

Space use behavior and multi-scale habitat selection of American marten (*Martes americana*) in northeastern Minnesota

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Chapter 1: Space use and habitat selection of American marten in Minnesota

Overview

Track counts and anecdotal reports indicate that the American marten (*Martes americana*) population in Minnesota has declined over the past 10 years. Previous work has demonstrated that marten populations respond negatively to habitat alterations that reduce forest age, structural complexity, or forest cover at low thresholds, but few studies have described marten habitat selection in Minnesota or the south-central portion of the marten range. We deployed radiocollars on 170 marten from 2008-2012 and used location data to describe space use behavior and habitat selection at landscape and stand scales. The majority of adult marten were residents in established home ranges, while juvenile marten were more likely to establish temporary home ranges or disperse from their capture site. Males used larger home ranges than females, and home range sizes were similar to those reported elsewhere. We evaluated habitat selection at both population and individual levels. Population-level selection considers habitat use by the average marten, while individual-level selection compares each individual marten's habitat use to habitat availability. At the population level, marten used habitat types in proportion to their availability at both landscape and stand scales. However, most individual marten used habitat types disproportionately, but there was a high degree of variability as to which forest cover types were preferred. Additional work is needed to identify the factors contributing to individual differences in habitat use and to determine whether individual differences affect access to prey species and other critical resources.

Introduction

Characterizing animal space use behavior and habitat associations is important for understanding how individuals interact with their environment to acquire the resources necessary for survival and reproduction. Habitat selection and space use behavior are ecologically important processes that integrate an animal's need for energy, nutrients, and other resources with the spatial heterogeneity of these resources in their environment. The type of resources animals acquire from their environment varies among species and may include food and water, access to mates, protection from the physical environment, movement corridors, and habitat features that reduce competition and/or predation (Powell 2012, Powell and Mitchell 2012). For animals of conservation concern, a detailed understanding of how individuals use habitat is necessary for predicting the effects of human- or climate-induced landscape alterations, identifying critical habitat for conservation protections, and designing management strategies to maintain adequate habitat on the landscape.

Space use behavior is commonly described by estimating the size of an animal's home range from location data and quantifying habitat associations and spatial requirements from these home range estimates. Home ranges are dynamic entities that reflect an animal's experience with and cognitive map of its environment (Powell 2000, Spencer 2012). Powell and Mitchell (2012) defined a home range as the portion of an animal's cognitive map that it keeps updated. While this definition is currently impossible to measure for free-ranging animals, it highlights that a home range is based on both spatial memory and a decision by the animal that should reflect fitness-based

tradeoffs. Home range size and position may change over the course of the year as a result of seasonal changes in resource availability and the physical environment.

Considerable effort has been invested on developing statistical models to quantify home range size and position from movement and location data with the goal of finding the best estimator (Powell and Mitchell 2012, Fieberg and Börger 2012). Location data are often used to estimate density of use, otherwise known as a utilization distribution, with respect to time spent in different areas (Powell 2000, Powell and Mitchell 2012, Fieberg and Börger 2012). More recently, models have been developed that incorporate movement paths into home range estimates (Fieberg and Börger 2012, Benhamou and Cornelis 2010, Bullard 1999, Moorcroft 2012). Despite advances in home range estimation methods, there has been relatively less effort to describe the biological processes that result in space use patterns (Powell and Mitchell 2012).

Home range sizes for American marten vary greatly among studies. Variation in home range size among studies is not correlated with body size, geography, or weather and climate indices (Buskirk and McDonald 1989, Smith and Schaefer 2002). However, direct comparison of home range estimates between studies is challenging because of differences in methods used to obtain locations, varied re-location frequency, and differences in software and/or method used to estimate home ranges among studies.

Despite variability in home range size, certain patterns are consistent among studies. Marten use much larger home ranges than predicted by body size (Harestad and Bunnell 1979, Lindstedt et al. 1986). Large home range sizes have important implications for management, because marten populations exist at low densities and

habitat loss can reduce occupancy at relatively low thresholds (Chapin et al. 1998).

Variation in home range size within a particular region has been linked to habitat quality and prey abundance. Marten have larger home range sizes in regenerating forests than in older forests (Thompson 1994), home range size is positively correlated with proportion of avoided habitat types within home ranges (Gosse et al. 2005) and marten expand home range sites as prey abundance decreases (Thompson and Colgan 1987). These results along with large spatial requirements suggest that selection of home range location influences individual fitness (Thompson et al. 2012).

Male marten home ranges are approximately twice as large as female home ranges (Buskirk and McDonald 1989, Katnik et al. 1994, Smith and Schaefer 2002, Dumyahn et al. 2007). Male and female home ranges overlap considerably, but male home ranges do not overlap with home ranges of other males (Clark et al. 1989, Katnik et al. 1994, Bull and Heater 2001). Home range size does not vary seasonally and most individual marten have a high degree of home range fidelity in successive years (Clark et al. 1989, Phillips et al. 1998, Bull et al. 2005). However, males occasionally change home range location in response to available space as a result of mortality of other males, and females have been observed abandoning rather than expanding home ranges as resource availability declines (Katnik et al. 1994, Phillips et al. 1998).

Habitat selection is a hierarchical process because selection at larger spatial scales limits available habitat types at smaller spatial scales (Johnson 1980, Urban et al. 1987). Analysis of habitat selection at broad spatial scales relies on assigning habitat types to preference categories based on the proportion of that cover type in the home range or

time spent in each habitat type relative to availability. At smaller spatial scales, site-attribute designs allow researchers to describe features such as vegetative cover and physical habitat structure that correlate with sites used for specific functions such as resting, denning, or foraging (Garshelis 2000). Marten select habitat at multiple spatial scales including landscape scale (home range scale; 2nd-order selection *sensu* Johnson 1980), stand scale (within home ranges; 3rd-order selection *sensu* Johnson 1980), and at the level of individual sites within stands. Most studies on within-stand habitat selection by marten have focused on selection of habitat elements for resting and denning (see Chapter 2).

Marten occupy a range of forest types at landscape and stand scales, although highest relative use occurs in mature forest stands. Mixed-wood and conifer stands are typically preferred (Potvin et al. 2000, Proulx 2006, Thompson et al. 2012), although there are some regional differences. In western North America, marten select mature conifer-dominated stands (Slough 1989, Latour et al. 1994, Bull et al. 2005, Slauson et al. 2007), while marten in eastern North America select mature deciduous and deciduous-dominated mixed-wood stands (Chapin et al. 1997, Potvin et al. 2000, Payer and Harrison 2003, Dumyahn et al. 2007). These differences likely reflect variation in distribution and abundance of important habitat features such as forest structure and prey abundance among forest types in different regions, but may also reflect differences in availability of forest types among regions. Habitat patches selected by marten are characterized by closed canopies, a high density of fallen logs and snags, large quantities of coarse woody debris, and large mean basal area of live trees (Spencer et al. 1983, Bowman and

Robitaille 1997, Payer and Harrison 2003, Bull et al. 2005, Fuller and Harrison 2005). Vertical and horizontal structure provides protection from predators and access to the subnivean layer for foraging and thermally efficient rest sites during winter (Buskirk and Powell 1994, Slauson 2007). However, most studies that have compared forest structure to relative use by marten took place in western and eastern North America with little data from the western Great Lakes region in the south-central portion of the marten range (but see Gilbert et al. 1997).

Habitat types used at lower proportions than expected based on availability include early successional forests regenerating from timber harvest or natural disturbances (Latour et al. 1994, Potvin et al. 2000, Chapin et al. 1998) and open, non-forested habitat types such as wetlands, open bogs, and meadows (Spencer 1983, Dumyahn 2007, Bull et al. 2005). However, marten will use young, recently disturbed and relatively open forest patches if there is adequate forest structure or prey density present (Latour et al. 1994, Paragi et al. 1996). In general, marten exhibit strong selection at the landscape scale, possibly because selection of home range location is related to individual fitness (Thompson et al. 2012). Occupancy declines when greater than 25-30% of the landscape is composed of stands regenerating from clear-cutting and other disturbance types (Chapin et al. 1998, Potvin et al. 2000). Habitat selection at landscape and stand scales appears to be similar for males and females and among age classes (Chapin et al. 1997, Dumyahn et al. 2007). However, there have been no direct comparisons of habitat use among dispersing and resident marten.

Track counts and anecdotal evidence suggest that the marten population has declined in Minnesota over the last ten years. We fitted American marten with radiocollars in northeastern Minnesota and used location data to describe space use behavior and habitat requirements of radiocollared marten. This work is necessary for several reasons. Home range sizes vary greatly across North America while marten space requirements in Minnesota may not be accurately reflected in the limited data that is available (Mech and Rodgers 1977). Habitat preferences have been studied extensively in eastern and western North America but few studies exist from central North America. Although studies have taken place on re-introduced populations in Michigan and Wisconsin, management status differ between these studies and the marten population in Minnesota. Variation in forest composition, topography, forest management history, and status of marten in central North America make extrapolation of results from other regions problematic. Forest harvest is known to impact marten, but most of these studies and those quantifying forest structural requirements of marten were done in different forest communities than those that exist within the marten range in Minnesota. We tested several hypotheses to determine which factors influenced home range size, space use behavior, and habitat use. We hypothesized that males would establish larger home ranges and that home range size would be influenced by age. We also predicted that juvenile marten would be more likely to disperse or establish temporary home ranges than adults because juveniles must locate unoccupied areas to establish a home range after leaving their natal territory. Furthermore, we hypothesized that habitat selection

would reflect use of stands with adequate structural complexity at both landscape and stand scales.

Study Area

Our study site was located in the central portion of the Superior National Forest (47°30'N, 91°52'W) in Lake and St. Louis counties of northeastern Minnesota (Fig. 1.1). The Superior National Forest is entirely publically owned, although there are state, county, and private land inholdings within the Superior National Forest boundary. Private land includes residential and commercial properties. In general, public land throughout the Superior National Forest is managed for timber harvest, recreation, and conservation of native plant and animal communities. Vegetation in northeastern Minnesota is characteristic of the Laurentian Mixed Forest Ecological Province (Minnesota Department of Natural Resources [MN DNR] 2013). Upland mixed coniferous-deciduous forest covered the majority of our study area (~69%). Mixed-wood forest consisted of aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), and white spruce (*Picea glauca*). Lowland conifer forest covered approximately 15% of our study area and included swamps dominated by black spruce (*P. mariana*), tamarack (*Larix laricina*), and white cedar (*Thuja occidentalis*). Upland conifer forest consisted of red pine (*Pinus resinosa*) and jack pine (*P. banksiana*) stands on shallow, rocky soils. Deciduous forest made up a relatively small proportion of our study area, and included stands of aspen, paper birch, red maple, and occasionally sugar maple (*Acer saccharum*).

Understory vegetation typically consists of beaked hazel (*Corylus cornuta*), mountain maple (*A. spicatum*), alder (*Alnus* spp.) in lowland areas, and saplings of common canopy species including aspen, birch, balsam fir, and black spruce. Historically, fire was the main form of disturbance, while logging is the major current disturbance type (White and Host 2008). In the Boundary Waters Canoe Area of northern Minnesota, smaller fires occurred at 4-year intervals pre-settlement, while larger fires occurred approximately every 25 years during the same time period (Heinselman 1973). Vegetation in regenerating clear-cut areas consisted of the same canopy and understory species typically found in forested stands along with raspberries (*Rubus* spp.), pin cherry (*Prunus pensylvanica*), and choke cherry (*P. virginiana*).

Northeastern Minnesota has a continental climate with long, cold winters and short, warm summers. Temperatures average 18.6°C in July and -14.7°C in January (NOAA 2013). The area receives an average of 71.0 cm of rainfall and 142.7 cm of snowfall annually, with persistent snow cover usually present from December to April. There is little topographical relief throughout the study area, with elevations ranging from 450 - 600 m above sea level. Permanent water in the form of lakes and rivers covers approximately 2.7 % of the study area (~4860 ha).

Marten are managed as a furbearer in Minnesota. Unregulated trapping and habitat loss from logging and development substantially reduced the marten population in Minnesota in the early twentieth century. Fur harvest was closed from 1935-1985 (Mech and Rogers 1977, Erb 2013). Currently, harvest is restricted to a 6-day season with a limit of 5 marten per trapper. Since the beginning of the study, $1,947 \pm 173$ (SE) marten

have been harvested annually in Minnesota, with $62\% \pm 2\%$ of the harvest taking place in Lake and St. Louis counties where the study site is located (Erb 2013).

Methods

Animal capture and radiotelemetry

Marten were captured from December through February each winter from 2007-08 through 2011-12. Marten were captured using cage traps (Tomahawk Model 106 or 108) baited with either deer (*Odocoileus virginianus*) or beaver (*Castor canadensis*) meat with a commercial lure placed in or above the trap. Traps were checked daily to ensure all captured marten were processed and released as soon as possible after capture. Captured marten were immobilized with ketamine (20 mg/kg) and xylazine (2 mg/kg; Kreeger and Arnemo 2012). While anesthetized, marten were placed on chemical hand warmers or heating pads connected to a power inverter and a 12 volt battery to keep the marten warm during processing. Respiration, heart rate, and body temperature were monitored while under anesthesia. Marten were fitted with a Holohil MI-2 radiocollar (30-35 g) and both ears were tagged with monel #1 tags (National Band and Tag Co., Newport, KY). Sex was determined, and a pre-molar was extracted for aging. We took morphological measurements including weight, body length, tail length, hind foot length, and chest, neck, and head circumference. After processing, xylazine was reversed with an injection of yohimbine (0.1 mg/kg) and marten were allowed to recover for 40 minutes before being released at the trap site. Animal capture and handling protocols were consistent

with guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Marten location data were collected at approximately 7-10 day intervals from a fixed-wing aircraft. We also radiotracked marten on foot to locate rest sites and reproductive dens. Coordinates were taken at rest and den site locations using handheld GPS receivers (GPSmap 76 or eTrex30, Garmin, Olathe, KS). Prior to generating home ranges from the location data, we introduced random error to duplicate locations (e.g., multiple locations at the same den or rest site) because certain bandwidth-selection algorithms are sensitive to identical x- and y-coordinates for >1 location (Silverman 1986). Random error was added to each duplicate location. Displacement distances were selected from a random normal distribution. Duplicate locations were displaced 11.3 ± 0.8 m, which corresponded to the maximum estimated error observed from our GPS receivers. Intensive radiotracking of females during the denning period resulted in lower average relocation interval for female marten compared to males. We randomly removed locations from female study animals during these months until there was no difference in average time between locations for males and females.

Home range and core area estimation

Home range and core area estimates were made using Geospatial Modeling Environment Version 0.7.2.1 (Beyer 2012, R Core Development Team 2011) and ArcMap 10.1 (Environmental Systems Research Institute Inc., Redlands, California). We generated annual home ranges using three different methods to examine how home range estimation

methods affected estimates of home range size and habitat selection. Annual 95% MCP home ranges were estimated for all marten with ≥ 20 locations over ≥ 200 days. We removed 5% of locations that were furthest from the arithmetic mean of all coordinates for each location set prior to generating an MCP home range (Rodgers and Kie 2011). We also estimated annual 95% home ranges using fixed-kernel density estimators (Worton 1987, 1989) for marten with ≥ 25 locations using two different bandwidth selection algorithms: least-squares cross-validation (LSCV) and plugin (Worton 1995, Jones et al. 1996, Gitzen et al. 2006). We used the plugin method because we felt that it produced home range estimates that fit our data better than other available methods. LSCV was used because it is one of the most common methods used for kernel analysis (Worton 1995, Rodgers and Kie 2011) and because other researchers have used LSCV with fixed-kernel density methods to estimate marten home range size (Dumyahn et al. 2007). A grid size of 10 m was used for both bandwidth selection methods. While adaptive-kernels have been used to estimate marten home ranges (Wright 1999, Bull and Heater 2001), we used fixed-kernel methods because adaptive-kernels resulted in over-smoothed estimates of the utilization distributions. We removed portions of home ranges overlapping lakes if they comprised $>3\%$ of home range area.

In addition to estimating home range size, we classified location sets into space use categories based on distribution of locations throughout the year. Marten were not classified into a space use category unless they had a sufficient number and duration of locations for MCP home range analysis. Marten were classified as residents if they appeared to have established a home range and had relatively few outliers. We classified

marten as dispersing if initial locations were relatively far apart and followed by establishment of a home range after movement across the landscape. Marten that initially appeared to have established a home range before moving a relatively large distance were classified as temporary residents. We compared proportion of marten in each space use category among sexes and age classes using a chi-square test of independence. Dispersal distances were calculated for all marten classified as temporary residents or dispersing. For dispersing marten, we calculated dispersal distance as the distance between initial capture site and the centroid of any apparent home range or activity center. If no home range was established before mortality and there was no apparent center of activity, we measured the distance between the location of the trap site and the mortality location. Dispersal distances for temporary residents were measured as the distance between centroids of partial-year home ranges. Dispersal distances were calculated in ArcMap10.1.

We used one-factor ANOVA to test for effects of home range estimation method (MCP, LSCV, plugin) on natural log-transformed home range sizes of resident marten. We tested for effects of age class and sex on natural log-transformed home range size of resident marten using two-factor ANOVA. Separate tests were run on each home range estimation method. Marten were classified into age classes based on age at capture. Because trapping occurred during winter, age estimates were in half year intervals rather than integers. Marten were classified as adults if they were ≥ 1.5 years old at time of capture because females can give birth to their first litter at 24 months old (Strickland et al. 1982). Marten that were 0.5 years old at capture were classified as juveniles. We

randomly selected a single set of annual locations for any marten tracked for multiple years.

