Evaluation of Environmental Factors Influencing American Marten Distribution and Density in New Hampshire

Donovan Drummey

University of Massachusetts Amherst

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EVALUATION OF ENVIRONMENTAL FACTORS INFLUENCING AMERICAN MARTEN DISTRIBUTION AND DENSITY IN NEW HAMPSHIRE

A Thesis Presented
by
DONOVAN B. DRUMMEY

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

February 2021

Environmental Conservation
Wildlife, Fish, and Conservation Biology
EVALUATION OF ENVIRONMENTAL FACTORS INFLUENCING AMERICAN MARTEN DISTRIBUTION AND DENSITY IN NEW HAMPSHIRE

A Thesis Presented
by
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DEDICATION

To my mother, for telling me to put the book down and go play outside, for saying “I love you - learn something!” every day as I left for school, and meaning it.

To my father, for being the one to introduce me to the woods, for encouraging me to talk about what I’d learned, and for being willing to explain and discuss anything, at any time.
ACKNOWLEDGEMENTS

I would first like to express my gratitude to my committee members. To my advisor, Dr. Chris Sutherland, thank you for answering obscure R code questions at all times of the day and night and creating an environment where I learned to understand, appreciate, and even enjoy statistics and coding. To Jill Kilborn, thank you for bringing this project to us in the first place, and for sharing your expertise and knowledge whenever I asked for it. To Dr. Toni Lyn Morelli, thank you for your enthusiasm, compassion, and encouragement throughout this process. Thank you also for inviting me to come trap red squirrels with you, providing me with a chance to see my first marten. Finally, to Dr. Sarah Emel, thank you for sharing your extensive knowledge of genetics, and for sharing my love of baking. I am grateful to have met each and every member of this committee; your friendship has been just as valuable as your insights and knowledge.

This work was made possible with support from US Fish and Wildlife Service’s Wildlife and Sportfish Restoration Program by providing Pittsman-Roberts funds to New Hampshire Fish and Game Department. Thank you to all the New Hampshire Fish and Game employees and volunteers who assisted with the camera trap deployments. Additional funding was also provided by the American Wildlife Conservation Foundation.

I would like to acknowledge the 25 undergraduate volunteers who handled the time-consuming task of identifying the species captured in each of the 197,000 camera trap images: Alex Ahlquist, Lili Allen, Mary Apessos, Desiree Bator, Emily Begonis, Amalia Butler, Drew Carrano, Molly Craft, Elise Daigle, Kara Duprey, Rachel Finn, Jillian Flanagan, Michael Heine, Jason Hodgkins, Evan Johnson, Kallin Lang, Julia Lemmi, Emily Mei, Sean Mulvaney, Tansy Remiszewski, Sam Rode, Sarah Spaulding, Jacob Yankee, and Suzanna Yeung. Everyone, your
enthusiasm, work ethic, and attention to detail made this whole process possible. I wish you all the best in your future endeavors!

Several other individuals have also made significant contributions over the course of this project. To Katie Callahan from the New Hampshire Fish and Game Department and my sister Demarest, thank you for your assistance with species identification. Ben Sharaf, thank you for your enthusiasm when searching for and collecting samples across the White Mountain National Forest as my summer intern. Dr. Lisa Komoroske, thank you for the use of your brand-new lab space. Dr. Alexej Sirén, your knowledge of marten and the New Hampshire landscape has been invaluable; thank you for always being willing to answer questions and talk.

Another group that has been hugely influential over the course of this project is the combined Sutherland and Morelli lab groups, aka WildThings. Your comments and suggestions have made me a more concise writer and eloquent speaker, while the community you provided made my time at UMass vibrant. Thank you all for your assistance and your friendship; I have certainly appreciated them both.

Last but not least, I would like to thank my family. Thank you to my mother and father, for encouraging me to pursue my passions, and supporting me every step of the way. Thank you to my siblings Demarest and Mason, for being only a phone call away, and answering ‘yes’ whenever I asked for something. Finally, thank you to my husband Shelby, for your patience with my late nights and grumpy days, and for being with me every step of the way.

I could not have done this without all of you. Thank you.
Though the American marten (*Martes americana*) is widely distributed across northern North America, habitat use and population abundance vary widely across the range. Due to its status as a furbearer, the species has been extensively researched, resulting in a large body of knowledge about the species’ ecology, distribution, and abundance, as well as drivers of population structure and dynamics. More recently, marten research has shifted focus to genetics, habitat associations, and estimation of population state variables. The rapid increase in estimation of states such as occupancy, abundance, and density has likely been driven by the increasing accessibility of noninvasive field technology, such as noninvasive genetic sampling and remote camera trapping, and by the statistical development of ecological hierarchical models. This convergence of advances in field and analytical methods is most apparent in the now widespread application of spatial capture-recapture, an approach that produces robust estimates of population densities and abundance that can be compared across time and space.

These new models are especially valuable near the edges of marten distribution where populations are often recovering from historic overexploitation, and expanding into areas they have previously been absent from. In these areas, detailed, landscape-scale understanding of marten populations is necessary in order to establish current conditions, effectively monitor changes, and predict what effect management actions may have on marten populations. I utilized
these models to study marten populations in New Hampshire where marten are a species of management interest, and recent recovery has led to their removal from the state endangered species list.

Through a collaborative effort with New Hampshire Fish and Game Department in the winters of 2017 and 2018, marten were surveyed across northern New Hampshire using a novel camera trap design that allows for the identification of individuals. These data were analyzed using spatial capture-recapture models, allowing me to evaluate habitat associations that explain spatial variation in marten density and provide a population status assessment for the New Hampshire marten population. Marten densities are highest in the White Mountain National Forest, though other protected lands in northern New Hampshire also appear to support larger populations. The greatest population densities coincided with deeper snows, increased canopy closure, and intermediate boreal biomass. These results provide additional support for several hypotheses explaining marten habitat use across their range while also providing novel insight that will inform active management of both marten and the habitat they occur in.

In addition to the population status assessment, I evaluated the relationship between estimates of occupancy and density in New Hampshire. Though utility of non-invasive methodology can decrease research costs, the need for individual identification in spatial capture-recapture models represents a cost increase over occupancy models. My results suggest that the two are positively correlated; however, occupancy is a poor predictor of the entire range of density, especially because the variables used to predict each of the state variables are different. Thus, occupancy is likely not a good proxy for density in New Hampshire, however it could be used to track general trends through time so long as density is re-evaluated periodically.
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CHAPTER 1
A REVIEW OF THE CURRENT UNDERSTANDING OF AMERICAN MARTEN
(Martes americana) DISTRIBUTION AND ECOLOGY

1.1 Introduction

American marten (Martes americana, hereafter marten) are a medium-sized carnivore of the family Mustelidae. They are a species of concern and protected in a number of states and provinces (California, Nevada, South Dakota, Wisconsin, Newfoundland, Vermont, and Nova Scotia) (Proulx et al. 2004; NHFGD 2015), and are a regional species of greatest conservation need (SGCN) in the North Atlantic-Appalachian region of the United States (Terwilliger Consulting 2013). Marten are also considered to be a representative or umbrella species (Hepinstall and Harrison 2001; Terwilliger Consulting 2013), an ecological indicator of healthy forests (Ruggiero et al. 1994), or an otherwise sensitive species (Ruggiero et al. 1994; Proulx et al. 2004).

Much research has been conducted on marten across their range, but they can be difficult to study due, in part, to their low population densities, relatively large home range sizes, and elusive behavior (Gese 2001; Gompper 2006; Buskirk et al. 2012; Monterosso et al. 2014). This research has addressed a wide range of aspects of marten ecology, with a strong emphasis on quantifying aspects of marten habitat use and preference. However, there is evidence of inconsistency across the range, although the research has not been comprehensively summarized to identify how the ecology of the species, including distribution, abundance, and habitat preferences differ in space (e.g., across their range), time (e.g., by season), or by sampling methodologies. In this review, I aim to identify patterns and trends in these aspects of American marten research which I will then use to create a suite of habitat predictor variables (i.e.,
competing hypotheses) to inform modeling efforts that seek to quantify spatiotemporal habitat associations in New Hampshire (see Chapter 2).

1.2 Marten Ecology

General description

American marten are sexually dimorphic, with males 20-40% larger than females, though similar in appearance (Ruggiero et al. 1994). A furbearing species, their fur is long and silky and varies from a pale blonde to dark brown, with lighter markings on their chest (Silver 1957; Clark et al. 1987; Ruggiero et al. 1994). Marten are solitary and exhibit intrasexual territoriality; adults establish and defend home ranges against members of the same sex, but will tolerate some overlap with individuals of the opposite sex, as well as with juveniles before they reach sexual maturity (Strickland et al. 1982; Clark et al. 1987; Powell 1994; Ruggiero et al. 1994; Payer et al. 2004).

Marten breed between June and August, with most breeding occurring during July (Clark et al. 1987; Mead 1994). Marten are polygamous, with both males and females breeding with multiple individuals (Ruggiero et al. 1994). Implantation is delayed until sometime in February, with parturition occurring between mid-March and late April (Clark et al. 1987; Ruggiero et al. 1994; Mead 1994). All parental care is provided by the mother (Ruggiero et al. 1994). Litters vary from 1 to 5 individuals, with an average of 2 to 3 (Ruggiero et al. 1994; Mead 1994). The kits are weaned after 6 weeks, around May (Clark et al. 1987; Ruggiero et al. 1994; Mead 1994). A week later, the kits emerge from the den and begin to follow their mother around (Clark et al. 1987; Ruggiero et al. 1994; Mead 1994). By June, a month later and when the mother is receptive to breeding again, the kits begin to explore on their own, though they are not yet ready
to leave their mother entirely (Clark et al. 1987; Ruggiero et al. 1994; Mead 1994). The kits may not be fully independent until August, when they will start dispersing in order to establish their own home ranges (Mead 1994). The timing of dispersal varies across the range, but often continues through October. Marten become sexually mature after 15 months, much later than other similarly sized mammals (Clark et al. 1987; Ruggiero et al. 1994; Mead 1994; Harlow 1994).

The taxonomic classification of the American marten has recently undergone a series of revisions. Initially, two North American marten species were identified in the late 1800s; the American marten and the Pacific marten (*Martes caurina*) (Dawson and Cook 2012). This description of the two as different species was brought into question, as the delineation was based on morphology, and the Pacific marten was designated a subspecies within *M. americana* in the 1950s (Clark et al. 1987; Ruggiero et al. 1994; Dawson and Cook 2012). More recently, phylogenetic research suggests they are indeed distinct species (Cook et al. 2001; Stone and Cook 2002; Small et al. 2003; Slauson et al. 2009; Dawson and Cook 2012; Dawson et al. 2017; Colella et al. 2018). The range of the American marten encompasses much of northern and eastern North America, while the Pacific marten inhabits the area between the Pacific Coast and the Rocky Mountains (Figure 1).

Since these taxonomic changes are so recent, much of the available information and research about North American marten species has treated the two as a single species. Moreover, the two marten species are very similar in aspects of their behavior, diet, phenology, and interactions with other co-occurring species. As such, in this review I refer to the two species collectively as marten when discussing aspects of ecology that are consistent between the species, but specifically mention when there are noted differences.
Prior to European colonization, martens were found contiguously along the western North American mountain ranges, along the Appalachians as far south as West Virginia, south of the Great Lakes, and into the Maritime Provinces of Canada (Gibilisco 1994; Proulx et al. 2004; Krohn 2012). During the late 1800s and early 1900s, marten distribution and populations experienced a significant contraction and decline. This change has long been attributed to the effects of land conversion for farming and overexploitation of the species for their fur (Clark et al. 1987; Gibilisco 1994; Ruggiero et al. 1994). However, Krohn (2012) suggests that the pattern of martens retreating from south to north does not align with the patterns of European settlement, and that changes in climate may better explain the northward contraction. The lack of recovery following reversals in land conversion trends and limits on marten trapping further support this theory.
Currently, marten are found across much of the boreal zones of North America (Figure 2). They are absent north of the treeline in the Arctic Circle, and the southern extent of their range aligns approximately with the coniferous-deciduous transition zone (Clark et al. 1987; Ruggiero et al. 1994; Thompson et al. 2012). Their current distribution is continuous from Alaska across north central Canada, south to the Great Lakes, and east to southern Quebéc and the Northeastern United States (Gibilisco 1994; Proulx et al. 2004; Krohn 2012). In the western US, marten range further south in strings of smaller island-like populations along the Cascades into Oregon and Washington, the Sierra Nevadas into California and Nevada, and the Rockies all the way to New Mexico (Clark et al. 1987; Gibilisco 1994; Ruggiero et al. 1994). Additional disjunct populations that do not appear to be connected to the main range exist in southwestern Saskatchewan and Manitoba, Nova Scotia, Newfoundland, and New York (Gibilisco 1994; Proulx et al. 2004; Dawson and Cook 2012).

In some areas, marten are recolonizing parts of their historical range, a shift facilitated by a number of translocation and reintroduction attempts in both Canada and the United States (Krohn 2012). These efforts have had varied success, and have helped to establish some isolated marten populations in Saskatchewan, Manitoba, and South Dakota (Slough 1994; Powell et al. 2012). Most of these reintroductions occurred between the 1970s and 1990s and recovery has been slow; Gibilisco (1994) stated that little population change occurred between the 1950s and 1990s. However, more recently, populations of marten have been discovered in southern Vermont (O’Brien et al. 2018) and the Apostle Islands in northern Wisconsin (Allen et al. 2018) where they were previously thought to be absent. This suggests that marten may be more widespread at their southern range limits than previously believed, but occur at low densities, limiting detection of the populations.
Marten are considered a boreal species, closely associated with coniferous species (Buskirk and Powell 1994; Ruggiero et al. 1994; Proulx et al. 2004). However, marten also inhabit mixed and deciduous forests in the northeastern United States (Payer and Harrison 2004; Proulx et al. 2004; Thompson et al. 2012). Regardless of the forest type, marten are associated with mid to late successional forests (Buskirk and Powell 1994; Sirén et al. 2015), complex horizontal and vertical forest structures (Ruggiero et al. 1994; Chapin et al. 1997; Potvin et al. 2000; Payer and Harrison 2004), and deep snowpack (Krohn et al. 1995; Krohn et al. 2004; Carroll 2007). These components, especially stand age, are not strict requirements, but receive greater use than other habitats that may be available suggesting a strong preference (Carroll 2007; Thompson et al. 2012). Juvenile marten appear to have even more flexible preferences, which could be a result of exclusion from preferred habitat by established adults (Buskirk and
Selection of habitat occurs at a variety of scales ranging from stand-level characteristics, such as forest type, to individual structures, such as snags for resting sites (Shirk et al. 2012; Thompson et al. 2012).

Despite frequent characterization as a forest specialist species that is dependent on coniferous cover, there exists a great deal of variation in associations with specific tree species. For example, Zielinski et al. (2001) found that marten sightings were most closely associated with Douglas fir in California, whereas marten selected against sites with the same species in British Columbia (Mowat 2006) and Oregon (Bull et al. 2005). McCann et al. (2014) evaluated fine-scale marten movement in Wisconsin and found hemlock-cedar forests to be of great importance, despite being a habitat marten are not otherwise associated with. This variation in responses suggests that aspects of marten ecology is region-specific. Viewing marten spatial population ecology through a regional lens may go some way towards reconciling apparent contradictions in the literature.

The spatial variation in habitat preferences suggests that major conservation threats to marten are also likely to vary regionally. One major threat that is consistent across the range is habitat conversion, primarily through timber harvest. Harvest can shift the composition of the forest patch to early successional hardwood species, which are generally not preferred by marten (Payer and Harrison 2000; Poole et al. 2004; Proulx 2006). Conversion to non-forested habitat is also detrimental to marten. Open areas, such as clearcuts, create large fragmentation related dispersal barriers (Ruggiero et al. 1994; Gibilisco 1994). They may forage around the edges of open spaces, especially if abundant logging debris provides cover from predators and sufficient cover to promote an abundance of prey. Population densities are much lower and home range sizes are greater in cut areas than they are in adjacent uncut areas. This suggests that some timber
harvest methods can decrease the overall quality of the habitat for marten use (Thompson and Harestad 1994; Payer and Harrison 2003).

Space use and movement

Home range size, and thus density, in this solitary species varies depending on the quality of available habitat. Generally, structure and canopy cover contribute to habitat quality more than stand age and overstory species composition (Poole et al. 2004; Mowat 2006; Godbout and Ouellet 2010). Timber harvest can decrease overhead cover, forest structure, and coarse woody debris thereby decreasing habitat quality (Thompson 1994; Payer and Harrison 2003; Fuller and Harrison 2005). Tree die-off due to insect outbreaks or disease may also decrease cover, but maintains structure so these areas retain value for marten habitat (Payer and Harrison 2000; Ivan et al. 2018). Application of certain silvicultural methods and post-harvest treatments can decrease the impact on suitability, but density is still likely to be lower in these areas (Fuller and Harrison 2005; Godbout and Ouellet 2010; Weibe et al. 2014).

Part of the reason that marten densities are so low is due to their territorial nature. Home range size varies greatly depending on habitat quality, resource availability, individual size, and sex, and can vary from less than 1km² to more than 15km², with male home ranges typically 2-3 times larger than females (Clark et al. 1987; Powell 1994; Ruggiero et al. 1994). Marten are active throughout the year, though they may utilize different portions of their home range during the winter than in the summer (Payer et al. 2004; Sirén et al. 2015; Moriarty et al. 2017). Despite these seasonal differences in space use, marten demonstrate strong site fidelity between years (Payer et al. 2004).
In general, marten avoid large open areas, which impacts both long and short distance movement. Though marten are known to travel up to 74km between sites (Fecske and Jenks 2002), they generally avoid crossing treeless areas greater than 5km (Ruggiero et al. 1994; Gibilisco 1994), so fragmented forest landscapes pose a significant barrier to dispersal between suitable sites. Marten also avoid openings within their own home ranges. When hunting, they stay under tree, shrub, or woody debris cover as much as possible and follow winding paths, often crossing and re-crossing their own paths as they search for prey (Clark et al. 1987; Ruggiero et al. 1994; Buskirk and Powell 1994). Marten do not seem to prefer to hunt during any specific time of the day, displaying highly variable activity patterns (Clark et al. 1987; Ruggiero et al. 1994; Sirén et al. 2016a). They primarily hunt on the ground, but are accomplished climbers and foray into trees to search for food (Clark et al. 1987; Ruggiero et al. 1994).

Winter weather conditions produce additional constraints on marten movement. Lower temperatures require a greater expenditure of energy to conserve heat, while deep snows hamper movement making traveling and hunting more difficult. To combat these challenges, marten have low foot-loads ratios; their feet act as snowshoes, which allows them to move on top of the snow instead of sinking into it (Krohn et al. 2004). They have limited fat reserves, but are able to mobilize them efficiently and can fast for up to 5 days, which enables them to shelter in place during particularly harsh conditions (Nieminen et al. 2007). To augment these physiological adaptations, marten also utilize a number of behavioral adaptations. They make extensive use of subnivean spaces in winter, both as space to hunt for mammalian prey (Raine 1981; Sherburne and Bissonnette 1994; Mustonen and Nieminen 2012) and to take advantage of the warmer temperatures under the snow while resting (Clark et al. 1987; Ruggiero et al. 1994; Buskirk and
Additionally, marten greatly reduce their activity levels from 14 hours in summer to only 4 in winter (Mustonen and Nieminen 2012).

**Interspecific interactions**

As a relatively small mammal, marten are vulnerable to predation by a wide variety of larger carnivores: fisher (*Pekania pennanti*), bald eagle (*Haliaeetus leucocephalus*), golden eagle (*Aquila chrysaetos*), red fox (*Vulpes vulpes*), great horned owl (*Bubo virginianus*), peregrine falcon (*Falco peregrinus*), bobcat (*Lynx rufus*), lynx (*Lynx canadensis*), wolf (*Canis lupus*), and coyote (*Canis latrans*) have all been recorded attacking and killing marten (Raine 1981; Clark et al. 1987; Ruggiero et al. 1994; Price et al. 2005; Romanski and Belant 2008; Pagel and Schmitt 2013; Woodford et al. 2013). Their vulnerability to aerial attack is largely believed to be the reason why marten avoid foraging in forest openings (Clark et al. 1987; Ruggiero et al. 1994). Despite the large number of potential predators, none are known to have significant population level impacts on the species (Clark et al. 1987).

