Using thinning as a management tool for gypsy moth: 
the influence on small mammal abundance

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Abstract

Silvicultural manipulations may be used to reduce forest susceptibility or vulnerability to defoliation by the gypsy moth. The effects of this management strategy on small mammal abundance were determined by pitfall trapping small mammals 1 year before silvicultural thinnings and for 3 years following thinning in a deciduous montane forest. \textit{Sorex cinereus} (masked shrew) was the most frequently captured small mammal, followed by \textit{Peromyscus} spp. (white-footed and deer mice) and \textit{Clethrionomys gapperi} (redback vole). We found significant differences between thinned and reference stands in total small mammal and \textit{Peromyscus} spp. abundance. There were no significant changes in \textit{S. cinereus} and \textit{C. gapperi} abundance as a result of thinning. The response of the small mammal community reflects the increased complexity of understory vegetation found on the study site as a result of thinning. Principal components analysis results indicated that both vegetation richness and abundance correspond with thinning treatment and likely indirectly affect small mammal abundance. Increased complexity may improve habitat quality, as well as enhancing invertebrate food supply, thereby influencing small mammals.

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1. Introduction

Since its accidental introduction into Massachusetts in 1869, the gypsy moth (\textit{Lymantria dispar} L.) has become one of North America’s most important forest pests. This is due, in part, to the extensive tree mortality that can occur after a gypsy moth outbreak. Despite numerous control attempts, the gypsy moth continues to expand its range into southeastern and midwestern states.

While direct suppression of gypsy moth populations with insecticides is the principal management approach, several other strategies are used that indirectly affect gypsy moth populations (e.g., classical biological control, mating disruption and silviculture). Among these, silvicultural manipulations that lower the likelihood of a gypsy moth outbreak in a forest have been used for nearly 100 years in North America (Behre et al., 1936), although the basis and objectives of various silvicultural approaches varies (Muzika and Liebhold, 2000). Silvicultural management is attractive economically and ecologically in part because it has the potential to reduce the susceptibility or vulnerability of forest stands to gypsy moth attack while...
benefiting wildlife, especially gypsy moth predators. One of the first attempts at defining a possible silvicultural management approach was developed by Fiske (1913), who determined that the removal of oak and other preferred food species could help reduce gypsy moth related damage to forests. The main purpose of gypsy moth management by silviculture is to remove trees that are likely to be killed or damaged by the gypsy moth, thus reducing stand susceptibility or vulnerability.

Susceptibility is the likelihood that a stand will be defoliated; it relates primarily to tree species composition, but can also be influenced by the abundance and distribution of natural enemies (Smith, 1985), and the habitat that supports these natural enemies. It has been hypothesized that forest stand susceptibility can be reduced by increasing tree growth and vigor, reducing gypsy moth habitat (resting and pupation locations) and the dominance of host trees, manipulating the habitat so that it is attractive to predators, and increasing the diversity of vegetation at the landscape level (Gottschalk, 1991). Vulnerability refers to potential tree mortality in a forest following defoliation. Like stand susceptibility, increasing the growth and vigor of residual trees can reduce forest stand vulnerability.

Small mammals are an important component for the gypsy moth (Bess et al., 1947; Campbell, 1974; Campbell and Sloan, 1976, 1977; Cook et al., 1995; Liebhold et al., 2000). It is critical, then, to understand the effects of silvicultural tactics on small mammal populations. The response of small mammals to even-age timber management has been extensively researched (Krull, 1970; Kirkland, 1977, 1990; Verme and Ozoga, 1981; Monthey and Soutiere, 1985), however, the response of small mammals to forest thinning has not received as much attention. Among the few studies, Suzuki and Hayes (2003) found that thinning in forests of the Pacific Northwest provides somewhat of an overall benefit to small mammal habitat.

