

Does Forest Thinning Affect Predation on Gypsy Moth (Lepidoptera: Lymantriidae) Larvae and Pupae?

SHAWN T. GRUSHECKY, ANDREW M. LIEBHOLD,¹ RICHARD GREER,² AND ROBERT LEO SMITH

Division of Forestry, West Virginia University, Morgantown, WV 26506

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ABSTRACT Predation on larvae and pupae of the gypsy moth, *Lymantria dispar* (L.) was studied in a leading-edge population in West Virginia. In 8 thinned and 8 uncut stands, rates of survival of larvae and pupae were monitored in 3 types of enclosures placed at 3 heights in the forest strata. The abundance of small mammals was measured within each of these stands using pitfall traps. 37% of larvae and 25% of pupae were killed by predators over the 3 d of observations each year. Thinning did not influence the proportion of larvae or pupae killed. Survival of larvae and pupae on the ground was significantly lower than that found on tree boles or in the foliage. Differences in survival among enclosure types indicated that invertebrates were the major predators of larvae, and small mammals were the major predators of pupae.

KEY WORDS *Lymantria dispar*, *Peromyscus*, *Sorex*, predation, small mammals, enclosures

THE GYPSY MOTH, *Lymantria dispar* (L.), was accidentally introduced near Boston in 1868 or 1869 (Liebhold et al. 1989). Since that time, it has expanded its range through most of the northeastern United States. In areas where this insect has become established and host tree species preferred by the gypsy moth dominate, populations often fluctuate considerably. Populations may exist at low densities for many years but then, for reasons that are not completely understood, densities may increase rapidly to very high densities such that trees are totally defoliated.

Predation by small mammals on gypsy moth pupae has been documented as a major source of mortality in low-density gypsy moth populations in North America (Bess et al. 1947, Campbell and Sloan 1977a, Elkinton et al. 1989, Cook et al. 1994). Campbell and Sloan (1977a) hypothesized that predation by small mammals regulated gypsy moth populations at low levels. However, Elkinton et al. (1989) reported that predation on gypsy moths was characterized more by a type II functional response (Holling 1959), rather than a type III response that would be necessary for population regulation.

Changes in the density of innocuous gypsy moth populations have been found to be directly related to the intensity of predation, which is in turn directly related to predator abundance (Elkinton et al. 1996). Furthermore, there is considerable evidence that the density of small mammals and intensity of predation is inversely related with forest stand susceptibility to defoliation in North America; intense predation by small mammals appears to be one of the key factors

explaining stand immunity from gypsy moth outbreaks (Bess et al. 1947; Smith 1985, 1989; Cook et al. 1994; Liebhold et al. 1998a).

Interest exists in the development of methods for minimizing forest pest problems through the use of silvicultural manipulations. Gottschalk (1993) presented guidelines for reducing forest susceptibility to gypsy moth outbreaks through the use of silviculture. Largely, this method consists of thinning to reduce total stand density and specifically to reduce the stand component represented by species that are highly preferred by the gypsy moth. However, susceptibility may be strongly affected by the abundance of small mammal predators. Thus, it is important to understand how these silvicultural manipulations affect small mammal abundance and predation levels.

Grushecky (1995) found that silvicultural manipulations described by Gottschalk (1993) caused an increase in the abundance of small mammals. There is still a need to understand whether this translates into an increase in predation rates. The objective of this study was to determine whether thinnings that reduce total stand density and/or the oak component result in a change in predation levels and a subsequent change in gypsy moth abundance. This study was also designed to determine the identity of gypsy moth predators affecting gypsy moth survival.

Materials and Methods

Study Area. This project was conducted on the 3,905-ha West Virginia University Forest, which comprises the northern half of the Coopers Rock State Forest. It is located ≈8 km northeast of Morgantown, WV in Preston and Monongalia counties.

¹ Northeastern Forest Experiment Station, U.S. Forest Service, Morgantown, WV 26505.

² Exxon Biomedical Sciences, Inc., East Millstone, NJ 08873.

