

**Small Mammals, Habitat, and Forest Restoration at
Seney National Wildlife Refuge**

by

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ABSTRACT

My study took place at Seney National Wildlife Refuge (SNWR) in the east-central Upper Peninsula of Michigan. Recently, SNWR forest management has attempted to build and maintain biological integrity through ecological restoration. In order to inform managers about wildlife habitat requirements, my study focused on the habitat use of small mammals. I investigated at which scale, macro- or microhabitat, habitat elements predicted the presence of small mammals. I predicted: 1) small mammal communities in near old-growth stands will be more abundant than in logged habitats proposed for restoration and 2) small mammal species composition, in mature and second-growth conifers and hardwoods, can be predicted by specific habitat characteristics such as coarse woody debris abundance and basal area of trees.

I trapped small mammals in eight hardwood stands, with four replicates each of mature and second-growth forest stands, and in nine coniferous sites with three replicates of each category (mature, second-growth, recently cut). Small mammals were live-trapped during July and August in 2004 and 2005; vegetation measurements were taken during the summer of 2005. At the macrohabitat scale, no significant differences were found between small mammal captures and site categories on either deciduous or coniferous plots even though differences in habitat structure among site categories existed (evident in the principle components analysis). However, my results supported the hypothesis that microhabitat features are important in predicting the distribution of small mammals. At the micro-scale, the binomial regression analysis identified three important habitat elements on which managers should concentrate restoration efforts: coarse woody debris, snags, and tree species diversity. Many other wildlife species depend on the same habitat elements as small mammals and a management focus on these three habitat components during restoration will help to obtain overall biological integrity.

INTRODUCTION

Over a century ago, extensive logging dramatically altered Michigan's Upper Peninsula forests. Large-scale deforestation began in the eastern Upper Peninsula (EUP) in 1835; loggers targeted principally white pines (*Pinus strobus*) until they were depleted in the early 1900s (Beyer et al. 1997). They then refocused on Eastern hemlock (*Tsuga canadensis*) and hardwoods (sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*)). Clear-cutting greatly diminished old-growth white pine and hemlock forests, leaving today's early successional forests of primarily jack pine (*Pinus banksiana*).

Logging remains important in the EUP, with paper companies owning 12% of the land (191,000 ha). In contrast, state and federal agencies own 53% of the land area (853,150 ha; Beyer et al. 1997). Seney National Wildlife Refuge (SNWR) comprises 38,650 ha of this public land. It is mostly second-growth forest; before its establishment in 1935, SNWR was used for agriculture and timber extraction. Today, SNWR serves as an important ecological reserve and is the home of many species, including threatened grey wolves (*Canis lupus*). Notably, 10,178 ha of SNWR are designated as protected Wilderness (Anderson 1982).

Recently, NWR forest management has attempted to build and maintain biological integrity. Ecological restoration is a common approach. In accordance with the National Wildlife Refuge System Improvement Act of 1997 (House Resolution 1420), SNWR managers have initiated an ecological restoration program to restore logged forests to approximate presettlement conditions. Forest restoration is often used in an attempt to compensate for many years of fire suppression (Covington 1997) or logging. The Act mandates that Refuges have a management goal to preserve biological integrity, defined as "the capability of maintaining and supporting a balanced, integrated, adaptive community of organisms, having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley 1981). A community with high biological integrity is one that has existed under natural conditions for some considerable period (Angermeier and Karr 1994). Unfortunately, preserving biological integrity is not a well-defined management goal. It is difficult, for example, to know what presettlement and "natural" conditions were, and to what extent they had been affected by Native Americans. However, efforts can be made to restore ecosystem components that are possible to manage.

Measuring biological integrity is difficult. In order to do this, SNWR managers wish to gather as much information as possible about the habitat requirements of all wildlife species on the Refuge. Most Refuge research has been focused on birds and a few individual species (e.g., wolves). Research on small mammal habitat use helps to broaden their knowledge. Small mammals are often used as an indicator species group (Carey and Johnson 1995; Carey and Harrington 2001; Pearce and Venier 2005) to reflect some aspects of “integrity.” A biological indicator is “an organism whose characteristics, such as presence or absence, population density, dispersion, reproductive success, are used as an index of attributes too difficult, inconvenient, or expensive to measure” (Landres et al. 1988). Small mammals are an appropriate indicator group in part because they have important ecosystem roles. They are primary consumers (Huntly 1991). After a disturbance such as fire, pioneering small mammals may be important seed sources for plant regeneration. Ectomycorrhizal fungi and nitrogen-fixing bacteria depend on consumption by small mammals for dispersal (Sieg 1987). Small mammals increase vegetation decomposition rates, and they are more efficient than both ungulates and insects at mineralizing organic matter (Hayward and Phillipson 1979). They are also prey for many larger mammals, birds, and reptiles. More broadly, niche separation of different small mammal species on the forest floor may be an indicator of the number of available trophic pathways (Carey and Harrington 2001).

Certain habitat elements are good predictors of the presence of small mammal species. For example, coarse woody debris is an important habitat component for small mammals (Harmon et al. 1986; Loeb 1993; Carey and Johnson 1995; Ford et al. 1997; Menzel et al. 1999; Bowman et al. 2000). Studying small mammal abundances and their associated habitat components in SNWR will give management additional information on how best to manage for biological integrity. In SNWR forests, the most common species are woodland deer mice (*Peromyscus maniculatus gracilis*), white-footed mice (*Peromyscus leucopus*), red-backed voles (*Clethrionomys gapperi*), short-tailed shrews (*Blarina brevicauda*), masked shrews (*Sorex cinereus*), and eastern chipmunks (*Tamias striatus*).

Here, I address macro- and microhabitat effects separately in both hardwood and conifer plots. Macrohabitat, as defined by Morris (1987), is the scale at which “the minimum area corresponds to that within which an average individual performs all of its biological functions (home range) during a typical activity cycle.” Microhabitat includes the “physical/chemical

variables that influence the allocation of time and energy by an individual within its home range” (Morris 1987). I investigate the following three questions. Do small mammal communities vary with the successional forest stage they live in? Data collection at which scale, macro- or microhabitat, more reliably predicts the presence of small mammals? Can SNWR use these variables to inform their management (restoration) decisions?

I hypothesize that small mammal abundances are affected by both macro- and micro-habitat structures. My first prediction is that small mammal communities in near old-growth stands will be more abundant than in logged habitats proposed for restoration because old-growth stands are more favorable for most native species than disturbed habitats (Carey 1995, Carey and Johnson 1995). My second prediction is that small mammal species composition, in old-growth and second-growth conifers and hardwoods, can be predicted by specific habitat characteristics such as coarse woody debris abundance and basal area of trees.

MATERIALS AND METHODS

Study area.-- My study site is in Seney National Wildlife Refuge, east-central Upper Peninsula, Schoolcraft County, Michigan (elevation 207-219 m; 46.16° - 46.35°N and 85.93° - 86.26°W). The Refuge (38,650 ha) contains wetlands and forests, including 10,178 ha that comprise the Strangmoor Bog National Natural Landmark and the Seney Wilderness Area. Overall, SNWR is 26% deciduous shrub wetlands, 26% perennial grass wetlands, and 24% forested evergreen upland. The remaining 24% varies greatly in habitat type (Tansy et al. 2003).