Decreasing forest susceptibility or vulnerability to gypsy moth defoliation via silvicultural thinning could have variable effects on small mammal communities. Because small mammals are important predators of forest insect pests, management practices that maintain or enhance their populations or their predatory impact should be considered when faced with defoliation by the gypsy moth (Yahner and Smith, 1991). Moreover, there is an increasing interest in incorporating ecological values in forest management approaches, irrespective of the primary objective. In this study, we intended to examine the effects of gypsy moth-oriented silvicultural management techniques on small mammal populations. Specifically, we wanted to determine if thinning influenced small mammal populations, and if so, to identify vegetation changes that correspond with a change in mammal abundance.

2. Methods

2.1. Study site description

This study was conducted on the 3905 ha West Virginia University Forest (WVUF) located approximately 12 km northeast of Morgantown, WV, USA. The elevation of the forest ranges from 318 to 795 m, with an average slope of 20% (Carvell et al., 1978). The forest cover types found at the West Virginia University Forest are of two general groups: cove hardwood and mixed oak. Cove hardwood types are normally dominated by yellow-poplar, *Liriodendron tulipifera* L., but also may include white oak, *Quercus alba* L., northern red oak, *Quercus rubra* L., eastern hemlock, *Tsuga canadensis* (L.) Carr., American basswood, *Tilia americana* L., and white ash, *Fraxinus americana* L. (Carvell et al., 1978). Mixed oak types are mainly dominated by oaks or a mixture of oak and hickory (*Carya* spp.).

Sixteen stands were delineated on the forest, ranging in size from 7.9 to 12.7 ha (mean = 10.2 ha). Stand age ranged from 55 to 62 years (mean = 58) and site index50 for northern red oak ranged from 64 to 96 (mean = 78). Eight of these stands were thinned in the winter of Year 1 (Y1) of this study. The remaining eight stands were not cut, and served as reference areas. Select harvests were done in accordance with gypsy moth management guidelines (Gottschalk, 1993), with the objectives of reducing the oak component, while increasing the vigor of remaining trees.

2.2. Field sampling

Within each stand, a series of pitfall traps was established along a grid. Since stands varied greatly in size, a varying number of pitfall traps was

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established within each stand, to help minimize variability in sampling intensity. The number of pitfall traps ranged from 10 in an 8.1 ha stand to 19 in a 12.5 ha stand. Each pitfall trapping plot was at least 100 m from the nearest trap. Overstory vegetation characteristics were also measured in each stand. The measurements included tree species, diameters, and heights of all trees found within 20 randomly located 0.04 ha plots in each stand. Mast samples were taken in overstory plots by randomly placing a 0.5 m radius funnel trap within each overstory plot. Mast was collected from the funnel traps each spring, then identified and weighed in the laboratory. Overstory vegetation and pitfall trapping plots frequently overlapped. Understory data were collected on three 10.5 m² plots located within each of the 20 overstory plots. The following data were collected on understory plots: percentage cover of woody and non-woody vegetation, seedling density and logging debris (slash) cover. Slash cover was measured using three categories: (i) 0–49% slash cover, (ii) 50–100% slash cover, (iii) 50–100% slash cover at least 1.2 m tall. Vegetation sampling plots were measured once a year during the study period.

Small mammals were captured weekly using pitfall traps during an 11-week period encompassing May–July. Data were collected for four consecutive years (Y1–Y4); the first year (Y1) represents preharvest data. Pitfall traps were constructed by affixing a square particleboard apron (29.8 cm × 29.8 cm) to a 19 cm deep, 2.51 cylindrical container. Each apron had a 15 cm circular hole in its center, where the plastic container was inserted to serve as the receptacle for any captures. The wooden apron was routed to form a shelf that ensured that the capture receptacle was flush with the apron. Each pitfall trap was filled with approximately 500 ml of propylene glycol, which served as both a killing agent and preservative.

During weekly monitoring, the propylene glycol was filtered to remove any captures. Discolored or old propylene glycol was discarded. Care was taken so that it did not come in contact with surrounding vegetation, so that any type of olfactory stimulus that could have altered trap success was prevented. Small mammals were collected and returned to the laboratory where they were frozen for future identification.

