., snowshoe hare (*Lepus americanus*) than previously thought.

Thompson and Curran (1995), and later Sturtevant et al. (1996) and Sturtevant and Bissonette (1997), hypothesized that the depauperate prey base in Newfoundland has restricted martens to older forests where meadow voles are most abundant (Thompson and Curran 1995). They further speculated that *M. a. atrata* are more strongly tied to mature and overmature conifer forests than *M. a.* in other parts of North America because of limited prey availability; this rationale has been used to explain observed differences in habitat selection in Newfoundland as compared to Maine (Bissonette et al. 1997). Sturtevant and Bissonette (1997) concluded that generalizations of habitat requirements developed from research throughout mainland North America may not apply to the local conditions of Newfoundland and that habitat management must recognize the constraints imposed on *M. a. atrata* by the limited prey resource.

Thus, I examine the habitat ecology of the endangered *M. a. atrata* in southwestern Newfoundland, the region of the island thought to contain the remaining core population (Thompson 1991, Forsey et al.1995). The objectives of this study were: 1) evaluate multi-scale habitat selection by martens across landscapes comprised of a range of habitat types, including mature and overmature coniferous forests, extensive areas of softwood scrub on poorer quality sites, regenerating clearcuts, areas of insect-killed overmature coniferous forest, and precommercially thinned softwood stands; 2) test the hypothesis that mature and overmature conifer stands were preferred by martens relative to other

forest types that occurred within their home range; and 3) compare the age structure and average daily survival of resident martens with differing amounts of mature and overmature forests in their home ranges. Additionally, I evaluated 11 *a priori* predictions used to assess 7 questions about habitat preferences of Newfoundland martens using empirical data collected from a sample of radio-marked martens, and evaluated habitat guidelines currently used by forest and wildlife managers in Newfoundland for delineating critical habitat, assessing environmental effects of industrial forest harvesting operations, and conserving habitat for Newfoundland martens.

## STUDY AREA

The study was conducted within a 1,900-km<sup>2</sup> area in southwestern Newfoundland between June 1995 and August 2000 (Figure 2.1). The boundary was defined as the effective trapping area and was determined by creating a 6.26 km buffer around all locations (buffer = diameter of the mean 95% minimum convex polygon mean; Chapter 1) where traps were placed to capture resident martens (Fuller 2006). The study area incorporated a little more than one half (55%) of the 2,078 km<sup>2</sup> PMSA - a provincially designated wildlife reserve established in 1972 for the protection of the Newfoundland marten (Forsey et al. 1995). The PMSA is considered to contain the largest concentration of *M. a. atrata* and is managed as a refuge from which martens can disperse to reoccupy surrounding areas of suitable habitat. Previous research on Newfoundland martens has been concentrated within the PMSA (Snyder 1984, Snyder and Bissonette 1987, Tucker 1988, Bissonette et al. 1988, 1989, Fredrickson 1990, Drew 1995, Thompson 1991, Thompson and Curran 1995, Drew and Bissonette 1997); the PMSA is closed to all landbased snaring and trapping (Forsey et al. 1995).



Figure 2.1. Map of the study area and spatial relationship to the Pine Marten Study Area (PMSA), a provincially designated wildlife reserve closed to snaring and trapping, created in 1972 for the protection of the Newfoundland marten.

The forests on the study area are comprised primarily of balsam fir (Abies balsamea) with white pine (*Pinus strobus*), larch (*Larix laricina*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*), the latter becoming more common on the eastern extreme of the study area. Forested regions of the study area are concentrated on the eastern and western thirds of the study area; the study area is bisected naturally by a higher-elevation plateau (18% of total study area) that is dominated by large lakes, coniferous scrub vegetation ( $\leq 6.5$  m forest on low productivity sites), bogs, and soil and rock barrens. This plateau likely supported few resident martens, and generally has been considered a barrier to dispersal and genetic exchange between local marten subpopulations in southwestern and southcentral Newfoundland (J. Brazil, Department of Environment and Conservation, Wildlife Division, personal communication). Consequently, I considered this portion of the study area to be unavailable to resident martens and restricted my trapping efforts and analyses to the eastern and western portions of the study area. Approximately one half (54%) of the eastern and western portions were forested.

The fir-dominated boreal forests in this region of western Newfoundland are atypical; natural disturbance is primarily caused by insect infestations and not fire (Bakuzis and Hansen 1965, Thompson et al. 2003). Hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) infestations occurred on the area during the mid-1980's resulting in a mosaic of insect-killed softwood stands ranging in size from 0.60 - 200 ha (median patch size = 2.85 ha). These insect-killed stands composed 2.4% of the available landscape (Table 2.1), were in various stages of decline
Vegetation Class	Code	Description	%
Bog / Barren	Bb	Open, generally treeless bogs; rock and soil barrens	22.0
Recent Cuts	Rc	Recent ( $\leq$ 5 years) cuts; residual patches of softwood and mixedwood	4.0
Scrub	Sc	Unmerchantable softwood $\leq 6.5$ m in height; generally low productivity sites	9.5
Regenerating Forest	Rf	Conifer regeneration $\leq 6.5$ m height, $\geq 75\%$ canopy closure	3.6
Precommercially Thinned	Pct	20- 30-year-old conifer stands, 7-17 years post-thinning, > 50% canopy closure; typical density of 1,500 stems/ha	3.4
Medium Open Softwood	Mos	Conifer stands, 6.6-12.5 m in height, $\leq 50\%$ canopy closure	13.3
Medium Closed Softwood	d Mcs	Conifer stands, 6.6-12.5 m in height, > 50% canopy closure	4.3
Tall Open Softwood	Tos	Conifer stands $\geq$ 12.6 m in height, $\leq$ 50% canopy closure	6.4
Tall Closed Softwood	Tcs	Conifer stands $\geq$ 12.6 m in height, > 50% canopy closure	10.9

Table 2.1. Description of vegetation classes and the percent of each class on the study area, southwestern Newfoundland, Canada.

Vegetation classes were derived from the provincial forest inventory (Anonymous 1991).

Vegetation Class	Code	Description	%
Insect-killed Stands	Ik	Insect-killed conifer stands, primarily $\geq$ 12.6 m in height, < 25% canopy closure;	2.4
		understory typically dense advanced softwood (Abies balsamea) regeneration	
Other <sup>a</sup>	n/a	Rare forest types, including hardwood, mixedwood, stand remnants, cleared land,	6.1
		transmission lines, roads, pits, and disturbed areas.	
Water <sup>a</sup>	n/a	All ponds, lakes, streams, and rivers	14.1

<sup>a</sup> Selection of these classes was not evaluated.

and regeneration, and typically had little to no crown closure, an abundance of snags in various stages of decay, and substantial volumes of coarse woody debris. Most of the insect-killed stands on the study area were 10-20 years post infestation and typically had a dense ground cover of balsam fir regeneration.

Forest harvesting, primarily for coniferous pulpwood production, has been ongoing on the study area for much of the last century and occurred during the study period with 4.0% of the area in recent ( $\leq$  5 years) clearcuts. Additionally, clearcutting began in the late 1970's and 3.6% of the available landscape for martens was in regenerating <6.5 m cuts (> 5 years since harvest) and 3.4% was comprised of 20- to 30-year-old clearcuts that had been subsequently precommercially thinned to reduce softwood stem densities (Table 2.1). Old-growth (> 80-years old; Thompson 1991, Thompson and Curran 1995, Sturtevant and Bissonette 1997) conifer forest comprised only 17.3% of the study area. Stands of scrub (unmerchantable softwood) forest  $\leq$  6.5 m in height, generally occurring on low-productivity wet sites, occupied 9.5% of the study area. Ponds, lakes, streams and rivers occupied 14.1% of the study area.

### **METHODS**

### Marten Capture and Radio Collaring

Martens were trapped for a 2- to 4-week period each summer (June – August) and each autumn (typically late September – early October) beginning in June 1995 and ending in August 2000. Martens were captured in collapsible Tomahawk ® live traps (18 x 18 x 48 cm) located every 1-2 km along roads and snowmobile trails, or along the shoreline of lakes and were spaced to maximize the likelihood that all potential marten

territories would include at least 1 trap. During winter, I used snowmobiles to access the study area to improve my trapping coverage.

On initial capture, martens were sexed, weighed, tagged, and fitted with radio collars using standard field procedures (Snyder and Bissonette 1987, Hodgman et al. 1994, Katnik et al. 1994, Bull et al. 1996, Chapin et al. 1997; Chapter 1). A first premolar (PM<sub>1</sub>) was removed from each marten for aging using cementum analysis (Matson's Laboratory, Milltown, MT); whenever possible a PM<sub>4</sub> tooth was extracted for confirmation from animals that died during the study. All females captured were assessed for evidence of lactation or suckling. Radio-collared martens were located every 7-10 days primarily using either an amphibious fixed-wing airplane (Cessna 185) or helicopter (Bell 206 B or Aerospatial A-star). Detailed methods of trapping, handling, and radio telemetry are described in Chapter 1.

### **Residency and Home-range Estimation**

Home-ranges were estimated for all resident martens using the Animal Movement Extension (Hooge et al. 1999) for ArcView ® 3.2 with Spatial Analyst (Environmental Systems Research Institute, Redlands, California). I classified a marten as resident if it met the following criteria:  $1 \ge 12$  months old;  $2 \ge 10$  locations over 90 days with locations  $\ge 24$  hours apart; and (3) mean minimum distance moved between consecutive locations (MINDIST; Harrison and Gilbert 1985) was  $\le$  mean + 3 SD MINDIST for all same-sex martens; these residency criteria were based on Phillips et al. (1998). I defined the biological year as 1 May – 30 April and pooled data to produce individual martenand year-specific databases. I tested for seasonal shifts in home-range area and did not calculate annual home ranges for animals that displayed discrete seasonal ranges. I

calculated 95% minimum convex polygon home ranges (Mohr 1947) for all resident adult  $(\geq 1 \text{ yr})$  martens with at least 19 locations during the biological year of 1 May – 30 April (i.e., area-observation curve asymptote; Chapter 1).

# **Habitat Mapping**

I created a habitat map of the study area using a geographic information system (ARCGIS ®; Environmental Systems Research Institute 1997). My initial landcover was the Provincial Forest Inventory (PFI), which was interpreted from 1:12,500-scale stereoscopic, black and white aerial photography taken in 1986; the minimum mapping unit used in the PFI was ca. 0.30 ha (S. Payne, Newfoundland Forest Service, personal communication).

The initial landcover was partitioned into 118 vegetation types based on dominant cover (e.g., softwood, mixedwood, hardwood, bog, barren, scrub, etc.), and stand height (7 classes; 1 = 0-3.5 m, 2 = 3.6-6.5 m, 3 = 6.6-9.5 m, etc.), and crown closure (4 classes; 1 = > 75%, 2 = 51 - 75%, 3 = 26-50%,  $4 = \le 25\%$ ). I increased stand height by 2.9 m (1 height class) for all stands occupying sites with a quality index of medium or better based on local growth and yield equations to account for changes in stand height between 1986 and the beginning of the study in 1995 (Anonymous 1991). Further, I incorporated annual updates for the PFI (i.e., forest harvesting, road construction, silvicultural activities, and insect disturbance) to produce year-specific landcover maps for each year of the study (i.e., 1995-2000).

During the first year of the study I observed significant use of areas mapped by the PFI as scrub forest (Scs). Because the Scs class was created to map forested areas below the merchantability threshold ( $\leq$  70 m3/ha) for economical forest harvesting, (G. Van

Dusen, Corner Brook Pulp and Paper Limited, personal communication), the Scs class represented a wide variety of structural conditions (i.e., 0-12.6+ m height; 0-100% crown closure). Subsequently, I reclassified all Scs identified from the original 1986 aerial photography into the 7 height and 4 crown-closure classes used for classifying merchantable forest; reclassification was based on stereoscopic re-evaluation of the original 1:12,500 scale aerial photography.

Stand height, successional stage, and overhead cover are consistently reported as the most important stand-scale attributes associated with habitat selection by the American marten throughout its geographic range (Koehler and Hornocker 1977, Allen 1982, Hargis and McCullough 1984, Snyder and Bissonette 1987, Buskirk and Powell 1994, Thompson and Harestad 1994, Payer and Harrison 2000, Payer and Harrison 2003). Accordingly, I combined the original 118 landcover types and created 11 vegetation classes (Table 2.1) based on forest composition and structural characteristics (i.e., stand height, crown closure). My Tall Open Softwood (Tos) and Tall Closed Softwood (Tcs) classes represented mature (61- 80-years old) and overmature (> 80-years old) coniferous forests hypothesized to be of paramount importance to Newfoundland martens (Snyder and Bissonette 1987, Bissonette et al. 1988, 1989, Drew 1995, Thompson 1991, Thompson and Curran 1995, Sturtevant et al. 1996, Bissonette et al. 1997, Sturtevant and Bissonette 1997).

Many of my original 118 vegetation types were either rare on the study area or lacked measures of height and/or crown closure. For that reason, I combined all rare or structurally uncharacterized vegetation types into a non-specific class "Other" (6.1% of study area) and excluded it from further habitat selection analyses.

## **Habitat Selection Indices**

Habitat selection is a hierarchical process (Johnson 1980) occurring from the geographical range of the species, to placement of the individual home range on the landscape (landscape-scale selection), to use of habitats within the home range (stand-scale selection), to selection of individual features (e.g., coarse woody debris, dens, within the home range (Orians and Wittenberger 1991, Manly et al. 2002)). Habitat selection at these various scales is not independent; decisions made by animals at lower hierarchical levels are influenced by decisions made at higher levels and often result in different patterns of selection across scales (Aebischer et al. 1993).

Accordingly, I evaluated both landscape- and stand-scale habitat selection by calculating selection indices (SI) for each vegetation class as:

$$SI = Ln$$
 (Use / Availability).

I used a Design III approach (Thomas and Taylor 1990, Manly et al. 2002), where use and availability of resource units (e.g., habitat classes) were estimated separately for each animal and thus the individual radio-marked animal, rather than the individual location, was the experimental (sampling) unit. Such an approach avoids the problems of pseudoreplication (Hurlbert 1984) inherent in field studies that treat the telemetry location as the sampling unit (Kenward 1992), eliminates the inflated apparent number of degrees of freedom of statistical tests (increased Type I error rate; Aebischer et al. 1993), and allows for variation among individuals (e.g., sex, age) as the basis for population inferences regarding resource selection (Alldredge and Ratti 1992, Aebischer et al. 1993, Manly et al. 2002). I used natural logs to rescale the SI and to center the index on zero; selection indices > 0 indicated preference, selection indices <0 indicated avoidance, and selection indices = 0 indicated use of a habitat type proportional to its availability. Use of natural logs also increases the independence of selection indices calculated from use-availability data and addresses issues of linear dependence and the unit-sum constraint inherent in proportional data (i.e., proportions describing use and availability sum to one over all resources (Aebischer et al. 1993). There is, however, no consensus on the statistical issues posed by the unit-sum constraint or the effectiveness of log transformations (McClean et al. 1998).

### Landscape-scale habitat selection

For landscape-scale habitat selection (2<sup>nd</sup>-order selection; Johnson 1980), I calculated a SI for each vegetation class by comparing the percent of each class within the home range (use) to the percent of the class available on the landscape (availability), for individual marten, on a year-specific basis. To determine the availability of each vegetation class on the landscape, I used year-specific study area boundaries based on the area I effectively trapped each year as calculated by Fuller (2006). Landscape-scale habitat availability (calculated after removing all water) was then defined as the year-specific study area minus all areas included within the 95% MCP home ranges of consexuals, to account for intra-sexual territoriality. There were also martens occupying the study area for which we had fewer than 19 locations (i.e., my home-range calculation criteria) for which I needed to calculate an area of occupancy (i.e., 95% MCP simulated home ranges). Accordingly, based on data from 30 individual martens (41-marten years) with a minimum of 30 radiolocations per animal I developed a regression equation to

predict home range area (i.e., 95% MCP Area ( $km^2$ ) = 0.013 (MINDIST) – 13.785,  $r^2$  = 0.79; Chapter 1) where MINDIST (Harrison and Gilbert 1985, Phillips et al.1998) equals the average distance moved between consecutive relocations. Fuller (2006) used this regression equation and MINDIST for all martens with 10-18 locations to calculate simulated home range for all martens with 10-18 annual locations. Because marten are intrasexually territorial (Katnik et al. 1994), simulated home ranges were used exclusively to estimate the area unavailable to consexual martens, and were not included in the sample of home ranges considered used by martens.

I further limited my analyses of landscape-scale selection to vegetation classes that had at least 2% availability on the landscape for individual martens, on a year-specific basis. By limiting my landscape-scale analyses, I eliminated the need for substitution values (i.e., small positive values such as 0.01 are substituted for each 0% use; Aebischer et al. 1993) when no observations (locations) are recorded for an animal in rare habitat types. This approach reduced interpretation problems associated with calculating selection indices for habitat types that were rare on my study area (Weir and Harestad 2003), and eliminated inflated Type I error rates associated with the use of substitution values in resource selection analysis (Bingham and Brennan 2004). I analyzed habitat use for these rare types using a Sign test (Conover 1999) to evaluate whether individual vegetation classes tended to be selected (SI > 0) or avoided (SI <0)

### **Stand-scale habitat selection**

I evaluated stand-scale habitat selection (within home range; 3<sup>rd</sup>-order selection; Johnson 1980) by determining the proportion of total locations in each of the 10 habitat classes (use) and availability as the proportion of each class (availability calculated after

removing all water) within the individual marten- and year-specific 95% MCP home range. To avoid computing spurious measures of habitat selection, I applied two criteria when calculating a stand-scale SI. First, I did not calculate a SI if the expected number of locations occurring in a particular vegetation class was < 2.0 (expected value = % of habitat class in the home range multiplied by the number of locations used to define the home range). Setting a minimum expected value of 2.0 avoided the issue of calculating a SI for vegetation classes that were rare within the home range. Thus, for animals having only the minimum number of locations required for home range calculation (i.e., 19 locations), a vegetation class would have to comprise > 10.5% of the home range before a SI was calculated. Secondly, if a vegetation class had an expected value > 2.0 but was unused (zero locations recorded in the habitat class) I arbitrarily substituted a 0.001 value for use so that the SI was mathematically defined; the latter approach is analogous to that proposed by Aebischer et al. (1993) for missing habitat types when using compositional analysis. SI values calculated using this approach (6.3%) correctly calculated a negative selection index (i.e., < 0, indicating avoidance) that were appropriate in scale (< 0, > -3) to selection indices calculated without using substitution values (Aebischer et al. 1993).