I classified hardwood and conifer study sites into three categories: reference stands, stands proposed for restoration, and treated stands. “Reference” stands were logged more than 100 years ago and have remained untouched since logging. “Proposed” stands were logged within the last 100 years (logging dates vary widely) and are targeted for restoration. “Treated” stands were logged within the last ten years as part of restoration efforts.

I trapped small mammals in hardwood stands in 2004 and in coniferous stands in 2005, because my goal was comparison of stands within each habitat type rather than across habitat types, and large annual variations in small mammal populations would have made year-to-year comparisons difficult. I trapped in eight hardwood stands, with four replicates each of proposed and reference stands. The Refuge had no available treated hardwood stands. All sites were at least 800 m apart to ensure sampling independence (Bowman et al. 2000). These sites are dominated by sugar maple, American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), paper birch (*Betula papyrifera*), and red maple (*Acer rubrum*). A total of nine coniferous sites were trapped with three replicates of each category (reference, proposed, treated). Coniferous sites were dominated by red pine (*Pinus resinosa*), white pine (*Pinus strobus*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*).

Field methods.--Seventeen study sites were selected from accessible coniferous and hardwood areas at the Refuge. Two parallel transects, 75 m apart, were placed within each site, at least 50 m from edges, and at least 20 m from any used road (Bowman et al. 2001). The starting point for each transect was chosen randomly from the range of locations that were logistically possible. Each transect consisted of 25 stations spaced 10 m apart. Two collapsible Sherman live traps (H.B. Sherman Traps, Inc., Tallahassee, FL), one large (8 x 9 x 23 cm) and one small (5 x 6 x 15 cm), were placed at each trap station.

In 2004, Tomahawk traps (Tomahawk Live Trap Company, Tomahawk, WI; 40 x 13 x 13 cm) were positioned at every other trap station. In 2005, Tomahawks were placed at every fourth station because sites were trapped simultaneously and I had a limited number of Tomahawk traps. The Tomahawk traps contained polyester fiberfill for insulation and were covered with leaf litter to provide shelter from the elements. Traps were placed at microsites that small mammals use, such as logs, burrows, and runways, and in areas that did not have direct sunlight (to prevent overheating). All traps were put within one m of the station and were baited with a 50:50 mixture of sunflower seeds and oats. Traps were checked in the morning (0700-1100 h) and evening (1800-2100 h); they remained open 24 hours a day. Capture methods followed the American Society of Mammalogists' (1998) guidelines, and were approved by the University Committee on the Use and Care of Animals at the University of Michigan (UCUCA protocol #7773).

Small mammals were live-trapped during July and August in 2004 and 2005 because this is when population numbers peak (Myers, unpubl. data). When possible, reference and proposed (or treated, in 2005) sites were trapped simultaneously to minimize temporal variation. The sampling effort was 1800 trap-nights in 2004 and 1700 trap-nights in 2005. Analysis does not include traps that were set off and therefore incapable of capturing a small mammal (Nelson and Clark 1973). Effort decreased in 2005 because I trapped two sites simultaneously and therefore had to use fewer Tomahawk traps at each site than in 2004 (11 versus 23). Each site was trapped for three consecutive nights.

For all captured animals I recorded the time of capture, station number, trap type, species, weight, tail and hind foot length, ear length (for *Peromyscus spp.* only), and any disturbance to the trap. Captured animals were categorized as juveniles or adults, determined by pelage and weight. Saliva samples were taken for *Peromyscus* that could not easily be identified to species. Reproductive status was determined, when possible, by the position of the testes (descended or abdominal) in males and state of the nipples (tiny versus enlarged with evidence of lactation such as hair removed near teats) in females. A patch of fur above the tail was clipped to mark individuals temporarily, allowing the identification of recaptures. Captured animals were released immediately after processing at the trap station. Temperature and precipitation at time of trap-checking were also recorded. Dead specimens were prepared and contributed to the University of Michigan's Museum of Zoology, Ann Arbor, Michigan.

All vegetation measurements were taken during the summer of 2005. Percent canopy cover was measured with a spherical densiometer (four readings in each cardinal direction) and percent slope was measured with a Suunto clinometer. Woody plants with a diameter at breast height (DBH) > 0.04 m and height > 1.0 m were defined as trees (Orrock and Pagels 2003). Tree species and DBH were recorded for all individuals within a five m radius around each trap station. I used the line intercept method to estimate coarse woody debris (CWD), following the method outlined in Harmon and Sexton (1996). I selected two randomly chosen five m transects that extended out from the trap location. For each piece of CWD (> 10 cm diameter and one m in length) encountered along the transect I recorded the following: decay class as defined by Harmon and Sexton (1996), length, and diameter. The volume of CWD was calculated according to the formula suggested by Harmon and Sexton (1996). All snags and stumps within a five m radius of each trap location were recorded. I recorded three attributes for snags: decay class, DBH, and height. For stumps, the base diameter and decay class were recorded.

I recorded percent cover within each five m radius at three layers: the herbaceous (0 - 0.5 m from forest floor), short (0.51 - 0.75 m), and tall (0.76 – 1.5 m) layers using the Braun-Blanquet scale (Braun Blanquet 1928). Ground cover percentage was visually estimated within two randomly chosen Daubenmire plots (one m square) that fell within the five m square. The following categories were used for ground cover: saplings, wood, dirt, grass, ferns, leaves, moss, lichen and slash (Bonham 1989). The dominant ground cover species for the entire five m square was also recorded at each station. See Table 1 for a complete list of measurements taken and used for the analysis.

Statistical analysis.-- Principle components analysis (R Development Core Team 2005) was used to characterize the differences in habitat variables among site treatments by visual observation of biplots (PC1 vs. PC2, PC1 vs. PC3, PC2 vs. PC3). Prior to the PCA, each variable was centered and scaled to have a mean of zero and a standard deviation of one. Eigenvalues were examined to determine how many principle components to interpret. All variables used in the binomial regression, except abundances of individual tree species, were included in the PCA. Since tree species abundances were not included in the PCA, I conducted a separate analysis of the simple distribution of tree species among site categories.

I also analyzed the tree species composition of each site. Trees that made up more than two percent of the total trees were included in the analysis. A two-sample *t*-test was used to compare species composition of the deciduous sites (between categories); one-way ANOVA was used to compare the coniferous sites (among categories).

At the macrohabitat scale, total small mammal captures were compared with a two-sample *t*-test for the two treatments (proposed, reference) in hardwoods. One-way ANOVA (SPSS version 12) was used to compare small mammal captures among the three treatments in coniferous stands (treated, proposed, reference). At the site level (micro-scale), trap success was defined as the total number of individuals caught (not including recaptures). Total small mammal captures and captures by species were analyzed at this scale. I analyzed species with captures that made up more than eight percent of the total captures.

