HOME RANGE AND MICROHABITAT ASSOCIATIONS OF THE SOUTHERN RED-BACKED VOLE (MYODES GAPPERI) IN NEW HAMPSHIRE FORESTS

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HOME RANGE AND MICROHABITAT ASSOCIATIONS OF THE SOUTHERN RED-BACKED VOLE (*MYODES GAPPERI*) IN NEW HAMPshire FORESTS

BY

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THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Master of Science
in
Natural Resources: Wildlife and Conservation Biology

September, 2018
This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources: Wildlife and Conservation Biology by:

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Dr. Russell G. Congalton, Professor, Natural Resources and the Environment

On May 23, 2018

Original approval signatures are on file with the University of New Hampshire Graduate School
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ABSTRACT

HOME RANGE AND MICROHABITAT ASSOCIATIONS OF THE SOUTHERN RED-BACKED VOLE (*MYODES GAPPERI*) IN NEW HAMPSHIRE FORESTS

by

Honora Barbara Tisell

University of New Hampshire, September, 2018

Resources, such as food and shelter, are unevenly distributed across the landscape at both macro and micro scales. Home range is one measure of space use that reflects an individual’s resource requirements (e.g., microhabitat characteristics) and competition for those resources (e.g., density dependence). This study focuses on the home range of the southern red-backed vole (*Myodes gapperi*), comparing field methods for estimating home range and modeling the microhabitat characteristics that define the core area of the home range. Southern red-backed voles (*Myodes gapperi*) are common to boreal forests, most often found in coniferous or mixed deciduous stands, and in the northeast, have an affinity for eastern hemlock (*Tsuga canadensis*). With eastern hemlock populations in decline due to the invasive eastern hemlock woolly adelgid (*Adelges tsugae*), it is unknown how *M. gapperi* space use will be affected.

From 2014-2017, southern red-backed voles were censused across 12 (~1 ha) grids using mark-recapture methods and for a subset of individuals radiotelemetry. Individual home range size, core area size, and core area overlap were calculated for adults using kernel density estimators from both mark recapture live trapping and radiotelemetry data. At each capture point,
forest structure, ground cover, and geographic features were measured to assess influence of microhabitat on home range and core area. Density was calculated on each grid for each year of the study using the POPAN parameterization of the Jolly-Seber model.

In this thesis, Chapter One presents the effects of *M. gapperi* density on individual home range and core area. Differences in size and overlap are examined within and between sexes, and estimates compared between the two field techniques, mark-recapture and radiotelemetry, often used to delineate home range and core area. Density did not affect space use and female voles shared area more often with males than other females. The home range size of males was larger than that of females, however, core area was consistently about 30% of total home range. Area estimates generated under mark-recapture and radiotelemetry were similar for females, but differed for males with larger home ranges calculated using radiotelemetry. Mark-recapture methods may have underestimated male home range as a consequence of the trapping grid being smaller than male home range.

Chapter Two identifies habitat characteristics at the macro and micro scale that influence *M. gapperi* space use. Macrohabitat differences were evaluated between trap stations that were visited and were not visited by *M. gapperi* and microhabitat characteristics were modeling within female *M. gapperi* core areas. *Myodes gapperi* are found in areas with higher eastern hemlock basal area and more coarse woody debris. Within these stands, female *M. gapperi* select for core areas closer to water, with greater red maple basal area, deeper leaf litter, and a greater density of hemlock stems.
CHAPTER 1

SOUTHERN RED-BACKED VOLE (MYODES GAPPERI) HOME RANGE AND OVERLAP:
A COMPARISON OF MARK-RECAPTURE AND RADIOTELEMETRY

INTRODUCTION

Where an animal concentrates their activity reflects a number of important ecological processes and behaviors. An individual’s home range is the space they use in their daily activities. The placement and size of the home range is an indicator of a species’ resource requirements (Burt 1943; Powell and Mitchell 2012; Spencer 2012) and is shaped by environmental factors, both abiotic conditions, such as temperature and water availability (Getz 1968), and biotic conditions, such as the distribution of food and habitat resources (Gore 1988; Börger et al. 2008). Intraspecific interactions, such as competition and sociality, can also lead to differences in home range size and placement among individuals based on sex and age (Jorgensen 1968; Bondrup-Nielsen and Karlsson 1985; Bondrup-Nielsen and Ims 1986). Population density can affect the strength of biotic interactions and often fluctuates widely among seasons and years for small mammals (Boonstra and Krebs 2012). For example, at high density, intraspecific competition is greater for resources and space which may lead to smaller home ranges (Adams 2001; Efford et al. 2015). Comparisons of home range over space and time are important for making informed management decisions and understanding the impact
disturbance, both natural and anthropogenic, may have on population dynamics and persistence (Jorgensen 1968; Spencer 2012).

Identifying an individual’s home range can be challenging because the area is not uniformly used. Areas in which an individual spends disproportionately more time are considered core areas (Samuel et al. 1985; Millspaugh et al. 2012a). These core areas often reflect nesting sites, resting areas, or areas of high resource abundance (Samuel et al. 1985; Millspaugh et al. 2006; Spencer 2012). An individual will often constrict their home range to surround a core area (e.g. nest site). Overall home range size is limited by the distance an individual can travel and readily return to their core area (Börger et al. 2008).

Modelling home range and distinguishing core areas requires relocation data. The ability to differentiate between areas of high and low use may vary depending on the tracking method used. Mark-recapture and radiotelemetry are two common field methods used to gather locational data. Choice of method can depend on the research question and terrain of study site (Fuller and Fuller 2012; Millspaugh et al. 2012b). An animal’s space use is strongly tied to their body size and the scaling relationships between body size, space use, and energetic requirements (Jetz et al. 2004; Millspaugh et al. 2012a) often dictates the method used to determine home range. In general, because smaller bodied mammals are more limited in their distances moved, both methods may be appropriate for measuring home range. For small mammals, only a few studies have compared the two field methods for home range estimates (e.g. Jones and Sherman 1983, *Microtus pennsylvanicus*; Desy et al. 1989, *Microtus ochrogaster*; Ribble et al. 2002, *Peromyscus boylii & P. truei*). However, these studies used minimum convex polygon estimators for home range size and this technique cannot give intensity of use estimates (Harris et al. 1990) and therefore cannot calculate a core area. More recent approaches including utilization
distribution (UD) kernel density estimators can calculate the intensity of use of an individual at any given point within their home range (Van Winkle 1975; Powell and Mitchell 2012) and can thus be used to identify areas of high intensity of use, or core areas (Samuel et al. 1985).