#### **Statistical Approach and Analyses**

Martens are intrasexually territorial (Powell 1979, 1994) and display fidelity to home range location (Phillips et al. 1998, Payer et al. 2004). Additionally, socially dominant animals presumably occupy higher quality habitats or home ranges, thereby increasing their fitness (i.e., increased survival and/or reproduction; Pulliam and Danielson 1991), in accordance with the ideal-despotic hypothesis as outlined by (Fretwell 1972). Thus, annual home ranges that are occupied consecutively by the same

individual are likely of higher quality. Therefore, I considered the individual yearspecific home range (95% MCP) as the unit of replication for habitat selection analysis. Hence, locational data used for home-range calculation were not pooled within individuals across years. As a result, animals that survived to be monitored more than 1 year would have contributed data for 2 or more years if sufficient locations were available to calculate a year-specific home range. This approach increased my statistical power while concurrently avoiding the underrepresentation of high quality portions of the study area that received repeated use by surviving resident animals throughout the study.

I conducted a multivariate analysis of variance (MANOVA) on ranked habitat selection indices to test the effects of sex and exposure to snaring and trapping (marten resident within or outside the closed PMSA) on habitat selection; data were pooled across sex, and exposure to snaring and trapping if P > 0.10. Subsequently, I used a nonparametric single factor analysis of variance on ranks (Kruskal-Wallis; Conover 1999:288) to test the hypothesis that martens used habitats in proportion to availability, and Fishers Least Significant Difference multiple comparison test (Conover 1999:288) to compare my *a priori* habitat questions (p.26) between pairs of vegetation classes. Use of rank habitat selection indices, without blocking on each individual animal, is statistically conservative but was required in this setting where not all animals had each of the 10 vegetation classes in their home range.

Additional to my primary question of regarding proportional habitat use at the standand landscape-scales, I evaluated 7 more specific questions using 11 pre-selected, pairwise comparisons of selection indices (SI) using Fishers's Least Significant Difference test. Specifically, I assessed the following questions: 1) at what stage of

maturity does a stand become marten habitat? (SI's compared: Tcs > Mcs, Tcs > Rf, Rf > Rc); 2) do martens in Newfoundland select old-growth forests above all other forest types? (SI's compared: Tcs > Mcs, Tcs > Ik, Tcs > Tos, Tos > Mos); 3) what are the effects of canopy closure, and the interaction of canopy closure and stand height, on habitat use? (SI's compared: Tcs > Mcs, Tcs > Tos); 4) are regenerating forests on productive sites used more than scrub forests on poor-quality sites? (SI's compared: Rf > Sc); 5) are bogs, recent cuts, and scrub forest selected differently by martens? (SI's compared: Rc = Bb, Sc = Bb); 6) are insect-killed stands used comparably to mature conifer stands regardless of overstory canopy closure? (SI's compared: Tcs = Ik, Tos = Ik); 7) are precommercially thinned stands selected equally to unthinned regenerating stands? (SI's compared: Pct = Rf). I used a binomial test with P = 0.50 (Sign test; Conover 1999) to test whether individual habitat classes tended to be preferred (SI > 0). This is the nonparametric equivalent to testing whether the frequency distribution of selection values for a habitat class included the value of zero.

My overarching assumption, generally supported by the published studies of marten habitat selection in general, and previous habitat work concerning Newfoundland martens in particular, was that the individual vegetation classes I identified did not all have equal value as habitat for martens. I considered a multiple comparison test significant (i.e., habitat selection significantly different between vegetation classes) if P < 0.10. Given sample size constraints, and the importance of conservative measures surrounding habitat management for an endangered species, I judged it more appropriate to balance the probabilities of committing a Type I (i.e., accepting the null hypothesis of equal habitat selection between pairs of vegetation classes) or Type II error (i.e., failure to detect

existing differences in selection between pairs of vegetation classes) by reducing the probability of committing a Type II error, as discussed by Caughley and Gunn (1996). For multiple comparison tests, I did not adjust my alpha level to control experimentwise error rate, judging that the latter procedure would have significantly decreased my ability (i.e., inflated Type II error rates) to discern habitat types of significantly different value to martens in Newfoundland, which potentially have greater conservation implications than Type I errors (Taylor and Gerrodette 1993).

### **Performance Of Martens In Relation To Mature And Overmature Forest**

I indexed population performance of martens in relation to their landscape use (home-range availability) for mature and overmature forest using two measures; yearclass age distributions (i.e., 5 age classes; 1, 2, 3, 4, 5+ years) and daily survival rates. To begin, I placed animals into 1 of 3 classes (i.e., low, medium, or high) based on the prevalence of mature and overmature (old-growth) forest within the home ranges; class boundaries were based on the 33<sup>rd</sup> and 66<sup>th</sup> percentiles for the distributional range of mature and overmature forest availability within the home ranges. Subsequently, I used a Chi-square test to compare age distributions between each of the three classes. I used a Spearman rank correlation ( $r_s$ ; Zar 1999) to examine the relationship between daily survival and the percent of the home range composed of mature and overmature forest. I calculated daily survival rates using program MICROMORT (Heisey and Fuller 1985) and tested whether daily survival was positively correlated with stand-scale (home range) availability of old growth.

## RESULTS

## **Home Ranges**

I captured 159 individual martens (Appendix) during 494 captures between June 1995 and August 2000, including 93 adults ( $\geq 1$  yr) and 54 juveniles (<1 yr); ages were not obtained for 12 animals). I equipped 155 of these animals with radio collars and collected a total of 5,086 locations. Of the 93 confirmed adults, 58 individuals were monitored for a sufficient period to meet my residency and asymptotic home-range criteria (Chapter 1), from which I produced 92 year-specific home ranges (43 male and 49 female ranges; Table 2.2). Each year-specific database was a product of all aerialtelemetry (88%), ground-telemetry (5%) and trapping (7%) locations (n = 2,861) that were separated by > 24 hours. Data were sufficient for only 1 year-specific home ranges for 32 of the 58 individual martens; however, 20 martens provided annual home ranges for 2 years, 5 for 3 years, and 1 marten estimates for each of the 5 years of the study. Mean number of relocations per annual home range was 31.3 (range 19-54).

# Habitat Selection and Availability

### Landscape-scale habitat availability

My trapping and monitoring intensity, hence my ability to document landscape-scale occupancy by martens, was greatest during the first 3 years of the study. Thus, landscape-scale habitat selection analyses were based on 95% MCP for 54 individual martens (29 males, 25 females) representing 84 marten years (40 males and 44 females) obtained during 1995 - 1997. I simulated home ranges (i.e., estimated area occupied using MINDIST) for an additional 24 individuals (13 male, 11 female) for which I had too few (i.e., 10-18) locations to calculate actual home ranges. Simulated ranges were

Study Area	Year	Males	Females	Totals
Section				
Little Grand Lake	1995	11	8	19
	1996	7	11	18
	1997	6	7	13
	1998 <sup>a</sup>	1	2	3
	1999	2	0	2
	Subtotal	27	28	55
Red Indian Lake <sup>b</sup>	1996	11	8	19
	1997	5	10	15
	1998	0	3	3
	Subtotal	16	21	37
Totals		43	49	92

Table 2.2. Numbers of home ranges (n = 92) obtained for 58 individual (31 males, 27 females) adult ( $\geq$  1 yr), resident martens used for habitat selection analyses, southwestern Newfoundland, 1995-1999.

<sup>a</sup> Landscape-scale (i.e., 2<sup>nd</sup>-order; Johnson 1980) selection was not evaluated in 1998 because capture effort was incomplete (i.e., only a portion of the study area was livetrapped).

<sup>b</sup> Radio-collaring and monitoring of marten in the Red Indian Lake area (i.e., eastern portion of the study area) began in May 1996.

deleted from the available habitat in the landscape for same-sex martens because of interspecific territoriality; however, simulated ranges were not used to quantify habitat use at the scale of the home range.

Bog and barren habitat (Bb) was the most common vegetation class available to martens on the study area with median landscape-scale availability of 25.6% (range 22.5-29.6%). Further, approximately one-third of the study area was non-forested or scrub (i.e., Bb and Sc habitat combined) with median landscape-scale availability of 35.8% (10<sup>th</sup> and 90<sup>th</sup> percentiles 33.7% and 39.5%, respectively). Mature and overmature forest (i.e., Tcs, Tos, Ik habitat classes combined), which are habitat types previously hypothesized to be required by Newfoundland martens, had a median landscape availability of only 25.4% (10<sup>th</sup> and 90<sup>th</sup> percentiles, 19.7% and 28.0%, respectively). Four vegetation types including overmature insect-killed stands (Ik), recent cuts  $\leq$  5-years old (Rc), young regenerating forest  $\leq 6.5$  m (Rf), and precommercially thinned stands (Pct), were rare on the study area (mean landscape-scale availability < 5%). Those four vegetation types accounted for all instances (n = 61) where calculation of a selection index for landscape-scale selection would have required use of a non-zero substitution for use; consequently they were excluded from my global test for landscape-scale habitat selection. Thus, no non-zero substitution selection indices were subsequently included in landscape-scale habitat analyses.

### Landscape-scale habitat selection

Landscape-scale selection indices did not differ between sexes ( $F_{Sex; 1, 5} = 1.11$ , P = 0.35), but did differ between animals inhabiting areas open or closed (PMSA) to snaring and trapping ( $F_{Area; 1,5} = 2.67$ , P = 0.02); therefore, I combined data across sexes, and

analyzed landscape-scale selection separately for animals inside versus outside the PMSA.

Adult resident martens did not randomly position their home range on the study area with respect to my 6 habitat classes, in both open and closed areas;  $F_{\text{Closed}; 5,330} = 14.85$ , P < 0.000; F<sub>Open; 5,162</sub> = 12.78, P < 0.000. Further, relative habitat preference, as indexed by the relative rankings of my 6 habitat classes, was very similar between areas (Table 2.3). Tall open softwood ranked highest and bog and barren ranked lowest in relative preference in both open and closed areas. Further, my significant area effect appears to have been a result of minor shifts in the relative rankings between the 2 medium-height softwood classes (i.e., Mos ranked 3<sup>rd</sup> or 2<sup>nd</sup>, and Mcs ranked 4<sup>th</sup> or 5<sup>th</sup> in relative preference on the closed and open areas, respectively). Further, selection indices were significantly different between open and closed areas for only the Tcs (negative on both areas) and Mcs (negative on both areas) classes. Thus, given the notable difference in the number of selection indices calculated in open (n = 168) versus closed areas (n = 336) and the relatively low availability of medium closed softwood habitat (i.e., median landscape availability = 4.10%; 75% of resident animals had  $\leq 5.2\%$ ; Figure 2.2), I viewed these changes in relative ranking between areas as biologically inconsequential, and pooled my data across areas to maximize my statistical power for detecting habitat selection.

Tall open-canopy softwood had the highest selection index and a distribution of selection values indicating that martens selected for this class at the landscape scale (Figure 2.2). Tall closed softwood, and medium open softwood had intermediate selection values and a distribution of selection values suggesting proportional use (i.e.,

Table 2.3. Relative habitat rankings (1 = highest relative preference) and median selection indices (SI) at the landscape scale for 54 adult ( $\geq$  1 yr), resident martens (29 males, 25 females) representing 84 marten years (40 male and 44 female), southwestern Newfoundland, 1995-1997. Vegetation class descriptions as per Table 2.1; Tcs = tall closed softwood, Tos = tall open softwood, Mcs = medium closed softwood, Mos = medium open softwood, Sc = scrub, Bb = bog and barren. Number of selection indices used in statistical comparisons was 336 and 168 for the closed and open area, respectively.

Habitat Class		Closed Area			Open Area		
	Ranking	Median SI	Range <sup>b</sup>	Ranking	Median SI	Range	
Tos	1	0.26	0.07 to 0.45	1	0.63	-0.24 to 0.83	0.865
Tcs	2	-0.03	-0.51 to 0.47	3	-0.33	-0.99 to 0.22	0.073
Mos	3	-0.02	-0.38 to 0.21	2	-0.02	-0.35 to 0.16	0.998
Mcs	4	-0.29	-0.96 to 0.70	5	-1.08	-1.85 to 0.31	0.000
Sc	5	-0.19	-0.58 to 0.04	4	-0.44	-0.73 to 0.18	0.778
Bb	6	-0.64	-1.32 to 0.11	6	-0.73	-1.22 to 0.46	0.140

<sup>a</sup> Comparison (2-sample t-test) of mean habitat rankings for individual vegetation classes between areas.

<sup>b</sup> Interquartile range

Figure 2.2. Boxplot of landscape-scale (i.e.,  $2^{nd}$ -order; Johnson 1980): habitat selection indices (a) and habitat availability (b) for 84 annual home ranges of 54 individual adult ( $\geq$ 1 yr) resident martens, southwestern Newfoundland, 1995-2000. Vegetation class descriptions as per Table 1; Ik = insect killed, Rf = regenerating forest, Tcs = tall closed softwood, Tos = tall open softwood, Mcs = medium closed softwood, Pct = precommercially thinned, Rc = recent cuts, Mos = medium open softwood, Sc = softwood scrub, Bb = bog and barren. Vegetation classes are displayed in rank order of relative preference from highest (Ik) to lowest (Bb). T is the Kruskal-Wallis test statistic. Selection indices > 0 indicate preference and values < 0 indicate avoidance; lower box boundary is the 25<sup>th</sup> percentile, line within the box marks the 50<sup>th</sup> percentile (median), and the upper box boundary is the 75<sup>th</sup> percentile. Whiskers below and above the box indicate the 10<sup>th</sup> and 90<sup>th</sup> percentiles, respectively.



median selection index centered on zero). Both scrub forest and bog and barren classes had lower selection values relative to mature and overmature forest, and generally were avoided. Surprisingly, medium closed softwood habitat ranked 2<sup>nd</sup> lowest in relative preference and below the selection index for scrub. However, medium closed softwood was uncommon on the study area (i.e., lowest landscape-scale availability of my six habitat classes) and had the greatest variation (range) in selection indices across animals. Consequently, my measure of selection and relative preference for this class is uncertain. I suspect where available on the landscape, medium closed softwood habitat would be used proportional to its availability.

Landscape-scale selection indices for my 4 rare habitat types (i.e., overmature insect-killed stands (Ik), recent cuts  $\leq$  5-years old (Rc), young regenerating forest  $\leq$  6.5 m (Rc), and precommercially thinned stands (Pct)) suggested that young regenerating forest was selected for (Sign test; P = 0.006). I had insufficient evidence to conclude that the Ik, Rc, or Pct were selected disproportionate to availability on the landscape (P > 0.18; Table 2.4)

Martens occupied home ranges not dominated by mature and overmature forest conditions. The median occurrence of mature and overmature forests (Tcs + Tos + Ik) within home ranges (i.e., landscape-scale measure of habitat use) occupied by resident, adult ( $\geq 1$  yr) martens was only 30.0% (range 10.7-75.6%; Figure 2.3). Seventy-five percent of martens had <36% mature and overmature types within their home ranges and 90% had  $\leq 45.2\%$ . Tall closed softwood stands (Tcs), which were previously hypothesized to be the most preferred marten habitat, did not receive the highest selection at the landscape-scale, and comprised only 12.5% of resident martens home ranges; 75%

Table 2.4. Results of landscape-scale selection analyses (non-parametric Sign Tests) for 4 rare ( $\leq$ 5% median availability) vegetation classes. Vegetation class descriptions as per Table 1; Rf = young regenerating forest, Ik = overmature insect-killed stands, Rc = recent cuts  $\leq$  5 years old, and Pct = precommercially thinned stands. Analyses based on data for 54 individual (29 males, 25 females) adult ( $\geq$ 1 yr), resident martens representing 84 marten years (40 males and 44 females), southwestern Newfoundland, 1995-1997.

Vegetation Class				
Rf	Rc	Ik	Pct	
55	19	40	35	
29	16	31	48	
84	35	71	83	
0.006	0.735	0.342	0.188	
	Rf 55 29 84 0.006	Rf Rc   55 19   29 16   84 35   0.006 0.735	Vegetation Class   Rf Rc Ik   55 19 40   29 16 31   84 35 71   0.006 0.735 0.342	

<sup>a</sup> Total number of landscape-scale selection indices calculated for each vegetation class.



Figure 2.3. Boxplot of habitat availability within the home range for vegetation classes with high relative preference (positive selection or proportional use; i.e., Ik, Tcs, Tos, Mcs, Pct, Rf, Rc), avoided vegetation classes (i.e, Mos, Sc, Bb) and mature and overmature vegetation classes (i.e., Ik, Tcs, Tos) for 92 annual home ranges of 54 individual adult ( $\geq 1$  yr), resident martens, southwestern Newfoundland, 1995-1999. Lower box boundary is the 25<sup>th</sup> percentile, line within the box marks the 50<sup>th</sup> percentile (median), and the upper box boundary is the 75<sup>th</sup> percentile. Whiskers below and above the box indicate the 10<sup>th</sup> and 90<sup>th</sup> percentiles, respectively.

of home ranges were comprised of <20.1% Tcs and 90% had < 34.0% Tcs. Although the Tcs, Tos, and Ik classes were based on height criteria (> 12.6 m), height was a reliable surrogate of age. Eighty-four percent of marten locations in those 3 classes were in stands categorized as > 80-years old.

#### **Stand-scale habitat availability**

Only 38 of the 92 (41%) home ranges included all habitat classes, with most home ranges having little or no availability for 1 or more habitat classes. Median habitat availability was < 3% for 4 of my 10 habitat classes (insect-killed, recent cuts, precommercially thinned and medium height open-canopy softwood; Figure 2.4).