The age distributions of populations, by species, in different site categories were compared using Fisher's Exact Test. *Peromyscus spp.* was the only species that I could reliably age and had adequate data to analyze. Captured *Peromyscus spp.* were classified as juveniles if they had a mass of less than 17.5 g (Van Horne 1982).

At the microhabitat scale, I used binomial regression to model habitat (independent) variables associated with the total captures (dependent variable) of each mammal species at a trap site. These regression models are not tests on specific variables and their relationship to small mammal captures. They are exploratory in nature and therefore a wide variety of potentially important variables to small mammals were included. Trapping success was defined as the number of captures at a single station (two Sherman traps). I chose not to use logistic regression because it incorporates only presence or absence data, while binomial regression can include multiple captures at a single station. The response variable for binomial regression is the number of successful trials out of the total number of trials. For this study, a trial consists of one trap night. At each station, I had a total of six trap nights (two traps x three nights) and the data consisted of the number of animals caught, not including recaptures, in those six trap nights for a maximum of six trials (two traps at a station for three nights). In other words, there were six total trials at each station, where each trial is defined by success (capture) or failure (no capture) at each trap.

Variables were chosen on the basis of hypothesized ecological importance for small mammals (Dueser and Shugart 1978). Redundant variables were eliminated based on inaccuracy

of measure (Mengak and Guynn 2003). Twenty-seven variables were included in the hardwoods regression; thirty variables were included in the coniferous regression (Table 1). To simplify the models, a stepwise model selection procedure was used. This allowed the addition or removal of a variable at any step of the procedure. The Akaike Information Criterion (AIC) was used to determine the addition or removal of variables. Confidence intervals of the regression parameters were calculated using profile likelihood using the R statistical package, stepwise regression procedure and profile likelihood from the MASS package (Venables and Ripley 2002). Profile likelihood is a method of estimating confidence intervals for multiple parameters. Significance of individual variables was determined using a likelihood ratio test comparing the full model to the model with the variable of interest removed.

I performed a binomial regression for each species (*Peromyscus spp.*, Eastern chipmunks, short-tailed shrews for hardwoods; *Peromyscus spp.*, Eastern chipmunks, least chipmunks, red-backed voles, shrews (*Sorex spp.*) in conifers) and for total small mammal captures. Only small mammal species that made up more than 8% of total captures were included. This led to the exclusion of northern flying squirrels (*Glaucomys sabrinus*), meadow jumping mice (*Zapus hudsonius*), red squirrels (*Tamiasciurus hudsonicus*), and woodland jumping mice (*Napaeozapus insignis*) due to low numbers of individuals captured.

MACRO ANALYSIS RESULTS

At the macrohabitat scale, no significant differences were found between total small mammal captures and site categories on either deciduous or coniferous plots. Similarly, I found no significant differences between captures by species (abundance > 8%) and site category. However, differences in habitat structure among site categories existed. To investigate this variability, I conducted a principle components analysis (PCA) on the habitat data and an analysis of tree species distribution among site categories.

Principle components analysis for habitat (vegetation) data.--I analyzed the first three principle components (PCs); cumulatively, they accounted for 81% of the total variance among the eight deciduous sites, and 90% of the total variance among the nine coniferous sites (Table 1, Table 2). PC plots (Figures 1 – 6) were used to analyze differences in habitat variables among site treatments (proposed, treated, reference). Values were the averages of all 50 site stations.

Hardwoods Principle Components Analysis

In the deciduous sites, coarse woody debris (CWD) girth is the most influential positive loading in PC1. PC1 is negatively correlated with the number of trees and snags, snag height, and total tree species. PC2 is positively correlated with total CWD pieces and average CWD length; PC2 is negatively correlated with tree basal area, standard deviation of tree DBHs, maximum DBHs, and total number of trees (in order of influence). For PC3, large positive loadings for snag size, number of tree species, and the abundance and size of CWD indicate a large positive correlation between the variable and PC3. PC3 is lower in value when the average canopy cover and the basal area of trees are low (Table 1).

The most noticeable trend is that all four proposed sites have low PC1 and PC2 values (Figure 1). The reference sites are more variable but are mostly high for PC1 and PC2. With the exception of one reference and one proposed site, proposed sites score high with PC3 and reference sites are on the low end (Figure 2, 3). That is, deciduous reference sites, compared to proposed sites, tend to have more CWD, bigger trees, and higher canopy cover. Proposed sites tend to have increased tree density, snag density, snag size, and snag height.

Conifers Principal Components Analysis

In the coniferous sites, PC1 comprises the following variables (from most influential to least): number tree species, tree size, average canopy cover, average CWD length, standard deviation of tree DBHs, average snag height, and CWD size and volume. There was no directional pattern with these variables and PC1, so PC1 is essentially an average of them. PC2 has high values when the average canopy cover, tree size, and snag height are high. PC2 is low when CWD size and abundance is large. Third, PC3 is high in value when sites have high tree and CWD abundance and low when snag height and DBH are high.

Treated sites are starkly different from reference and proposed sites in PC1 and PC3. Figures 4 and 5 show that all three treated sites have high PC 1 values; proposed and reference sites are lower on PC 1. PC2 is not very useful in deciphering vegetation differences among site categories due to the high variability among sites (Figure 4, 6). All three reference sites have high values of PC3; all three proposed sites have relatively low PC3 values. Overall, coniferous reference sites have higher values for total number of trees, total number of CWD pieces, total tree species, and maximum tree DBHs. Proposed sites tend to have higher snag heights, larger snags, low maximum tree DBH, and low number of tree species. Treated sites have low values for all vegetation variables; most notably treated sites are low on total tree species, tree size, and the CWD volume.

Tree species abundance.--On my deciduous plots, 71% of the trees were sugar maples. There were no significant ($p < 0.05$) differences between reference and proposed sites. The following three species were more abundant (not significantly) in reference stands than in proposed stands: American beech, Eastern hemlock, yellow birch. All other species were more abundant in proposed stands (sugar maple, red maple, paper birch, hophornbeam, black cherry, American basswood) (Figure 7).

Black spruce was the most common (27%) species found in the coniferous sites. Significant differences were found with one-way ANOVA with jack pines ($F = 6.01$; $df = 2, 6$; $p = 0.037$) and red maples ($F = 7.618$; $df = 2, 6$; $p = 0.023$). Reference sites contained the highest percentage of white pine, red maple, balsam fir, and trembling aspen. Jack pine and red pine were most commonly found in proposed sites. In treated sites, black spruce, big-toothed aspen, red oak predominated (Figure 8).

Small mammal captures.-- In 2004, 2400 trap nights resulted in the capture of 265 individuals of eight species in the deciduous sites (Table 5). Species captured included woodland deer mouse and white-footed mouse (70%), eastern chipmunk (15%), short-tailed shrew (11%), and northern flying squirrel (3%). In 2005, I trapped for 2700 trap nights and caught 226 individuals of 11 species. The main species captured were woodland deer mouse and white-footed mouse (38%), red-backed vole (20%), *Sorex spp.* (14%), eastern chipmunk (8%), least chipmunk (8%), masked shrew (6%), and meadow jumping mouse (3%). *Peromyscus spp.* (*P. maniculatus gracilis* or *P. leucopus*) were the only two species caught at every site both years. I found no significant differences in age distributions among site categories for *Peromyscus spp.* (other species were not analyzed).

