RESOURCE UTILIZATION AND MOVEMENTS OF AMERICAN MARTEN (*MARTES AMERICANA*) IN THE EASTERN UPPER PENINSULA, MICHIGAN

By

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ABSTRACT

RESOURCE UTILIZATION AND MOVEMENTS OF AMERICAN MARTEN (*MARTES AMERICANA*) IN THE EASTERN UPPER PENINSULA, MICHIGAN

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The goal of my thesis was to quantify fine scale American marten (*Martes americana*) space use, resource selection, and movement behaviors in the Eastern Upper Peninsula of Michigan. I had two main objectives, to: 1) quantify the relationships among stand-level forest inventory data, Euclidean distances, and marten space use in the East Unit of the Hiawatha National Forest (HNF), and 2) quantify marten movement behaviors and relate those behaviors to weather factors. In Chapter 1, I describe marten space use (quantified from 12 GPS-tagged marten) in the form of utilization distributions, and relate those distributions to typical forest inventory and available GIS data. I found that forest inventory data, summarized at the stand level, were poor predictors of marten space utilization. I found some support for site productivity and tree density as positive correlates of resource use. I suggest that at the stand-level, site productivity is the variable that best integrated multiple forest attributes, thereby better representing the complex forest structure knowingly used by marten. In Chapter 2, I examine daily and seasonal movements and correlated these movements to weather variables. I found that average daily movement rates were 13.28 m/min (SE = 0.48), and that marten were most active during winter (and least active during fall). My results indicated that marten in the HNF did not follow predictable daily activity patterns, and that movement rates were best explained by unmeasured characteristics related to individual marten and season. I found weak support that temperature and precipitation affected daily movement rates, with movement rates decreasing as temperature increased, and movement rates increasing on days with more precipitation. My results indicated that weather is a poor predictor of marten activity and that movements are greatest in winter, likely increasing their susceptibility to harvest and predation.

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Introduction

American marten (*Martes americana)* are members of the Mustelidae family and are considered a species of management concern for several national forests in the United States, including the Hiawatha National Forest (HNF) in the Upper Peninsula of Michigan. National Forests where marten occur are required to manage for their habitat (Dumyahn *et al.* 2007). Additionally, marten are an important recreational species that is harvested for fur in some U.S. States and Canadian Provinces, and marten are culturally important to some Native American tribes (e.g., as clan animals). Thus, interest in marten populations is generally high among natural resource management agencies, Native American tribes, and the trapping community. Marten are sensitive to environmental change (USDA 2006), and can thus provide an early warning signal about ecosystem health (USDA 2014, USDA 2006).

The types of habitat selected by marten vary by geographic location (Buskirk and Powell 1994, Bissonette *et al.* 1997, Potvin *et al.* 2000). Although marten located in the western portions of the U.S. and Canada prefer late-successional coniferous forests (Buskirk and Powell 1994), in the Great Lakes Region marten may occupy areas that are dominated by deciduous forest types, and mixed coniferous and deciduous forests (Chapin *et al.* 1997, Potvin *et al.* 2000, Payer and Harrison 2002). Marten also rely on complex structural features near the forest floor (USDA 2014, Buskirk and Powell 1994). Ground cover that consists of coarse woody debris (CWD) such as downed logs, snags, stumps, and exposed root masses, and low hanging branches and shrubs, provide denning and resting sites (Buskirk and Powell 1994), habitat for prey (Clark and Campbell 1977, Corn and Raphael 1992, Sturtevant and Bissonette 1996), and escape cover from predators such as great horned owls (*Bubo virginianus*), eagles (*Haliaeetus spp.* and *Aquila chrysaetos*), fishers (*Martes pennanti*), red fox (*Vulpes vulpes*), and coyotes (*Canis latrans)* (Clark *et al.* 1987, Payer and Harrison 2002, Drew and Bissonette 1997, Thompson 1994). Complex structural features near the forest floor also provide thermal protection during the winter

(Taylor and Buskirk 1994), and interstitial spaces beneath the snow layer (Clark and Campbell 1977, Corn and Raphael 1992, Sherburne and Bissonette 1994).

Martens usually occupy areas with >30% tree canopy cover; but for resting and foraging they prefer 40% to 60% canopy cover (Spencer *et al.* 1983, Clark *et al.* 1987, Watkins 2011). Marten typically avoid open areas and landscapes where overhead canopy cover and mature trees are absent (Heinemeyer 2002, Cushman *et al.*2011). However, vertical stems from regenerating trees and coarse woody debris can provide adequate security cover when overstory canopy cover is absent (Drew and Bissonette 1997).

Prior to European settlement, marten occupied both peninsulas of Michigan. Landscape changes resulting from logging, fires, and human settlements, along with overharvesting, caused marten to be extirpated, with the last confirmed sighting in the Upper Peninsula of Michigan from Marquette County in 1939 (Manville 1948, Williams *et al.* 2007, Skalski *et al.* 2011). Marten were reintroduced in the western portion of the Upper Peninsula in the 1950s, and the eastern portion of the Upper Peninsula in the late 1980s and early 1990s (Williams *et al.* 2007, Earle *et al.* 2001). Additionally, 85 marten were reintroduced to the northern Lower Peninsula at two sites in the 1980s. As the marten population grew in the Upper Peninsula, a trapping season was authorized in 2000 (Williams *et al.* 2007). As part of the trapping season, Michigan Department of Natural Resources – Wildlife Division annually monitor marten harvest.

Marten populations are challenged by a rapidly changing climate, and have been identified as a moderately vulnerable species on the Climate Change Vulnerability Index (CCVI) (Hoving *et al.* 2013). This ranking indicates that range and population declines due to climate changes are expected. Some have speculated that high quality habitat can help alleviate the negative impacts of climate change on wildlife (e.g., Franklin *et al.* 2000). Habitat management may be particularly important for populations that are isolated, as is the situation for marten in the HNF. Hence, studies on marten spatial ecology and resource selection in these areas can provide critical information to guide habitat management.

The goal of my study was to quantify fine scale (both spatially and temporally) marten space use, resource selection, and movement behaviors in the HNF of the Eastern Upper Peninsula of Michigan. Here, fine spatial scale refers to forest stands (average ~6 ha in the HNF study area) and marten GPS telemetry locations (generally 6 m average positional accuracy). Fine temporal scale refers to attempting a marten location every 15 min for an approximately 2-week period (life of the collar). The spatial domain was the East Unit of the HNF, and the temporal domain was 2016-2017. I relied on marten telemetry data, spatially explicit forest inventory data (summarized at the stand level) from the HNF, Euclidean distance measurements, and Daymet daily weather estimates.

Study Area

The East Unit of the HNF is located in the eastern Upper Peninsula of Michigan (Figure 0.1) and has been managed by the United States Forest Service (USFS) since 1931. The southern boundary of the East Unit borders both Lake Michigan and Lake Huron near the city of St. Ignace. The northern boundary includes Lake Superior, west of Sault Ste. Marie (USDA Forest Service 2017; Figure 0.1). The East Unit includes approximately 1,538 km^2 and 70 km of shoreline along lakes Michigan, Huron, and Superior (Figure 0.1). At the time of this study, ecosystems included beach ridges and dunes, outwash plains with lowland coniferous forests, bedrock controlled ground moraines with northern hardwoods, and pine (*Pinus* spp.) and aspen (*Populus* spp.) forests (USDA 2011). Additionally, northern hardwood and mixed forest types were widespread; the most common tree species included sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), red pine (*P. resinosa*), northern white cedar (*Thuja occidentalis*), eastern larch/tamarack (*Larix laricina*), jack pine (*P. banksiana*), spruce (*Picea* spp.), and balsam fir (*Abies balsamea*) (USDA Forest Service 2017). Proximity to the Great Lakes has a profound effect on weather in this region. Summer temperatures average 21° C, but along the Great Lakes shoreline temperatures are cooler by 5° to 8° C. Average snowfall varies from 137 cm along lakes Michigan and Huron to 610 cm along Lake Superior (USDA Forest Service 2017).

Current land and marten habitat management in the East Unit, originally established as the Marquette National Forest, has evolved significantly over the last 80 years. After extensive logging in the late 1800s and early 1900s major fires swept through this region, damaging soils and preventing natural reforestation (USDA 2017). To prevent future timber shortages, the federal government subsequently acquired lands throughout the Great Lakes region. Early (late 19th and early 20th centuries), and forest management practices were established by Congressional Acts to protect wildlife populations, conserve soil and water, and provide recreational opportunities to the public (USDA 2017). During the Great Depression (1930s), the government established the Civilian Conservation Corps (CCC) to create jobs. In the East Unit of the HNF, the CCC began rehabilitating by planting trees, controlling white pine (*P. strobus*) blister rust, suppressing fires, and constructing roads, trails, and campgrounds (USDA 2017). Today in the East Unit, the Forest Service continues to protect Great Lakes shorelines, and maintain healthy ecosystems through management practices that not only allow timber harvesting but also protect northern habitats for wildlife. The HNF has an active timber management program. For example, in 2009 the East Unit harvested approximately 49,554 m^3 of lumber dominated by red pine, jack pine and aspen (USDA 2011).

APPENDIX

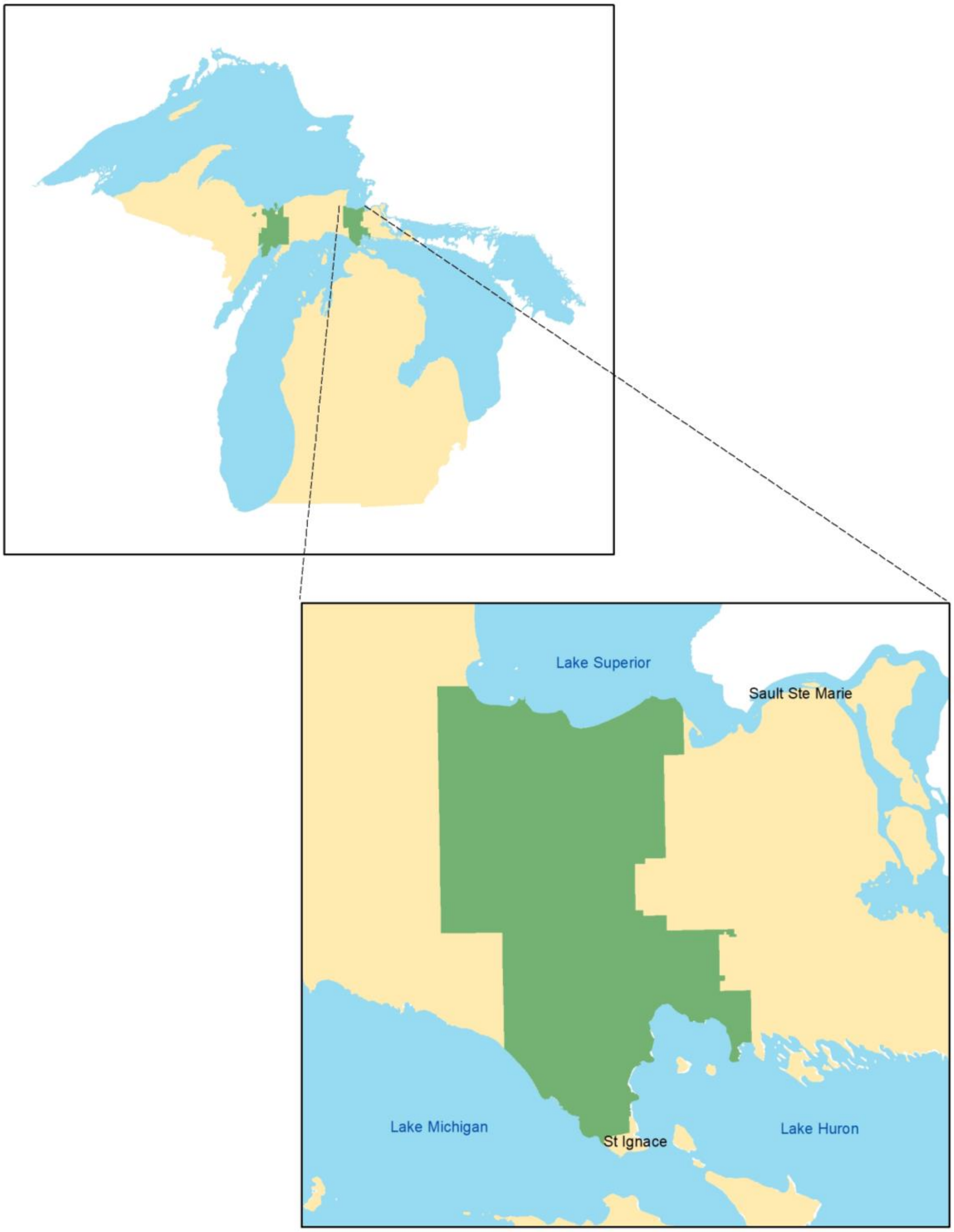

Figure 0.1. Hiawatha National Forest in the Upper Peninsula of Michigan (shaded green). Inset: East Unit of the Hiawatha National Forest. This unit includes approximately 1538 km^2 and 70 km of shoreline along lakes Michigan, Huron, and Superior.