Mast samples were collected in 0.5 m radius funnel traps. A trap was randomly placed within each plot during the study period. Mast was collected from the traps each spring, then identified and weighed in the laboratory.

2.3. Statistical analysis

Analysis was conducted on total small mammal abundance as well on the abundance (number per 100 trap nights) of *Peromyscus* spp., *S. cinereus* and *C. gapperi*; these species comprised approximately 90% of the total captures. The capture of mice and their subsequent soaking in propylene glycol made separation of the genus *Peromyscus* difficult, so all *Peromyscus* were combined for the analysis. Percentage data were arcsine square-root transformed, while all other variables were log₁₀ transformed.

To ensure that pretreatment differences did not confound results, the abundance of small mammals and vegetation variables collected in the first year (Y1) were compared between subsequently thinned and unthinned stands using Student’s *t*-tests. Since small mammals were captured in the same trap locations during the 4 year period, repeated measures analysis of variance was used to test for differences in their abundance among years and between treatments for the years following treatment application (Gurevitch and Chester, 1986). Repeated measures ANOVA also was used to test for differences in vegetation structure and composition. Univariate tests of hypotheses were used if the Greenhouse-Geisser (G-G) epsilon was greater than 0.75 (indicating no violations of sphericity assumptions), otherwise, multivariate test results were reported (Hatcher and Stepanski, 1994).

Principal components analysis (PCA) was used to describe the vegetational gradients in the post-harvest habitat data set. Post-harvest vegetation data (Y2, Y3, Y4) were averaged at the plot level for analysis. Pearson correlations were used to determine the degree of association between small mammal abundance in post-treatment years and the major vegetation gradients as determined by PCA.

Because of its importance to small mammals, potential differences in slash (logging residues) between thinned and reference stands were tested using a chi-square test of independence. Relationships between small mammal captures and slash cover were made by averaging post-harvest small mammal
captures and slash cover values in plots where both were collected (not all vegetation plots were pitfall trapping plots, \( n = 171 \)) and obtaining Spearman = s rank correlation coefficients.

3. Results

Overstory, as well as understory vegetation characteristics were similar in both thinned and reference stands before logging (Table 1). In reference stands, northern red oak had the greatest basal area (9.44 m\(^2\) ha\(^{-1}\)), followed by yellow-poplar (5.77 m\(^2\) ha\(^{-1}\)), red maple (\( Acer rubrum \) L.) (3.85 m\(^2\) ha\(^{-1}\)) and chestnut oak (\( Quercus montana \) Willdenow) (3.15 m\(^2\) ha\(^{-1}\)). Thinned stands were also dominated by northern red oak (9.56 m\(^2\) ha\(^{-1}\)), yellow-poplar (7.75 m\(^2\) ha\(^{-1}\)), red maple (3.67 m\(^2\) ha\(^{-1}\)), and chestnut oak (2.57 m\(^2\) ha\(^{-1}\)). As a result of thinning, total tree basal area was reduced by 28% in thinned stands immediately after harvest, whereas the basal area of Quercus spp. was reduced by 32%. Owing to mortality, over the 4 year period, however, there were reductions in total basal area and Quercus basal area of 33 and 50%, respectively. Even in unthinned stands, by the end of the 4 years, total basal area had declined 15%. After thinning, total mast weight was 8% higher in reference stands; however, Quercus spp. mast weight was 6% higher in thinned stands after harvest.

Although borderline, we found no differences in total basal area (\( F = 4.33, P = 0.0564 \)), or oak basal area (\( F = 3.65, P = 0.0769 \)) between treated and reference stands as a result of thinning (Table 1). Of the understory vegetation characteristics analyzed, only % shrub cover did not show a general increase after thinning (Table 1). However, only seedlings less than 0.3 m tall were found in significantly greater numbers in thinned stands (\( F = 6.19, P < 0.05 \)).

The year \( \times \) treatment interaction was not significant (\( F = 2.24, P > 0.10 \)), therefore, this difference was apparent each year following harvesting.