Table 1. Characteristics of stands used for predation studies on the West Virginia University Forest, including both experimental and environmental factors

Stand	Area, ha	Treatment ^a	No. plots	Age, yr	Site index ^b	% Tot. reduction ^c	% Pref. reduction ^d
1	12.29	T	14	58	89	29.56	39.86
2	11.23	R	14	59	78	—	—
3	12.70	T	14	57	76	28.91	43.73
4	11.68	R	10	56	76	—	—
5	11.76	R	13	59	73	—	—
6	10.82	T	14	58	80	32.06	17.45
7	9.08	DT	9	55	94	17.19	29.71
8	7.97	D	10	58	96	—	—
9	9.20	T	11	58	69	33.94	29.67
10	9.84	R	11	60	67	—	—
11	9.80	T	9	58	83	37.57	38.24
12	9.97	R	9	56	78	—	—
13	7.86	DT	10	60	64	31.97	30.18
14	8.06	D	10	60	67	—	—
15	12.45	DT	14	62	80	34.15	32.32
16	11.72	D	10	58	74	—	—

^a T, stands that were thinned during the winter of 1989; R, stands that served as reference; D, stands that were defoliated; DT, stands that were both thinned and then defoliated.

^b Site index₅₀ for northern red oak.

^c Percentage reduction in total basal area in stands that were thinned.

^d Percentage reduction in preferred tree species basal area in stands that were thinned. Preferred tree species include *Quercus* spp., *Tilia americana*, and *Populus* spp.

The university forest is situated on Chestnut Ridge, which is the western-most ridge of the Allegheny Mountains, and is within the unglaciated Allegheny Plateau. The topography of the area is the result of differential erosion of resistant Pottsville sandstone and less resistant Pennsylvanian rocks (Carvell et al. 1978). Elevation on the forest ranges from 318 to 795 m, the average slope being 20% (Carvell et al. 1978).

The forest types found at the university forest are of 2 general groups—Appalachian mixed hardwood (cove hardwood) types, and mixed oak types. Cove hardwood types are normally dominated by yellow poplar, *Liriodendron tulipifera* L., with mixtures of white and red oak, *Quercus* spp.; eastern hemlock, *Tsuga canadensis* (L.) Carr.; American basswood, *Tilia americana* L.; and white ash, *Fraxinus americana* L., depending on site characteristics. Mixed oak types are typically found on more arid sites and are dominated by oaks *Quercus* spp. or are of an oak–hickory, *Carya* spp., composition.

Design. In 1989, a study was initiated at the university forest to assess the feasibility of silviculture as a gypsy moth management tool. Sixteen stands with a total area of 163.2 ha were delineated in 1989 on the forest. Stands ranged in size from 7.86 to 12.7 ha (mean, 10.2 ha). Stand age ranged from 55 to 62 years (mean, 58 yrs) and site index₅₀ for northern red oak *Quercus rubra* L., ranged from 64 to 96 (mean, 78) (Table 1). Eight of these stands were thinned in 1989. The remaining 8 stands were not cut, and served as reference areas. The objective of these thinnings was to reduce the quantity of trees that were susceptible or vulnerable to gypsy moth damage (Gottschalk 1993). Six of these stands also received a >50% reduction in canopy cover caused by gypsy moth defoliation in 1990 and 1991. Gypsy moth defoliation was

therefore considered a 2nd treatment in the analyses, thinning being the 1st.

Within each stand, a 100-m grid was established so that sampling plots could be defined. A random number of plots was chosen, using the preestablished grid, to sample small mammal populations and to measure predation. Variable numbers of sampling plots were chosen within each stand, based on its area, so that sampling intensity was consistent (Table 1). Predation and population sampling points did not coincide.

Predation Studies. To determine the importance of various predators (e.g., vertebrates versus invertebrates), the survival rate of gypsy moth larvae and pupae was examined inside 3 types of exclosures deployed in 183 points. The 1st exclosure was constructed using 2.54-cm mesh netting (chicken wire), which was designed to exclude avian predators. The 2nd was constructed using 1.27-cm screen, which was designed to exclude both avian and mammalian predators. The last had no mesh; it was considered a reference to naturally occurring predation.