Fisher are of particular interest as they are both competitor and predator. Despite the fact that fisher are up to 5x the size of marten, the two species exploit an almost identical prey base and share a significant range overlap (Fisher et al. 2013; Manlick et al. 2017). The relationship between the two is largely mediated by snow conditions, where marten are more snow-adapted (Clark et al. 1987; Buskirk and Powell 1994; Ruggiero et al. 1994; Krohn et al. 1995; Krohn et al. 2004; Pozzanghera et al. 2016). In fact, competition with fisher has been proposed as an important reason for the apparent stalling of the marten range expansion (Sirén and Morelli 2019).
Marten are generalist predators and most species are consumed opportunistically and in proportion with their availability, with common high frequency species including mice, voles, squirrels, lagomorphs, and birds (Clark et al. 1987; Martin 1994; Ruggiero et al. 1994; Zielinski and Duncan 2004; Slauson and Zielinski 2017). Notable exceptions where certain prey species dominate marten diet include red-backed voles (*Clethrionomys spp*) which are highly important across the majority of the range (Martin 1994), snowshoe hare (*Lepus americanus*) in southeast Manitoba (Raine 1981), mice on Vancouver Island (Nagorsen et al. 1989), and *Microtus spp* voles in Newfoundland (Gosse and Hearn 2005; Hearn et al. 2006). There is also some evidence that larger species with higher calorific value may actually be more important even though they are consumed less frequently (Martin 1994; Cumberland et al. 2001). There is no strong evidence that marten diet varies by sex or age, though there is some variation by region, again related to their opportunistic feeding ecology and prey availability (Martin 1994; Nagorsen 1994; Hales et al. 2008; Robitaille and Laurence 2007). Generally, marten diet is most varied in the southern parts of their range and less complex the further north the population is located (Martin 1994; Ruggiero et al. 1994). There is also some variation in diet throughout the year when seasonal food sources are available. In summer, marten consume insects, bird eggs, nestlings, and young small mammals; in autumn, increased amounts of vegetative material, especially fruit, berries, and nuts are consumed (Martin 1994; Bull 2000; Slauson et al. 2017). Carrion is an important food source in winter (Raine 1981; Gosse and Hearn 2005; Hales et al. 2008).

**Population dynamics and pressures**

Marten populations are considered stable across much of their range, although there is large variation in reported values (Table 1). While density is a state variable that can be easily compared across space and time, relatively few studies across the range report density estimates.
Of those that do report, estimates range from less than 0.5 individuals/km$^2$ to 1.8 individuals/km$^2$. Much of this variation has been attributed to habitat quality, but other factors have been proposed.

One source of inter-year variability is resource availability. For example, the four- and six-fold increases in populations exposed to little or no harvest pressure, respectively, were linked to changes in small mammal availability in Montana (Weckwerth and Hawley 1962) and Ontario (Thompson and Colgan 1987). Such large fluctuations in marten abundance have not been reported in harvested populations, although numerical responses in harvest rates have been. Jensen et al. (2012) linked a 6.5x increase in fur harvest following years when soft mast crops failed. Though the magnitude of increase is similar, untrapped populations increased when resources were plentiful, while trapped populations increased when resources were scarce. In the case of Jensen et al. (2012), the fluctuations are likely a reflection of individual susceptibility to capture, rather than changes in marten abundance. This suggests that harvest acts as another population regulation mechanism.

In the 30 states and provinces in which marten currently occur, they are trapped in 22 (Table 1). Many of these regions utilize trapping records to monitor population changes and adaptively set harvest (Hiller et al. 2011). There are a number of limitations with using trapping data to infer population size or trends (DeVink et al. 2011). Furbearer harvests are notoriously sensitive to market prices and thus trapper effort, but oftentimes information on trapper effort is not collected uniformly across all jurisdictions (Ruggiero et al. 1994). Trapping is naturally biased towards male martens, due to their larger home ranges, and thus exposure to more traps. However, it can disproportionately affect juveniles when trapping coincides with dispersal, or with females when it coincides with active gestation (Ruggiero et al. 1994; Strickland 1994).
Due to these biases, harvesting not only has the potential to reduce density, it can skew estimates of sex and age structure (Payer and Harrison 1999; Fortin and Cantin 2004; Payer et al. 2004). Variable food availability can add temporal dynamics to these trapping biases. For example, Jensen et al. (2012) not only found that marten harvests were larger in years where mast crops failed; proportionally fewer juveniles and more females were captured as well.

Table 1. Marten status, trends, and reported density values across the 30 jurisdictions in their current distribution. Table adapted from Proulx et al. 2004.

<table>
<thead>
<tr>
<th>State/Province</th>
<th>Furbearer</th>
<th>Protected</th>
<th>Population Trend</th>
<th>Reported Densities</th>
<th>Estimation Method*</th>
<th>Citation(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.17-0.55</td>
<td>D</td>
<td>Flynn et al. 2009</td>
</tr>
<tr>
<td>Alberta</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>British Columbia</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.33</td>
<td>D</td>
<td>Mowat &amp; Paetkau 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.24-0.37</td>
<td>D</td>
<td>Poole et al. 2004</td>
</tr>
<tr>
<td>California</td>
<td>x</td>
<td>unknown</td>
<td></td>
<td>0.07-0.33</td>
<td>S</td>
<td>Slauson et al. 2017</td>
</tr>
<tr>
<td>Colorado</td>
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<td>unknown</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Idaho</td>
<td>x</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Labrador</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maine</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.4-1.2</td>
<td>D</td>
<td>Soutiere 1979</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.14-0.68</td>
<td>D</td>
<td>Phillips 1994</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.08-0.15</td>
<td>D</td>
<td>Payer &amp; Harrison 1999</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.61</td>
<td>D</td>
<td>Kelly et al. 2009</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.08</td>
<td>S</td>
<td>Clare et al. 2017</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.18-0.34</td>
<td>S</td>
<td>Clare et al. 2019</td>
</tr>
<tr>
<td>Manitoba</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Michigan</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minnesota</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montana</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>1.12-1.66</td>
<td>D</td>
<td>Hawley 1955</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.19-1.70</td>
<td>D</td>
<td>Hawley &amp; Newby 1957</td>
</tr>
<tr>
<td>Nevada</td>
<td>x</td>
<td>unknown</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newfoundland</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>State/Province</td>
<td>Furbearer</td>
<td>Protected</td>
<td>Population Trend</td>
<td>Reported Densities</td>
<td>Estimation Method*</td>
<td>Citation(s)</td>
</tr>
<tr>
<td>---------------------</td>
<td>-----------</td>
<td>-----------</td>
<td>------------------</td>
<td>-------------------</td>
<td>-------------------</td>
<td>---------------------------------------</td>
</tr>
<tr>
<td>New Brunswick</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>New Hampshire</td>
<td></td>
<td></td>
<td>increasing</td>
<td>0.43-0.6</td>
<td>S</td>
<td>Sirén et al. 2016b</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.39-0.43</td>
<td>S</td>
<td>Linden et al. 2018</td>
</tr>
<tr>
<td>New York</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northwest Territories</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.156</td>
<td>D</td>
<td>Latour et al. 1994</td>
</tr>
<tr>
<td>Nova Scotia</td>
<td>x</td>
<td>unknown</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ontario</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>1.2-1.9</td>
<td>D</td>
<td>Francis &amp; Stephenson 1972</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.4-2.4</td>
<td>D</td>
<td>Thompson &amp; Colgan, 1987</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.05-1.8</td>
<td>D</td>
<td>Thompson 1994</td>
</tr>
<tr>
<td>Oregon</td>
<td>x</td>
<td>stable</td>
<td>stable (dec. in coastal mountains)</td>
<td>1.13</td>
<td>S</td>
<td>Linnell et al. 2018</td>
</tr>
<tr>
<td>Quebec</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.24-0.43</td>
<td>D</td>
<td>Godbout &amp; Ouellet 2008</td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>South Dakota</td>
<td>x</td>
<td>unknown</td>
<td></td>
<td>0-0.69</td>
<td>D</td>
<td>Smith et al. 2007</td>
</tr>
<tr>
<td>Utah</td>
<td>x</td>
<td>stable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vermont</td>
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<td>unknown</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Washington</td>
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<td>stable (dec. in coastal mountains)</td>
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<td>x</td>
<td>unknown</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wyoming</td>
<td>x</td>
<td>unknown</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yukon</td>
<td>x</td>
<td>stable</td>
<td></td>
<td>0.4-0.6</td>
<td>D</td>
<td>Archibald &amp; Jessup 1984</td>
</tr>
</tbody>
</table>

*S = spatially explicit estimation, D = abundance-derived estimation. Spatially-explicit methods, such as SCR, incorporate an estimate of space use, meaning that the effective area sampled is known, and estimates of abundance can be converted to true density. Abundance-derived methods, such as the simple calculation of N individuals/area surveyed, cannot estimate the effective space, only the study area surveyed, and thus cannot accurately estimate true density. Many of these derived methods depend on intensively surveying the study area and assuming all individuals are captured, which means the final estimates are likely conservative.
1.3 Patterns in Recent Marten Research

Search criteria

To identify patterns in marten research across their range, I reviewed the literature, including both academic articles and technical reports. In April of 2018, I used the Web of Science search engine to search the titles, abstracts, and keywords for any articles that matched the search terms “American marten” or “*Martes americana*.” I was particularly interested in recent research that coincided with the development of hierarchical models (e.g., occupancy models, capture-recapture methods, and spatial capture-recapture methods), as they provide inference about error-corrected state variable that allow for more appropriate comparison across systems and studies. All articles were downloaded, and I reviewed the abstracts to ensure the article truly matched my search requirements.

Articles in which American marten were mentioned only as an example or in the literature cited were removed, as were any articles that actually studied closely related Eurasian marten species. After I began reviewing the articles, I discovered that some focused on certain sub-species of American marten (i.e., Humboldt marten, *M. humboldtensis*, Newfoundland marten, *Martes atrata* and Pacific marten, *M. caurina*). To ensure I also captured articles that referred only to certain subspecies, I re-ran the search using the subspecies names as additional search terms in August. I re-ran the search one more time at the end of 2018 to capture any articles written over that year, resulting in a total of 183 articles. I extracted meta information about each article and recorded article details, field and statistical methods used, and the results reported (Table 2).
**Table 2.** Data collected from each article for the literature review.

<table>
<thead>
<tr>
<th>Paper Details</th>
<th>Field Methods</th>
<th>Habitat-Specific Survey Details</th>
<th>Statistical Methods &amp; Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st Author</td>
<td>Field survey method(s)</td>
<td>Habitat data collected</td>
<td># marten observations</td>
</tr>
<tr>
<td>Year published</td>
<td>Bait(s) used</td>
<td>Data source</td>
<td># marten individuals</td>
</tr>
<tr>
<td>Journal</td>
<td>Season surveyed</td>
<td>GIS grain size (m)</td>
<td>Home range size</td>
</tr>
<tr>
<td>Title</td>
<td>Months surveyed</td>
<td>Habitat survey details</td>
<td>Statistical method</td>
</tr>
<tr>
<td>State/Country</td>
<td>Years surveyed</td>
<td>Response type</td>
<td>Response variable</td>
</tr>
<tr>
<td>Locality</td>
<td>Study duration (months)</td>
<td>Resource selection level (I, II, or III)</td>
<td>Descriptive results</td>
</tr>
<tr>
<td>Coordinates</td>
<td>Survey duration (days)</td>
<td>Significant habitat variables</td>
<td>Predictor variables</td>
</tr>
<tr>
<td>Ecoregion</td>
<td># of sites</td>
<td></td>
<td>Significant variables</td>
</tr>
<tr>
<td>Topic</td>
<td># of units per site</td>
<td></td>
<td>Detectability</td>
</tr>
<tr>
<td>Other species surveyed</td>
<td>Total trap nights</td>
<td></td>
<td>Density</td>
</tr>
<tr>
<td>Marten (sub)species surveyed</td>
<td>Telemetry frequency</td>
<td></td>
<td>Occupancy</td>
</tr>
<tr>
<td>Study area</td>
<td>Survey details</td>
<td>Capture Probability</td>
<td>Survival</td>
</tr>
<tr>
<td>Notes</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Geographic distribution of marten research**

Between 2000 and 2018, American marten research has been conducted throughout their range albeit unevenly (Figure 3). In order to evaluate spatial patterns, articles were categorized by Level I Ecoregions, as defined by the United States Environmental Protection Agency (CECWG 1997; Omernick and Griffith 2014). In North America, marten range overlaps with six ecoregions (Table 3). Marten research has not, however, been conducted proportionally to the ecoregional composition of the range. In the studies reviewed, northern, montane, and coastal
forests are overrepresented, temperate forests are approximately in proportion, and the Hudson Plains and taiga are underrepresented (Table 3).

Figure 3. Map showing the distribution of marten research sites across North America and the different EPA ecoregions. Most study locations are approximate. Figure does not include research from 7 articles that utilized museum specimens from a large number (>10) of areas.

Even within the ecoregions, research was clustered, highlighting potentially important spatial biases in recent marten research. There are two research hotspots on the west coast; the Alexander Archipelago which is primarily focused on the introgression zone between Pacific and American marten (n = 17), and the Sierra Nevada mountains, a portion of Pacific marten range (n = 16). We note that this bias is one largely related to the productivity (in terms of publishing) of specific research groups. A third research hotspot, which includes a variety of topics and research groups, is the Upper Peninsula of Michigan where a large number of reintroduction projects have occurred and marten are recovering (n = 19, Powell et al. 2012).
Table 3. Distribution of area, papers, and study sites by ecoregion within marten range in North America.

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>Area (km²)</th>
<th>% of Total</th>
<th>Papers</th>
<th>% of Total</th>
<th>Study Sites</th>
<th>% of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal forest</td>
<td>383345</td>
<td>0.05</td>
<td>30</td>
<td>0.17</td>
<td>35</td>
<td>0.15</td>
</tr>
<tr>
<td>Hudson plain</td>
<td>313963</td>
<td>0.04</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td>Northern forest</td>
<td>2427549</td>
<td>0.32</td>
<td>97</td>
<td>0.54</td>
<td>97</td>
<td>0.42</td>
</tr>
<tr>
<td>Montane forest</td>
<td>1687730</td>
<td>0.22</td>
<td>68</td>
<td>0.38</td>
<td>81</td>
<td>0.35</td>
</tr>
<tr>
<td>Taiga</td>
<td>2365319</td>
<td>0.31</td>
<td>10</td>
<td>0.06</td>
<td>11</td>
<td>0.05</td>
</tr>
<tr>
<td>Temperate forest</td>
<td>61401</td>
<td>0.01</td>
<td>4</td>
<td>0.02</td>
<td>4</td>
<td>0.02</td>
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<tr>
<td>TOTALS</td>
<td>7597344</td>
<td>180</td>
<td>229</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Outside of these hotspots, marten research tends to focus on interest in marten as either a furbearer, protected species, or reintroduced population. One pattern that is clearer is areas where marten research has not recently occurred. The Hudson plain is virtually unsampled, as is the taiga outside of Alaska. Research has been particularly sparse in the Canadian provinces in the central and western parts of marten range (Yukon, Northwest Territories, Saskatchewan, and Manitoba), as well as northern Quebec and the maritime provinces to the east. In the United States, the populations in the Rocky Mountains are also poorly studied. In some of these areas, such as the Rocky Mountains, the lack of recent marten research may be related to populations being especially small and difficult to monitor. Additionally, access in some of these areas, such as northern Manitoba and Saskatchewan, is limited, making research difficult to conduct. In the other poorly studied areas, marten are actively managed as a furbearing species and are within the core of marten range, rather than on the edges. In these places where the populations are stable, marten are a lower research priority than they are elsewhere. The lack of research in these regions may limit our understanding of marten dynamics in these areas and delay management responses to changes in the populations there.
Field methods

Of the field methods used, studies using collars (both VHF and GPS) were the most common, followed by genetic analysis (Table 4). The source of genetic samples varied, and included (in order of most to least prevalent) trapper carcasses, hair snares, live traps, museum specimens, and scat surveys. Camera traps were the third most common method, followed by snow tracking. Most methods were used infrequently, making it difficult to determine if there were any trends in their use over this time period. However, genetic analysis and camera trap use increased markedly over this period, while captive observation, diet analysis, and use of track plates sharply decreased (Table 5). There are also regional differences in method used. Nearly all of the surveys in the taiga were multi-regional genetic surveys. In the northern forests, collars were used the most frequently, followed by genetic analyses and snow tracking. Surveys in the montane and coastal forests were most frequently genetic analyses, followed by camera traps and collars. In temperate forests, historic records were analyzed twice, and diet analysis and snow track surveys were each used once.
**Table 4.** Most commonly utilized field methods for marten research between 2000 and 2010.

<table>
<thead>
<tr>
<th>Field Method</th>
<th>Frequency</th>
<th>Field Method</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collars</td>
<td>47</td>
<td>Track surveys</td>
<td>4</td>
</tr>
<tr>
<td>Genetic analysis</td>
<td>37</td>
<td>Trapper surveys</td>
<td>4</td>
</tr>
<tr>
<td>Camera traps</td>
<td>29</td>
<td>Direct observation</td>
<td>3</td>
</tr>
<tr>
<td>Snow tracking</td>
<td>22</td>
<td>Simulation</td>
<td>3</td>
</tr>
<tr>
<td>Track plates</td>
<td>17</td>
<td>Expert surveys</td>
<td>2</td>
</tr>
<tr>
<td>Harvest records</td>
<td>11</td>
<td>Hair snares</td>
<td>2</td>
</tr>
<tr>
<td>Live traps</td>
<td>9</td>
<td>Historical records</td>
<td>2</td>
</tr>
<tr>
<td>Body analysis</td>
<td>8</td>
<td>Fossil remains</td>
<td>1</td>
</tr>
<tr>
<td>Diet analysis</td>
<td>8</td>
<td>Nest surveys</td>
<td>1</td>
</tr>
<tr>
<td>Captive observation</td>
<td>7</td>
<td>Roadkills</td>
<td>1</td>
</tr>
<tr>
<td>Pooled data</td>
<td>7</td>
<td>Small mammal trapping</td>
<td>1</td>
</tr>
<tr>
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Table 5. Breakdown of the most commonly used field methods by year in recent marten literature. Excludes methods used only once between 2000 and 2018.

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As expected, the field methods used were directly related to specific research objectives (Table 6). For example, questions related to marten distribution, occurrence, occupancy, abundance, and density were addressed using data collected from camera traps. Space use and habitat preferences were almost exclusively investigated using data from collars, although collar data were also used to understand marten behavior and demographic rates. The impact of fragmentation on population structure and barriers to movement, especially in the context of reintroductions and recovery, were investigated using molecular methods (including inference about genetic structure and diversity).

**Table 6.** Breakdown of the most commonly used field methods by research topic in recent marten literature. Excludes methods used only once between 2000 and 2018.

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In terms of marten seasonality, the bulk of research occurred between the months of October and March (fall-spring), but peaked in January. This is likely because it limits research to a time period outside of dispersal, mating, or care of young, when marten movement is minimal; this is important in order to meet assumptions of certain models. Surveys that include the spring and summer months (Apr-Aug) were typically part of full-year studies, where the objective is to compare between-season differences in marten activity. Certain field methods are also preferred in different seasons. Snow track surveys are obviously limited to the winter months, but camera trapping and hair snares are also most frequently used in the winter months, i.e., between January and March. Track plates are used mostly from late summer to early fall, when conditions are driest, and collars are typically deployed and monitored (remotely or by physical tracking) most frequently in the fall and winter. Other field methods, including live trapping and scat surveys, are used relatively evenly across the seasons.

There was also some geographic structure in research focus and, correspondingly, field methods. Most research on genetic structure occurred in western parts of the range where populations of Pacific and American marten co-occur, but also occurred in areas where there is interest in other subspecies such as the Newfoundland (M. a. atrata) and Humboldt (M. c. humboldtensis) marten. While attempts to understand the impacts of landscape connectivity on genetic patterns are distributed across their range, studies tended to be clustered around reintroductions and translocations areas (e.g., Michigan, Wisconsin, and Vermont).

Camera traps also tend to be used with these populations near the edges of marten distribution. These areas are sometimes only recently colonized or do not have clear records of historic marten occurrences. In these studies, the interest is in determining if marten are at all present, and if they are, at what population densities. These studies are almost entirely in the
forest fragments along the Rocky, Cascade, and Sierra Nevada Mountains, and in the northeastern United States. Camera traps are sensible choices in these areas because marten densities here are often very low and as a result, monitoring is challenging.

Use of the final major field method used, collars, dominates much of the research in central, stable portions of marten distribution. The interest in these regions is largely driven by marten’s status as a furbearer. Here, research focuses around understanding marten habitat preferences and requirements which is used to inform forest management and trapping regulations.