### **Stand-scale habitat selection**

After screening for low (< 2.0) expected values and missing habitat classes, I calculated 458 selection indices out of a possible 920 (10 types x 92 home ranges); no animals provided SI for all 10 possible habitat classes. Use of habitat classes did not differ between sexes ( $F_{1,8} = 1.16$ , P = 0.32) or among animals inhabiting areas open or closed (PMSA) to snaring and trapping ( $F_{1,8} = 1.20$ , P = 0.30); therefore, sex and exposure to snaring and trapping were dropped as explanatory covariates for subsequent analyses. At the stand scale, martens did not use habitat classes in proportion to their availability (T = 75.6, n = 458, P < 0.0001; Figure 2.4). Martens displayed selection for insect-killed stands (Ik; median use/availability ratio of 1.46; one-sided Sign test, P = 0.054, n = 25) and avoidance of medium-height, open-canopied softwood (Mcs; P < 0.000, n = 75), coniferous scrub (Sc; P < 0.000, n = 43), and bog and barren (Bb) vegetation types (P < 0.000, n = 68). The 6 remaining habitat classes (ordered by

Figure 2.4. Boxplot of stand-scale (i.e.,  $3^{rd}$ -order; Johnson 1980): habitat selection indices (a) and habitat availability (b) for 92 annual home ranges of 58 individual adult ( $\geq 1$  yr) resident martens, southwestern Newfoundland, 1995-2000. Vegetation class descriptions as per Table 1; Ik = insect killed, Rf = regenerating forest, Tcs = tall closed softwood, Tos = tall open softwood, Mcs = medium closed softwood, Pct = precommercially thinned, Rc = recent cuts, Mos = medium open softwood, Sc = softwood scrub, Bb = bog and barren. Vegetation classes are displayed in rank order of selection from highest (Ik) to lowest (Bb). *T* is the Kruskal-Wallis test statistic. Selection indices > 0 indicate preference and values < 0 indicate avoidance; lower box boundary is the 25<sup>th</sup> percentile, line within the box marks the 50<sup>th</sup> percentile (median), and the upper box boundary is the 75<sup>th</sup> percentile. Whiskers below and above the box indicate the 10<sup>th</sup> and 90<sup>th</sup> percentiles, respectively.



decreasing relative preference) including regenerating forests (Rf), tall closed softwood (Tcs), tall open softwood (Tos), medium closed softwood (Mcs), precommercially thinned forest (Pct), and recent cutovers (Rc), were used in proportion to their availability within the home range (Figure 2.4).

I explored whether seasonal variation in habitat use was a factor in my habitat selection results (Buskirk and Powell 1994). To begin, I coded all telemetry points (n = 2,271) used to generate my home ranges as either summer (snow-free period of May 1 – 30 November) or winter (1 December – 30 April) locations and calculated the percent of seasonal use observed in each of my 10 habitat classes. I used Chi-square ( $X^2$ ) analysis to test if habitat use was independent of season. Seasonal distribution of locations did not differ across my 10 habitat types between summer and winter ( $X^2 = 11.53$ , df = 9, P = 0.24; Table 2.5).

### **Performance of Martens in Relation to Mature and Overmature Forest**

Median availability of mature and overmature forests for animals with low, medium, and high availability was 20.7%, 30.0% and 41.5%, respectively. Year-class age distributions were not different ( $X^2 = 4.489$ , df = 8, P = 0.81) among classes. Similarly, daily survival of martens was not positively correlated with increasing stand-scale availability for mature and overmature forests ( $r_s = -0.04$ , P > 0.5).

### A Priori Habitat Questions

I evaluated 7 *a priori* questions concerning habitat selection and relative preference at 2 spatial scales (i.e.,  $2^{nd}$  - and  $3^{rd}$  -order habitat selection; Johnson 1980; Table 2.6). In general, comparisons of relative preference between pairs of habitat classes (predictions 1-11; Table 2.6) indicated similar patterns of habitat selection by martens across spatial Table 2.5. Seasonal comparison of vegetation class use by Newfoundland martens during summer and winter for 58 individual (31 males, 27 females) adult (≥ 1 yr), resident marten (92 marten years) located 2,271 times in southwestern Newfoundland, Canada, 1995-1999.

Habitat Class	Summer <sup>a</sup>	% Summer Locations <sup>b</sup>	Winter	% Winter Locations <sup>c</sup>	Total
Bog / Barren	142	9.1	53	7.4	195
Insect-killed	131	8.4	56	7.9	187
Cutover	61	3.9	38	5.3	99
Medium Closed Softwood	107	6.9	33	4.6	140
Medium Open Softwood	198	12.7	99	13.9	297
Precommercially Thinned	109	7.0	61	8.6	170
Regenerating Forest	165	10.6	77	10.8	242
Scrub	102	6.5	44	6.2	146
Tall Closed Softwood	324	20.8	160	22.5	484
Tall Open Softwood	220	14.1	91	12.8	311
Totals	1559		712		2271

<sup>a</sup> Summer was defined as the snow-free period (i.e., 1 May-30 November); winter was defined as 1 December-30 April.

<sup>b</sup> Percent of summer (1 May-30 November) locations observed in habitat class.

<sup>c</sup> Percent of winter (1 December-30 April) locations observed in habitat class.

Table 2.6. Twelve predictions tested to evaluate 7 *a priori* questions related to habitat selection by 58 individual (31 males, 27 females) adult ( $\geq$  1 yr), resident endangered Newfoundland martens at the stand- (i.e., 3<sup>rd</sup> -order; Johnson 1980) and landscape-scales (i.e., 2<sup>nd</sup> -order; Johnson 1980), southwestern Newfoundland, Canada, 1995-1999.

Habitat Question	Prediction <sup>a</sup>	Stand	Landscape
1) When does a conifer-dominated stand	Tcs is used more than Mcs (1)	No, $n = 87^{b}$ , $P = 0.125$	Yes, n = 168, P = 0.004
become marten habitat and what are the	Tcs is used more than Rf (2)	No, n= 110, P = 0.470	No <sup>c</sup>
breaks in the forest height continuum?	Rf is used more than Rc (3)	Yes, n= 65, P = 0.057	Yes <sup>d</sup>
2) Do Newfoundland marten select old-	Tcs is used more than Mcs (1)	No, n = 87, P = 0.125	Yes, n = 168, P = 0.004
growth forest above all other forest types?	Tcs and Ik are used equally (4)	No, n = 92, P = 0.031	Yes <sup>e</sup>
	Tcs is used more than Tos (5)	No, n = 135, P = 0.386	No, n = 168, P < 0.999
	Tos is used more than Mos (6)	Yes, n = 142, P = 0.004	Yes, n = 168, P < 0.000
3) What are the effects of canopy and the	Tcs is used more than Mcs (1)	No, n = 87, P = 0.125	Yes, n = 168, P = 0.004
interaction of canopy and height on use of	Tcs is used more than Tos (5)	No, n = 135, P = 0.386	No, n = 168, P = 0.999
stands by marten?			

Habitat Question	Prediction <sup>a</sup>	Stand	Landscape
4) Are young regenerating forests on	Rf is used more than Sc (7)	Yes, n = 86, P = 0.000	Yes <sup>f</sup>
productive sites used more than scrub forests			
on poor-quality sites?			
5) Are bogs, recent cuts, and scrub selected	Rc and Bb are used equally (8)	No, n = 90, P = 0.005	No <sup>g</sup>
differently?	Sc and Bb are used equally (9)	No, n = 111, P = 0.082	Yes <sup>h</sup>
6) Are insect-killed stands used comparably	Tcs and Ik are used equally (4)	No, n = 92, P = 0.031	Yes <sup>e</sup>
to mature conifer stands regardless of canopy	Tos and Ik are used equally (10)	No, n = 91, P = 0.018	No <sup>i</sup>
closure density?			
7) Are precommercially thinned stands used	Pct and Rf are used equally (11)	Yes, n = 70, P = 0.184	No <sup>j</sup>
equally to young regenerating forest?			

<sup>a</sup> Several predictions are consistent with > 1 habitat question; predictions 1 to 7 are one-sided tests.

<sup>b</sup> Number of selection indices pooled between habitat classes

<sup>c</sup> Rf selected for at the landscape level (Sign test, P = 0.006); Tcs used proportionally (Sign test, P = 0.585).

Table 2.6 Continued.

<sup>d</sup> Rf is selected for at the landscape level (Sign test, P = 0.006); Rc used proportionally (Sign test, P = 0.735)

<sup>e</sup> Ik and Tcs both used proportionally at landscape level.

<sup>f</sup> Rf is selected for at landscape scale (Sign test, P = 0.006); Sc is avoided (Sign test, P = 0.003).

<sup>g</sup> Rc used proportionally at landscape level (Sign test, P = 0.735); Bb is avoided (Sign test, P < 0.000).

<sup>h</sup> Bb and Sc are avoided at landscape level (Sign test,  $P \le 0.003$ ); Rc used proportionally (Sign test, P = 0.735).

<sup>i</sup> Tos is selected for at landscape level (Sign test, P < 0.000); Ik used proportionately (Sign test, P = 0.342).

<sup>j</sup> Rf is selected for at landscape scale (Sign test, P = 0.006); Pct used proportionately (Sign test, P = 0.188).

scales. Overall, there was little evidence to support the paradigm that Newfoundland martens prefer overmature forests relative to all other available forest types (question #2, predictions 1, 4, 5, 6, Table 2.6). Tall ( $\geq$  12.6 m) closed softwood (Tcs) stands were selected over medium (6.6-12.5 m) closed stands at the landscape-scale, but not at the stand scale; both types were used in proportion to availability (P = 0.125) at the stand scale. Notably, Mcs had low landscape-scale availability (Figure 2.2), thus the selection results for that class may be equivocal at the landscape-scale. Insect-killed (Ik) stands were selected over Tcs at the stand-scale, but both types were used in proportion to their availability at the landscape-scale. Further, tall-open (canopy closure < 50%) softwood stands were selected similarly to Tcs at both the stand and landscape-scales. Higher relative preference for taller stands was suggested by greater selection for Tos stands compared to medium-open stands (Mos) at both the stand- and landscape-scales. However, young regenerating forests (Rf) were selected for by martens at the landscapescale (Sign test, P = 0.006), whereas Tcs was used proportional to availability (Sign test P = 0.585) at that scale. At the scale of the stand, selection indices for Rf and Tcs did not differ (Fisher's LSD test, P = 0.470; question #1, prediction 2, Table 2.6). Martens did not select for mature forest stands with closed canopies relative to similar-height stands with more open canopies. Selection indices for Tcs were not greater (one-sided test) than for Tos at the stand- (Fisher's LSD test, P = 0.386) or landscape- (P = 0.999) scales (question #3, prediction 5, Table 2.6).

The paradigm that martens avoid young regenerating forests was not supported by my results. The selection index for the Rf class was higher than for Tcs (prediction 2,

Table 2.6) and Tos (Figure 2.2) at the landscape-scale. At the stand-scale, Rf ranked second only to Ik (Figure 2.4) and was not significantly different from the selection index for Tcs stands (prediction #2, Table 2.6). Although my Rf class included 2 height categories (height class 1 = 0.3.5 m, height class 2 = 3.6-6.5 m), 99.2% (n = 242) of radiolocations observed in the Rf class were in stands > 3.5 m. Thus, I suggest a cautionary approach and consider that my results indicating high relative preference for regenerating stands are applicable only to stands > 3.5 m in height.

Recent cuts (Rc) had lower selection indices at the stand-scale than the Rf class (question #1, prediction 3; Fisher's LSD test, P = 0.057; Table 2.6). At the landscape-scale, Rc was used in proportion to availability (Sign test, P = 0.735), whereas Rf was selected for (Sign test, P = 0.006) by martens. Although martens used Rc at both scales, that class had lower relative preference than Rf, which was characterized by higher tree heights, stocking densities, and overhead cover. Both Rc and scrub forests (Sc), which occurred on poor quality sites, were selected over bogs and barrens (Bb) at the stand-scale (question #5, predictions 8, 9; Table 2.6; Fisher's LSD test, P < 0.082). At the landscape-scale, Rc was used proportionate to availability (Sign test, P = 0.735), whereas Sc and Bb were avoided (Sign test, P < 0.003) by martens.

Despite their low canopy cover and general absence of live overstory, Ik stands had the highest relative preference at the stand-scale (Figure 2.4). The Ik stands were used proportionate to availability at the landscape-scale (Figure 2.2), and had stand-scale selection indices that were not different from Tcs (question #5, prediction 4, Table 2.6; Fisher's LSD test, P = 0.031). Selection for Ik exceeded the indices documented for Tos stands at the stand-scale (question #5, prediction 10, Table 2.6; Fisher's LSD test, P = 0.018); at the landscape-scale Ik was used proportional to availability (Sign test, P = 0.342), whereas Tos stands were selected for (Sign test, P < 0.000) by martens.

Lastly, I had insufficient evidence to conclude that stand-scale selection indices differed between regenerating stands that had been precommercially thinned (Pct) and those that were not thinned (Rf) (question #7, prediction 11, Table 2.6; Fisher's LSD test, P = 0.184). At the landscape-scale, Pct was used proportionate to availability (Sign test, P = 0.188), whereas, Rf was selected for (Sign test, P = 0.006) by martens.

## DISCUSSION

#### **Habitat Associations**

#### Landscape-scale

Resident adult martens on the study area established territories composed of a broad range of vegetation types. In contrast, previous studies of habitat relationships of Newfoundland martens (Snyder and Bissonette 1987, Bissonette et al. 1988, 1989, Drew 1995, Thompson 1991, Thompson and Curran 1995, Sturtevant et al. 1996, Bissonette et al. 1997, Sturtevant and Bissonette 1997) concluded that mature and overmature coniferous forests were a strict habitat requirement. Mature and overmature coniferous stands did not dominate the composition of home ranges and accounted for  $\leq 35\%$  of the home ranges for 75% (n = 92) of the adult resident martens that I monitored. Further, mature and overmature forest comprised <50% of the home ranges for 94% of my adult resident martens. Martens did not select for home ranges dominated by mature and overmature coniferous forests over other forest classes, including mid-successional and young regenerating softwood forests. Further, martens occupying home ranges dominated by mature and overmature forest did not exhibit higher survival rates. Finally, age distributions were not different among martens with high, intermediate, and low amounts of mature and overmature forest in their home range. In other words, my results do not indicate that martens on my study site with home ranges composed of little mature and overmature forest were compromising their fitness; no evidence was apparent of an "ideal dominance" distribution (Fretwell and Lucas 1970), or that animals occupying territories dominated by mature and overmature forest benefited from "superior" habitats (Thompson 2004).

At the landscape scale (i.e.,  $2^{nd}$ -order selection; Johnson 1980), martens selected for or proportionally used almost all forest classes including mature and overmature forest, closed-canopied, mid-successional stands, regenerating forest > 3.5m, precommercially thinned regenerating forests, and recent cuts when choosing where to position their home range. Closed-canopied, mid-successional forest, scrub forest < 6.6 m, and bogs and barrens were selected against relative to their availability in the landscape when martens established home ranges; however, these classes still represented substantial portions of home ranges of adult martens. Median home-range availability for these avoided classes was 28.1% (range = 4.7-54.3%).

My results indicate that Newfoundland martens occupy home ranges composed of a much wider array of habitat classes than has previously been hypothesized. In fact, martens occupied home ranges with little mature and overmature forest and did not select for areas dominated by those classes when establishing home ranges. Comparable or higher selection for regenerating forest relative to Tcs stands at both scales suggests that Newfoundland martens are more generalist in their habitat preferences than previously hypothesized. I conclude that a variety of forest age, stocking, and successional classes

are suitable for home range occupancy by Newfoundland martens and that these types, in aggregate, determine probability of home-range occupancy across the landscape. This conclusion has been further supported in companion studies that evaluated thresholds of home-range occupancy useful for predicting landscape-scale occupancy by martens (Fuller 2006).

# Stand-scale

Within their home ranges, resident adult martens selected for or proportionally used all forested classes, including mature and overmature forest, closed-canopied midsuccessional stands, regenerating forest > 3.5 m, precommercially thinned regenerating forests, and recent ( $\leq$  5 years) cuts, with the exception of open-canopied mid-successional softwood stands, which were avoided. Martens exhibited avoidance of only medium open softwood stands, low (< 6.6 m) scrub forest and nonforested habitats (i.e., bogs and barrens) at the stand-scale.

My results generally agree with recent habitat selection studies indicating that forests need not be "overmature" to provide suitable habitat for American martens (Katnik 1992, Payer 1999, Potvin et al. 2000, Poole et al. 2004, Fuller and Harrison 2005). In Maine, American martens utilized a wide range of forest conditions, and exhibited similar selection indices for a variety of mature, second-growth stands, including conifer, mixed, and deciduous classes (Katnik 1992, Payer 1999). Whereas those researchers did not detect significant selection against immature forests 6-9 m in height, martens in Maine strongly selected against regenerating clearcuts <6 m in height (Katnik 1992, Payer 1999, Fuller and Harrison 2005). My results are consistent with
Chapin et al.'s (1997) and Payer and Harrison's (2003) conclusions that forest structure, rather than forest age *per se*, determines stand-scale habitat suitability for martens.

My results show even stronger agreement with those reported by Potvin et al. (2000) for American martens in second-growth boreal forests in Quebec where no selection (i.e., proportional use) of coniferous habitats, including, overmature (> 80 years), mature (60-80-years old), immature (30- 60-years old), and recent (<4 years) clearcuts with dense regeneration was reported. Within established territories, I documented high use (positive selection or proportional use) of regenerating softwood forests and recent cuts. This finding is inconsistent with previous conclusions for Newfoundland martens, but is consistent with results published by Potvin et al. (2000) for American martens. Contrary to results reported by Snyder and Bissonette (1987), my findings suggest that Newfoundland martens do not avoid forest stands recently (<20 years) altered by logging; martens also did not avoid regenerating stands that had been precommercially thinned. I suspect that the substantial use of younger-aged forests exhibited by martens in this study is directly related to the ability of regenerating forests to support prey for martens, in particular snowshoe hare (*Lepus americanus*), and to reduced necessity to seek escape cover from mammalian predators (i.e., fisher (*Martes pennanti*), coyotes (*Canis latrans*)) in the depauperate faunal landscape of Newfoundland (Dodds 1983, Hearn et al. 2006).

Only 3 of my 10 vegetation classes (i.e., poorly-stocked-mid-successional-softwood, scrub forest, and bog-barren) did not receive proportional use or positive selection by martens at the stand-scale. These results are inconsistent with previous research (Snyder and Bissonette 1987, Bissonette et al. 1988, 1989, Drew 1995, Thompson 1991, Thompson and Curran 1995, Sturtevant et al. 1996, Bissonette et al. 1997, Sturtevant and

Bissonette 1997) and the presumed stand-scale habitat requirements for overmature forest by Newfoundland martens. I conclude that the stand-scale guidelines currently being used to manage marten habitat in Newfoundland are too narrowly defined.