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Chapter 1 - Resource Utilization of American Marten in the Hiawatha National Forest in the Upper Peninsula of Michigan

Abstract

I examined resource utilization of American marten (*Martes americana*) in the Hiawatha National Forest (HNF) in the eastern Upper Peninsula of Michigan. In cooperation with the Inland Fish and Wildlife Department of the Sault Ste. Marie Tribe of Chippewa Indians, I GPS collared twelve marten (11 males, one female) from March 2016 through July 2017 and used Brownian bridge movement models to portray utilization distributions for each marten. I used the utilization value at each GPS location as the response variable in generalized linear mixed models with forest stand ID as a random effect. Stands in my study area averaged 5.97 ha (SE = 0.11). Fixed effects included forest inventory measurements summarized at the stand level (i.e., basal area, stand age, tree diameter, and tree density class), a site productivity index, and distances from marten locations to nearest opening and high traffic road. I acquired 7,930 locations (660.8 locations/marten over approximately 14 days), and found that site productivity was the most consistent correlate of marten utilization, followed by tree density. Marten use was generally higher in more productive sites and in stands with higher tree densities (although this relationship was not consistent across all marten). Basal area, stand age, and tree diameter were of limited value in describing marten utilization. Some marten (n=3) appeared to negatively respond to openings, and the effect of high traffic roads was mixed. When summarized at the stand level, I found that individual metrics of vegetation structure typically collected during standard forest inventory were of limited value for describing marten resource utilization. Rather, I found that an index to site productivity (that indirectly related to forest structure complexity) was the metric that most consistently correlated with marten habitat use. At the stand-level, I recommend that managers consider multivariate measures of forest structure, combined with site productivity to portray marten habitat. I

also recommend that managers consider the potential negative effects of openings on marten core use areas.

Introduction

Marten (*Martes americana*) tend to occupy older (≥ 80 years) coniferous forests throughout much of their range (Buskirk and Powell 1994, Powell *et al.* 2003, Payer and Harrison 2003), however, in some areas marten have been found using mid-successional, coniferous or mixed coniferous-deciduous forests (Payer and Harrison 2003), and even areas dominated by young deciduous forests (Poole et al. 2004). Structural attributes found in older forests, like multi-storied canopies, snags, and abundant downed wood allow marten to avoid predators while resting or hunting (Drew 1995, Bull *et al.* 2005, McElhinny *et al.* 2005, Cushman 2011), and provide habitat for and access to prey (Corn and Raphael 1992, Buskirk and Powell 1994). Presumably, young- and mid-successional (≤ 80 years) forests that support marten provide these structural attributes (Bowman and Robitaille 1997, Payer and Harrison 2003, Poole *et al.* 2004, Porter *et al.* 2005, Hearn *et al.* 2010, Powell *et al.* 2009). Variation in forest ages and cover types used by marten underscores the importance of identifying site-specific features that contribute to suitable marten habitat (Payer and Harrison 2003, Shirk *et al.* 2014).

Given that marten are closely associated with complex forest structure, they generally avoid recently clearcut areas and openings with sparse canopy cover (Bull *et al.* 2005, Thompson and Harestad 1994, Pereboom *et al.* 2008). In Maine, use of clearcuts by martens was seasonal (Steventon and Major 1982). During winter marten avoided clearcuts, whereas in summer they used clearcuts to supplement their diet with raspberries (*Rubus* spp.; Soutiere 1979). During summer, regenerating hardwood and softwood trees in clearcuts presumably provided adequate overhead cover (Hawley and Newby 1957, Herman and Fuller 1974).

Martens generally have a negative relationship with roads. In some locations roads can be the primary source of mortality (e.g., Cervinka *et al.* 2015, Ruette *et al.* 2015). Some roads also can serve as barriers to marten dispersal and movements (e.g., Ruiz-Gonzalez *et al.* 2014, Li *et al.* 2014, Howell *et al.* 2016). For example, martens will use low-traffic roadways for travel and hunting (e.g., Robitaille and Aubry 2000), but roads with high traffic volumes can serve as movement barriers (e.g., Howell *et al.* 2016).

Marten unequivocally rely on complex forest structure, but our ability to adequately quantify that structure is typically restricted to vegetation inventories summarized at the stand level. Here, a stand refers to an operationally defined patch of relatively homogenous vegetation. In typical natural resource information systems, stands tend to be mapped at 1's to 10's of hectares resolution, with boundaries ecologically, operationally (e.g., along roads), or administratively defined. Stand-level summaries form the basis for timber assessments and, by default, often for wildlife habitat assessments. However, habitat utilization patterns exhibited by animals occur at multiple scales (Johnson 1980). For resource managers that are required to consider marten habitat, understanding the utility of stand-level data for management is important.

The goal of my study was to quantify marten resource utilization and relate utilization to stand-level summaries of typical forest inventory data. I also evaluated marten utilization in regards to high-traffic roads and openings. I hypothesized that forest inventory metrics indicative of older forest conditions (e.g., high basal area, larger tree diameters) would positively correlate with marten use. I also predicted that site productivity would positively correlate with marten use, as areas with higher productivity tend to provide more structural complexity (Hargis *et al.* 1999, Buskirk and Zielinski 1997, Larson *et al*. 2008). Lastly, I predicted that marten space use would negatively correlate with openings and high-traffic roads. Quantifying how the relationships between marten space use, structural attributes that are measured during standard forest inventory, and proximity metrics that can be derived from GIS provide insights into marten ecology useful to forest planning and habitat management.

Methods

Marten Trapping

To encompass a variety of forest types, I overlaid a 5.2 km^2 square grid on the East Unit of the HNF in the Upper Peninsula of Michigan (Figure 1.1). Only grid cells that were 100% inside the HNF boundary (not borders or shoreline) were available for sampling (Figure 1.1A). This cell size is roughly twice the home range size of marten in the East Unit of the HNF (Sault Tribe Inland Fish and Wildlife Department, unpublished data), thereby having the potential to encompass multiple home ranges. I selected 30 grids cells using generalized random tessellation stratified (GRTS) sampling (Stevens and Olsen 2003). This procedure randomly selects spatially distributed samples from a discrete population while reducing the chances of spatial clustering (Stevens and Olsen 2003). These grid cells formed the focal locations for marten trapping. In collaboration with the Inland Fish and Wildlife Department of the Sault Ste. Marie Tribe of Chippewa Indians, I trapped within selected grid cells from March 2016 through September 2016. Because of low capture rates within the initially selected grid cells, we expanded the trapping area from September 2016 through July 2017 to a 36.25 km^2 hexagon centered on each cell. We also opportunistically trapped areas that historically supported marten in and around these larger areas. Once a marten was collared in a grid cell, we moved to a different area. If no marten were trapped in an area after approximately 5 days, we moved to the next grid cell.

We captured marten using Tomahawk 201 and 204 live traps (Tomahawk Live Trap Company, Tomahawk, WI). We placed traps next to coarse woody debris and then covered the traps with leaf litter, conifer boughs, tree bark, fallen logs, or natural debris found in the area. In winter we cut 19 L buckets in half and covered each trap with straw and a half-bucket. Cover over the traps helped keep marten dry and hidden. We baited traps with meat that included chicken, venison, pork, beef, or fish heads. After placing the meat at the back of the trap, we placed a commercial call lure called Gusto (Caven's Gusto, Pennock, PA) on a branch above the trap.

We anesthetized marten using a facemask on a portable vaporizer with isoflurane in a 100% oxygen carrier, with an induction setting of 5% and a maintenance setting of 2-3%. We weighed each marten using a digital scale and monitored temperature, heart rate, and breathing during the collaring procedure. For marten weighing >833 g we fit a 30g LiteTrack30 collar (SIRTRACK, Hawkes Bay, NZL). I programmed the collars to attempt a location every 15 min (Moriarty and Epps 2015, Kie 2013). Based on this setting, I estimated that the GPS battery would last 12 days, with the VHF beacon lasting an additional 30 days. After collaring, we placed marten in a completely enclosed holding box and waited for recovery, typically <10 min. Marten were released at the point of capture when fully recovered. I used VHF triangulations to monitor the general locations of marten for the duration of VHF collar life. Because these collars required manual downloading to retrieve the GPS data, we started re-trapping marten after about 2 weeks, corresponding to the time period when GPS battery life was predicted to end. We used the same procedure except that traps were purposefully placed where VHF tracking suggested the marten were concentrating their activity. I plotted average daily movement rates since capture to evaluate effects of the collaring process on marten space use. Locations from days that showed a capture effect were removed from the analysis. Marten were trapped and handled using approved protocols from the Institutional Animal Use and Care Committee at Michigan State University (12/15-185-00) and the Inland Fish and Wildlife Department of the Sault Ste. Marie Tribe of Chippewa Indians.

Utilization Distributions

I used Brownian Bridge Movement Models (BBMM) to analyze the GPS telemetry data because the data were temporally autocorrelated (Kranstauber *et al.* 2012, Byrne *et al.* 2014). The BBMMs were specifically designed to describe animal movements and portray utilization distributions from temporally autocorrelated data (Horne *et. al.* 2007, Marzluff *et al.* 2004, Moriarty *et al.* 2016, Aebischer *et al.* 1993, Nielson *et al.* 2013). Prior to analysis, I removed locations with a Dilution of Precision (DOP) >10; DOP ≤10 have acceptable locational error (Lewis *et al.* 2007, D'Eon and Delparte 2005). I created a utilization distribution for each collared marten using the kernelbb function in the adehabitatHR package (Calenge 2006) in the program R Studio (R Core Team 2017). I exported the utilization distributions as rasters from RStudio for use in ArcGIS 10.2.1. Once in ArcGIS, I extracted raster values for each covariate that corresponded to every marten location. Thus, each marten location was assigned a measure of forest structure like tree density, basal area, and tree size and proximity value (i.e., distance to nearest opening, distance to nearest well-traveled road).

Modeling

For each marten, I used generalized linear mixed modeling (GLMM) with HNF stand as a random effect. I used stand identifier as a random effect because multiple marten locations often occurred within the same stand (and forest inventory data were summarized at the stand level). Fixed effects included basal area, stand age, diameter at breast height (DBH), site productivity, tree density classes, distance to nearest opening, and distance to nearest well-traveled road (Tables 1.1, 1.2). I selected these attributes based on findings from published marten literature (Hargis *et al.* 1999, Payer and Harrison 2002, Sturtevant *et al.* 1997, Tiedemann *et al.* 2002). Basal area, stand age, DBH and tree size and density came directly from the HNF. Basal area, stand age, and DBH were continuous data, whereas tree size and density were ordinal data that ranged from no trees to densely stocked (4 density categories) and openings to sawtimber sized (4 size categories), respectively (Table 1.1). I used site productivity rankings from Schaetzl *et al.* (2012) and coded those 1 – 5, representing low to highly productive sites (Table 1.1). To evaluate the assumption that site productivity positively correlated with forest complexity, I calculated an additive structural complexity index from tree basal area, DBH, and density (Barnett et al. 1978), and looked for a positive relationship between the index and site productivity. I measured Euclidean distance from marten locations to the nearest edge of an opening (as classified in the HNF stand layer) in ArcGIS (Table 1.2). Openings in the HNF stand layer ranged in size from <0.1 to 454.3 ha, and were defined as having a tree basal area and DBH measurement of zero. I also measured Euclidean distance from marten locations to nearest high traffic road in ArcGIS. I identified roads with the potential for higher traffic volumes based on an HNF classification ranging from 1 – 5, with 4 and 5 indicating that the road was routinely maintained and rated for passenger vehicle comfort (Table 1.2).

I produced a correlation table for the continuous fixed effects and identified those with a correlation > 0.5 as potentially redundant (Dormann *et al.* 2012); I did not include redundant variables in the same candidate model. Using all possible combinations of uncorrelated variables, I identified 40 to 76 candidate models for each marten and ranked those models using AICc (Burnham and Anderson 2002). To run the GLMMs, I used the lmer function in the lme4 package in RStudio (Bates *et al.* 2015). Each marten potentially had unique models based on correlation results (Table 1.4). For candidate models with ΔAIC < 7.0 for individual marten (Burnham and Anderson 2002), I used model averaging in the MuMIn package in R (Bartoń 2016) to produce a single model. I deemed model parameters significant if 95% confidence intervals did not overlap 0. I subsequently looked for consistency of parameters (i.e., sign, significance) among marten to identify important predictors.