This study evaluates 1) whether *Myodes gapperi* density influences home range or core area size and the amount of shared area, 2) whether there are differences in home range and core area size and overlap between sexes and 3) whether home range and core area estimates differ by the field methods of mark-recapture grid trapping and radiotelemetry. *Myodes gapperi* is widespread throughout Canada and the northern United States (Merritt 1981), and typically associated with montane boreal forests (Miller and Getz 1972). Like many small mammals, it is both short-lived and highly fecund and known to have years of high density and low density (Boonstra and Krebs 2006; Sullivan et al. 2017). Females are thought to be territorial and exclude conspecific females from their defended home range (Perrin 1979; Bondrup-Nielson and Karlsson 1985). Estimates of home ranges during the breeding season for females have been calculated using traditional mark-recapture live-trapping methods and suggest home range size may vary among hardwood and softwood forests (Bondrup-Nielson 1986a). Although *M. gapperi* are associated with eastern hemlock (*Tsuga canadensis*) in northern forests (Miller and Getz 1972; Yamasaki et al. 1999), little is known of their patterns of home range or space use activity among forest stands in this region.

**METHODS**

**Mark-recapture**

*Myodes gapperi* were captured at the Bartlett Experimental Forest, White Mountain National Forest, New Hampshire (44° 3’ 7.2” N, 71° 17’ 25.1” W). Twelve mark-recapture grids
were established in each of three forest types, softwood (n = 4), mixed (n = 4), and hardwood (n = 4). Forest type was distinguished by the percentage of hardwood basal area in which hardwood grids had an average of 91% hardwood basal area, mixed grids had an average of 52.5% hardwood basal area, and softwood grids had an average of 25.5% hardwood basal area. Dominant hardwood species include American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) and dominant softwood species include eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*). Grids were standardized as an 8 x 8 station array with 15m spacing (64 stations, ca. 1.1 ha). One Sherman live trap (H. B. Sherman Co., Tallahassee, Florida) was placed at each station and a pitfall trap at every other station. Both trap types were used to facilitate sampling of the entire small mammal assemblage (Stephens and Anderson 2014).

Mark-recapture surveys were conducted at each grid over four consecutive days in each summer month (June-August) from 2014-2017. Traps were baited with bird seed and polyester fiber was provided for insulation. Traps were checked twice a day at dawn and dusk. Captured animals were identified to species, and the sex, weight (g), age class (juvenile, sub-adult, and adult), and reproductive condition of each individual was recorded. Age was determined based on body size and reproductive condition (e.g., testes position and vaginal perforation). Individuals were marked with a unique identification number using either an ear tag (model 1005-1; National Band and Tag Company, Newport, Kentucky) or a Passively Integrated Transponder (PIT; model HPT9 (9mm x 2.1mm) BioMark, Inc, Boise, Idaho). Incidental mortalities were processed as voucher specimens and deposited in natural history collections.
Radiotelemetry

In 2017, VHF radio collars (BD-2XC 0.75g; Holohil Systems Ltd., Carp, Ontario, Canada) were placed on both adult male and female *Myodes gapperi* (*n* = 23; weight ≥ 19g) that were captured on one of the mark-recapture grids. Radio collars were ≤ 4% of each individual’s body weight to ensure collars did not interfere with daily activity and behavior (Millspaugh et al. 2012b). Collars were equipped with a TYGON sleeve that fastened around the animal’s neck to avoid chafing.

Individuals were collared from July to August with collars on for an average of 16 days ± 2.24. Individuals were tracked twice daily while collared except in cases where weather conditions prohibited tracking or the signal could not be located. Locations were marked with GPS coordinates (Garmin GPSMAP 64s). The protocol for small mammal trapping and radiotelemetry was approved by the University of New Hampshire Animal Care and Use Committee (protocol # 120708, 140304, 160507) and followed guidelines outlined by the American Society of Mammalogists (Sikes et al. 2016).

Modeling home range and core area

Home ranges were modelled with a utilization distribution (UD) kernel density model (Worton 1989) which determines the probability of finding an individual at any given point within their home range (Van Winkle 1975). Models were calculated for each adult male and female that was captured ≥ 5 times either on the mark-recapture grids within a year or with radiotelemetry. The home range was delimited at the 95% UD isopleth to ensure potentially misleading outliers did not skew area estimates (Anderson 1982).
Core areas within the home range are those that have a proportionally higher intensity of use (Samuel et al. 1985; Vander Wal and Rodgers 2012) and were calculated following Vander Wal and Rodgers (2012) by plotting the utilization distribution area (size of region within UD isopleth) against the volume and calculating the point at which the slope of the fitted line was equal to 1. This point marks the isopleth value that was used to define the boundary of the core area (Vander Wal and Rodgers 2012). Core areas were identified and home ranges were calculated using the ‘adehabitatHR’ package (Calenge 2006) in the R software (R Core Team 2017).

A fixed kernel with smoothing bandwidth selected by reference was used to decrease bias for home range estimations and to accommodate our small sample sizes (Worton 1989; Seaman et al. 1991; Kie 2013). A fixed kernel uses a fixed value over the plane of location points (Kie 2013) and results in fine scale detail in the UD home range estimate (Worton 1989; Vander Wal and Rodgers 2012). The reference bandwidth controls the size of the kernel based on the density of locations points (Worton 1989) and assumes the kernel density UD has a bivariate normal distribution (Worton 1989; Kie 2013).

Size of home range and core area were compared between males and females using a Welch two-sample t-test. A linear regression was used to assess whether number of locations impacted home range estimates under both methods and for both sexes. Home ranges (95% isopleth) and core areas were exported as shapefiles and projected into QGIS (QGIS Development Team 2018) to calculate overlap between individuals for each year. Overlap was derived by calculating the percent of area that was shared between one individual and their neighbors for both home range and core area. Degree of overlap was evaluated separately for neighbors of the same and different sex. A Welch two-sample t-test was used to determine
whether the amount of overlap was different between the methods of mark-recapture and radiotelemetry.

**Estimating population density**

Mark-recapture data were used to estimate the population density of *M. gapperi* separately for each grid in each summer using the POPAN parameterization (Schwarz and Arnason 1996) of the Jolly-Seber model (Jolly 1965; Seber 1965; Krebs 1999) implemented in the R software (R Core Team 2017) package ‘RMARK’ (Laake 2016) with an integrated interface to program MARK (White and Burnham 1999). The Jolly-Seber model assumes the population is “open” between monthly trapping sessions in which individuals may be born, die, emigrate, or immigrate (Jolly 1965; Seber 1965; Krebs 1999). The time within the trapping session must be negligible compared to the time between trapping sessions (Krebs 1999). Our three mark-recapture trapping sessions were each 4-days with an interval of three weeks satisfying such a requirement. The Jolly-Seber model also assumes that each individual 1) has the same probability of entering a trap (are not “trap happy” or “trap shy”), 2) has the same probability of surviving between trapping sessions, and 3) is marked and marks are not lost (Krebs 1999). POPAN parameterized Jolly-Seber models further assume births have a multinomial distribution and that captures are derived from a super population (Schwarz and Arnason 1996). A 30-meter boundary strip was used to augment the grid and account for the effective area sampled (Burnham and Anderson 2002).

We tested eight POPAN parameterized Jolly-Seber density models with constant or time-dependent parameters. Models were ranked using Akaike’s information criterion (AIC). Because of the small sample sizes, we used the second-order AIC (AICc) which includes a bias-correction
term (Burnham and Anderson 2002). The highest ranked model for all grids had constant survival (φ), constant catchability (p) and constant probability of entrance (b). Models with time-dependent parameters were either ranked low or did not converge.