Regional habitat associations

Over 200 variables were evaluated in the 71 articles that focused on marten habitat associations. The vast majority of these focused on describing characteristics of marten home ranges (second order selection, Johnson 1980), or marten use of specific features within their home range (third order selection). More recently, likely due to the development of both noninvasive monitoring techniques and hierarchical statistical models, other aspects of marten spatial population ecology, such as occupancy and abundance, have been investigated. Of the 149 variables tested more than 100 of these were found to be ‘significant’, but only 17 were significant in more than two studies. For marten home range characteristics, the variables that were consistently found to be significant were forest type, canopy closure, forest structure, and human influence (Table 7).

In their review of marten habitat associations from literature between 1993 and 2010, Thomson et al. (2012) suggest marten selection occurs at multiple scales, and that clear differences appear in different regions of marten range. Generally, high quality marten habitat is
associated with mature mixed and coniferous forest types, though specific tree species associations vary across their range. In general, it is suggested that marten are not restricted to specific forest types, but they do represent areas of higher frequency of use. Additionally, adults may exclude juveniles from preferred habitat, which can obscure some of these forest species associations (Ruggiero et al. 1994; Paragi et al. 1996). Nonetheless, my review found similar consistent regional relationships between marten and their environments.

Table 7. Habitat variables most frequently found to be significant, across all three resource selection levels (Johnson 1980). First level selection describes species distribution, second level describes species home range, and third level describes species use of features within their home range.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Resource Selection Level</th>
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<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Forest type</td>
<td>1</td>
</tr>
<tr>
<td>Canopy closure</td>
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</tr>
<tr>
<td>Developmental stage</td>
<td>0</td>
</tr>
<tr>
<td>Coarse woody debris</td>
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</tr>
<tr>
<td>Elevation</td>
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<tr>
<td>Roads</td>
<td>0</td>
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<tr>
<td>Terrain ruggedness</td>
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<tr>
<td>Coniferous</td>
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<tr>
<td>Snags</td>
<td>0</td>
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<tr>
<td>Snow depth</td>
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</table>

Research in the northern forests focused more on the effects of stand age rather than composition. In this region, marten are associated with mature, especially coniferous, forests, while maple and regenerating forests are typically avoided. An interesting aspect of marten habitat in this region was the difference between natural open areas (i.e. insect defoliated or burned) and human-created openings (i.e. timber harvest). Multiple studies found that marten preferred natural openings due to the greater structural remnants in these areas compared to timber harvested areas (Payer and Harrison 2000; Gosse et al. 2005; Godbout and Ouellet 2008; Hearn et al. 2010; Cheveau et al. 2013). In montane and coastal forests, tree species associated
with marten habitat were generally mesic species such as Douglas fir, while xeric sites were avoided, though this was not as consistent. There was only one article that evaluated species associations in the taiga; Tigner et al. (2015) found marten were associated with upland forests, including mixes of white spruce and aspen, but avoided lowland black-spruce dominated wetlands and areas with sparse cover. Studies in the temperate forests note a greater utilization of mixed and deciduous stands than is observed in other parts of their range (Payer and Harrison 2003; Poole et al. 2004; Dumyahn et al. 2007).

In some instances, forest composition and age were found to be less important than other habitat variables. A number of authors found that marten use of space did not greatly differ between harvested or young stands and older mature stands (Potvin et al. 2000; Hearn et al. 2010; Seip et al. 2018). They suggest that this is because structure, in the form of coarse woody debris, snags, logs, and other habitat features, is of greater importance. These features provide habitat for prey species, access to subnivean sites, and potential resting and denning sites for marten. Some authors additionally suggest that prey availability in these areas further explains marten space use (Payer and Harrison 2003; Vigeant-Langlois and Desrochers 2011). It is important to note that in the 66 articles that investigated marten habitat associations, 40 included variables related to composition, 20 included variables related to structure, and only 10 included variables related to age. Twelve considered composition and structure simultaneously, seven considered composition and age, and two considered structure and age. Only one article investigated all three measures of habitat simultaneously, which greatly limits our ability to understand the interactions between and relative importance of stand composition, structure and age.
Despite these inconsistencies in what constitutes ‘habitat’ for marten in terms of forest age and composition, marten are consistently and positively associated with canopy closure, especially coniferous cover, throughout their range. This response is sensible, considering marten avoidance of open areas where they are at greater risk of predation. Zielinski et al. (2001) found that marten occupancy rates were greatest in areas with canopy closure above 60%, though other authors have reported thresholds as low as 20% and as high as 80% (Bowman and Robitaille 1997; Smith and Schafer 2002). Interestingly, marten in New Brunswick were found to be positively associated with deciduous canopy closure and negatively associated with coniferous canopy closure; this apparent discrepancy is likely due to New Brunswick’s location in the temperate ecoregion, which has a greater deciduous component than the other ecoregions (Nams and Bourgeois 2004). Poole et al. (2004) found that marten respond negatively to overstory removal; marten either shifted their home ranges in response or, if more than 37% of the total canopy cover was removed, disappeared from the study area altogether.

Human activity generally has a negative impact on marten activity. Tested sources of human influence included distance to logged areas, area logged, distance to recreational sites and trails, distance to human structures, distance to nearest road, and road density (Clevenger et al. 2001; Slauson et al. 2007; Kirk et al. 2009; Slauson and Zielinski 2009; Hiller et al. 2011; Landriault et al. 2012; Wiebe et al. 2013; Baltensperger et al. 2017; Aylward et al. 2018; Seip et al. 2018). Marten activity is negatively associated with road density, though distance to road was not found to have a significant effect (Aylward et al. 2018). Marten avoid logged areas, especially larger ones (Slauson et al. 2007; Slauson and Zielinski 2009). The only other human-related variable that was found to have a significant impact on marten activity was the distance to
the nearest trail or recreation site; as the distance increased, so did marten activity (Baltensperger et al. 2017).

Several other variables are commonly cited in earlier literature as likely to impact marten, though they were not evaluated extensively in the articles reviewed. These include snow depth and the presence of fisher. Snow is thought to mediate the interaction between the two species, so they are likely correlated to some extent (Krohn et al. 1995; Sirén et al. 2019). Though the two are closely linked in the literature, only three studies evaluated the effects of both, and none found the combination of the two variables to be important.

A total of 14 articles evaluated the effects of snow on marten activity, but only five showed an effect. Marten were positively associated with deeper snow conditions in all five studies (Wilbert et al. 2000; Wiebe et al. 2014; Gompper et al. 2016; Koen et al. 2016; Pozzanghera et al. 2016). This apparent lack of support in the recent literature is particularly interesting, considering how frequently marten are described as a snow-adapted species (Raine 1981; Ruggiero et al. 1994; Krohn et al. 1995). It does appear, however, that the five articles that found an effect used fine-scale data collected in situ, whereas the other nine used weather station or remotely sensed data, suggesting a mismatch between the scale at which marten respond to variation in snow and the available coarse-scale snow data products, an issue recently highlighted by Sirén et al. (2018). It is also worth considering how snow is quantified (Pruitt 2005); snow depth was found to be significant more often than measures of cumulative snowfall or length of snow season.

The effect of fisher on marten activity was tested in a number of articles (11), with only three reporting important effects. In Alberta, fisher had a negative effect on marten (Fisher et al. 2013). In Wisconsin, marten were positively associated with fisher presence (Manlick et al.
2017; McCann et al. 2017). It is worth noting that all of these articles utilized furtrapper harvest rates or observed presences of both species. Barner et al. (2018) and Blanchet et al. (2020) have questioned the validity of equating species co-occurrence as interspecific interactions, which may explain why the results from these articles were inconclusive.

Another important aspect of marten space use is the factors influencing home range size. Reported marten home range sizes are highly variable. The smallest reported values come from coastal Oregon, and are less than 1km$^2$ for adult females (Linnell et al. 2018; Baldwin et al. 2008). Some of the largest reported values come from Newfoundland, with male home ranges averaging at 27km$^2$, and Labrador, with reported averages of 45km$^2$ (Smith and Schafer 2002; Hearn et al. 2010). A number of factors likely contribute to this observed variation. First, males are not only larger than females, they maintain significantly larger home ranges as well (Gosse et al. 2005; Dumyahn et al. 2007; Hearn et al. 2010). Male home ranges can be up to four times larger than female home ranges, though more typically they are between 40-50% larger (Slauson et al. 2008; Shirk et al. 2014; Moriarty et al. 2017). This greater home range size is, in part, an effect of male home ranges overlapping with multiple female home ranges. It is important to consider the overlap, variation between the sexes, and the male bias in marten sampling when calculating home range sizes.

Much of the remaining variability in home range size is due to the influence of habitat quality. Quality can be related to a number of habitat characteristics, but generally home ranges are smaller in higher quality sites, and larger in adjacent lower quality sites. Sites in Newfoundland are thought to be particularly large due to lack of available prey (Gosse et al. 2005; Hearn et al. 2010). In other locations, home range is influenced by timber harvest such that marten utilizing harvested areas maintain larger home ranges (Poole et al. 2004; Godbout and
Oullet 2008; Cheveau et al. 2013). Finally, marten may defend larger home ranges in winter than they do in summer, likely due to the limited availability of food resources (Moriarty et al. 2017; but see Sirén et al. 2016b).

Statistical methods

The research topic and objectives strongly influence which statistical methods are used to study marten (Table 8). Most research investigating marten behavior or biology was focused on identifying differences between groups of marten, such as sex (Robitaille and Cobb 2003; Schulte-Hostedde et al. 2011), age (Miller and Nagorsen 2008), residential status (Boonstra et al. 2018), sub-group (Nieminen et al. 2007; Howell et al. 2016), season (Gilbert et al. 2009), or study area (Robitaille and Aubry 2000; Moriarty et al. 2017). Common statistical tests used include Student’s t-test, ANOVA, and related paired and non-parametric tests. Though these tests for differences are commonly used for a variety of topics, they are limited in that they generally can only assess the effect of a single variable at a time, limiting our understanding of how multiple variables interact to affect marten.

Articles focused on evaluation of various or novel methods for surveying marten also often test for differences. Here, the focus is to evaluate differences in marten responses to different techniques (Belant 2005; Mortenson and Moriarty 2014) or the results from different analyses (Potvin et al. 2001; Bridger 2016). Methods research also frequently describe the utility of new methodologies without statistically evaluating them. Such descriptive results are usually supplementary to other inferences, and also commonly used to describe observations of marten outside their known distribution or results from genetic studies. A large portion of habitat research also searches for compositional differences between potential marten sites (Payer and
Table 8. Division of the types of statistical tests used to evaluate different research questions in recent marten research.

<table>
<thead>
<tr>
<th></th>
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<th>Descriptive</th>
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<th>Metric</th>
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Marten habitat research depends heavily on inferences about relationships between habitat variables and marten activity such as home range size (Potvin et al. 2000; Hearn et al. 2010; Cheveau et al. 2013), site use (Porter et al. 2005; Godbout and Ouellet 2010), occurrence (Slauson et al. 2007), or detectability (Mowat 2006). Common methods used to test for relationships include regression and generalized linear models (GLMs). This class of methods can evaluate the effect of a single predictor on a response but can also accommodate large numbers of predictor variables. Testing for relationships is thus very flexible and can generate detailed descriptions of marten responses. The third type of inference commonly used in habitat research is associations. The most common example of this is $X^2$ tests. Like relationships,
associations can evaluate the effects of many variables at a time. However, they utilize categorical, rather than continuous information. Because of this, they cannot estimate the precise value of each category; they can only evaluate if categories are used in greater or lower proportions than expected, based on availability in the landscape.

Genetic and diet research depends less on statistical tests and more on calculation of various measures of genetic diversity (i.e., homozygosity, inbreeding coefficients, genetic distance) and diet complexity (i.e., Levin’s index, Shannon diversity index). These metrics are valuable because they rely on existing formulas and can often be compared to results from other regions, time periods, or studies. Most of these metrics require samples be collected from as many individuals as possible, and are thus dependent on intrusive field methods (i.e., live capture, hunter carcasses), though some less intrusive methods (i.e., scat surveys, hair snares) can be used in certain instances.

Another calculated metric that is often used in marten research is home range size. Home range size is related to other common measures of marten populations; occurrence, abundance, occupancy, and density. Occurrence and occupancy data both utilize presence/absence data to determine characteristics of a species’ distribution in a given area. However, occupancy incorporates detectability – a measure of our ability to observe a species if it is present on the landscape – into its models (MacKenzie 2006; Powell and Gale 2015). This means that occupancy can estimate the probability that unsampled areas contain marten, not just describe which of the surveyed areas had marten. Similarly, abundance and density are both measures of how many individuals occupy an area. Unlike occurrence and occupancy, observations are of known individuals, not just presence/absence data. Density, often calculated with mark-recapture or spatial capture-recapture models, also incorporates an explicit measure of space utilization.
This means that density is a measure of the number of individuals per unit of area, while abundance is a spatially implicit function of the total number of individuals observed (Royle et al. 2014; Powell and Gale 2015). Like occupancy, density incorporates detectability, which means it can be used to estimate density across unsampled portions of the landscape.

Occupancy and capture-recapture models are both relatively new statistical methods. The use of both methods has been increasing since their introduction in the early 2000s, especially in the last few years, suggesting that the utility and interpretability of these models outweighs the additional costs incurred due to survey effort compared to occurrence and abundance (Figure 4). Occupancy rates varied across ecoregions and across study sites within each article. These articles compared occupancy rates within their study sites to determine how much of an effect certain habitat types (Baldwin et al. 2008), season (Zielinski et al. 2015; Clare et al. 2017), or human activity (Slauson et al. 2017; Ivan et al. 2018) had on marten. Population density followed similar patterns to average home range size. The highest densities reported, >1 individual per km², were Ontario and Oregon, where home ranges were the smallest (Thompson et al. 2008; Linnell et al. 2018). The lowest densities reported, < 0.2/km², came from Maine and Quebéc, relatively close to the large home ranges reported in Newfoundland and Labrador (Godbout and Ouellet 2008; Clare et al. 2017), and the Alexander Archipelago in Alaska (Flynn et al. 2009).
1.4 Conclusion

American marten are a species of interest across much of their range. In my review, I categorized research topic, field methodology, and statistical analyses to identify spatiotemporal patterns in recent marten research. By dividing marten range up by ecoregions, it was possible to broadly synthesize consistent patterns in observations driven by the underlying variation across the ecoregions. Research on the species varied by region, topic, and over time.

Though marten research is relatively well distributed, there are a few places that stand out either for being a hotspot of activity, or an area where no research has recently occurred. Hotspots tend to be either around recovering populations (i.e., the Upper Peninsula of MI), or near populations of the recently declared Pacific marten (CA and southeast AK). Major gaps exist in northern and central parts of American marten range. These areas are remote, making
research difficult to conduct. Moreover, marten populations in these regions are considered stable, so research tends to prioritize other species.

Some field methodologies have increased in use over the period reviewed. In the early 2000s, collars were the most common survey method used. Though collar use has remained relatively consistent, camera traps and genetic analysis have increased in popularity over time. This is likely due in part to the increasing affordability of both camera trap systems and genetics work. These largely non-invasive methodologies may continue to increase in popularity as they can produce large volumes of high-quality data with relatively little effort. Camera traps in particular are growing in popularity. Novel methodologies make it possible for researchers to gather individual-level data from the cameras (Sirén et al. 2016b, Clare et al. 2017), and numerous tools have been developed to assist in management of photo data (Young et al. 2018), further increasing the utility of the method.

Regardless of the method used, recent research is dominated by analysis of habitat preferences and requirements, exploring how spatial distribution impacts the species across their full range. Unsurprisingly for such a widely distributed species, marten exhibit some variation in habitat requirements and preferences. Marten are associated with different tree species in different regions of North America, but generally, they prefer coniferous forests. This relationship is not exclusive; marten will utilize other forest types, so long as other habitat requirements are met. Consistently, forest structure, in the form of coarse woody debris availability, height complexity, and canopy closure, is found to be more important than stand age or specific tree associations. This structure provides ample resting sites, access to subnivean space, and protection from predators. In general, this variation has important implications for
understanding geographic variation in marten ecology such as home range size and habitat preferences.

Additional research is needed to better understand marten near the edges of their distribution, where the species continues to expand into parts of their historical range. As evidenced by some of the recent discoveries in places where marten were thought to be extinct, undetected populations may already exist in these areas. Dynamics in these areas are likely to be volatile, as small populations are more vulnerable to stochastic changes in the environment around them. Moreover, understanding the dynamics of recovering populations in one area may better prepare managers for studying their own populations, or considering the potential of a translocation to supplement small populations, or to create new populations.

In under-researched portions of the range, managers may want to consider if new research projects are warranted to update known population statistics. Many of these regions depend on harvest records to monitor marten populations, which have numerous biases and limitations to their utility. It would be valuable to re-survey some of these populations, especially if they have not been surveyed in over two decades, in order to evaluate long-term population trends. Additionally, new methodologies for studying animal occupancy, abundance, space use, and resource selection are currently underutilized across marten range. Many of these methodologies have never been used in the jurisdictions with populations of marten that are considered stable. Establishing baselines would be beneficial both for long-term monitoring and by providing estimates that are comparable across regions.

My own research will use one of these new statistical models, spatial capture-recapture (SCR), to estimate marten densities and determine habitat associations in New Hampshire. I will use the information gained in this review to generate a candidate list of habitat variables to
consider for my own model development. This information will provide context for New Hampshire Fish and Game to make better management decisions for marten research in the Northeast. Additionally, I will also add to the body of literature available to wildlife managers and conservation practitioners across North America that will inform their own decisions, benefiting the species into the future.
CHAPTER 2
MODELING AMERICAN MARTEN DENSITY AND HABITAT ASSOCIATIONS IN NEW HAMPSHIRE

2.1 Introduction

Many mammal species have experienced significant declines in the northeastern United States, reaching population lows in the beginning of the 1900s (Foster et al. 2002). While a range of ecological and anthropogenic drivers have contributed to these declines, the most significant stressors have been landscape change, overharvest, or a combination of the two (Foster et al. 2002). As the 20th century progressed, many species have benefitted from the development of hunting and trapping regulations and the widespread reforestation that occurred following farm abandonment. Species like white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), fisher (*Pekannia pennanti*), and black bear (*Ursus americanus*) have, in recent decades, recolonized large parts of their historic range, and are becoming common ‘backyard and roadside’ species in some areas (Foster et al. 2002). Other species, for example Canada lynx (*Lynx canadensis*) and American marten (*Martes americana*), show signs of recovery yet remain uncommon across much of the region.

Historically, the American marten was found throughout Maine, New Hampshire, New York, Vermont, and western Massachusetts (Figure 5). At their lowest levels in the early 1900s, marten were limited primarily to Maine, with an isolated population in upstate New York and small remnant populations in New Hampshire and Vermont (Clark et al. 1987; Whitaker and Hamilton 1998; Kelly et al. 2009). Currently, their known range encompasses much of Maine, the Adirondack region of New York, northern New Hampshire, including the White Mountain National Forest, northern Vermont, and a recently confirmed population in southern Vermont in
the Green Mountain National Forest (Aylward 2017; O’Brien 2018). This recovery has been
driven by a combination of natural recolonization and human-assisted translocations (Kelly

The recently identified southern Vermont population clearly demonstrates why marten
recovery is difficult to monitor and quantify. While marten were largely thought to be extirpated
in the state by the early 1900s, recent genetic data suggest that this southern population could be
a remnant population supplemented by individuals translocated from Maine and New York
appears an established marten population existed at densities so low it remained undetected for
decades (Aylward 2017). This is perhaps not surprising given that systematic landscape scale
monitoring has not been implemented across the region and that their behavior makes them
notoriously difficult to monitor: marten have relatively large home range sizes for their size,
exist at low population densities, and are elusive and difficult to detect (Gompper et al. 2006;
Monterroso et al. 2014). Combined, these factors make sighting marten a very unlikely event
without dedicated, systematic search methods, especially in areas with low population densities.

In New Hampshire, population indices estimated using opportunistic sightings and
incidental captures, sign surveys, and telemetry of collared individuals suggest that marten
populations are recovering and potentially expanding their range (Kilborn et al. 2009; Sirén et al.
2015). Throughout their range, marten management and conservation depends on robust
estimates of population metrics that evaluate not only distribution but also abundance. (Pollock
et al. 2002; Keiter et al. 2017). To date, there had been no formal statewide, landscape-scale,
assessments of marten density allowing for a robust estimate of population size. Effective marten
management will be dependent on the development of replicable, cost effective survey methods that will result in estimates of both distribution and abundance that can be compared over time.