A core area represents the part of an animal's home range where use is concentrated (i.e., the part of the home range used at maximum intensity; Vander Wal and Rodgers 2009). We estimated core areas of annual fixed-kernel home ranges using area/probability curves (Vander Wal and Rodgers 2009, Powell 2000). A linear area/probability curve indicates random use of a home range and functions as a testable null hypothesis, whereas a concave relationship indicates clumped space use (Powell 2000). We estimated core areas for all marten with ≥ 25 locations distributed over ≥ 200 days. We used fixed-kernel methods to calculate the area of isopleth values between 5-95% at 5% intervals. The area of each isopleth was divided by that of the 95% isopleth to determine the percent of home range area represented by each isopleth value. Percent of home range area was transformed using the natural logarithm, transformed values were plotted as a function of isopleth value, and an exponential regression function was fit to these data (Bingham and Noon 1997, Powell 2000). This exponential regression function was not forced through the origin, because animals must occupy some minimal, non-zero amount of space (Vander Wal and Rodgers 2009). We used the first derivative of the regression equation to determine the isopleth value for which the slope was equal to one (Vander Wal and Rodgers 2009). A separate area/probability curve was used to determine the core-area isopleth for LSCV and plugin home range methods for each resident marten.

We summarized the isopleth value predicting the core area and used ANOVA to determine whether sex or age class influenced the isopleth value representing the core area. We used ANOVA on core areas to test for effects of age class and sex on core area size of marten. Core areas were natural log-transformed so that data were homoscedastic and normally distributed. We used paired *t*-tests on isopleth values estimating the core area and natural log-transformed core area sizes to test whether LSCV and plugin methods produced different estimates of marten core area size or isopleths used to define the core area.

Home range fidelity

Eleven marten (5 females, 6 males) were monitored for multiple years (range 2-4) and had enough locations for separate home range estimates each year. To determine home range fidelity, we calculated overlap between consecutive pairs of annual home ranges using a coincidence index (Cole 1949, Ferreras et al. 1997, Burdett 2008). The formula we used was:

$$C\% = \frac{2A \cap B}{A + B} \times 100$$

where C% is the coincidence index, or estimate of overlap between consecutive home ranges, $A \cap B$ is the area of overlap between consecutive home ranges, A is the area encompassed by the first home range, and B is the area encompassed by the second home range. We did not estimate fidelity for marten monitored in multiple years unless they were a resident for at least two full years. For marten with >2 years of locations, we

calculated a coincidence index for each consecutive pair of home ranges and used the average of these indices in further analysis. Coincidence indices were calculated separately for MCP and the two types of fixed-kernel home ranges.

Habitat selection

We determined habitat selection of marten by comparing proportion of used and available habitat at two spatial scales. To determine how marten select home ranges at the landscape scale, we estimated availability of habitat types throughout the study area by generating 50 random points within the study area and used ArcMap 10.1 to buffer each random location by the average home range size. The study area was defined as the 100% MCP of all marten locations. We compared cover type composition between home range estimators and buffered random points using chi-squared goodness-of-fit tests to determine whether cover types were used in proportion to their availability with each marten as the experimental unit (Neu et al. 1974). When the results of the chi-square test were significant, we used Bonferroni confidence intervals to determine which cover types were used differently than expected based on availability.

Individuals within a population may select habitat differently. We used chi-square goodness-of-fit tests to compare landscape-wide habitat availability to individual habitat use to determine whether there were individual-based differences in habitat selection. When individual chi-square tests were significant, we calculated Manly-Chesson selection indices for each cover type to determine which cover types were being used at a higher or lower proportion to their availability (Potvin et al. 2000; Chesson

1983, Manly et al. 1993). The Manly-Chesson selection index was calculated using the formula:

$$\alpha_i = \frac{Pu_i/Pa_i}{\sum_{i=1}^k Pu_i/Pa_i}$$

where Pu_i is the proportion of habitat i within the home range and Pa_i is the proportion of habitat type i across the landscape. Selection indices greater than $1/k$ for k different habitat types indicate the habitat type is used in greater proportion than expected (i.e., selected) and indices less than $1/k$ suggest lower proportional use (i.e., avoided). We used the non-parametric Kruskal-Wallis test to compare relative selection of each habitat type by individual marten. Kruskal-Wallis tests were used because data were non-normal and were not homoscedastic. When Kruskal-Wallis tests were significant, we used the mean score of each habitat type to rank individual selection of each habitat type relative to others. All figures displaying Manly-Chesson indices have a horizontal line to indicate the average $1/k$ value for each test.

Stand-scale habitat selection (3rd-order selection, Johnson 1980) was determined using two different methods. First, we compared cover type composition between home ranges and core areas. We also compared the cover type composition of individual locations to home range habitat composition. We used all three home range estimation methods separately. Comparison of cover type composition between core areas or actual locations and home ranges was made using chi-square goodness-of-fit tests and Bonferroni confidence intervals with individual marten as the experimental unit. We also

used Manly-Chesson indices and Kruskal-Wallis tests on individual comparisons to characterize stand-level selection at the individual level.

We tested for sex-based differences in habitat selection by comparing Manly-Chesson selection indices among males and females at landscape and stand scales. Student's t-tests were used if data satisfied conditions for this test. For non-normal indices, we used the Kruskal-Wallis non-parametric test. Separate tests were performed on each habitat type.

To determine the effect of telemetry location error on habitat use we simulated up to 300 m of error for all locations using Geospatial Modeling Environment software (Beyer 2012). Displacement distances were selected from a uniform distribution as a worst-case scenario analysis. We used a chi-square goodness of fit test to compare cover type composition between telemetry locations and 10 replicates of simulated error with the individual marten as the experimental unit.

Cover type composition of various locations and buffered regions was determined using Land Use Land Cover (LULC) classified LANDSAT satellite imagery collected from 1995-1996 (MN DNR 2001). These data are available in both raster and vector formats and have a resolution of 30 m. LULC data was approximately 95% accurate when first classified (MN DNR 2001). However, because the source imagery was collected 10-15 years ago, we took several steps to improve classification accuracy. Regenerating forest, which may now be young forest, and areas logged since these data sets were collected represented the two cover types where error was most likely to occur. We used aerial photographs to digitize recent clear-cuts from 1991 through 2012. The

majority of imagery used came from Farm Services Administration color orthophotos. Imagery used to map clear-cuts was collected in 1991, 2003-2004, 2005, 2006, 2007, 2008, 2009, 2010, and 2011. We removed LULC data within digitized clear-cuts and merged clear-cut polygons with remaining LULC data to make year-specific habitat layers for each study year from 2008 through 2012. To improve the accuracy of patches classified as regenerating forest in the original data set, we compared LULC data to aerial photos and re-classified regenerating patches as necessary. We assessed the accuracy of the final land cover data by comparing cover types derived from our habitat layer to ground-truthed habitat type at 141 prey transect locations and 99 random sites used for vegetation sampling. Classification accuracy was summarized overall and by forest cover type.

Structural complexity of habitat types

We quantified forest structure among different forest cover types because structural complexity is an important habitat component for marten. Plot locations were randomly selected within upland conifer, lowland conifer, deciduous, and mixed coniferous-deciduous forest cover types. Stands were classified as mixed-wood in LULC data if neither coniferous or deciduous trees made up >67% of the canopy. To avoid confounding effects of stand age we stratified cover types into five age classes: 20-40 yr, 40-60 yr, 60-80 yr, 80-100 yr, and >100 yr. Distribution of plots within cover type-age strata was balanced, except that there were not enough >100 yr deciduous stands for adequate sample sizes. We increased the number of 80-100 yr old deciduous stands to

compensate for the lack of >100 year old sample locations. Stand ages were determined using data obtained from the Field Sampled Vegetation (FSVeg) data provided by the U.S. Forest Service.

At each sample location, we measured a single circular 0.04 ac (14.6 m diameter) plot. Basal area and tree density were calculated by measuring the diameter at breast height (dbh) of all live trees within the sample plot. Canopy closure was measured with a convex spherical densiometer using Strickler's modification (Strickler 1959). We averaged the canopy closure measurements positioned at the plot boundary at three bearings (30°, 150°, and 270°) from the plot center. Understory cover density was measured using a cover pole. We took readings at heights of 0.5 m, 1.0 m, 1.5 m, and 2.0 m. The cover pole was placed at the plot boundary where canopy closure was measured, and we took readings from the center of the plot. Density and volume of coarse woody debris (CWD) was measured along three transects from plot center to plot boundary at 30°, 150°, and 270°. We measured CWD if it intersected the sampling transect and met the following criteria: diameter ≥ 7.6 cm at intersected with sampling transect; diameter of ≥ 7.6 cm for ≥ 91.4 cm in length; and met criteria for classification into decay classes 1-4 (Woodall and Monleon 2008). Volume was estimated as the volume of a cone frustrum, using length and diameter measurements at each end. Sapling density was calculated as the average of three measurements taken on micro-plots (4.14 m diameter) centered at the intersection between CWD transects and the plot boundary. Snag density was measured by counting the number of standing dead trees within the plot, and snag volume was estimated as the volume of a cone frustrum, using the height and diameters at

the small and large ends. Finally, we estimated the density of potential resting and denning structures by counting structures used by marten (see Chapter 2) at all vegetation plots. Potential structures were only counted if they were large enough for a marten to enter and fit completely within. Measurement protocols were largely based on USDA Forest Service's Forest Inventory Analysis (FIA) protocols. Because FIA data is collected nationwide every 5-10 years, using FIA protocols will allow our results to be directly comparable to estimates of forest structure collected elsewhere and will allow us to assess habitat suitability in the future without collecting additional data ourselves (Zielinski et al. 2006).

Statistical analysis

All statistical tests were performed using JMP software (JMP v.10.0, Statistical Analysis System Institute Inc., Cary, NC). Data were transformed when necessary to meet criteria for ANOVA and other parametric tests. Significance level for all statistical tests was set at $\alpha=0.05$.

Results

We captured and radiocollared 170 American marten (89 males, 81 females) from 2008-2012. The average time between locations was 10.2 ± 0.1 days. We categorized annual space use behavior for 112 annual location sets from 86 marten with sufficient sample size and sample durations for home range estimation. Of these location sets, 80 (71%) were classified as residents, 15 (13%) dispersed after capture, and 17 (15%)

established temporary home ranges after capture but later dispersed to a new territory. We classified five marten that we lost radio-contact with before obtaining adequate sample size into space use categories because they were harvested by fur trappers outside of our study area allowing us to assess their movement over the landscape through time. One of these marten was classified as a temporary resident because it appeared to establish a home range before dispersing, while the remaining four were classified as dispersing. Including these marten, 68% were residents, 16% dispersed after capture, and 15% were temporary residents. Space use classifications were not equally distributed among age classes ($\chi^2 = 21.69$, *d.f.* = 2, $P < 0.0001$). Juvenile marten were more likely to disperse or establish temporary home ranges than adults. Fifty-five percent of juveniles were non-residents, while 86% of adults were residents. There was no difference in space use category among males and females ($\chi^2 = 5.22$, *d.f.* = 2, $P = 0.074$).

Non-resident marten dispersed 17.4 ± 6.4 km from the trap location to an established home range or mortality location, although average dispersal distance was skewed by a few marten that dispersed large distances. The five marten that dispersed out of our study area and were trapped by fur-trappers dispersed 59.8 ± 21.2 km (range: 17.4 – 130 km), while the remaining 18 non-residents dispersed 5.6 ± 1.1 km (range: 0.8 – 19.4 km). We did not have sufficient sample sizes to test for the effect of sex on dispersal distance, but males and females had similar average dispersal distances (males: 17.3 ± 7.6 km; females: 17.5 ± 11.1 km) and large dispersal events were documented for both sexes (130 km for female and 86 km for male).

We calculated MCP home ranges for 83 resident location sets and fixed-kernel home ranges for 77 resident location sets. This included location sets for four dispersing marten that established home ranges within three weeks of capture. Locations prior to home range establishment were removed for these marten before delineating home ranges. After randomly selecting one annual home range per marten that was monitored for multiple years, we used 66 fixed-kernel and 70 MCP home ranges for further analysis. Preliminary analysis indicated that there was a significant effect of year on home range size ($F_{4,197} = 5.13, P = 0.0006$). However, distribution of sex and age classes among years was not balanced and likely confounded the effects of year on home range size. We did not have large enough sample sizes to compare the effects of sex, age class, and year together, so we removed year as a factor in our analysis. Home range method affected annual home range size estimates ($F_{2,199} = 37.14, P < 0.0001$). Home range size was larger for both kernel-based methods compared to MCP home ranges, and there was no difference between LSCV- and plugin-based kernel home ranges (Table 1.1).

ANOVA tests for the effects of sex and age class on home range size were significant for all home range estimation methods (MCP: $F_{3,59} = 8.52, P < 0.0001$; plugin: $F_{3,55} = 10.94, P < 0.0001$; LSCV: $F_{3,55} = 10.02, P < 0.0001$). There was a significant sex effect on home range size regardless of estimation method (MCP: $F_{1,59} = 13.3, P = 0.0006$; plugin: $F_{1,55} = 18.78, P < 0.0001$; LSCV: $F_{1,55} = 14.27, P < 0.0004$), but age class was not a significant factor (MCP: $F_{1,59} = 0.081, P = 0.78$; plugin: $F_{1,55} = 0.35, P = 0.56$; LSCV: $F_{1,55} = 0.80, P = 0.38$). Average male home ranges were more than twice as large as those of females (Table 1.1). There was a significant interaction between sex and age

class for LSCV-based kernel home ranges ($F_{1,55} = 4.98, P = 0.03$), and a marginally significant interaction effect for MCP and plugin home ranges (MCP: $F_{1,59} = 3.33, P = 0.07$; plugin: $F_{1,55} = 3.32, P = 0.07$). The effect of sex on home range size depended on age class. Home range size was similar for juvenile males and females, but adult males used significantly larger home ranges than adult females. Juvenile females had larger mean home range size than adult females, while juvenile males maintained smaller home ranges than adult males.

Area/probability curves suggested that marten did not use space within their home ranges randomly but instead concentrated their use within a portion of their home range (Figure 1.2). Isopleth values used to estimate the core area varied among individuals (Table 1.2). Isopleth values were not significantly different between plugin and LSCV core areas ($F_{1,132} = 1.54, P = 0.22$). Sex and age class did not affect the isopleth values corresponding to core area for the plugin method ($F_{3,55} = 2.24, P = 0.094$), but there were marginally significant effects of sex and age class on isopleth value for LSCV core areas ($F_{3,55} = 2.58, P = 0.06$). Female LSCV core area isopleth values were larger than those of males ($F_{1,55} = 4.13, P = 0.047$), and juveniles had larger isopleth values than adults ($F_{1,55} = 4.04, P = 0.049$).

Core area estimation method did not influence core area size estimates ($F_{1,55} = 1.52, P = 0.22$). Males used larger core areas than females (plugin: $F_{1,55} = 23.42, P < 0.0001$; LSCV: $F_{1,55} = 18.90, P < 0.0001$), but age class did not influence core area size (plugin: $F_{1,59} = 0.079, P = 0.78$; LSCV: $F_{1,55} = 0.39, P = 0.54$). There was also a significant interaction of sex and age class on core area size (plugin: $F_{1,55} = 3.76, P =$

0.058; LSCV: $F_{1,55} = 5.37$, $P = 0.024$). As with home range size, adult males used larger core areas than adult females, while the difference between sexes was reduced for juveniles.

Marten demonstrated a high degree of fidelity to annual home ranges (Table 1.3), although marten monitored for >3 years provided some evidence that home range position shifts more over longer time periods ($n = 3$). Estimates of home range fidelity appeared to be consistent among home range estimation methods, although we did not have adequate sample sizes to test for a significant difference. Average overlap among consecutive home ranges was $70\% \pm 3.4\%$ for 95% MCP's, $76\% \pm 1.6\%$ for LSCV-smoothed fixed kernel home ranges and $73\% \pm 2.8\%$ for plugin-smoothed fixed kernel home ranges. Fidelity was lower for core areas than for home ranges, suggesting that marten shift areas of intensive use within home ranges from one year to the next. Overlap among consecutive years was $64\% \pm 2.2\%$ for LSCV-based fixed-kernel core areas and $58\% \pm 2.1\%$ for plugin-based fixed-kernel core areas.

Habitat Selection

Our habitat data layer had an overall classification accuracy of 88%. Deciduous forests stands were correctly classified 65% of the time, while lowland coniferous forest had a classification accuracy of 85%. Accuracy of all other individual cover types was $\geq 93\%$ (coniferous forest: 93%; mixed coniferous-deciduous forest: 95%; young and regenerating forest: 100%). We checked all misclassified deciduous stands and determined that 13 out of 14 classification errors occurred when small deciduous patches

were classified as mixed coniferous-deciduous forest in the LULC. Mixed-wood forest represented the matrix within which the misclassified deciduous stands were embedded. Thus, our habitat data accurately classified broader scale stand type but did not have high enough resolution to detect smaller deciduous patches within mixed-wood stands. Excluding these errors resulted in an overall classification accuracy of 93% and a classification accuracy of 98% within deciduous stands that were not small patches within mixed-wood forest.