Analysis of variance (ANOVA) was used to test if density changed with year or habitat type. Linear regression models were used to test whether the size and overlap of home range and core area estimates from mark-recapture grids changed with changes in density. These analyses were conducted in the R software (R Core Team 2017).

RESULTS

Home range and core area estimates

A total of 417 unique individuals of Myodes gapperi were captured from 2014-2017. Forty-two females and 35 males were captured ≥ 5 times allowing home range to be calculated (Table 1.1). Of the 77 home ranges calculated, 12% were on hardwood grids, 60% on softwood grids, and 28% on mixed grids. Twenty-three M. gapperi were collared in the summer of 2017. Of these, home range was modeled for the 21 (10 females, 11 males) that had ≥ 5 locations (average 16.2 ± 2.15 SE locations). The average weight of the collared females was 25.39 ± 1.4 SE grams and of collared males was 25.53 ± 1.06 SE grams.

There was no significant difference in size of home range (95% isopleth) or core area calculated by mark-recapture (MR) and radiotelemetry (RT) for females or males (Figure 1.1 & Table 1.2). All core areas were calculated to be between the 59-62% isopleth for both methods. Core area was on average 32.80% ± 0.34 of the home range area. A Welch two-sample t-test showed that male home range is significantly larger than female home range (t = -6.5751, df = 50.234, P < 0.0001) and that male core area is significantly larger than female core area (t = -
Number of relocations did not affect the home range estimate for MR females, RT females, or MR males, but did affect the home range estimate for RT males ($r^2 = 0.5188$, $F = 9.702$, $df = 9$, $P = 0.0124$) with more locations leading to a decrease in the size of the male home range (Figure 1.2).

Patterns of shared space use did not differ significantly between the methods of MR and RT (Table 1.3) and were pooled to examine proportion of overlap within and among sexes (Table 1.4). Eighty-five percent of marked females occurred on grids with another individual (either male or female) whereas 95% of males occurred on grids with another individual. Of these individuals, less than half (45%) of females overlapped core areas whereas 86% of males overlapped female core areas. A female shared less of her home range and core area with neighboring females than with males (Figure 1.3). Females shared their home range and core area with males at a significantly greater percentage than they shared area with other females (Table 1.4). Figure 1.4 shows representative home range placement and overlap for mark-recapture and radiotelemetry.

Density

Density estimates from mark-recapture data ranged from 1.09 voles/ha to 26.29 voles/ha across the grids and years 2014-2017 (Figure 1.5). A chi-squared test for outliers (Dixon 1950) found the highest value of density, 26.29, to be an outlier ($X^2 = 20.176$, $P < 0.001$). With that outlier removed, the average density across grids and years was calculated at $5.49 \pm 0.69$ $M. gapperi$ per hectare. Density did not differ significantly among years ($F = 1.12$, $df = 37$, $P = 0.362$) or with an interaction between year and habitat type ($F(6,29) = 0.205$, $P = 0.972$).
Four of the 77 individuals occurred on the grid with the highest (outlier) density and their home ranges were included in these analyses of density-dependence as removing them did not affect the overall pattern. Density did not influence female home range size ($r^2 = 0.06785, F = 2.911, df = 40, P = 0.09571$) or male home range size ($r^2 = 0.05037, F = 1.75, df = 33, P = 0.1949$). Density did not affect female core area ($r^2 = 0.06961, F = 2.993, df = 40, P = 0.09134$) or male core area ($r^2 = 0.04024, F = 1.384, df = 33, P = 0.2479$). The proportions of shared area for core area and for home range were not density dependent for either males or females (Figure 1.6).

**DISCUSSION**

This study assessed whether home range or core area size were density dependent or varied between mark-recapture and radiotelemetry field methods for both female and male southern red-backed voles. We found no marked fluctuations in the density of *M. gapperi* across the four-year period (approximately ~ 5-6 voles/ha each year). However, there was spatial variation in density among grids, most notably with one mark-recapture grid in one year reaching high-density (26.29 voles/ha) while a grid a short distance away had low-density (1.64 voles/ha). We found home range and core area size were not density dependent. This is counter to many studies on terrestrial vertebrates (Adams 2001). However, another study looking across years also found that *M. gapperi* home range did not change with density in mixed forests of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) within Alberta, Canada (Bondrup-Nielson 1987). Longer-term studies of *M. gapperi* have found both stable densities across years (Mihok 1979; Fuller 1985; Boonstra and Krebs 2012), and boom and bust 4-year (Elias et al. 2006; Fauteux et al. 2015) and 7-year (Sullivan et al. 2017).
cycles. Density independence from home range dynamics suggests environmental factors (e.g. seasonality, Beer 1961; Boonstra and Krebs 2012 or habitat quality and type, Bondrup-Nielsen 1987) or interspecific interactions (e.g. competition, Dufour et al. 2015 or different foraging approaches, Mitchell and Powell 2004) may be structuring space use among *M. gapperi* in this region.

Amount of home range or core area overlap can show how individuals within a species interact with each other and the territoriality of a species (Jorgensen 1968). Female *M. gapperi* shared more of their area with males than other females. Females had very little overlap between core areas (~18%) which suggests that females actively defend or avoid other female’s core areas. Previous studies using mark-recapture grids have also suggested that female *M. gapperi* are territorial (Perrin 1979; Bondrup-Nielsen and Karlsson 1985). Females are likely defending their nests during the summer months, which are located within the core area of their home range and the areas directly around nest sites are important for gathering resources to rear young.

The patterns of shared space we documented among males as well as among males and females is indicative of a promiscuous breeding strategy (Merritt 1981). Males did not exclude other males from home range or core areas, suggesting they are not guarding one particular female. Male home ranges often overlap with multiple females and females were often sharing their home range and core areas with multiple males. These patterns highlight that to males, females are a resource sought out during the breeding season for mating opportunities (Bondrup-Nielsen 1986a).

Home range and core area estimates were not significantly different between mark-recapture and radiotelemetry methods for either female or male *M. gapperi*. This is consistent with previous studies of other vole species (Jones and Sherman 1983; Desy et al. 1989), however
Desy et. al (1989) found that mark-recapture derived home ranges were smaller than radiotelemetry derived home ranges, but only for individuals that were caught < 8 times. Desy et. al (1989) did not specify how sex was handled in their analysis and this result could have been a byproduct of sex differences; in our study we saw an effect of location number on home range estimates, but only for males. Previous studies on other small rodents found that radiotelemetry methods estimated larger home ranges than mark-recapture methods (Bergstrom 1988; Ribble et al. 2002). Studies on small to medium-sized marsupials [Sunquist et al. 1987 common opossum (Didelphis marsupialis); Bradshaw and Bradshaw 2002 honey possum (Tarsipes rostratus); Lira and Fernandez 2008 neotropical opossum (Philander frenatus)] have also found radiotelemetry to consistently yield larger home range estimates when compared to mark-recapture. These studies, in combination with our work, suggests differences between mark-recapture and radiotelemetry estimates may be species or system-specific.