Year accounted for a significant amount of the variation in seedlings greater than 1.52 m tall (\( F = 5.64, P < 0.05 \)) and total understory vegetation cover (\( F = 16.58, P < 0.005 \)). There were significantly more seedlings over 1.52 m tall in Y3 than in Y2 (\( F = 6.25, P < 0.05 \)). Likewise, total understory vegetation cover was significantly greater in Y3 than in Y2 (\( F = 36.03, P < 0.001 \)) (Table 1).

There were no significant differences in vegetation characteristics between thinned and uncut stands before harvesting (Table 2).

A total of 2030 small mammals, representing 13 species, were captured over the 4-year study period (62,832 trap nights) (Table 3). The masked shrew, \( Sorex cinereus \), was the most frequently captured small mammal, comprising 41.8% of the total catch. Deer mice, \( Peromyscus \) spp., represented 33.7%, and the redback vole, \( Clethrionomys gapperi \), represented 13.6% of the total captures. As with the vegetation, we found no significant differences in small mammal abundance among stands in small mammal abundance or the abundance of the three most common species (Table 2, Fig. 1).

<table>
<thead>
<tr>
<th>Variable measured</th>
<th>Preharvest*</th>
<th>Year 2</th>
<th>Year 3</th>
<th>Year 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ref</td>
<td>Thn</td>
<td>Ref</td>
<td>Thn</td>
</tr>
<tr>
<td>Total basal area (m(^2) ha(^{-1}))</td>
<td>30.1</td>
<td>31.1</td>
<td>30.4</td>
<td>22.3</td>
</tr>
<tr>
<td>Oak basal area (m(^2) ha(^{-1}))</td>
<td>15.3</td>
<td>14.9</td>
<td>15.1</td>
<td>10.1</td>
</tr>
<tr>
<td>Non-woody vegetation (%)</td>
<td>3.4</td>
<td>3.2</td>
<td>5.9</td>
<td>4.7</td>
</tr>
<tr>
<td>Seedlings ≤ 0.3 m tall</td>
<td>3614.6</td>
<td>2917.4</td>
<td>1702.3</td>
<td>3308.6</td>
</tr>
<tr>
<td>Seedlings 0.31–1.52 m tall</td>
<td>466.8</td>
<td>441.1</td>
<td>349.7</td>
<td>520.8</td>
</tr>
<tr>
<td>Seedlings &gt; 1.52 m tall</td>
<td>16.4</td>
<td>25.6</td>
<td>34.3</td>
<td>51.6</td>
</tr>
<tr>
<td>Shrub cover (%)</td>
<td>2.5</td>
<td>2.3</td>
<td>5.4</td>
<td>3.5</td>
</tr>
<tr>
<td>Total vegetation cover (%)</td>
<td>33.6</td>
<td>29.9</td>
<td>34.8</td>
<td>41.1</td>
</tr>
</tbody>
</table>

*Ref* and *Thn* represent unthinned and thinned stands, respectively.

* Pre-thinning year.
Over the post-treatment years, total small mammal abundance \((F = 10.41, P < 0.05)\) and deer mice abundance \((F = 8.74, P < 0.010)\) both were significantly greater in thinned than in reference stands (Figs. 1 and 2). Differences among years in total small mammal abundance also existed \((F = 14.31, P < 0.0001)\). There was a significant decline in total small mammal abundance from Y3 to Y4 \((F = 42.46, P < 0.0001)\).

There were also significant differences among years of deer mice \((F = 12.39, P < 0.001)\), masked shrew \((F = 9.57, P < 0.001)\), and redback vole abundance \((F = 10.50, P < 0.005)\) (Fig. 2). We found a significant decline in both deer mice \((F = 11.09, P < 0.001)\) and masked shrew \((F = 25.03, P < 0.001)\) abundance between Y3 and Y4 (Fig. 2). The abundance of masked shrew increased significantly between Y2 and Y3 \((F = 5.25, P < 0.05, \text{Fig. 2})\), whereas redback vole abundance \((F = 21.2, P < 0.001)\) declined significantly during this same period. There were no significant treatment by year interactions.