![Historic and current distribution map of American marten](image)

**Figure 5.** Historic (hatched) and current (blue) distribution of American marten in the northeastern United States and southeastern Canada. Current distribution map adapted from the IUCN Redlist Digital Distribution map for American marten (IUCN 2016). Historic map adapted from Gibilisco (1994), Proulx et al. (2004), and Krohn (2012).

Occupancy surveys can be designed to target multiple species, resulting in a greater breadth of data compared to species-specific density surveys (Burton et al. 2015). However, in many cases, density is the preferred population metric, as it provides spatially explicit estimates of population size that can be compared over space and through time (Royle et al. 2014). The use of spatial capture-recapture (SCR) and similar models is increasing, due to their valuable inferences about ecological processes such as population density, movement, and space use (Royle et al. 2014; Burton et al. 2015).

Although density and occupancy are related, and the relationship is almost exclusively positive (Brown 1984; Gaston et al. 2000), density estimation requires that individuals are
recognizable, and thus generally requires more intensive survey methodologies than occupancy estimation. Numerous researchers have used relatively low-cost occupancy estimates as an index for true density for numerous species, though these indices are often not calibrated with true density estimates for the study area nor tested for sensitivity to changing population sizes, limiting their applicability (Gaston et al. 2000; Jones 2011). Moreover, the relationship is likely to be non-linear, as density is able to increase even after occupancy reaches a maximum of 1 (Clare et al. 2015). Despite the limitations with using occupancy as an index for density, the potential reduction in research costs makes it worth evaluating the relationship for marten in New Hampshire.

Density estimation at large scales was not easily achievable for American marten until Sirén et al. (2016) developed a camera trap design for identifying individual marten using uniquely identifiable chest markings (e.g., by shape, size and, to a degree, color). As a proof-of-concept, Sirén et al. (2016) demonstrated that individual identification of American marten from camera trap imagery was possible. The resulting data could be analyzed using SCR to generate density estimates that can be used to update population baselines and provide a benchmark for future conservation and monitoring efforts in New Hampshire.

Careful deployment of camera traps can result in observations of a single individual at multiple locations as well as repeated visits to the same sites to provide valuable information about space use at the individual scale. SCR models can then be used to estimate detection probabilities and density estimates (Efford 2004; Royle et al. 2018). This camera trap setup was demonstrably efficient and effective at generating individual encounter histories in both the original New Hampshire study and in a separate study conducted using a slightly modified camera trap in Maine (Clare et al. 2017). However, the relatively small scale of the two studies
(~484 and 494km$^2$, respectively) precluded robust inferences about the population status of American marten statewide.

I employed this novel camera trap setup across a much larger portion of New Hampshire, in areas representative of marten habitat across their range in the state. Using spatially varying covariates identified in Chapter 1 (Table 1), I identified factors influencing marten density and generated the first spatially explicit statewide estimate of marten population size. Finally, acknowledging that this large-scale camera trapping effort may not be a sustainable monitoring solution, I investigate occupancy-density relationships by comparing my spatially explicit density estimates with recently developed statewide occupancy estimates (Sirén et al. 2019), and discuss the potential for increasing the efficiency of future monitoring efforts.

### 2.2 Methods

**Study Area**

Camera surveys were conducted across state, federal, and private lands during the winters of 2017 and 2018 (02 Feb to 07 Apr and 22 Jan to 24 Apr, respectively) in the Northeastern Highlands across northern New Hampshire (Coos, Grafton, and Carroll County), USA (Griffith et al. 2009). The region boasts some of the highest points in the eastern United States which are concentrated within the White Mountain National Forest (McNab and Avers 1994; Griffith et al. 2009). The forests are transitional, with boreal spruce-fir forests to the north shifting to deciduous forests to the south (Griffith et al. 2009). Valleys are dominated by hardwood forests of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), mixed with other hardwoods and eastern hemlock (*Tsuga canadensis*). As elevation increases, hardwood forests shift to include balsam fir (*Abies balsamea*), red spruce
(Picea rubens), and other spruce species before transitioning to pure spruce-fir forests. At the highest elevations, forests shift to stunted balsam fir, krummholz, and other alpine communities (Griffith et al. 2009). Climate is variable, with warm summers and cold winters, but evenly distributed precipitation throughout the year (McNab and Avers 1994). Mean annual temperatures vary between 3 and 7°C, with January being the coldest month and July the warmest (McNab and Avers 1994). Annual precipitation varies, from 91 to 178 cm, and snowfall from 244 to 406 cm; both precipitation and snowfall increase locally with elevation (McNab and Avers 1994). Study sites occurred primarily at mid-elevation zones (270 to 1470m) in both unmanaged and commercially managed forests (Figure 6).

**Figure 6.** (Left) Distribution of camera sites across the study area in northern New Hampshire, and (right) general setup of a sampling line. Each line consists of 5-10 2x2km grid blocks, approximately the home range size of an American marten in New Hampshire, connected by snowmobile trails (in white). Three cameras (circles with crosses) were randomly placed within each block a minimum of 300m apart from one another. In both images, the color gradient represents elevation.

**Field Methods**

Camera trap methodology primarily followed Sirén et al. (2016). In short, these methods depend on capturing images of martens’ unique chest markings so that individuals can be
identified without physical capture and marking. To maximize the likelihood that individuals can be identified from images, cameras were set opposite a ramp leading to a platform, above which is a baited board (Figure 7). This setup forces the marten to reach up to the bait, exposing their chest markings (Figure 7).

Figure 7. Three example photographs from the camera traps. In each image, the shape and color of each marten’s unique chest markings are clearly visible, and hence can be used for individual identification. The constructed ramps leading up to a platforms and the baited boards above are also visible.

The sampling frame was defined by dividing the northern three New Hampshire counties into 4km² grid cells, or blocks, approximately the size of a marten home range (Sirén et al. 2016; Figure 6). Any cells that did not contain a snowmobile or hiking trail were removed as they would not be accessible under winter and deep snow conditions. From the remainder, clusters of 5-10 cells connected by trails were selected for sampling, referred to as a trap line. Three cameras were placed a minimum of 300m apart within each selected block, ensuring that multiple cameras were located within a single marten’s home range.

The choice to use snowmobile trails to define the sampling areas was motivated by accessibility, but it is important to acknowledge the potential biases that this may introduce to the data. First, the increased human activity at these sites may result in marten avoidance of these
areas, especially along the larger snowmobile trails. While roads have been found to negatively impact marten movement (Robitaille and Aubry 2000; Howell et al. 2016; Sirén et al. 2017), researchers in California found that off-highway vehicle use did not impact marten occupancy or detectability (Zielinski et al. 2008). Therefore, I felt that proximity to snowmobile trails would not unduly impact my density estimates, especially as cameras were set away from trails (53 ± 42m).

The other potential bias my site selection may have introduced is spatial; it may limit how representative the areas sampled are of the wider landscape. To address these spatial concerns, I ensured that the number of connected blocks was small (5-10) relative to the total number sampled (138) and multiple cameras were placed in each sampled block. The latter point ensures maximal spatial representation within the grid-based design.

Cameras were set on the northern side of a tree, limiting false triggers due to bright light and white-out caused by low-angle sunlight. The bait boards were pre-constructed and carried to the sites, and ramps were constructed from materials available at the site. The boards were baited with an open can of sardines, and a pea-sized amount of commercial skunk lure was applied to the trunk of the tree. In 2017, as per Sirén et al. (2016), cameras were placed 60-80cm from the platform which resulted in poor quality images due to focal length differences between the 2011/2012 and 2017/2018 models of the Bushnell Trophy Cam used in Sirén et al (2016) and this study, respectively (Bushnell Corporation, Overland Park, KS, USA). To correct for this in 2018, and informed by pre-season experimentation, the distance between the camera and platform was increased to 250cm. Camera settings were similar in the two years: cameras were set to take 3 pictures when triggered, with a ten second cooldown between triggers. Due to the limited number of cameras (30 in 2017, 45 in 2018), cameras were deployed using a rotating
schedule to maximize the area surveyed (Sun et al. 2014). Cameras were set for a minimum of 10 days (11.7 ± 1.7) before being moved. In 2017, cameras were re-baited after 5 days, although, after preliminary analysis suggested that rebaiting did not alter detection probability (unpublished data), traps were not rebaited in 2018, which enabled the sampling of more lines.

*Photo Processing*

All photos were compiled and processed using the Microsoft Access database program Colorado Parks and Wildlife Photo Warehouse (CPW: Ivan & Newkirk 2016). The program has the functionality to require a minimum of two independent observers per photo with a final decision required for images with conflicting species or individual identification. For this study, each image was processed by two independent observers from a pool of 25 trained undergraduate students over the two years. Once all images were identified to species level, all images within 30 minutes of each other at a camera were assigned to a single independent cluster, or visit (O’Brien et al. 2003). All marten images were then extracted for the process of individual identification. All images within a visit were used to determine whether an individual chest pattern was identifiable or not, based on angle of the marten relative to the camera and image quality. Identifiable individuals were added to a catalogue of individuals which was used as a reference as visits were processed. The individual identification step involved several rounds of cross-referencing the individual catalogue. This allowed me to eliminate cases where a single individual had multiple names, including situations where the same individuals were observed in both years, or where multiple individuals with similar markings were assigned to a single name despite being separated by an unreasonable distance. A complete description of the protocols for organizing images, species identification, individual identification, and managing multiple observers is provided in Appendix A.
Variable Selection and GIS Data Management

My analysis was focused on explaining spatial variation in marten density, which required spatial representations of factors hypothesized to influence density. Habitat covariates were selected based on hypotheses derived from a literature review (Chapter 1), or were suggested by local experts as being particularly important for the management of marten in New Hampshire (Appendix B). Specifically, I was interested in the effects of aboveground biomass, forest type, snow conditions, canopy characteristics, and ruggedness of the terrain on marten density. For a complete list of all variables that were initially considered, see Appendix C.

Biomass is an established proxy for forest age (McGarigal et al. 2017). Marten are often associated with older, more developed forest stands, as these forests provide them with a variety of habitat and food resources (Buskirk and Powell 1994; Sirén et al. 2015). However, tree species grow and accumulate biomass at different rates over time (Teck and Hilt 1991). Thus, stands of different forest types of similar ages may have very different biomass values. To account for this variability, I generated forest type-specific biomass layers, allowing me to evaluate the impact of biomass while controlling for forest type. These layers were calculated using the biomass layer and a reclassified version of the Designing Sustainable Landscapes project’s landscape layer, Subsysland (Subsys; Appendix D; McGarigal et al. 2020).

The forest type-specific biomass layers were created by overlaying biomass with each of the three forest types (Figure 8). This allowed me to treat these combined habitat-biomass layers as a single continuous variable, rather than needing to include two separate variables in each model. It is worth noting that boreal biomass and hardwood biomass are inversely related to one another in the region. As marten are associated with coniferous species across much of their range, though mixed forest types may gain importance in eastern forests, I focused on the boreal
variable for my analyses (Thompson et al. 2012). I expect marten densities to increase with boreal biomass, but acknowledge that there is possibly an optimal biomass level beyond which densities may again decrease.

Figure 8. Process for creating forest type-specific biomass layers. The continuous biomass layer (a) is overlaid with binary forest layers (b). This results in separate continuous biomass layers for each forest type (c).

Marten are well adapted for snowy conditions, with low foot load ratios relative to their body size, and make extensive use of subnivean space for resting and foraging (Krohn et al. 1995; Krohn et al. 2004). Snow conditions may also mediate interactions between marten and their primary competitor, fisher, resulting in marten being associated with deeper snows where the two species co-occur (Krohn et al. 1995; Sirén and Morelli 2019). As fisher are widely present across the New Hampshire landscape, I expect marten will be associated with snowier locations.

Forests with greater canopy closure may be better habitat for marten. Risk of aerial predation is elevated in open forests, resulting in avoidance of these areas (Clark et al. 1987; Ruggiero et al. 1994). Though different thresholds have been reported, general consensus is that as canopy closure increases, so too does habitat quality (Bowman and Robitaille 1997; Zielinski et al. 2001; Smith and Schafer 2002; Poole et al. 2004). Marten densities will likely increase with canopy closure in my study.
The final variable being considered, terrain ruggedness, can provide protected denning and resting sites for marten (Bull and Heater 2000; Shelley 2008). I quantified ruggedness using the Vector Ruggedness Measure (VRM, Sappington et al. 2007). Similar to biomass, I expect that there is an optimal ruggedness level; below the optimum, the terrain becomes increasingly uniform and may eventually provide no additional resting sites, while above the optimum, the terrain is increasingly rough until it becomes cliff-like and impassable.

All of these predictor variables were accessible from publicly available GIS data layers. Some variables required combining data from multiple political jurisdictions into a single layer in order to encompass the entire area of interest, or were derived from the publicly available layers (Appendix C). If necessary, layers were resampled to ensure all layers were at a 30x30m resolution. GIS data were processed both in ArcMap (Esri Inc. 2015) and R (R Core Team 2019). For a full workflow of all spatial data processing, see Appendix E.

Once all derived covariate layers were generated, a spatial smooth was applied so that each 30m x 30m pixel value represented a spatial average of the surrounding area defined by a Gaussian kernel with a scale parameter of 590m, which translates to an area of 4.235 km², an approximation of a marten home range size. These smoothed layers were then z-transformed to reduce computation times for the models.

Data Analysis

Spatial capture-recapture (SCR) methods extend traditional capture-recapture methods to include a spatially explicit encounter model that addresses the potential biases from individuals located closer to detectors being more likely to be detected. Estimates of the parameters of the spatial encounter model are based on the pattern and frequency of spatial recaptures (Royle et al.
The ability to estimate the spatial scale over which detection is likely means that the effective area sampled by a set of detection devices is explicit and absolute density can be estimated. Thus, SCR simultaneously produces estimates of detectability, the scale of detectability (and hence space use), and of most interest, spatially explicit estimates of density.

In SCR models, individuals are represented by their activity centers, analogous to a home range. These activity centers are assumed to be either distributed across the landscape uniformly, or according to a spatially varying intensity function if using spatial covariates. These activity centers are unobserved latent variables that are estimated based on the spatial pattern of detections. The area within which activity centers are assumed to occur is referred to as the state space ($S$), and should be a buffered area around the traps that is large enough to include the activity centers of all individuals that have a non-zero probability of detection. I use a discrete representation of $S$, defined as a grid of points which represent the centroids of each 250 x 250m pixel that is within a 4km buffer of a camera. Given the differences in sampling effort between years, this resulted in a state space consisting of 11055 and 23903 points in 2017 and 2018, respectively. The inferential objective is to use the encounter history data to estimate the point-specific density which can be modeled as a function of habitat covariates. For example, in my case, where I am interested in testing for the influence of boreal biomass ($\text{Biom}$), snow depth ($\text{Dpth}$), canopy closure ($\text{Clsr}$), and terrain ruggedness ($\text{VRM}$) on spatial variation in marten density, I have the following log-linear model:

$$\log(d(s_i)) = \beta_0 + \beta_1 \text{Year} + \beta_2 \text{Biom}_i + \beta_3 \text{Biom}_i^2 + \beta_4 \text{Dpth}_i + \beta_5 \text{Clsr}_i + \beta_6 \text{VRM}_i + \beta_7 \text{VRM}_i^2$$

where $d(s_i)$ is the density at pixel $i$, $\beta_0$ is the intercept and $\beta_1:7$ are the regression coefficients relating density to the spatial covariates which are to be estimated. I note that I include a year effect to allow for any variation between years. As marten density may either increase linearly or
maximize at certain habitat values, I included squared terms to accommodate expected quadratic responses for biomass and VRM.

The detections of individual $i$ at trap $j$ during occasion $k$ ($y_{ijk}$) are assumed to be Bernoulli random variables with success probability $p_{ijk}$:

$$y_{ijk} \sim \text{Bernoulli}(p_{ijk})$$

The probability $p_{ijk}$ is itself a declining function of the distance between an individual’s activity center ($s_i$) and a trap location ($x_j$). Here I apply the half-normal encounter model to describe the detection probability:

$$\logit(p_{ijk}) = p_0 \exp(-\text{dist}(x_j, s_i)^2 / 2\sigma^2)$$

where $p_0$ is the baseline detection probability, or the probability of detection when a trap is located precisely at an individual’s activity center, $\sigma$ describes the distance from the activity center over which the probability of detection decreases, and $\text{dist}(x_j, s_i)$ is the distance between a trap location and an individual’s activity center. The probability of detecting an individual is a function of individual, trap, or occasion-specific covariates. In my case, I am interested in the effects of individual-specific learned trap behavior ($b_i$), trap-specific variable fisher presence ($\text{Fish}_j$), and trap-by-occasion-specific variables snow depth and Julian day ($\text{JDay}_j$) on detectability such that I have the following logit model:

$$\logit(p_{0ijk}) = \alpha_0 + \alpha_1 \text{Year}_j + \alpha_2 b_i + \alpha_3 \text{Fish}_j + \alpha_4 \text{Dpth}_k + \alpha_5 \text{JDay}_{jk} + \alpha_6 \text{JDay}_{jk}^2$$

Once again, I note that I include a year effect to allow for variation in base detection rates between years, and a quadratic response for Julian day to reflect changes in marten detectability over the course of the trapping season.
In total, I was interested in quantifying the effects of 5 covariates on density, 5 on baseline detection, and 2 on space use (Table 9). Considering all combinations of parameters resulted in a total of 46 encounter models and 72 density models. Using the sequential approach described by Morin et al. (2020), I evaluated all detection models \((p_0\) and sigma, the observation process) using the fully parameterized density model (the state process) shown above. Once the most supported detection model was identified, it was carried over and used while comparing density models.

I analyzed the SCR data using the R package oSCR (Sutherland et al. 2018) and used AIC to rank and compare models (Akaike 1974). Model selection was conducted using the principle of parameter redundancy described by Arnold (2010). Once the top model was selected, I could use the calculated covariate coefficients \((\alpha\) and \(\beta\) values) to predict total marten abundance for the entire state. This predictive layer could then be cropped to investigate smaller regions of interest, such as the area actively surveyed by the cameras, or state space, and the northern three counties of New Hampshire.

### Table 9. List of the variables included for consideration for each SCR model component and their abbreviations.

<table>
<thead>
<tr>
<th>Density ((d))</th>
<th>Baseline detection ((p_0))</th>
<th>Space use ((\sigma))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field season (Year)</td>
<td>Field season (Year)</td>
<td>Null</td>
</tr>
<tr>
<td>Boreal biomass (Biom)</td>
<td>Behavior (b)</td>
<td>Field season (Year)</td>
</tr>
<tr>
<td>Boreal biomass(^2) (Biom2)</td>
<td>Fisher presence (Fisher)</td>
<td></td>
</tr>
<tr>
<td>Snow depth (Dpth)</td>
<td>Snow depth (Dpth)</td>
<td></td>
</tr>
<tr>
<td>Canopy closure (Clsr)</td>
<td>Julian day (JDay)</td>
<td></td>
</tr>
<tr>
<td>VRM (VRM)</td>
<td>Julian day(^2) (JDay2)</td>
<td></td>
</tr>
<tr>
<td>VRM(^2) (VRM2)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Comparison of SCR and Occupancy Models**

Concurrent with my camera trapping study, Sirén et al. conducted an independent landscape-scale camera trapping initiative was conducted that focused on evaluating abiotic and
biotic factors influencing occupancy rates of carnivores in New Hampshire, including the American marten. Sirén et al. (2019) have produced spatially explicit estimates of species-specific occupancy that coincide spatially and temporally with the density estimates produce in this study. This provides a unique opportunity to explicitly investigate the marten occupancy-density relationship using independent data sources. Of note, both studies investigated similar covariates at the same spatial scale of influence (i.e., the smoothing scale, $\sigma = 592.4$ m). In their study, Sirén et al (2019) found that marten occupancy was positively related to snow depth and boreal biomass, with an additional year effect for each season sampled (Table 10).