Number of locations had an impact on the size of radiotelemetry male home range with more locations leading to a decrease in home range size. This may be due to males having larger home ranges and as location points are added there becomes greater precision in the reference smoothing bandwidth used to calculate the UD kernel density. Because males typically range farther than females (Bondrup-Nielsen 1987) they are more likely to range outside of a telemetry receiver’s ability to pick up the signal. Our data support this with 7 of 11 males missing location data on a given survey session due to inability to locate a signal. Five of these males returned to within signal strength range in a subsequent day; the remaining 2 may have experienced a collar failure or a predation event. In contrast, three of 12 females had missing location data due to inability to locate a radiotelemetry signal however, the signal was never located again for those three females indicating possible collar failure or predation event. Because dispersal is sex biased
such that males disperse more often and farther (Greenwood 1980) and we restricted collars to adults, dispersal events are unlikely to explain these lost signals.

Home range and core area estimates under mark-recapture and radiotelemetry were not significantly different for females or for males. However, male home range and core area estimates were larger (although not significantly different, $P = 0.16$) when calculated from radiotelemetry (2.1 ha) than from mark-recapture (1.3 ha). These mark-recapture grids are 1.1 ha in size and our findings suggest grid size may be truncating the male home range such that mark-recapture estimates approximate grid size at 1.3 ha and radiotelemetry estimates exceed mark-recapture estimates by over 50% (Figure 1.4). Although robust estimates of male *M. gapperi* home range size may require larger grids (closer to 3 ha) or radiotelemetry, female home ranges can be effectively calculated from 1 ha grids. Overall, our findings suggest mark-recapture and radiotelemetry provide similar estimates of home range and core area size for *M. gapperi* and possibly other small mammal species.
Table 1.1. Summary of the trap nights (one trap, set for 24-hour period) and captures for *Myodes gapperi* from 2014-2017. Total captures include number of times each individual was captured. Home ranges were calculated from individuals with 5 or more captures (77 home ranges). Grids were standardized; however, trap nights vary based on bear disturbance. If a trap was disturbed by bear and unable to catch an animal, then the trap night was considered lost.

<table>
<thead>
<tr>
<th>Year</th>
<th>Trap nights</th>
<th>Captures</th>
<th># Home ranges</th>
</tr>
</thead>
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<td></td>
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</tr>
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</tr>
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</tr>
<tr>
<td>2017</td>
<td>8738</td>
<td>112</td>
<td>346</td>
</tr>
</tbody>
</table>
Table 1.2. Comparison of mark-recapture (MR) and radiotelemetry (RT) methods on the size of home range and core area. Area is recorded as mean size in hectares ± SE. A Welch two-sample t-test was conducted to compare estimates between methods.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Distribution</th>
<th>Method</th>
<th>Mean size (ha)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Home range</td>
<td>MR (n = 42)</td>
<td>0.402 ± 0.048</td>
<td>0.7547</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RT (n = 10)</td>
<td>0.370 ± 0.043</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Core area</td>
<td>MR (n = 42)</td>
<td>0.135 ± 0.016</td>
<td>0.6055</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RT (n = 10)</td>
<td>0.117 ± 0.014</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>Home range</td>
<td>MR (n = 35)</td>
<td>1.329 ± 0.142</td>
<td>0.1617</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RT (n = 11)</td>
<td>2.107 ± 0.501</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Core area</td>
<td>MR (n = 35)</td>
<td>0.448 ± 0.050</td>
<td>0.2092</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RT (n = 11)</td>
<td>0.701 ± 0.184</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.3. Comparison of estimates of shared space use between mark-recapture and radiotelemetry methods. Proportion of overlap was measured for both home range and core area and a t-test was conducted separately within and among sexes. Overlap was considered the total proportion of the area shared. Comparison was conducted on proportions but, for clarity, results are shown as percent ± SE. Number of overlapping individuals is the average number of individuals that shared space with each focal individual ± SE.

<table>
<thead>
<tr>
<th>Focal individual</th>
<th>Shared individual</th>
<th>Distribution</th>
<th>Method</th>
<th>Mean overlap (%)</th>
<th>P-value</th>
<th># overlapping individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Female</td>
<td>Core area</td>
<td>MR (n = 16)</td>
<td>20.41 ± 4.42</td>
<td>0.3169</td>
<td>1.37 ± 0.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 3)</td>
<td>9.57 ± 2.71</td>
<td></td>
<td>1.33 ± 0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Home range</td>
<td>MR (n = 27)</td>
<td>39.45 ± 5.65</td>
<td>0.3608</td>
<td>1.70 ± 0.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 8)</td>
<td>29.23 ± 6.79</td>
<td></td>
<td>2.75 ± 0.45</td>
</tr>
<tr>
<td>Male</td>
<td>Female</td>
<td>Core area</td>
<td>MR (n = 28)</td>
<td>65.27 ± 6.76</td>
<td>0.6060</td>
<td>1.86 ± 0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 8)</td>
<td>57.41 ± 15.65</td>
<td></td>
<td>2.75 ± 0.45</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Core area</td>
<td>MR (n = 31)</td>
<td>91.95 ± 2.64</td>
<td>0.1929</td>
<td>2.32 ± 0.16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 9)</td>
<td>77.84 ± 9.69</td>
<td></td>
<td>3.33 ± 0.55</td>
</tr>
<tr>
<td>Male</td>
<td>Female</td>
<td>Core area</td>
<td>MR (n = 26)</td>
<td>31.41 ± 4.37</td>
<td>0.2974</td>
<td>1.96 ± 0.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 10)</td>
<td>22.88 ± 6.30</td>
<td></td>
<td>2.10 ± 0.43</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>Home range</td>
<td>MR (n = 28)</td>
<td>49.23 ± 5.12</td>
<td>0.1162</td>
<td>2.57 ± 0.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 10)</td>
<td>64.40 ± 6.45</td>
<td></td>
<td>3.00 ± 0.60</td>
</tr>
<tr>
<td>Male</td>
<td>Male</td>
<td>Core area</td>
<td>MR (n = 30)</td>
<td>57.82 ± 5.04</td>
<td>0.4493</td>
<td>1.53 ± 0.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 9)</td>
<td>66.19 ± 10.95</td>
<td></td>
<td>3.56 ± 0.44</td>
</tr>
<tr>
<td></td>
<td>Home range</td>
<td>MR (n = 31)</td>
<td>74.06 ± 4.45</td>
<td>0.1703</td>
<td>1.81 ± 0.15</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RT (n = 9)</td>
<td>86.45 ± 5.82</td>
<td></td>
<td>4.00 ± 0.50</td>
</tr>
</tbody>
</table>
Table 1.4. Summary of shared space within and among female and male *M. gapperi*. Averages reflect areas generated under both mark-recapture and radiotelemetry as no differences were detected between methods (Table 3). Overlap was considered the total proportion of the area shared between members of the overlap sex. Comparisons were conducted on proportions but, for clarity, are shown as percent ± SE. Significance were calculated using two-sample t-tests.