MICRO ANALYSIS RESULTS

Binomial regression.--In deciduous sites, the regression results show that more CWD at a station meant a greater number of captures was likely (Table 6); CWD was positively correlated with total captures and individual species captures. Total captures were positively associated with average snag DBHs, number of CWD pieces, and average CWD length. Total captures were negatively associated with the average snag height and average canopy cover. At the species level, I could predict an increase in *Peromyscus spp.* captures from the average length and the total number of CWD pieces. I found a negative association between *Peromyscus spp.* captures and the total CWD volume. Eastern chipmunk captures increased with an increase in the average snag DBH and the total CWD volume; they were negatively associated with average snag height and average canopy cover. Lastly, short-tailed shrew captures increased with high abundances of six tree species (highly significant for Eastern hemlock, paper birch, and sugar maple), amount of CWD, and black spruce abundance and they decreased with lower total number of trees, and average tree DBH.

In coniferous sites, total captures of all species were most positively significantly associated with the number of CWD pieces and total tree species (Table 7). Total captures were negatively influenced by only one variable, the abundance of red pines. Captures of *Peromyscus spp.* were positively associated with maximum tree DBHs, average snag DBHs, average canopy cover, and total pieces of CWD; they were negatively associated with average tree DBHs, number of tree species, number of stumps, and with four species of trees (red maple, black spruce, red and jack pine). A positive association for eastern chipmunk captures was found with the total number of CWD pieces, and I could predict captures based on a negative association with average snag DBH and abundance of black spruces. Least chipmunk captures were positively associated with the average length of CWD. Negative associations included average canopy cover and abundance of red pines. I found a positive association between red-backed vole captures and total tree species; abundance of jack pine, snag and stump abundance, average tree DBHs; and black spruce and white pine abundance. Balsam fir abundance and total tree basal area negatively influenced red-backed vole captures. Lastly, *Sorex spp.* captures were predicted by the number of CWD pieces, total tree species, and abundance of black spruce (positive associations). *Sorex spp.* captures were negatively associated with average canopy cover and trembling aspen abundance.

DISCUSSION

As has been found in many small mammal habitat studies, my results supported the hypothesis that microhabitat features are important in predicting the distribution of small mammals. At the micro-scale, the regression analysis identified three important habitat elements on which managers should concentrate restoration efforts: coarse woody debris (CWD), snags, and tree species diversity. The macro analysis failed to find associations between habitat and captures.

Micro scale.--The microhabitat results supported my prediction that presence of small mammals can be predicted by specific habitat characteristics; the regression analysis showed many associations between habitat measurements and captures. Since my research goal was to identify features that SNWR managers can use for their restoration, I chose easily manipulated habitat features that were consistently important for multiple species. SNWR restoration should focus on restoring the following habitat components: CWD pieces, snags, and tree diversity.

The number of CWD pieces was positively associated with total small mammal captures in hardwoods and conifers. Of the CWD variables in the regression analyses, total CWD pieces was the only variable that was consistently important. Managers should therefore focus on number of pieces, rather than CWD size (see Zollner and Crane (2003) for a discussion on ways to manage for CWD). Even with *Peromyscus* mice, an abundant habitat generalist (Seagle 1985; Martin and McComb 2002), I found that CWD abundance was still a significant predictor of *Peromyscus* presence. Menzel et al. (1999) also found that *Peromyscus* abundance was strongly positively correlated with CWD in western North Carolina's northern hardwoods.

Small mammals at Seney responded not only to ground CWD, they also used areas with woody material in the form of snags. Snags serve a similar function as CWD; they provide shelter, nesting places, and travel paths for small mammals. Unlike CWD, however, the total number of snags had no influence on small mammal captures. Interestingly, I found that Eastern chipmunk captures were positively associated with average snag DBH in hardwoods and negatively associated with the same variable in coniferous stands. This contradictory finding illustrates the importance of analyzing capture data separately for habitat types. Overall, most small mammals preferred short snags with a large DBH, perhaps because they are more decayed or accessible. Because I found several relationships with snags, managers performing restoration

should preserve snags. My recommendation is to preserve older, large trees and existing snags if selective logging is used.

Based on the regression results, tree species diversity should be maximized when restoration involves planting, especially conifers. High tree diversity is often found in old-growth forests. I found that only short-tailed shrews were positively associated with high tree diversity in hardwoods. But in coniferous sites, total small mammal, red-backed vole, and *Sorex spp.* captures all were positively associated with tree diversity. This contrast between hardwoods and conifers likely exists because Seney's coniferous forests have higher tree diversity and more variation than its hardwoods.

Lastly, due to the variety of habitat elements that I and others found to be important for different small mammal species, restoration should focus on maximizing habitat heterogeneity (Carey et al. 1999; Manning and Edge 2004). The regression analysis highlighted many other habitat elements other than those previously mentioned. In the deciduous sites the following habitat components were associated with captures: high (positive association) maximum tree DBH, low (negative association) average tree DBH, low number of trees, and low canopy cover. In conifers, the following variables had associations: high and low tree DBH, high maximum tree DBH, low total tree basal area, high and low number stumps, and high and low canopy cover. More associations were also found with certain tree species (Table 6, 7). This incredible range of associations demonstrates the variety of habitat preferences of small mammals.

Macro scale.-- Small mammal capture data did not support my prediction that small mammal communities in near old-growth stands are more abundant than in logged habitats proposed for restoration. Regardless of the differences in vegetation structure among site categories uncovered in the PCA analysis, I found no significant differences in small mammal captures among these categories. Others, however, have identified macro-scale patterns for some small mammal species, particularly the red-backed vole (Jerry 1984; Sullivan et al. 2000; Pearce and Venier 2005). Perhaps at SNWR red-backed voles are not more abundant in mature forests because the patches of mature forest are very small; this does not allow for an accumulation of a large red-backed vole population. The same may be true for other small mammal species at SNWR that are typically found in mature forests elsewhere.

Although I found no macro-scale associations, large-scale influences on small mammal distributions probably exist. Morris (1987) suggests that prey abundance and seed availability are determined by macrohabitat. Predator distribution, which I did not measure, may also have an effect on small mammal populations (Krohne and Burgin 1990; Morris 1996). Lastly, social factors likely influence distributions at the macro-scale; competition with adults often drives juveniles into less desirable habitat (source-sink dynamics).

Future Directions.--At Point Pelee National Park in southern Ontario, Morris (1987) found that macrohabitat variables more effectively predicted small mammal density than microhabitat characteristics. Morris used vastly different types of macrohabitat than I did. He made two macro comparisons: mature forest versus a sumac (*Rhus spp.*) dominated area and grassland versus old field. These habitats are considerably more different from each other than my macro comparison of different forest successional stages (reference, proposed, treated). If I had compared small mammal captures between vegetation types (hardwoods versus conifers) I would have found significant macrohabitat differences as well. Thus the type of macrohabitat comparison researched should be examined closely when comparing results from different studies and when designing studies that investigate different scales of habitat use.