# **Historical Considerations**

The differences in conclusions reached in this study versus previous studies regarding the habitat requirements of Newfoundland martens are likely attributable to the history of the spatial decline and range contraction of this island population. During the early 1900's, excessive harvesting resulted in the decline and extirpation of furbearer populations, in particular martens, throughout North America (Yeager 1950, de Vos 1951, Hagmeier 1956, Quick 1956, Strickland and Douglas 1981, Gibilisco 1994, Krohn et al. 1994, Strickland 1994). A similar history of decline during this same period was documented for the marten (Bangs 1913, Dodds 1983) and other species in Newfoundland; the Newfoundland wolf was extirpated between 1910 and 1923 (Allen and Barbour 1937); beaver (*Castor canadensis*) were nearly eliminated (Cameron 1958, Payne 1975); and caribou (*Rangifer tarandus*), lynx (*Lynx canadensis*), and otter (*Lutra canadensis*) populations were reduced so that harvest seasons were closed (Dodds 1983).

By the mid 1950's, the distribution and habitat occupancy of martens in Newfoundland was restricted to the inaccessible areas of mature and overmature timber remaining on the island (Bergerud 1969) where forest harvesting was absent, human access was limited due to the lack of roads, and overexploitation by trappers was precluded by poor access. Thus, the co-occurrence of martens with areas of mature and overmature forest types, by default, defined the scope of observed habitat use.

Logically, the earliest work on martens in Newfoundland sought to understand the mechanisms behind this apparent habitat restriction (Snyder 1984, Snyder and Bissonette 1987, Bissonette et al. 1989, Tucker 1988, Frederickson 1990, Drew 1995, Thompson and Curran 1995, Sturtevant et al. 1996, Sturtevant and Bissonette 1997). By necessity, essentially all of this earlier work was conducted on the only substantial population of martens remaining on the island within the core of the PMSA, an area dominated by inaccessible overmature softwood forests or very recent cuts (which had low relative preference in the present study). Based on the insecurity of marten habitat outside of the PMSA (i.e., open to trapping and snaring), and the premise that martens would occur in uncut softwood-dominated areas, study areas were restricted in size and few adult resident martens were monitored. I conclude that the limited range of forest age classes represented within the PMSA reduced the range of forest conditions available for martens to occupy; therefore, providing limited inferences to past researchers regarding the range and quality (i.e., fitness; Thompson 2004) of habitat suitable for use and occupancy.

Unfortunately, remnant populations of an endangered species do not always find refuge in habitats of highest quality (i.e., highest individual fitness), but often persist in habitats where the original cause of the decline (e.g., trapping and snaring) is excluded (Caughley and Gunn 1996). Lomolino and Channel (1995, 1998) reported that endangered species often occur near the periphery of their former ranges. Because the periphery of a species' range typically represents less than optimal conditions, studies of habitat use by these populations can be misleading (Caughley and Gunn 1996). As pointed out by Van Horne (1983), many factors define habitat, and habitat suitability and habitat quality should not be inferred from simple occupancy.

The incompleteness of past assessments of habitat associations of Newfoundland martens was further suggested during my first year of work within the RIL region of the study area. Despite local expert opinion that marten habitat suitability there was marginal due to lack of mature and overmature coniferous stands, 17 adult ( $\geq 1$  yr) resident martens were captured during the first 4 days of trapping in 1996. Subsequent fieldwork over the next 3 years captured a total of 93 martens in this region of the study area and confirmed breeding of an adult resident marten population displaying multi-year occupancy of home ranges (Chapter 1), and multi-year survival (Chapter 3). Many of those individuals were included in the data reported herein.

### **Factors Affecting Local Habitat Associations**

Newfoundland martens are a genetically distinct population operating outside a relatively genetically homogeneous population of American martens occupying mainland Canada (Kyle and Strobeck 2003). The Newfoundland population has been geographically and reproductively isolated from mainland populations for the last 7,000 years (South 1983). By comparison, Newfoundland martens are large (mean body weight of males = 1,275 g, n = 40; Chapter 1) when compared to martens from nearby mainland populations in Quebec (males = 937 g, n = 67, Potvin and Breton 1997) and Maine (males = 808 g, n = 134; Chapter 1). Further, martens in Newfoundland have disproportionately large home ranges (males = 27.6 km<sup>2</sup>, n = 43; Chapter 1) when compared to Quebec (males = 7.4 km<sup>2</sup>, n = 40; Potvin and Breton 1997) and Maine (males =  $3.8 \text{ km}^2$ , n = 135; Chapter 1), and elsewhere throughout the North American range (Buskirk and McDonald 1989). I suspect these ecological attributes are a direct consequence of the historical setting in which the Newfoundland population evolved,

including a depauperate mammalian community composed of a disproportionate number of predators, few prey species, and only 1 native vole (Dodds 1983, Hearn et al. 2006).

My results indicate that marten in Newfoundland position and maintain territories in a highly, naturally fragmented landscape; more than 50% of martens had home ranges composed of > 42% avoided vegetation classes (i.e., Bb, Sc, Mos). Further, results from a companion study contrasting landscape composition and configuration indicated that Newfoundland marten occupy landscapes with much lower landscape availability of suitable habitat (32%) versus marten in Maine (51%) and initially are much less sensitive to low levels of habitat loss (Fuller 2006).

# Habitat-Selection and Food

Many factors such as sex, age, season, reproductive status, and body size, affect the size of an animal's home range (Harestad and Bunnell 1979, Phillips et al. 1998, Payer 1999, McLoughlin and Ferguson 2000, Poole et al. 2004). Habitat productivity or variation in food availability, however, is likely the most important factor affecting territoriality and home-range size within carnivores (Lindstedt et al. 1986, Powell 2000, McLoughlin and Ferguson 2000), including martens (Thompson and Colgan 1987). Bateman (1986) reported that the meadow vole was the main small mammal prey for Newfoundland martens; subsequently, previous researchers (Thompson and Curran 1995, Sturtevant et al. 1996, and Sturtevant and Bissonette 1997) have hypothesized an "obligate association" of Newfoundland martens with overmature softwood because of its higher habitat quality (density) for meadow voles. I suspect this conclusion places too much emphasis on voles as the principle food resource for Newfoundland martens and hence, the importance of overmature softwood.

Recent data on the diet of Newfoundland martens based on 704 samples (679 scats; 25 stomach contents) indicate that, although Newfoundland martens utilize meadow voles extensively (80% frequency of occurrence in summer scats; n = 400), meadow voles occurred in only 47% of scats during winter (n = 236; Gosse and Hearn 2005). Further, frequency of occurrence of snowshoe hares in the diet of Newfoundland martens increased 10-fold from 2.8% in summer to 28% in winter. Cumberland et al. (2001) equated a 31% frequency of occurrence of larger prey (i.e., 8% snowshoe hare, 12% grouse, and 10.8% red squirrel (Tamiasciurus hudsonicus)) to 95% of the caloric intake by martens in New Brunswick. Large prey, such as hares, are more easily digested and have a higher metabolizable energy per unit volume than mice and voles (Zielinski 1986).

Gosse and Hearn (2005) concluded that hares may be a vital food resource for Newfoundland martens during the critically-limiting winter season (Thompson 1986, Buskirk et al. 1988). Snowshoe hare densities, and overall prey biomass, reported by Thompson and Curran (1995) for 40-year-old semi-mature stands were 7-8 times higher than in 60-year-old mature stands, and 22-23 times higher than in 81+-year-old overmature stands (my calculations). The higher relative prey biomass in regenerating forests stands may explain the relatively high selection of those classes by martens during this study. The difference in caloric value between a 30 g (n = 45; B. J. Hearn, unpublished data) meadow vole and a 1300-1400 g (Joyce 2001) snowshoe hare (Poole and Graf 1996, Cumberland et al. 2001), coupled with higher hare densities in younger forests, likely explains why Newfoundland martens use regenerating forests extensively. Notably, harvests of American martens in Canada are historically synchronized with snowshoe hare numbers (Bulmer 1974, Fryxell et al. 1999); at the stand scale, snowshoe

hare densities are greatest in younger ( $\leq 10-30$  years), dense-conifer stands (Parker 1986, Thompson 1988, Hodges 2000).

Low vole densities across all forest types in Newfoundland may also reduce the relative profitability of voles to martens. Although, vole densities reported by Thompson and Curran (1995) and Sturtevant and Bissonette (1997) were highest in overmature stands, densities were exceptionally low in all forest types, ranging from only 0.01 to 0.54 snap-trap captures per 100 trap-nights (Thompson and Curran 1995). I hypothesize that Newfoundland martens feed by searching for large prey while capturing smaller prey opportunistically, as reported for martens in Ontario (Thompson and Colgan 1990). Thus, it seems unlikely that overmature forests would provide the most suitable habitat conditions, particularly in winter when martens are most energetically stressed (Buskirk and Harlow 1989) and prevalence of hares increases in the diet (Thompson and Colgan 1990).

Thompson and Colgan (1991) estimated that, based on energetics, martens in Ontario could not survive exclusively on small rodents during late winter. If, as suggested, habitat preferences of mustelids parallel those of their prey species (Zielinski et al.1983, Buskirk and MacDonald 1989, Buskirk and Powell 1994, Lode 1994) and if martens forage to maximize captures of large prey (Thompson and Colgan 1990, 1991), I view it as unlikely that mature and overmature coniferous forests can be considered a strict habitat requirement for Newfoundland martens.

# **Predator Avoidance**

Avoidance of avian and mammalian predators has been proposed as a significant selective pressure to explain why American martens are associated with mature closed-

canopy forests, avoid areas without overhead cover (Hawley and Newby 1957, Herman and Fuller 1974, Pulliainen 1981, Spencer et al. 1983, Hargis and McCullough 1984, Buskirk and Powell 1994), and are restricted to stands with many large trees where they can use their arboreal ability for escape (Hodgman et al. 1997, Payer and Harrison 2003). While predation risk may be a dominant habitat selection pressure elsewhere, Newfoundland martens contend with relative few potential predators. Thus, Newfoundland martens may have experienced ecological release (Whittaker 1998) from this selective pressure that has allowed them to expand their habitat use into areas with greater prey densities, but less secure cover, relative to mainland populations of American martens.

Fishers, which are an important natural predator of martens (Hodgman et al. 1997, Krohn et al. 1995, Krohn et al. 1997, Payer 1999), are absent in Newfoundland (Dodds 1983). Further, lynx or their tracks were not observed on the study area during 5 years of extensive aerial and ground fieldwork and were not suspected in any mortality observed during the study (Chapter 3). Similarly, coyotes or their tracks, were also rarely observed (n < 5) during the study. Likewise, avian predators capable of taking martens are generally uncommon in southwestern Newfoundland when compared to mainland North America (Gosse and Montevecchi 2001), and were not implicated in the deaths of any radio-marked individuals (Chapter 3). Red foxes (*Vulpes vulpes*) were common on the study area and were the most common natural predator of martens during this study (Chapter 3).

I suggest that, given the relatively few predators of martens in Newfoundland, predator avoidance may not have been as significant a factor in shaping habitat

associations as in populations of American martens studied elsewhere. This may allow martens to utilize a wider range of forest conditions, while meeting their needs for escape cover. Consequently, stands of limited height but with closed canopies, or recent cuts with dense regeneration and/or abundant woody debris might be sufficient for martens to minimize the risk of mammalian and avian predation. Niche expansion in the absence of competitors and predators, coupled with higher prey availability in regenerating stands, may partially explain the substantial use of younger-aged forests by martens during this study.

# CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Past studies of habitat selection concluded that Newfoundland martens were more dependent on old-growth coniferous forests than populations of American martens inhabiting mainland North America. Those findings were not supported by my results. To the contrary, martens in Newfoundland utilized a broad range of forest-stand conditions and displayed use of a wider range of forest-stand types than previously suggested for *M. a. atrata* in Newfoundland or for *M. a.* elsewhere in North America.

This multi-scale assessment of habitat selection by martens in Newfoundland suggests that habitat associations are broader and more complex than previously documented and that habitat quality for martens does not necessarily equate with the extent and degree of maturity of conifer-dominated stands. Mature and overmature forests accounted for  $\leq 35\%$  of the home-range composition for 75% of the martens in this study, with no indication that individual fitness was compromised.

I conclude that the depauperate prey base, and specialized habitat requirements of available prey (Thompson and Curran 1995, Sturtevant et al. 1996, Sturtevant and

Bissonette 1997, Bissonette et al. 1997) combined with the limited number of potential predators on the island, has broadened, rather than constrained, the habitat choices made by Newfoundland martens. Habitat for any terrestrial species is not simply a set of specific cover types (Patton 1992, Hall et al. 1997), but a concept that describes a particular combination of resources (e.g., food, vegetation types) and environmental conditions (e.g., temperature, presence or absence of predators and competitors, spatial arrangement of resources) that in concert, determines the suitability of an environment for individuals (Van Horne 1983, Hall et al. 1997, Garshelis 2000). I conclude that a wide range of forest habitat conditions may be suitable for use and occupancy by Newfoundland martens if martens are protected from human-related causes of mortality; trapping and snaring were the primary causes of marten mortality outside of the PMSA (Chapter 3).

Newfoundland martens appear capable of utilizing a mix of forest conditions that, in aggregate, determine patterns of habitat use and occupancy. From a management perspective, my results suggest that current habitat interpretations for martens in Newfoundland are overly conservative. More importantly, my results indicate that a much broader range of stands are potentially used by martens in Newfoundland than previously thought. I recommend that areas managed for marten occupancy at the scale of the home range should include > 30% mature and overmature (Tcs + Tos + IK) forest, which represented the median value observed for martens during my study. Second, my results should not be simplified and interpreted to suggest that landscapes composed solely of regenerating forests, precommercially thinned forests, and recent cuts are sufficient to allow occupancy by resident martens. Median representation of

precommercially thinned forests, regenerating forests, and recent cuts within home ranges of adult resident martens was < 1.0%, 6.7%, and < 1.0% respectively and collectively these younger age classes had a median availability of 14.8% ( $75^{th}$  and  $90^{th}$  percentiles 29.25% and 36.5%, respectively). Thus, martens did not occupy landscapes comprised solely of younger-aged forests. I recommend that home-range size landscapes suitable for marten not contain > 30% younger-aged forest. Finally, companion research suggests that the percent of suitable habitat within the home range is the most important predictor of occupancy for martens in Newfoundland and that probability of occupancy declines in a non-linear fashion as suitable habitat falls 60% (Fuller 2006). Thus, areas managed for marten should ensure that home-range size landscapes maintain sufficient suitable habitat to ensure relatively high probability of occupancy (Fuller 2006).

The historical refugium for Newfoundland martens in the provincial wildlife reserve (i.e., Pine Marten Study Area; PMSA) where martens have previously been studied does not represent the full range of habitat conditions that this endangered population is capable of occupying. Recent restrictions on trapping and snaring have allowed resident adult animals to occupy, select for, and survive in a wider range of habitat conditions than exists in the central portion of the PMSA. The central portion of the PMSA is comprised primarily of mature and overmature forest classes (used in proportion to availability by martens during this study) and bogs and barrens (both classes were avoided by martens). Thus, a wider range of suitable habitat conditions exists outside of the central portion of the PMSA if martens are allowed to expand into these areas via conservative management of trapping and snaring mortality (Chapter 3).

Forest management on publicly-owned land in Newfoundland and designation of critical habitat for this endangered population may also need to be reconsidered in light of my findings. Maintenance of martens in landscapes where wood harvesting will be a dominant human activity will require forest-harvesting prescriptions that recognize the constraints already imposed by the highly-fragmented nature of the natural landscape (Chapter 1), while retaining stand- and landscape-scale habitat conditions within required limits. These limits will need to consider natural fragmentation, the presence of mature and overmature forest, the prevalence of younger forests, as well as the representation of avoided vegetation types, within landscapes managed for martens. Further, management of human-caused mortality for martens will need to ensure that populations can be maintained in currently occupied areas and established in new areas of potential habitat to allow the recovery of this provincially- and federally-listed endangered species.

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# CHAPTER 3: SURVIVAL AND CAUSE-SPECIFIC MORTALTIY OF ENDANGERED NEWFOUNDLAND MARTENS INSIDE AND OUTSIDE A WILDLIFE PRESERVE: IMPLICATIONS FOR RECOVERY ABSTRACT

The American marten (Martes americana) is a forest-dependent carnivore often associated with mature forest conditions. Recently-logged forests have been postulated to be suboptimal habitat and timber harvesting and the associated loss of mature and overmature timber has been postulated to reduce marten survival. However, martens are a highly valued furbearer and overexploitation (trapping) has also been implicated in the decline of marten populations following the construction of logging roads associated with forest harvesting. Past studies have suggested that the Newfoundland marten (M. a.*atrata*), an endangered population endemic to the island of Newfoundland, is habitat limited due to forest-harvesting operations and the loss of overmature (> 80-years old) coniferous forests. Furthermore, these studies have also suggested that the Newfoundland marten is more dependent on these forest types than populations inhabiting mainland North America due to the ecological setting for this island population (e.g., depauperate prey base). Newfoundland marten populations declined in the early 1900's due to overexploitation; however, populations have failed to recover since closure of the season in 1934. Currently, an unknown number of martens are incidentally killed in snares set for snowshoe hares (Lepus americanus) and traps set for furbearers other than marten each year, particularly in areas where forest harvesting has increased road access. I documented cause-specific mortality factors, and survival rates of a sample of radiocollared juvenile (n = 44) and adult (n = 122) marten inside and

outside a the Pine Marten Study Area (PMSA) wildlife reserve, and used an informationtheoretic approach to developed a suite of candidate models to assess how the survival of adult resident marten populations was influenced by variables indexing home-range habitat composition, and risk to human-related mortality related to road access from roads. I monitored survival of juvenile marten from October to April and developed a suite of candidate models to assess the timing and pattern of juvenile mortality. I documented 52 mortalities during the study; human-caused mortality accounted for 45.3% of overall mortality but 71.9% of mortality outside the reserve. Models best characterizing survival of adults indicated a strong positive additive effect of increased habitat availability within the home range, and increasing distance from roads where snowshoe hare (Lepus americanus) snaring and trapping of furbearers is legal. These models fit the observed data better that models associating marten survival solely with one or more habitat types purported to offer high survival value (overmature forest) or lower individual survival probability (recently-logged forest). Annual survival of adult martens was 0.83 for both males and females. Survival of juvenile marten from October to April was 0.76 for juveniles inside the reserve but only 0.51 for marten in areas open to snaring and trapping. Models describing juvenile survival suggested that increased juvenile mortality outside the reserve was coincident with the onset of the snaring and trapping season. Marten populations outside the PMSA are likely maintained by dispersal from the PMSA reserve or other untrapped regfugia. Recovery of this endangered population and recapture of this historical range will require prolonged positive growth from source populations; however, martens recolonizing historical range

must be protected from human-related sources of mortality to allow recovery of this species at risk.