<table>
<thead>
<tr>
<th>Focal individual Distribution</th>
<th>Shared individual</th>
<th>Mean overlap (%)</th>
<th>P-value</th>
<th># overlapping individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female Core area</td>
<td>Female (n = 19)</td>
<td>18.69 ± 3.84</td>
<td>&lt; 0.0001</td>
<td>1.37 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>Male (n = 36)</td>
<td>63.52 ± 6.21</td>
<td></td>
<td>2.06 ± 0.15</td>
</tr>
<tr>
<td>Female Home range</td>
<td>Female (n = 35)</td>
<td>37.14 ± 4.64</td>
<td>&lt; 0.0001</td>
<td>1.94 ± 0.16</td>
</tr>
<tr>
<td></td>
<td>Male (n = 40)</td>
<td>88.78 ± 3.06</td>
<td></td>
<td>2.55 ± 0.18</td>
</tr>
<tr>
<td>Male Core area</td>
<td>Female (n = 36)</td>
<td>29.04 ± 3.62</td>
<td>&lt; 0.0001</td>
<td>2.00 ± 0.17</td>
</tr>
<tr>
<td></td>
<td>Male (n = 39)</td>
<td>59.76 ± 4.59</td>
<td></td>
<td>2.00 ± 0.20</td>
</tr>
<tr>
<td>Male Home range</td>
<td>Female (n = 38)</td>
<td>53.22 ± 4.24</td>
<td>&lt; 0.0001</td>
<td>2.68 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>Male (n = 40)</td>
<td>76.84 ± 3.75</td>
<td></td>
<td>2.30 ± 0.22</td>
</tr>
</tbody>
</table>
Figure 1.1. Estimates of home range and core area size utilizing mark-recapture and radiotelemetry methods for both adult female and male *M. gapperi*. Boxplots denote 25th, 50th and 75th percentiles: whiskers represent the lowest and highest datum within the 1.5 interquartile range. Dots represent outliers. Welch two-sample t-tests were used to compare methods with no differences determined significant.
Figure 1.2. Linear regression to assess whether home range area was sensitive to the number of locations for *M. gapperi* females (top/green) and males (bottom/yellow). Each data point represents the size of an individual’s home range and number of locations used to calculate that home range area. The shaded area represents the 95% confidence interval. Mark-recapture (left) data are compiled over 2014-2017 and radiotelemetry data (right) are from 2017. The regression for radiotelemetry males was the only significant regression (P = 0.0124).
Figure 1.3. Mean proportion of shared area between individuals. Female-male refers to the proportion of female home range that is shared with male individuals and male-female refers to the proportion of male home range that is shared with females. Boxplots denote 25th, 50th and 75th percentiles: whiskers represent the lowest and highest datum within the 1.5 interquartile range. Dots represent outliers.
Figure 1.4. Representative *M. gapperi* home ranges calculated using locations gathered through mark-recapture (left) and radiotelemetry (right). These data are not paired: for clarity, grids with greater sample sizes have been depicted here. Filled polygons represent female individuals and lines represent male individuals. The white box is the mark-recapture grid.
Figure 1.5. Density estimates for *M. gapperi* each year. Boxplots denote 25\textsuperscript{th}, 50\textsuperscript{th} and 75\textsuperscript{th} percentiles: whiskers represent the lowest and highest datum within the 1.5 interquartile range. Dots represent outliers. Density was modelled using the POPAN parameterized of Jolly-Seber models. ANOVA was used to compare among years and did not detect any significant differences. Outlier was removed from analyses (see text).
Figure 1.6. Comparison of whether shared space is density dependent. Shaded areas are 95% confidence intervals of linear regression model $R^2$ and p-values provided.
CHAPTER 2:

SOUTHERN RED-BACKED VOLE (MYODES GAPPERI) MICROHABITAT ASSOCIATIONS IN NEW ENGLAND FOREST STANDS

INTRODUCTION

Small mammals are an important component of a forest's ecosystem. They are embedded in many levels of the forest food web as both dispersers of seeds and fungal spores (Maser and Nussbaum 1978; Elias et al. 2006; Stephens et al. 2016) and as prey to a wide range of predator species (Hanski et al. 1991). They also serve as vectors for parasites, bacteria, and viruses that cause zoonotic disease (Ecke et al. 2017). Given that small mammals contribute to a set of diverse ecosystem functions and services, understanding the environmental factors that structure their distribution and habitat associations may inform on forest management and health.

Animals select for particular habitat characteristics at multiple spatial scales. Macrohabitats reflect coarse differences in abiotic and biotic conditions. At this scale, habitat selection reflects the placement of an individual’s home range on the landscape (Morris 1987; Rosenzweig 1991; Jorgensen 2004). A home range is the area an individual uses in their daily movement patterns (Burt 1943). Finer scale heterogeneity in conditions are captured through microhabitat characteristics which influence the behavior of the individual within their home range. Core areas are those areas where an individual spends a disproportionately greater amount of time and reflect the microhabitat or specific resource and environmental requirements that individuals are keying in on to survive and rear young (Morris 1987; Drickamer 1990). Therefore, core areas reflect areas of high resource quality and often contain nesting sites.
Identifying which microhabitat characteristics make up a core area can provide insight into which resources are most important for a species. This is particularly the case for small mammal species (mass < 250g) because they live and interact with their environment at a micro-scale.

The southern red-backed vole (*Myodes gapperi*, Vigors 1830) is broadly distributed in North America, but most typically found in northern mountainous forest systems (Miller and Getz 1972; Merritt 1981). This species is an important disperser of mycorrhizal fungi (Linzey and Linzey 1973; Orrock and Pagels 2002) which contributes to overall forest health. As forests experience increasing pressure under climate change, invasive pests, and human disturbances it is important to identify characteristics that structure a species home range to ensure the effects of forest disturbance can be predicted and mitigated. This study aims to evaluate the macrohabitat and microhabitat characteristics that structure southern red-backed vole space use.

**METHODS**

**Study System & Mammal Data Collection**

Small mammal surveys were conducted at the Bartlett Experimental Forest, White Mountain National Forest, New Hampshire (44° 3’ 7.2” N, 71° 17’ 25.1” W). Mark-recapture grids were established within three forest types that were categorized by the percentage of hardwood basal area (HBA, see Stephens et al. (2017): hardwood (n = 4, avg. 91% HBA), mixed (n = 4, avg. 52.5% HBA), and softwood (n = 4, avg. 25.5% HBA). Dominant hardwood species include American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) and dominant softwood species include eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*).
Each grid consists of an 8 x 8 array of Sherman live traps (H. B. Sherman Co., Tallahassee, Florida) with each trap placed 15m apart (~1 ha). Captured individuals were identified to species, and sex, weight (g), age class (i.e. juvenile, sub-adult, and adult), and reproductive condition were recorded. Age class was determined based on body size and reproductive condition (e.g., testes position and vaginal perforation). Individuals were marked with a unique identification number using either an ear tag (model 1005-1; National Band and Tag Company, Newport, Kentucky) or a Passively Integrated Transponder (PIT; HPT9 (9mm x 2.1mm) BioMark, Inc, Boise, Idaho) and released. Location data for generating home range and core areas came from mark-recapture and radiotelemetry surveys in the summer of 2017. Trap visitation data used to assess macrohabitat affinity came from mark-recapture surveys in the summers of 2013-2017. Of the fifteen small mammal species (9 rodents, 6 shrews) that have been captured on the grids, the southern red-backed vole is among the five most common, which collectively represent ca. 90% of all captures.