<table>
<thead>
<tr>
<th>Occupancy covariate</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept(2014)</td>
<td>-0.507</td>
<td>0.424</td>
</tr>
<tr>
<td>Year2015</td>
<td>-0.25</td>
<td>0.583</td>
</tr>
<tr>
<td>Year2016</td>
<td>-1.158</td>
<td>0.594</td>
</tr>
<tr>
<td>Year2017</td>
<td>-0.12</td>
<td>0.574</td>
</tr>
<tr>
<td>Year2018</td>
<td>-1.084</td>
<td>0.501</td>
</tr>
<tr>
<td>Year2019</td>
<td>-0.427</td>
<td>0.489</td>
</tr>
<tr>
<td>Maximum snow depth:</td>
<td>1.612</td>
<td>0.202</td>
</tr>
<tr>
<td>Boreal forest biomass:</td>
<td>0.425</td>
<td>0.145</td>
</tr>
</tbody>
</table>

While a formal analysis of the occupancy-density relationship was not the primary objective of this chapter, it is of great interest to the New Hampshire Fish and Game Department (NHFG), who are responsible for managing and monitoring marten in New Hampshire, as it will provide important guidance when evaluating an information-effort trade-off for developing future monitoring strategies. As such, I provide a descriptive assessment of the marten occupancy-density relationship. First, using the model of Sirén et al (2019), I computed the expected occupancy over the state of New Hampshire at the 2x2km scale, the approximate size of a typical marten home range. Then, using the most supported model from the SCR analysis
(see above), I computed the expected density for the same 2x2km grid summing the predictions of abundance of the associated 250m x 250m pixels from the SCR analysis. The resulting occupancy and density estimates were summarized by their respective 10% centile brackets (mean and standard error) in order to evaluate whether occupancy is an adequate predictor of density.

2.3 Results

**Camera data**

The camera trapping effort resulted in 4393 trap nights across both years and more than 46000 images of American marten (see Table 11 for a breakdown by year). Marten were detected more frequently in the 2017 season than in 2018 (107236 vs 90174 images respectively), despite fewer 2017 trap nights (1556 and 2837, respectively, Table 11). Although there were more images in 2017, there were more independent visits in 2018. Of the 768 independent visits across both years, individual identification was made in 525. Identification rates averaged 68%: 80% in 2017, and 62% in 2018. They resulted in a total of 116 individuals: 37 in 2017 and 82 in 2018 (Appendix F). Of the 116 individuals observed, most individuals were captured at a single site (n = 80; 69%), 22 (19%) were captured at 2 sites, 12 (10%) at 3 sites, and a single individual at 4 and 5 sites. Most individuals were captured fewer than 5 times (n = 77; 66%); a majority of these were observed only once (n = 29; 25%). Relatively few individuals were observed on 10 or more independent visits (n = 13; 11%); one individual was captured in 28 separate visits at three sites over the course of 8 days.
Table 11. Summary of camera trap survey results from the two winters surveyed. Surveys effort was divided by trap lines, a set of adjacent 2x2km blocks connected by snowmobile trails. Each block contained 3 cameras placed at least 300m apart from one another.

<table>
<thead>
<tr>
<th></th>
<th>2017</th>
<th>2018</th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of lines surveyed</td>
<td>5</td>
<td>12</td>
<td>17</td>
</tr>
<tr>
<td>No. of blocks surveyed</td>
<td>50</td>
<td>88</td>
<td>138</td>
</tr>
<tr>
<td>No. of camera sites</td>
<td>150</td>
<td>260</td>
<td>410</td>
</tr>
<tr>
<td>Average days deployed</td>
<td>10.4</td>
<td>10.9</td>
<td>10.7</td>
</tr>
<tr>
<td>Total trap nights</td>
<td>1556</td>
<td>2837</td>
<td>4393</td>
</tr>
<tr>
<td>Total images</td>
<td>107236</td>
<td>90176</td>
<td>197412</td>
</tr>
<tr>
<td>No. of species</td>
<td>17</td>
<td>29</td>
<td>30</td>
</tr>
<tr>
<td>Total marten images</td>
<td>37334</td>
<td>9482</td>
<td>46816</td>
</tr>
<tr>
<td>Average visit length (min)</td>
<td>14.87</td>
<td>6.49</td>
<td>9.64</td>
</tr>
<tr>
<td>No. of independent marten visits</td>
<td>290</td>
<td>478</td>
<td>768</td>
</tr>
<tr>
<td>No. visits with known individual</td>
<td>231</td>
<td>294</td>
<td>525</td>
</tr>
<tr>
<td>No. visits with unknown individual</td>
<td>59</td>
<td>184</td>
<td>243</td>
</tr>
<tr>
<td>Identification rate</td>
<td>79.7%</td>
<td>61.5%</td>
<td>68.3%</td>
</tr>
<tr>
<td>No. of individuals</td>
<td>37</td>
<td>82</td>
<td>116*</td>
</tr>
<tr>
<td>Average visits per individual</td>
<td>6.24</td>
<td>3.59</td>
<td>4.41</td>
</tr>
<tr>
<td>No. individuals with &gt; 1 visit</td>
<td>33</td>
<td>57</td>
<td>88*</td>
</tr>
<tr>
<td>No. individuals at &gt; 1 location</td>
<td>18</td>
<td>20</td>
<td>36*</td>
</tr>
</tbody>
</table>

*Three individuals were captured in both years, so the sum of 2017 and 2018 does not equal the total.

**SCR analysis – selecting the encounter model**

Considering all combinations of effects on $\sigma$ and $p_0$ resulted in 46 possible encounter models, which I compared using AIC using the fully specified density model (see equation above) (Appendix G). The greatest support was for models that allowed for between-year variation in baseline detection but assumed space use ($\sigma$) to be constant across years (Table 12).
While there are models within 2 AIC units of this AIC-top model, using the principle of parameter redundancy (Arnold 2010; Leroux 2019) I can conclude that all other terms are uninformative factors. More specifically, when comparing one model to another with one additional term, if the more complex model does not have a lower AIC after the penalization for additional model complexity, that additional parameter is considered to be redundant, or uninformative. Indeed, this is the case for the effects of sampling day, fisher presence, and snow depth (Table 12). Therefore, the encounter model structure that includes year-specific \( p_0 \) and constant \( \sigma \) are used in the second modeling stage where I test hypotheses about spatial variation in density.

### Table 12. Top performing (<10 ΔAIC) detection models. These models held density constant at the full parameterization (Year + Biom + Biom\(^2\) + Dpth + Clsr + VRM + VRM\(^2\)), while varying the two detection parameters, baseline detection and space use. Here I report the 23 models with the null model for sigma given there was no support for the year effect on sigma.

<table>
<thead>
<tr>
<th>Density ((d))</th>
<th>Baseline detection ((p))</th>
<th>Space use ((\sigma))</th>
<th>logL</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>~full</td>
<td>~b + Year</td>
<td>~1</td>
<td>1229.91</td>
<td>12</td>
<td>2483.82</td>
<td>0</td>
</tr>
<tr>
<td>~full</td>
<td>~b + Year + JDay + JDay(^2)</td>
<td>~1</td>
<td>1228.22</td>
<td>14</td>
<td>2484.44</td>
<td>0.62</td>
</tr>
<tr>
<td>~full</td>
<td>~b + Year + JDay</td>
<td>~1</td>
<td>1229.24</td>
<td>13</td>
<td>2484.48</td>
<td>0.66</td>
</tr>
<tr>
<td>~full</td>
<td>~b + Dpth + Year</td>
<td>~1</td>
<td>1229.25</td>
<td>13</td>
<td>2484.51</td>
<td>0.69</td>
</tr>
<tr>
<td>~full</td>
<td>~b + Year + Fisher</td>
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SCR analysis – modeling variation in detection and density

Considering all combinations of the 5 habitat covariates results in a total of 72 density models which, using the top encounter model above, I compared using AIC (Appendix G). Again, based on the principle of parameter redundancy (Arnold 2010), I ended up with a single top supported model, i.e., all models with lower AIC models were either more complex models with uninformative parameters or simpler models with less support (Table 13; Leroux 2019).

The top encounter model indicated that marten exhibited a strong positive behavioral response ($\alpha_2 = 2.614$, se = 0.217), meaning that individuals were more likely to be detected after their initial detection. This translates to a near tenfold increase in encounter rate (Table 14).

Detection was higher in 2017 than in 2018 ($\alpha_1 = -0.520$, se = 0.218, Table 14). The space use parameter, which was assumed to be constant across years, was $\sigma = 872$ m (CI: 754-1009). Using a conversion ($HR_{95} = \pi (\sqrt{5.99 * \sigma})^2$), this translates to an estimate of the 95% home range area at 14.32 km$^2$.

The most supported model, based on AIC model comparisons, included the effect of year, snow depth, a quadratic effect of boreal biomass, and canopy closure (Table 13). Density was higher in 2018 than in 2017 ($\beta_1 = 0.471$, se = 0.254), and within the state space was 0.16 (CI: 0.09-0.28) and 0.26 (CI: 0.15-0.46) marten per km$^2$ in 2017 and 2018, respectively. Statewide density was 0.05 (CI: 0.02-0.13) and 0.09 (CI: 0.04-0.19) for 2017 and 2018, respectively. Support for the quadratic effect of boreal biomass shows that density is highest at intermediate
values of boreal biomass \( \beta_2 = 0.713, \text{ se } = 0.332 \) and \( \beta_3 = -0.214, \text{ se } = 0.108 \) Figure 9a). Density was positively associated with snow depth \( \beta_4 = 0.242, \text{ se } = 0.154 \), Figure 9b) and canopy closure \( \beta_5 = 1.350, \text{ se } = 0.340 \), Figure 9c).

I use the modeled relationships between density and spatial covariates to generate statewide density predictions for each year (Figure 10) that can be used to visualize variation in density according to the most supported model. Moreover, I can use these predictions to generate the first robust statewide estimate of marten population size for New Hampshire. The resulting estimates of abundance within the camera trapping study area, generated by summing expected pixel densities across the state space is 112 (CI: 65-193) and 390 (CI: 228-681) for 2017 and 2018, respectively. If we extrapolate abundance over the entire state, predictions were 1286 (CI: 583 - 3048) and 2061 (CI: 1020 - 4477) for 2017 and 2018, respectively.
Table 13. Top performing (<5 ΔAIC) density models. These models held base detection and space use at the top model derived above, while density was allowed to vary.

<table>
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Figure 9. Effect of (a) biomass, (b) snow depth, and (c) canopy closure on marten densities. In each case, one habitat variable was allowed to vary while the other two were held constant at their mean values. The x-axis represents the range of values which sampling occurred. Ribbons around each line represent the 95% confidence interval.
The best supported occupancy model included the effects of boreal biomass and snow depth. My analysis identified similar covariates as being important for explaining density, though there were some notable differences between the two models. Boreal biomass and snow depth positively influenced both occupancy and density. However, density was further influenced by the quadratic term for boreal biomass and canopy closure. The quadratic term was not found to
influence occupancy. The final variable in the top density model, canopy closure, was not considered in the occupancy model.

To account for this, I also compared the occupancy model to a like-for-like density model, referred to as the “matched” model, such that the two models contained the same covariates (Table 15). While this model is not the best fitting density model, it would potentially allow me to evaluate how much of the model noise from the top model comparison was due to the mismatch in tested variables, rather than the actual relationship between occupancy and density. I repeated the comparison steps described above using the matched, rather than the top, density model. Because the effect of year was additive in both the occupancy and SCR models, I used a single year (2017) of statewide model predictions for the comparison of the occupancy and density models. Generally, while the models identified similar areas for having high marten occupancy or density, especially the White Mountain National Forest, the locations where the highest values are concentrated varies from model to model (Figure 11).

Comparing the top occupancy and density models, there is a strong positive relationship \( (r = 0.76) \), but there is a lot of variation around that relationship as well (Figure 12a). In contrast, the matched model shows a stronger correlation \( (r = 0.85) \), with less variability but a much shallower slope, suggesting that variability in occupancy doesn’t correspond to associated changes in density (Figure 12b). In order to better understand how the density models differ across the range of expected occupancy values, and hence where the occupancy-density relationship may be incorrectly specified using the matched comparison, I calculated the relative differences in density between the top and matched models \( \left( \frac{\text{matched density} - \text{top density}}{\text{top density}} \right) \) at each of the occupancy centiles (Figure 12c). In general, the matched model produces positively biased
density estimates when occupancy is below 0.5, and negatively biased density estimates at higher occupancy (here bias is relative to the most supported model). Though the matched model is positively biased almost as frequently as it is negatively biased, there is much greater range of values to the positive bias. In other words, when the matched model underestimates density, it tends to underestimate by only a small percentage, up to 50%; when the matched model overestimates density, the range of values is much higher, exceeding 300%. This relationship arises from the shallower slope of the occupancy-density relationship for the matched model, which also has lower variance because it ignores significant spatial variation in density (e.g., variation related to the non-linear boreal biomass effect and the additional canopy cover effect), and also because it shares the same model structure resulting in correlated expected values.

| Table 15. Parameter estimates for the habitat variables in the top occupancy model, top SCR model, and the matched SCR model. |
|-----------------|-----------------|-----------------|
|                | Occupancy$^1$   | Density – top model$^2$ | Density - same model structure$^3$
| Year           | -1.084          | 0.471           | 0.648          |
| Boreal Biomass | 1.612           | 0.713           | 0.192           |
| Boreal Biomass$^2$ | -              | -0.214          | -              |
| Snow Depth     | 0.425           | 0.242           | 0.273           |
| Canopy Closure | na$^*$          | 1.350           | -              |

$^*$Canopy closure was not a candidate variable considered for the occupancy model.

$^1\Psi \sim Year + BorealBiom + Depth$

$^2D \sim Year + BorealBiom + BorealBiom$^2 + SnowDepth + CanopyClosure

$^3D \sim Year + BorealBiom + Depth$
Figure 11. Maps showing the predicted marten (a) occupancy, (b) density based on the top model, and (c) density based on the matched model (i.e., with the same covariate structure as the occupancy model) for the three northernmost counties in New Hampshire. All three maps are of the 2017 predictions, and at a 2x2km resolution.

Figure 12. Evaluation of the relationship between the occupancy model and the two density models. From left to right, the plots show (a) the relationship between occupancy and the top density model, (b) the relationship between occupancy and the matched density model (i.e., with the same covariate structure as the occupancy model), and (c) showing how the two density models differ from one another over the range of occupancy values. For each plot, the data are summarized into 10% percentiles, thus the blue points represent the central tendency (a, b = mean; c = median) for that segment, the horizontal bars the confidence interval around the occupancy values, and the verticals bars the confidence interval around the density values.
2.4 Discussion

In this chapter, I combined a landscape scale camera trapping effort, using a camera trap design for identifying individual American marten, with well-established statistical methods for population density estimation. I showed how such an approach provides important information about drivers of spatial variation in marten density and provide the first estimate of New Hampshire abundance. Working closely with project partners, I set out to test hypotheses about how both the manageable components of northern forests (i.e., boreal biomass and canopy structure) and environmental characteristics (i.e., snow depth) structure density across space.

Inference about marten spatial ecology

I found that density was positively associated with canopy closure and snow depth, exhibited a non-linear (peaked) response to boreal biomass, and was higher in 2018 than in 2017. The effect of canopy closure is striking with density remaining near 0 until canopy closure reaches about 60%, beyond which density increases exponentially (Figure 9c). This apparent threshold is consistent with previous work in both the western United States (Zielinski et al. 2001), where marten detection rates were highest in dense (60-100% closure) areas, and eastern Canada (Bowman and Robitaille 1997), where average canopy closure at utilized sites was near 80%. My results, therefore, support the hypothesis that marten avoid forest openings as a predator avoidance strategy (Ruggiero et al. 1994).

Snow depth also positively impacted density, although the effect size was not as large as for canopy cover (Figure 9b). Indeed, this relationship was expected given that marten are a snow-adapted species, with numerous behavioral and physiological adaptations for snowy conditions. Similar linear relationships between snow depth and occupancy have been observed in Alaska (Pozzanghera et al. 2016) and the Adirondacks (Gompper et al. 2016). The consistency
of this relationship across marten range, regardless of realized range of depths evaluated in each study, suggests that other factors may be influencing the relationship between marten and snow. Numerous authors have noted that other snow metrics, such as compaction and crust development, seem to influence marten movement patterns (Raine 1983; Sirén et al. 2017) and occupancy (Pozzanghera et al. 2016). This influence is often attributed to intraguild competition, especially with fisher; it is generally hypothesized that fisher outcompete marten, but cannot forage as efficiently in fluffy snow (Krohn et al. 1995; Fisher et al. 2013; Gompper et al. 2016; Manlick et al. 2017; Zielinski et al. 2017). My results show additional support for the expectation that marten thrive in areas in deeper snow; however, the presence of a strong fisher population across southern regions in the state may be excluding them from areas where snow conditions are otherwise suitable (Sirén and Morelli 2019).

Density peaked when boreal biomass reached intermediate levels, around 80 Mg/hectare (Figure 9a). Boreal forests around this value of biomass are generally mid-successional, dominated by a mixture of pole-sized to small saw timber. Thus, my results are not consistent with existing literature that describes marten as an old forest specialist (Buskirk and Powell 1994; Ruggiero et al. 1994). However, it is consistent with a growing body of evidence that suggests that forest age is less important than stand structure. Research in British Columbia (Poole et al. 2004), Maine (Payer and Harrison 2004), Ontario (Bowman and Robitaille 1997), Québec (Potvin et al. 2000), and Wisconsin (McCann et al. 2014) suggests that structure, especially in terms of horizontal complexity such as coarse woody debris availability, is a greater driver of marten activity than stand age. Though I did not directly measure stand structure, my results suggest that marten are associated with more structurally complex forests in New Hampshire; this includes both mid-successional forests, which contain greater amounts of coarse
woody debris than old growth (Sturtevant et al. 1997), and higher-elevation boreal forests, which tend to be older and structurally complex but are shorter (and thus have less overall biomass) due to stunting caused by exposure (Anderson et al. 2013).

As expected, marten displayed a learned behavioral response to the traps that increased their detectability, commonly referred to as “trap-happiness.” Though the effect of baited traps has long been considered a potential source of bias in data collection, the value of increased detectability and repeated captures outweighs the potential alteration of individual behavior and movement (Stewart et al. 2019). This is especially true for models, like SCR, where the interest is in determining the presence of individuals on the landscape, not fine-scale individual movement. The risk is likely further limited in species, like marten, that display strong territorial behaviors that would prevent individuals from foraging far outside of their home range.

**Year effects**

Though camera trapping effort was higher in 2018 (i.e., more cameras in wider spatial coverage), this did not result in a greater total number of images, nor total number of individual marten identified. Additionally, visit duration decreased in 2018, reducing my ability to positively identify the individuals observed. This change in visitation rate between the years therefore resulted in an expected difference in the estimated SCR detection rate: detection was higher in 2017. However, I also found a year effect on density, such that density was higher in 2018.

To understand this seemingly contradictory pattern, where increased effort did not result in additional observations, it is necessary to look at ecological processes that underlay this pattern. The 2017 field season followed a typical summer, but the 2018 season came after a mast
year for cone species and mountain ash. Marten can directly benefit from mast production, especially beech nuts and soft mast, as they are a supplemental food source (Jensen et al. 2012). Moreover, small mammal prey species can respond rapidly to mast production, with populations responding functionally by altering their use of space and distribution (Hallworth et al. in preparation). Moreover, Conrad and Reitsma (2015) found that numerical responses in small mammal populations could be observed in the spring following a mast year; this could indicate that reproduction is higher during the mast season, or survival is higher in the winter following the mast, resulting in more available small mammal prey during my trapping season.

Marten may also respond immediately to the increased prey availability following a mast year by reducing their home range size and foraging patterns (i.e., functionally, Jensen et al. 2018). As they do not need to search as intensively for food, their search time and radius will likely decrease, which in turn will decrease their likelihood of encountering a camera trap. Moreover, the greater availability of resources may reduce the attractiveness of the camera bait, thus reducing the amount of time marten were willing to spend at a trap attempting to extract bait (Jakubas et al. 2005).

Masting cycles offer an intuitive explanation for why detection was higher during the 2017 season. As the 2018 season followed a mast year, marten likely were responding to increased availability of food resources. The response we observed did not seem to include decreasing home range size, as $\sigma$ was constant across the two years. Thus, the reason for the decreased detectability in 2017 can likely be attributed to these alterations in foraging patterns and decreased attractiveness of the bait, as the marten were already sated.

The influence of masting cycles on marten density is less straightforward. In 2018, total density was higher than in 2017 (0.26 individuals/km, compared to 0.16), representing a 62%
increase between years. Marten populations are known to fluctuate in response to prey availability, sometimes wildly (Weckwerth and Hawley 1962; Thompson and Colgan 1987; Jensen et al. 2012). However, these numerical responses are delayed such that marten population increases occur a year after prey populations increase, a common pattern in predator-prey relationships. Thus, it is unlikely that the higher marten populations values from 2018 are solely driven by processes associated with masting cycles.