Habitat use at the scale of telemetry locations was not influenced by telemetry error for >90% of location sets. For the 8 sets in which there was a difference between simulated error locations and actual locations, there were no consistent patterns for which cover types were different among coniferous, deciduous, mixed-wood, and lowland conifer stands. However, the proportion of simulated error locations in young/regenerating forest, wetlands, and shrubby grassland was consistently lower than in actual telemetry locations. Comparison of ground locations to flight locations at mortality sites and rest sites indicated that actual telemetry error may have been less than estimated.

There was no significant difference between LSCV and plugin home range size, so we buffered random points by the average size of both methods (8.3 km²). We also buffered random points by the average MCP home range size because MCP home ranges were significantly smaller than those produced from fixed-kernel methods. Home ranges and core areas produced using different methods had similar proportions of habitat types (Table 1.4). We removed deciduous forest, wetlands, and other non-forested habitat

types for analysis of landscape-scale habitat selection because they collectively made up <5% of the landscape. However, these habitat types were not removed for individual analyses at the stand-scale if they made up >5% of the home range or core area. Similarly, any habitat type not found within individual home ranges was not included in tests of stand level habitat selection. We analyzed habitat selection using all home range estimates, but only report habitat selection for plugin fixed-kernel home ranges and core areas because home ranges for plugin, LSCV, and MCP had similar proportions of forest cover types.

At the landscape scale, marten used habitat types in proportion to their availability when comparing average home range composition to habitat within random buffered points ($\chi^2 = 3.32$, $d.f. = 4$, $P = 0.51$; Figure 1.3a). Individually, 60 out of 66 marten selected habitat types disproportionately within their home ranges, although selection patterns varied by individual (Figure 1.3b). No forest cover types were selected or avoided by all marten. Instead, each habitat type was selected by some individuals and avoided by others. Manly-Chesson selection indices were significantly different among cover types (Kruskal-Wallis, $H_4 = 63.2$, $P < 0.0001$). Coniferous forest, lowland conifer/bog, and mixed-wood forests all had higher rank scores than young/regenerating forests and shrubby grassland, indicating marten were more likely to select these cover types. When marten used each of these more preferred cover types less than expected based on availability, they increased the use of one or more other forest types (Figure 1.3c). Fifty-six percent of marten using less mixed-wood forest increased their use of coniferous forest, 50% selected lowland conifer, and 28% used more deciduous forest.

Marten using less coniferous forest selected more lowland conifer (44%), mixed-wood (36%), and deciduous stands (36%), while marten using less lowland conifer supplemented their home ranges with more conifer (62%), mixed-wood (53%), and deciduous stands (26%). Approximately 8% of marten used each of the four main forest types in proportion to or less than expected but increased use of shrubby grassland and young/regenerating habitats.

At the stand scale, average marten core areas had similar habitat proportions as home ranges ($\chi^2 = 1.03$, $d.f. = 4$, $P = 0.45$; Figure 1.4). Individually, 28 marten selected core areas with similar habitat composition as home ranges, while 38 marten demonstrated selection for different habitat types within their home range. Marten using habitat types disproportionately did not all prefer the same forest types. However, Manly-Chesson selection indices were significantly different among habitat types (Kruskal-Wallis, $H_4 = 17.87$, $P = 0.0013$). Mixed-wood stands were more likely to be selected within core areas followed by lowland conifer/bog and coniferous forest (Figure 1.4). Shrubby grassland and young/regenerating stands were more likely to have Manly-Chesson indices reflecting less use than expected. All marten selected deciduous, coniferous, mixed-wood, or lowland conifer/bog or a combination of multiple forest types at a greater proportion in core areas relative to home ranges.

Comparison of habitat composition of telemetry locations to that of home ranges supported the stand-level selection patterns observed using core areas to define use within the home range (Figure 1.4). Forty-five marten (68%) showed selection for habitat types within their home range. Eighty-percent of marten that used habitat types

disproportionately within their home range used more mixed-wood stands, 56% used more coniferous stands, and 40% used more lowland conifer stands. Manly-Chesson indices were significantly different among forest cover types (Kruskal Wallis, $H_4 = 43.27$, $P < 0.0001$), with highest relative selection of mixed-wood and coniferous stands followed by moderate selection for lowland conifer and lowest relative selection for young/regenerating stands and shrubby grassland. The similarity between the two tests of stand-level selection suggest that marten prefer mixed-wood and coniferous forest at this scale.

Overall, males and females selected habitat similarly at both scales. At the landscape scale, males had significantly higher selection indices for lowland conifer than females (Kruskal-Wallis test, $H_1 = 5.93$, $P = 0.015$). At the stand scale, male selection indices were higher for shrubby grassland ($t = 2.92$, $P = 0.004$). Selection indices were similar for all other cover types at both scales, including no difference for any habitat type at the stand scale based on telemetry locations.

Forest Structure

Vegetative characteristics varied among forest cover types (Table 1.5). Understory cover density and density of root-mass tip-ups were higher in lowland conifer forest, while canopy closure, average tree diameter, basal area, and density of snags and trees were lower in lowland conifer stands. Mixed-wood stands had higher canopy closure, higher tree density, and less horizontal cover. Snag density was highest in deciduous stands, while upland coniferous and mixed-wood stands had higher basal area than deciduous

and lowland conifer stands. Snag volume and CWD in decay class 2 were marginally significant, both occurring at higher volumes in deciduous stands. Lowland conifer stands had significantly more potential resting and denning structures than other forest types. Most of the potential structures counted at random sites were ground-based structures that were abundant in lowland coniferous forest. There was no difference in sapling density, CWD volume (including total and decay classes 1, 3, and 4), stump density, or average diameter of snags between cover types.

Stand age also influenced structural complexity (Table 1.6). Volume of CWD in decay classes 1 and 3, average diameter of trees and snags, basal area, and snag volume all increased with stand age. Mean CWD volume and snag density both increased with stand age, but these effects were not statistically significant. Sapling density was the only habitat variable that decreased with increasing stand age. Available rest sites were significantly more abundant in older stands, especially those >100 years old. However, there were few deciduous stands >100 years old, and this result may be an interaction between stand age and cover type because old-growth lowland conifer stands had the highest mean ground-burrow density. There was no difference in understory cover density, canopy closure, CWD volume, stump density, root-mass tip-up density, or tree density among age classes.

Discussion

Evaluating space use behavior and habitat selection by marten in Minnesota is necessary for proper management because martens have low reproductive potential, live at

low densities, and respond negatively to landscape-scale habitat alterations at low thresholds (Chapin et al. 1998). Although marten generally occupy mature forest stands, selection for specific forest types varies geographically (Thompson et al. 2012) and relatively little research on habitat use has been conducted in the western Great Lakes region in the south central portion of the marten range. Identifying broad-scale selection patterns in Minnesota provides a basis for additional work to determine how marten interact with their environment to obtain critical resources. Track surveys and anecdotal information suggests that the marten population in Minnesota has declined over the past 10 years (Erb 2011). Marten populations are sensitive to progressive clear-cut logging, which reduces stand age and/or complexity of woody structure (Chapin et al. 1998, Potvin et al. 2000, Thompson and Harestad 1994), and fur-trapping, which can dramatically affect demographic rates, population age structure, and spatial relationships among marten (Hodgman et al. 1994, Payer et al. 2004, Katnik et al. 1994). Habitat use information is necessary to evaluate habitat suitability as a potential contributor to declining population trends in Minnesota.

Space use and home range characteristics

Most of the marten that we monitored (68%) were classified as residents based on spatial distribution of locations. Other studies have found similar proportions of residents (Pauli et al. 2012), although our results may over-estimate the percentage of residents because we only classified location sets for marten with adequate location samples to estimate an annual home range. We lost radio-contact with a portion of the

marten with insufficient sample sizes for home range analysis, while others were apparent residents but did not survive long enough for us to obtain enough locations to calculate a home range.

Sex or age could potentially influence space use behavior if males and females use space differently, or if young individuals make dispersal movements away from their natal territory prior to establishing a home range. We did not find a significant difference in the proportion of residents, temporary residents, and dispersing marten among males and females, although absolute proportion of residents was greater for males (74% for males, 59% for females). Female marten space use may be more dynamic than that of males. In Maine, females were more likely to abandon existing home ranges (Phillips et al. 1998). Juveniles were more likely to be classified as dispersing or temporary residents and were likely dispersing out of their natal territory to establish a new home range. Temporary residents often did not move into a second putative home range until April or May. Juvenile temporary residents may have remained in their natal territory through winter prior to dispersal. Alternatively, the decision to disperse and establish a new home range could be influenced by other factors such as intrasexual territoriality (Katnik et al. 1994) or reductions in resource availability (Thompson and Colgan 1987).

Average dispersal distances were similar to those reported elsewhere (Johnson et al. 2009, Pauli et al. 2012). Most marten disperse moderate distances (5-20 km), while a smaller proportion of marten make long-distance dispersal movements (130 km in our study; 214 km, Johnson et al. 2009). Long-distance dispersal events are more likely with less habitat fragmentation (Johnson et al. 2009), probably because landscape connectivity

does not limit movement. Thus, marten have the dispersal abilities to establish connectivity among population sources and sinks throughout a large landscape, but fragmentation from progressive clear-cutting or climate-change induced changes in vegetative cover could reduce the genetic connectivity among marten populations in the future (Wasserman et al. 2012).

Home range size estimates for radiocollared marten in our study were within the range of values reported elsewhere (Smith and Schaefer 2001). Estimates of marten home range sizes are typically less than 12 km² for males and less than 7 km² for females (Smith and Schaefer 2002, Buskirk and MacDonald 1989), although average home ranges >25 km² have been reported (O'Doherty et al. 1997, Bull and Heater 2001, Gosse et al. 2005). Winter home ranges in Wisconsin were smaller than our estimates, although differences in sampling frequency and home range estimation method make direct comparison problematic. Habitat composition is a factor in home range size in some jurisdictions (Gosse et al. 2005), but we found no evidence that home range size varied predictably with any forest cover type.

MCP home ranges were significantly smaller than fixed-kernel home ranges. Sample size could have resulted in larger fixed-kernel home range sizes, as small sample sizes can result in over-smoothed kernel density estimates and increase the probability of including unused portions of the landscape within the home range boundary (Fieberg and Börger 2012, Seaman et al. 1999). However, MCP's may be more biased by outlying points, and do not take into account relative intensity of use among different portions of the home range. Furthermore, MCP's may underestimate use of habitat on the MCP

boundary. We felt that both methods used together provide a reasonable estimate of home range size and an adequate unit to determine patterns of habitat selection because average sample size was >30 , habitat composition was similar among home range estimation methods (Table 1.4), and radiotelemetry tracking observations generally supported our home range estimates.

We found that sex and age influenced home range and core area size. Use of larger home ranges by males is a consistent pattern throughout North America (Buskirk and McDonald 1989, Smith and Schaefer 2002). Males may have larger home ranges in part because of larger body size and higher energetic demands (Katnik et al. 1994), because females are more selective of fine-scale habitat (Phillips et al. 1998), or because males benefit from establishing home ranges that overlap with multiple females. By itself, age class was not a significant factor in home range size, but there was a significant interaction between sex and age class. Adult males used more space than adult females, while the difference between home range and core area size of juvenile males and juvenile females was reduced. Furthermore, juvenile females had larger home ranges than adults while juvenile males had smaller home ranges than adult males. Differences in social organization among males and females may account for this pattern. Juvenile males may be less dominant and be more sensitive to intrasexual aggression than juvenile females. Alternatively, juvenile females may tend to use a larger area while becoming familiar with their environment before eventually settling into a smaller home range. Some dispersing females made diffuse use of an area before apparently settling into a smaller portion of the landscape, whereas dispersing males tended to make more directed

movements prior to home range establishment. Seasonal shifts in home range position may be more likely for juvenile females as a result of seasonal changes in resource abundance or refinement of habitat preference over time. In Maine, males were more likely to change home range location as unoccupied space becomes available (Phillips et al. 1998).

Relatively few studies have analyzed marten core area size, and those that have defined core areas arbitrarily. In Wisconsin, marten apparently concentrated their time in core areas, although habitat composition was not different between home ranges and core areas (Dumyahn et al. 2007). Defining core areas using area/probability curves is quantitatively repeatable and biologically significant because it is based on spatial distribution of telemetry locations and does not rely on arbitrarily-determined isopleth values (Vander Wal and Rodgers 2009, Powell 2000). Area/probability curves suggested all marten concentrate their time in a subset of their home range rather than using all portions of their home range evenly or randomly. Concentrated use likely allows marten to maximize fitness by gaining information about a well-confined part of the landscape (Spencer 2012). The isopleth value corresponding to the core area varied among individual marten. Differences in core area isopleth may reflect differences in spatial abundance of resources. However, there were marginally significant effects of sex and age on core area isopleth value, indicating consistent differences in space use among these groups.

Home range fidelity for marten monitored in multiple years was high for all home range estimation types and similar for males and females. High fidelity suggests that the

benefits of becoming familiar with a particular portion of the landscape outweighs the costs of maintaining this familiarity. A greater familiarity with the environment promotes fitness through the process of learning where critical resources and habitat elements are and developing a cognitive map of the location of these fitness-promoting features on the landscape (Spencer 2012). As martens occupy the same landscape, they may become more familiar with habitat features that reduce predation and may become better able to identify locations where foraging efficiency is maximized. However, martens had lower fidelity to core areas. One possible explanation is that they respond to short-term, fine-scale fluctuations in resource availability within their home ranges.

Habitat Selection

Despite the overall high classification accuracies, our habitat data did not have the resolution to detect small deciduous stands within a matrix of mixed coniferous-deciduous forest. Our results may under represent use of small deciduous patches within the forested landscape matrix, although the low availability of deciduous stands across our study area suggests that selection for these stands across broad spatial and temporal scales is unlikely. Other work has shown that marten movement patterns are influenced by small habitat patches that are not detectable in coarse land cover data sets (McCann 2011). Martens moved toward and with more sinuosity in hemlock-cedar patches in Wisconsin (McCann 2011), but few studies have investigated habitat composition and use by martens at such small grain sizes. Additional work is needed to characterize fine-

scale habitat use and determine the extent to which marten respond to habitat configuration at smaller spatial scales.

Overall, telemetry error did not influence habitat selection results. However, differences in cover type composition between telemetry locations and simulated error locations indicated that use of wetlands, shrubby grassland, and young/regenerating forest might have been overestimated for eight marten. One possible explanation is that these marten were located more frequently in forest edges, increasing the probability of incorrect habitat classification. Habitat fragmentation increases forest edge density. In highly fragmented environments, marten may increase relative use of forest edges while avoiding crossing open non-forested and regenerating cover types (Cushman et al. 2011). Another possibility is that home ranges with smaller average patch size have more potential telemetry errors because the probability of habitat classification errors increases with more forest edge.

Most habitat selection analyses occur at the population level, either by pooling animal telemetry locations or estimating use for the average individual (Aebischer et al. 1993, Garshelis 2000). While significant deviations in habitat use at the population level demonstrate consistent responses throughout the population, both approaches have potential problems. Pooled locations may artificially inflate sample sizes and corresponding degrees of freedom if sample size corresponds to number of locations rather than number of individual and mask behavioral differences among individuals within a population. Using average habitat use allows comparisons with individual animals as the sampling unit, but still may fail to capture individual differences in habitat

use if increased use of a particular habitat type by a subset of individuals is balanced by decreased use of that habitat by other individuals. Recently, more attention has been given to differences in resource use among populations of animals (e.g., differences in prey specialization [Elbroch and Wittmer 2013]). Individual differences may result from learned behavior, individual preferences, differences in resource availability, or other factors (Estes et al. 2003).

We found contrasting results between individual- and population-level habitat analyses. At the population level, marten in our study used cover types in proportion to their availability at both landscape and stand scales. One possible explanation for the lack selection patterns is that marten can acquire critical resources from multiple habitat types. Vegetation data provides support that woody structure is similar among habitat types. Although some of the variables we measured were different among forest cover types, all cover types generally had sufficient structural characteristics compared to other values reported in the literature (Payer and Harrison 2004). However, all cover types had lower average snag density, sapling density, and CWD volume than recommended (Payer and Harrison 2004). Other factors that could influence marten habitat use within forest stands include prey availability, predator density or predation risk, and competition with other marten (i.e., density-dependent effects). However, without data to determine whether these factors varied among cover types and without understanding how habitat features influence individual fitness or population demography, it is difficult to evaluate the extent to which habitat features are limiting across the landscape.

At the individual level, most marten used habitat types disproportionately to availability at both landscape and stand scales. Selection patterns varied significantly among individual marten at both scales, and all cover types were selected by some individuals and avoided by others. Marten using any particular mature forest type less than expected based on availability showed a corresponding increase in use of one or more other habitat types. Individual differences may reflect differences in availability of habitat at more local scales, individual preferences, or a combination of factors. These results suggest that all mature forest types have the potential to provide adequate resources for marten. More work is needed to assess the distribution of resources within forest stands and to identify factors influencing selection patterns at the individual level.

Contrary to other studies (reviewed in Thompson 2012), we found that marten were more selective of habitat types within their home range than they were while establishing a home range from available habitat at the landscape-scale. There was more variability in Manly-Chesson selection indices at the landscape level compared to the stand level. At the stand-scale, our results between the two different methods were consistent and indicated that individual marten select mixed-wood stands and avoid young/regenerating stands and shrubby grassland habitat within their home ranges. Mixed-wood stands may be preferred at the stand scale because of the increased vegetative structure relative to other habitat types. Mixed-wood stands had higher canopy closure, higher density of trees and snags, more snag volume, and moderate to high CWD volume compared to other habitat types. Mixed-wood stands also tend to have higher small mammal densities (Lovallo and Anderson 1996, Fuller et al. 2004),

which has been associated with higher marten densities and increased habitat use (Thompson and Colgan 1987). These stands also provide abundant resting and denning opportunities in all seasons (see Chapter 2).