Before being placed within exclosures, laboratory-reared gypsy moth larvae and pupae were attached to 20 by 20 cm. burlap squares. Larvae were tethered to burlap with thread (Weseloh 1988), whereas pupae were secured using beeswax (Smith 1985). Larvae were deployed in late June and the pupae were deployed in late July during the summers of 1989–1992. These time frames coincided with the periods that late larval and pupal stages naturally occur within the area being studied.

Three stations were located at each of 183 points; stations were within 15 m of the point, but at least 5 m apart. At 1 tree at each station, 1 exclosure was secured to the base of the tree, another was secured to the tree trunk, and the last was fastened to an overhanging branch (<3 m high). The exclosures were placed in

alternating locations at each station, so there were 9 enclosure–location combinations per plot. The enclosures were monitored for 3 d during each year and the extent and type of predation on larvae and pupae were recorded daily. Larvae or pupae that were fragmented or missing were considered predated. Those that remained intact were considered surviving.

Gypsy moth egg masses were counted on twenty 0.01-ha plots (Liebhold et al. 1998b) in every stand each year. The number of egg masses per hectare was estimated from these counts.

Small Mammal Trapping. To determine the effect of small mammal abundance on predation rates, we captured small mammals with large-capacity pitfall traps during the summers of 1989 through 1992. Traps were checked once a week for a period of 11 wk each year. The pitfall traps were constructed by affixing a square particle board apron to a cylindrical container (19 cm deep). Each apron had a hole (15 cm diameter) in its center, where the plastic container was inserted to serve as the receptacle for any captures. The wooden apron was used to ensure that the traps were flush with the ground.

Each pitfall trap was partially filled with ≈ 5 cm of propylene glycol, which served as both a killing agent and preservative. During each monitoring visit, the propylene glycol was filtered to remove any captures. Specimens were then taken to the laboratory and frozen for future identification.

Analyses. The proportion of larvae and pupae killed by predators was determined at the stand level within each enclosure–height combination, then transformed to a k value ($-\log_{10}[\text{survival} + 0.1]$) for analyses. A split-plot analysis of variance (ANOVA) was used to determine if any differences existed in the proportion of gypsy moth larvae and pupae that survived within each stand. The ANOVA model can be stated as follows:

$$Y_{ijklm} = \mu + a_i + y_k + h_l + e_m + s_{ij} + y_k^*s_{ij} + (y)_{ik} + (h)_{il} + (e)_{im} + (he)_{lm} + (he)_{ilm} + \varepsilon_{ijklm}$$

where Y_{ijklm} represents the proportion of gypsy moth larvae–pupae surviving predation (k value), μ is the overall mean, a_i is the main effect of treatment, y_k is the main effect of year, h_l is the main effect of enclosure height, e_m is the main effect of enclosure type, s_{ij} is a random effect caused by stands within each treatment, $y_k^*s_{ij}$ is a random effect caused by the interaction between year and stands within each treatment, $(y)_{ik}$, $(h)_{il}$, $(e)_{im}$, $(he)_{lm}$, and $(he)_{ilm}$ are interaction terms, and ε_{ijklm} is a random effect that represents all uncontrolled variability.

To test for differences between treatments, s_{ij} was used as the error term. To test for differences between years and the interaction between year and treatments, $y_k^*s_{ij}$ was used as the error term.

When expressed as a k factor [$-\log(\text{survival})$ (Varley et al. 1974)], total predation can be partitioned into mortality caused by mammals, invertebrates, and birds:

$$k_{\text{total}} = k_{\text{mammal}} + k_{\text{invertebrate}} + k_{\text{birds}}$$

It is thus obvious that predation in reference (no enclosure) pupae was the same as total mortality:

$$k_{\text{control}} = k_{\text{mammal}} + k_{\text{invertebrate}} + k_{\text{birds}}$$