There is the possibility that the increase in estimates of density between the two years is an artifact of the changes in sampling methodology and distribution. My decision to not re-bait cameras partway through their deployment was motivated by data that suggested that this had no effect on the number of individuals observed, thus I do not expect that rebaiting had an effect on estimates of abundance and density. Sirén et al. (2016) found that the length of time between rebaits did influence their ability to identify individuals, which my results corroborated, but again, this should not have affected my estimates.

This leaves the increased survey effort as the only remaining explanation for some (or all) of the differences in density. If the additional sites surveyed in 2018 represented higher quality marten habitat than those surveyed in 2017, I would expect average density in the study area to increase. This was likely the case here as the bulk of the new sites occurred in the White Mountain National Forest, which I have previously established represent high quality marten habitat. This is further corroborated when considering only sites that were surveyed in both years; when I re-ran the top density model using only these data, average density for the two years was practically identical (2017 = 0.14, CI: 0.06-0.38; 2018 = 0.15, CI: 0.07-0.43). This illustrates the importance of representative sampling in SCR models, and underscores the need to carefully consider the study area that should be sampled, especially if the intent is to produce
comparable estimates of density. It also raises the question about whether there is spatial variation in the associations between habitat structure and marten density as well as variation in density itself (e.g., density dependence, or divergent local adaptations). For example, is the density-habitat relationship the same in the White Mountain National Forest and the private northern forests, which have different management histories and habitat distributions?

Absence of data on sex

Though I accounted for changes in detectability caused by individual behavioral response, I did not account for variation due to differences in space use between sexes. As is common across many sexually dimorphic species, marten males defend home ranges significantly larger than females do (Clark et al. 1987; Ruggiero et al. 1994). As a result of these larger ranges, male movements, and hence space use, tend to be larger, which has been shown to be important for density estimation (Sollmann et al. 2011).

Unfortunately, sexing martens visually is extremely difficult, although not impossible. For example, Sirén et al. (2016) used front foot size in relation to camera trap footholds of known (collared) individuals to identify sex of 5 individuals. However, small sample sizes, coupled with known overlap between male and female marten size distributions (Clark et al. 1987) and the difficulty of sexing juvenile individuals (Sirén et al. 2016) meant I did not use this approach.

Within the SCR model, inclusion of sex results in a separate estimate of baseline detection ($p$) and space use ($\sigma$). Exclusion of these variables results in a single estimate of $p$ and $\sigma$, which will fall somewhere between the true sex-specific values. The direction of the bias will be impacted by the ratio of captured males to females. For example, if males (the group with larger home ranges) make up a disproportionate amount of the captures, density estimates will
undervalue the true state of the population. If the sex ratio of the sample is proportional to the sex ratio of the population, then density estimates should be generally unbiased.

Generally, live capture of marten is biased towards males, a result of their increased spatial use, though seasonality, underlying population structure, and trapping pressures can affect encounter rates (Ruggiero et al. 1994; Royle et al. 2006; Belant 2007). If my camera traps followed the general trend and were biased towards males or juveniles, then my estimates of abundance and density would be a conservative representation of the New Hampshire marten population. However, Sirén et al. (2016) observed nearly equal captures of males and females in their camera trap study, suggesting that the traps do not disproportionately sample certain groups. As I surveyed using the same methodology during a similar season in a geographically similar area, it is plausible that my capture rates also were also evenly distributed amongst the sexes. Additionally, my estimate of sigma ($\sigma = 872 \text{m}$) was consistent with Sirén et al. (2016; 790-1173m, sex not differentiated) and Linden et al. (2018; 468-932m, sex differentiated), further supporting the hypothesis that my cameras sampled in proportion to the marten population. Ultimately, this suggests that not including sex information, which was not available, is unlikely to have resulted in biased estimates of abundance and density.

*Comparisons with previous estimates*

Reported densities across the full marten range are highly variable, but my results (2017: 0.16 and 2018: 0.26) tend to fall on the lower end of the distribution of values (*Chapter 1*, Table 1). It is important to note, however, that many of these other studies utilize abundance-based density estimates (i.e., converted to density using an arbitrarily defined spatial extent), rather than estimated from spatially-explicit models of density (e.g., SCR), and are thus prone to biases and are not directly comparable to my estimates (Powell and Gale 2015). Nonetheless, it is
interesting to note that many of the highest derived estimates of marten density from across the marten range come from interior parts of marten distribution. In contrast, New Hampshire represents the southern range limit for marten; the general expectation is that individuals near range limits often exhibit differential habitat use and selection compared to individuals in the core of the range, and densities at the range edge are lower than in the core (Brown 1984; Gaston et al. 2000; Pironon et al. 2017). Moreover, interactions between biotic and abiotic limitations can further impact a species’ attempts to expand their range even when suitable habitat is available (Sirén and Morelli 2019). As a result, marten near the range limit may select less ideal habitat, resulting in larger required home ranges and lower population densities.

If only the spatially-explicit estimates from other areas are considered, average density estimates in New Hampshire were similar to those reported in California (0.07-0.33: Slauson et al. 2017) and Maine (0.08-0.34: Clare et al. 2017; 2019), much lower than in Oregon (1.13: Linnell et al. 2018), and lower than previously reported in New Hampshire (0.43-0.6: Sirén et al. 2016; 0.39-0.43: Linden et al. 2018). Interestingly, the populations studied in California are also near the southern range limit, so they may be exhibiting a similar response as marten in New Hampshire. Northern Maine is further from the southern range limit, but the populations sampled in the Maine study are located primarily within actively managed forest land. Combined with historical land management, especially clearcutting, this may represent suboptimal marten habitat. It is also worth noting that estimates for the Maine study are based on a small number of individuals with a limited number of recaptures (55 detection events associated with 15 individuals). The much higher densities in Oregon may be attributable to the different subspecies, *M. a. humboldtensis*, present in the area, and are the highest spatially-explicit values reported in any North American marten species.
The much lower average American marten densities in my study than in other recent publications in New Hampshire is worth additional consideration. Sirén et al. (2016) surveyed for marten in 2011 and 2012 around Mt Kelsey. Linden et al. (2018) re-analyzed this data using a model that integrated the camera trap data with telemetry data. Fortuitously, Sirén et al. (2016) surveyed under similar masting conditions as I did, such that both of our first survey seasons, 2011 and 2017, preceded a mast crop, and our second seasons, 2012 and 2018, followed the mast crop. In both studies, detectability was higher in the first season, while density was higher in the second. This would seem to confirm that the effect of masting cycles on marten detectability is consistent, and was not just an effect of the particularly large masting event that occurred in 2017 (Jensen et al. 2012; Hallworth et al. in preparation).

To directly compare my estimates to those from Sirén et al. (2016) and Linden et al. (2018), which overlapped spatially and used the same method, I calculated total density for the same spatial extent used by Sirén et al (2016). My estimates of total density were 0.10 (CI: 0.6-0.18) and 0.16 (CI: 0.09-0.28), for 2017 and 2018, respectively, which was less than half that reported by Siren et al (2016: 0.43 (0.25-0.75); 2017: 0.60 (0.35-1.01), respectively, (Table 16).

Some of the differences may be indicative of changes to the SCR analysis. Though all three models included similar variables for σ and base detection rate (i.e., year, behavioral response), the density models were quite different. Sirén et al. (2016) used no habitat covariates to account for spatial variation in marten density, Linden et al. (2018) included a single variable, distance to mixed forest, while my models incorporated multiple habitat covariates. However, SCR is generally robust to misspecification of the spatial density model: estimates of total density (i.e, population size) are similar regardless of whether the spatially varying or spatially invariant density models are applied (Efford & Fewster 2013). Instead, there was likely an actual
change in the marten population over the 5 years between 2011/2012 and 2017/2018. Shortly after Sirén et al. (2016) surveyed for marten on Mt Kelsey, parts of the forest were harvested. The effects of timber harvest on marten habitat selection and space use have been well documented (Potvin et al. 2000; Poole et al. 2004; Fuller and Harrison 2005; Thompson et al. 2012; Cheveau et al. 2013; Moriarty et al. 2016). Likely, the forest harvest in the Mt Kelsey area returned parts of the landscape to earlier successional stages, which are less suitable for marten habitat. This decreased suitability is reflected in the results from my survey, as less suitable habitat would result in fewer marten being present in the area, and thus overall density also being lower. This was clearly apparent in the surveys, where Sirén et al. (2016) observed 13 individuals in 2011 and 15 in 2012, while I observed only 5 individuals in 2017 and 4 in 2018.

<table>
<thead>
<tr>
<th>Author and Model</th>
<th>Average Density</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sirén 2011 Cameras</td>
<td>0.43</td>
<td>0.25</td>
<td>0.75</td>
</tr>
<tr>
<td>Sirén 2012 Cameras</td>
<td>0.60</td>
<td>0.35</td>
<td>1.01</td>
</tr>
<tr>
<td>Sirén 2012 Live-trap</td>
<td>0.45</td>
<td>0.16</td>
<td>1.22</td>
</tr>
<tr>
<td>Linden 2011/12 Cameras</td>
<td>0.39</td>
<td>0.29</td>
<td>0.56</td>
</tr>
<tr>
<td>Linden 2011/12 Integrated</td>
<td>0.43</td>
<td>0.32</td>
<td>0.61</td>
</tr>
<tr>
<td>Drummey 2017</td>
<td>0.10</td>
<td>0.06</td>
<td>0.18</td>
</tr>
<tr>
<td>Drummey 2018</td>
<td>0.16</td>
<td>0.09</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Using my SCR model, I was able to produce robust predictions of statewide population size using a fit-for-purpose combination of field and analytical methods. These estimates are higher than previously reported, and provide an important benchmark for future monitoring and conservation efforts in New Hampshire and the northeastern range more generally (Table 17). Though my average density values are low compared to estimates produced in other studies, my maximum predicted density values for 2017 and 2018 (up to 0.63 and 1.01
individuals/km², respectively) are much closer to the upper end of reported marten densities. These density hotspots occurred within the White Mountain National Forest, though other protected areas in northern New Hampshire outside of the White Mountain National Forest also supported relatively high population densities in 2017 and 2018 (up to 0.51 and 0.82, respectively). In addition to encompassing the highest predicted marten densities in New Hampshire, the White Mountain National Forest represents approximately 14% of the total land area in New Hampshire, but supports more than 40% of the statewide marten population. These density hotspots likely represent the core habitat for marten in New Hampshire, acting as source populations.

<table>
<thead>
<tr>
<th>Author and Model</th>
<th>Abundance</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sirén 2011</td>
<td>701</td>
<td>411</td>
<td>1052</td>
</tr>
<tr>
<td>Sirén 2012</td>
<td>930</td>
<td>533</td>
<td>1372</td>
</tr>
<tr>
<td>Drummey 2017</td>
<td>1286</td>
<td>583</td>
<td>3048</td>
</tr>
<tr>
<td>Drummey 2018</td>
<td>2061</td>
<td>1020</td>
<td>4477</td>
</tr>
</tbody>
</table>

In similar studies, where researchers investigated the relationship between occupancy and density, comparisons are typically made using occupancy and density estimates derived from the same data and model structures, and, perhaps as should be expected then, typically result in regression models with very good fit (Clare et al. 2015: $R^2 = 0.95$; Linden et al. 2018: $R^2 = 0.94$). My lower value may be due, in part, to the independent data sets utilized for the two models, limiting potential spatial autocorrelation. Though sampling for my comparison occurred concurrently, sampling locations were not the same and were selected independently of one another.
I also saw that, while occupancy and density are closely related and are likely affected by similar habitat covariates, they may not respond to them in exactly the same way. I demonstrated this with boreal biomass, which was linear in the top occupancy model, but quadratic in the top density model. Moreover, my inclusion of an additional density covariate, canopy closure, showed that there can be different drivers of occupancy and density patterns and therefore using expectations of one as a proxy of the other is not straightforward. On the one hand, comparing 'best' models shows a strong positive relationship, but a lot of variation around that relationship, perhaps more than would be acceptable for informing management. On the other hand, the matched model provided a weaker but more precise relationship between occupancy and density, but is biased across the range of occupancy values because the models miss important spatial structure. Moreover, was saw that the relationship between occupancy and density seemed to saturate as occupancy approached 1; this may further limit the utility of occupancy as a proxy for density.

2.5 Management Implications and Recommendations

Over the course of this project, I was able to successfully scale up the novel camera trap method developed by Sirén et al. (2016) to survey at the landscape level (greater than 1,800 km²). I demonstrated that not only were the field methods feasible for use at the large scale; when combined with SCR models, the methods allowed me to predict baseline density and abundance estimates for marten in the state of New Hampshire. These models allow for a refined, and more mechanistic, understanding of the factors that influence spatial variation in marten density in heterogeneously managed landscapes. My results provide important benchmarks for future marten management and research, enabling the New Hampshire Fish and
Game Department to track population changes and trends as marten continue to recover in the state.

Though statewide estimates were the ultimate goal of my research, I would be cautious when interpreting the predicted density and abundance values. Though I extrapolated over the entire state, I only sampled across the northern three counties of New Hampshire; as a result, I did not sample habitat in proportion to its availability (Figure 13). In particular, low values of boreal biomass were common across New Hampshire, but were rarely surveyed; snow depth was slightly biased to higher values than were present at the state level; and canopy closure was strongly skewed towards very higher levels.

The effect of these sampling biases can be clearly seen in the statewide estimates (Figure 10). A large proportion of the state, mostly south of the White Mountain National Forest, is predicted to have very low abundance and density, primarily due to the decreased availability of boreal forests in this region, and the decreased winter snowfall. The influence of southern New Hampshire on the statewide estimates results in very low averaged density values and abundance estimates with high uncertainty. Due to this, I would recommend the focus instead be on the predictions for northern New Hampshire; though the sampling is still not completely representative, it is far more similar to the area surveyed. Moreover, very few individuals have been observed further to the south; likely, individuals observed in southern New Hampshire are dispersing from the northern part of the state, rather than representing stable populations in this region. As we know that marten populations are close to 0 or absent in the south, despite my predictions suggesting that marten are present but at low densities, it is reasonable to take the estimates of abundance and density within northern New Hampshire to be representative of the entire state, i.e., focusing on their known distribution, or at least not in areas we know they do not
occur. This may change as marten continue to recover and expand, in which case, targeted
surveys will be necessary to determine if marten habitat usage is similar in northern and southern
New Hampshire, despite the difference in what habitat is available.

In addition to establishing baseline population estimates, I was also able to quantify the
effects of abiotic and biotic factors on the spatial distribution of marten. The surveys described in
this chapter prioritized a representative sampling of the range of habitat and environmental
conditions hypothesized to be important for marten, allowing me to quantify effect sizes over a
representative range of conditions. These results also offer important insights about the current
distribution of marten, which can therefore be used to predict additional marten range shifts and
the role landscape-scale forest management can play in improving connectivity and hence, the
continued recolonization of the historic range.

Figure 13. Distribution of values for each of the habitat covariates in the top model at three spatial
scales: the state of New Hampshire, the three northernmost counties, and the actual area surveyed by the
camera traps. The x-axes for each variable are scaled; the y-axes on all charts is probability density.
Overall, it appears that survey efforts failed to survey very low boreal biomass layers, snow depth was
slightly biased to higher values, and canopy closure was heavily surveyed at the highest levels.
Importantly, this provides critical information that will be valuable for informing how forests are managed in the future, or more specifically, predict how forest management decisions are likely to affect the standing marten populations. My results indicate that two forest characteristics, aboveground boreal biomass and canopy closure, influence marten distribution on the New Hampshire landscape. Marten densities peak at intermediate biomass levels (~80 Mg/ha), and decline to near 0 when canopy closure drops below 60%. These two values can be used as guidelines for establishing future habitat management recommendations, as well as for identifying priority marten habitat in New Hampshire. However, it is important to note that closure alone is not sufficient to explain marten habitat preferences; it must be coupled with other variables related to forest type, age, and structure. Otherwise, all canopy closure is doing in a model is testing for whether a site is forested or not. This may be especially true for my model, where the vast majority of sites surveyed were forested (i.e., only 5% of the surveyed area was below 60% closure) and thus could artificially inflate the importance of this variable.

The final environmental variable found to influence marten densities, snow depth, cannot be directly managed. However, it is still an important consideration for marten management, especially as changing climatic conditions may alter habitat suitability in the future. Identifying priority areas that could act as climate refugia (Morelli et al. 2016) will benefit long-term management of American marten, as will identifying areas south of the current range where marten could potentially expand to in the near future.

There are several factors that should be considered prior to conducting additional SCR surveys in New Hampshire. First, future surveys should consider the influence of masting events on marten detectability. The amount of effort required to encounter a marten is much higher after a successful masting season; thus, targeting non-mast years would result in more captures per
unit of effort. This may be less of a concern when surveying over a multi-year period, as masting occurs every 2-3 years in the northeast (Hallworth et al. *in preparation*).

The large variability in observed density between 2017 and 2018 illustrates the importance of scale when comparing estimates. The variation disappeared when the analysis was re-run using only areas that were surveyed in both years. Indeed, at least some of the variation we report between the two years is likely to be an artifact of 2018 being a better-informed model with the inclusion of very high-quality habitat in the White Mountains. Density is comparable across sites and times; however, if you want to monitor change at a specific site, you need to ensure that the scope of the two comparison points matches. For NHFGD, this does not mean all future surveys must contain all the sites I surveyed, an unreasonable expectation for a state that has varied research needs and limited funding. It means that baselines specific to the areas being resurveyed should be produced from my data for comparison, rather than trying to compare a small area to all of northern New Hampshire. Representative survey areas should be identified so that useful baselines can be established prior to future surveys.

While the camera trap methodology developed by Sirén et al. (2016) is less intensive than live-capture or telemetry, it still requires more effort than occupancy-based camera surveys. My results indicate that there is a positive relationship between the two. However, mismatches between the habitat covariates that drive each of the metrics may make occupancy an insufficient index for density. It may be possible to use occupancy surveys to track general trends, but periodic density surveys would still be necessary in order to accurately and effectively monitor marten density and abundance. Development of an integrated model that combines annual occupancy models with periodic SCR models could improve precision (Chandler and Clark...
2014), though this would require the development of a nested survey design, as opposed to the independent datasets used in my comparison.

Several additional investigations could further improve our understanding of marten habitat requirements and space use in New Hampshire. First, our understanding of the relationship between aboveground biomass and stand complexity is insufficient. While biomass is correlated with stand age, stand age is not necessarily correlated with stand complexity, the actual habitat variable martens are thought to respond to. Directly linking biomass to complexity through field-based investigations will confirm whether there is a relationship, and thus, if biomass is an acceptable, remotely-sensed alternative for stand complexity.

The influence of survey effort on density estimates deserves further investigation. Generally, I would recommend using the 2018 estimates as the state benchmark, as this survey was informed by far more data (260 cameras sites and 478 marten visits in 2018, compared to 150 cameras and 290 visits in 2017). However, if future surveys are not going to occur on the same scale as the 2018 survey, then comparisons should at least be made using priority areas that coincide with the current sampling, and smaller scale comparisons should be made.

Finally, the camera trap data from both Sirén et al. (2016) and this thesis should be reanalyzed using occupancy models. This would allow for 1) identification of changes in occupancy between 2011/2012 and 2017/2018, 2) direct comparison between occupancy models developed using different camera trap designs for 2017/2018, and 3) comparison between occupancy and density models developed from a single dataset. These investigations could help identify recent range expansions, efficacy of different camera designs for occupancy models, and whether the relationship between occupancy and density is impacted by the use of separate datasets. Furthermore, this last investigation could help inform the development of a nested
modeling approach similar to Chandler and Clark (2014) should the state decide to utilize this approach.