We found few differences in habitat use between male and female marten. Males had higher selection indices for lowland conifer at the landscape scale and females demonstrated less selection for shrubby grassland at the stand scale, but both males and females used all habitat types on some level. Males and females would be expected to utilize habitat differently if they partitioned food or other resources that were patchily distributed and only occurred in certain habitat types. Lack of strong differences between males and females implies that marten either are not partitioning resources at a coarse scale or that habitat types generally all contain enough resources for both males and females. While there is some data suggesting that male and female marten exploit different prey resources on islands (Nagorsen 1994), there was a large degree of overlap in diet use and other studies have failed to find any evidence for diet partitioning (Thompson and Colgan 1990). Similarly, there is little evidence for differences in habitat selection among males and females at broad spatial scales (Chapin et al. 1997, Dumyahn et al. 2007).

While our results suggest that multiple forest cover types can provide suitable habitat for marten, fine-scale differences in resource availability may exist between habitat types. If resources are not distributed homogeneously among habitat types, differences in habitat use may alter an animal's ability to meet energetic and nutrient demands and influence individual fitness. Potential factors influencing marten habitat

use include predation risk (Brainerd et al. 1995), relative prey availability (Thompson and Colgan 1987), and density-dependent effects such as competition (Thompson et al. 2012). Use of different habitat types could influence survival if predator densities or structural features that reduce predation risk vary among forest types. For example, bobcats (*Lynx rufus*) select lowland conifer and lowland deciduous forest in Wisconsin (Lovallo and Anderson 1996), and forest structural characteristics have been hypothesized to function in predator avoidance by marten (Buskirk and Powell 1994, Buskirk and Ruggiero 1994). Prey-availability is influenced by both prey abundance and presence of habitat features that promote efficient foraging behaviors (Andruskiw et al. 2008). Furthermore, differences in relative rates of prey encounter and successful capture could affect movement costs and influence the ability of marten to meet energetic demands. More work is needed to understand the factors influencing variation in habitat use by different individuals, relate fine-scale habitat use to landscape level availability of habitat types, and identify how habitat influences individual fitness and population demography.

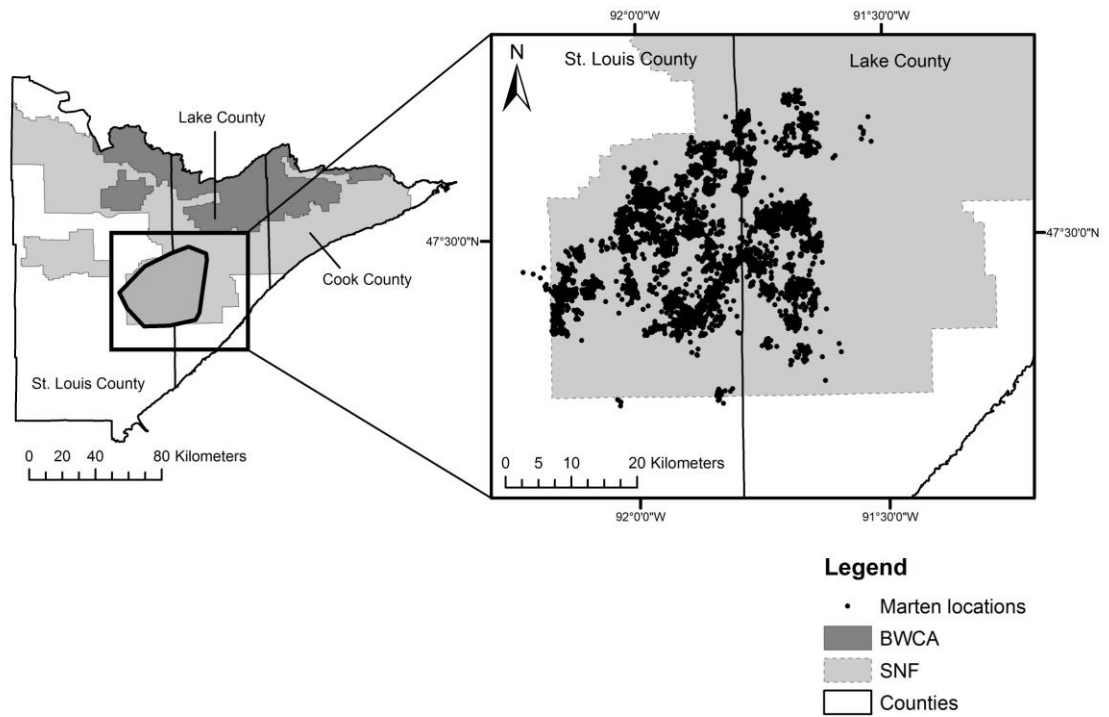


Figure 1.1. American marten study area in the Superior National Forest, Minnesota, United States. Points represent telemetry locations of 170 American marten wearing radiocollars from 2008-2012.

Table 1.1. Summary statistics for 95% minimum convex polygon (MCP) and 95% fixed-kernel home ranges estimates (km²) of resident American marten in Minnesota. Fixed-kernel home ranges were estimated using two different smoothing parameters using the program Geospatial Modeling Environment: least-squares cross validation (LSCV), and Plugin.

	<i>n</i>		$\bar{X} \pm SE$		Range	
	♂	♀	♂	♀	♂	♀
MCP	46	24	4.8 ± 0.5	2.3 ± 0.3	1.3 - 14.4	0.7 - 6.6
Plugin	42	24	9.9 ± 0.9	4.7 ± 0.5	3.0 - 24.2	1.6 - 11.8
LSCV	42	24	11.5 ± 1.1	5.5 ± 0.7	3.5 - 28.6	1.8 - 15.6

Table 1.2. Summary statistics for fixed-kernel isopleth values predicting core-area size for American marten estimated with annual telemetry locations. Fixed-kernel utilization distributions were estimated using both least-squares cross-validation (LSCV) and Plugin smoothing parameter settings within Geospatial Modeling Environment.

	<i>n</i>		Isopleth (%)		Core Area (km ²)	
	♂	♀	♂	♀	♂	♀
Plugin	42	24	55.7 ± 0.2	56.8 ± 0.5	3.1 ± 0.3	1.3 ± 0.1
LSCV	42	24	56.1 ± 0.2	57.1 ± 0.5	3.5 ± 0.3	1.6 ± 0.2

Table 1.3. Home range and core area fidelity for radiocollared American marten monitored for ≥ 2 full years in northeastern Minnesota from 2008-2012. Overlap of home ranges and core areas in consecutive years was calculated using a coincidence index.

	Home Ranges		Core Areas	
	<i>n</i>	Overlap (%)	<i>n</i>	Overlap (%)
MCP	8	69.4 \pm 3.4	-	-
Plugin	7	73.3 \pm 2.5	7	57.9 \pm 2.1
LSCV	7	75.8 \pm 1.6	7	63.6 \pm 2.2

Table 1.4. Proportion (mean \pm SE) of habitat types within home ranges and core areas of radiocollared American marten in Minnesota. Home ranges were made using 95% MCP and 95% fixed-kernel methods, while core areas were made using fixed-kernel methods. Fixed-kernel home ranges and core areas were made using two different bandwidth selection algorithms (Plugin and least-squares cross-validation [LSCV]).

Habitat	95% MCP	95% Kernel		Core Areas	
		PLUGIN	LSCV	PLUGIN	LSCV
Mixedwood forest	32.4 \pm 3.3	32.7 \pm 1.7	32.4 \pm 1.7	35.6 \pm 2.4	34.9 \pm 2.4
Lowland conifer/bog	29.9 \pm 3.0	30.0 \pm 1.9	28.9 \pm 1.9	29.9 \pm 2.4	29.8 \pm 2.4
Coniferous forest	13.7 \pm 1.4	13.2 \pm 1.0	13.0 \pm 1.0	14.2 \pm 1.5	14.0 \pm 1.5
Deciduous forest	1.4 \pm 0.1	1.4 \pm 0.4	1.4 \pm 0.4	1.3 \pm 0.5	1.3 \pm 0.5
Regenerating/Young forest	12.9 \pm 1.3	14.5 \pm 1.0	14.4 \pm 1.0	11.0 \pm 1.2	11.6 \pm 1.2
Shrubby grassland	6.3 \pm 0.7	5.3 \pm 1.0	5.4 \pm 1.0	5.4 \pm 1.3	5.4 \pm 1.3
Non-forested habitats	2.9 \pm 0.3	3.6 \pm 0.5	3.8 \pm 0.5	2.2 \pm 0.5	2.5 \pm 0.5

Table 1.5. Vegetative characteristics (mean \pm SE) of 4 forest cover types sampled 2012-13 in the Superior National Forest, Minnesota. Letters denote significant differences based on ANOVA and Tukey's HSD ($P < 0.05$).

Habitat variable	Forest cover types				Statistic	P
	Deciduous	Upland Conifer	Mixed-wood	Bog/Lowland Conifer		
Overhead cover (%)	85.1 \pm 2.2 a,b	85.2 \pm 2.3 a,b	87.7 \pm 2.1 a	77.5 \pm 2.1 b	$F_{3,98} = 4.42$	0.0059*
Understory cover (%)	54.4 \pm 4.1 a,b	46.8 \pm 4.3 b	48.3 \pm 3.9 b	66.0 \pm 3.9 a	$F_{3,98} = 4.79$	0.0037*
Sapling Density (no./ha)						
Total Saplings	1838.5 \pm 424.8	2879.3 \pm 442.9	2077.5 \pm 408.8	2498.5 \pm 408.8	$F_{3,98} = 1.14$	0.3367
Coniferous saplings	118.6 \pm 348.6 b	2213.2 \pm 363.4 a	787.1 \pm 335.4 b	2178.2 \pm 335.4 a	$F_{3,98} = 9.00$	<.0001*
Deciduous saplings	1719.9 \pm 260.6 a	666.1 \pm 271.7 b,c	1290.4 \pm 250.7 a,b	320.3 \pm 250.7 c	$F_{3,98} = 5.94$.0009*
Tree variables						
tree density (no./ha)	483.0 \pm 60.8 b	667.2 \pm 63.4 a,b	837.1 \pm 58.5 a	473.6 \pm 58.5 b	$F_{3,98} = 8.54$	<.0001*
diameter (cm)	21.4 \pm 1.1 a,b	23.9 \pm 1.1 a	20.9 \pm 1.0 a,b	19.0 \pm 1.0 b	$F_{3,96} = 3.54$.0175*

Table 1.5 (continued)

Habitat variable	Forest cover types				Statistic	P
	Deciduous	Upland Conifer	Mixed-wood	Bog/Lowland Conifer		
Tree variables, cont.						
basal area (m ² /ha)	19.4 ± 2.5 b	29.7 ± 2.6 a	30.5 ± 2.4 a	14.8 ± 2.5 b	$F_{3,97} = 9.77$	<.0001*
deciduous species	17.7 ± 1.7 a	3.6 ± 1.8 b	12.3 ± 1.7 a	0.6 ± 1.7 b	$F_{3,98} = 20.60$	<.0001*
coniferous species	1.7 ± 2.2 c	26.1 ± 2.3 a	18.2 ± 2.1 a,b	14.2 ± 2.1 b	$F_{3,97} = 21.28$	<.0001*
Snag variables						
density (no./ha)	121.3 ± 21.6 a	85.3 ± 22.5 a,b	94.7 ± 20.8 a,b	37.4 ± 20.8 b	$F_{3,98} = 2.76$.0465*
diameter (cm)	18.4 ± 1.8	21.8 ± 2.8	21.4 ± 1.8	20.5 ± 2.3	$F_{3,55} = 0.58$	0.6288
volume (m ³ /ha)	26.0 ± 5.9 a	21.2 ± 6.1 a	18.5 ± 5.6 a	5.8 ± 5.6 a	$F_{3,98} = 2.27$	0.0855
CWD volume (m ³ /ha)						
total volume	14.7 ± 3.1	12.6 ± 3.3	12.0 ± 3.0	9.1 ± 3.0	$F_{3,98} = 0.58$	0.6295

Table 1.5 (continued)

Habitat variable	Forest cover types				Statistic	P
	Deciduous	Upland Conifer	Mixed-wood	Bog/Lowland Conifer		
CWD volume, cont.						
decay class 1	0.6 ± 1.0	1.8 ± 1.0	1.1 ± 0.9	3.4 ± 0.9	$F_{3,98} = 1.70$	0.172
decay class 2	9.6 ± 2.2 a	6.3 ± 2.3 a	2.3 ± 2.1 a	2.8 ± 2.1 a	$F_{3,98} = 2.39$	0.074
decay class 3	3.2 ± 1.4	2.9 ± 1.5	5.1 ± 1.3	2.0 ± 1.3	$F_{3,98} = 0.97$	0.412
decay class 4	1.3 ± 1.0	1.6 ± 1.0	3.5 ± 1.0	0.9 ± 1.0	$F_{3,98} = 1.41$	0.245
Stump density (no./ha)	178.4 ± 40.7	232.7 ± 42.5	193.9 ± 39.2	171.8 ± 39.2	$F_{3,98} = 0.43$	0.731
Exposed root-mass density (no./ha)	9.5 ± 7.7 b	10.3 ± 8.0 b	24.2 ± 7.4 a,b	41.9 ± 7.4 a	$F_{3,98} = 4.03$.0095*
Potential Rest Sites (no./ha)	26.2 ± 30.8 b	62.1 ± 32.1 b	123.4 ± 30.0 b	279.8 ± 30.0 a	$F_{3,98} = 13.81$	<.0001*
Sites Measured	25	23	27	27		

Table 1.6. Vegetative characteristics (mean \pm SE) in stands of five different age classes measured in the Superior National Forest, Minnesota from 2012-13. Letters denote significant differences based on ANOVA and Tukey's HSD ($P < 0.05$).

Habitat variable	Stand age					Statistic	P
	20 - 40 yr	40 - 60 yr	60 - 80 yr	80 - 100 yr	>100 yr		
Overhead cover (%)	89.1 \pm 1.9	83.4 \pm 2.1	83.9 \pm 2.2	87.3 \pm 2.1	85.7 \pm 2.7	$F_{4,83} = 1.40$	0.25
Understory cover (%)	53.3 \pm 4.7	51.1 \pm 5.2	54.1 \pm 5.5	54.0 \pm 5.3	51.1 \pm 6.8	$F_{4,83} = 0.07$	0.99
Sapling Density (no./ha)							
Total Saplings	3330.5 \pm 420.6 a	2171.9 \pm 462.8 a	1758.8 \pm 489.2 a	1743.5 \pm 475.5 a	1437.7 \pm 608.2 a	$F_{4,83} = 2.63$	0.04*
Coniferous saplings	1987.6 \pm 402.3	1573.7 \pm 442.6	930.3 \pm 467.9	562.9 \pm 454.7	853.6 \pm 581.7	$F_{4,83} = 1.78$	0.14
Deciduous saplings	1343.0 \pm 265.7	598.3 \pm 292.4	828.5 \pm 309.1	1180.6 \pm 300.4	584.1 \pm 384.3	$F_{4,83} = 1.32$	0.27
Tree variables							
Tree density (no./ha)	656.8 \pm 70.7 a	704.3 \pm 77.8 a	503.8 \pm 82.3 a	687.3 \pm 80.0 a	665.1 \pm 102.3 a	$F_{4,83} = 0.97$	0.43
Mean tree diameter (cm)	18.1 \pm 1.0 c	19.2 \pm 1.2 b,c	24.3 \pm 1.2 a	23.4 \pm 1.2 a,b	24.6 \pm 1.5 a	$F_{4,82} = 6.96$	<0.001*

Table 1.6 (continued)

Habitat variable	Stand age					Statistic	P
	20 - 40 yr	40 - 60 yr	60 - 80 yr	80 - 100 yr	>100 yr		
Tree variables, cont.							
Basal area (m ² /ha)	18.0 ± 2.7 c	21.1 ± 3.0 b,c	25.7 ± 3.1 a,b,c	30.7 ± 3.0 a,b	36.0 ± 3.9 a	$F_{4,83} = 5.07$	0.0010*
deciduous species	5.1 ± 2.2 b	6.7 ± 2.5 b	8.8 ± 2.6 a,b	17.6 ± 2.5 a	7.9 ± 3.2 a,b	$F_{4,83} = 3.89$	0.0060*
coniferous species	12.9 ± 2.9 b	14.4 ± 3.2 a,b	16.9 ± 3.3 a,b	13.1 ± 3.2 b	28.1 ± 4.1 a	$F_{4,83} = 2.71$	0.0353*
Snag variables							
density (no./ha)	41.3 ± 23.4 a	68.9 ± 25.7 a	101.5 ± 27.2 a	135.5 ± 26.4 a	119.0 ± 33.8 a	$F_{4,83} = 2.21$	0.0745
mean DBH (cm)	17.3 ± 2.7 a,b	17.1 ± 2.3 b	19.9 ± 2.4 a,b	26.4 ± 2.1 a	20.8 ± 2.6 a,b	$F_{4,47} = 2.89$	0.0320*
volume (m ³ /ha)	8.2 ± 6.3 a	8.8 ± 6.9 a	22.5 ± 7.3 a	33.8 ± 7.1 a	32.0 ± 9.1 a	$F_{4,83} = 2.92$	0.0257*
CWD volume (m ³ /ha)							
total volume	7.4 ± 3.2	9.6 ± 3.6	12.2 ± 3.8	19.8 ± 3.7	18.4 ± 4.7	$F_{4,83} = 2.17$	0.0789