Female southern red-backed voles (n= 10; weight ≥ 19g) caught on the mark-recapture grids in 2017 were fit with VHF radio collars (BD-2XC 0.75g; Holohil Systems Ltd., Carp, Ontario, Canada) to better assess their space use and habitat affinity. Collars were equipped with a TYGON sleeve that fastened around the individual’s neck to avoid chafing. Radio collars were ≤ 4% of the individual’s body weight to ensure collars did not interfere with daily activity and behavior (Millspaugh et al. 2012b). Only females were used in these analyses because the home ranges of males are influenced by factors other than microhabitat characteristics as males use females as a resource (Bondrup-Nielson 1986b) and may therefore bias analysis of the microhabitat selection.
Individuals were collared from July to August 2017 and collars were removed after 16 days (± 2.24) on average. Individuals were tracked twice daily except in cases of poor weather conditions that prohibited tracking or when the signal could not be located. Locations of tracked individuals were marked with GPS coordinates (Garmin GPSMAP 64s). The protocol for small mammal trapping and radiotelemetry was approved by the University of New Hampshire Animal Care and Use Committee (protocol # 120708, 140304, 160507) and followed guidelines outlined by the American Society of Mammalogists (Sikes et al. 2016).

Habitat characteristics

Habitat characteristics were measured at each trap station on every grid and at each tracked location when locations were greater than one meter apart. Characteristics were placed into three categories: forest structure (n = 20), ground cover (n = 7), and geographic feature (n = 1) (Table 2.1). Forest structure was measured in five-meter radius plots around trap stations (see Stephens et al. 2017) and three-meter radius plots around tracked locations; measurements included the diameter at breast height (DBH) of 9 tree species and unidentified snags and a count of the understory stems (trees with a DBH < 3 cm) of 9 tree species and unidentified snags (Table 2.1). Basal area per hectare (BA) of each tree species was calculated from DBH. Percent ground cover was measured using a one-meter-squared plot and recorded for six categories: forbs, shrubs, leaf litter, moss, and soil. Leaf litter depth (mm) was measured at the center of each one-meter-squared plot. The volume of coarse woody debris (CWD) was calculated by measuring the length and width of woody debris within the three-meter radius around each trap station and tracked location. The geographic feature, distance to stream (m), was extracted from the National Hydrologic Layer (Simley and Carswell Jr 2009) using 2.5m buffers using ArcGIS.
v10.3 (ESRI, Inc., Redlands, California, USA). All measured habitat characteristics were considered for both macro and micro scale habitat assessments.

**Modeling home range and core area**

Home ranges were modelled with a utilization distribution (UD) kernel density model (Van Winkle 1975; Worton 1989) using a fixed kernel smoothing bandwidth selected by reference. The home range was delimited at the 95% UD isopleth to ensure potentially misleading outliers did not skew area estimates (Anderson 1982). A fixed kernel with smoothing bandwidth selected by reference was used to decrease bias for home range estimations and to accommodate our small sample sizes (Worton 1989; Seaman et al. 1991; Kie 2013).

Core areas were calculated following Vander Wal and Rodgers (2012) by plotting the utilization distribution area (size of region within UD isopleth) against the volume and the point at which the slope of the fitted line was equal to 1. This point marks the isopleth value that was used to define the boundary of the core area (Vander Wal and Rodgers 2012). Home range and core area were modeled for each collared female who was located ≥ 5 times using the ‘adehabitatHR’ package (Calenge 2006) via R 3.5.0 software (R Core Team 2017).

**Assessing habitat associations**

Primary habitat associations (on the macro scale) were based on mark-recapture data from 2013-2017 and a two-sample t-test, with unequal variance, was used to determine significant differences in habitat characteristics between visited trap stations and not visited trap stations. Visited trap stations were trap stations that had caught a minimum of one red-backed vole in any year while not visited trap stations were those that never caught a red-backed vole.
Fine scale habitat associations (on the micro scale) were determined by creating a microhabitat profile of the core area using logistic regression model selection. First, an interpolated surface was generated for each of the microhabitat characteristic using the data collected at all mark-recapture trap stations and locations tracked with radiotelemetry. Radiotelemetry provides resolution at a finer scale than the 15m spacing of the trap stations on the mark-recapture grid as it tracks the natural movements of the individual. Interpolated surfaces were calculated using inverse distance weighting in QGIS (QGIS Development Team 2018) (Figure 2.1). The modeled core area and home range area for each female (n = 10) were overlaid onto the interpolated surface and vegetation and physiographic values were extracted. Sampling habitat within each female’s home range was area-standardized with 18 random points placed in the core area and 42 in the home range to give an average of 1 point in every 66.67 m² (average female home range size = 0.40 ha see Chapter 1).

Habitat characteristics were standardized before entering logistic regression models and collinearity was tested (no correlation values were > 0.60). Logistic regression model selection and importance ranking was performed within the package ‘glmulti’ in the R software using a genetic approach due to the large starting variable set (Calcagno and Mazancourt 2010). Models were ranked with Akaike Information Criterion (AIC). The top model was selected (ΔAIC = 0) as having covariates most likely to explain the response. AIC is known to rank overparameterized models more highly than models with less parameterization (Arnold 2010). To adjust for over parameterization, covariates were tested for non-significance with likelihood ratio tests to compare the full model to a model without the effect in question. The final model was determined by dropping covariates deemed non-significant (p-value > 0.05) under the likelihood ratio tests. An exhaustive model set was then run to calculate cumulative AIC weights.
(relative importance values) which we interpret as the strength of support for each covariate (Burnham and Anderson 2002). As posterior probabilities over the set of hypotheses, relative importance values > 0.70 and > 0.90 were interpreted as moderate and strong evidence, respectively.

**RESULTS**

Of 768 trap stations on the 12 mark-recapture grids, 48% caught a red-backed vole between 2013-2017. Trap-station based analysis of macrohabitat associations found voles were captured in areas that had significantly more eastern hemlock \( t = -5.0977, df = 721.46, P < 0.001 \), more coarse woody debris (CWD) per hectare \( t = -2.0904, df = 747.53, P = 0.037 \), and less American beech basal area \( t = 8.0637, df = 691.41, P < 0.001 \) (Figure 2.2).

Female red-backed voles \( (n = 10) \) had an average home range size of 0.370 ha ± 0.043 with a core area size of 0.117 ha ± 0.014 (Chapter 1). All core areas were calculated to be between the 59-62% isopleth.