For the macrohabitat comparison, the heterogeneous nature of SNWR led to high amounts of habitat variation within categories and within sites. For example, the treated sites were highly variable in the extent of logging, ranging from treeless clear-cuts to second-growth with a few selectively logged large trees. This variation within categories may have confounded differences in small mammal populations since category replicates were not identical in habitat features. Substantial variation within sites also occurred. Most of the reference sites were very small and often only just large enough for two transects. Within these small habitat patches, a few of the red and white pine dominated reference sites had small patches of black spruce bog within them. This led to some trap stations that were located in boggy areas; black spruce bog areas most likely have a different small mammal community than a mature coniferous habitat. Similar variation existed in proposed and treated sites. All of this variability may have resulted in increased variation in the small mammal captures within categories, making it difficult to observe trends at the macro scale. Studies with only small patches of habitat available should

have as many macro-scale replicates as possible. This replication will help to minimize the effects of high variation among sites.

Future microhabitat studies can enhance my study design. Researchers should measure habitat elements at a finer scale than I did; I suggest that vegetation measurements of one m around the trap station are appropriately small. Additionally, my study was strictly observational; experimental studies that manipulate habitat elements will more specifically pinpoint how those components affect small mammals. Based on my findings, future small mammal habitat use studies in the upper Midwest that investigate CWD, snags, and tree diversity will be most informative. Most significantly, my sample size was small with few replicates; these should always be maximized when possible. The study was also short in duration. Research on small mammal habitat use should be conducted during all seasons since habitat use likely shifts with resource availability.

At SNWR, the habitat requirements of other wildlife species must also be considered since managers are interested in landscape level restoration (not targeting a single species). Fortunately, many other wildlife species depend on the same habitat elements as small mammals. MacNally et al. (2002) found that a CWD decrease diminishes avian diversity. There is ample evidence that snags are important for wildlife such as birds (Walter and Maguire 2005), *Myotis* bats (Ford et al. 2006), and American martens (*Martes americana*; Porter et al. 2005). A management focus on CWD, snags, and tree diversity will help to obtain overall biological integrity.

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APPENDIX 1. TABLES AND FIGURES

Table 1. All habitat measurements recorded and used for analysis.

category: treated, proposed, reference	CWD: # pieces
trees: total basal area	CWD: avg decay class
trees: total #	CWD: avg DBH (cm)
trees: total # species	CWD: total volume (m ³)
trees: avg DBH (cm)	canopy cover: avg (% open)
trees: minimum DBH (cm) trees	cover: herbaceous (categorical)
trees: maximum DBH (cm) trees	cover: short (categorical)
trees: standard deviation DBH (cm)	cover: tall (categorical)
stumps: total basal area	cover: dominant ground cover species
stumps: total #	slope: %
stumps: avg decay class	ground cover: % sapling
snags: total basal area	ground cover: % wood
snags: total #	ground cover: % dirt
snags: avg decay class	ground cover: % grass
snags: avg DBH (cm)	ground cover: % ferns
snags: minimum DBH (cm)	ground cover: % leaves
snags: maximum DBH (cm)	ground cover: % moss
snags: avg height (m)	ground cover: % lichen
	ground cover: % slash

Table 2. Definitions of variables used in both coniferous and deciduous binomial regression.

Code	Measurement (5-m radius around trap station)	Unit
cat	site category (treated,proposed, reference)	treat, pro, ref
trees	total number of trees (all species)	number trees
dbhavg	average DBH of trees	cm
dbhmax	maximum DBH	cm
dbhsd	standard deviation of DBH	cm
basal	total basal area of trees	cm/m ²
species	total tree species	number species
stumps	total number of stumps	number stumps
snags	total number of snags	number snags
snagdbh	average DBH of snags	cm
snagh	average height of snags	m
cwd	total number pieces of CWD	number pieces
cwddb	average CWD DBH	cm
cwdvolume	total volume of CWD	m ³
cwdlavg	average length of CWD	m
avgcc	average canopy cover (% open)	percentage
wood	average % ground cover that is wood	percentage
balsam fir	total number of balsam fir	number trees
red maple	total number of red maple	number trees
sugar maple	total number of sugar maple	number trees
paper birch	total number of paper birch	number trees
hophornbeam	total number of hophornbeam	number trees
big-toothed aspen	total number of big-toothed aspen	number trees

Deciduous analysis only: black cherry, American basswood, Eastern hemlock, yellow birch, American beech

Conifer analysis only: white ash, black spruce, jack pine, red pine, white pine, trembling aspen, red oak, white cedar

Table 3. Hardwoods: PCA loadings from principle components analysis. Bold numbers are the most influential loadings on that principle component.

Variable	PC 1	PC 2	PC 3
trees: total species	-0.23	-0.30	0.34
trees: total number	-0.26	-0.36	-0.05
trees: total basal area	0.18	-0.41	-0.17
trees: average DBH	0.36	0.05	-0.01
trees: maximum DBH	0.26	-0.38	-0.07
trees: standard deviation of DBHs	0.15	-0.39	0.05
CWD: total number pieces	0.37	0.13	0.30
CWD: average DBH	0.40	-0.15	0.07
CWD: average length	0.31	0.10	0.25
CWD: total volume	0.33	-0.19	-0.07
snags: average DBH	0.18	-0.04	0.50
snags: average height	-0.26	-0.23	0.44
snags: total number	-0.16	-0.34	0.15
average canopy cover	0.08	-0.24	-0.47
Percentage of total variance	36.60	29.70	14.60
Cumulative percentage of variance	36.60	66.30	80.90

Figure 1. Hardwoods: PC1 versus PC2 biplot. See Table 2 for variable code (in red) definitions. Pro = proposed, ref = reference sites.

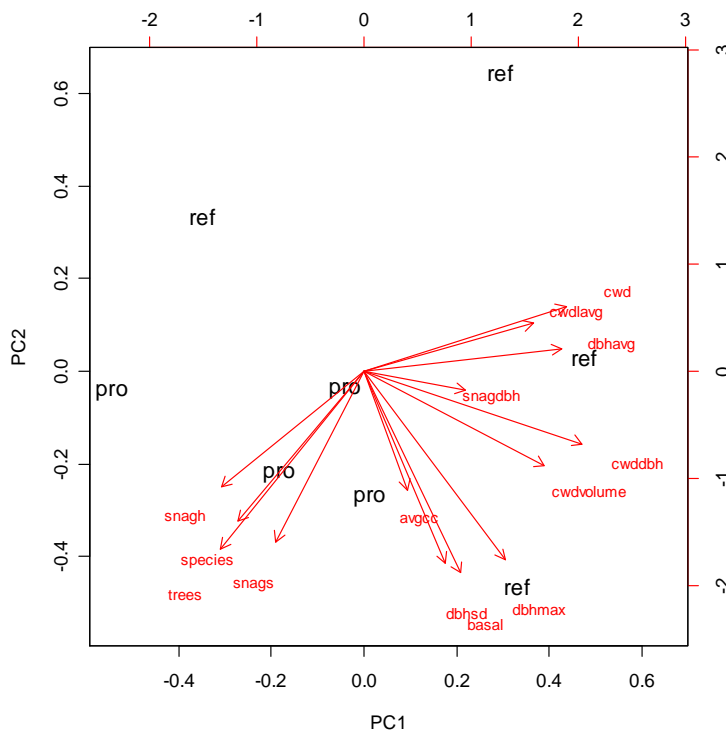


Table 4. Conifers: PCA loadings from principle components analysis. Bold numbers are the most influential loadings on that principle component.