Slash levels differed among thinned and reference stands \((\chi^2 = 260.63, \text{d.f.} = 2, P = 0.001)\). The number of subplots with slash covering <50% of their area was similar in thinned and reference stands. However, there were 239 subplots in thinned stands with >50% slash cover, as compared to FIVE subplots in reference stands. Likewise, there were 79 subplots with >50% slash cover that was at least 1.2 m tall in the thinned stands, as compared to four plots in the reference stands.

After thinning, the first three principal components (PCs) accounted for 51.8% of the variation in the vegetation data set (Table 4). Multivariate analysis of variance results indicated that thinning explained a significant amount of the variation in the three principal components \((F = 25.8, P = 0.0001)\). Specifically, univariate tests showed that thinning explained a significant amount of the variation in PC3 \((F = 35.9, P = 0.0001)\) and PC3 \((F = 24.12, P = 0.0001)\) scores. Because our objectives were to

Table 2
Result of Student’s \(t\)-test to examine pre-treatment differences among stands for small mammal abundances and vegetation characteristics

| Species                      | \(T\)  | Prob. > |\(|T|\) |
|------------------------------|--------|---------|-------|
| Total small mammal abundance | -0.2008 | 0.8438  |       |
| Peromyscus spp.              | 0.7379 | 0.4728  |       |
| S. cinerus                   | -0.0917 | 0.9282  |       |
| C. gapperi                   | -0.1830 | 0.8574  |       |
| Total basal area (m²/ha)     | -0.8057 | 0.4339  |       |
| Oak basal area (m²/ha)       | 0.3434 | 0.7364  |       |
| Non-woody vegetation (% cover) | -0.1780 | 0.8613  |       |
| Seedlings ≤ 0.3 m tall       | 1.8556 | 0.0847  |       |
| Seedlings 0.31–1.52 m tall   | 0.1838 | 0.8568  |       |
| Seedling > 1.52 m tall       | -1.0477 | 0.3125  |       |
| Shrub cover                  | 0.2259 | 0.8245  |       |
| Total vegetation cover       | 0.9215 | 0.3724  |       |

*Ref’ and ‘Thn’ represent unthinned and thinned stands, respectively.*
determine the influence of thinning on small mammal abundance, only vegetational gradients represented by PC1 and PCA3 were included in subsequent results.

Principal component 1 (PC1) appeared to represent a gradient from thinned stands, which had more basal area in yellow-poplar, as well as higher levels of seedling, shrub, and total understory cover, to reference stands, which had more red maple, hickory, and oak basal area, and therefore virtually no understory cover.

PC3 represented a gradient from thinned stands, which had higher non-woody vegetation cover, to reference stands, which had more oak and total basal area.

Total small mammal \( (r = 0.32, P < 0.0001) \), deer-mice \( (r = 0.22, P < 0.005) \), and masked shrew \( (r = 0.17, P < 0.05) \) captures were significantly positively correlated with PC1. Total small mammal \( (r = -0.15, P < 0.05) \) and masked shrew \( (r = -0.16, P < 0.05) \) captures were significantly negatively correlated with PC3 (Table 4).

Table 4
Summary of principal components analysis of vegetation plots after thinning on the West Virginia University Forest, and the Pearson correlation between vegetation variables and principal component scores \( (r, \text{Prob.}) \)