Results

Marten Trapping

We trapped marten for 5,922 trap nights. We caught 12 marten that were collared (11 males and 1 female) and 10 marten (1 male and 9 females) that were too small to collar (i.e., <833 g). These trapping results suggested that smaller marten (generally females) were using the same areas as larger marten (generally males). On average, we caught a marten for collaring every 269 trap nights; trap success was higher in March, April and May compared to July, August, October, and November (75.5 and 608.1 trap nights/marten, respectively). Martens that were not collared weighed an average of 608.3 g (505g-706g). The average weight of martens that were collared was 1064.64 g (891g-1335g).

Collar Performance

Prior to deployment, I tested every collar by attempting to acquire at least one location; 100% of the collars were functional. The GPS batteries lasted on average 14.7 days (SE = 1.09; range = 13-18), collecting an average of 660.8 locations (SE = 167.6; range 374 – 1061) per marten, with 620.1 (SE = 160.5) of the fixes (94%) having DOP < 10. The average collar fix rate was 45% (SE = 9), comparable to other GPS studies on marten (Moriarty *et al.* 2015). These collars were found to have an average positional accuracy of 6 meters (DOP ≤10). I found no difference in average daily movement rate as time from capture increased (Figure 1.2), hence all GPS collar locations were used in the resource utilization model. Additionally, average marten home ranges from my study (male = 9.67 km^2, female = 4.46 km^2) approximated home range estimates from other estimates in the Great Lakes Region (e.g., 4.3 – 15.7 km^2; Davis 1978, Mech and Rogers 1977).

Resource Utilization

On average, I found that marten GPS locations were in forested stands with a relatively wide range of basal areas (14.0 – 32.7 m^2/ha), including forested stands with no merchantable timber (i.e., basal area = 0; Table 1.1). Average stand ages used by marten were >33 (range = 0 – 135) years, but recently cut and permanent openings were also used (stand age = 0; Table 1.1). I found that average stem diameters of used stands were >15.1 cm (Table 1.1). Areas used by marten in this study generally contained small diameter trees overall (upper range = 46 cm, with most <35 cm; Table 1.1). Marten consistently used forested stands that were relatively dense (i.e., stocking code >3), with moderate productivity (productivity code generally > 2; Table 1.1). Most marten had a broad range of productivity classes that they used, with codes generally ranging from 1 to 5 (Table 1.1).

I found that marten GPS locations were >167 m (range = 0 – 1,117 m) from openings on average, with relatively low variability among individuals (most SEs < 14 m; Table 1.2). However, all marten were documented using non-forested areas during all seasons (i.e., opening distance minimum = 0; Table 1.2). Marten tended to use habitats that were >440 m from high traffic roads, but this pattern was highly variable (SE ranged from 13.9 – 50.3 m; Table 1.2). Anecdotally, I found that the marten collared in November, corresponding to the firearm deer season in Michigan, was farthest from maintained roads (mean = 5,072 m; Table 1.2).

For each marten, I found that model averaging resulted in relatively simple (i.e., ≤3 parameters) models for the majority (11 of 12) of marten (Table 1.3). On average, each marten had 8.8 (SE = 0.6) competing models, with the top-ranking models accounting for 0.26 to 0.96 weight of evidence (Table 1.4). The majority (8 of 12) of top-ranking models included only the random effects, indicating that unmeasured attributes of the stand or individual marten were explaining the most variability in resource utilization.

The most consistent (10 of 12 marten) fixed effects that appeared in marten resource utilization models included site productivity and tree density (Table 1.3). Other variables with some support (2-3 marten) among marten included basal area, distance to openings, and distance to roads (Table 1.3). Stand age and stem diameter received limited support (1 and 0 marten, respectively; Table 1.3). Of the most consistently appearing variables, site productivity was significant for 6 (of 10) marten, however the direction of the effect was variable (Table 1.3). For tree density, the relationship tended to be positive (i.e., as tree density increased probability of marten use increased), but few (8 of 10) of the relationships were significant (Table 1.3). For the limited number of marten (n=3) that appeared to respond to openings, the relationship was consistently significant and positive, indicating that high use areas tended to occur farther from openings (Table 1.3).

Discussion

The positive relationships between marten and complex forest structure is undisputed. Marten have been shown to use areas with higher basal areas or tree densities (>40m^2/ha and 1,054 live trees/ha; Spencer *et al.* 1983, Payer and Harrison 2003, Bull *et al.* 2005, Godbout and Ouellet 2010, Sanders *et al.* 2017), older forests (≥ 80 years; Slauson and Zielinski 2009, Wiebe *et al.* 2013, Sanders *et al.* 2017), and forests that contain larger diameter trees (>70 cm; Slauson and Zielinski 2009, Erb *et al.* 2010, Sanders *et al.* 2017). However, these structures may not consistently be restricted to mature or old forest types (e.g., Vigeant-Langlois and Desrochers 2011, Hearn *et al.* 2010). I found that standard forest inventory measures that included basal area, stand age, and tree diameter, summarized at the stand level, were poor predictors of marten space use in the eastern Upper Peninsula of Michigan. This finding highlights some of the challenges faced by natural resource managers that rely on forest inventory databases to describe marten habitats. Short-term (i.e., daily, weekly) marten resource utilization decisions likely occur at fine scales (e.g., individual trees, localized patches of downed wood; Wiebe *et al.* 2014, Sanders *et al.* 2017) that are undetectable in stand-level forest inventories. Additionally, consistent responses by martens to forest inventory metrics across large landscapes may not be expected, as marten selection of forest structures can vary depending on landscape context of home ranges (Hearn *et al.* 2010, Shirk *et al.* 2014). In these instances, combinations of factors like site productivity and forest type, along with information on structural complexity, will likely provide more consistent insight into why marten are using certain areas.

Complex forest structures are more likely to develop on productive sites (Hargis *et al.* 1999, Buskirk and Zielinski 1997, Larson *et al*. 2008). Indeed, in my study a coarse ranking of site productivity was the most consistent correlate to marten resource use patterns. I found that marten use increased as site productivity increased. Stands with higher productivity develop complex forest structure more rapidly than low productivity stands (Larson *et al.* 2008). Additionally, highly productive forests provide enough nutrients for quick growth after a disturbance like timber harvest (Page-Dumroese 2010). Following disturbances on the HNF, early successional trees (including balsam fir, spruce, and aspens) rapidly colonize highly productive sites (USDA 2011, USDA Forest Service 2017), providing complex structure suitable for marten foraging (Larsen *et al.* 2008, Payer and Harrison 2003, Baker 1992). These densely treed areas provide cover for marten and key habitat for prey like snowshoe hare (*Lepus americanus*) and ruffed grouse (*Bonasa umbellus*) (Vigeant-Langlois and Desrochers 2011, Fuller and Harrison 2005, Potvin *et al.* 2000).

Openings with sparse overstory vegetation (<30% cover) generally do not provide enough cover for marten or their prey (Vigeant-Langlois and Desrochers 2011, Fuller and Harrison 2005, Potvin *et al.* 2000, Baker 1992). In these low cover areas mortality risks for marten are higher and these places are generally avoided (Bull *et al.* 2005, Thompson and Harestad 1994, Pereboom *et al.* 2008). However, I found that marten temporarily use and cross openings in HNF. For example, in November a marten crossed a large (67.9 ha) emergent wetland opening and stayed in a relatively small island (0.18 ha) of sparse trees. I suspect that the emergent vegetation in this wetland provided enough cover to facilitate movement to the island of trees (Buskirk and Zielinski 2003, Buskirk and Powell 1994).

Contrary to other studies (Cervinka *et al.* 2015, Ruette *et al.* 2015), I failed to find a strong road effect on marten space use. In my study area, high traffic roads were relatively scarce, but low traffic roads were common. Roads may correspond to areas where less prey occurs (Vos and Chardon 1998, Rondinini and Doncaster 2002), however I frequently observed marten crossing and traveling down low-traffic roads. My results highlight the importance of road type when describing marten habitat use. I documented marten mortality from road kill on high traffic roads during my study, but also observed marten using low-traffic roads for travel and foraging,

I acknowledge several limitations to my study. My forest inventory data were spatially limited to the stand scale, which represented average forest structure condition across multiple hectares, a spatial scale that may not align with short-term marten decisions on resource use. As such, stand-level averages of forest structure likely represent a scale mismatch and hence it is not surprising that no single variable was a good predictor of marten space use. Additionally, marten affinity for complex forest structure suggests that no single variable should be a strong predictor. Rather, marten are likely responding to the combination of forest structural attributes that includes interactions among the variables I used. These factors likely contributed to the random effects models outperforming other models for explaining marten resource utilization. I further acknowledge that my results are based on a limited number of marten that were mainly males, monitored intensively over a short temporal window. This sampling design has been shown to reliably portray marten home ranges (Moriarty 2014), but only represents a sex-biased and relatively short assessment of resource utilization. Over a short temporal window, proximate factors (e.g., interaction with a predator or conspecific, disturbance by humans or pets) other than habitat could significantly affect resource utilization.

Given the ecological, recreational, and cultural importance of marten in Michigan, understanding how marten populations interact with vegetation structure, land use patterns, and site productivity are important contributions to marten conservation. I encourage natural resource managers to cautiously use stand-level forest inventory data to quantify marten habitat, as singularly these measures inadequately portrayed high use areas. My results suggest that site productivity is an important consideration and I encourage managers to combine forest inventory data with site productivity. I also encourage managers to recognize that some martens positioned high use areas away from openings, thereby suggesting some sensitivity to non-forested areas. Lastly, my results indicated that high-traffic roads in the East Unit were not consistent determinants of marten resource utilization.

APPENDIX

Table 1.1. Basal area, stand age, diameter at breast height (DBH), site productivity, and tree density for stands used by American marten on the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

		Basal Area (m^2/ha)		Stand Age (yrs)		DBH (cm)		Tree Density (stems/ha)[a]		Productivity[b]	
Marten	Month	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	Mode	Range	Mode	Range
A	March	23.6 (0.7)	0, 46	33 (2)	0, 100	16.5 (0.5)	0, 29.7	4	1, 4	2	1, 5
B	March	24.2 (0.5)	0, 41	65 (3)	0, 97	21.6 (0.3)	0, 26.7	4	1, 4	2	1, 5
C	March	23.2 (1.1)	0, 41	81 (2)	0, 104	17.7 (0.5)	0, 24.9	4	1, 4	2	1, 4
D	April	16.8 (0.4)	0, 32	50 (1)	0, 92	20.9 (0.3)	0, 31.2	3	1, 4	1	1
E	May	28.9 (0.5)	0, 53	78 (2)	0, 125	19.9 (0.3)	0, 29.5	4	1, 4	2	2, 5
F	May	19.3 (0.3)	0, 51	65 (1)	0, 128	18.7 (0.3)	0, 40.6	4	1, 4	1	1, 2
G	July	32.7 (0.5)	0, 49	52 (3)	0, 135	25.6 (0.3)	0, 30.5	4	1, 4	3	3, 5
H	August	28.1 (0.3)	0, 49	50 (2)	0, 112	22.2 (0.3)	0, 27.2	4	1, 4	3	2, 5
I	August	14.0 (0.5)	0, 40	47 (1)	0, 131	15.1 (0.3)	0, 46.0	4	1, 4	2	1, 5
J	August	28.4 (0.3)	0, 48	59 (1)	0, 122	18.5 (0.3)	0, 30.5	4	1, 4	3	2, 5
K	October	22.8 (0.5)	0, 32	65 (4)	0, 96	22.4 (1.0)	0, 40.6	4	1, 4	3	2, 5

Table 1.1. (cont'd).

		Basal Area (m^2/ha)		Stand Age (yrs)		DBH (cm)		Density (stems/ha)[a]		Productivity[b]	
Marten	Month	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	Mode	Range	Mode	Range
L	November	15.7 (0.3)	0, 36	75 (1)	0, 130	15.8 (3.0)	0, 29.0	4	1, 4	4	2, 5

[a] Ordinal data, where 1 = non-stocked, 2 = low stocking, 3 = medium stocking, and 4 = high stocking, based on Huron National Forest stocking codes.

[b] Ordinal data, where 1 = Productivity Index 5, 2 = Productivity Index 8, 3 = Productivity Index 9, 4 = Productivity Index 11, and 5 = Productivity Index 14, based on Schaetzl *et al.* 2012 productivity indices. Schaetzl *et al.* (2012) rank productivities from 0 as the least productive to 19 as the most productive.