For the microhabitat assessment within the core areas, twelve of the 28 habitat covariates were included within the top model and of those 12, three were determined non-significant through likelihood ratio tests. Therefore, the final model that best fit our data contained nine covariates from forest structure (red maple BA, yellow birch BA, hemlock stems, beech stems, and snag BA), ground cover (moss, CWD, and leaf litter depth), and geographic features (distance to steam) (Table 2.2). Calculated cumulative AIC weights of the covariates from the top model revealed 6 habitat characteristics as very important > 0.90 (distance to stream, red maple BA, leaf litter depth, yellow birch BA, hemlock stems) and 2 (moss, beech stems) as moderately important > 0.70 (Table 2.3) in microhabitat selection.
DISCUSSION

Macrohabitat associations were identified by comparing areas that had captured at least one red-backed vole to areas that had not captured any red-backed voles. Our findings support previous studies that suggest voles select for macrohabitats with coarse woody debris (CWD) and eastern hemlock (Yamasaki et al. 1999; Fauteux et al. 2013; Craig et al. 2014). CWD is an important structural element that provides cover and nest sites (Maser and Trappe 1984; Bowman et al. 2000; Fauteux et al. 2012). Decayed wood also provides moist micro-conditions and can facilitate nutrient cycling which contributes to availability of fungi (Maser and Trappe 1984), a primary food source for the southern red-backed vole (Linzey and Linzey 1973; Orrock and Pagels 2002).

Female red-backed voles are known to be territorial and exclude conspecific females from their defended home ranges and core areas (Bondrup-Nielson and Karlsson 1985; Chapter 1). Territoriality suggests the required resources to rear young and survive must be encompassed within the core area. Females selected core areas closer to water, with more red maple basal area, greater leaf litter depth, less yellow birch basal area, and more hemlock stems. Proximity to water may correspond with the poor kidney function of the southern red-backed vole which requires greater intake of water in their diet, either via vegetation or free-standing water (Getz 1968). While southern red-backed voles primarily eat fungi, they are opportunists and will eat a variety of foods including seeds (Linzey and Linzey 1973; Orrock and Pagels 2002). It is likely females select for areas with red maple as a secondary food choice. Red maple seeds are abundantly available for a short period during the year and fluctuate in volume year to year.
In addition to food items, microhabitat conditions may also reflect locomotor mode and structural conditions that promote predator avoidance. Southern red-backed voles may be selecting for deeper leaf litter because they are sub-fossorial and develop extensive tunneling systems. Deeper leaf litter layers may help facilitate these burrows. Although we did not see a correlation between leaf litter depth and hemlock basal area ($r = 0.158$), deeper leaf litter is often associated with eastern hemlock forests due to acidic soils which slow decomposition rates (Orwig et al. 2002; Evans 2004). Our finding that hemlock stems may be important to core area selection supports previous studies that demonstrated that red-backed voles prefer close-to-the-ground vegetation (Lovejoy 1975) or dense shrub coverage (Miller and Getz 1972). There is a strong tendency of small mammals to move and forage under cover to avoid risk of predation.

Conclusion

Eastern hemlock forests in New England are declining as the eastern hemlock woolly adelgid (*Adelges tsugae*, Annand 1928) moves northward (McClure 1991; Orwig et al. 2002; Ellison et al. 2005). Eastern hemlocks are a long-lived, shade tolerant foundation species (Ellison et al. 2005) that affect numerous populations of forest-dwelling species including ants (Record et al. 2018), birds (Tingley et al. 2002), salamanders (Siddig et al. 2016), and small mammals (Degrassi 2018), but little is known on how the loss of eastern hemlock may impact individual behavior or habitat selection on a micro-scale. There is no known tree species that can replace the ecological function of eastern hemlocks in New England forests (Evans 2004). This study demonstrated that red-backed voles select for macrohabitats with eastern hemlock and that
within these eastern hemlock stands, females are selecting for microhabitats with water, red maple, deep leaf litter for burrowing, and young hemlocks for possible cover (Table 2.3). As a foundation species, eastern hemlock influences biogeochemical and biophysical processes, including microclimate (Lustenhouwer et al. 2012) and stream flow (Brantley et al. 2015). Together, these critical processes create microhabitat conditions that may influence core habitat selection of southern red-backed voles and possibly other species that depend on eastern hemlock.