<table>
<thead>
<tr>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>2.65</td>
<td>1.88</td>
</tr>
<tr>
<td>Percent</td>
<td>22.12</td>
<td>15.70</td>
</tr>
<tr>
<td>Cumulative percent</td>
<td>22.12</td>
<td>37.82</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>0.52 (0.0001)</td>
<td>-0.17 (0.0195)</td>
</tr>
<tr>
<td>Total understory cover</td>
<td>0.67 (0.0001)</td>
<td>0.34 (0.0001)</td>
</tr>
<tr>
<td>Total basal area</td>
<td>-0.09 (0.1973)</td>
<td>-0.13 (0.0842)</td>
</tr>
<tr>
<td>Oak basal area</td>
<td>-0.35 (0.0001)</td>
<td>0.48 (0.0001)</td>
</tr>
<tr>
<td>Black cherry basal area</td>
<td>-0.06 (0.3825)</td>
<td>0.54 (0.0001)</td>
</tr>
<tr>
<td>Red maple basal area</td>
<td>-0.56 (0.0001)</td>
<td>-0.06 (0.4344)</td>
</tr>
<tr>
<td>Yellow-poplar basal area</td>
<td>0.38 (0.0001)</td>
<td>-0.62 (0.0001)</td>
</tr>
<tr>
<td>Seedlings ≤ 0.3 m tall</td>
<td>0.47 (0.0001)</td>
<td>-0.51 (0.0001)</td>
</tr>
<tr>
<td>Seedlings 0.31–1.52 m tall</td>
<td>0.77 (0.0001)</td>
<td>0.27 (0.0003)</td>
</tr>
<tr>
<td>Seedlings &gt; 1.52 m tall</td>
<td>0.62 (0.0001)</td>
<td>0.50 (0.0001)</td>
</tr>
<tr>
<td>Non-woody cover</td>
<td>-0.03 (0.6605)</td>
<td>0.36 (0.0001)</td>
</tr>
</tbody>
</table>
4. Discussion

The response of small mammals to timber harvesting is strongly influenced by the degree to which vegetation is altered (Van Horne, 1981; Medin and Booth, 1989). Large-scale alterations such as clearcutting may alter habitat to such an extent that small mammal abundance is affected; however, thinning is likely to produce little direct effect on small mammals (Gore, 1988). Since changes in small mammal habitats will be more pronounced in stands that are clearcut, it is difficult to compare results from this study to those involving even-aged management techniques. However, most of the previous research has involved clearcutting, and little work has been done with thinning, especially related to gypsy moth management.

In this study, small mammals were more abundant in stands that were thinned. Monthey and Soutiere
(1985) also found that the abundance of small mammals was greater in partially cut than uncut woodlands. However, roughly 50% of the total tree basal area was removed in that study, which would likely have affected ground level vegetation and therefore, small mammal abundance to a greater degree. Most other studies found no response in total small mammal abundance after thinning (Martell, 1983; Klein and Michael, 1984; Brooks and Healy, 1988). Suzuki and other studies have shown no difference in the abundance of deer mice between selectively cut or thinned stands and uncut sites (Campbell and Clark, 1980; Martell, 1983; Brooks and Healy, 1988; Medin and Booth, 1989). It is difficult to explain the effect of thinning in our study because of the differential habitat use exhibited by species in this genus. The deermouse, *Peromyscus maniculatus nubiterae*, and white-footed mouse, *Peromyscus leucopus novaborancensis* are sympatric in forest habitats of Appalachia (Wilson, 1945; Klein, 1960; Wolff and Hurlbutt, 1982; Barry et al., 1984; Buckner and Shure, 1985) and occur in a wide range of habitat types. Both species have been captured and have shown microhabitat separation in the study area (Violet, 1973; Bardwell, 1979). However, *P. maniculatus* shows greater affinity to higher elevation habitats in the Appalachian Mountains, to larger openings, or to areas with larger trees (Wilson, 1945; Klein, 1960; Barry et al., 1984; Buckner and Shure, 1985; Parren and Capen, 1985). Attributes common to both *P. maniculatus* and *P. leucopus*, such as food preferences (Hamilton, 1941) can explain the increased abundance of deer mice in thinned stands, although our findings do not allow to distinguish the deermouse from the white-footed mouse.

Deermice association with PC1 was can be attributed to the increased cover offered by these areas and/or an increased food supply. Areas with more complex understories have been found to support a greater abundance of insects (Lovejoy, 1975), and may supply greater quantities of soft mast (Cooper et al., 1993). Sites with greater arthropod abundance support more deer mice (Mastrota et al., 1989) because insects make up a large proportion of their diet (Hamilton, 1941; Williams, 1959; Van Horne, 1982). Mice of this genus also rely heavily on acorn mast (Wolff, 1996), which can explain the correlation between the abundance of deer mice and PC3. Mast alone may not constitute a sufficient diet (Smith, 1962; Getz, 1968); however greater mast supplies in thinned stands could have...