Table 1.2. Distances to nearest openings and maintained, high traffic roads from American marten telemetry locations on the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

		Opening (m)		Roads (m)	
Marten	Month	Mean (SE)	Range	Mean (SE)	Range
A	March	306.4 (12.9)	0, 969	494.1 (18.5)	14, 1580
B	March	310.0 (13.1)	0, 757	442.3 (20.7)	8, 1586
C	March	418.8 (32.9)	0, 927	660.4 (37.4)	1, 1393
D	April	527.1 (9.6)	0, 995	1260.3 (22.0)	2, 2317
E	May	246.8 (7.1)	0, 579	612.6 (18.6)	3, 2083
F	May	149.7 (5.0)	0, 591	894.1 (24.0)	3, 2006
G	July	167.0 (4.6)	0, 382	2808.0 (50.3)	729, 3750
H	August	395.7 (7.6)	0, 893	1303.5 (23.6)	72, 2229
I	August	323.6 (7.5)	0, 1117	760.2 (24.9)	18, 2828
J	August	458.9 (12.3)	0, 1058	1155.1 (69.79)	10, 4784
K	October	235.3 (10.7)	0, 675	2204.6 (52.8)	959, 2949
L	November	293.1 (7.9)	0, 831	5072.0 (13.9)	4031, 6149

Table 1.3. Generalized linear mixed model averaged coefficients (95% confidence intervals), by individual marten, for variables used to describe resource utilization in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017. NA denotes a variable that was not included in the model averaging for individual marten. Bold-face indicates that the 95% confidence interval did not overlap 0.

Marten	Basal Area	Stand Age	DBH	Density	Productivity	Opening	Roads
A	NA	NA	NA	0.008	**0.0196**	NA	NA
				(-0.08, 0.06)	(0.002, 0.037)		
B	NA	NA	NA	-0.077	**0.0191**	NA	NA
				(-0.16, 0.003)	(0.004, 0.033)		
C	NA	NA	NA	-0.027	NA	NA	NA
				(-0.13, 0.106)			
D	NA	NA	NA	NA	NA	NA	**0.0006**
							(0.0005, 0.0007)
E	NA	NA	NA	-0.022	-0.021	**0.0005**	NA
				(-0.10-0.056)	(-0.05, 0.014)	(0.0002, 0.0007)	
F	NA	NA	NA	NA	-0.050	NA	NA
					(-0.16, 0.06)		

Table 1.3. (cont'd).

Marten	Basal Area	Stand Age	DBH	Density	Productivity	Opening	Roads
G	NA	NA	NA	0.028	**-0.067**	NA	**-0.0001**
				(-0.051, 0.107)	(-0.013, -0.011)		(-0.0001, -0.00008)
H	NA	NA	NA	0.028	**-0.055**	**0.0004**	NA
				(-0.051, 0.107)	(-0.09, 0.024)	(0.0003, 0.0006)	
I	**-0.0009**	NA	NA	**0.038**	-0.025	NA	NA
	(-0.0002, -0.0006)			(0.019, 0.057)	(-0.088, 0.038)		
J	NA	NA	NA	0.007	**0.066**	NA	NA
				(-0.026, 0.012)	(0.007, 0.126)		
K	NA	NA	NA	0.064	-0.013	NA	NA
				(-0.052, 0.180)	(-0.121, 0.095)		
L	**0.0016**	**0.0014**	NA	**0.049**	**0.121**	**0.0001**	**-0.0001**
	(0.001, 0.002)	(0.001, 0.002)		(0.0389, 0.0586)	(0.034, 0.207)	(0.00007, 0.0002)	(-0.0002, -0.0001)

Table 1.4. Candidate resource utilization models for individual marten with AICc weight >0, Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

Marten	Model Number	Model	AICc	Delta	Weight
A	1	UD~ random effect	-493.1	0.00	0.878
	2	UD~ productivity	-488.1	4.97	0.073
	3	UD~ density	-486.3	6.77	0.030
	4	UD~ DBH	-484.0	9.06	0.009
	5	UD~ near open	-481.8	11.28	0.003
	6	UD~ density + productivity	-481.3	11.80	0.002
	7	UD~ basal area	-479.5	13.60	0.001
	8	UD~ stand age	-479.4	13.73	0.001
	9	UD~DBH + productivity	-479.0	14.05	0.001
	10	UD~ near road	-478.5	14.59	0.001
B	1	UD~ random effect	-333.8	0.00	0.637
	2	UD~ density	-331.0	2.75	0.161
	3	UD~ productivity	-330.6	3.12	0.134
	4	UD~ density +productivity	-328.3	5.49	0.041
	5	UD~ DBH	-326.5	7.30	0.017
	6	UD~ DBH + productivity	-323.8	10.00	0.004
	7	UD~ basal area	-323.3	10.46	0.003
	8	UD~ basal area + productivity	-320.8	12.95	0.001
	9	UD~ stand age	-320.3	13.46	0.001
C	1	UD~ random effect	-3.5	0.00	0.903
	2	UD~ density	2.5	5.98	0.045
	3	UD~ productivity	3.6	7.08	0.026
	4	UD~ DBH	4.5	8.02	0.016
	5	UD~ near open	7.6	11.11	0.003
	6	UD~ stand age	9.2	12.72	0.002
	7	UD~ density + productivity	9.6	13.11	0.001
	8	UD~ basal area	10.2	13.74	0.001

Table 1.4. (cont'd).

Marten	Model Number	Model	AICc	Delta	Weight
	9	UD~ near road	11.4	14.97	0.001
D	1	UD~ near road	-389.0	0.00	0.958
	2	UD~ DBH + near road	-381.5	7.53	0.022
	3	UD~ near open + near road	-380.9	8.15	0.016
	4	UD~ near road + stand age	-377.1	11.86	0.002
E	1	UD~ random effect	-352.0	0.00	0.562
	2	UD~ near open	-351.1	0.92	0.355
	3	UD~ density + near open	-345.4	6.61	0.021
	4	UD~ density	-345.1	6.90	0.018
	5	UD~ productivity	-345.0	6.93	0.018
	6	UD~ near open + productivity	-343.9	8.12	0.010
	7	UD~ DBH	-342.8	9.17	0.006
	8	UD~ stand age	-342.1	9.88	0.004
	9	UD~ DBH + near open	-342.0	9.97	0.004
	10	UD~ near open	-338.3	13.72	0.001
	11	UD~ density + productivity	-338.2	13.81	0.001
	12	UD~ density + near open + productivity	-338.1	13.87	0.001
F	1	UD~ random effect	-725.1	0.00	0.892
	2	UD~ productivity	-719.9	5.17	0.067
	3	UD~ density	-717.2	7.91	0.017
	4	UD~ near road	-716.4	8.66	0.012
	5	UD~ DBH	-715.0	10.03	0.006
	6	UD~ stand age	-713.1	11.94	0.002
	7	UD~ density + productivity	-712.0	13.12	0.001
	8	UD~ near road + productivity	-711.1	13.95	0.001
G	1	UD~ random effect	-378.6	0.00	0.672
	2	UD~ productivity	-376.8	1.82	0.270
	3	UD~ density	-372.5	6.16	0.031

Table 1.4. (cont'd).

Marten	Model Number	Model	AICc	Delta	Weight
	4	UD~ density + productivity	-370.4	8.20	0.011
	5	UD~ DBH	-369.9	8.71	0.009
	6	UD~ DBH + productivity	-367.9	10.72	0.003
	7	UD~ stand age	-367.3	11.35	0.002
	8	UD~ basal area	-364.8	13.83	0.001
H	1	UD~ near open + productivity	-90.5	0.00	0.783
	2	UD~ near open	-87.3	3.21	0.158
	3	UD~ density + near open + productivity	-84.0	6.45	0.031
	4	UD~ DBH + near open + productivity	-82.1	8.35	0.012
	5	UD~ density + near open	-81.0	9.46	0.007
	6	UD~ productivity	-79.7	10.81	0.004
	7	UD~ DBH + near open	-79.1	11.41	0.003
	8	UD~ near open + productivity + stand age	-76.9	13.57	0.001
	9	UD~ basal area + near open + stand age	-75.8	14.64	0.001
I	1	UD~ DBH + near road	-173.4	0.00	0.724
	2	UD~basal area + DBH + density + near road	-170.9	2.51	0.416
	3	UD~ DBH + near road + productivity	-167.0	6.46	0.029
	4	UD~ basal area + DBH + near road	-165.0	8.41	0.011
	5	UD~basal+DBH+density+road+productivity	-163.9	9.54	0.006
	6	UD~ basal area + density + near road	-162.2	11.24	0.003
	7	UD~DBH+ density + near road + productivity	-159.7	13.76	0.001
J	1	UD~ random effect	-260.6	0.00	0.747
	2	UD~ productivity	-258.1	2.55	0.209
	3	UD~ density	-253.8	6.79	0.025
	4	UD~ DBH	-251.3	9.31	0.007
	5	UD~ density + productivity	-251.3	9.36	0.007
	6	UD~ DBH + productivity	-248.6	12.04	0.002
	7	UD~ stand age	-246.6	12.04	0.001

Table 1.4. (cont'd).

Marten	Model Number	Model	AICc	Delta	Weight
K	1	UD~ random effect	-2.4	0.00	0.843
	2	UD~ density	2.3	4.77	0.078
	3	UD~ productivity	3.6	6.05	0.041
	4	UD~ DBH	4.6	7.03	0.025
	5	UD~ density + productivity	8.4	10.85	0.004
	6	UD~ near open	9.0	11.47	0.003
	7	UD~ basal area	9.9	12.33	0.002
	8	UD~ DBH + density	10.0	12.48	0.002
	9	UD~ DBH + productivity	10.7	13.16	0.001
	10	UD~ stand age	11.2	13.63	0.001
L	1	UD~ basal area +near road	-590.8	0.00	0.257
	2	UD~ density + near road	-590.6	0.22	0.230
	3	UD~ basal area + near road + productivity	-590.1	0.75	0.177
	4	UD~ density + near road + productivity	-589.7	1.17	0.143
	5	UD~density + near open + near road	-588.4	2.41	0.077
	6	UD~density+near open+near road+prod.	-587.7	3.10	0.055
	7	UD~ near road + stand age	-585.7	5.10	0.020
	8	UD~ basal area + near open + near road	-585.3	5.56	0.016
	9	UD~basal area+near open+near road+prod.	-584.8	6.08	0.012
	10	UD~ near road + productivity + stand age	-584.7	6.11	0.012
	11	UD~ near open + near road + stand age	-579.9	10.97	0.001
	12	UD~ near open + near road + productivity + stand age	-579.1	11.74	0.001