Table 1.6 (continued)

Habitat variable	Stand age					Statistic	P
	20 - 40 yr	40 - 60 yr	60 - 80 yr	80 - 100 yr	>100 yr		
CWD volume, cont.							
decay class 1	0.8 ± 0.9 b	0.8 ± 1.0 b	0.4 ± 1.0 b	1.3 ± 1.0 b	7.7 ± 1.3 a	$F_{4,83} = 6.24$	0.0002*
decay class 2	4.0 ± 2.4	3.8 ± 2.7	4.3 ± 2.8	8.8 ± 2.8	6.2 ± 3.5	$F_{4,83} = 0.59$	0.6699
decay class 3	1.1 ± 1.5 b	2.4 ± 1.6 a,b	4.6 ± 1.7 a,b	7.7 ± 1.7 a	3.1 ± 2.2 a,b	$F_{4,83} = 2.42$	0.0547
decay class 4	1.5 ± 1.1	2.7 ± 1.3	2.8 ± 1.3	2.0 ± 1.3	1.4 ± 1.6	$F_{4,83} = 0.24$	0.9132
Stump density (no./ha)	152.6 ± 38.4	181.6 ± 42.3	255.4 ± 44.7	165.2 ± 43.5	194.7 ± 55.6	$F_{4,83} = 0.86$	0.4933
Exposed root-mass density (no./ha)	18.1 ± 7.9	12.5 ± 8.7	10.5 ± 9.2	33.0 ± 8.9	27.0 ± 11.4	$F_{4,83} = 1.09$	0.3655
Potential Rest Sites (no./ha)	75.0 ± 28.0 b	68.9 ± 30.7 b	91.0 ± 32.5 b	105.7 ± 31.6 b	275.8 ± 40.4 a	$F_{4,83} = 5.14$	0.0009*
Sites Measured	23	19	17	18	11		

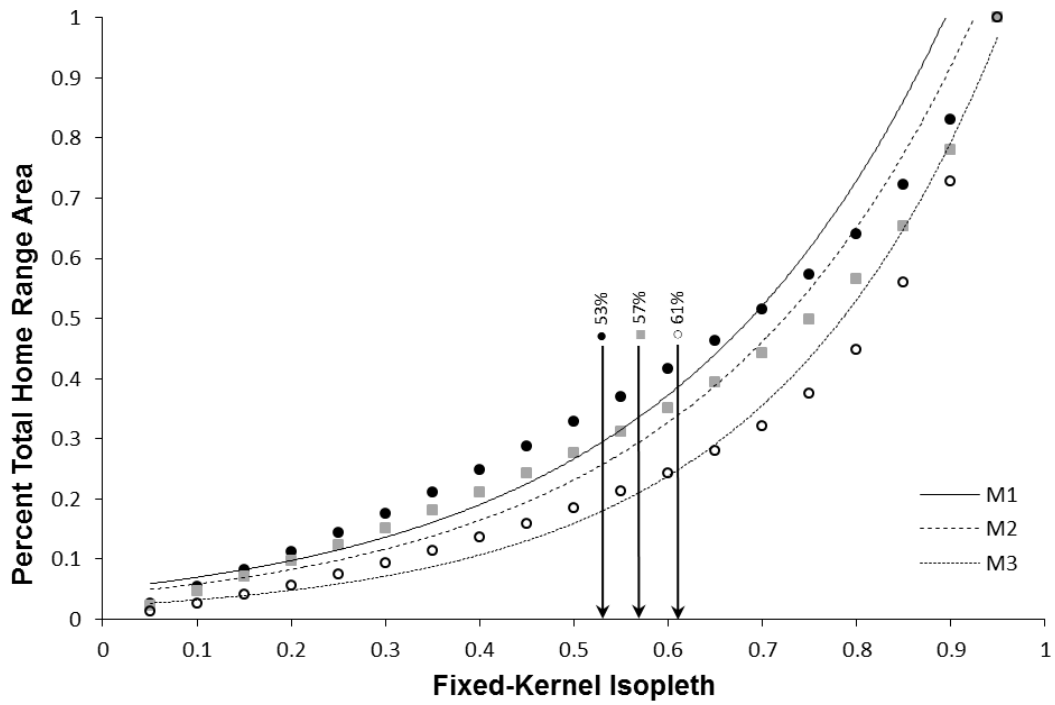


Figure 1.2. Area/probability curve estimating core area isopleth values for three radiocollared American marten from northeastern Minnesota monitored from 2008-2012. Inflection points of exponential regression curves indicate the isopleth value corresponding to the core area (arrows). All marten demonstrated clumped space use within their home range, but core area isopleth values varied among individuals.

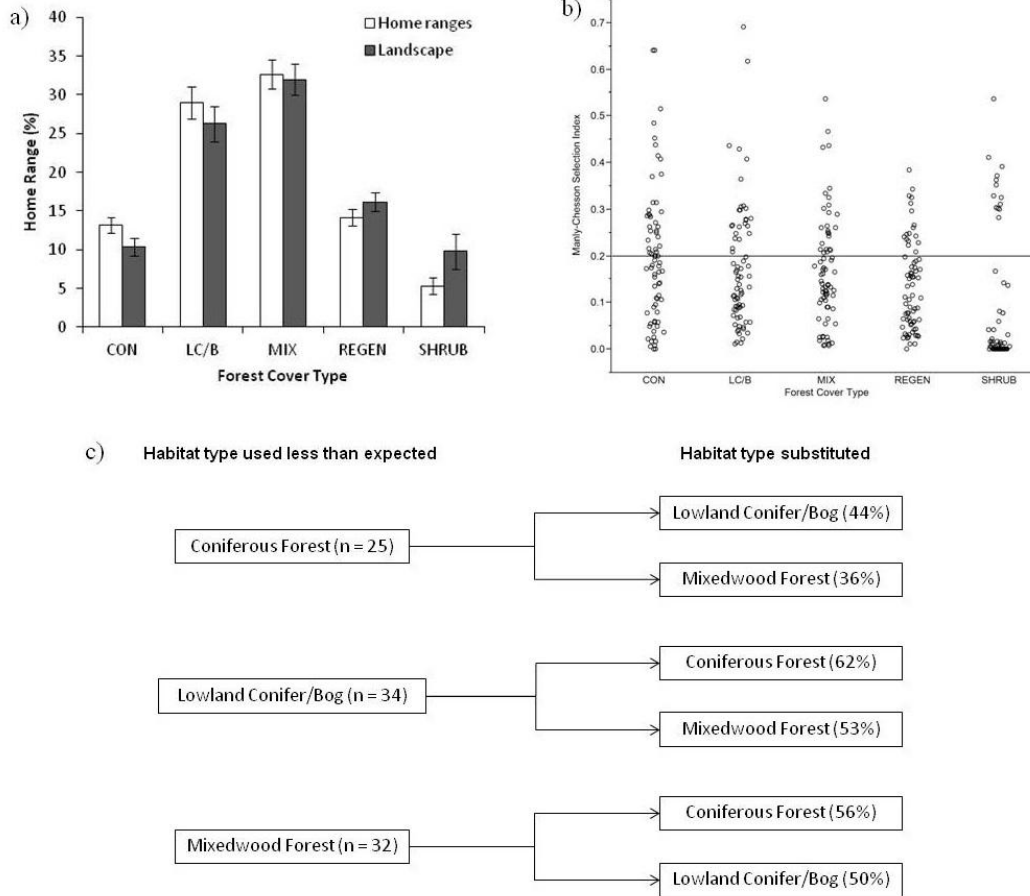


Figure 1.3. Landscape-scale habitat selection of radiocollared American marten in Minnesota. a) Average proportion of habitat types within plugin fixed-kernel home ranges was compared to proportion of available habitat across the landscape. b) Manly-Chesson selection indices were calculated for all marten that used cover types disproportionately to availability. c) When more available forest types were used in lower proportion than expected based on availability, marten increased use of one or more other cover type. The two most selected cover types are represented even though some marten increased use of >2 cover types. Percentages sum to greater than 100% because most marten increased use of more than one cover type.

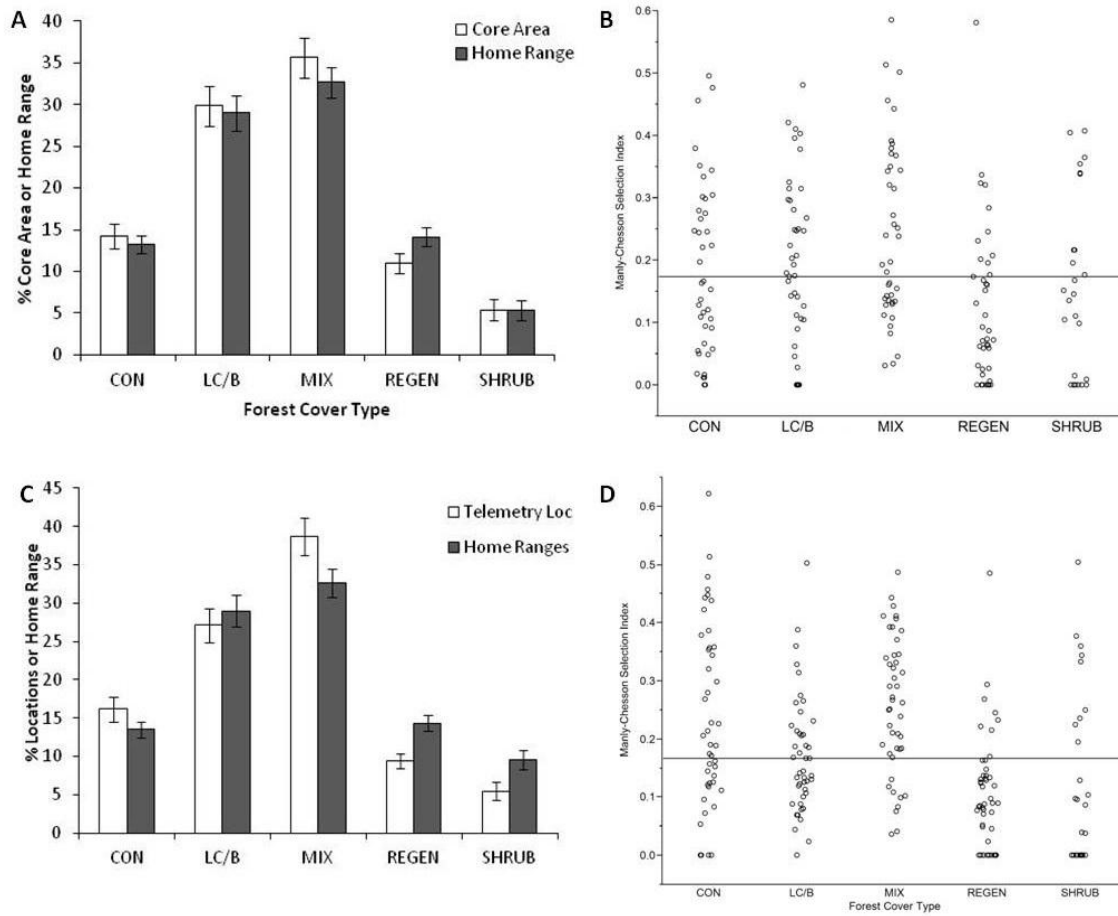


Figure 1.4. Stand-scale habitat selection of radiocollared American marten in Minnesota. A) Habitat composition of core areas and home ranges. B) Manly-Chesson selection indices for 38 marten using different proportions of habitat types in core areas than in home ranges. C) Habitat composition of telemetry locations and home ranges. D) Manly-Chesson selection indices for marten for which habitat composition of telemetry locations deviated from habitat available in home ranges.

Chapter 2: Selection of rest sites and reproductive dens by American marten in
Minnesota

Overview

Rest sites and reproductive dens are important habitat elements that facilitate recruitment and protect marten from predators and inclement weather during periods of inactivity. We deployed radiocollars on 202 marten from 2007 to 2013 and used radiotelemetry to locate 200 rest sites (35 females, 25 males) and 31 reproductive dens (16 females). Marten selected above-ground rest sites more often during summer, while winter rest sites were predominantly in subnivean or subterranean structures. A greater proportion of females used rest sites in tree cavities compared with males. Males used tree branches more frequently than females. Females used both above- and below-ground sites as reproductive dens. We measured forest structural characteristics at 31 reproductive dens, 62 rest sites, and 102 random sites from 2012-2013. Marten selected rest sites and reproductive dens in mature, structurally complex forest stands. Sites used by marten had higher coarse woody debris volume, higher snag density, and larger mean tree and snag diameter compared to random sites. Forest management practices aimed at supporting marten populations should retain stands of mature, structurally complex forest to maintain resting and denning habitat.

Introduction

Determining selection of microhabitat sites provides an understanding of how animals interact with their environment at small spatial scales to meet specific life-history needs or obtain particular resources. Rest sites and reproductive dens are two important microhabitat sites used by American marten (*Martes americana*) that contribute to individual fitness. Rest sites protect marten from predators, harsh weather, and thermal stress during periods of inactivity, while dens facilitate recruitment by providing these same benefits to females and their kits. Lack of suitable habitat for resting and denning may reduce population viability through reduced survival or recruitment (Ruggiero et al. 1998, Brainerd et al. 1995, Birks et al. 2005), yet data on rest site and den selection from the western Great Lakes region in the south-central portion of the marten range is limited (Gilbert et al. 1997). A better understanding of selection of rest sites and dens for this region is necessary for developing habitat management strategies, particularly because selection patterns are influenced by regional availability of suitable habitat elements (Brainerd 1995, Raphael and Jones 1997).

Marten use a variety of structures as rest sites including cavities in live trees and snags, tree branches, witches' broom structures caused by broom rust fungus (*Melampsorella* and *Chrysomyxa* spp.), hollow logs, slash or log piles, stumps, tree root-masses, underground burrows, rock piles, and anthropogenic structures (Buskirk et al. 1989, Raphael and Jones 1997, Gilbert et al. 1997, Bull and Heater 2000). Rest site selection is influenced by availability of suitable sites (Raphael and Jones 1997), predation risk (Brainerd et al. 1995), prey availability (Buskirk and Powell 1994), and

thermal properties of resting structures (Buskirk et al. 1989, Taylor and Buskirk 1994). Past studies have not found differences in selection of resting structures between males and females (Raphael and Jones 1997), but vertical position of rest sites changes seasonally for both sexes. Most studies report increased use of above-ground sites during summer and increased selection of subnivean or subterranean resting structures during winter (Raphael and Jones, Spencer 1983, Gilbert et al. 1997). Subnivean rest sites, particularly those associated with coarse woody debris (CWD), provide a thermally protective resting environment and are an important component of thermoregulation during winter (Buskirk et al. 1989, Taylor and Buskirk 1994).

Behavior at rest sites may also vary seasonally, although most studies have focused on structure selection and site characteristics rather than behavior at rest sites. During the winter, marten re-use rest sites more frequently than in spring (Wilbert et al. 2000). Re-used winter sites tend to be subnivean sites associated with deep snow, and re-use is more common during periods of extreme cold. However, beyond re-use frequency little is known about behavioral aspects of rest site use such as activity patterns at rest sites, presence of or response to other species at rest sites, or territorial behaviors such as scent-marking.

Dens are classified as either natal dens, where parturition occurs and females provide initial maternal care, or maternal dens, where females move their kits after leaving the natal den (Buskirk and Ruggiero 1994). Parturition occurs from late March through April, and females move kits to multiple maternal dens until kits become fully independent by late summer or early fall (Strickland et al. 1982, Ruggiero et al. 1998).

As kits mature and are weaned, females spend less time at dens and duration of activity away from dens increases (Henry et al. 1997). Dens also may be an important site for social interaction prior to mating. Males were observed at 6 of 16 maternal dens monitored using motion-activated cameras in Oregon (Jones et al. 1997), although no evidence of paternal care has been documented (Buskirk and Ruggiero 1994).

Marten use many of the same structures for denning as they do for resting, although dens are typically in more secure structures than rest sites because they must protect kits when females leave the den to forage. Approximately 40% of dens are located in hollow cavities in live trees and snags (Ruggiero et al. 1998, Buskirk and Ruggiero 1994). Other structures used for denning include hollow logs, burrows in rock piles or rocky soil, squirrel middens, stumps, tree root-mass tip-ups, and slash piles (Gilbert et al. 1997, Raphael and Jones 1997, Bull and Heater 2000). Den selection is influenced by availability of potential sites on the landscape, availability of potential sites within individual home ranges, and individual differences in den site preference (Raphael and Jones 1997, Ruggiero et al. 1998). Natal dens are often in more secure structures such as tree cavities and underground burrows (Ruggiero et al. 1998, Bull and Heater 2000). Some authors have suggested that females select above-ground structures for natal dens and move kits to ground-based sites as they mature (Wynne and Sherburne 1984), but this pattern is not consistent among studies (Ruggiero et al. 1998).