We made 2 assumptions about how the various enclosures functioned: First, it was assumed that the 2.5-cm mesh excluded birds but not invertebrates or mammals:

$$k_{2.5} = k_{\text{invertebrate}} + k_{\text{mammal}}$$

Second, we assumed that the 1.3-cm mesh excluded all but invertebrate predators:

$$k_{1.3} = k_{\text{invertebrate}}$$

Based upon these assumptions, we estimated predation by each of the 3 types of predators from predation rates observed in the various enclosures:

$$k_{\text{invertebrate}} = k_{1.3}$$

$$k_{\text{mammal}} = k_{2.5} - k_{1.3}$$

$$k_{\text{bird}} = k_{\text{control}} - k_{2.5}$$

Least-squares regression techniques were used to determine if any relationships existed between gypsy moth larval and pupal mortality (both total mortality, k_{control} , and mortality caused by small mammals, k_{mammal} , were used as dependent variables), and independent variables: catch per unit effort (CPUE = number of small mammals per 100 trap nights) of small mammal predators and gypsy moth egg mass density. Data on the survival of gypsy moth larvae and pupae in reference enclosures were pooled among the ground and trunk and were considered the field survival rate.

Least-squares regressions also were used to assess the impact of small mammal abundance and predation rates at time T on gypsy moth populations at time $T+1$ (e.g., time T represents predation rates in 1989, time $T+1$ represents gypsy moth populations in 1990). Gypsy moth egg mass density, total small mammal abundance, *Peromyscus* spp. abundance, and *Sorex cinereus* (Kerr) (masked shrew) abundance were \log_{10} -transformed to help linearize their relationship with the proportion of larvae or pupae killed.

The effects of thinning and defoliation on gypsy moth larval and pupal survival when small mammal predators were the only source of mortality also was explored. ANOVA was used to determine if any differences existed in the survival rate of gypsy moth larvae and pupae between treatments.

Several researchers (Smith and Lautenschlager 1981, Weseloh 1988, Elkinton et al. 1989) have discussed the problems associated with accurately estimating natural predation rates. In this study we used survival of tethered pupae and larvae only as relative measures of natural predation; the proportion of gypsy moth larvae or pupae surviving on our study sites was not used as an estimate of actual survival in field populations.

Table 2. Small mammal capture summary from 1989 to 1992 in stands used to conduct predation studies on the West Virginia University Forest

Species	No. captures	% of total
Masked shrew	849	41.93
<i>Sorex cinereus</i> Kerr		
White-footed and deer mice	685	33.83
<i>Peromyscus</i> spp.		
Southern red-backed vole	277	13.68
<i>Clethrionomys gapperi</i> Vigors		
Woodland jumping mouse	85	4.20
<i>Napaeozapus insignis</i> Miller		
Pine vole	37	1.83
<i>Microtus pinetorum</i> LeConte.		
Northern short-tailed shrew	29	1.43
<i>Blarina brevicauda</i> Say		
Eastern chipmunk	25	1.23
<i>Tamias striatus</i> L.		
Smoky shrew	20	0.99
<i>Sorex fumeus</i> Miller		
Pygmy shrew	11	0.54
<i>Sorex hoyi</i> Baird		
Longtail shrew	3	0.15
<i>Sorex dispar</i> Batchelder		
Hairytail mole	2	0.10
<i>Parascalops breweri</i> Bachman		
Least shrew	1	0.05
<i>Cryptotis parva</i> Say		
Star-nose mole	1	0.05
<i>Condylura cristata</i> L.		
Total	2,025	100.00

Results

Overstory vegetation characteristics were similar in both thinned and reference stands before logging. Northern red oak had the greatest basal area, followed by yellow-poplar; red maple, *Acer rubrum* L.; and chestnut oak, *Q. prinus* L. As a result of thinning, total tree basal area and basal area of species preferred by the gypsy moth were reduced by 31% and 33% respectively (Table 1). There was no change in the ranking of the most common tree species after thinning.