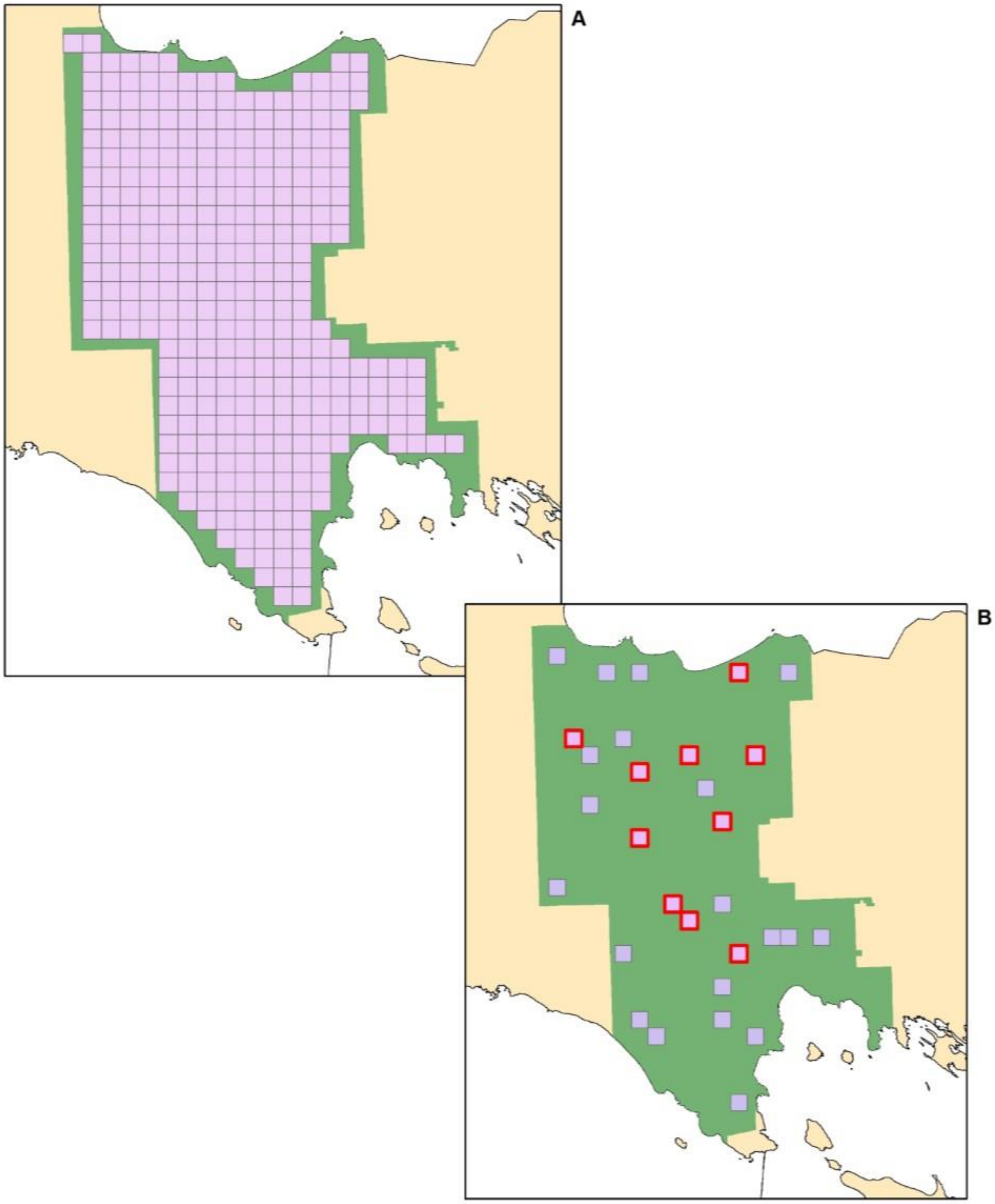

Figure 1.1. East Unit of the Hiawatha National Forest, eastern Upper Peninsula of Michigan. A) 5.2 km^2 grid cells within the East Unit boundary that were available for random selection. B) Grid cells selected using generalized random tessellation stratified (GRTS) sampling (purple). Red outlined grid cells are where marten were collared.

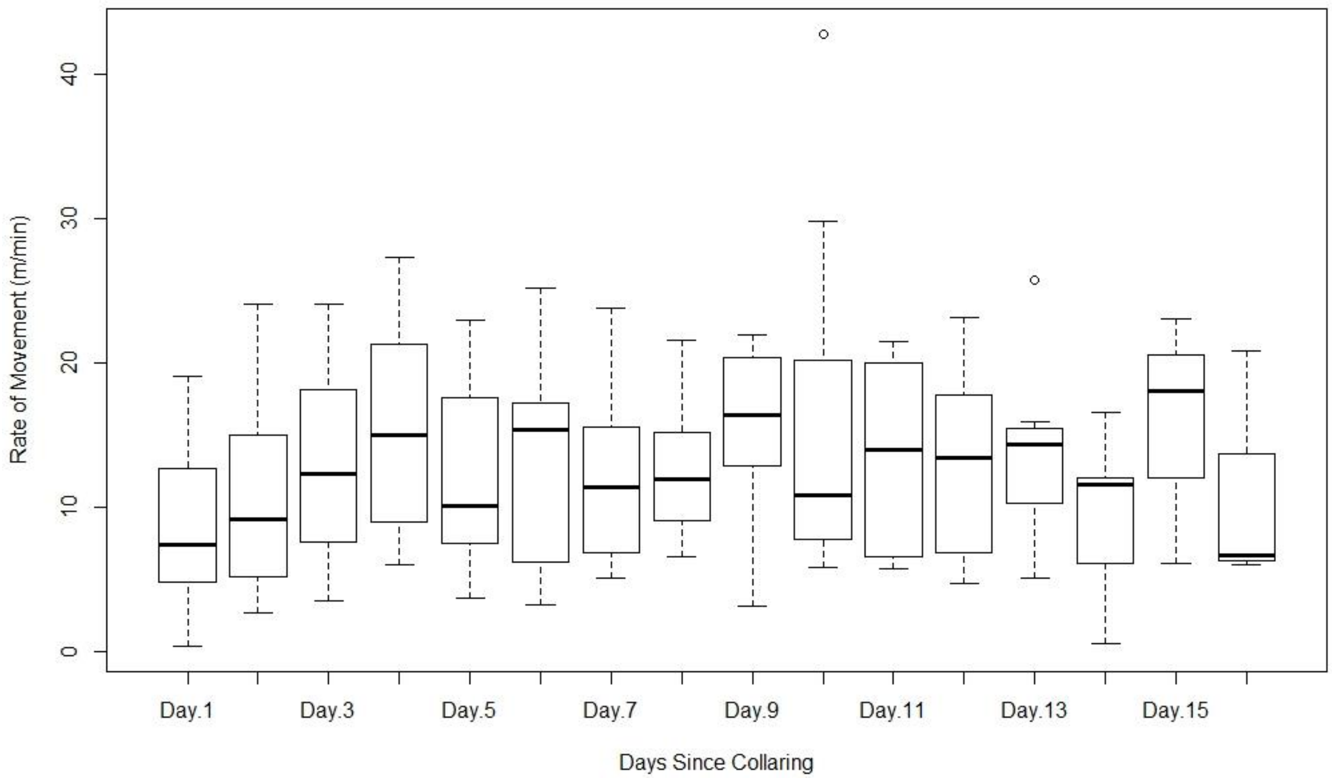

Figure 1.2. Average daily rate of movement of marten (n=12) after collaring, Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

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Chapter 2 – Weather-related Movements of American Marten in the Hiawatha National Forest, Michigan

Abstract

As American marten (*Martes americana*) move they respond to biotic and abiotic factors. For species that are vulnerable to predation and trapping like marten, movement behaviors in response to weather and season can inform harvest regulations and research activities. I examined the daily, seasonal, and weather related movements of marten in the Hiawatha National Forest (HNF) in the eastern Upper Peninsula of Michigan. I GPS collared 12 (11 males, 1 female) marten and attempted to collect a location every 15 minutes. I downloaded 7,930 locations (660.8 locations/marten), and for each successive GPS fix I calculated average hourly rate of movement by season. To model abiotic factors affecting movement rates, I used hourly rate of movement as a dependent variable in generalized linear mixed models with fixed effects that included interpolated weather estimates from Daymet. Individual marten and season were used as random effects in the models. On average, I found that marten moved 13.3 m/min, and that hourly movement rates did not differ throughout a 24-hr day. I also found that marten moved significantly less in fall than winter, spring, and summer. I failed to find a significant weather effect on marten movement rates, but limited evidence supported the hypotheses that daily movement rates increased as: 1) maximum daily temperatures decreased, and 2) as precipitation increased. My results indicate that fall is a difficult time to capture marten as movement rates are significantly lower, and that weather cannot be used to reliably predict when marten move.

Introduction

Movement ecology of harvested wildlife species can provide insights into capture effort and animal vulnerability (Gilchrist *et al.* 2005, Cushman *et al.* 2011, Nams and Bourgeois 2005). More broadly, information on animal movements has been used to understand population distributions (Turchin 1991), resource use (Birchfield and Deters 2005), distribution strategies (Small and Rusch 1989), and patterns of space use (Kenward *et al.* 2001). Until recently, studies on animal space use tended to ignore the connection between successive locations, instead analyzing the characteristics of locations themselves (Kernohan 2001). Recent advances in telemetry technology and analytical techniques have increased the ability to quantify animal activities between locations and include analyses on directionality (Pace 2001), movement rates (Forester *et al.* 2007, Frair *et al.* 2005), and relating environmental variables to movement choices (Cushman *et al.* 2011). Movement characteristics and behaviors are often linked directly to critical life history processes like foraging (Heinrich 1979), reproduction (Martin 1994), predator avoidance (Frair *et al.* 2005), and dispersal (Broquet *et al.* 2006). Thus, understanding factors that relate to animal movement behaviors is important to management and research.

American marten (*Martes americana*) are a forest habitat specialist with significant ecological, recreational, and cultural importance. Generally little is known about marten movement ecology, especially in regards to seasonal and daily movement rates. Studies indicate that marten are more active during summer (~60% of the day) compared to winter (~16% of the day; Stone 2010; Bull and Heater 2000; Powell *et al.* 2003). In a similar study in Ontario, Canada, Thompson (1986) found that marten were more active in the spring, summer, and fall (42 – 67% of the day) compared to winter (21% of the day). Moriarty (2014) speculated that higher summer activity was related to availability of food, presence of predators, and activities associated with reproduction. Decreases in winter activity may be related to fewer active predators, consumption of larger prey that reduces foraging time, lack of reproductive activities, and thermal stress during cold temperatures (Stone 2010, Moriarty 2014). Generally, males travel greater distances than females (Thompson 1986).

Prior to development of satellite-based GPS collars that were light enough for marten, our knowledge of marten movement behaviors was primarily limited to locations collected through VHF telemetry. Oftentimes, inference from VHF data was restricted by low fix rates (resulting in large time intervals between successive fixes) and locational accuracy. Commercially available GPS collars for marten are relatively new (within the last 5 years) and offer an opportunity to improve our understanding of movement ecology. For other species, satellite-based technology for studying animal movements has proven effective for quantifying habitat use (Nielson *et al.* 2009), identifying stopover areas (Sawyer *et al.* 2009, Kochert *et al.* 2011), migration routes (Takekawa *et al.* 2010, White *et al.* 2010), and for recreating movement paths (Witt *et al.* 2010).

The goal of my study was to characterize marten movement behaviors in the eastern Upper Peninsula of Michigan to inform capture activities and to better understand environmental factors affecting movements. Using GPS telemetry data, I described seasonal movement rates and activity patterns, and correlated weather factors to movement rates. I expected movement rates to be higher in summer, and because marten are generally thought to be nocturnal (Zalewski 2000, Buskirk 1983, Strickland *et al.* 1987), I expected movement rates to be higher at night. Marten are also poor thermoregulators (Buskirk *et al.* 1988, Buskirk *et al.* 1989), so I hypothesized that precipitation would negatively affect marten movements. Also related to thermoregulation, I hypothesized that as maximum temperature increased, daily movement rates would decrease. Similarly, when minimum temperature decreased I expected marten movement rates to decrease. I predicted that as the difference between daily maximum and minimum temperature increased (i.e., large daily changes in temperature), marten movements would increase. Lastly, I hypothesized that as solar radiation increased (i.e., bright, sunny days), marten movement rates would decrease. The ability to predict periods of high marten movements based on weather data could result in greater trapping efficiencies for research purposes, and provide insight into periods of potentially high capture vulnerability during public trapping seasons.

Methods

Marten Trapping

To capture marten across the East Unit of the Hiawatha National Forest, I overlaid a 5.2 km^2 square grid within the Forest Service property boundary and only used grid cells that were 100% inside this area (not borders or shoreline; Figure 2.1A). I selected this grid size to encompass multiple marten home ranges; this area is roughly twice the home range size of marten in the East Unit of the HNF (Sault Tribe Inland Fish and Wildlife Department, unpublished data). I used generalized random tessellation stratified (GRTS) sampling to select 30 grid cells for trapping (Figure 2.1B). This procedure randomly selects spatially distributed samples from a discrete population using an algorithm that avoids spatial clustering (Stevens and Olsen 2003). I trapped marten in collaboration with the Inland Fish and Wildlife Department of the Sault Ste. Marie Tribe of Chippewa Indians within selected grids from March 2016 through September 2016. From September 2016 through July 2017, we expanded trapping effort to a 36.25 km^2 hexagon centered on the GRTS selected grid because of low capture rates. Towards the end of the study we also opportunistically trapped areas known to historically support marten. For grid- and hexagon-based trapping, we moved to a different area once a marten was collared. Our overall strategy was to collar marten across a broad, partially unbiased area (Figure 2.1).

We captured marten using Tomahawk 201 and 204 live traps (Tomahawk Live Trap Company, Tomahawk, WI). We placed traps next to coarse woody debris and covered them with leaf litter, conifer boughs, tree bark, fallen logs, or natural debris found in the area. In winter we cut 19 L buckets in half and covered each trap with straw and a half-bucket. Cover over the traps helped keep marten dry and hidden. We baited traps with meat: chicken, venison, pork, beef, or fish heads. After placing the meat at the back of the trap, we placed a commercial call lure, called Gusto (Caven's Gusto, Pennock, PA), on a branch above the trap.