Marten select rest sites and dens in mature, structurally-complex forest stands, although sites in second-growth forest and regenerating burns are occasionally used (Baker 1992, Latour et al. 1994). Complex vertical and horizontal woody structure

associated with late-successional forests is an important component of rest sites and dens used by marten. Marten select sites with closed canopies, large diameter trees and snags, and large volumes of coarse woody debris (CWD) and snags (Raphael and Jones 1997, Ruggeiro et al. 1998, Bull and Heater 2000). Structural complexity increases as forest stands age due to natural successional processes such as tree senescence and canopy gap-formations. Marten may select rest sites and dens in mature forest because they are more likely to have potential sites due to increased structural complexity, or because these characteristics increase fitness. For example, CWD increases foraging efficiency and provides access to subnivean rest sites (Andruskiw et al. 2008, Sherburne and Bissonette 1994, Corn and Raphael 1992), while forest stands with closed canopies may be more protective from predation by raptors and dense understory vegetation may provide escape cover from mammalian predators. Although mature forest stands may provide better resting and denning habitat, matrix habitats may complement mature forest if they provide denning or resting opportunities or if mature forest is highly fragmented and less available (Caryl et al. 2012).

Despite the importance of rest sites and dens to survival and reproduction of individual marten, few studies have described selection patterns for the western Great Lakes region in the south central portion of the marten range. Previous work in the western marten range has demonstrated the importance of large diameter structures for rest and den sites, yet selection of resting and denning sites depends on availability of potential sites on the landscape (Raphael and Jones 1997). Availability of important resting and denning habitat features can be altered by timber harvest. Our objectives

were to characterize rest site and den selection in Minnesota because of the lack of data from this region. We located rest sites and reproductive dens used by radiocollared marten and described selection of resting and denning structures (4th-order selection *sensu* Johnson 1980) and identify important components of the site around resting and denning structures (3rd-order selection *sensu* Johnson 1980). Because of concern that the marten population in Minnesota declined over the last ten years, we were also interested in assessing whether resting and denning habitat was limiting in our study area and providing quantitative estimates of forest structural attributes important to marten that could be used by managers to improve or monitor habitat suitability.

Study Area

Our study area was located in northeastern Minnesota (47°30'N, 91°52'W) in portions of Lake and St. Louis counties (Fig. 2.1). The study area is entirely within the central portion of the Superior National Forest. The Superior National Forest is managed for timber harvest, biological conservation, and recreation. While the Superior National Forest is entirely federal land, there are other ownerships within the forest boundary, including state, county, and private land holdings. Northeastern Minnesota has a continental climate with long, cold winters and short, warm summers. Temperatures average 18.6°C in July and -14.7°C in January (NOAA 2013). The area receives an average of 71.0 cm of rainfall and 142.7 cm of snowfall annually, with snow cover usually present from December to April. There is little topographical relief throughout

the study area, with elevations between 450 and 600 m above sea level. Permanent water in the form of lakes and rivers covers approximately 2.7 % of our study area (~4860 ha).

Our study area consists of a matrix of four main forest cover types that are characteristic of the Laurentian Mixed Forest Ecological Province (MN DNR 2013). The most abundant forest type is mixed coniferous-deciduous forest. Mixed-wood forests consist of aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), white pine (*Pinus strobus*), and white spruce (*Picea glauca*). Lowland conifer forests dominated by black spruce (*P. mariana*), tamarack (*Larix laricina*), and white cedar (*Thuja occidentalis*) covered approximately 15% of our study area. Upland conifer forest consisted of red pine (*Pinus resinosa*) and jack pine (*P. banksiana*) stands on shallow, rocky soils. Deciduous stands comprised of aspen, paper birch, red maple, and sugar maple (*Acer saccharum*) were present, but accounted for a relatively small proportion of our study area except as small patches within a larger matrix of mixed-wood forest. Understory vegetation in upland forest stands consists of beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), and saplings of common canopy species. Alder (*Alnus* spp.) is common in the understory of lowland forests and in non-forests shrublands between forest stands. Fire was the main natural disturbance historically, while logging is the major current disturbance type. Clear-cutting is the predominant harvest method, although clear-cutting reserves and pre-commercial and commercial thinning are also common. Young and regenerating stands consist of dense saplings and understory species typically found in mature forest stands.

Methods

Animal capture

Marten were captured from December through February each winter between January 2008 and February 2012. We used cage traps (Tomahawk Model 106 or 108) baited with deer (*Odocoileus virginianus*) or beaver (*Castor canadensis*) meat with commercial lure placed in or above the trap. Traps were covered with plastic grain bags and balsam fir boughs to protect captured marten from wind and moisture and checked daily. Captured marten were immobilized with ketamine (20 mg/kg) and xylazine (2 mg/kg; Kreeger and Arnemo 2012). Marten were placed on chemical hand warmers or heating pads while anesthetized to minimize hypothermia. We monitored respiration, heart rate, and body temperature of marten while under anesthesia. Marten were fitted with a Holohil MI-2 radiocollar (30-35g) and both ears were tagged (monel #1, National Band and Tag Co., Newport, KY). While anesthetized, we determined sex, extracted a pre-molar for aging, took morphological measurements, and collected hair samples. After processing, xylazine was reversed with an injection of yohimbine (0.1mg/kg) and marten were allowed to recover for 40 minutes before being released at the trap site. Animal capture and handling protocols were consistent with guidelines established by the American Society of Mammalogists (Sikes et al. 2011).

Locating rest sites and reproductive dens

We used radiotelemetry to locate rest sites and reproductive dens used by radiocollared marten from 2008-2013. We used characteristics of the transmitter signal

to determine whether marten were resting or active. If the signal was steady for ≥ 2 minutes, we attempted to locate the rest site or den site that was being used. While radiotracking a resting marten, we monitored the signal every 2-3 minutes and did not continue if the marten became active. We determined the exact site used for resting or denning based on telemetry signal, including relative position within habitat elements such as hollow logs, tree cavities, and ground-based structures with multiple openings. Identification of den or rest site structure was aided by presence of tracks leading to sites during the winter or visual sighting of the marten within the site. We did not include any sites in our analysis if the marten was located in a structure that did not appear to be a rest or den site (e.g., standing on a small branch without any potential structures nearby). Once rest sites and potential dens were located, we took coordinates at the site using handheld GPS receivers (GPSmap 76 or eTrex30, Garmin, Olathe, KS). After a den or rest site was confirmed, we marked the location with flagging and returned to the site when the marten was not present to measure structural characteristics. Measurements taken varied by rest structure and included the diameter (diameter at breast height, dbh), height, and species of tree-based structures; tree species, length, diameter at the small and large end, and decay class for all hollow logs; tree species, maximum width, maximum length, average diameter, and origin for log piles; and diameter and substrate type for all burrows. We also measured height of the rest site or den for above-ground sites and snow-depth for any sites located during winter. Site characteristics such as forest type, hydrological regime, and dominant tree species were recorded for comparison with GIS-based land cover data. Radiocollared marten were also located at 7-10 day intervals

throughout the year from a fixed-wing aircraft, which allowed us to compare rest/den selection to use of forest cover types throughout the year.

Effort to locate reproductive dens was focused on the early to mid-denning period from late April through June each year. When age data were available before this time period, we concentrated our effort on adult females. However, these data were generally unavailable, and as a result we attempted to locate all females that were thought to be an adult during capture and handling. Potential den structures were only considered reproductive dens if the presence of kits at these sites was confirmed through direct observation, video probe, or indirect observation using passive infrared cameras. We classified reproductive dens as natal or maternal dens based on time of year and relative kit development based on video or pictures taken at the site. Sites located from late April through early May tended to be natal dens, although there were some instances of females moving kits in early May. We summarized structures used as reproductive dens and compared the proportion of various den structures between natal and maternal dens using a Fisher's Exact Test.

Rest sites were located from 2008 through 2013, although effort to locate rest sites varied throughout this time period. Between 2008 and 2011, rest sites located were almost exclusively from females during the denning period while attempting to identify reproductive dens. From January 2012 to August 2013, we located rest sites year-round for both males and females. Rest sites were located opportunistically, although we attempted to locate rest sites for as many marten as possible and rarely sampled the same individual >1 time per month. With one exception, we did not locate marten from the

ground within 10 days of capture to reduce the chance of capture-related effects on rest site selection and behavior.

We classified rest sites into four different seasons based on historical climate data and phenology. Winter (1 November – 30 March) corresponded to months characterized by persistent snow cover and average temperatures near freezing, and summer (1 June – 31 August) corresponded to months with the highest average temperatures and full leaf cover. Spring (1 April – 31 May) and fall (1 September – 31 October) season dates represented the transitional periods between winter and summer temperature extremes, and were characterized by fluctuating temperatures, changing vegetative cover, and transitional behavior by other wildlife species such as migrating birds. We classified sites from April 2013 as winter due to heavy snowfall, persistent snow cover, and below average temperatures. We summarized proportion of various resting structures by season and used a chi-square test of independence to determine whether vertical position of rest sites varied by season. We tested for differences in proportion of resting structures between males and females using a Fisher's Exact Test. If the results of the Fisher's Exact Test were significant, we used Bonferroni z-tests to determine which structures were used in different proportions by males and females.

Habitat characteristics at rest sites and dens

We measured forest structural attributes around rest structures, reproductive dens, and random points to identify habitat variables that correlated with sites around structures selected by marten. Vegetative features were measured using circular, 0.02-ha circular

plots (0.04-ac; 7.3 m [24 ft] radius). Two plots were measured at all rest sites and dens. The first plot was centered on the rest/den structure or random location (center plot). A second plot was centered 36.6 m (120 feet) from the rest or den structure at an angle of 120°, 240°, or 360° (surrounding plot). Using two plots allowed us to examine forest structure at two spatial scales around rest and den structures. The direction of the surrounding plot for each den or rest site was determined randomly, although a different direction was selected if the plot location was in a non-forested cover type based on the random angle. Only one plot was measured at random sites. Measurement protocols are largely based on the U.S. Forest Service's Forest Inventory and Analysis (FIA) protocols. Because FIA data is collected periodically, our data will allow our results to be used to predict changes in habitat suitability over time with minimal additional marten-specific data collection (Zielinski et al. 2006).

We measured vegetation plots at all reproductive dens and a subset of rest sites. Rest sites were randomly selected so that we measured an equal number of sites per season and an equal number of male and female sites. When possible, we avoided measuring multiple sites for the same individual in the same season. If the site had changed dramatically as a result of natural or anthropogenic disturbance between when it was located and when we visited the site for vegetation sampling, we did not measure the site. Random locations were selected within upland conifer, lowland conifer, deciduous, and mixed coniferous-deciduous forest cover types using Geospatial Modeling Environment (Beyer 2012) and classified Landsat-based Land Use Land Cover data (LULC). Because LULC data was from source imagery collected in 1995-1996 (MN

DNR 2001), we improved classification accuracy by mapping recent disturbances (see Chapter 1). Cover types were stratified by age to avoid over-sampling any particular age class. Age strata included 20-40, 40-60, 60-80, 80-100, and ≥ 100 year old stands. We measured ≥ 3 plots per cover-type-age strata and ≥ 25 plots per forest cover type. Random sites occurring more than two kilometers from a road or trail were discarded because we had very few rest sites or dens this far from a trail.

At each plot location, we measured forest structural features that have been shown to be important to marten in the literature (Payer and Harrison 2004). Basal area and tree density were calculated by measuring the dbh of all live trees within the sample plot. Canopy closure was measured at three points along the plot boundary with a convex spherical densiometer using Strickler's modification (Strickler 1959). Measurements were taken at bearings of 30° , 150° , and 270° from the plot center and canopy closure at each site averaged to obtain an estimate of canopy closure for the plot. Understory cover density was measured using a cover pole (Griffith and Youtie 1988). The cover pole was placed at the plot boundary where canopy closure was measured, and measurements were taken from the plot center. We took readings at heights of 0.5 m, 1.0 m, 1.5 m, and 2.0 m. Density and volume of coarse woody debris (CWD) was measured along three transects from plot center to plot boundary at 30° , 150° , and 270° . CWD was counted and measured if it intersected the transect, was ≥ 7.6 cm where it intersected the transect, was ≥ 7.6 cm for at least 91.4 cm (36 in) in length, and was classified in decay classes 1-4. Volume was estimated as the volume of a cone frustrum, using length and diameter measurements at each end. Sapling density was calculated as the average of three

measurements taken on micro-plots (4.14 m diameter) centered at the intersection between CWD transects and the plot boundary. Finally, snag density was measured by counting the number of standing dead trees within the plot, and snag volume was estimated as the volume of a cone frustrum, using the height and diameters at the small and large ends. Snag heights were estimated using a clinometer (Model PM5, Suunto, Vantaa, Finland). We also counted the number of potential resting structures at each site to determine whether different habitat types provided more resting opportunities for marten. We looked for cavities and witches' brooms in all trees within the plot and searched the ground for any potential burrows. Burrows and cavities were only counted as a potential structure if the opening was large enough for a marten to enter (i.e., >7.5 cm diameter) and the potential structure contained enough space for an adult marten to fit completely within. We used a tape measure to assess whether these conditions were met, and we did not count any structure unless we could verify that these criteria.

We used ANOVA to test for differences in forest structure among different cover type-age strata. Because of small sample sizes within individual strata, we combined age classes and tested for differences between two age-classes: 20-60 years and >60 years. These age classes represent young to mature and mature to old-growth forests, respectively. For rest sites and dens, we compared each variable among center and surrounding plots using paired *t*-tests. We tested for effects of season and sex on structural features at rest sites using Two-Way ANOVA. One-Way ANOVA was used to test for differences in structural complexity between natal and maternal dens. Finally, we used One-Way ANOVA to test for differences among rest sites, reproductive dens, and

random sites. If there was no effect of season or sex on structure at rest sites, they were pooled for comparison to random sites. Similarly, dens were pooled for this analysis if there was no difference in structural features between natal and maternal den.

Cover type selection

Dens and rest sites are selected from stands occurring within a marten's home range. To determine whether certain cover types were favored for resting and denning, we compared distribution of dens and rest sites among forest cover types to expected distribution based on telemetry locations. Because we did not have adequate sample sizes for most marten to test for selection at the individual level, we averaged the cover type composition for marten from which we located at least one rest or den site. To determine whether there are seasonal differences in selection of cover types for resting, we grouped rest sites by season and compared each to the proportion of habitat used for all rest sites. Cover type composition was compared using chi-square goodness-of-fit tests and Bonferroni z-tests.

Monitoring behavior at rest sites

To describe behavior at rest sites, we monitored a subset of rest sites using passive infrared cameras. We deployed either Reconyx Silent Image RM30 black and white or Reconyx RapidFire PC85 color cameras (Reconyx, Inc., Holmen, Wisconsin). Cameras were mounted to trees or logs approximately 1-1.5 meters from the ground. Distance from the camera to rest site entrance varied slightly as a result of differing availability of

trees for mounting the camera. When possible, cameras were placed approximately 5 m from the site, facing the site opening or suspected travel route if the rest site appeared to have multiple openings. Tree-based structures were monitored with a camera facing the tree bole from the apparent direction of travel. Cameras were set to take 2, 5, or 10 pictures per trigger event without delay between consecutive triggers. We left cameras at rest sites 21.3 ± 2.4 days (range 1 – 49 days) depending on season and whether cameras were needed to monitor potential reproductive dens. Most cameras were not checked again until they were removed, but we checked and changed memory cards for cameras when they were suspected reproductive dens, if we located the marten using the same site while the camera was deployed, or if the site was close to a road or trail. We selected rest sites to monitor opportunistically, but avoided repeated monitoring of the same individuals. We attempted to balance camera deployments among sexes and seasons.

Pictures were divided into individual events and the species triggering the camera was identified for all events that contained an animal. We divided picture sets into multiple events and identified the species in each event. An event was defined as all pictures from a single trigger or series of triggers separated by ≤ 5 minutes. Picture events of marten were examined to determine whether the marten was radiocollared. For each rest site monitored, we summarized the total number of events, the number of events for each separate species, and the time between marten events. We pooled the number of events of common marten prey species as well as marten predators. We also described behavior observed at rest sites (e.g., prey-related behaviors, scent-marking, etc.) and summarized the number of events by behavior. We also determined how often marten re-

visited and re-used rest sites and compared re-use frequency to that obtained from radiotelemetry.

Statistical analysis

All statistical tests were performed using JMP software (JMP v.10.0, Statistical Analysis System Institute Inc., Cary, NC). Data were transformed when necessary to meet criteria for ANOVA. Significance level for all statistical tests was set at $\alpha=0.05$

Results

From 2008-2013 we located 16 natal dens and 15 maternal dens used by 16 female marten (Table 2.1). Dens were located in structurally sound, protective habitat elements. Reproductive den structures included cavities in trees and snags (55%), burrows in rocky soil (20%), burrows under the base of trees/snags (13%), hollow logs (7%), burrows under stumps (3%), and burrows associated with the exposed root-masses of wind-fallen trees (3%). Natal dens were located from 19 April – 18 May, while maternal dens were located from 10 May – 12 July. We located natal dens in four different structures, although 14 out of 16 natal dens were located in just two different structures: cavities in trees and snags, and burrows in rocky soil. Cavities in trees and snags accounted for 68% of all natal dens. Maternal dens were also located predominantly in tree/snag cavities (40%). Maternal dens were located in five different structures, although 13 of 15 natal dens were found in three of these structures: cavities in

trees and snags, burrows in rocky soil, and burrows under the base of trees or snags (Table 2.1). Natal dens were mostly in above-ground, tree-based structures (69%), while the majority of maternal dens were located at ground level (60%). However, there was no statistically significant difference in vertical position among natal and maternal dens ($\chi^2 = 2.58$, $d.f. = 1$, $P = 0.11$).