As expected, total as well as oak basal area declined after thinning, but profound changes in understory vegetation characteristics, taken alone, were not detected. Despite this, PCA defined vegetational gradients that clearly separated thinned and reference stands. Since small mammals can be found in a large number of plant communities, associations between their abundance and habitat gradients would be a better indicator of their habitat affinities, rather than with individual vegetational parameters.

Understory vegetation complexity is an important factor influencing the abundance of small mammals (Dueer and Brown, 1980; Mastrota et al., 1989). The relative abundance of small mammals has been found to be greater in areas where the litter, ground, and shrub layers of vegetation are well developed (Clough, 1987). Similarly, we found that small mammal abundance was higher in areas where shrub, non-woody, and total understory cover, as well as seedling densities, were higher. Thinning not only provided enough new growing space to increase understory vegetation growth, it also provided higher levels of slash, in the form of tree tops and abandoned logs. Logs and slash are important structural microhabitat features as they can shield small mammals from predators and provide abundant refuges and foraging habitat (McCloskey, 1975; Kaufman et al., 1983; Yahner, 1988; Moses and Boutin, 2001). Both vegetation growth and increased slash levels increased the complexity of the understory, thereby increasing food supplies and expanding the amount of foraging and escape cover available to small mammals.

Small mammal abundance in thinned stands returned to levels similar to that found in reference stands during the final year of the study. This may indicate that small mammals responded to the initial harvest, i.e. to increased levels of slash and initial vegetative growth. Since thinnings were relatively light, residual trees may have been able to quickly fill the gaps left after thinning. Moreover, decomposition would account for decline in slash levels, thereby returning the habitat to its preharvest condition.

Although we found a thinning effect, several studies have shown no difference in the abundance of deer mice between selectively cut or thinned stands and uncut sites (Campbell and Clark, 1980; Martell, 1983; Brooks and Healy, 1988; Medin and Booth, 1989). It is difficult to explain the effect of thinning in our study because of the differential habitat use exhibited by species in this genus. The deermouse, *Peromyscus maniculatus nubiterae*, and white-footed mouse, *Peromyscus leucopus novaborancensis* are sympatric in forest habitats of Appalachia (Wilson, 1945; Klein, 1960; Wolff and Hurlbutt, 1982; Barry et al., 1984; Buckner and Shure, 1985) and occur in a wide range of habitat types. Both species have been captured and have shown microhabitat separation in the study area (Violet, 1973; Bardwell, 1979). However, *P. maniculatus* shows greater affinity to higher elevation habitats in the Appalachian Mountains, to larger openings, or to areas with larger trees (Wilson, 1945; Klein, 1960; Barry et al., 1984; Buckner and Shure, 1985; Parren and Capen, 1985). Attributes common to both *P. maniculatus* and *P. leucopus*, such as food preferences (Hamilton, 1941) can explain the increased abundance of deer mice in thinned stands, although our findings do not allow to distinguish the deermouse from the white-footed mouse.

Deermice association with PC1 was can be attributed to the increased cover offered by these areas and/or an increased food supply. Areas with more complex understories have been found to support a greater abundance of insects (Lovejoy, 1975), and may supply greater quantities of soft mast (Cooper et al., 1993). Sites with greater arthropod abundance support more deer mice (Mastrota et al., 1989) because insects make up a large proportion of their diet (Hamilton, 1941; Williams, 1959; Van Horne, 1982). Mice of this genus also rely heavily on acorn mast (Wolff, 1996), which can explain the correlation between the abundance of deer mice and PC3. Mast alone may not constitute a sufficient diet (Smith, 1962; Getz, 1968); however greater mast supplies in thinned stands could have...
resulted in greater winter survival of deermice. Although abundance of small mammals may not always be a good indicator of habitat quality (Van Horne, 1983; Vickery et al., 1992), increased hard and soft mast levels, along with higher invertebrate densities could have been enough to elicit the positive response of deermice to thinning.