We anesthetized marten using a facemask on a portable vaporizer with isoflurane in a 100% oxygen carrier, with an induction setting of 5% and a maintenance setting of 2-3%. We weighed marten and constantly monitored their temperature, heart rate, and breathing during the collaring procedure. We only collared marten weighing >833 g. While under anesthesia, we fit marten with a 30g LiteTrack30 collar (SIRTRACK, Hawkes Bay, NZL). I programmed the collars to attempt a location every 15 min (Kie 2013, Moriarty and Epps 2015,). Based on this setting, I estimated that the GPS battery would last 12 days, with the VHF beacon lasting an additional 30 days. After full recovery in an enclosed container, marten were released at the point of capture. We used VHF triangulations to monitor marten locations for the duration of collar life. Because these collars required manual downloading to retrieve data, we started re-trapping marten after about 2 weeks. We used the same trapping techniques except that traps were purposefully placed where the VHF tracking results suggested the marten were concentrating their activities. Marten were trapped and handled using approved protocols from the Institutional Animal Use and Care Committee at Michigan State University (12/15-185-00) and Inland Fish and Wildlife Department of the Sault Ste. Marie Tribe of Chippewa Indians.

Daily Movement

I calculated average daily and hourly movement distances for marten using the as.ltraj function in the adehabitatHR package (Calenge 2006) in RStudio (RStudio Team 2015). I first calculated distances traveled between successful locations, and then divided this value by the time stamp of the second location in the sequence (expressed as m/min). I summarized these data for all marten by hours within a day and seasonally. I defined seasons as winter (December, January, February, March), spring (April and May), summer (June, July, August), and fall (September, October, November). I tested for a seasonal difference in daily movement rates using a Kruskal-Wallis test (R Core Team 2017).

Weather Related Movements

I acquired weather data from Daymet (Thornton *et al.* 2016). These data were interpolated from weather station measurements and portray several daily variables as 1 km^2 grid cells across North America (Thornton *et al.* 2016). To model the relationships between average daily movement of martens and weather data, I included total precipitation of the previous day (t-1), precipitation on the same day (t), precipitation for the next day (t+1), solar radiation (t), snow water equivalent (t), maximum temperature (t), minimum temperature (t), vapor pressure (t), change in temperature during the day (tmax-tmin), and change in vapor pressure from previous day. I hypothesized that precipitation and temperature would play a role in marten movements because they struggle to thermoregulate (Buskirk *et al.* 1988). Since marten are a cold adapted species, as maximum temperature increases their movements should decrease (Cushman *et al.* 2011), and as low temperature decreases past a thermoregulatory threshold, their movements should decrease (Buskirk *et al.* 1988, Buskirk *et al.* 1989). Solar radiation refers to the intensity of sunlight reaching the ground and can be used to infer cloud cover.

I used a generalized linear mixed model (GLMM) to explore relationships between average marten movement rates (AMMRs) per day and the 10 weather variables (fixed effects). Additionally, I used individual marten and season as random effects in the GLMM. I initially identified correlated (>0.5; Dormann *et al.* 2012) fixed effects and then built a candidate model set using different combinations of uncorrelated variables. I ranked the candidate model set using AICc (Burnham and Anderson 2002), and for models within AICc <7 from the top ranking model I used model averaging (Bartoń 2016). I deemed a covariate significant if the 95% confidence interval of the parameter estimate did not overlap 0.

Results

Marten Trapping

We trapped marten from March 2016 through July 2017 for 5,922 trap nights. We caught and collared 12 marten (11 males and 1 female) around 10 of our focal areas (Figure 2.1B). We also caught 10 marten (1 male and 9 females) that were too small to collar, suggesting that our collared marten were found in habitats similar to other marten. Annual trapping success was 269 nights/marten; trap success was higher in late winter and spring (83 and 68 trap nights/marten, respectively) than summer and fall (391 and 1259 trap nights/marten, respectively). Martens that were not collared weighed an average of 608.3 g (505 g-706 g). The average weight of martens that were collared was 1064.64 g (891 g-1335 g). Telemetry data were collected in late winter (March; n = 3 marten), spring (n = 3), summer (n = 4), and fall (n = 2).

Daily Movements

I tested every collar prior to deployment by acquiring at least one location; 100% of the collars were functional as received from the company. The 12 collared marten produced 7,930 locations. The batteries in the GPS lasted on average 14.7 days (SE = 1.09; range = 13-18), collecting an average of 660.8 locations (SE = 167.6; range 374 – 1061) per marten, with 620.1 (SE = 160.5; 94%) of the fixes with DOP < 10. The average collar fix rate was 44.9% (SE = 9), comparable to other short-term GPS studies on marten (Moriarty *et al.* 2015). The average time lag between successful fixes was 34.7 minutes (SE = 1.17). An average of 43.1 successful locations (SE = 2.4) per day per marten was obtained. I found that collars had an average positional error of 6 m (DOP ≤10). I found no difference in daily movement rates related to the trapping and collaring process (Figure 2.2), so all data were used in my analysis.

When pooled across all seasons, I found that marten movements throughout the 24-hour day were highly variable, with no significant differences among hours within a day (Figure 2.3). On average, marten moved <5 m/min regardless of hour, although rapid movements (>100m/min) were recorded for all times of the day (Figure 2.3). Maximum observed movement rate exceeded 350 m/min (Figure 2.3).

My results indicated that marten were active throughout the day from late winter to fall, with variability in seasonal movements lower in fall and summer (Figure 2.4). I found no significant differences in hourly movement rates of marten within a season (Figure 2.4), however movement rates among seasons differed (Kruskal-Wallis test, $\chi2 = 102.41$, $p < 0.001$; Figure 2.5). In contrast to other studies, I found that average hourly movement rates were higher in late winter (mean =18.16 m/min, SE = 1.80), but with considerable variability (Figure 2.4). Movement rates in spring and summer were similar (mean = 16.55 m/min, SE = 1.86; mean = 13.9 m/min, SE = 0.99, respectively), and lowest during fall (mean = 7.29 m/min, SE = 0.85).

Weather Related Movements

I analyzed daily movement rates and weather for 9 of the 12 marten (Daymet data were only available for 2016). Summer and fall received higher average daily precipitation than late winter, solar radiation was comparable across the 3 seasons, and temperatures were cooler in late winter (summer and fall were comparable; Table 2.1). I observed larger changes in temperature in summer and fall compared to winter, and lower vapor pressure in winter (Table 2.1). Changes in vapor pressure were more variable in summer and fall (Table 2.1).

The top-ranking model accounted for 59% weight of evidence and included only the random effects (Table 2.3), indicating that unmeasured characteristics of martens and seasons explained the most variation in daily movement rates. Univariate temperature and precipitation models dominated the competing models ($\Delta AIC < 7.0$; Table 2.3), with these models accounting for an additional 33% weight. Though not significant, precipitation and temperature coefficients from model averaging indicated that as precipitation increased marten daily movement rates increased, and as temperature increased movement rates decreased (Table 2.4).

Discussion

My results indicated that American marten (mostly adult males in my sample) in the Hiawatha National Forest do not exhibit daily movement patterns similar to those found in other studies. I found that average daily movement rates were relatively consistent throughout a 24-hour period, regardless of season. Others found that both male and female marten activity was higher during daylight hours during summer and nocturnal in the winter (Zielinski *et al.* 1983, Martin 1987). Zielinski *et al.* (1983) suggested that the nocturnal pattern in winter was potentially related to capturing prey at night. Animal movements generally result from foraging (Heinrich 1979), reproduction (Martin 1994) and avoiding predators (Frair *et al.* 2005), among other factors. For animals with minimal fat reserves and high metabolism like marten, foraging is a dominant component of daily activities. The lack of variation in hourly movement rates within a day from my study was likely related to my sample being mostly adult male marten. Adult male marten move in the spring and summer for mating purposes and during the winter for foraging (Buskirk and Zielinski 1997, Drew and Bissonette 1997).

I found that marten moved significantly slower during fall compared to other times of the year (Figure 2.3). In the eastern Upper Peninsula of Michigan, fall corresponds to an increase in the availability of prey like voles (Getz *et al.* 2006), red squirrels (*Tamiasciurus hudsonicus*), and numerous soft mast species, likely reducing the search times required for marten to successfully forage. Others have found that marten were more active during summer than winter (Thompson 1986, Thompson and Colgan 1994), whereas I found that marten were most active during late winter. Buskirk *et al.* (1988) suggested that marten were more active in winter to aid in thermoregulation. Another possible explanation could be the availability of prey. During winter prey availability decreases because the majority of small mammal activity is subnivean, some prey significantly reduce their activity patterns, many bird species have migrated (Martin 1994), and soft mast is generally unavailable. Limited availability and access to food during winter may cause marten to travel greater distances.

Because marten are poor thermoregulators due to their small size and moderately effective fur (Buskirk *et al.* 1988, Buskirk *et al.* 1989), I expected weather conditions like precipitation and temperature to have negative relationships with movement rates. I failed to find a significant weather factor that influenced adult marten movements on the HNF. Zalewski *et al.* (2004) suggested that marten slowed their rate of movements as temperatures decreased, with speeds highest in summer and lowest in fall and winter. My temperature model-averaged coefficients were all negative, lending support to the observation by Zalewski *et al.* (2004). My model-averaged coefficients for precipitation were positive, indicating that marten movement rates increased as precipitation increased. This was a pattern I also observed with trapping success, and may be related to thermoregulation or prey activity but the causal mechanism(s) remains unclear.

The solar radiation variable represented a measure of hotness as influenced by temperature and sun exposure (Thornton *et al.* 2016); I failed to find a relationship between marten daily movement rates and solar radiation. Vapor pressure increases the ability for some animals (rodents) to smell (Vander Wall 2003), because higher humidity causes higher air conductance (Zalewski 1997). Some marten prey (e.g., shrews; Otto and Roloff 2012) increase activity with precipitation, which occurs when water vapor pressure is saturated (Vander Wall 2003). Although I predicted that marten movement would positively relate to water vapor pressure, I failed to find a significant relationship.

I caution that my results are based on a limited number of marten (mostly males) that were monitored intensively for relatively short time spans. The combination of frequent fixes over short time frames (i.e., ~ 2 weeks) has been shown to reasonably represent marten home ranges (Moriarty 2014, Thomasma 1996, Strickland and Douglas 1987), and although I collected hundreds of fixes for each marten, the ~2-week time frame provided limited opportunities for individual marten to experience a wide range of weather conditions. Additionally, marten may make movement decisions based on weather at temporal scales finer than a day. A limitation of the Daymet data was that weather variables were summarized over a 24 hr period.

This study provides insights into movement rates of American marten in the East Unit of the HNF, Upper Peninsula of Michigan. The results of my study increased our understanding of marten movement behavior (quantified rates, by day and season), and demonstrated that readily available weather data were not useful predictors of marten movement behaviors. Hence, relying on daily weather forecasting to improve marten capture success (presumably because of increased movements) will probably not be effective.

APPENDIX

Table 2.1. Average (SE) and range of daily weather conditions, by season, experienced by collared American marten on the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

	Winter		Spring		Summer		Fall	
Weather	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
Precipitation (t-1) (mm)	2.1 (0.6)	0, 13	NA	NA	5.2 (1.4)	0, 35	6.0 (2.6)	0, 38
Precipitation (mm)	2.2 (0.6)	0, 13	NA	NA	5.2 (1.4)	0, 35	5.4 (2.6)	0, 38
Precipitation (t+1) (mm)	2.1 (0.6)	0, 13	NA	NA	5.8 (1.4)	0, 35	5.3 (2.6)	0, 38
Solar Radiation (W/m^2)	311.1 (16.2)	144, 455	NA	NA	328.1 (13.3)	157, 467	309 (20.8)	154, 435
Snow Weight Equiv. (kg/m^2)	129.5 (1.2)	120, 140	NA	NA	0 (0)	0	0 (0)	0
Maximum Temperature (°C)	6.4 (0.5)	2, 10	NA	NA	22.7 (0.6)	10, 30	20.8 (1.0)	11, 26
Minimum Temperature (°C)	-2.1 (0.5)	-11, -1	NA	NA	10.7 (0.6)	-2, 18	9.3 (1.0)	-1, 16
Delta Temperature (°C)	8.5 (0.4)	4, 12	NA	NA	12.0 (0.4)	7, 18	11.5 (0.6)	600, 1800
Vapor Pressure (Pa)	530 (17)	280, 640	NA	NA	1314 (50)	520, 2080	1206 (37)	7, 17
Delta Vapor Pressure (Pa)	12 (17)	-200, 160	NA	NA	-9 (39)	-600, 600	10 (48)	-320, 400

Table 2.2. Model selection using AICc for weather related movement rates of American marten in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017. All models with AICc weight >0.