# **INTRODUCTION**

The American marten (*Martes americana*) is a widely distributed forest carnivore inhabiting much of boreal North America from Alaska to Labrador (Hagmeier 1956, Strickland and Douglas 1987, Gibilisco 1994). Preferred habitat for martens has often been postulated to include features (e.g., complex physical structure, canopy closure) most commonly found in "old" forests (Thompson and Harestad 1994). These structural features have been considered important for predator avoidance (Herman and Fuller 1974, Pulliainen 1981, Hargis and McCullough 1984), access to prey (Sherburne and Bissonette 1984, Thompson and Colgan 1987, Thompson and Curran 1995, Sturtevant and Bissonette 1997), provision of maternal den sites (Bergerud 1969, Ruggiero et al. 1998) or thermoneutral resting sites (Buskirk et al. 1988, Taylor and Buskirk 1994).

Martens are a highly-valued furbearer (Archibald and Jessup 1984, Strickland and Douglas 1987), are vulnerable to overexploitation (Quick 1956, Strickland and Douglas 1987, Hodgman et al. 1994), and historically were eliminated from many areas of former range via overtrapping (Yeager 1950, deVos 1951, Hagmeier 1956). Nonetheless, the decline of marten populations in several regions has been directly attributed to the loss of preferred habitat via logging (Yeager 1950, Bergerud 1969, Dodds and Martell 1971, Thompson 1991, Thompson and Harestad 1994, Bissonette et al. 1989). Thompson and Colgan (1987) asserted that marten survival is compromised by habitat degradation when mature and overmature forests are logged, and that survival in cut (logged) areas is reduced, primarily via increased natural mortality via predation. The effects of timber

harvesting (and the attendant loss of older forests) on the survival of marten populations is confounded, however, when forest harvesting also increases human access via the construction of forest harvesting roads, which increase opportunities for exploitation via trapping. For example, trapping mortality accounted for 19 of 25 mortalities (76%) on Thompson and Cogan's (1987) study area in northcentral Ontario, but marten populations in both mature forest and logged areas were exploited via trapping. Moreover, losses to trapping were 3 times greater than losses to natural causes, with trapping mortality (81.2%, n = 11) actually higher on their mature forest sites than on their logged site (71.4%, n = 14). Further, their conclusion of increased natural mortality rates on logged sites forests was based on few deaths (i.e., n = 6) and hinged on a single mortality (4 deaths in logged forests and 2 deaths in uncut forests). Potvin and Breton (1997) also reported higher rates of mortality among martens on logged sections of their study area in comparison to their unharvested sites. But trapping was permitted on their unharvested (mature forest) areas, and was prohibited on their logged areas; thus trapping mortality on their unharvested sites may have been partially compensatory. The latter possibility is supported by the collective evidence from Hodgman et al. (1994) and Hodgman et al. (1997) which suggests that natural mortality is comparable or actually higher in untrapped areas dominated by mature forest conditions, and that differences in overall survival of marten in logged and unlogged areas are largely attributable to differences in access for trappers and to higher human-caused mortality (trapping) where logging and forest roads are prevalent. Finally, Payer (1999), who simultaneously evaluated the effects of timber harvesting and trapping on marten on 3 forest-management scenarios (i.e., an untrapped forest reserve dominated by mature forests, an untrapped, extensively

clearcut industrial forest, and a trapped, extensively clearcut industrial forest), found no differences in natural mortality rates between his 3 forest-management treatments, suggesting that trapping mortality on his trapped industrial forest site was largely additive.

The endangered Newfoundland marten is a genetically-distinct population (*Martes americana atrata*) of the American marten (Kyle and Strobeck 2003) restricted to the island of Newfoundland. Historically, martens occurred throughout most of the forested regions of the island (Bergerud 1969); however, by the early 1900's the Newfoundland marten population was in decline (Bergerud 1969). In response to increasing concern about the status of marten in the province, trapping of marten was prohibited in 1934. Nonetheless, marten distribution and populations continued to decline and by the 1950's had been eliminated from the central region of the province (Bergerud 1969). In 1973, the Pine Marten Study Area, a 2,078-km<sup>2</sup> wildlife reserve in southwestern Newfoundland, was established to protect the remaining core population (Snyder 1984, Forsey et al. 1995). The PMSA is considered to contain the largest concentration of martens remaining on the island (Thompson 1991, Forsey et al. 1995) and is managed as a refuge from which martens can disperse to reoccupy surrounding areas of suitable habitat (Bissonette et al. 1988).

Excessive trapping, in combination with habitat loss due to logging and fire, had been suggested as factors contributing to the early decline of martens in Newfoundland (Thompson 1991, Forsey et al. 1995). More emphatically, however, habitat loss via timber harvesting of mature (61- 80-years old) and old-growth (> 80-years old) softwood forest has been widely cited as the principle factor currently limiting recovery of the

Newfoundland marten (Bissonette et al. 1988, Thompson 1991, Forsey et al. 1995, Thompson and Curran 1995, Schneider 1997). The association of Newfoundland marten with mature and overmature timber has been hypothesized to be of even higher significance for this island population relative to American martens elsewhere in North American because of a depauperate prey base, specialized habitat requirements of available prey, and fluctuating microtine populations (Thompson and Curran 1995, Bissonette et al. 1997, Sturtevant and Bissonette 1997). Consequently, conservation efforts for much of the last three decades have focused on maintenance of habitat postulated as preferred, in particular old-growth coniferous forest (Bissonette et al. 1988, Thompson 1991, Drew 1995, Thompson and Curran 1995, Schneider 1997, Bissonette et al. 1997).

Thompson and Curran (1995:2063) also suggested, however, that the Newfoundland marten may be restricted from using a wider selection of habitat types due to incidental mortality as martens disperse from the PMSA to second-growth forests that are open to trapping (of furbearers other than martens) and snaring of snowshoe hare (*Lepus americana*). To date, little effort has been directed at examining incidental mortality of martens in areas outside the PMSA as a potential explanation of why remnant marten populations have failed to recover since the closure of trapping and why remnant marten populations were restricted to areas with little human access, restrictions on trapping, and predominately uncut forests (but see Chapter 2).

An undetermined number of martens are incidentally taken each year in snares and traps set for snowshoe hares (*Lepus americanus*) and furbearers (Proulx et al. 1994, Forsey et al. 1995, Fisher et al. 2005); however, actual survival rates, causes of

mortalities, and fates of individually radiomarked animals have not been available (Schneider 1997). Further, most previous field studies of Newfoundland martens (e.g., Snyder 1984, Snyder and Bissonette 1987, Bissonette et al. 1988, Fredrickson 1990, Drew 1995, Drew and Bissonette 1997) have been conducted inside the PMSA, an area dominated by mature and overmature timber where human access is limited and snaring and trapping prohibited. Thus, the relative importance of human-caused mortality in limiting recovery of the species and recolonization of historical range (Bergerud 1969) outside the PMSA has not been evaluated.

As part of a larger 5-year study of the spatial ecology, habitat use, food habits (Gosse and Hearn 2005), and population dynamics, I radio-collared martens in southwestern Newfoundland between June 1995 and August 2000 and collected data on mortality factors and survival rates. In this paper, I document cause-specific mortality factors for martens inside and outside the PMSA, and use a contemporary modeling approach (Johnson and Omland 2004) to estimate survival. Further, I use an informationtheoretic approach (Burnham and Anderson 2001) to develop a suite of *a priori* models to assess the relative support for the competing hypotheses posed by Thompson and Curran (1995) and Thompson and Colgan (1987) to explain factors which increase survival in martens, which are: 1) increased availability of mature forest types increases marten survival; 2) increased availability of logged forest habitat increases natural mortality rates of marten and thereby decreases marten survival; and 3) Newfoundland martens occupying areas outside the PMSA reserve, suffer increased mortality rates (i.e., lower survival) due to incidental mortality in traps (i.e., neck snares and foot-hold traps) set for furbearers and in wire neck snares set to capture snowshoe hares.

# STUDY AREA

The study was conducted within a 2,278-km<sup>2</sup> area in southwestern Newfoundland between June 1995 and August 2000 (Figure 3.1). The boundary of the study area was determined by creating a minimum convex polygon (MCP) using all locations (Chapter 2) for all resident martens (Chapter 1) and included 54% of the PMSA. I used the term untrapped region of the study areas to refer to the PMSA; traditional snaring for snowshoe hares (Proulx et al. 1994, Fisher et al. 2005) and trapping for furbearers was permitted on the 987-km<sup>2</sup> portion of the study area outside the PMSA (Forsey et al. 1995, Thompson and Curran 1995).

The forests on the study area are composed primarily of balsam fir (*Abies* balsamea), with white pine (*Pinus strobus*), larch (*Larix laricina*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*), the latter becoming more common on the eastern extreme of the study area. Forested regions of the study area are concentrated on the eastern and western thirds of the study area; the study area is bisected naturally by a higher-elevation plateau (18% of total study area) that is dominated by large lakes, coniferous scrub vegetation  $\leq 6.5$  m, bogs, and soil and rock barrens, habitat types avoided by marten in Newfoundland (Chapter 2). Consequently, this plateau likely did not support resident marten; previously, this plateau had been considered a barrier to dispersal and genetic exchange between local marten subpopulations in southwestern and southcentral Newfoundland. I considered this portion of the study area to be unavailable to resident martens and restricted my trapping efforts to the eastern and western portions of the study area. Fifty-four percent of the eastern and western portions of the study area are forested.



Figure 3.1. Map of the study area and spatial relationship to the Pine Marten Study Area (PMSA), a provincially designated wildlife reserve closed to snaring and trapping, created in 1972 for the protection of the Newfoundland marten. The Red Indian Lake region of the study area was open to snaring and trapping during the study.

The fir-dominated forests in this region of boreal forest are atypical in that natural disturbance is primarily caused by insect infestations and not fire (Bakuzis and Hansen 1965, Thompson et al. 2003). Hemlock looper (*Lambdia fiscellaria*) and spruce budworm (*Choristoneura fumiferana*) infestations occurred on the area during the mid-1980's, which resulted in a mosaic of insect-killed softwood stands (median patch size = 2.85 ha, range =0.60 - 200 ha). These insect-killed stands comprised 2.4% of the available landscape (Table 2.1), were in various stages of decline and regeneration, and typically had little to no crown closure, an abundance of snags in various stages of decay, and substantial volumes of coarse woody debris. Most of the insect-killed stands on the study area were 10-20 years post infestation and typically had a dense ground cover of balsam fir regeneration.

Forest harvesting, primarily for coniferous pulpwood production, has been ongoing on the study area for much of the last century with 4.0% of the study area in recent ( $\leq$  5 years) clearcuts. Additionally, clearcutting began in the late 1970's and 3.6% of the available landscape for martens was in regenerating < 6.5 m height cuts (> 5 years since harvest) and 3.4% was composed of 20- to 30-year-old clearcuts that had been subsequently precommercially thinned to 1,500 stems per ha (Table 2.1). Old-growth (> 80-years old; Thompson 1991, Thompson and Curran 1995, Sturtevant and Bissonette 1997) conifer forest comprised only 17.3% of the study area. Stands of scrub (unmerchantable softwood) forest  $\leq$  6.5 m in height, generally occurring on lowproductivity wet sites, occupied 9.5% of the study area. Ponds, lakes, streams and rivers occupied 14.1% of the study area. Potential terrestrial predators of martens resident on the study area included red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and lynx (*Lynx canadensis*), of which only the red fox is common. Coyotes became established in Newfoundland in the mid 1980's (Parker 1995), but densities on the study area (snow track observations) appeared very low during the study period. Similarly, no lynx or lynx tracks were observed on the study area during 5 years of field work. Potential avian predators included the great-horned owl (*Bubo virginianus*) and hawk owl (*Surnia ulula*); however, raptors are uncommon in western Newfoundland relative to mainland North America (Gosse and Montevecchi 2001).

#### METHODS

# Marten Capture and Radio Collaring

Martens were trapped for a 2- to 4-week period each summer (June – August) and each autumn (typically late September – early October) beginning in June 1995 and ending in August 2000. Martens were captured in collapsible Tomahawk ® live traps (18 x 18 x 48 cm) located every 1-2 km along roads and snowmobile trails, or along the shoreline of lakes. Traps were spaced to maximize the likelihood that all potential marten territories would include at least 1 trap. During winter, I used snowmobiles to access the study area to improve my trapping coverage.

On initial capture, martens were sexed, weighed, tagged, and fitted with radio collars using standard field procedures (Snyder and Bissonette 1987, Hodgman et al. 1994, Katnik et al. 1994, Bull et al. 1996, Chapin et al. 1997; Chapter 1). A first premolar (PM<sub>1</sub>) was removed from each marten for aging using cementum analysis (Matson's

Laboratory, Milltown, MT); whenever possible a  $PM_4$  was extracted from animals that died during the study for confirmation of initial aging.

Radio-collared martens were located every 7-10 days using either an amphibious fixed-wing airplane or a helicopter. Whenever a mortality signal was detected, the carcass was located and the dead marten was examined, as well as physical evidence at the mortality site, to make an initial evaluation of the cause of death. I used carcass characteristics (e.g., location, wounds, intercanine puncture distance), collar condition (e.g., buried, cut), and physical evidence at the carcass location (e.g., scats, tracks, cached carcass) to assign a tentative cause of death. All carcasses were collected, frozen and subsequently examined by a veterinary pathologist at the Atlantic Veterinary College, Charlottetown, Prince Edward Island, to evaluate the field assessment. Detailed methods of trapping, handling, and radio telemetry are described in Chapter 1.

# **Survival Analyses**

I used the known-fate model in program MARK (White and Burnham 1999) to estimate survival rates of juvenile (< 1yr) and adult ( $\geq$  1 yr) martens. I converted field telemetry data for individual animals into a live-dead (LDLD) encounter history for each biweekly period of the biological year, beginning 1 May. I excluded all encounter histories for the first week after each marten was captured and radiocollared to allow for a period of acclimation. Animals that died because of research related causes, those whose radiocollared failed prematurely, as well as those that survived until the end of the study, were right censored (Winterstein et al. 2001). Encounter histories for individual martens from successive years were treated as independent samples, (i.e., marten year as the unit of sampling replication) which allowed me to partition the radiotelemetry history

of individuals who shifted patterns of residency (e.g., dispersed outside the PMSA reserve) or whose telemetry history spanned two or more biological years (e.g., juveniles who survived to be subsequently monitored as adults).

# A Priori Modeling

# Adults

I structured a set of *a priori* (candidate) models relating survival of martens to five metrics describing composition and spatial position of the individual marten home range; these metrics were treated as covariates in the individual encounter histories. For all marten with  $\geq 10$  annual locations, I constructed a 95% MCP, and then quantified the composition of home ranges using three measures: 1) the percent of mature and overmature (MOM) coniferous forest (i.e., previously postulated as required habitat for Newfoundland marten, Thompson 1991, Thompson and Curran 1995, Drew 1995, Bissonette et al. 1997, Sturtevant and Bissonette 1997); 2) the percent suitable (Suitable) habitat; and 3) the percent of the home range composed of recently (Cut) stands. Suitable habitat types for Newfoundland martens was based on stand-scale habitat analyses (Chapter 2) and a companion study (Fuller 2006), and was defined as: insect-killed (IK) stands, primarily  $\geq 12.6$  m tall, < 25% canopy closure with a dense understory; precommercially thinned 20- 30-year old conifer stands (PCT), 7-17 years post thinning with > 50% canopy closure and typical densities of 1,500 stems /ha; medium height (6.6-12.5 m tall) closed (> 50% canopy closure) conifer stands; tall ( $\geq$  12.6 m) open canopy ( $\leq$ 50% canopy closure) conifer stands; tall closed-canopy conifer stands; and conifer regeneration (RF)  $\leq 6.5$  m in height with  $\geq 75\%$  canopy closure. Cut habitat was defined as recent ( $\leq$  5-years old) clearcuts with residual patches of conifer and mixedwood, PCT,
and RF to represent the logged forests studied by Thompson and Colgan (1987); median home-range availability (n = 224) was 14.7% (range 0 – 66.6%). Based on my areaobservation curves (Chapter 1, Figure 1.5), 19 locations were necessary to meet asymptotic home range estimates, whereas 10 locations would estimated approximately 55% of the 95% MCP home-range area.

For animals with fewer than 10 locations during a sampling year annual I used three approaches to estimate home-range composition and spatial position: 1) for animals monitored in previous, or subsequent years, I used the averages of the metrics for the home ranges from previous or subsequent years; 2) I pooled locations across consecutive biological years for animals with 10 locations in either year; or 3) I simulated a home range (3 males, 3 females) by calculating a geometric center from all available locations (all animals had  $\geq$  4 locations) and simulated a circular home range around that point using a radius equal to that documented for 43 males (radius = 3,131 m) and 49 females (radius = 2,015 m) with  $\geq$  19 locations.

To quantify an individual marten's risk to incidental (i.e., snaring and trapping) mortality, I calculated two metrics: 1) the distance (Distance) from the geometric center of the home range to the nearest road where snaring and trapping is permitted; and 2) the presence or absence of a road (Road) providing legal trapping and snaring access within the actual home range. I hypothesized that an animal's risk to incidental mortality would decrease with increasing distance from a trapping road and modeled DISTANCE as a function, where risk decreased to zero beyond the home-range boundary (radius of the mean sex-specific home-range boundary was > 3,131 m for males, > 2,015 m for females).

Home-range area, and movement rates (MNDIST) differed between adult male and female martens (Chapter 1, Table 1.3). Further, sex-specific differences in natural survival rates and vulnerability to trapping have been documented in other populations of martens throughout North America (Archibald and Jessup 1984, Strickland and Douglas 1987, Thompson and Colgan 1987, Fortin and Cantin 1994, Hodgman et al. 1994, Payer 1999). Thus, I evaluated my set of candidate models separately for males and females. All variables used in survival models were examined for pairwise correlation and were retained if r < 10.951 (Burnham and Anderson 2002).