In general, harvested stands had higher numbers of masked shrews, but there was no significant difference in their abundance between thinned and reference stands. Similarly, Martell (1983) found no difference in the number of masked shrew to forest thinning have been varied (Klein and Michael, 1984; Monthey and Soutiere, 1985). The relationships found between masked shrew abundance, PC1, and PC3, again show that masked shrews preferred areas where understory vegetation complexity is high. Abundance of shrews also has been correlated positively with percent cover of slash and fallen logs (Hahn and Michael, 1980; Yahner, 1988). Conditions in thinned stands would be expected to enhance masked shrew habitat because of increased food supplies and shelter from predators. It has been suggested that high abundance of fallen logs can reduce shrew foraging efficiency (Yahner, 1988). However, this has not been tested and seems counter-intuitive. We believe that the low-intensity of the harvest operation did not alter the habitat enough sufficiently to affect masked shrew populations.

Most researchers have documented a positive response of redback vole to selectively cut or thinned forested sites (Campbell and Clark, 1980; Martell, 1983; Monthey and Soutiere, 1985; Medin and Booth, 1989). The redback vole is commonly found in areas with a complex ground cover (e.g. shrubs, herbs, seedlings, and debris) (Miller and Getz, 1973; Lovejoy, 1975; Monthey and Soutiere, 1985; Yahner, 1988; Medin and Booth, 1989), and because of its inability to exist in water-limited environments (Getz, 1968; Miller and Getz, 1973) it may be the most influenced by cover. From these studies, we would expect redback voles to be associated with PC1 and PC3. However, our results do not correspond with the literature. Perhaps the relatively small number of redback vole captures influenced the relationships shown in these data. Moreover, as with the masked shrew, the lack of response exhibited by redback vole to harvesting may have been due to the relatively limited duration and intensity of thinning.

Small mammals are an important component of eastern forest ecosystems. The response of small mammals to logging depends on the type and severity of the harvest. Since silvicultural operations associated with minimizing defoliator impact do not remove a large proportion of the total tree basal area, ground level vegetation may not severely altered. However any increases in vegetational complexity or debris cover can influence small mammal abundance by altering forest floor microhabitats. Increased complexity provides small mammals with effective foraging and resting cover as well as increasing the available amount of invertebrates and plant foods.

In general, thinning had a positive influence on the small mammal abundance in our study. Thinning also reduced the oak component of residual stands, potentially decreasing its susceptibility to gypsy moth defoliation. Increases in the abundance of deermice, an important gypsy moth predator, could also reduce forest susceptibility to gypsy moth defoliation via increased predation. However, thinning did not have an effect on predation rates at our site (Grushecky et al., 1998), nor did the thinning directly affect population dynamics of gypsy moth (Liebhold et al., 1998). Although small mammals are important components of oak dominated ecosystems, particularly in the multiple trophic relationship of small mammals, gypsy moth, and mast (Liebhold et al., 2000), recent data have shown that predation by small mammals is inadequate to stabilize populations of gypsy moth (Elkinton et al., in press). Nevertheless, silvicultural gypsy moth management is an important management strategy, and has the potential to reduce forest susceptibility/vulnerability to gypsy moth infestation via many mechanisms. Such approaches also further the incorporation of ecological values in traditional forest management approaches.

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References


Fiske, W.F., 1913. The gypsy moth as a forest insect, with suggestions as to its control. US Bur. Ent. Cir. 164, Washington, DC.


Smith, R.L., Acorn consumption by white-footed mice, West Virginia University Agricultural Experimental Station Bull. 482T, 15 pp.


Yahner, R.H., Smith, H.R., 1991. Small mammal abundance and habitat relationships on deciduous forested sites with different susceptibility to gypsy moth defoliation. Environ. Manage. 15, 113–120.