We located 200 rest sites used by 66 marten during 213 resting events (Table 2.2). Marten used twelve different structures as rest sites. Resting structures included platforms on tree branches, bird nests, or witches' brooms (32%); cavities in trees and snags (23%); burrows under trees, snags, or stumps (13%); hollow logs (9%); burrows in rocky soil (8%); and log piles (7%). For each marten, we located 2.9 ± 0.3 rest sites (range 1 – 11). Marten were located in rest sites that they had previously used on nine occasions (4.5% of total rest sites). Re-used sites were used 2.2 ± 0.1 times (range 2 – 4) based on radiotelemetry tracking data alone. However, because we generally avoided tracking marten more than once per month, this estimate is a minimum.

We located 54 winter rest sites (32 male sites, 22 female sites), 77 spring rest sites (12 male sites, 65 female sites), 55 summer rest sites (21 male sites, 34 female sites), and 14 fall rest sites (11 male sites, 3 female sites; Table 2.2). The most common winter rest structures were burrows under the base of trees/snags (22%), burrows with no above-ground structure (19%), and burrows in or under log piles (13%). The two most common resting structures in spring and summer were tree cavities and witches' brooms, while the most common resting structure in fall was burrows under the base of trees or snags (21%). Vertical position of rest site varied by season ($\chi^2 = 49.14$, $d.f. = 3$, $P < 0.001$;

Figure 2.2). Rest sites were predominantly in subnivean and subterranean structures during the fall (60%) and winter (81%). Spring and summer rest sites were mainly located in elevated positions such as cavities in trees and snags, witches' brooms, and tree branches.

Selection of resting structures varied between males and females (Fisher's Exact Test, $P = 0.002$; Figure 2.3, Table 2.3). Males rested more frequently on tree branches than females (95% Bonferroni confidence intervals; males $17 \pm 8.5\%$ of rest sites; females $4 \pm 3.5\%$ of rest sites), while females selected rest sites in tree/snag cavities more frequently than males (95% Bonferroni confidence intervals; females $31 \pm 8.1\%$ of rest sites; males $11 \pm 6.9\%$ of rest sites). There was no difference in proportion of male and female rest sites among other resting structures.

Marten selected forest cover types for resting and denning in different proportions than expected from telemetry locations (Figure 2.4). Dens did not occur in all forest cover types, but were predominantly in mixed-wood and lowland coniferous stands. Rest sites occurred in all forest cover types, including young regenerating stands, although sites in young forest were often associated with patches of remnant forest within the logged matrix. Marten preferred mixed-wood stands for rest sites, while young/regenerating forest and shrubby grassland was avoided. There was not a significant difference in proportion of habitat types used for resting and denning (Fisher's Exact test, $P = 0.20$), although marten appeared to be more selective of which habitat types they used for denning.

Vegetative characteristics

We measured vegetative characteristics at 332 total plots including 102 random sites, 31 reproductive dens, and 86 rest sites from June – September 2012 and June – August 2013. Random sites were distributed evenly among forest types and age-classes. We measured plots in 25 deciduous, 23 upland conifer, 27 lowland conifer, and 27 mixed-wood stands. We measured a subset of the total rest sites that were identified, including 25 winter rest sites, 25 spring rest sites, 24 summer rest sites, and 12 fall rest sites.

Most vegetative characteristics were not significantly different between center plots and surrounding plots. At reproductive dens, summer canopy closure ($t = 2.49$, $P = 0.01$), mean tree diameter ($t = 3.68$, $P = 0.0007$), and sapling density ($t = 2.19$, $P = 0.019$) were all higher at center plots than surrounding plots. Total basal area ($t = 2.13$, $P = 0.018$), basal area from conifer trees ($t = 2.35$, $P = 0.011$), snag density ($t = 1.77$, $P = 0.041$), and density of potential resting sites ($t = 4.06$, $P < 0.0001$) were significantly higher at center plots for rest sites compared to surrounding plots. Differences in center and surrounding plots were generally accounted for by changes in forest cover type between the two plots. We report results for the center plot only for vegetative characteristics that were not different between center and surrounding plots.

Natal and maternal den sites had similar vegetative structure. None of the variables we measured were significantly different between natal and maternal dens among center or surrounding plots. Because there were no differences, we pooled natal and maternal dens prior to comparing to rest sites and random sites.

There were few effects of sex and season on vegetative characteristics at rest sites. Sapling density was significantly higher at female rest sites ($F_{7,66} = 3.37$, $P = 0.004$; sex effects, $F_{1,66} = 11.34$, $P = 0.0013$), and there was a significant interaction between season and sex on sapling density ($F_{3,66} = 3.65$, $P = 0.017$). The difference in sapling density between male and female rest sites was more pronounced in the fall and summer, while male and female sites had more similar sapling density during the spring and winter. Females also tended to have higher understory cover density than males (sex effect, $F_{1,66} = 9.64$, $P = 0.003$), but the trend was not statistically significant when taking seasonal variation into account ($F_{7,66} = 2.09$, $P = 0.057$). Because of the lack of significant effects, we pooled all rest sites to compare vegetative structure to random sites.

Marten selected sites for resting and denning that had more woody structure than random sites, although there was variation in which vegetative characteristics were significant for dens and rest sites (Table 2.4). Rest sites and reproductive dens had more CWD (Kruskal-Wallis, $H_2 = 17.93$, $P < 0.0001$), including more CWD in decay class 2 ($H_2 = 15.19$, $P = 0.0005$) and decay class 3 ($H_2 = 15.5$, $P = 0.0004$) for rest sites. Mean snag diameter was higher at rest sites and dens ($H_2 = 11.1$, $P = 0.004$), mean tree diameter was higher at den sites ($F_{2,193} = 6.42$, $P = 0.002$), and snag density was higher at rest sites ($H_2 = 13.85$, $P = 0.001$). Dens also had higher sapling density ($F_{2,195} = 8.19$, $P = 0.0004$), higher density of deciduous saplings ($F_{2,195} = 3.62$, $P = 0.029$), and more potential resting and denning structures ($H_2 = 10.1$, $P = 0.006$) compared to random sites and rest sites. All other measured variables were similar between rest sites, den sites, and random sites.

Behavior at rest sites

We deployed cameras at 25 rest sites and recorded 452 events over 572 total camera-days. There were 80 events that failed to capture an animal, many of which were caused by vegetation moving from the wind. Most camera deployments occurred at female rest sites during spring and summer as we were monitoring potential den sites. We monitored nine summer rest sites (4 male, 5 female), seven spring rest sites (7 female), six winter rest sites (2 male, 4 female), and three fall rest sites (2 male, 1 female). Each deployment lasted 22.9 ± 2.3 days (range 7 - 50) and captured 18.1 ± 5.9 events (range 0 – 127).

We captured a total of 140 events with marten, including 118 events of radiocollared marten, 18 events of martens without radiocollars, and 4 marten events in which we could not determine whether the marten was wearing a radiocollar or not. We were able to confirm that the rest site was re-used in 60 of the marten events representing 49 re-uses. For the remaining marten events, marten were visiting the site without entering the resting structure or we could not determine whether the site was being re-used from the pictures taken. We classified these events as re-visits to avoid over-estimating the number of times a site was re-used. Marten re-visited 13 and re-used 8 of the 25 sites monitored. Excluding sites that did not capture any marten events, sites were re-used 0.22 ± 0.07 times/camera-day (range: 0.03 – 0.5 times/camera-day) and revisited 0.18 ± 0.07 times/camera-day (range: 0.04 – 0.82 times/camera-day). Males and females had similar number of re-uses per deployment (males: $n = 3$, range 1-18; females: $n = 5$, range 1-14) and re-visits per deployment (males: $n = 7$, range 1-19; females: $n = 6$, range

2-32). We were able to determine the time spent resting for 10 out of 49 re-uses. During these resting events, marten spent 3.4 ± 0.4 h using the rest site (range 0.5 – 5.1 h). Time between consecutive marten events was 1.5 ± 0.3 days (range 0.4 hours – 23.1 days).

We classified marten behavior at rest sites into six categories (Table 2.5). Some events contained more than one behavior, particularly with longer events that included multiple consecutive camera triggers or when the marten displayed one behavior before or after using the rest site. The most prevalent behavior was surveillance, with marten often surveying their surroundings before entering or just after leaving the rest site, occasionally standing upright and scanning all directions. Territorial behaviors included scent-marking near the site opening by rubbing parts of the body on the ground or by urinating/defecating and investigating apparent scent marks of other marten. At one rest site, we observed a radiocollared female marking above the site entrance before leaving and a marten without a radiocollar smell the mark approximately four hours later without entering the site. We also recorded one direct, aggressive interaction between two marten. We occasionally observed marten carrying or consuming prey at rest sites. One event contained a squirrel climbing a tree and a marten smelling the base of the tree and looking towards the top approximately three minutes later. There were no apparent differences in behavior frequency by sex, except that males were not observed grooming or scratching. We did not have an adequate sample to determine whether behavior varied by season, although marten re-used rest sites more frequently in the winter. It was also easier to observe behavior during the winter because winter rest sites were predominantly in subterranean and subnivean structures that were easier to monitor with a camera.

In addition to marten, we identified nine other species from 234 events including seven species of mammal (197 events) and 2 categories of bird (6 events; Table 2.6). The most common species present at rest sites were red squirrels and white-tailed deer. Squirrels were often observed feeding and occasionally entered the rest site. We captured four species of mammalian carnivores besides marten visiting sites including fisher (*Martes pennanti*), weasel (*Mustela* spp.), otter (*Lontra canadensis*), and black bear (*Ursus americanus*). Fishers were observed at three marten rest sites. Fishers investigated the rest site entrance at all sites in which they were observed. One rest site was visited by a fisher on four different occasions. There were also 31 events in which the animal triggering the camera could not be determined.

Discussion

Marten use a variety of structures as rest sites and reproductive dens. Reproductive dens were in more protective structures than rest sites because dens need to protect kits while females leave the den to forage. Although we located dens in six different structures, 56% of dens were in tree cavities. Our results did not support the hypothesis that females establish natal dens above the ground and then shift preference to ground-level sites as kits mature (Wynne and Sherburne 1984). While natal dens were predominantly located above the ground, a substantial number of natal dens were positioned at ground level, and a large portion of maternal dens remained in tree cavities. Females were less selective of maternal dens, using a wider range of structures.

Rest site selection varied seasonally. Marten increased use of subnivean and subterranean resting structures during the winter and used more elevated, tree-based structures during the summer. Winter rest sites were also re-used more frequently than rest sites in other seasons, as has been reported elsewhere (Wilbert 2000). Greater use of subnivean and subterranean rest sites during winter is a consistent pattern previously observed for American marten (Buskirk et al. 1989, Chapin et al. 1997, Raphael and Jones 1997) and Eurasian pine marten (*Martes martes* [Pulliainen 1981]). Rest site selection is an important behavioral component of thermoregulation that allows American marten to decrease metabolic rate during the winter (Buskirk et al. 1989, Gilbert et al. 2009) and likely serves a similar purpose for other species of marten. Marten are energetically constrained during winter due to high thermal conductance with their environment due to high mass-specific surface area (Harlow 1994), shorter and less-insulating fur compared to other northern mammals (Scholander 1950), and lack of body fat reserves to insulate against heat loss or provide a backup energy source (Buskirk and Harlow 1989). Subnivean rest sites associated with CWD provide a resting microenvironment where temperatures are generally above ambient during winter (Buskirk et al. 1989). Air pockets trapped within the snow likely provide insulation at these sites, while partially decomposed woody debris reduces heat loss due to its low thermal conductance (Buskirk et al. 1989). Rest sites also become increasingly important during winter when activity levels decline and more time is spent resting (Thompson and Colgan 1994).

Despite the thermal properties of ground-based sites, approximately 20% of the winter rest sites we located were in above-ground structures including cavities in trees and snags, tree branches, and witches brooms. During the winter, snow depth, wind, and air temperature influence which resting site provides the best thermal microenvironment (Buskirk et al. 1989, Taylor and Buskirk 1994, Wilbert et al. 2000). When snow depths are not sufficient to provide protection from predators, and ambient temperature is higher than the temperature in resting microenvironments, use of tree cavities and tree branches increases (Wilbert et al. 2000). In such conditions, high wind speeds are associated with selection for cavities instead of branches (Wilbert et al. 2000). Deep snow, high wind speed, and low ambient temperatures make subnivean sites more favorable (Wilbert et al. 2000). Although we did not record temperature data, we observed a general trend of increased use of above-ground rest sites during winter with less severe weather. For example, we located more above-ground rest sites during winter 2011-2012 (60% above-ground), which was a mild winter with higher average temperatures and less snowfall, compared to 2012-2013 (5% above-ground), which had more typical winter temperatures and above average snowfall.

During the summer, increased use of above-ground structures could be caused by site availability, relaxing of energetic constraints, or predator avoidance strategies. Without snow cover, some of the subnivean rest sites are not available because they would fail to provide a protective environment from predators or shelter from environmental conditions. Tree-based structures such as branches, witches brooms, and nests do not change in availability, but they fail to provide a thermally protective

environment during the winter. Above-ground rest sites may also provide better protection from predators that are less able to capture marten in trees. Common mammalian predators of marten include bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), red fox (*Vulpes vulpes*), and other marten (Hodgman et al. 1997, Bull and Heater 2001, Hearn 2007). Of these species, only fisher and marten are well adapted for climbing trees. However, without additional information on interactions between marten and other predators throughout the year, it is not possible to determine the extent to which predation risk influences selection for different resting structures throughout the year.

We found that although male and female marten used many of the same habitat elements for resting, each sex used certain types of resting structures more than the other. Other studies have not reported differences in site use by males and females (Raphael and Jones 1997), but female Eurasian pine marten (*M. martes*) use more tree cavities than males (Brainerd et al. 1995). Multiple factors could contribute to differences in rest site use by males and females including predator avoidance and differences in fine-scale habitat ecology. Natural mortality is female biased for most marten populations (Hodgman et al. 1997), and selection of rest and den sites may reflect relative abundance of predator species (Brainerd et al. 1995). Arboreal cavities may reduce predation risk by providing a protective environment that excludes larger-bodied mammalian carnivores. Size-limitation for larger male marten could also influence relative use of arboreal cavities, but diameter of tree cavity and burrow entrances were similar for males and females despite males being larger-bodied.

Vegetative structure is an important component of sites selected by marten for resting and denning. Sites selected by marten in Minnesota have large volumes of CWD, high densities of snags, large diameter trees and snags, and high density of saplings. The role of CWD in marten habitat ecology is well established. CWD serves as habitat for prey species such as red-backed voles (*Myodes gapperi*; Bowman et al. 2000, Ucitel et al. 2003), increases winter foraging efficiency (Andruskiw et al. 2009), improves thermal properties of resting microenvironments during winter (Buskirk et al. 1989), and provides marten with access to the subnivean layer for resting and foraging by creating openings in the snow (Corn and Raphael 1992). Sound, hollow pieces of CWD also serve as resting structures. Large diameter trees and snags are more likely to have developed cavities that serve as rest sites and also are an indicator of forest age. High sapling densities at reproductive dens may function as escape cover, although little is known about anti-predator behavior and few tests of hypotheses about how habitat features influence marten-predator interactions.

Vegetative characteristics were mostly similar between center and surrounding plots, natal and maternal dens, and rest sites used in different seasons. The lack of many significant differences suggests that marten are selecting sites from within mature forest stands. Based on measurements taken in our random plots, forested stands in Minnesota develop adequate quantities of physical structure around 60-80 year post disturbance (Chapter 1, Table 1.5). As stands mature, senescence and canopy disturbances promote the development of snags and downed woody material and provide canopy openings for regeneration of saplings in the forest understory.

Martens preferred mixed-wood stands for both resting and denning, while they typically did not use young/regenerating forest and open stands consisting of shrubby vegetation unless they contained patches of remnant mature forest. Mixed-wood forest had a high density of potential rest and den site structures and relatively high snag density compared to other cover types (Chapter 1, Table 1.5). In addition to physical habitat structure, mixed-wood forests have relatively high densities of small mammalian prey species (Lovallo and Anderson 1996, Fuller et al. 2004). Proximity to foraging sites may be an important aspect of rest site selection, particularly in winter when exposure to ambient temperatures is energetically costly, but data on movement and fine-scale habitat use is limited.

Using passive-infrared cameras at rest sites allowed us to observe behavioral patterns of marten and document presence of other species at marten rest sites. Overall, marten re-visited 52% of sites and re-used 32% of sites. Continuous monitoring using cameras provided better estimates of re-use frequency than telemetry because we did not re-locate individual marten frequently enough to accurately document this behavior. Re-use frequency and number of marten events per deployment were higher during the winter than in other seasons. Re-use frequency increases as ambient temperature decreases (Wilbert et al. 2000), suggesting more thermally protective sites are of increased importance. However, our results may underestimate how often sites are used in other seasons because ground-based winter rest sites were easier to monitor with cameras than tree-based rest sites.

We found that 24% of rest sites monitored were used or visited by more than one marten. This suggests that rest sites may be important sites for intraspecific interactions. We observed territorial behaviors such as scent-marking and aggression between marten. It is also possible that sites are used cooperatively by parent-offspring or sibling pairs preceding or during dispersal. Establishing genetic relatedness among marten using a common site would be required to examine this possibility, and there is currently no data to support this possibility.

Collectively, our results suggest that suitable habitat for denning and resting is available throughout the landscape in northeastern Minnesota. Marten are able to make use of a wide range of structures for resting and denning. Although marten selected resting and denning sites in mature mixed-wood stands more frequently than in other mature forest types, mixed-wood forest was abundant throughout our study area. Furthermore, other mature forest types provide similar levels of woody structure that was correlated with sites selected by marten. However, age is an important aspect of resting and denning habitat because many resting and denning structures do not fully develop until stands reach advanced age and because vegetative structure at these sites develops with stand age. Forest management practices aimed at supporting marten populations should retain stands of mature, structurally complex forest to maintain resting and denning habitat across the landscape.