Model[a]	k	AICc	Delta AIC	Weight	Cum. Weight
Rate~null	3	670.5	0	0.592	0.592
Rate~tmax	4	674	3.48	0.087	0.679
Rate~prcp	4	674.3	3.78	0.075	0.753
Rate~tmin	4	674.4	3.94	0.069	0.822
Rate~prcpps	4	675.5	5.01	0.041	0.863
Rate~prcppr	4	675.9	5.37	0.034	0.897
Rate~swe	4	676.5	5.97	0.025	0.922
Rate~prcp+tmax	5	677.8	7.29	0.013	0.935
Rate~prcp+tmin	5	678.1	7.64	0.011	0.946
Rate~prcpps+tmax	5	678.8	8.28	0.008	0.954
Rate~prcpps+tmin	5	679.1	8.64	0.007	0.961
Rate~prcppr+tmax	5	679.5	8.95	0.005	0.966
Rate~prcp+prcpps	5	679.5	9.02	0.005	0.971
Rate~prcppr+tmin	5	679.9	9.36	0.004	0.976
Rate~srad	4	680.4	9.91	0.003	0.979
Rate~prcp+swe	5	680.5	10.02	0.003	0.982
Rate~prcpps+prcppr	5	680.7	10.18	0.003	0.986

Table 2.2. (cont'd).

Model	k	AIC	Delta AIC	Weight	Cum. Weight
Rate~deltavp	4	680.9	10.43	0.002	0.988
Rate~prcpps+swe	5	681.4	10.85	0.002	0.990
Rate~prcppr+swe	5	681.8	11.28	0.002	0.992
Rate~prcp+prcpps+tmax	6	682.9	12.35	0.001	0.993
Rate~vp	4	683	12.46	0.001	0.995
Rate~prcp+prcpps+tmin	6	683.4	12.85	0.001	0.996
Rate~prcp+prcppr+tmax	6	683.5	12.96	0.001	0.997
Rate~prcp+prcppr+tmin	6	683.7	13.25	0.001	0.998
Rate~srad+tmax	5	683.8	13.25	0.001	0.999
Rate~prcpps+prcppr	5	684	13.55	0.001	1.000

[a] tmax = maximum temperature, prcp = precipitation, tmin = minimum temperature, prcpps = precipitation (t+1), prcppr = precipitation (t-1), swe = snow weight equivalent, srad = solar radiation, vp = vapor pressure

Table 2.3. Generalized linear mixed model averaged coefficients (95% confidence intervals) for daily weather variables used to describe marten movement rates in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017. NA denotes a variable that was not included in the model averaging.

Model Variable	Estimate	Std. Error	95% Confidence Interval
(Intercept)	12.47315	2.53361	7.41, 17.54
Precipitation (t-1) (mm)	0.04229	0.06772	-0.09, 0.18
Precipitation (mm)	0.054087	0.07528	-0.10, 0.20
Precipitation (t+1) (mm)	0.05897	0.06660	-0.07, 0.19
Solar Radiation (W/m^2)	NA	NA	NA
Snow Weight Equiv. (kg/m^2)	0.03661	0.02595	-0.02, 0.09
Maximum Temperature (°C)	-0.10969	0.17367	-0.46, 0.24
Minimum Temperature (°C)	-0.05521	0.16795	-0.39, 0.28
Delta Temperature (°C)	-0.16553	0.26099	-0.69, 0.36
Vapor Pressure (Pa)	NA	NA	NA
Delta Vapor Pressure (Pa)	NA	NA	NA

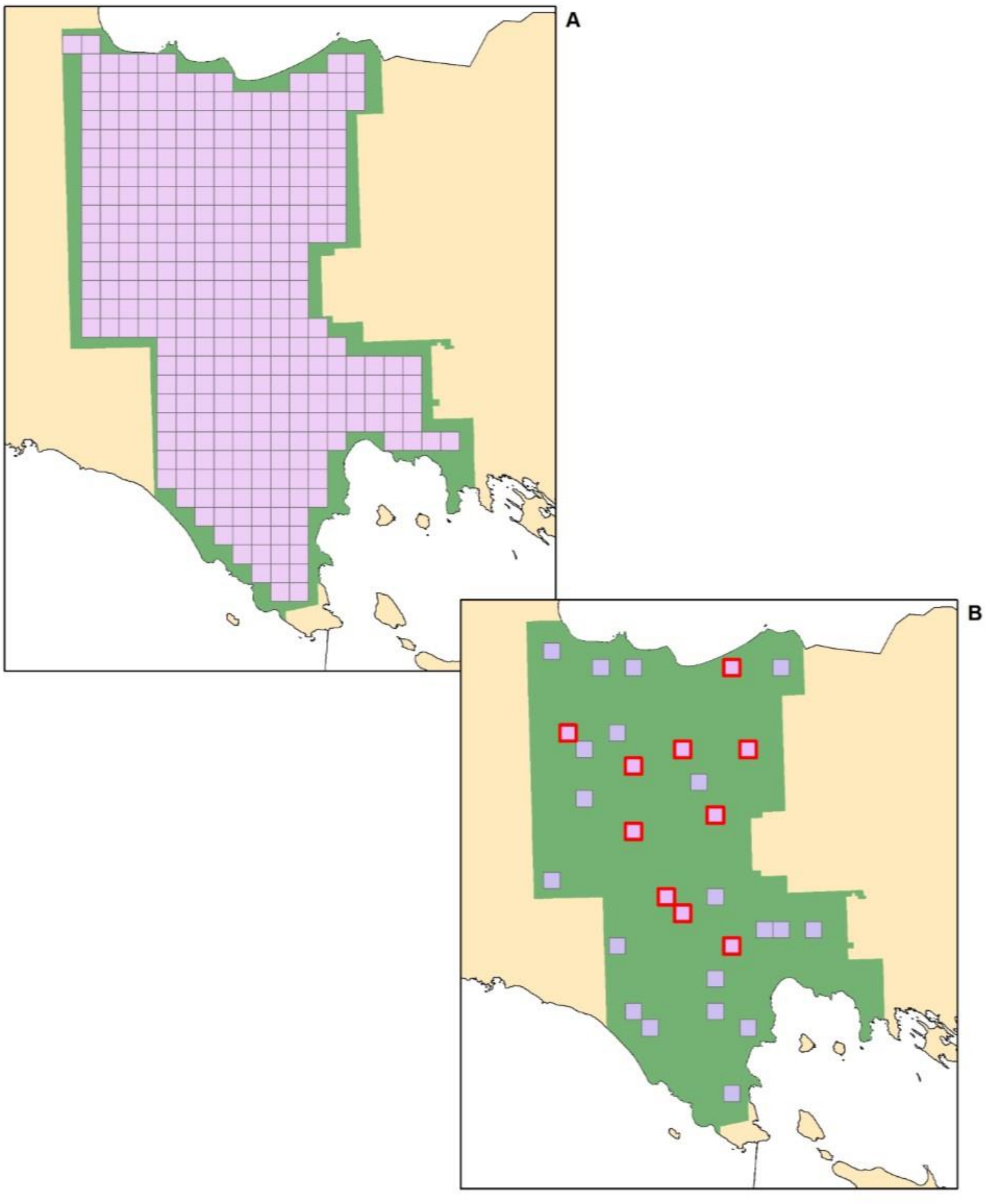

Figure 2.1. Selection of Randomly Selected Trapping Grids. A. Grids that fall completely within the East Unit of the Hiawatha National Forest. B. Grids selected using generalized random tessellation stratified (GRTS) sampling. Highlighted grids are where marten were collared.

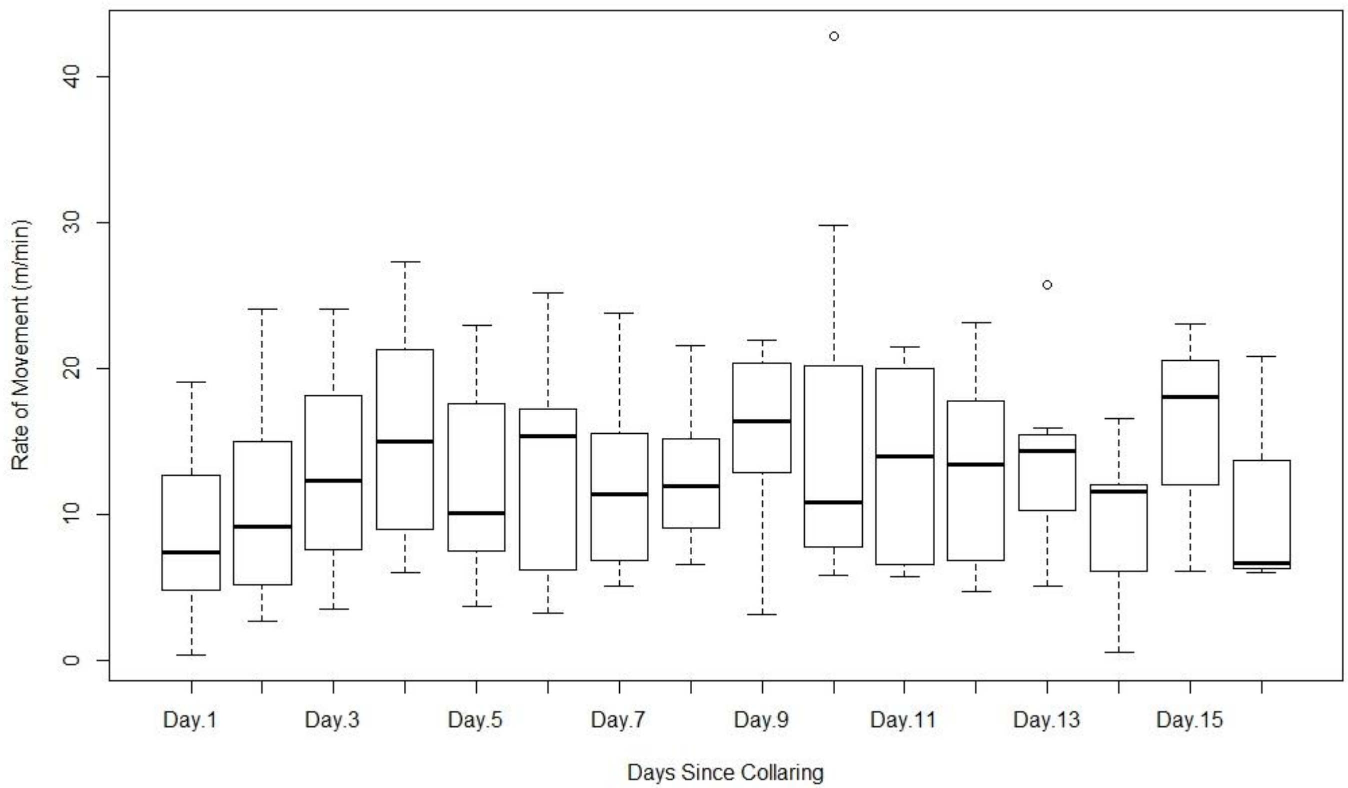

Figure 2.2. Average daily marten movement rate after collaring in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