Ultimately, this research has produced information necessary for the New Hampshire Fish and Game Department to effectively protect American marten populations and habitat within the state while simultaneously contributing to the growing body of information about marten habitat associations, monitoring, and management. This information can be used to inform decision-making, habitat management, research plans, and other wildlife management activities. The recommendations here will hopefully prove beneficial to American marten, leading to their continued recovery in New Hampshire.
APPENDICES
APPENDIX A

CPW PHOTO WAREHOUSE INSTRUCTIONS

Basic Protocol for Marten Identification – Project Setup

This document was put together for the 2017/18 New Hampshire marten identification program by Donovan Drummey. If there are any questions about this document or the use of the CPW program, let me know. E-mail: ddrummey@umass.edu

This guide provides the basics of using the CPW Photo Warehouse program for the American marten identification, though the basics are the same for any project. For a more detailed description of the program and some of its capabilities, read the User Guide (a copy is saved to each of the Photo Lab computers; it can also be accessed at http://cpw.state.co.us/learn/Pages/ResearchMammalsSoftware.aspx)

Terminology:

There are several words used to describe aspects of this project that will be commonly used throughout this guide. They are defined below:

- **Line** - A line is a group of blocks and traps that are in a similar area to one another. In the image below, each color represents a different line. There are a total of 6 lines on the project this season.
- **Block** - A block is a 2km x 2km area that is being sampled. In the image below, each square is a block. There are generally 10 to 11 blocks per line.
- **Trap** - A trap is a game camera set to capture images of American marten chest badges. For this project, there are three traps in each of the sampled blocks.
- **Observer**: Any individual who uses the program to ID images
- **Set, Check, and Pull**: When setting a trap, there are three dates of importance; the day it was set up (Set), the day it was taken down (Pull), and any times in between the two that a staff member visited the camera (Check). Checks are done to ensure the battery hasn’t run out, the SD card isn’t full, and there is still bait in the trap. When IDing photos and on the data sheets, you will notice they are sorted into ‘Check’ (from Set to Check) and ‘Pull’ (from Check to Pull) folders. Make sure you know which one you are working on!
There are some words used to describe actions in CPW Warehouse, defined below:
Switchboard – The main page of the CPW program (see image below)
Form – Any of the pages accessed by clicking on one of the options on the Switchboard.

Accessing the files
All the files for this project are stored on the ‘tfuller’ external drive (usually next to the Lenovo computer), within the ‘Marten’ folder. There should be two documents and a folder there. The access file is the database itself; to work on the marten database, click on this, and not the link on the computer desktop. The spreadsheet ‘Camera Data’ contains the information on each of the traps; unique IDs, coordinates, time and date set, and other notes. Open the ‘Winter 2017’ folder and you will see the traps are sorted into their lines. Select the line you will be working on, and all of the traps in that line will appear.

Each trap has a folder whose name consists of three parts: a number, a letter, and a number (some may have an additional letter at the end).
- The first number corresponds to the unique sampling block number. There are only 10 or 11 sampling blocks to a line, but they are all numbered sequentially (line A includes block 1-10, line B includes blocks 11-20, etc.). Some blocks may be missed due to weather and/or time constraints (i.e., there is no block 10).
- The letter refers to which of the three cameras within a block the trap was. Each block should have 3 traps in it; an A, a B, and a C.
- The second number is the number on the trap, which should be visible in the pictures.

Routine actions:
The database should be backed up once a week at minimum, and preferably after every time it is used to process photos. To do so, close the CPW startup menu and click the ‘File’ button. Select ‘Save As’ to open the Save menu. ‘Back up Database’ is in the Advanced options, directly above the large ‘Save As’ button.
On the 1st of every month, the database should be compacted and repaired. This keeps the database smaller, and can help keep the program from bogging down. Do this by clicking on
‘File’ in the Access page (close out of the CPW window). Click on ‘Info’ in the left-side column, and select the ‘Compact and Repair Database’ option.

Setting up a new project
1. Before beginning, compile a list of the camera locations (including coordinates), a list of expected species, and a list of any additional features you may want to record (i.e., age, sex, ID, tagged/collared).
2. Add the first area to the Study Areas table (Switchboard >> Add or Edit Study Areas).
   **Even if you only have 1 area, you need to complete this step in order to process photos.** Assign a Name, Abbreviation (max 3 letters), and Description. Save (Ctrl + S) before closing the window (the symbol to the left of the row will change from a pencil to an arrow).
3. Once the Study area(s) are set, add camera locations (Switchboard >> Add or Edit Locations). For each camera, select the study area from the dropdown menu and assign a location name (i.e., camera code). You can also add coordinates in UTM or lat/long format (recommended). Use NAD83 for UTMs, and WGS84 for Lat/Long. Additionally, Lat/Long should be in decimal degrees. Save (Ctrl + S) before closing the window.
   *You can do steps 4 and 5 now, or do them later through either the Photo ID form or the Switchboard.*
4. Add your expected species (Switchboard >> Edit the Species List). Enter the common name, genus, and species. If you like, you can assign a keyboard shortcut, a shorter name that will appear in the dropdown menus (i.e., ‘Lynx’ instead of ‘Canada Lynx’), or assign a species to a group. Remember to save (Ctrl + S) before you close the window. You can delete species by clicking the ‘X’ to the left of the row.
   You can create groups (i.e., carnivores, ground-nesters, raptors, ungulates) by clicking the ‘Add or Edit Groups’ button on the bottom right of the window. Enter the group name, then save (Ctrl + S) before closing the ‘Groups’ window. You can delete groups by clicking the ‘X’ to the left of the row.
5. Add the features and details you wish to record (Switchboard >> Edit Species Details). Each detail must be added for each species you want it to apply to (if you want to know if any individuals of any species was collared, you would need to have a row for each species). Save (Ctrl + S) before closing the window.

Preparing for Importing Photos:
6. Add the visits for each camera (Switchboard >> Add or Edit Visits). There are three types of visits: Set, Check, and Pull. Set is the first day a camera begins sampling (the day it is turned on/put up). Checks are when the camera is sampling before and after (and possibly during) a visit (such as rebaiting a camera trap). Pull is the last day the camera is sampling (the day it is turned off/removed). The time between a set and a pull at a location is referred to as a deployment. Toward the bottom of the Visits window, click the ‘Add New Visit’ button. Keep adding additional visits by clicking the ‘Next Visit’ button.
   *For the marten project, there should be a set, check, and pull for each folder. The dates should be in the ‘Camera Data’ spreadsheet.*

Importing Photos:
7. Photos can only be added to a check or a pull, not a set (because no pictures should have been taken before the camera was set). There are two options for importing photos:
a. Import using the ‘Load Photos’ button while in the ‘Add New Visit’ window. You can also access this screen by clicking the ‘Edit’ button to the right of a visit in the ‘Add or Edit Visits’ window. This method is recommended.

b. Can also import using ‘Import Photos’ button found directly in the Switchboard window. This is very similar to the import option in the ‘Load Photos’ window in ‘Add New Visit’, however, you need to already have a check or pull visit entered in addition to a set to which the photos will be associated.

In the popup window, select the visit you are interested in and the folder where those images are on the hard drive. Not every Check and Pull has images associated with it. Select the ‘Include subfolders’ option, and deselect the ‘Copy images’ option. Allow the photos to load before attempting to do anything else.
Basic Protocol for Marten Identification – Instructions for Observers

PHOTO ID DYNAMICS ON CPW PHOTO WAREHOUSE

Standard protocol calls for at least two people to review and ID each photo. This is easily done in Photo Warehouse, so long as everyone who enters data signs in on their own name (see step 3 below). If the two observers assign the same species to an image, it is marked as ‘verified’ and no further action is needed. If the two observers assign a different species to the image (i.e., one puts in gray squirrel but the other thought it was a red squirrel), then the image is flagged as ‘pending’ in the database. A third person – a ‘referee’ – will need to reconcile the image before it can be verified.

BASIC PHOTO IDENTIFICATION

   (File Explorer -> tkfuller@eco.umass.edu (F:) -> Marten -> Marten Surveys)
2. Select ‘ID Photos’ on the Switchboard.
3. Enter your name into the form that pops up.
4. Select the folder you want to work in (red). Select ‘only photos that need ID’ (blue) to hide any photos that have already been identified. Make sure you are the individual currently logged in (orange).

5. ID the photos in the folder.
   a. Select the species and number of individuals of each species in the image (red). Select the ‘X’ on the right to delete a record.
   b. Other tools: Batch ID (orange) and Highlight (blue). See ‘Advanced Photo Identification’ for more information.
   c. Non-standard identifications:
      i. Snow: an image where snow was covering the camera
ii. Date: an image of a whiteboard with the date and time on it (check that the time is within 10 minutes or so of what is on the bottom of the image; if not, note that in the comments on the data sheet)

iii. Staff: an image of someone setting up/taking down the camera

iv. Scan: an automatically triggered image taken by the camera every day around 2:00 PM, used to ensure camera was functioning all days it was deployed

v. Human: a person who is NOT staff walking by

vi. None: an image where no animal appears

vii. Unknown: an image with something in it, but you can’t tell what it is

6. When you start a folder, put your initials and the start date on the appropriate line of the data sheet on the table next to the computer. When you finish a folder, add the completion date. If a folder is empty (some of them are), write ‘empty’ in the Initials column, so that we know it has been looked at.

**ADVANCED PHOTO IDENTIFICATION**

*Highlight*

Used for flagging photos that are of good quality for later use in reports, papers, and publicity documents (i.e., the photo is particularly clear, or contains an animal doing something funny/unusual). To highlight an image, simply select the box next to ‘Highlight’ on the photo ID form.

*Batch ID*

Used to ID multiple images at one time. Put the first image of the batch on the left, and the last image of the batch on the right. Select the species, and click ‘Apply ID.’

*I often find it helpful to have the folder open in the File Explorer as I am IDing. It allows me to quickly scan through the images, making it easier to find the beginning and end of a batch. Keep in mind that the cameras were set to take photos in clusters, so batches should be multiples of 3!*
Adding tags to photos

Used to mark the location of a difficult to see animal. While in the ‘Photo ID’ form, click on the animal to create an orange box around it. Click inside the box to delete the tag.
Adding a new species

Type in the name and progress to the next image. When the program asks if you want to add the species, select ‘Yes.’
**Basic Protocol for Marten Identification – Guide to Using Photo Modules**


***You do not need to have CPW downloaded on the computer to use modules***

**Downloading the module**

Go to the Box folder ([https://umass.app.box.com/folder/51139334845](https://umass.app.box.com/folder/51139334845)). Select the Line of interest, and open the folder. Choose the site you want to work on from the list. Download the whole folder by clicking on the ‘More Options’ icon (circled in green), to the right of the folder name and file count, and selecting the ‘Download’ option (blue). Follow the prompts and download the module to a location on your computer. If the folder is zipped, unzip it before proceeding.

**Opening the module**

The module has two components – a folder with the images, and an Access Runtime Application named ‘PhotoID.’ The photos are necessary in order to view the images in the module, but you may not otherwise need to open this folder at all. Click on the Runtime app to open the module, ignoring any security warnings. This will open a simplified version of CPW’s Photo ID form. Enter your name into the pop-up log-in form, click through to create your Observer ID, and you are set to begin IDing.
IDing photos

ID the photos in the folder.

a. Select the species and number of individuals in the image (red). Select the ‘X’ on the right to delete a record. If there is more than one species, add the second species on the second row.

b. Useful tools: Only images that need ID (pink), Keyboard Shortcuts (green), Batch ID (orange) and Highlight (blue). See ‘Advanced Photo Identification’ for more information.

i. Only images that need ID: toggle on and off to hide images you have already identified. Especially useful to do when you think you are done with the site, to ensure you did not accidentally skip any images.

ii. Highlight: Used for flagging photos that are of good quality for later use in reports, papers, and publicity documents (i.e., the photo is particularly clear, or contains an animal doing something funny/unusual). To highlight an image, simply select the box next to ‘Highlight’ on the photo ID form.

iii. Keyboard Shortcuts: Some species are linked to keyboard shortcuts, so that you do not need to click through the dropdown menu each time. Instead, you can just hit the appropriate key on the keyboard. For example, hitting ‘d’ will
autofill the field with ‘date.’ Click on ‘Keyboard Shortcuts’ to see the full list of them.

iv. **Batch ID:** Used to ID multiple images at one time. Put the first image of the batch on the left, and the last image of the batch on the right. Select the species, and click ‘Apply ID.’

*I often find it helpful to have the folder of photos open in the File Explorer as I am IDing. It allows me to quickly scan through the images, making it easier to find the beginning and end of a batch. Keep in mind that the cameras were set to take photos in clusters, so batches should be multiples of 3! Be careful if Batch IDing any photos of ‘None.’ Often you will find a red squirrel or something else small ran by somewhere in the middle of the batch.*

![Batch ID screenshot](image)

v. **Adding a new species:** Type in the name and progress to the next image. When the program asks if you want to add the species, select ‘Yes.’ Add the details to the list (species and genus) and click ok.

![Unknown Species](image)

vi. **Adding tags to photos:** Used to mark the location of a difficult to see animal. While in the ‘Photo ID’ form, click on the animal to create an orange box around it. Click and drag to create a larger box. Click inside the box to delete the tag.
c. Important non-animal identifications:
   i. Snow: an image where snow was covering the camera (blurry)
   ii. Date: an image of a whiteboard with the date and time on it (check that the time is within 10 minutes or so of what is on the bottom of the image; if not, make a note of how far off it is, and let me know)
   iii. Staff: an image of someone setting up/taking down the camera (usually in the first and last dozen images)
   iv. Human: a person who is NOT staff walking by (usually in the middle)
   v. Scan: Each camera was set to take a photo at 2PM (14:00) every day. Unfortunately, because of some of the camera settings, they took a whole sequence of images. The first image from the scan sequence, usually at 14:00 (but may be at 13:59) is the ‘scan’ photo. Only 1 image per day should be a scan; the others are ‘None’
   vi. None: an image where no animal appears
   vii. Unknown and unknown bird: an image with something in it, but you can’t tell what it is

**Finishing a module**

When you finish a model, re-name the Runtime App to include your initials and the site number (i.e., PhotoID_DD_119A3). Upload just the runtime file (not the folder of photos) to the folder in the Box. Shoot me a quick e-mail when you finish 2-3 modules, and include any important comments, such as ‘Clock off by 1 hour,’ ‘Images out of focus,’ ‘Camera malfunctioning,’ or ‘Really cool image of a moose around image 236.’ Let me know if you have questions at any point in time – I generally try to respond within a day! ddruemmey@umass.edu
APPENDIX B

ADDITIONAL HYPOTHESES

Additional literature-derived hypotheses explaining American marten spatial distribution that were ultimately not included in analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hypothesis</th>
<th>Source</th>
<th>Reason for elimination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecotone Elevation</td>
<td>Elevation does not directly impact marten distribution, but it is correlated with a number of other environmental variables (i.e., forest type, precipitation, etc) more directly impact marten. Many researchers utilize this variable to account for some of this variation, though interactions between elevation and latitude may complicate the relationships.</td>
<td>Zielinski et al. 2015</td>
<td>Elevation is an indirect way of quantifying numerous other variables we can more directly quantify. Moreover, elevation is correlated with measures of terrain ruggedness, which is unsurprising considering that they are derived from elevation.</td>
</tr>
<tr>
<td>Landcover (NLCD, NETH, forest/ nonforest)</td>
<td>Marten are associated primarily with softwood forests across much of their range, though mixedwood types may gain importance in eastern forests.</td>
<td>Thompson et al. 2012</td>
<td>While landcover is an important variable which we did include in our analysis, there were several potential ways of classifying the landscape to choose between. The NLCD dataset was discarded as the main forest categories (hard/soft/mixed) are strict and based on reflectance values, rather than underlying ecological processes. The NETH dataset better describes forest patterns, but was discarded in favor of the Subsys layer, which is an updated version of the NETH data. We considered a forest/nonforest dataset as well, but discarded this as marten do not inhabit all forest types.</td>
</tr>
<tr>
<td>Protection status</td>
<td>Forests with a protected status, such as state ownership or land easements, are often older and more complex than surrounding areas. These areas may represent core marten habitat.</td>
<td>Kirk et al. 2009, Ivan et al. 2018</td>
<td>Though protected lands may contain core habitat, this variable lacks predictive power across the large portions of NH forests that are not protected. Additionally, protection status may just be an indirect way of measuring stand age and complexity, which we can measure more directly with biomass.</td>
</tr>
</tbody>
</table>
APPENDIX B (CONT.)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hypothesis</th>
<th>Source</th>
<th>Reason for elimination</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Road density</strong></td>
<td>Marten are frequently described as being forest specialists and wary of humans. Increased human activity and associated development may deter marten from an area.</td>
<td>Ruggiero et al. 1994</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompper et al. 2006</td>
<td></td>
</tr>
<tr>
<td><strong>Stream density</strong></td>
<td>Water is an important resource for many species. For marten, it can be an immediate resource and also provide additional hunting and foraging opportunities. These areas may also have more complex structure as a result of NH’s best management practices for timber harvest in riparian areas.</td>
<td>Kirk et al. 2009</td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX C
GIS DATA SOURCES