Variable	PC 1	PC 2	PC 3
trees: total species	-0.36	-0.11	0.08
trees: total number	-0.09	-0.11	0.56
trees: total basal area	-0.33	0.21	0.20
trees: average DBH	-0.33	0.21	-0.09
trees: maximum DBH	-0.36	0.15	0.12
trees: standard deviation of DBHs	-0.33	0.18	0.16
CWD: total number pieces	-0.19	-0.37	0.33
CWD: average DBH	-0.17	-0.50	-0.19
CWD: average length	-0.30	-0.34	-0.11
CWD: total volume	-0.20	-0.48	-0.18
snags: average DBH	-0.22	0.07	-0.44
snags: average height	-0.23	0.19	-0.46
average canopy cover	-0.33	0.25	0.09
Percentage of total variance	52.40	22.10	15.50
Cumulative percentage of variance	52.40	74.50	90.00

Figure 4. Conifers: PC1 versus PC2 biplot from the PCA. See Table 2 for variable code (in red) definitions. Pro = proposed, ref = reference, tre = treated sites.

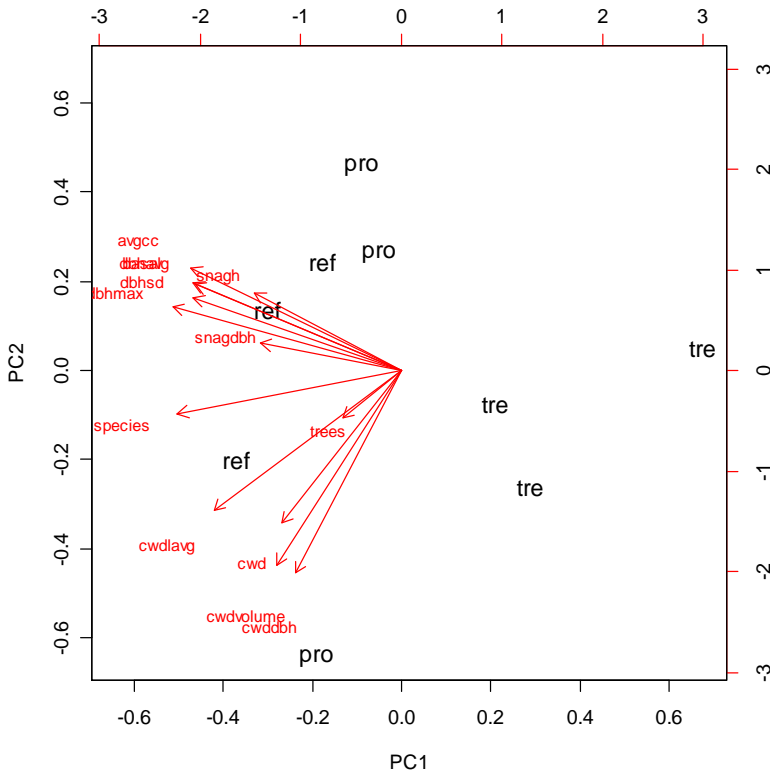


Figure 5. Conifers: PC3 versus PC1 from the PCA. See Table 2 for variable code (in red) definitions. Pro = proposed, ref = reference, tre = treated sites.

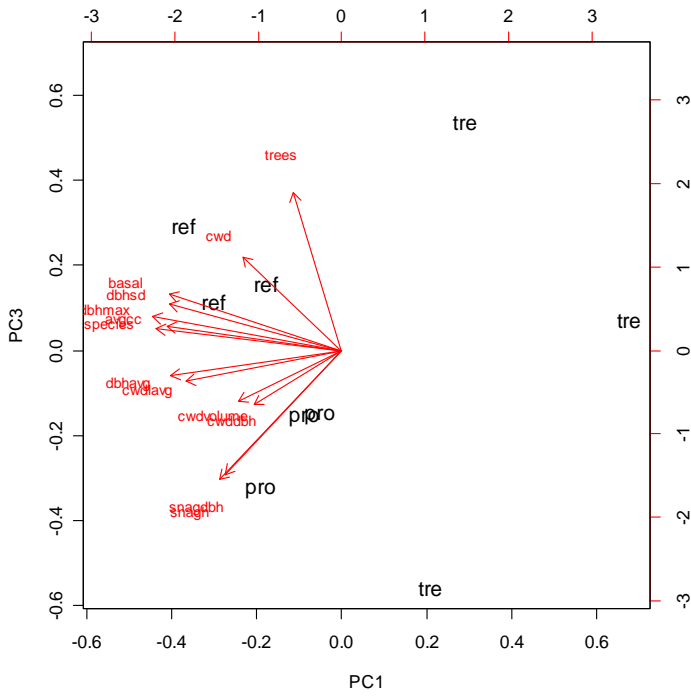


Figure 6. Conifers: PC2 versus PC3 from the PCA. See Table 2 for variable code (in red) definitions. Pro = proposed, ref = reference, tre = treated sites.

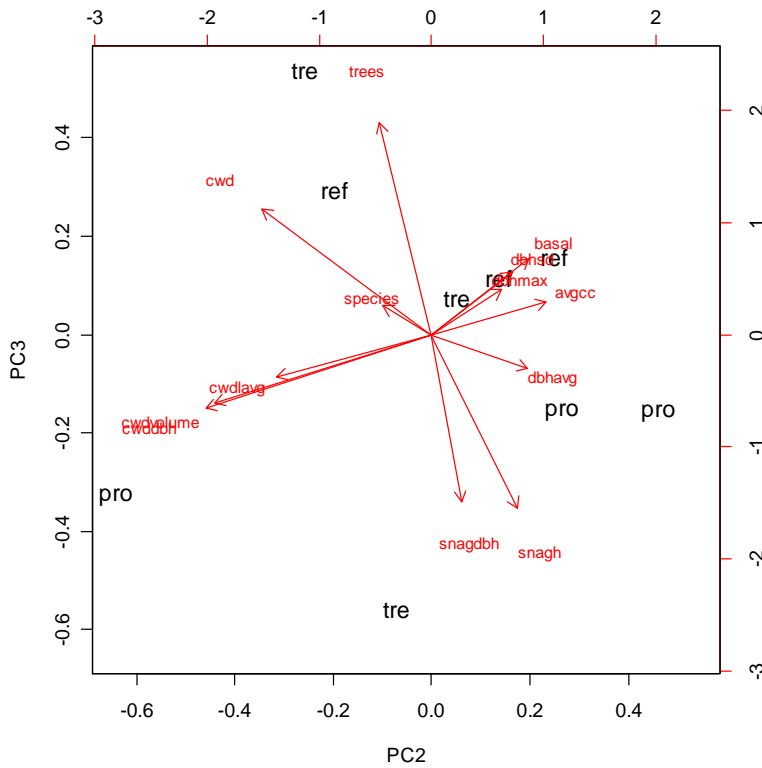


Figure 7. Deciduous sites: total number of trees by site category. Only tree species with > 2% of total tree abundance included. No significant differences ($p < 0.05$) with two-sample t -test.