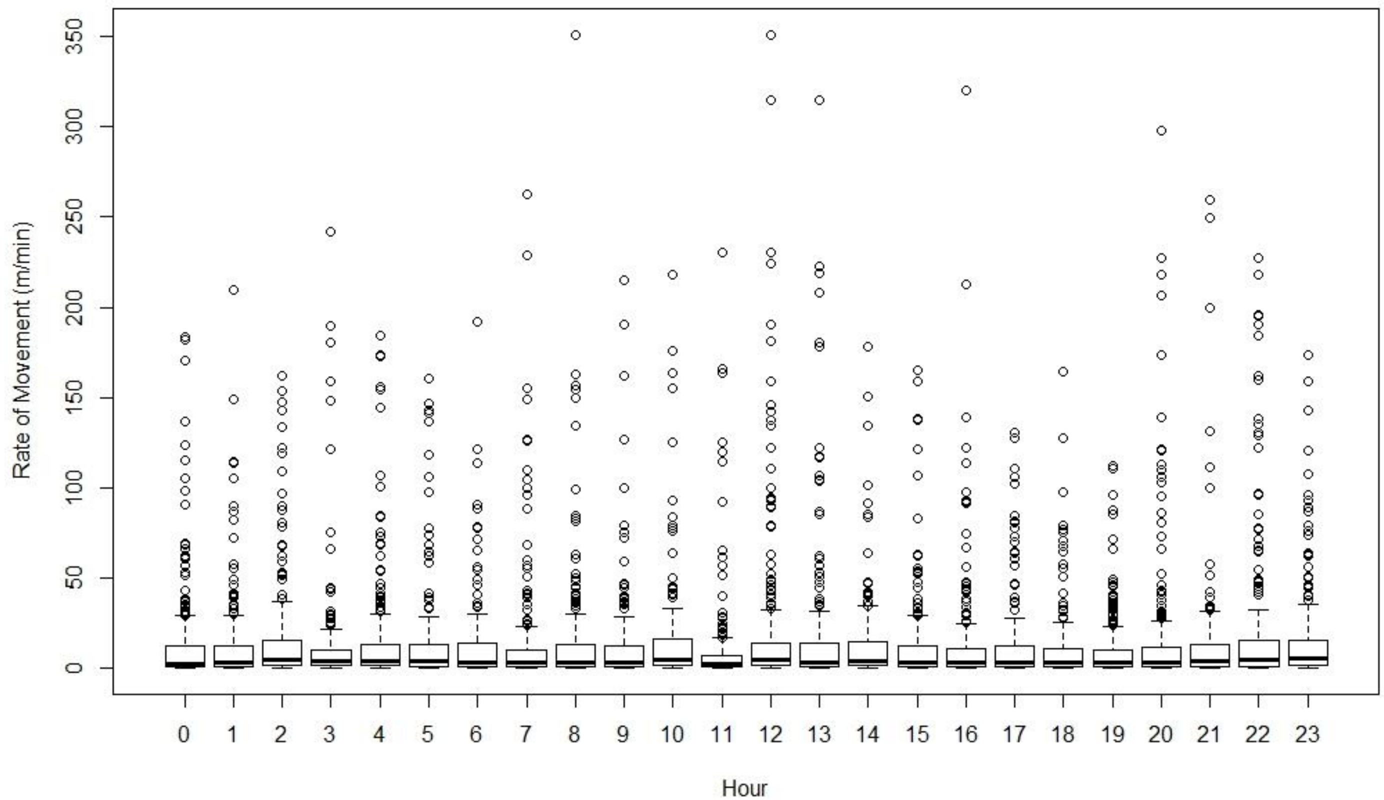

Figure 2.3. Movement rate per hour for American marten in a 24-hour day in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017. Box plots show the mean (dark bar), 75% quartile (box), 95% confidence interval (whiskers), and outliers.

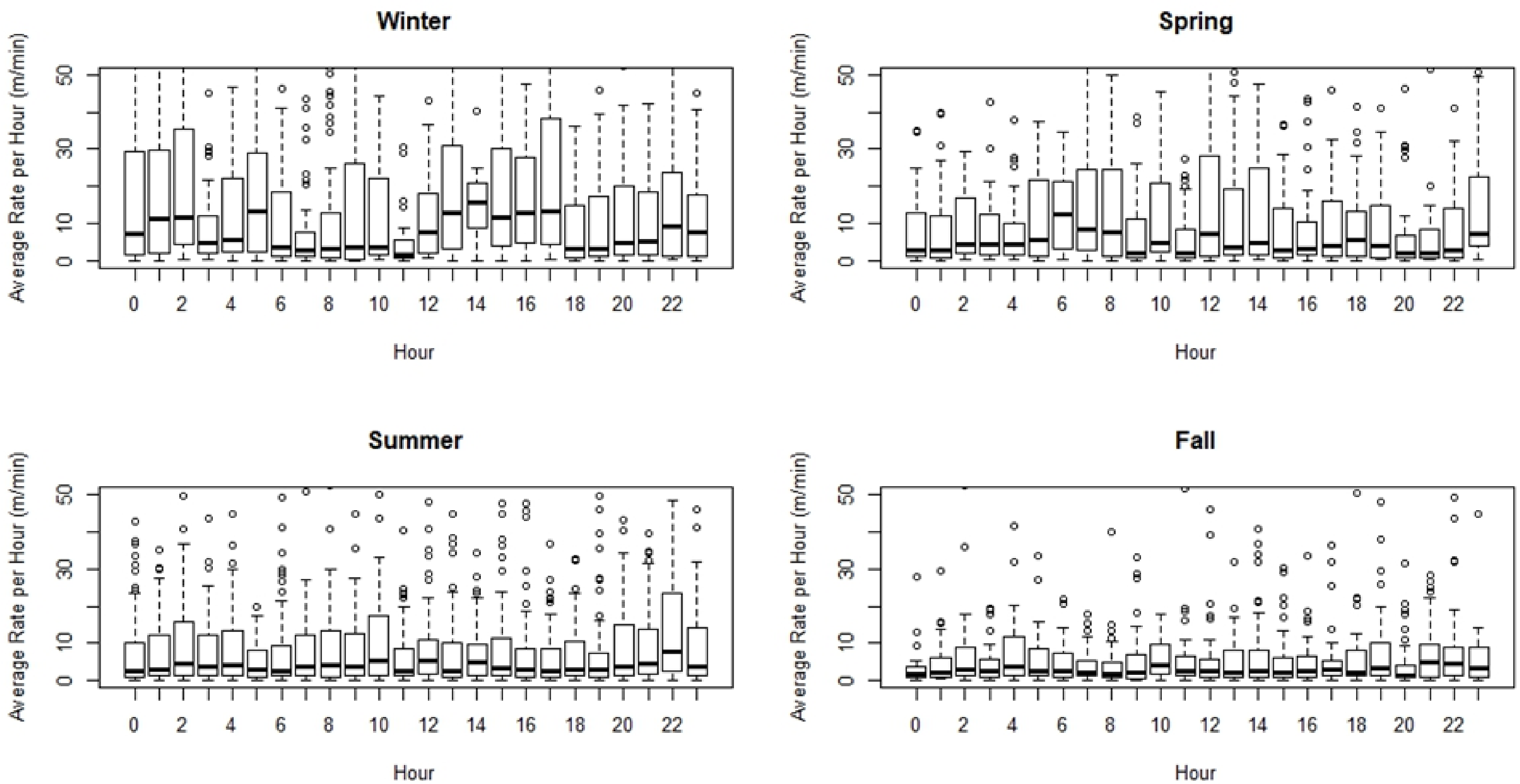

Figure 2.4. Movement rate per hour, by season, for American marten in a 24-hour day in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017. Box plots show the mean (dark bar), 75% quartile (box), 95% confidence interval (whiskers), and outliers.

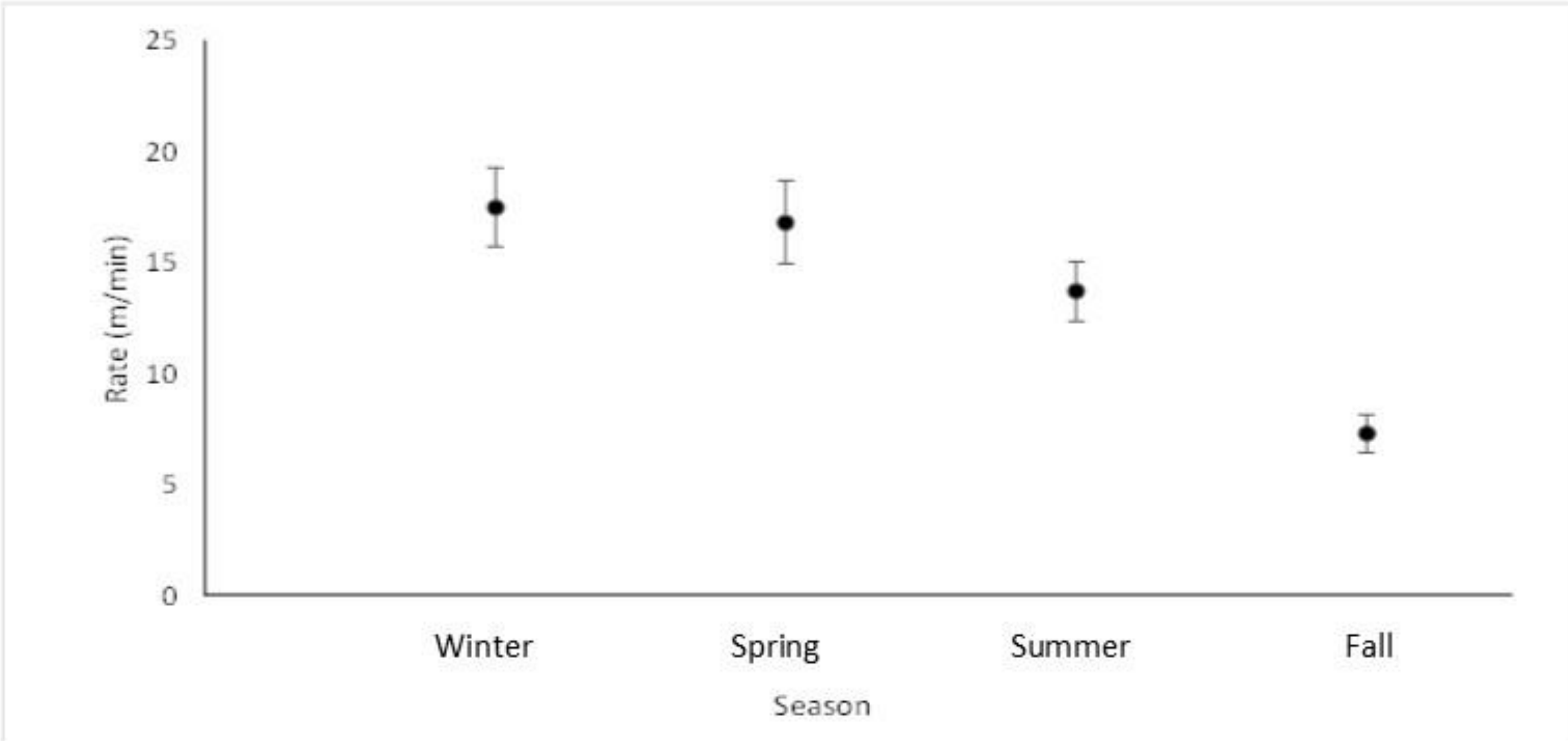

Figure 2.5. Seasonal average movement rates with 95% confidence intervals for American marten in the Hiawatha National Forest, eastern Upper Peninsula of Michigan, March 2016 – July 2017.

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Conclusions

The purpose of my thesis was to improve our understanding of marten resource utilization and movement behaviors in the East Unit of the Hiawatha National Forest (HNF). I modeled resource utilization of marten that were captured across a broad site productivity and forest type gradient throughout HNF. I found that marten resource utilization in this area could not be explained from stand-level, univariate metrics of forest structure collected as part of standard forest inventory. Rather, my results indicated that site productivity was a more useful metric, with marten use positively related to site productivity. I also found that activity centers for some marten were negatively related to distance from opening, even though all marten were documented to use openings (2.4% of locations). The effects of high-traffic roads on marten resource utilization were minimal, and for those marten that were influenced by roads the responses were both positive and negative. My study showed that resource utilization by individual marten in the HNF is highly variable, and given the variables I evaluated unpredictable.

I also quantified when and how far marten moved daily, seasonally, and in relation to weather conditions. Marten were active throughout the day, and more active in late winter than summer and least active in fall. Movement decisions can be highly individualized based on current and past experiences and seasonal life history demands. My results support this observation; the random effects that accounted for individual marten and seasons received the most model support. I observed weak precipitation and temperature relationships with movement rates, the direction of those relationships were intuitively correct. I found weak evidence that marten movement rates decreased as temperatures increased, and that movement rates increased on days with precipitation. My interest in the effects of weather on movements partially stemmed from observations I made while trying to trap marten. I observed that marten seemed more trappable in association with precipitation events, so I posited that weather could be used to improve trapping efficiency. The effects of weather on movement can also be helpful in knowing how marten in the HNF may respond to the weather ramifications of climate change. Marten movement rates slowed when there was a large change in temperature during the day.

Limitations of this work include: 1) the short-temporal aspect of the collar that recorded marten locations (GPS collar only active on average 14.7 days), and 2) the use of HNF forest inventory data at the stand level that were likely coarser than the marten habitat selection process. Additional data more accurately portraying the forest inventory at a finer scale rather than stand level may be more helpful in identifying if there are pockets of different measurements within a stand that determine high use.

Results from my work can be used to assist the HNF in forest management decisions regarding marten management. The HNF should manage for forest structural complexity (e.g., leave snags, downed wood, facilitate multi-storied forest structure), and recognize that site productivity affects the complexity of forest structure (i.e., more complex forest structure tends to occur on higher quality sites). Targeted efforts for increasing forest structural complexity to enhance marten habitat may be particularly effective on low productivity sites. I also recommend that the HNF include information on snags and downed wood in their standard forest inventory system, as these habitat elements are used by multiple wildlife species, including marten. The next phase of research should look at point-level data (as opposed to stand-level summaries) from the forest inventory as a predictor of marten resource utilization. Additionally, an analysis of marten movement rates through different forest types could prove insightful, with the hypothesis that movement rates would be highest through less desirable forest types (like openings).