Complete list of all density and detection covariates initially considered and the source(s) for the data. Variables in bold were ultimately retained as candidate variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Source</th>
<th>Links(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td>Continuous measure of aboveground tree biomass, in Mg/ha</td>
<td>2017 Forest Above-ground Biomass, Northeast (Designing Sustainable Landscapes project)</td>
<td><a href="http://jambaprovost.ads.umass.edu/web/lcc/dsl/dslinks.htm">http://jambaprovost.ads.umass.edu/web/lcc/dsl/dslinks.htm</a></td>
</tr>
<tr>
<td>Ecotone</td>
<td>Binary variable describing whether and area is within the transitional zone (1) or not (0)</td>
<td>Derived</td>
<td>Provided courtesy of M. Hallworth. Ecotone calculated following methodology by Foster et al. 2015.</td>
</tr>
<tr>
<td>Fisher presence</td>
<td>Binary variable describing whether fisher were detected (1) or not (0) at camera trap</td>
<td>Derived</td>
<td>Derived from camera trap data. Result is associated with each camera, NOT a raster layer.</td>
</tr>
<tr>
<td>Landcover (NETH)</td>
<td>Stack of binary variables describing whether a pixel contained the target landcover class (1) or not (0).</td>
<td>Derived 2013 Terrestrial Habitat for the Northeast US and Atlantic Canada (TNC)</td>
<td>The categorical NETH raster was converted into a stack of rasters, with one binary layer for each forest habitat class.</td>
</tr>
<tr>
<td>Landcover (forest/ nonforest)</td>
<td>Binary variable describing whether an area is forested (1) or not (0).</td>
<td>Derived 2013 Terrestrial Habitat for the Northeast US and Atlantic Canada (TNC)</td>
<td>The categorical NETH raster was reclassified into 2 categories; forest or nonforest, resulting in a single binary layer.</td>
</tr>
</tbody>
</table>
### APPENDIX C (CONT)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Source</th>
<th>Links(s)</th>
</tr>
</thead>
</table>
| **Landcover (Subsys)** | Stack of binary variables describing whether a pixel contained the target landcover class (1) or not (0). | *Derived*  
2020 Subsysland (Designing Sustainable Landscapes Project) | The categorical Subsys raster was reclassified into 3 categories; boreal, hardwood, and mixedwood forests, then converted into a stack of rasters, with one binary layer for each forest habitat class. [http://umassdsl.org/](http://umassdsl.org/) |
| **Landcover (NLCD)** | Stack of binary variables describing whether a pixel contained the target landcover class (1) or not (0). | *Derived*  
2016 National Landcover Database (USGS) | The categorical NLCD raster was converted into a stack of rasters, with one binary layer for each forest habitat class. [https://www.sciencebase.gov/catalog/item/5dadee41e4b09fd0c9d8ed](https://www.sciencebase.gov/catalog/item/5dadee41e4b09fd0c9d8ed) |
| **Protection status** | Binary variable describing whether an area is under a form of land protection (1) or not (0) | *Mosaicked;*  
CAN – 2018 Registre des Aires Protégées au Québec  
USA – 2018 USGS Protected Areas Data (PAD-US) | [https://www.donneesquebec.ca/recherche/fr/dataset/aires-protegees-au-quebec](https://www.donneesquebec.ca/recherche/fr/dataset/aires-protegees-au-quebec)  
| **Road density** | Linear measure of the length of road within an area, in km/km² | *Mosaicked, then derived;*  
CAN – 2015 Road Network Files  
ME – 2019 ME E911 Roads  
NH – 2013 NH GRANIT Public Roads  
VT – 2019 VT Road Centerlines | Density derived using Line Density tool in ArcMap.  
[http://www.granit.unh.edu/data/downloadfreedata/category/databycategory.html](http://www.granit.unh.edu/data/downloadfreedata/category/databycategory.html)  
[https://open.canada.ca/data/en/dataset/8e089409-8b6e-40a9-a837-51fcb2736b2c](https://open.canada.ca/data/en/dataset/8e089409-8b6e-40a9-a837-51fcb2736b2c)  
[https://www.maine.gov/megis/catalog/](https://www.maine.gov/megis/catalog/) |
| **Snow conditions** | Continuous measures of a variety of precipitation-related variables; snow depth (in meters), snow-water equivalence (SWE; in m), and total snowcover days were evaluated | annual Snow Data Assimilation System (SNODAS) | [https://nsidc.org/data/g02158](https://nsidc.org/data/g02158) |
### APPENDIX C (CONT)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Source</th>
<th>Links(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Terrain ruggedness</strong></td>
<td>Continuous index measures of variation in the topography; numerous methods of calculating ruggedness exist, but we utilized TRI and VRM</td>
<td>Derived</td>
<td>Derived from the elevation products described above. TRI calculated using methods described by Wilson et al. 2007. VRM calculated using methods described by Sappington et al. 2007.</td>
</tr>
</tbody>
</table>
Reclassification scheme for converting the many forested habitat types from Subsys into the three main forest types. All other habitat types were classified as ‘other’ for analysis.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hardwood</td>
<td>5640</td>
<td>Laurentian-Acadian Northern Hardwood Forest: typic</td>
</tr>
<tr>
<td></td>
<td>5642</td>
<td>Laurentian-Acadian Northern Hardwood Forest: high conifer</td>
</tr>
<tr>
<td></td>
<td>5644</td>
<td>Laurentian-Acadian Red Oak-Northern Hardwood Forest</td>
</tr>
<tr>
<td></td>
<td>5649</td>
<td>Laurentian-Acadian Northern Hardwood Forest: moist-cool</td>
</tr>
<tr>
<td></td>
<td>562</td>
<td>Acadian Sub-boreal Spruce Flat</td>
</tr>
<tr>
<td></td>
<td>566</td>
<td>Acadian-Appalachian Montane Spruce-Fir-Hardwood Forest</td>
</tr>
<tr>
<td></td>
<td>5650</td>
<td>Acadian Low Elevation Spruce-Fir-Hardwood Forest</td>
</tr>
<tr>
<td></td>
<td>5740</td>
<td>Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Isolated</td>
</tr>
<tr>
<td></td>
<td>5742</td>
<td>Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Lake/pond: any size</td>
</tr>
<tr>
<td></td>
<td>5747</td>
<td>Northern Appalachian-Acadian Conifer-Hardwood Acidic Swamp: Smaller river floodplain/riparian</td>
</tr>
<tr>
<td></td>
<td>5750</td>
<td>Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Isolated</td>
</tr>
<tr>
<td></td>
<td>5752</td>
<td>Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Lake/pond: any size</td>
</tr>
<tr>
<td></td>
<td>5757</td>
<td>Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Smaller river riparian</td>
</tr>
<tr>
<td></td>
<td>5758</td>
<td>Laurentian-Acadian Alkaline Conifer-Hardwood Swamp: Smaller river floodplain</td>
</tr>
<tr>
<td>Boreal</td>
<td>999</td>
<td>Northeastern Coastal and Interior Pine-Oak Forest</td>
</tr>
<tr>
<td></td>
<td>5630</td>
<td>Laurentian-Acadian Pine-Hemlock-Hardwood Forest: typic</td>
</tr>
<tr>
<td></td>
<td>5639</td>
<td>Laurentian-Acadian Pine-Hemlock-Hardwood Forest: moist-cool</td>
</tr>
<tr>
<td></td>
<td>5930</td>
<td>Appalachian (Hemlock)-Northern Hardwood Forest: typic</td>
</tr>
<tr>
<td></td>
<td>5938</td>
<td>Appalachian (Hemlock)-Northern Hardwood Forest: drier</td>
</tr>
<tr>
<td></td>
<td>5939</td>
<td>Appalachian (Hemlock)-Northern Hardwood Forest: moist-cool</td>
</tr>
<tr>
<td></td>
<td>6040</td>
<td>North-Central Appalachian Acidic Swamp: Isolated</td>
</tr>
<tr>
<td></td>
<td>6042</td>
<td>North-Central Appalachian Acidic Swamp: Lake/pond: any size</td>
</tr>
<tr>
<td></td>
<td>6045</td>
<td>North-Central Appalachian Acidic Swamp: Great Lakes</td>
</tr>
<tr>
<td></td>
<td>6047</td>
<td>North-Central Appalachian Acidic Swamp: Smaller river riparian</td>
</tr>
<tr>
<td></td>
<td>6048</td>
<td>North-Central Appalachian Acidic Swamp: Smaller river floodplain</td>
</tr>
</tbody>
</table>
Download GIS layers; import layers and camera data to Create ‘Extent’ item based on camera locations

If necessary, merge multi-state/multi-item layers into

If necessary, use line files to create density rasters

Crop all layers to ‘Extent’ item

Save all raster files in .tif format and export to R.

While it would be more convenient to do all spatial data processing in a single system, ArcGIS is more efficient at processing certain actions, while R allows for greater control over certain actions and more complex analyses. The compromise here was to do a few steps in ArcMap that R struggles with, in order to provide a set of map layers that are easily processed in R.

The purpose of the “Extent” item is to have a shape that encompasses more than your study area. This will reduce edge effects caused by trying to generate averages near the edge of map borders. If your extent is sufficiently large, cells that are affected by these problems will not be part of the ultimate analysis. We achieved this by placing a 50km buffer around all camera sites with the Buffer tool, then used the Feature Envelope to Polygon to define a rectangle encompassing the buffered area.

Some layers, such as the roads and water data, were only available at the state level, while others, such as elevation, were available in standardized survey grids. As the extent incorporated multiple states and grids, it was necessary to download the layers from each location and combine them using the Merge (for vectors) or Mosaic tool (for rasters).

For the road and water layers, we were interested in the density (km/km²) of the features, not their specific locations. These values were calculated from the vector layers using the Line Density tool.

While R can handle cropping layers, very large rasters can take a long time to process. Rather than crop some layers in ArcGIS and some in R, all layers were cropped in ArcGIS for consistency, and to make use of ArcGIS’ ability to project ‘on the fly.’

TIFs are relatively small files, and can easily be read into R using the raster package.
SNODAS data is structured such that there is a raster layer for every day, for each of the 6 available precipitation variables. This stack must be trimmed to the variable of interest, study area, and the dates of interest. Once this is complete, a single raster layer of average values can be produced.

Overlying biomass with the landcover layers incorporates differential growth rates, and allows for the two layers to be treated as a single continuous variable.

SNODAS data is structured such that there is a raster layer for every day, for each of the 6 available precipitation variables. This stack must be trimmed to the variable of interest, study area, and the dates of interest. Once this is complete, a single raster layer of average values can be produced.

Overlying biomass with the landcover layers incorporates differential growth rates, and allows for the two layers to be treated as a single continuous variable.

These two measures of terrain ruggedness are derived from elevation, aspect, and slope, which can all be calculated from digital elevation maps.
General R Code Used for Processing Spatial Data

###Load libraries
library(raster)
library(rgdal)
library(rgeos)
library(spatialEco)
library(gridprocess)
library(gridkernel)
library(oSCR)

###Set directory for map layers
mdir<"C:\Users\Donovan Drummey\Documents\School\UMass Amherst ECo\Marten\Maps"

###Take the original SNODAS data, unpack it, extract yearly data, and calculate averages.
c <- readOGR("C:/Users/Donovan Drummey/Documents/School/UMass Amherst ECo/Marten/Maps/Base layers/Cams_50kmExtent.shp")
  #This shape is used to crop the SNODAS data to the area of interest
dpth <- brick('Data/Map Layers/snodas_NE.nc', varname = 'depth')
dpth <- crop(dpth, c)
dates_dpth <- as.Date(as.character(getZ(dpth)), '%Y%m%d')

# Winter 2016-2017
winter_2016_dpth <- which(as.numeric(format(dates_dpth,'%Y')) %in% 2016 &
                         as.numeric(format(dates_dpth,'%m')) %in% c(10,11,12)) # Oct-Dec 2016
winter_2016_dpthb <- which(as.numeric(format(dates_dpth,'%Y')) %in% 2017 &
                         as.numeric(format(dates_dpth,'%m')) %in% c(1,2,3,4,5)) # Jan-May 2017
winter_2016_dpth <- c(winter_2016_dptha,winter_2016_dpthb)

# Winter 2017-2018
winter_2017_dptha <- which(as.numeric(format(dates_dpth,'%Y')) %in% 2017 &
                         as.numeric(format(dates_dpth,'%m')) %in% c(10,11,12)) # Oct-Dec 2017
winter_2017_dpthb <- which(as.numeric(format(dates_dpth,'%Y')) %in% 2018 &
                         as.numeric(format(dates_dpth,'%m')) %in% c(1,2,3,4,5)) # Jan-May 2018
winter_2017_dpth <- c(winter_2017_dptha,winter_2017_dpthb)

#Calculate average depth for each winter
dpth_16_17_mean <- calc(subset(dpth,winter_2016_dpth), mean)/10
dpth_17_18_mean <- calc(subset(dpth,winter_2018_dpth), mean)/10

dpth_stack <-stack(dpth_16_17_mean,dpth_17_18_mean)
dpth_mean<- calc(dpth_stack, fun = mean)
dpth_stack<- stack(dpth_stack,dpth_mean)
names(dpth_stack) <- c("Depth 2016-17", "Depth 2017-18", "Depth Mean")
writeRaster(dpth_stack, "Data//Map Layers//dpth_stack2016_2018", format = "GTiff", overwrite=TRUE)

###Take the landcover data, reclassify into the different habitat breakdowns, and stack the layers.

dsl<- raster("C:\Users\Donovan Drummeyp\Documents\School\UMass Amherst ECo\Marten\Maps\TIFs\DSL_50kmExtent.tif")

lnd.dat<- read.csv("Data//Map Layers//lnd.csv") #a table containing your reclassification key
lnd.dat$TNC_Code<- as.numeric(lnd.dat$HABITAT)

lndcvr<- reclassify(dsl, lnd.dat[,c(1,13)]) #DSL data (updated US-only TNC), re-classified by boreal/hard/mixed according to Alexej

#Determine the names for all landcover types, and assign the names to the appropriate values
atr<- as.data.frame(freq(lndcvr, useNA = 'no'))
colnames(atr)<- c("Values", "Freq")

atr<- merge(atr, lnd.dat[, c(11,13)], by.x = "Values", by.y = "DSL_Code")
atr<- distinct(atr)

#Create binary layers for all variables of interest
lcov.rasts <- list()

for(i in 1:nrow(atr)){
  lcov.rasts[[1]] <- lndcvr
  lcov.rasts[[paste(atr[2,1])]] <- lndcvr==atr$Values[i]
  lcov.rasts <- stack(lcov.rasts)
}

names(lcov.rasts)<- c("DSL_50kmExtent", as.character(atr$HabitatClass))
lcov.rasts2<- lcov.rasts2[[1:4]] #remove 'other' class

writeRaster(lcov.rasts, "Data//Map Layers//lndcvr", format = "raster")

###Import map layers. Reproject as necessary. Create any derived rasters. Save final products.

depth_stack<- brick("Data//Map Layers//dpth_stack2016_2018.tif")
depth<- depth_stack[[3]] #the first 2 layers are the individual annual averages; the 3rd layer is the overall average for the 2 winters
lcov.rasts<- brick("Data//Map Layers//lndcvr.grd")
biom<- raster(paste0(mdir,"TIFs\Biom_50kmExtent.tif"))
elev<- raster(paste0(mdir,"TIFs\Elev30m_50kmExtent.tif"))

depth@crs
lcov.rasts@crs
biom@crs
elev@crs

newproj<- "+proj=aea +lat_1=29.5 +lat_2=45.5 +lat_0=23 +lon_0=-96 +x_0=0 +y_0=0 +datum=NAD83 +units=m +no_def"

depth<- projectRaster(depth, crs = newproj, res = 30)
elev<- projectRaster(elev, crs = newproj, res = 30)
#biom and lndcvr did not need to be reprojected

#Create biomass-habitat overlay layers
biom_b<- biom * lcv.rasts2[[2]]
biom_h<- biom * lcv.rasts2[[3]]
biom_m<- biom * lcv.rasts2[[4]]
biom.rasts<- brick(biom_b, biom_h, biom_m)
names(biom.rasts)<- c("Boreal", "Hardwood", "Mixedwood")

vrm<- vrm(elev, s = 3)
writeRaster(depth, "Data//Map Layers//Depth_50kmExtent.tif")
writeRaster(lcv.rasts, "Data//Map Layers//Lndcvr_50kmExtent.grd")
writeRaster(biom.rasts, "Data//Map Layers//BiomxLand_50kmExtent.grd")
writeRaster(vrm, "Data//Map Layers//VRM_50kmExtent.tif")

###Create smoothed rasters for all habitat covariates. Save final products.
#Setup parameters for gaussian smooth
area<- 4.235 #area, in km, of the average female marten home range
radius_m<- sqrt(4.235/pi) * 1000
diameter<- radius_m * 2
sig <- (diameter/1.96)/2 # 1.96 gets us to 1sd of the kernel, 2 converts from diameter to a radius

depth<- raster("Data//Map Layers//Depth_50kmExtent.tif")
depth_smooth <- gaussiansmooth(as.grid(depth), sd = sig) # sd is in map units, and is equivalent to 1 sd (radius/1.96)
depth_smooth.rast  <- raster(depth_smooth)
writeRaster(depth_smooth.rast, "Data//Map Layers//Depth_50kmExtent_smooth.tif")

vrm<- raster("Data//Map Layers//VRM_50kmExtent.tif")
vrm_smooth <- gaussiansmooth(as.grid(vrm), sd = sig)
vrm_smooth.rast <- raster(vrm_smooth)
writeRaster(vrm_smooth.rast, "Data//Map Layers//VRM_50kmExtent_smooth.tif")

biom.rasts<- brick("Data//Map Layers//BiomxLand.W_50kmExtent.grd")
biomboreal_smooth <- gaussiansmooth(as.grid(biom.rasts[[1]]), sd = sig)
biomboreal_smooth.rast <- raster(biomboreal_smooth)
biomhard_smooth <- gaussiansmooth(as.grid(biom.rasts[[2]]), sd = sig)
biomhard_smooth.rast <- raster(biomhard_smooth)
biomixed_smooth <- gaussiansmooth(as.grid(biom.rasts[[3]]), sd = sig)
biomixed_smooth.rast <- raster(biomixed_smooth)
biomland_smooth <- stack(biomoboreal_smooth.rast, biomhard_smooth.rast, biomixed_smooth.rast)
names(biomland_smooth) <- list("BiomxBoreal", "BiomxHardwood", "BiomxMixedwood")
writeRaster(biomland_smooth, "Data//Map Layers//BiomxLand_50kmExtent_smooth")

###Create scaled rasters for all habitat covariates. Save final products. Create squared rasters as necessary.
depth <- raster("Data//Map Layers//Depth_50kmExtent_smooth.tif")
vrm <- raster("Data//Map Layers//VRM_50kmExtent_smooth.tif")
biomXland <- brick("Data//Map Layers//BiomxLand_50kmExtent_smooth.grd")
biomB <- biomXland[[1]]
biomH <- biomXland[[2]]
biomM <- biomXland[[3]]

depth.mu <- cellStats(depth, "mean")
depth.sd <- cellStats(depth, "sd")
scaled_depth <- (depth - depth.mu) / depth.sd
writeRaster(scaled_depth, "Data//Map Layers//Depth_50kmExtent_scaled.tif")

vrm.mu <- cellStats(vrm, "mean")
vrm.sd <- cellStats(vrm, "sd")
scaled_vrm <- (vrm - vrm.mu) / vrm.sd
writeRaster(scaled_vrm, "Data//Map Layers//VRM_50kmExtent_scaled.tif")

biomB.mu <- cellStats(biomB, "mean")
biomB.sd <- cellStats(biomB, "sd")
scaled_biomB <- (biomB - biomB.mu) / biomB.sd
writeRaster(scaled_biomB, "Data//Map Layers//Biom-Boreal_50kmExtent_scaled.tif")

biomH.mu <- cellStats(biomH, "mean")
biomH.sd <- cellStats(biomH, "sd")
scaled_biomH <- (biomH - biomH.mu) / biomH.sd
writeRaster(scaled_biomH, "Data//Map Layers//Biom-Hard_50kmExtent_scaled.tif")

biomM.mu <- cellStats(biomM, "mean")
biomM.sd <- cellStats(biomM, "sd")
scaled_biomM <- (biomM - biomM.mu) / biomM.sd
writeRaster(scaled_biomM, "Data//Map Layers//Biom-Mixed_50kmExtent_scaled.tif")

#Create table of mu and sd values, for back-transforming data after analysis
mu_sd <- data.frame(Var = rep(NA, 5), Mu = rep(NA, 5), SD = rep(NA, 5))
mu_sd$Var <- list("Depth", "VRM", "BiomB", "BiomH", "BiomM")
mu_sd$Mu <- list(depth.mu, vrm.mu, biomB.mu, biomH.mu, biomM.mu)
mu_sd$SD <- list(depth.sd, vrm.sd, biomB.sd, biomH.sd, biomM.sd)
save(mu_sd, file = "Data//Map Layers//ScalingTable.RData")

# make squared variables
vrm2 <- scaled_vrm^2
writeRaster(vrm2, "Data//Map Layers//VRM2_50kmExtent_scaled.tif")

biomB2 <- scaled_biomB^2
writeRaster(biomB2, "Data//Map Layers//Biom-Boreal2_50kmExtent_scaled.tif")

biomH2 <- scaled_biomH^2
writeRaster(biomH2, "Data//Map Layers//Biom-Hard2_50kmExtent_scaled.tif")

biomM2 <- scaled_biomM^2
writeRaster(biomM2, "Data//Map Layers//Biom-Mixed2_50kmExtent_scaled.tif")

### Extract raster data to ssDF for SCR analysis.

depth <- raster("Data//Map Layers//Depth_50kmExtent_scaled.tif")
vrn <- raster("Data//Map Layers//VRM_50kmExtent_scaled.tif")
vrm2 <- raster("Data//Map Layers//VRM2_50kmExtent_scaled.tif")
biomB <- raster("Data//Map Layers//Biom-Boreal_50kmExtent_scaled.tif")
biomB2 <- raster("Data//Map Layers//Biom-Boreal2_50kmExtent_scaled.tif")
biomH <- raster("Data//Map Layers//Biom-Hard_50kmExtent_scaled.tif")
biomH2 <- raster("Data//Map Layers//Biom-Hard2_50kmExtent_scaled.tif")
biomM <- raster("Data//Map Layers//Biom-Mixed_50kmExtent_scaled.tif")
biomM2 <- raster("Data//Map Layers//Biom-Mixed2_50kmExtent_scaled.tif")

# stack biomass rasters for easier extraction
biomdat <- stack(biomB, biomB2, biomH, biomH2, biomM, biomM2)

### Overwrite the existing extract.rast function; this function extracts the mean of a buffered area
# NOTE: IF USING SMOOTHED LAYERS, LEAVE buffer = “NULL”
extract.rast2 <- function(ss, rast, mult = 1, cov.name = "val.1", buffer=NULL, method="simple", fun = mean){
  for(i in 1:length(ss)) {
    tmpS <- ss[[i]][, c("X", "Y")]*mult
    r1 <- raster::extract(rast, tmpS, buffer=buffer, fun = fun, na.rm=T)
    ss[[i]][, cov.name] <- r1
  }
  return(ss)
}

ssDF <- extract.rast2(ss = ssDF, rast = depth, mult = 1000, cov.name = "SnowDepth")
ssDF <- extract.rast2(ss = ssDF, rast = vrm, mult = 1000, cov.name = "VRM")
ssDF <- extract.rast2(ss = ssDF, rast = vrm2, mult = 1000, cov.name = "VRM2")
ssDF <- extract.rast2(ss = ssDF, rast = biomdat, mult = 1000, cov.name = c("BorealBiom", "BorealBiom2", "HardBiom", "HardBiom2", "MixedBiom", "MixedBiom2"))
APPENDIX F

INDIVIDUAL MARTEN CAPTURE SUMMARIES

Summary of individual marten captures for the two field seasons. The total number of sites each individual was captured at is reported, as is the total number of times the individual was captured across those sites. Summaries for individuals captured in both years (Eyeball, Stripe, and Tern) are divided by field season.

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# APPENDIX G

## COMPLETE MODEL LISTS

Full list of all detection models fit, and the model results. Density was held constant at the full parameterization \((D \sim Year + BorealBiom + BorealBiom^2 + Depth + Canopy Closure + VRM + VRM^2)\). Base detection \((p)\) and space use \((\sigma)\) were allowed to vary such that all possible combinations of variables were considered.

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Full list of all density models fit, and the model results. Base detection \((p)\) and space use \((\sigma)\) were held at the top model, while density was allowed to vary such that all possible combinations of variables were considered.

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