In addition, individual tree loss of eastern hemlocks, caused by hemlock woolly adelgid infestation, opens the otherwise closed canopy and allows more light to reach the forest floor which stimulates growth of hardwood species (Kizlinski et al. 2002; Farnsworth et al. 2012). Our study demonstrates that eastern hemlock cover (stems) is important in core area selection (0.98 importance, Table 2.3) and hardwood species (i.e. beech stem growth and yellow birch basal area) are actively being selected against (Tables 2.2 and 2.3). The loss of foundation eastern hemlock trees will likely influence home range placement of southern red-backed voles and therein the ecological interaction and dispersal of eastern hemlock seed and mycorrhizal fungi (Stephens et al. 2017) in New England forests.
<table>
<thead>
<tr>
<th>Microhabitat characteristic</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forest structure</strong></td>
<td></td>
</tr>
<tr>
<td>Diameter at breast height (DBH) (cm):</td>
<td></td>
</tr>
<tr>
<td>American beech (<em>Fagus grandifolia</em>)</td>
<td></td>
</tr>
<tr>
<td>Balsam fir (<em>Abies balsamea</em>)</td>
<td></td>
</tr>
<tr>
<td>Eastern hemlock (<em>Tsuga canadensis</em>)</td>
<td></td>
</tr>
<tr>
<td>Paper birch (<em>Betula papyrifera</em>)</td>
<td></td>
</tr>
<tr>
<td>Red maple (<em>Acer rubrum</em>)</td>
<td></td>
</tr>
<tr>
<td>Red spruce (<em>Picea rubens</em>)</td>
<td></td>
</tr>
<tr>
<td>White ash (<em>Fraxinus americana</em>)</td>
<td></td>
</tr>
<tr>
<td>White pine (<em>Pinus strobus</em>)</td>
<td></td>
</tr>
<tr>
<td>Yellow birch (<em>Betula alleghaniensis</em>)</td>
<td></td>
</tr>
<tr>
<td>Snag</td>
<td></td>
</tr>
<tr>
<td><strong>Stems:</strong></td>
<td></td>
</tr>
<tr>
<td>American beech (<em>Fagus grandifolia</em>)</td>
<td></td>
</tr>
<tr>
<td>American witch-hazel (<em>Hamamelis virginiana</em>)</td>
<td></td>
</tr>
<tr>
<td>Balsam fir (<em>Abies balsamea</em>)</td>
<td></td>
</tr>
<tr>
<td>Eastern hemlock (<em>Tsuga canadensis</em>)</td>
<td></td>
</tr>
<tr>
<td>Hobblebush (<em>Viburnum lantanoides</em>)</td>
<td></td>
</tr>
<tr>
<td>Red spruce (<em>Picea rubens</em>)</td>
<td></td>
</tr>
<tr>
<td>Striped maple (<em>Acer pensylvanicum</em>)</td>
<td></td>
</tr>
<tr>
<td>White ash (<em>Fraxinus americana</em>)</td>
<td></td>
</tr>
<tr>
<td>Yellow birch (<em>Betula alleghaniensis</em>)</td>
<td></td>
</tr>
<tr>
<td>Snag</td>
<td></td>
</tr>
<tr>
<td><strong>Ground cover</strong></td>
<td></td>
</tr>
<tr>
<td>Leaf litter depth (mm)</td>
<td></td>
</tr>
<tr>
<td>Coarse woody debris (CWD, volume per hectare)</td>
<td></td>
</tr>
<tr>
<td>Percent cover:</td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td></td>
</tr>
<tr>
<td>Leaf litter</td>
<td></td>
</tr>
<tr>
<td>Moss</td>
<td></td>
</tr>
<tr>
<td>Shrub</td>
<td></td>
</tr>
<tr>
<td>Soil</td>
<td></td>
</tr>
<tr>
<td><strong>Geographic feature</strong></td>
<td></td>
</tr>
<tr>
<td>Distance to stream (m)</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2. Summary of output from the best (ΔAIC = 0) generalized logistic regression model of the microhabitat characteristics. Those microhabitat characteristics (n = 3) deemed not significant under likelihood ratio tests were excluded. Table includes coefficient estimates, standard error (SE) and confidence intervals (lower and upper 95%), and significance (p-value) test of the null hypothesis (coefficient = 0). BA = basal area (cm), CWD = coarse woody debris.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>Lower</th>
<th>Upper</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.6536</td>
<td>0.0983</td>
<td>-0.8498</td>
<td>-0.4640</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>hemlock stems</td>
<td>0.3693</td>
<td>0.1073</td>
<td>0.1600</td>
<td>0.5817</td>
<td>0.0006</td>
</tr>
<tr>
<td>beech stems</td>
<td>-0.2204</td>
<td>0.1123</td>
<td>-0.4445</td>
<td>-0.0037</td>
<td>0.0496</td>
</tr>
<tr>
<td>yellow birch BA</td>
<td>-0.4229</td>
<td>0.1591</td>
<td>-0.7872</td>
<td>-0.1551</td>
<td>0.0079</td>
</tr>
<tr>
<td>red maple BA</td>
<td>0.4163</td>
<td>0.1203</td>
<td>0.1900</td>
<td>0.6614</td>
<td>0.0005</td>
</tr>
<tr>
<td>snag BA</td>
<td>0.1551</td>
<td>0.0895</td>
<td>-0.0279</td>
<td>0.3346</td>
<td>0.0831</td>
</tr>
<tr>
<td>moss</td>
<td>-0.2501</td>
<td>0.1092</td>
<td>-0.4733</td>
<td>-0.0439</td>
<td>0.0220</td>
</tr>
<tr>
<td>leaf litter depth</td>
<td>0.3653</td>
<td>0.1006</td>
<td>0.1695</td>
<td>0.5650</td>
<td>0.0003</td>
</tr>
<tr>
<td>distance to stream</td>
<td>-0.7423</td>
<td>0.1187</td>
<td>-0.9834</td>
<td>-0.5175</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>CWD</td>
<td>-0.1455</td>
<td>0.1022</td>
<td>-0.3602</td>
<td>0.0455</td>
<td>0.1546</td>
</tr>
</tbody>
</table>
**Table 2.3.** The relative importance for each variable from the top model (ΔAIC = 0). Importance is calculated from the sum of Akaike weights of all models in which the predictor is present resulting in a balanced model set. BA = basal area, CWD = coarse woody debris.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Relative importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.000</td>
</tr>
<tr>
<td>distance to stream</td>
<td>1.000</td>
</tr>
<tr>
<td>red maple BA</td>
<td>0.998</td>
</tr>
<tr>
<td>leaf litter depth</td>
<td>0.996</td>
</tr>
<tr>
<td>yellow birch BA</td>
<td>0.986</td>
</tr>
<tr>
<td>hemlock stems</td>
<td>0.981</td>
</tr>
<tr>
<td>moss</td>
<td>0.814</td>
</tr>
<tr>
<td>beech stems</td>
<td>0.719</td>
</tr>
<tr>
<td>snag BA</td>
<td>0.640</td>
</tr>
<tr>
<td>CWD</td>
<td>0.537</td>
</tr>
</tbody>
</table>
Figure 2.1. Example of interpolated surfaces calculated from the microhabitat characteristics with female home range and core areas overlaid. Interpolated surface of distance to stream (left) and red maple basal area (right). Darkest red areas represent clusters of red maple trees, dark blue represents the path of the stream. Each pixel is 0.5m$^2$ in size.
Figure 2.2. Comparison of the three significant macrohabitat characteristics at visited trap stations and not visited trap stations. Boxplots denote 25th, 50th and 75th percentiles: whiskers represent the lowest and highest datum within the 1.5 interquartile range. Dots represent outliers.
LITERATURE CITED


LAAKE, J. L. 2016. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK.
93:948–958.


APPENDIX

University of New Hampshire
Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3584

01-Apr-2014

Rowe, Rebecca J
Natural Resources & the Environment, James Hall Rm 136
Durham, NH 03824

IACUC #: 140304
Project: Abiotic and Biotic Drivers of Small Mammal Community Structure in the White Mountain National Forest
Category: D
Approval Date: 21-Mar-2014

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used. The IACUC made the following comment(s) on this protocol:

1. All principal investigators/instructors are responsible for knowing about zoonotic diseases, safety issues, laws, and regulations applicable to the proposed field study activity, taking appropriate precautions, instructing/informing project personnel and students ahead of time about pertinent issues accordingly, and ensuring project personnel review the collection permit before capturing/trapping/handling any animals. Please contact the UNH Office of Environmental Health & Safety (603/862-4041) with any questions.
2. The investigator is responsible for obtaining any necessary permits for capturing animals as proposed in the study.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill A. McCaughey, Ph.D.
Chair

cc: File
University of New Hampshire

Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

27-Aug-2012

Rowe, Rebecca J
Natural Resources & the Environment, James Hall Rm 114
Durham, NH 03824

IACUC #: 120708
Project: Species Vulnerability to Environmental Change: Insights from Land-Use Legacies
Category: D
Approval Date: 22-Aug-2012

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

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If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill A. McCaughey, Ph.D.
Chair

cc: File
University of New Hampshire
Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

16-Jun-2016

Rowe, Rebecca J
Natural Resources & the Environment
James Hall Rm 136
Durham, NH 03824-2601

IACUC #: 160507
Project: The Population and Community Ecology of Small Mammals in the White Mountain National Forest
Approval Date: 16-Jun-2016

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used. The IACUC made the following comment(s) on this protocol:

1. The investigator is responsible for obtaining any necessary permits for capturing animals as proposed in the study.
2. All principal investigators/instructors are responsible for knowing about zoonotic diseases, safety issues, laws, and regulations applicable to the proposed field study activity, taking appropriate precautions, instructing/informing project personnel and students ahead of time about pertinent issues accordingly, and ensuring project personnel review the collection permit before capturing/trapping/handling any animals. Please contact the UNH Office of Environmental Health & Safety (603/862-4041) with any questions.

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2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill A. McGaughey, Ph.D.
Chair

cc: File