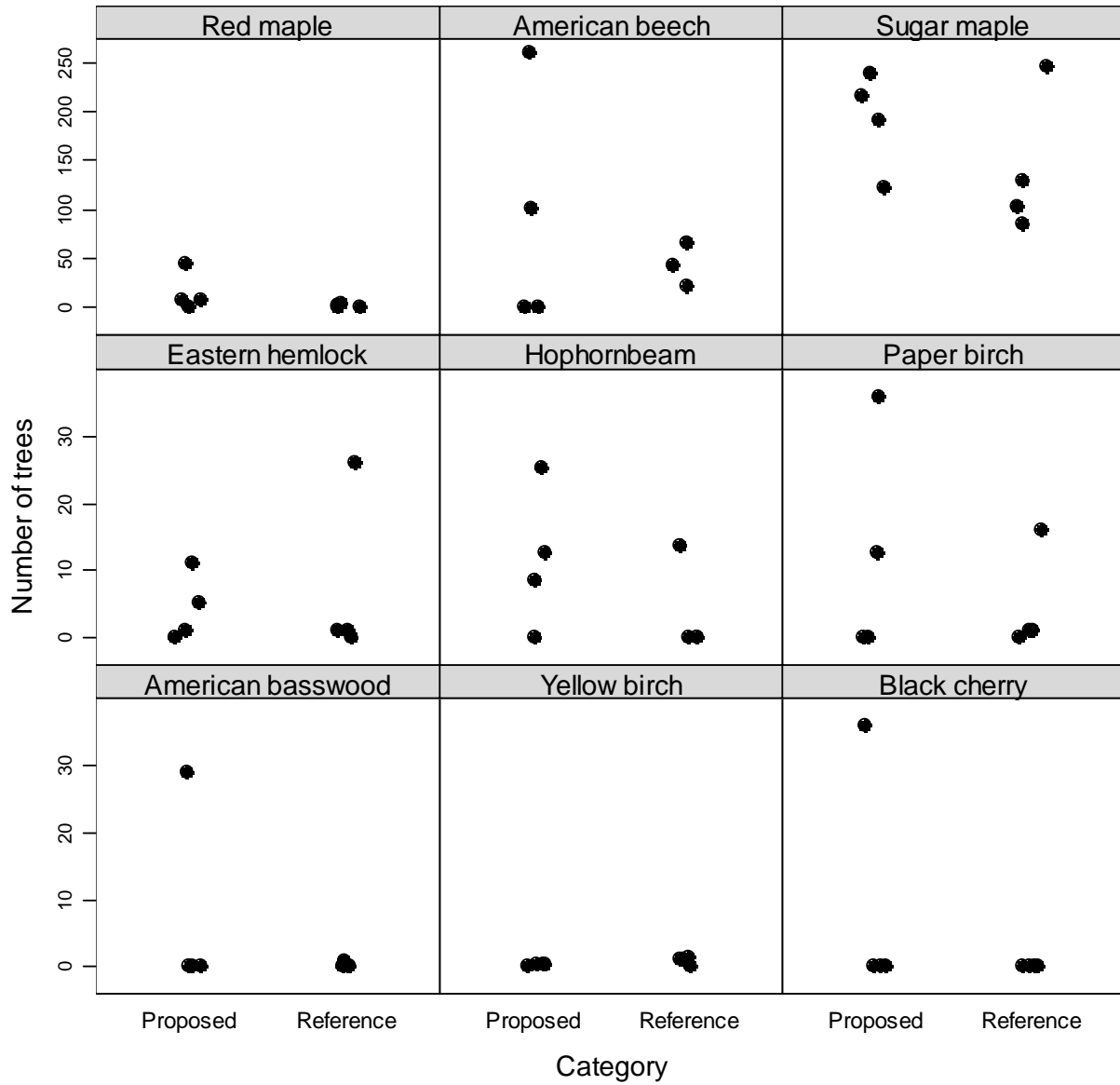


Figure 8. Coniferous sites: total number of trees by site category. Only tree species with > 2% of total tree abundance included. Significant differences ($p < 0.05$) with one-way ANOVA: jack pines ($F = 6.01$; $df = 2, 6$; $p = 0.037$) and red maples ($F = 7.618$; $df = 2, 6$; $p = 0.023$).