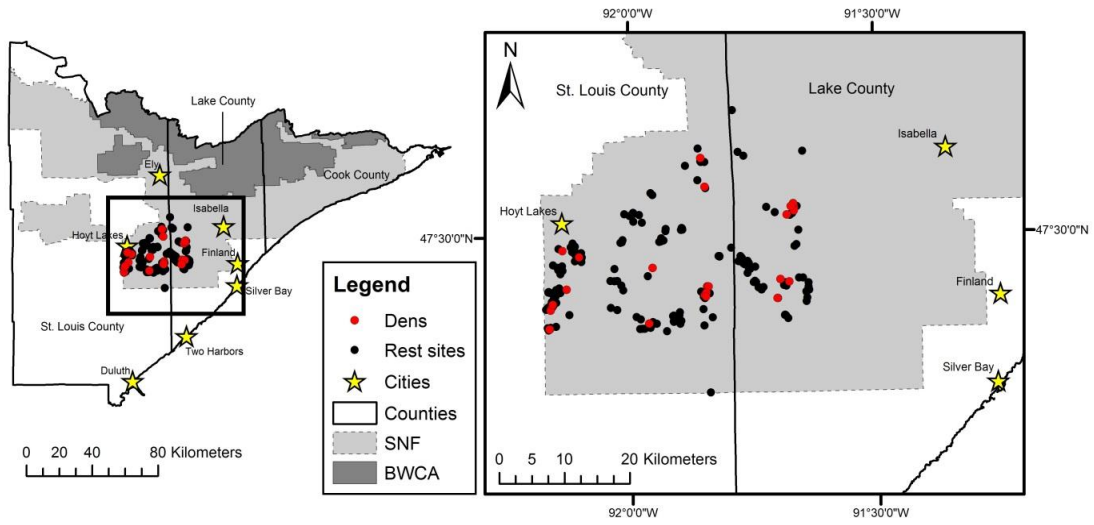


Figure 2.1. Locations of rest sites and reproductive dens used by 30 male and 41 female radiocollared American marten in the Superior National Forest, Minnesota, from 2008-2013.

Table 2.1. Structures used as reproductive dens by 16 radiocollared female American marten located in northeastern Minnesota from 2008-2013. Natal dens are the site of parturition, while maternal dens are structures used for maternal care after parturition.

	Natal		Maternal		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Burrow in rocky soil	3	19	3	20	6	19
Burrow under tree/snag			4	27	4	13
Burrow under stump	1	6			1	3
Burrow in exposed root mass			1	7	1	3
Cavity in tree/snag	11	69	6	40	17	55
Hollow log	1	6	1	7	2	7
<i>Total</i>	16		15		31	

Table 2.2. Resting structures used by 30 male and 36 female radiocollared American marten located in northeastern Minnesota from 2008-2013. Rest site selection varied by season. Marten used more above-ground rest sites during the snow-free period and more subnivean and subterranean structures during the winter.

	Winter		Spring		Summer		Fall	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Above-ground rest sites								
Cavity in tree/snag	2	3.7	27	35.1	15	27.3	2	14.3
Elevated hollow log			1	1.3	2	3.6		
Stick/grass nest	1	1.9	5	6.5	3	5.5		
Tree branch	4	7.4	4	5.2	9	16.4	1	7.1
Witches' broom	4	7.4	15	19.4	15	27.3	2	14.3
Ground-level rest sites								
Burrow under tree/snag	12	22.2	4	5.2	2	3.6	3	21.4
Burrow under stump	4	7.4					1	7.1
Burrow in rocky soil	5	9.2	7	9.1	2	3.6	2	14.3

Table 2.2 (continued)

	Winter		Spring		Summer		Fall	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Ground burrow	10	18.5	1	1.3				
Exposed rootmass	5	9.3	1	1.3	1	1.8	1	7.1
Hollow log			9	11.7	4	7.3	1	7.1
Log pile	7	13	3	3.9	2	3.6	1	7.1
Total	54		77		55		14	

Table 2.3. Comparison of resting structures used by 30 male and 36 female radiocollared American marten located in northeastern Minnesota from 2008-2013. Proportion of resting structures is significantly different between males and females for resting structures marked with an asterisk.

	Male		Female		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Above-ground rest sites						
Cavity in tree/snag*	8	10.5	38	30.6	46	23.0
Elevated hollow log			3	2.4	3	1.5
Stick/grass nest	4	5.3	5	4.0	9	4.5
Tree branch*	13	17.1	5	4.0	18	9.0
Witches' broom	15	19.7	21	16.9	36	18.0
Ground-level rest sites						
Burrow under tree/snag	8	10.5	13	10.5	21	10.5
Burrow under stump	3	3.9	2	1.6	5	2.5
Burrow in rocky soil	6	7.9	10	8.1	16	8.0
Ground burrow	4	5.3	7	5.6	11	5.5
Exposed rootmass	3	3.9	5	4.0	8	4.0
Hollow log	5	6.6	9	7.3	14	7.0
Log pile	7	9.1	6	4.8	13	6.5
Total	76		124		200	

Table 2.4. Vegetative characteristics (mean \pm SE) of rest sites, reproductive dens, and random sites measured in the Superior National Forest, Minnesota from 2012-13. Letters denote significant differences based on ANOVA/Tukey HSD or Kruskal-Wallis tests.

Habitat variable	Rest Sites	Den Sites	Random Sites	Statistic	P
Canopy Closure (%)	80.7 \pm 1.2	82.2 \pm 2.1	84.2 \pm 1.1	$F_{2,195} = 2.22$	0.11
Understory cover (%)	54.2 \pm 2.7	62.1 \pm 4.6	53.9 \pm 2.3	$F_{2,195} = 1.34$	0.27
Sapling Density (no./ha)					
Total Saplings	2416.9 \pm 233.6 a	4022.9 \pm 399.2 b	2236.3 \pm 199.6 a	$F_{2,195} = 8.19$	0.0004*
Coniferous saplings	1032.4 \pm 209.1	1816.2 \pm 399.4	1294.8 \pm 178.6	$F_{2,190} = 1.58$	0.21
Deciduous saplings	1384.5 \pm 154.3 a	1618.5 \pm 294.8 a	941.5 \pm 131.8 a	$F_{2,190} = 3.62$	0.029*
Tree variables					
Tree density (no./ha)	624.9 \pm 38.1	513.9 \pm 65.2	625.1 \pm 32.6	$F_{2,195} = 1.27$	0.28
Mean tree diameter (cm)	23.2 \pm 0.65 a,b	25.4 \pm 1.1 a	21.2 \pm 0.56 b	$F_{2,193} = 6.42$	0.0020*

Table 2.4 (continued)

Habitat variable	Rest Sites	Den Sites	Random Sites	Statistic	<i>P</i>
Tree variables, cont.					
Basal area (m ² /ha)	27.6 ± 1.7	29.5 ± 2.98	23.9 ± 1.5	$F_{2,194} = 2.03$	0.134
deciduous species	11.6 ± 1.3	12.7 ± 2.2	8.6 ± 1.1	$F_{2,195} = 2.32$	0.10
coniferous species	15.9 ± 1.7	16.7 ± 2.9	15.2 ± 1.5	$F_{2,194} = 0.57$	0.57
Snag variables					
density (no./ha)	138.5 ± 13.9 a	71.4 ± 23.7 b	73 ± 11.8 b	$H_2 = 13.85$	0.001*
mean DBH (cm)	23.5 ± 2.2 a	25.4 ± 4.1 a	23.5 ± 1.9 b	$H_2 = 11.1$	0.0038*
volume (m ³ /ha)	41.7 ± 5.3	29.7 ± 9	34.6 ± 4.5	$H_2 = 2.89$	0.24
CWD volume (m ³ /ha)					
total volume	33.7 ± 3.9 a	19.9 ± 6.6 a	12.1 ± 3.3 b	$H_2 = 17.93$	0.0001*

Table 2.4 (continued)

Habitat variable	Rest Sites	Den Sites	Random Sites	Statistic	<i>P</i>
CWD volume, cont.					
decay class 1	2.7 ± 0.85	1.9 ± 1.45	1.8 ± 0.73	$F_{2,195} = 0.34$	0.71
decay class 2	15 ± 2.3 a	6.1 ± 3.9 a,b	5.1 ± 1.96 a	$H_2 = 15.19$	0.0005*
decay class 3	13.4 ± 2.7 a	7.4 ± 4.5 a	3.3 ± 2.3 b	$H_2 = 15.5$	0.0004*
decay class 4	2.5 ± 0.62	4.5 ± 1.1	1.9 ± 0.53	$F_{2,195} = 2.37$	0.096
Stump density (no./ha)	156.4 ± 17.5	135.6 ± 29.8	140.1 ± 14.9	$H_2 = 2.85$	0.24
Exposed root-mass density (no./ha)	32.6 ± 5.6	33.3 ± 9.5	17.98 ± 4.7	$H_2 = 2.64$	0.27
Potential Sites (no./ha)	178.4 ± 23.6 a,b	294.4 ± 44.6 b	129.7 ± 19.95 a	$H_2 = 10.1$	0.0064*

Table 2.5. Marten behavior observed at rest sites of radiocollared marten using passive-infrared cameras.

Behavior	No. Events	% Marten Events
Surveillance	88	63%
Re-using structure	67	48%
Grooming/scratching	17	12%
Territorial behavior	15	11%
Prey-related activities	6	4%

Table 2.6. Species observed at rest sites of radiocollared marten monitored using passive infra-red cameras to monitor behavior.

Species	No. Events
Red Squirrel (<i>Tamiasciurus hudsonicus</i>)	149
American Marten (<i>Martes americana</i>)	140
White-tailed deer (<i>Odocoileus virginianus</i>)	28
Hare (<i>Lepus americanus</i>)	10
Fisher (<i>Martes pennanti</i>)	6
Bird (Passerines)	4
Ruffed Grouse (<i>Bonasa umbellus</i>)	2
Black Bear (<i>Ursus americanus</i>)	2
Weasel (<i>Mustela</i> spp.)	1
Otter (<i>Lontra canadensis</i>)	1
Unknown	31

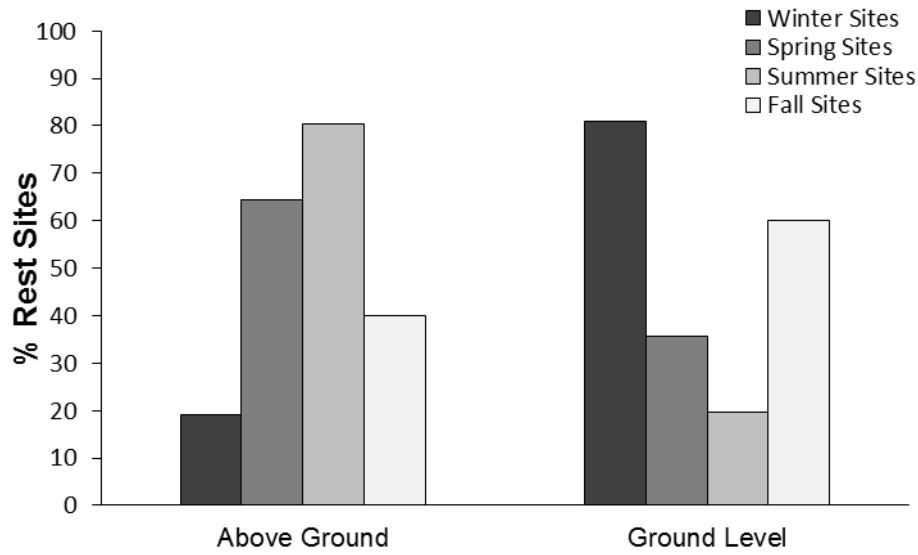


Figure 2.2. Vertical position of rest sites used by American marten during 213 resting events in northeastern Minnesota from 2008-2013. Proportion of above-ground and ground-level rest sites was significantly different among seasons ($P < 0.001$). Summer rest sites were predominantly in above-ground structures, while winter rest sites were in subnivean and subterranean structures.

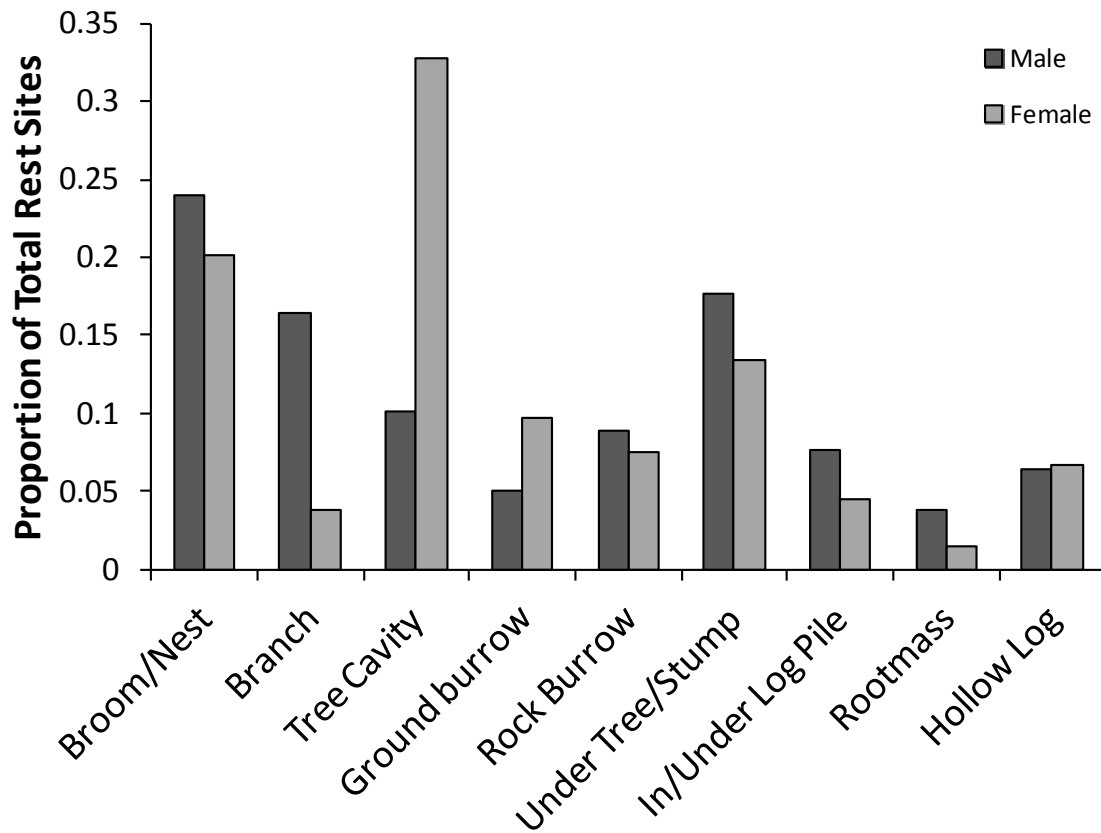


Figure 2.3. Selection of rest site structure for 30 male and 36 female radiocollared American marten located in northeastern Minnesota, 2008-2013. Males and females did not use resting structures in equal proportions (Fisher's Exact Test, $P = 0.002$). Males selected rest sites in tree branches more frequently than females, while female rest sites were more frequently in cavities in trees and snags compared to males.

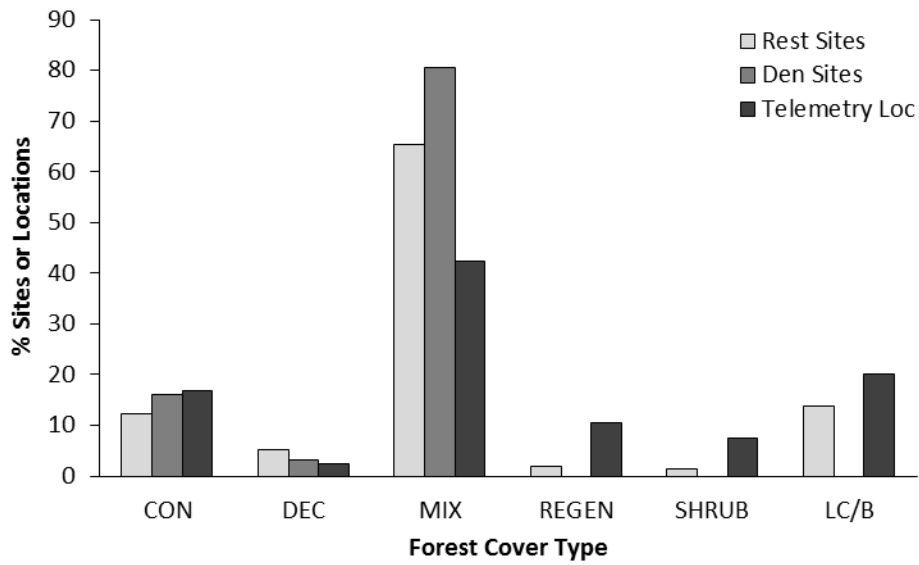


Figure 2.4. Forest cover type composition of rest sites, dens, and telemetry locations of radiocollared American marten in Minnesota. Telemetry locations are only those collected for marten for which we have located at least one rest site or den. Cover types included coniferous (CON), deciduous (DEC), and mixed-wood (MIX) forests, young/regenerating forest (REGEN), shrubby grassland (SHRUB), and lowland conifer forests/bogs (LC/B).

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