# **Juveniles**

Juvenile martens were normally not captured until late September - early October and were not considered residents (i.e., did not occupy exclusive territories) during their first year. Consequently, I could not develop individual covariates based on the composition and spatial location of the home range. Therefore, I calculated juvenile survival for the 30-week period of 2 October to 31 April by calculating 15 biweekly survival rates, and structured models to investigate the timing of mortality for juveniles inside and outside the reserve with respect to the onset of the snaring and trapping season in early October. I compared models assuming a constant biweekly survival probability versus those that partitioned the 30-week period in to a 6-week (i.e., 3 biweekly periods) early snaring and trapping season period, a late (6-week) snaring and trapping season, and a 18-week winter period. I hypothesized that: 1) survival of juvenile marten in areas open to snaring and trapping would be lower than for juveniles inside the PMSA; 2) mortality would be concentrated during the earliest part of the snaring and trapping seasons (October to mid-November); 3) survival of juvenile martens inside the PMSA

would not display a seasonal (interval) pattern (i.e., would be best described by models treating biweekly survival probability as constant during October to April).

## **Model Selection**

I evaluated the rank and relative support for competing model using Akaike's Information Criterion following the guidelines of (Burnham and Anderson 2002). MARK ranks competing models using a  $\Delta AIC_c$  score, giving the model with the most support in the observed data set a  $\Delta AIC_c$  value of zero. Values of  $\Delta AIC_c$  from 0-2 are considered to have substantial and potentially equal support, > 2.0 -7 suggest considerable support for a real difference between models, and values > 10 suggest strong evidence to support differences between models (Burnham and Anderson 2002).

## RESULTS

I captured 159 individual martens during 494 captures between June 1995 and August 2000, including 93 adults ( $\geq 1$  yr) and 54 juveniles (<1 yr); ages were not obtained for 12 animals) of which I monitored 147 individual martens for survival (Table 3.1). Many juvenile marten either survived (n = 19) or dispersed outside the PMSA (n = 4) and were subsequently monitored while occupying areas open to snaring and trapping. Respectively, I monitored survival of adult and juvenile martens for an average of 505.9 (n = 55) and 104.1 (n = 19) days inside the PMSA and for 332.4 (n = 67) and 116.6 (n = 28) days, outside the PMSA (Table 3.1).

#### **Cause-specific Mortality**

There were 10 marten mortalities that were related to research activities (i.e., livetrapping, immobilization or radiocollaring of martens). These 10 mortalities were associated with 494 captures (handling events) yielding a 2.0% research-associated

Table 3.1.	Total number	of martens r	nonitored ar	nd total	number	of individua	s radiocollar	ed by age	and sex of	class in th	ne untrapp	ed and
trapped re	gions of the stu	ıdy area, sou	thwestern N	ewfour	ndland, 1	995-2000.						

Number	PMSA (Untrapped)				Red Indian Lake Region (Trapped)				oped)	TOTAL	
	Males <u>Females</u> Total		Total	Males		Females		Total			
	Juveniles	Adults	Juveniles	Adults	Total	Juveniles	Adults	Juveniles	Adults	Total	
Monitored	12	30	7	25	74	18	35	10	32	95	169 <sup>a</sup>
Individuals	12 <sup>b</sup>	24 <sup>c</sup>	7 <sup>b</sup>	23 <sup>c</sup>	66	15 <sup>b</sup>	30 <sup>d</sup>	10	26 <sup>d</sup>	81	147

<sup>a</sup> One juvenile male escaped from a rabbit (neck) snare due to the protection of the radiocollar, but was subsequently trapped in a leg-hold trap; this individual was treated as two radiomarked samples (i.e., death from snaring, death from trapping).

<sup>b</sup> Four juvenile martens (2 males, 2 females) dispersed from the untrapped regions and into the trapped region of the study area and contributed to data for both areas

<sup>c</sup> Eight juvenile martens (6 males, 2 females) survived their juvenile year and provided survival data as adults.

<sup>d</sup> Eleven juvenile martens (5 males, 6 females) survived their juvenile year and provided survival data as adults.

mortality rate. Seven of these martens died because of the entanglement or entrapment of their radiocollars. These marten were included in the survival analysis up to their date of last known contact alive; however, their fates were censored from the study and are not represented in the data presented in Table 3.2.

I documented 52 mortalities of martens during the study (Table 3.2). Twenty-one martens (18 adults, 3 juveniles) died in the untrapped region, whereas 31 marten (19 adults, 12 juveniles) mortalities were documented in the trapped region of the study area. Twenty-nine marten mortalities (55.8%) were associated with natural causes, including 16 cases of predation. Red fox accounted for a minimum of 56.3% (n = 16) of predator mortalities. Based on the distance between intercanine puncture marks, one juvenile marten was killed by a coyote; the first known marten mortality attributed to this newlyestablished canid on the island. Most of the martens killed by red fox (and the single covote kill) had puncture wounds in the thorax region and/or skulls, had extensive subdermal hemorrhage (indicating predation rather than scavenging; Bull and Heater 2001), were typically intact (not consumed) and were often buried or covered with vegetation. I suspect that several of the 6 mortalities attributed to unknown predators were also caused by red fox; intraspecific predation was suspected in only 1 of these 6 cases. Of the remaining 13 natural mortalities, 1 adult female accidentally choked while eating a small mammal and 1 adult male died as a result of a massive infection caused by a bite wound; this likely occurred during an intraspecific fight. Exact cause of death could not be determined for 11 of the 13 natural mortalities; however, several of these animals were judged to be in poor body condition and likely died of starvation.

Table 3.2. Sources of mortality by age and sex class for radiocollared Newfoundland martens in untrapped and trapped portions of the study area, southwestern Newfoundland, 1995-2000.

	Untrapped								
Mortality Source	Adult		Juv	venile	Α	Adult		venile	Totals
	Male	Female	Male	Female	Male	Female	Male	Female	
Predation									
Red fox	2	4	0	0	0	3	0	0	9
Coyote	0	0	0	0	0	0	1	0	1
Unknown predator	1	1	1	1	0	2	0	0	6
Other natural causes	6	3	0	1	1	2	0	0	13
Subtotal Natural	9	8	1	2	1	7	1	0	29
Snaring	1	0	0	0	8	2	5	1	17
Trapped	0	0	0	0	1	0	2	3	6
Subtotal Human	1	0	0	0	9	2	7	4	23
Totals	10	8	1	2	10	9	8	4	52

Three marten carcasses were recovered from the canopy of trees. One of these marten, recovered from the canopy approximately 10 m above the ground, was an intact carcass sowing no indication of predation (i.e., puncture wounds, subdermal hemorrhage); the other 2 martens were only partial carcasses. The latter 2 carcasses may have represented avian predation or scavenging. Two other marten carcasses were recovered from ground dens with hare snares embedded in their necks. Both of these martens (1 adult male, 1 adult female) were in poor body condition, were 20-30% below mean sex-specific body weight, and apparently succumbed to injuries and died after escaping from hare snares.

Human-caused mortality accounted for 45.3% (24/53) of all deaths. Incidental mortality of martens in snares set for hares accounted for 75.0% and trapping (i.e., fox snares, leg-hold traps, body-gripping steel traps) accounted for 25.0% of human-caused mortality (n = 24, Table 3.2). Further, two additional adult males were right censored from the study due to radio transmitter failure, but subsequently died because of human-related mortality, one in a hare snare and the other in a fox snare. These mortalities were reported by the individuals who had trapped the radiocollared animals; however, these observations were not included in the survival analyses.

Cause-specific mortality was notably different between the trapped and untrapped regions of the study area (Figure 3.2). Predictably, natural mortality accounted for essentially all mortality (95.2%; n = 21) in the untrapped region; however, one resident adult male was illegally killed in a hare snare set just inside the boundary of the PMSA. In contrast, natural mortality accounted for only 28.1% of the deaths in the trapped region of the study area and human-caused mortality accounted for the remaining 71.9%.



Figure 3.2. Relative causes of mortality for 52 martens in the untrapped (n = 21) and trapped (n = 31) regions of the study area, southwestern Newfoundland, 1995-2000; samples sizes are presented above bars.

Within the trapped region of the study area, snaring and trapping accounted for 90.9% (n = 10) of the mortality of adult males, and 91.7% (n = 12) of the mortality of juvenile martens. All snaring and trapping mortalities (n = 24, Table 3.2) occurred between 10 October and 24 January. In contrast, death due to natural causes was the principle source of mortality for adult females outside the reserve (7 of 9). A comparison of the relative number of natural and human-related mortalities observed inside and outside the PMSA suggests that human-caused mortalities may be at least partially compensatory to natural mortality at the levels of human exploitation experienced on my study area.

# Survival

### Adult Survival

There was low to moderate association between variables in my pairwise correlations (i.e., median of correlation coefficients; r = 0.38 for males, r = 0.35 for females, Table 3.3 and 3.4). Distance and Road were most highly correlated for both males and females but coefficients did not exceed 0.82; thus all variables were retained for modeling.

Annual survival of adult males was estimated using 112 encounter histories for 65 individual martens. The process of model selection indicated that Suitable and Distance were important variables explaining survival of adult males and both variables were included in all 6 of the top competing models (AIC<sub>c</sub>  $\leq$  2.4, Table 3.5); both Suitable and Distance were positively associated with survival (i.e.,  $\beta > 0.0$ , confidence interval did not overlap with 0.0, Table 3.6). These 6 competing models collectively contained 96% of the weight of evidence explaining survival of adult males. Three other covariates were

	Cut	Suitable	MOM	Distance	Road
Cut	1.00				
Suitable	0.30	1.00			
MOM	-0.54	0.54	1.00		
Distance	-0.50	0.31	0.57	1.00	
Road	0.25	-0.25	-0.29	-0.82	1.00

Table 3.3. Pearson correlation coefficients among 5 variables<sup>a</sup> used in MARK models to explain survival of adult male martens, southwestern Newfoundland, 1995-2000.

<sup>a</sup> Suitable = % home range comprised of suitable habitat types. Suitable habitat (Chapter 2, Fuller 2006) was defined as: insect-killed (IK) stands, primarily  $\geq$  12.6 m tall, < 25% canopy closure with a dense understory; precommercially thinned 20- 30-year old conifer stands (PCT), 7-17 years post thinning with > 50% canopy closure and typical densities of 1,500 stems /ha; medium height (6.6-12.5 m tall) closed (> 50% canopy closure) conifer stands; tall ( $\geq$  12.6 m) open canopy ( $\leq$  50% canopy closure) conifer stands (TOS); tall closed-canopy conifer stands (TCS); and conifer regeneration (RF)  $\leq$  6.5 m in height with  $\geq$  75% canopy closure. Cut habitat was defined as IK + PCT + RF. MOM habitat was defined as IK + TCS + TOS. Distance = the distance (m) from the geometric center of the home range to the nearest road where snaring and trapping is permitted. Road = the presence or absence of a road providing legal trapping and snaring access inside the home range.

	Cut	Suitable	MOM	Distance	Road
Cut	1.00				
Suitable	0.44	1.00			
MOM	-0.52	0.39	1.00		
Distance	-0.35	0.29	0.48	1.00	
Road	0.16	-0.26	-0.21	-0.72	1.00

Table 3.4. Pearson correlation coefficients among 5 variables<sup>a</sup> used in MARK models to explain survival of adult female martens, southwestern Newfoundland, 1995-2000.

<sup>a</sup> Suitable = % home range comprised of suitable habitat types. Suitable habitat (Chapter 2, Fuller 2006) was defined as: insect-killed (IK) stands, primarily  $\geq$  12.6 m tall, < 25% canopy closure with a dense understory; precommercially thinned 20- 30-year old conifer stands (PCT), 7-17 years post thinning with > 50% canopy closure and typical densities of 1,500 stems /ha; medium height (6.6-12.5 m tall) closed (> 50% canopy closure) conifer stands; tall ( $\geq$  12.6 m) open canopy ( $\leq$  50% canopy closure) conifer stands (TOS); tall closed-canopy conifer stands (TCS); and conifer regeneration (RF)  $\leq$  6.5 m in height with  $\geq$  75% canopy closure. Cut habitat was defined as IK + PCT + RF. MOM habitat was defined as IK + TCS + TOS. Distance = the distance (m) from the geometric center of the home range to the nearest road where snaring and trapping is permitted. Road = the presence or absence of a road providing legal trapping and snaring access inside the home range.

Table 3.5. Candidate models relating survival of adult ( $\geq 1$  yr) male martens (n = 65), southwestern Newfoundland, 1995-2000, in rank order of support using Akaike's Information Criteria. Survival models included individual covariates describing home range composition, (i.e., % suitable habitat (Suitable), % cut (Cut), % mature and overmature (MOM)), and measures of relative risk to snaring and trapping (i.e., distance from the center of the home range to nearest road where snaring and trapping is permitted (Distance), presence of a road where snaring and trapping is permitted within the home-range area (Road)).

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_{c}$	Weights	$ML^b$	K <sup>c</sup>	Deviance
Suitable + Distance	260.2	0.0	0.30	1.00	2	256.2
Suitable + Distance + Road	260.7	0.5	0.24	0.79	3	254.7
Cut + Suitable + Distance	262.0	1.8	0.12	0.40	3	256.0
MOM + Suitable + Distance	262.2	2.0	0.11	0.37	3	256.2
Cut + Suitable + Distance + Road	262.4	2.2	0.10	0.33	4	254.4
MOM + Suitable + Distance + Road	262.6	2.4	0.09	0.30	4	254.6
Cut + MOM + Suitable + Distance + Road	264.5	4.2	0.04	0.12	5	254.4
Suitable	269.9	9.7	0.00	0.01	1	267.9

Table 3.5. Continued.

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_c$	Weights	$ML^b$	K <sup>c</sup>	Deviance
Suitable + Road	270.6	10.4	0.00	0.00	2	266.6
Suitable + MOM	271.8	11.6	0.00	0.00	2	267.8
Suitable + Cut	271.9	11.7	0.00	0.00	2	267.9
Cut + MOM + Distance + Road	273.6	13.4	0.00	0.00	4	265.6
Cut + MOM	281.5	21.3	0.00	0.00	2	277.5
MOM + Distance + Road	319.1	58.9	0.00	0.00	3	313.1
MOM + Distance	319.8	59.6	0.00	0.00	2	315.8
MOM + Road	323.4	63.2	0.00	0.00	2	319.4
MOM	328.7	68.5	0.00	0.00	1	326.7
Cut + Distance + Road	677.9	417.7	0.00	0.00	3	671.9
Cut + Distance	699.8	439.6	0.00	0.00	2	695.8
Cut + Road	723.5	463.3	0.00	0.00	2	719.5

Table 3.5. Continued.

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_c$	Weights	$ML^b$	K <sup>c</sup>	Deviance
Cut	740.1	479.9	0.00	0.00	1	738.1
Distance + Road	1706.2	1446.0	0.00	0.00	2	1702.2
Road	1754.9	1494.7	0.00	0.00	1	1752.9
Distance	1866.4	1606.2	0.00	0.00	1	1864.4

<sup>a</sup> See Table 3.3 for a detailed description of model variables..

<sup>b</sup> Model Likelihood.

<sup>c</sup> Number of parameters estimated.

				_	_	-				
Model	Suita	<u>ble</u>	Cut		MOM		Distan	<u>ce</u>	Road	
	β	95% CI	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Males										
S + D	8.7	7.7, 9.7					0.002	0.0004, 0.0035		
S + D + R	9.0	7.9, 10.2					0.002	0.0005, 0.0051	-0.62	-1.6, 0.3
C + S + D	8.9	7.5, 10.3	-0.7	-3.7, 2.4			0.002	0.0004, 0.0037		
M + S + D	8.6	5.5, 11.6			0.22	-4.2, 4.7	0.002	0.0004, 0.0035		
C + S + D + R	8.8	7.4, 10.2	1.0	-3.3, 5.3			0.003	0.0005, 0.0054	-0.85	-2.2, 0.5
M + S + D + R	9.5	5.9, 13.1			-0.73	-5.6, 4.2	0.003	0.0004, 0.0054	-0.68	-1.7, 0.4
Females										
C + M + D			5.2	2.7, 7.7	10.8	8.8, 12.8	0.001	0.0001, 0.0027		
C + M + D + R			5.8	2.8, 8.8	10.8	8.8, 12.7	0.001	0.0001, 0.0036	-0.48	-1.7, 0.7
C + M + D + K			5.0	2.0, 0.0	10.0	0.0, 12.7	0.001	0.0001, 0.0030	-0.40	-1.7, 0.7

(R) on the survival of adult resident martens for the top 6 competing models, southwestern Newfoundland, southwestern Newfoundland, 1995-2000. Estimates are for sex-specific competing models (i.e.,  $AIC_c \le 2.4$ , Tables 3.5 and 3.7).

Table 3.6. Regression coefficients (β) for the effect of covariates Suitable (S), Cut (C), MOM (M), Distance (D) and Road

present in 1 of the top 6 competing models (i.e., Road, Cut, and MOM). Road was always negatively associated with survival in the 2<sup>nd</sup>- 5<sup>th</sup>- and 6<sup>th</sup>-ranked models, whereas covariates MOM and Cut alternated between having positive and negative association with survival depending on the model structure; however, the confidence intervals of  $\beta$ coefficients for all 3 of these additional covariates substantially overlapped 0.0 in all of the models where they appeared (Table 3.6). In contrast, the  $\beta$  coefficients for the Suitable and Distance variables in the top-ranked model did not span 0.0.

There was little support for any model containing only a single habitat variable (i.e., MOM, Cut, or Suitable) and or a single human-risk covariate (i.e., Distance, Road); AIC<sub>c</sub>  $\geq$  9.7). Suitable was the most highly-ranked (8<sup>th</sup>) single-variable model with a model likelihood of 0.01. Models which incorporated only risk covariates (i.e., Distance, Road) were ranked lowest of all the candidate models. The single variable MOM model, which based on previous work (Snyder and Bissonette 1987, Thompson and Curran 1995, Sturtevant and Bissonette 1997) was considered "required" habitat, had essentially no support (i.e., model likelihood (ML) < 0.00). Additionally, the MOM habitat model when combined with variables indexing risk to human mortality still had no support (i.e., 14<sup>th</sup>-ranked model, ML of < 0.00). The top model containing MOM was the 4<sup>th</sup>-ranked model (i.e., M + S + D) but the addition of the MOM variable did not explain any additional variation in adult male survival (i.e., 95% CI strongly overlapped 0.0 (-4.2 – 4.7); Table 3.6) and the more parsimonious model S + D (top-ranked model) was > 100 times more plausible.

These findings suggest that survival in adult males was positively influenced by the additive effects of suitable habitat and increased distance from a road where hare snaring

and trapping of furbearers (other than martens) was legal. Annual survival of adult males derived from the average of my 6 competing ( $\Delta AICc \leq 2.4$ , Table 3.5) models, based on the mean value for individual covariates, was 0.83 (range 0.82 - 0.84).