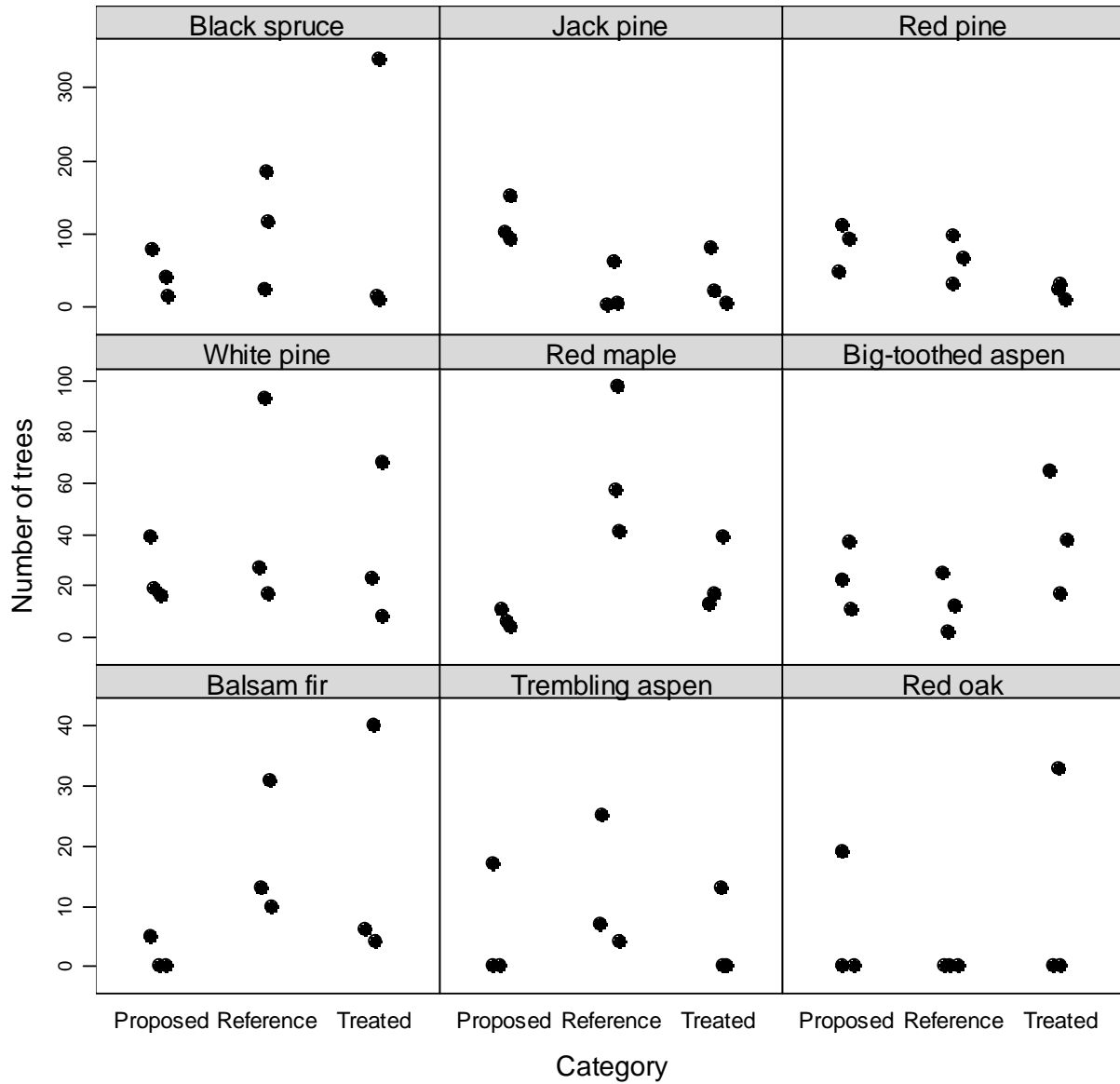


Table 5. Total captures by site. H = hardwoods sites, 2004. C = coniferous sites, 2005.

Site	Category	Total	<i>Pero- myscus spp.</i>	E. chip- munk	Short- tailed shrew	Red- backed vole	<i>Sorex spp.</i>	Masked shrew	Least chip- munk	N. flying squirrel	Meadow jumping mouse	Red squirrel	Woodland jumping mouse
H1	ref	66	45	8	11	1	0	0	0	1	0	0	0
H2	ref	37	26	11	0	0	0	0	0	0	0	0	0
H3	ref	15	5	7	3	0	0	0	0	0	0	0	0
H4	ref	25	15	2	6	0	0	0	0	2	0	0	0
H5	prop	56	34	10	6	0	1	0	0	4	0	0	1
H6	prop	27	24	1	1	1	0	0	0	0	0	0	0
H7	prop	24	22	2	0	0	0	0	0	0	0	0	0
H8	prop	15	14	0	1	0	0	0	0	0	0	0	0
H	TOTAL	265	185	41	28	2	1	0	0	7	0	0	1
H	%		70%	15%	11%	1%	0%	0%	0%	3%	0%	0%	0%
C1	ref	26	16	0	1	3	3	2	1	0	0	0	0
C5	ref	31	20	1	1	5	2	0	2	0	0	0	0
C8	ref	24	6	0	2	4	7	5	0	0	0	0	0
C3	prop	29	11	0	0	9	2	1	0	4	2	0	0
C6	prop	27	4	5	0	10	2	1	2	0	3	0	0
C7	prop	21	4	0	0	3	9	0	4	0	1	0	0
C2	treat	22	5	0	1	6	3	3	4	0	0	0	0
C4	treat	26	8	11	0	4	1	1	0	0	0	0	1
C9	treat	20	12	0	0	1	2	0	4	0	0	1	0
C	TOTAL	226	86	17	5	45	31	13	17	4	6	1	1
C	%		38%	8%	2%	20%	14%	6%	8%	2%	3%	0%	0%

* No Tomahawks or recaptures included

Table 6. Deciduous sites: likelihood ratio test (LRT) statistics and p-values for each variable in the regression analysis are reported. Variables highlighted in red are negatively associated and grey values are positively associated with small mammal captures. Degrees of freedom = 1. P-values < 0.001 are in bold.

	Total (all species)		<i>Peromyscus spp.</i>		Eastern chipmunk		Short-tailed shrew	
	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value
trees: avg DBH							5.53	0.0187
trees: max DBH							7.57	0.0059
trees: total #							22.98	1.640E-06
trees: total species							6.85	0.0088
snags: avg DBH	12.32	0.0004			15.50	8.237E-05		
snags: avg height	5.88	0.0153			5.54	0.0186		
CWD: # pieces	4.78	0.0287	3.90	0.0482				
CWD: avg length	5.19	0.0227	4.75	0.0293				
CWD: volume			6.08	0.0137	7.45	0.0063		
canopy cover: %	5.66	0.0174			6.04	0.0140		
balsam fir							5.58	0.0182
Eastern hemlock							19.43	1.042E-05
hophornbeam							5.09	0.0241
paper birch							15.98	6.405E-05
sugar maple							18.24	1.947E-05
yellow birch							10.33	0.0013

Table 7. Coniferous sites: likelihood ratio test (LRT) statistics and p-values for each variable in the regression analysis are reported. Variables highlighted in red are negatively associated and grey values are positively associated with small mammal captures. Degrees of freedom = 1. P-values < 0.001 are in bold.

	Total (all species)		<i>Peromyscus spp.</i>		Eastern chipmunk	
	p-value	LRT	p-value	LRT	p-value	LRT
trees: avg DBH			0.0080	7.02		
trees: max DBH			0.0260	4.96		
trees: basal area						
trees: total species	0.0408	4.19	0.0364	4.38		
stumps: total #			0.0230	5.17		
snags: avg DBH			0.0157	5.83	0.0121	6.30
snags: avg height			0.0266	4.92		
CWD: # pieces	0.0053	7.76	0.0391	4.26	0.0210	5.32
canopy cover: %			0.0038	8.38		
black spruce			0.0015	10.09	0.0012	10.53
jack pine			0.0256	4.98		
red maple			0.0473	3.93		
red pine	0.0162	5.78	0.0038	8.36		
	Least chipmunk		Red-backed vole		<i>Sorex spp.</i>	
	p-value	LRT	p-value	LRT	p-value	LRT
trees: avg DBH			0.0230	5.17		
trees: basal area			0.0089	6.84		
trees: total species			3.245E-06	21.67	0.0023	9.30
stumps: total #			0.0230	5.17		
snags: total #			0.0161	5.80		
CWD: # pieces					0.0011	10.67
CWD: avg length	0.0260	4.96				
canopy cover: %	0.0212	5.31			0.0006	11.69
balsam fir			0.0079	7.06		
black spruce			0.0177	5.63	0.0039	8.32
jack pine			0.0014	10.16		
red pine	0.0313	4.64				
trembling aspen					0.0186	5.54
white pine			0.0250	5.02		