Annual survival of adult females was estimated using 112 encounter histories for 57 individual marten. Covariates Cut, MOM, and Distance appeared in the top 2 models (Table 3.7) and all 3 covariates were positively ( $\beta > 0.0$ ) associated with survival (Table 3.6). These competing models (AIC<sub>c</sub>  $\leq$  1.4) contained 81% of the weight of evidence explaining variation in survival of adult females. The best habitat only model Cut + MOM was ranked 4<sup>th</sup> ( $\Delta$ AIC<sub>c</sub> = 5.2) and was similar in structure to the top-ranked model (i.e., C + M + D, Table 3.7); however, the top-ranked model included the human-risk variable Distance and was > 13 times more plausible. Similar to the modeling results for males, Road was negatively association with adult female survival (Table 3.7) but the confidence interval for the  $\beta$  coefficient for this covariate included 0.0 (Table 3.6) suggesting uncertainty in the predictive power of this covariate.

Nine of the 10 top models for adult females included variables indexing risk to human-caused mortality as an additive effect (Table 3.7); however, comparable to the rankings for males, candidate models containing only risk variables, ranked lowest of all candidate models. Thus, modeling results for females are comparable to those of males, suggesting that survival in adult females was positively influenced by the additive effects of habitat and reduced risk to human-related mortality. Annual survival of adult females, derived from the average of my two competing models, and based on the mean value of individual covariates, was identical to that of adult males (i.e., 0.83, range 0.82 - 0.84).

Table 3.7. Candidate models relating survival of adult ( $\geq 1$  yr) female martens, southwestern Newfoundland, 1995-2000, in rank order of support using Akaike's Information Criteria. Survival models included individual covariates describing home range composition, (i.e., % suitable habitat (Suitable), % cut (Cut), % mature and overmature (MOM)), and measures of relative risk to snaring and trapping (i.e., distance from the center of the home range to nearest road where snaring and trapping is permitted (Distance), presence of a road where snaring and trapping is permitted within the home-range area (Road)).

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_{c}$	Weights	$ML^b$	K <sup>c</sup>	Deviance
Cut + MOM + Distance	220.8	0.0	0.54	1.0	3	214.8
Cut + MOM + Distance + Road	222.2	1.4	0.27	0.50	4	214.2
Cut + MOM+ Suitable + Distance + Road	223.9	3.0	0.12	0.22	5	213.8
Cut + MOM	226.1	5.2	0.04	0.07	2	222.0
Suitable + MOM + Distance + Road	227.8	6.9	0.02	0.03	4	219.8
Suitable + Distance	228.9	8.1	0.01	0.02	2	224.9
Suitable + Distance + Road	230.2	9.4	0.00	0.01	3	224.2
Cut + Suitable + Distance	230.6	9.7	0.00	0.01	3	224.5
Cut + Suitable + Distance + Road	232.2	11.4	0.00	0.00	4	224.2

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_{c}$	Weights	$\mathrm{ML}^{\mathrm{b}}$	K <sup>c</sup>	Deviance
Suitable + Road	234.9	14.1	0.00	0.00	2	230.9
Suitable + MOM	236.5	15.7	0.00	0.00	2	232.5
Suitable	238.3	17.4	0.00	0.00	1	236.3
Suitable + Cut	238.5	17.7	0.00	0.00	2	234.5
MOM + Distance	245.2	24.3	0.00	0.00	2	241.1
MOM + Distance + Road	246.2	25.4	0.00	0.00	3	240.2
MOM + Road	248.0	27.1	0.00	0.00	2	244.0
Mom	257.3	36.5	0.00	0.00	1	255.3
Cut + Distance + Road	526.0	305.2	0.00	0.00	3	520.0
Cut + Distance	529.2	308.4	0.00	0.00	2	525.2
Cut + Road	606.7	385.9	0.00	0.00	2	602.7

Table 3.7. Continued.

 Table 3.7.
 Continued.

			AIC <sub>c</sub>			
Model <sup>a</sup>	AIC <sub>c</sub>	$\Delta AIC_{c}$	Weights	$\mathrm{ML}^{\mathrm{b}}$	K <sup>c</sup>	Deviance
Distance + Road	1456.4	1235.5	0.00	0.00	2	1452.3
Distance	1529.1	1308.3	0.00	0.00	1	1527.1
Road	1597.6	1376.7	0.00	0.00	1	1595.6

<sup>a</sup> See Table 3.3 for a detailed description of model variables.

<sup>b</sup> Model Likelihood.

<sup>c</sup> Number of parameters estimated.

### Juvenile Survival

Survival models for the October-April interval were constructed for juvenile martens based on 47 encounter histories for 44 individuals (27 males, 17 females). Models based on differences in survival by area and partitioned into 3 time intervals best described my observed data for juveniles (Table 3.8). The top 2 competing models (AIC<sub>c</sub>  $\leq$  1.0) incorporated an area effect and collectively these 2 models contained 82% of the weight of evidence. The top-ranked model partitioned survival outside the reserve into 3 intervals (i.e., an early- and a late-fall trapping and snaring season interval, and a late winter interval), and treated survival of juveniles in the PMSA as a constant survival probability over the period. This model was 1.65 times more likely than the 2<sup>nd</sup>-best model and 3.2 times more likely the 3<sup>rd</sup>-ranked model which did not incorporate an area effect. The structure of my top-ranked model corroborated my *a priori* view that survival of juveniles was lower in areas open to snaring and trapping, and that mortality was concentrated shortly following the onset of the snaring and trapping season (Figure 3.3). There was no support in the data for differences in juvenile survival between sexes but the analyses likely were affected by low statistical power. Juvenile survival rates for the 7-month interval (i.e., October to April) based on the average of my 2 competing models was 0.76 and 0.51 for martens inside and outside the PMSA reserve, respectively.

## DISCUSSION

My results suggest that incidental mortality associated with hare snaring and fur trapping significantly influences survival of Newfoundland martens. Human-caused mortality accounted for nearly one half (45.3%) of the mortalities documented during the study, and 71.9% of all mortalities of martens outside the reserve.

Table. 3.8. Table. 3.5. Candidate models describing survival of radiocollared juvenile (< 12-months old) martens (n = 44) inside the Pine Marten Study Area (PMSA) and in areas outside the reserve open to snaring and trapping (STA), southwestern Newfoundland, 1995-2000. Models are ranked from lowest to highest AIC<sub>c</sub> based on Akaike's Information Criteria.

Model	AIC <sub>c</sub>	$\Delta AIC_{c}$	AIC <sub>c</sub> Weights	ML	K	Deviance
Constant survival in PMSA; early fall, late fall, and winter intervals for STA	119.5	0.00	0.51	1.00	4	111.4
Early fall, late fall, and winter intervals calculated separately for PMSA and STA	120.5	1.0	0.31	0.60	6	108.3
PMSA and STA data pooled; early fall, late fall and winter intervals	121.8	2.3	0.16	0.31	3	115.8
Rate (30-week interval) calculated separately for PMSA and STA	127.7	8.2	0.01	0.02	2	123.7
PMSA and STA data pooled; single (30-week) interval	128.7	9.2	0.01	0.01	1	126.7
PMSA (single 30-week interval); STA survival (15 biweekly) intervals	135.7	16.2	0.00	0.00	16	102.2
PMSA (15 biweekly) intervals; STA (15 biweekly) intervals	156.4	36.9	0.00	0.00	30	91.1
PMSA (15 biweekly) intervals; STA (15 biweekly) intervals + Sex	158.5	39.0	0.00	0.00	31	90.8
PMSA (15 biweekly) intervals; STA (15 biweekly) intervals + Sex + Sex * Area interaction	159.7	40.2	0.00	0.00	32	89.7



Figure 3.3. Survival functions for juvenile radiocollared martens from 2 October to 31 April (15 biweekly intervals) in the PMSA (solid circles) and in areas open to snaring and trapping (open circles). Functions were generated by the best-fitting model depicting juvenile survival, southwestern Newfoundland, 1995-2000.

Models best characterizing survival of both adult males and adult females incorporated variables indexing risk to human-caused mortality (as indexed by the presence or absence of a road where snaring and trapping is permitted with home-range boundaries, or the distance of a road from the home-range centre) as an additive effect, and fit the observed data better that models associating marten survival solely or in combinations of habitat types purported to offer high survival value (MOM) or lower individual survival probability (Cut). Further, mature and overmature forest, supposedly required habitat for Newfoundland marten, was not a dominant variable explaining survival for either adult males or adult females. Moreover, a positive association of survival with the extent of the home range that had been logged (i.e., Cut) was observed for both males and females, and Cut occurred in 2 of the competing models ( $\Delta AIC_c < 2.4$ ) for males and both of the competing ( $\Delta AIC_c < 1.4$ ) models for females. These results contradict Thompson and Cogan's (1987) conclusion that logging *per se* decreases marten survival.

Models which incorporated only variables for habitat effects or only covariates indexing risk to human-risk habitat did not perform well and all had model likelihoods of  $\leq 0.07$  (Table 3.5 and Table 3.7). Suitable habitat appeared to be strongly (positively) associated with male survival, appearing in all six of our top competing models with positive  $\beta$  coefficients and tight confidence intervals that never included 0.0 (Table 3.6). Further, the single variable model Suitable ranked eighth and was the highest ranking single-variable model for males, outperforming models structured with only variables related to risk of human-related mortality, suggesting increasing amounts of suitable habitat was a strong determinant of survival in males. Survival of male martens was

further improved with distance from a road open to snaring and trapping. Adult female survival was also strongly (positively) associated with habitat variables (i.e., MOM and Cut), with increased explanatory power with the addition of the variable distance. There was however, significant (P < 0.05) correlation between all of my covariates with the exception of Cut and Road (P > 0.10), thus my study design was not sufficient to separate the relative importance of trapping and snaring versus the habitat-composition of the home-range in determining adult survival. Overall, I interpret the collective weight of evidence from the modeling exercise to indicate that survival of adult martens was positively influenced with increasing amounts of habitat and further enhanced by increasing distance from roads where snaring and trapping are legally permitted.

Few studies have estimated annual survival rates of martens, particularly in areas where exploitation is prohibited. Hodgman et al. (1994) and Payer (1999) reported annual survival rates of 0.87 and 0.95 for adult (> 1 yr) males, and 0.53 and 0.62 for adult females, respectively, for an unharvested marten population inhabiting a forest reserve (Baxter State Park; closed > 50 yr to trapping and > 35 yr to timber harvesting) in northcentral Maine. As well, Payer (1999) reported annual survival rates of 0.82 for adult males and 0.81 for adult females in the 130-km<sup>2</sup> untrapped industrial forest adjacent to this reserve. Finally, Bull and Heater (2001) reported a mean (n = 4 years) annual survival of 0.63 (range 0.55 - 0.71; 14-18 martens tracked per year) for marten  $\ge$  9months old (sexes pooled) for an unharvested marten population in northeastern Oregon. My estimate of 0.83 annual survival for both adult males and adult females, despite the occurrence of considerable human-related mortality, particularly for adult males (Table 3.2), is comparable to those reported for unharvested populations and appreciably higher than the 0.64 annual survival rate previously reported by Bissonette et al. (1988) for Newfoundland martens inside the core of the PMSA (rate calculated as simple % surviving, data pooled between sexes and juveniles and adults).

My observations of higher rates of natural mortality (Figure 3.3) for adult females in trapped populations is consistent with the results of both Hodgman et al. (1997) and Payer (1999) and collectively all three studies suggest that low levels of human-related mortality may not be additive for adult females. Mean density of lactating females reported by Payer (1999) was nearly identical in trapped and untrapped industrial forest  $(0.04-0.06 \text{ per km}^2)$  but 3 times higher  $(0.15 \text{ km}^2)$  in the untrapped reserve, suggesting that habitat availability is overriding in determining density of adult females. Survival of juvenile ( $\geq$  5-months old) martens from October to April was relatively high inside the reserve (0.75) and approximately 50% higher (0.51) than for juveniles outside the reserve. Additionally, survival curves of juvenile martens (generally considered more vulnerable to trapping mortality; Soukkala 1983, Strickland and Douglas 1987, Hodgman et al. 1994) suggested that increased mortality of juveniles outside the reserves was coincident with the onset of the snaring and trapping season. This difference in survival of juveniles was directly attributable to human-caused mortality indicating that humanrelated mortality in my study had a strong additive effect. Human-related mortality was also significant for adult males outside the reserve and modeling results suggested an important additive effect that reducing exposure to snaring and trapping mortality would increase male survival. Collectively, my results suggest that marten in preserves have the additive advantage of increased access to suitable habitat components and elimination of any additive component of mortality to human-related snaring and trapping activity.

Estimates of human-related mortality for marten populations outside the reserve likely underestimated the potential effects of human-related mortality on marten populations relative to many other areas on the island. Trapping, which has the potential to exceed sustainable levels (Hodgman et al. 1994, Fortin and Cantin 1994), was nearly absent on my sites during the study period. Despite requests by wildlife officials for local trappers to conduct trapping activities as usual, the individual trapper who traditionally trapped a large portion of the study area where the majority of my radiocollared marten were resident, did not trap because he was confident he would remove all resident martens within the first few weeks of the trapping season. In support of this view, Hodgman et al. (1994) documented only 11% and 20% survival of juvenile male (n = 8)and female (n = 9) martens, and only 12.7% and 42.6% survival of adult male (n = 20)and adult female (n = 21) martens during the trapping season on an intensively-trapped study area in northcentral Maine. Additionally, the majority of the trapped mortality documented by Hodgman et al. (1994) occurred in the first 2 weeks of the 6-week trapping season, compelling them to conclude that shortening the trapping season would have little effect on improving the overall annual survival rate and thus, sustainability of the harvested population. Thus, I speculate that incidental trapping mortality, if trapping is conducted at levels more typical of areas being actively trapped for furbearers in other parts of the island, in concert with accidental snaring mortality, would generate substantial additive mortality and effectively eliminate martens from areas of the island that might otherwise be suitable for occupancy.

Consistent with previous research (Soukkala 1983, Archibald and Jessup 1984, Strickland and Douglas 1987, Fortin and Cantin 1994, Hodgman et al. 1994, Payer 1999)

I observed high trapping mortality among adult males and juveniles in the trapped region of the study area. Yeager (1950) suggested that male marten are more vulnerable to trapping because they have a larger territory (hence larger foraging areas), which increases their chance of encountering traps. Home-range sizes of martens in Newfoundland are disproportionately large (Chapter 1, Table 1.5), a likely consequence of a naturally fragmented landscape and a naturally depauperate prey base (Dodds 1984, Hearn et al. 2006; Chapter 1, Table 1.1). Further, martens in Newfoundland have high rates of movement as indexed by minimum distance moved between consecutive telemetry locations (Chapter 1, Table 1.3). Thus, given these ecological characteristics, combined with the naturally high movement rates and long distances (Bowman et al. 2002, B.J. Hearn, unpublished data) traveled by dispersing juveniles (Strickland 1994), I speculate that martens in Newfoundland may be more susceptible to incidental mortality from hare snaring and trapping than mainland martens. Given the functional link between territory size and animal density (Fuller et al. 2001, Jetz et al. 2004), it seems reasonable to suggest that relatively low levels of spatially-distributed snaring and trapping pressure might be sufficient to eliminate martens over large areas of Newfoundland. Further, the limited prey base available to martens in Newfoundland (Chapter 1, Tables 1.1 and Table 1.5) may require higher adult survival to compensate for lower juvenile survival and natality relative to mainland populations with higher prey diversity.

There was a striking difference in cause-specific mortality factors inside versus outside the reserve. Nearly three quarters of all marten mortality documented outside the reserve was incidental mortality in hare snares and traps. Further, human-related

mortality was the dominant mortality factor ( $\geq 87.5\%$ ) for all age and sex classes on the trapped region of the study area with the exception of adult females (22.2%). This reduced human-related mortality of adult females on the trapped region of the study area may have been the consequence of lower vulnerability to traps and hare snares based on their smaller home-range sizes (Yeager 1950) and lower movement rates (Buskirk and Lindstedt 1989; Chapter 1, Table 1.2), reduced levels of snaring and trapping activity on the study area experienced during this study, and the higher natural mortality rates of adult females evident in this study (Table 3.2) and reported elsewhere (Hodgman et al 1997, Payer 1999, Fryxell et al. 2001). However, over 26 million snare nights are set per year in Newfoundland to capture snowshoe hare (Fisher et al. 2005) with annual harvest averaging over 1,000,000 hares per year (range 200,000 to 2,000,000; Joyce 2001). Furthermore, Hodgman et al. (1994) reported a nonsustainable (0.574) mortality rate for adult females during a 6-week trapping season in Maine. Archibald and Jessup (1984) noted that growth of marten populations in the Yukon was highest in unharvested populations, suggesting that harvest mortality was primarily additive, and Thompson and Colgan (1987) suggested that trapping mortality of martens in Ontario was additive during years of low prey availability. Although my data suggested that mortality by human sources may partially compensate for natural mortality in Newfoundland (Figure 3.2), mortality would likely become additive where hare snaring, fox snaring, and trapping of furbearers in steel traps is permitted. This likely explains why martens have not persisted outside of protected areas in Newfoundland, or successfully recolonized previously-logged areas following regenerating of suitable habitat.

Female martens do not produce their first litter until 24 months of age (Strickland and Douglas 1987, Fortin and Cantin 1994, Mead 1994), have relatively small litters (Strickland and Douglas1987, Fortin and Cantin 1994), a relatively short reproductive life span, and appear to have a higher natural mortality rate (Strickland et al. 1982, Hodgman et al. 1994, Payer 1999, this study). Fryxell et al (2001) reported that although displaying a potential life span of 13 years, few animals lived to age 6 in their harvested population in Ontario. Thus, as noted by Krebs et al. (2004) for wolverine populations and Eberhardt (1990) for other low-density populations with inherently low potential rates of increase, maintenance of high adult female survival rates is paramount. Payer (1999) documented a median age of only 2 years among 80 nonjuvenile ( $\geq$  1-year old) resident martens in both harvested and unharvested populations in Maine. Phillips (1994) also reported no difference in age structure of females between an untrapped reserve and a trapped industrial forest in Maine. The median age of adult ( $\geq 1$ -year old) females at first capture during this study was also 2 (n = 76) for both the PMSA (n = 37) and the area outside the reserve (n = 39). Collectively, these data suggest that females in many marten populations have limited opportunities for reproduction; thus survival and recruitment of juvenile females into the breeding segment of the population may be of significant demographic concern to maintain positive rates of increase.

Previously, both Frederickson (1990) and Drew and Bissonette (1997) noted red fox predation on martens in Newfoundland; however, this study is the first to document red fox as the predominate predator of martens in Newfoundland. Given the limited number of potential predators in Newfoundland compared to mainland North America (Dodds 1984, Gosse and Montevecchi 2001, Hearn et al. 2006), foxes may experience ecological

release on the island. Moreover, essentially all of the martens killed by red fox were not consumed, suggesting interference competition. Marten (*Martes martes*) populations in Scandinavia increased in the 1980s, following a decline of red fox due to a sarcoptic mange epidemic, which was hypothesized to result from reduced risk of predation (Lindström et al. 1994; Helldin 1998) or reduced competition for *Microtus* prey (Storch et al. 1990). Further, it is noteworthy that live-trapping captures of martens in the Main River watershed (on the Northern Peninsula of Newfoundland) increased in 2005 following a recent (2002-2004) rabies outbreak that virtually eliminated red fox from the local landscape (M. McGrath, Newfoundland and Labrador Inland Fish and Wildlife Division, unpublished data). Thus, trapping pressure if targeted on red fox might actually improve survival of resident marten and dispersing juveniles through community-level effects.

### **PROPOSED CHRONOLOGY OF INITIAL DECLINE**

Trapping pressure on marten in Newfoundland must have been considerable at the turn of the century and was likely the principal cause of the decline and retraction of Newfoundland marten to remote, inaccessible tracts of virgin (i.e., old-growth areas) timber, as documented by Bergerud (1969). Both snowshoe hare and lynx populations irrupted (Dodds 1960, Joyce 2001) between 1896 and 1912 following the introduction of the hare during the period 1865-1876 (Dodds 1960); lynx populations irrupted to the point that in 1900, the government passed the "Lynx Extermination Bill" to control the populations (Dodds 1960).

The decline in marten numbers and distribution on the island of Newfoundland (Bangs 1913, Bergerud 1969, Dodds 1983, Forsey et al. 1995) was coincident with the

overexploitation and decline of marten and fisher populations throughout their North American ranges (Burt 1946, Yeager 1950, de Vos 1951, Quick 1956, Hagmeier 1956, Dodds and Martel 1971, Gibilisco 1994, Strickland and Douglas 1981, Krohn et al. 1994, Strickland 1994), as well as pine marten (*Martes martes*) and wolverine (*Gulo gulo*) populations in Scandinavia (Brainerd 1990, Landa et al. 1997, Helldin 2000). During this period (i.e., 1890-1940), the average annual marten harvest in Canada declined approximately 75% from 86,469 (1890-1900) to 22,883 (1930-1940; Novak et al. 1987).

A similar history of decline was also documented for other species in Newfoundland during this period: the Newfoundland wolf (*Canis lupus beothucus*) was extirpated between 1910 and 1923 (Allen and Barbour 1937); beaver (*Castor canadensis*) were nearly eliminated (Cameron 1958, Payne 1975); and caribou (*Rangifer tarandus*), lynx, and otter (*Lutra canadensis*) populations were so severely reduced that harvest seasons were closed (Dodds 1983). Likewise, trapping for martens on the island of Newfoundland was prohibited beginning in 1934 (Forsey et al. 1995).

The introduction of the snowshoe hare to Newfoundland, while providing an important future prey item (Gosse and Hearn 2005), may have simultaneously introduced substantial human-related incidental mortality in hare snares, and increased incidental mortality in furbearer traps, as both lynx and likely red fox populations irrupted following the first cyclic high of the snowshoe hare at the turn of the last century (Dodds 1960, Joyce 2001). By the mid 1950's, the distribution of martens in Newfoundland was restricted to the inaccessible areas of mature and overmature timber remaining on the island (Bergerud 1969) where forest harvesting was absent, human access was limited, thus overexploitation by trappers precluded by poor access. Understandably, with little

additional knowledge about the relative importance of other factors limiting this population, the restricted habitat association of martens to overmature forest and the expanding harvesting of mature and overmature forest, was interpreted as the explanation for the continual decline of the marten (Thompson 1991, Thompson and Curran 1995, Sturtevant and Bissonette 1997, Bissonette et al. 1997). My results suggest that mortality of marten incidental to hare snaring and furbearer trapping is the predominant reason why marten have not expanded outside of protected areas.

## CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This study documented survival rates of juvenile and adult (≥ 1 yr) Newfoundland marten inside and outside the PMSA wildlife reserve. Annual survival rates of both juvenile and adult marten inside the reserve were high and in agreement with those recorded for other unharvested populations; the marten population inside the reserve was likely a source population. In contrast, human-caused mortality was the prevailing source of mortality outside the reserve. Marten populations outside the reserve are likely experiencing negative rates of growth (i.e., sinks; Pulliam 1988, Pulliam and Danielson 1991) and are being maintained by dispersal from the PMSA reserve or other untrapped natural regfugia (Quick 1950de Vos 1951, Strickland 1994) inaccessible to humanrelated sources of mortality.

Newfoundland marten currently are absent from many areas of their historical range (Bergerud 1969). This historical range contraction was likely the result of elimination of marten via incidental mortality of martens from hare snaring and trapping from areas of otherwise suitable habitat. Thus recovery of this endangered population and recapture of this historical range will require prolonged positive growth from existing source

populations, particularly within the core range of the species in southwestern Newfoundland. Further, marten recolonizing historical range must be protected from excessive human-related mortality. Concomitant research, based on empirical data collected from a subset of the radiocollared marten (Chapter 2), suggest that habitat associations of Newfoundland marten are likely broader than previously understood. Thus, it appears that marten are capable of utilizing a broader range of stands than previously thought if protected from human-related mortality. However, recolonization of historical habitat where industrial forest operations are a dominant human activity will also require forest harvesting prescriptions that recognize the stand- and landscape-scale habitat attributes required by marten in Newfoundland. Recently developed predictive habitat occupancy models (Fuller 2006) will play a critical role in identifying historical range that currently has the highest probability of occupancy (suitability) where management regimes to eliminate human-related mortality can be initiated.

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APPENDIX

Table A1. Marten capture history. Sex, age, capture date, total number of captures, passive integrated transponder (PIT) tag number, and weight (g) at first capture for 72 and 87 martens captured in the Little Grand Lake and Red Indian Lake regions of the study area, respectively, southwestern Newfoundland, June 1995-August 2000.

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
Little (	Grand Lak	e Area				
1	F	А	21-Jun-95	11	122445146A	750
2	F	А	21-Jun-95	8	n/a	950
3	F	Y	24-Jun-95	6	n/a	700
4	F	А	27-Jun-95	11	n/a	700
5	$F^2$	n/a	28-Jun-95	17	n/a	570
6	F	А	30-Jun-95	4	n/a	775
7	F	Y	16-Oct-95	6	n/a	550
8	F	Α	09-Nov-95	5	n/a	600
9	F	Y	22-Feb-96	5	n/a	600
10	F	Α	28-Jun-96	3	n/a	730
11	F	А	03-Jul-96	3	n/a	1000
12	F	А	04-Jul-96	10	122451244A	700
13	F	J	11-Jul-96	2	n/a	500
14	F	J	11-Jul-96	1	n/a	510

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
15	F	А	01-Oct-96	4	122447134A	800
16	F	Y	02-Oct-97	2	n/a	800
17	F	J	03-Oct-97	4	n/a	710
18	F	А	04-Oct-97	2	n/a	845
19	F	J	07-Oct-97	1	n/a	680
20	F	А	24-Mar-98	2	122439512A	790
21	F	J	28-Oct-98	6	122451226A	~
22	F	J	28-Oct-98	2	122427751A	725
23	F	J	29-Oct-98	4	121414111A	800
24	F	J	30-Oct-98	1	121252710A	~
25	F	Y	30-Oct-98	4	121576551A	~
26	F	n/a	15-Mar-99	1	122445237A	750
27	F	Y	23-Jun-99	1	121447754A	800
28	F	Y	23-Jun-99	3	122569444A	775
29	F	А	09-Jul-99	1	122422271A	680
30	F	Y	29-Sep-99	1	122422540	825
31	F	А	30-Sep-99	3	n/a	800
32	$F^3$	J	30-Sep-99	1	122567240	800
33	F	J	30-Sep-99	4	122557760	710
34	F	А	04-Oct-99	1	122936510	760

Table A1. Continued.

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
35	М	J	01-Oct-93	9	n/a	1064
36	Μ	J	04-Oct-93	9	n/a	~
37	Μ	J	04-Oct-93	12	n/a	912
38	Μ	J	06-Nov-93	11	n/a	1250
39	Μ	J	22-Feb-95	17	122519691A	1100
40	Μ	Y	04-Apr-95	7	n/a	1300
41	Μ	А	22-Jun-95	7	n/a	1250
42	Μ	А	22-Jun-95	11	n/a	1200
43	Μ	Y	23-Jun-95	5	n/a	1500
44	М	А	24-Jun-95	1	n/a	1325
45	М	n/a	28-Jun-95	11	122422256A	1450
46	Μ	А	29-Jun-95	1	n/a	1450
47	М	Y	29-Jun-95	5	116531732A	1150
48	М	J	18-Oct-95	1	n/a	1100
49	М	А	02-Jul-96	7	n/a	1025
50	М	А	25-Sep-96	2	n/a	1525
51	Μ	J	28-Sep-96	6	121248353A	1025
52	М	А	30-Sep-96	1	n/a	1500
53	Μ	Y	11-Mar-97	8	n/a	1160
54	М	А	07-Jul-97	1	n/a	1350

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
55	М	А	02-Oct-97	2	n/a	1150
56	М	J	04-Oct-97	1	n/a	1000
57	М	А	06-Oct-97	2	121135485A	1170
58	М	А	27-Mar-98	1	n/a	1475
59	М	J	28-Oct-98	8	121576231A	1215
60	М	J	29-Oct-98	3	122445624A	~
61	М	J	30-Oct-98	3	122525237A	950
62	М	J	31-Oct-98	1	121147733A	1150
63	М	А	01-Nov-98	3	121552650A	1250
64	М	J	12-Mar-99	2	122445544A	1000
65	М	Y	26-Jun-99	1	121161222A	1240
66	Μ	Y	28-Jun-99	2	122449673A	1225
67	М	Y	08-Jul-99	2	122428770A	1260
68	М	J	29-Sep-99	5	122444537	1000
69	М	J	29-Sep-99	5	122811283	1100
70	М	J	30-Sep-99	1	122531313	1100
71	М	J	03-Oct-99	1	122433193	950
72	Μ	J	04-Oct-99	2	122422212	1060
Red In	dian Lake	Area				
73	F	А	18-May-96	1	n/a	700

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
74	F	А	18-May-96	9	n/a	950
75	F	А	19-May-96	1	n/a	750
76	F	А	19-May-96	1	n/a	750
77	F	А	20-May-96	6	121121340A	750
78	F	А	22-Jul-96	3	122553732A	625
79	F	J	24-Jul-96	1	n/a	500
80	F	J	24-Jul-96	1	n/a	660
81	F	n/a	26-Jul-96	1	n/a	840
82	F	J	28-Jul-96	1	n/a	660
83	F	А	30-Jul-96	4	n/a	825
84	F	А	17-Oct-96	4	n/a	750
85	F	А	19-Oct-96	1	n/a	850
86	F	А	22-Oct-96	2	n/a	725
87	F	А	22-Oct-96	1	n/a	725
88	F	А	23-Oct-96	1	n/a	700
89	F	J	24-Oct-96	1	n/a	775
90	F	А	13-Jun-97	1	n/a	1025
91	F	J	12-Sep-97	2	n/a	640
92	F	А	14-Sep-97	1	n/a	700
93	F	А	16-Sep-97	2	121477525A	690

Table A1.	Continued.
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No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
94	F	А	16-Sep-97	1	n/a	775
95	F	Y	10-Jun-98	2	121244715A	700
96	F	Y	12-Jun-98	1	121575545A	850
97	F	J	07-Oct-98	1	121355694A	750
98	F	Y	07-Oct-98	5	121616456A	700
99	F	Y	07-Oct-98	2	121155446A	700
100	F	J	07-Oct-98	2	121259546A	1000
101	F	J	09-Oct-98	2	116446685A	850
102	F	J	09-Oct-98	1	none	800
103	F	J	12-Oct-98	3	121357164A	750
104	F	J	14-Oct-98	1	121351333A	750
105	F	J	20-Nov-98	1	122554145A	650
106	F	Y	06-Jun-99	1	122422452A	700
107	F	Y	07-Jun-99	1	122433563A	750
108	F	Y	09-Jun-99	1	122553327A	700
109	F	Y	10-Jun-99	2	122433167A	825
110	F	Y	14-Sep-99	2	121155760A	875
111	F	n/a	09-Jun-00	1	122531594A	850
112	М	А	18-May-96	4	121509185A	1200
113	Μ	А	19-May-96	1	n/a	1300

Table A1.	Continued.
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No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
114	М	А	19-May-96	3	n/a	1200
115	М	А	19-May-96	1	n/a	1450
116	М	А	19-May-96	2	n/a	1500
117	М	А	19-May-96	3	n/a	1250
118	М	А	20-May-96	4	n/a	1300
119	М	А	20-May-96	2	n/a	1150
120	М	А	20-May-96	3	n/a	1200
121	М	А	21-May-96	3	n/a	1300
122	М	J	24-Jul-96	3	n/a	610
123	М	J	25-Jul-96	1	n/a	875
124	М	А	28-Jul-96	4	n/a	1015
125	М	J	18-Oct-96	1	n/a	1000
126	М	J	20-Oct-96	3	n/a	1100
127	М	Y	15-Jun-97	2	n/a	1100
128	М	А	19-Jun-97	2	121611127A	1250
129	М	J	12-Sep-97	1	n/a	1100
130	М	J	16-Sep-97	1	n/a	1300
131	М	А	04-Jun-98	1	121133645A	~
132	М	А	05-Jun-98	4	121256537A	1275
133	М	Y	05-Jun-98	2	121613111A	1000

Table A1. Continued.

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
134	М	А	07-Oct-98	4	121352270A	1100
135	М	n/a	07-Oct-98	3	121261696A	1200
136	М	Y	08-Oct-98	2	121147396A	1300
137	М	J	08-Oct-98	3	121155696A	1150
138	М	Y	08-Oct-98	2	121355656A	1150
139	М	J	08-Oct-98	1	121515447A	1200
140	Μ	А	10-Oct-98	1	121473155A	1450
141	М	J	10-Oct-98	3	121215374A	1000
142	М	J	10-Oct-98	2	116563222A	1100
143	М	J	13-Oct-98	1	121233564A	1300
144	М	J	15-Oct-98	2	121261494A	1250
145	М	n/a	02-Jun-99	1	121474096A	1125
146	М	Y	02-Jun-99	2	121259511A	1100
147	М	n/a	02-Jun-99	1	122373444A	1450
148	М	Y	03-Jun-99	2	116631752A	1360
149	М	Y	03-Jun-99	3	122418692A	1200
150	М	А	04-Jun-99	1	122418220A	1260
151	М	Y	06-Jun-99	1	121422231A	1250
152	М	Y	09-Jun-99	1	122521250A	1200
153	М	Y	10-Sep-99	2	122433247A	1110
Table A1. Continued.

No.	Sex	Age Class <sup>1</sup>	First Capture	Total Captures	PIT Tag #	Weight
154	М	n/a	11-Sep-99	5	121353220A	1090
155	М	J	12-Sep-99	2	122444623A	1050
156	М	J	16-Sep-99	1	122566323A	1060
157	М	n/a	21-Jun-00	3	121164454A	1160
158	М	n/a	24-Jun-00	1	121576647A	1110
159	Μ	n/a	22-Jul-00	1	121247570A	1380

<sup>1</sup> Age at first capture.

<sup>2</sup> Originally captured in October 1993 during a previous study; minimum age 2 years.

<sup>3</sup> Originally captured in October 1993 by Drew (1995).

## **BIOGRAPHY OF THE AUTHOR**

Brian J. Hearn was born in St. John's, Newfoundland, Canada, and graduated from the University of New Brunswick, Fredericton in 1979, where he obtained a Bachelor of Science in Forestry with a double major in Forestry and Wildlife Biology. From 1979-1984, Brian was employed as a Wildlife Biologist with the Newfoundland Wildlife Division, where he conducted field research on the Newfoundland Arctic hare (*Lepus arcticus*). This research formed the basis for his Master of Science degree (Wildlife Ecology) from the University of Wisconsin, Madison in 1985. Brian published two papers from his Master's research, one in the *Canadian Journal of Zoology* (1987) and the other in the *Wildlife Society Bulletin* (1988).

Between 1987 and 1990, Mr. Hearn was employed as a Research Biologist with the Newfoundland Wildlife Division in Goose Bay, Labrador where he was involved in research and management of various woodland caribou (*Rangifer tarandus*) herds. He published two papers on his caribou work – authoring one in the *Canadian Journal of Zoology* and as a co-author for a paper published in *Rangifer*. In 1990, Mr. Hearn took a position with Natural Resource Canada, Canadian Forest Service, where he is currently employed as a Forest Wildlife Ecologist.

In 1995, Brian initiated a 5-year cooperative research project with the Newfoundland Inland Fish and Wildlife Division, Corner Brook Pulp and Paper, Abitibi Consolidated, and the Western Newfoundland Model Forest to study the ecology and population demography of the endangered Newfoundland Marten (*Martes americana atrata*). After 3 years of conducting field research, Brian entered the Doctoral program in Wildlife Ecology at the University of Maine in September 1998. Brian returned to

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Newfoundland in December 1998, and completed fieldwork in August 2000. In 2005, Brian co-authored a paper on the seasonal diet of martens in Newfoundland that appeared in the *Canadian Field Naturalist*, and in 2006 authored a paper on the discovery of the introduction of the Southern Red-backed Vole (*Clethrionomys gapperi*) to Newfoundland and the implications of this introduction for the Newfoundland marten, also in the *Canadian Field Naturalist*. Brian has been a member of the Newfoundland Marten National Recovery Team since 1996, and Co-chair of the team since 2001. He also serves on two other national recovery teams; the Southern Labrador Woodland Caribou Herds Recovery Team, and the Newfoundland Red Crossbill (*Loxia curvirostra percna*) Recovery Team. Brian is presently a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in May 2007.