Small Mammals. Thirteen species of small mammals (a total of 2,025 individuals) were captured over the 4-yr study period (62,832 trap nights) (Table 2). The most abundant species of small mammals captured were *Sorex cinereus* Kerr, which made up 41.9% of the total catch, and *Peromyscus* spp., which represented 33.8% of the total catch, all of which are gypsy moth predators. Research has shown that *Peromyscus leucopus* R. (Fisher) is the most effective gypsy moth predator (Smith and Campbell 1978, Smith and Lautenschlager 1981). However, *Peromyscus maniculatus* W. and *Peromyscus leucopus* R. are sympatric in Appalachia (Wilson 1945, Klein 1960, Barry et al. 1984) and have similar food preferences (Hamilton 1941). Therefore, it is likely that *Peromyscus maniculatus* M. is also an effective gypsy moth predator. Individuals within the genus *Peromyscus* were grouped for the analysis because they occupy similar niches, and their capture and subsequent soaking in propylene glycol made identification difficult.

Larval Studies. Of the 4,380 larvae deployed after thinning, 63% survived predation over the 3-d obser-

Table 3. Gypsy moth larval and pupal *k* values among treatments

Treatment	Larvae <i>k</i> value	Pupae <i>k</i> value
Thinning	0.16a	0.08a
Reference	0.14ac	0.08a
Defoliation	0.10b	0.05a
Thinned and Defoliated	0.11bc	0.05a

Means with the same letter are not significantly different at $\alpha = 0.05$ (ANOVA).

vation period. The overall survival rate of tethered larvae (1989–1992) was 65%.

Survival rates of larvae differed among treatments ($F = 4.26$; $df = 3,12$; $P = 0.0289$); *k* values in thinned stands were significantly greater than those found in defoliated stands (Table 3). Larval survival rates when only small mammal predators were considered were not different among treatments ($F = 0.38$; $df = 3,32$; $P = 0.7645$); however, differences among years were apparent ($F = 5.07$; $df = 2,32$; $P = 0.0122$). Survival of larvae was significantly higher in 1991 and 1992 than in 1990.

Exclosure height also was important ($F = 122.57$; $df = 2,320$; $P = 0.0001$); significantly fewer larvae survived on the ground than on the trunk, and a greater number were predated on the trunk than in the foliage (Table 4). Likewise, exclosure size had an effect on the proportion of larvae surviving ($F = 18.90$; $df = 2,320$; $P = 0.0001$); significantly fewer larvae survived in reference exclosures than in 2.54-cm-mesh exclosures and in 2.54- versus 1.27-cm-mesh exclosures (Table 4).

The effect of treatment was not the same over all exclosure heights ($F = 2.84$; $df = 6,320$; $P = 0.0105$). Survival of larvae on the ground was the lowest in control (*k* value = 0.32) and thinned (*k* value = 0.30) stands, compared with that found in defoliated (*k* value = 0.19) and in thinned-defoliated stands (*k* value = 0.22). Survival of larvae on the trunk was significantly greater in thinned and defoliated stands (*k* value = 0.09) and significantly less in thinned stands (*k* value = 0.13) than in control (*k* value = 0.11) and defoliated (*k* value = 0.10) stands. In the foliage, significantly more larvae survived in defoliated stands (*k* value = 0.02) than in control (*k* value = 0.04), thinned and defoliated (*k* value = 0.04), and thinned

Table 4. Gypsy moth larval *k* values found at all heights, exclosures, and height-exclosure combinations during the summers of 1990–1992 on the West Virginia University Forest

Exclosure size, cm	Exclosure Location			
	Ground	Trunk	Foliage	Total
Reference	0.38	0.15	0.06	0.18a
2.54	0.26*	0.12*	0.04	0.13b
1.27	0.19*	0.07*	0.05	0.10c
Total	0.27a	0.11b	0.05c	0.14

* significant increase in larval survival by exclosure size. Values with the same letter are not significantly different (Duncan multiple range test).

Table 5. Gypsy moth larval and pupal k values when only invertebrate, small mammal, or bird predation was considered

	Larvae			Pupae		
	Ground	Trunk	Foliage	Ground	Trunk	Foliage
Invertebrate k	0.191	0.066	0.041	0.037	0.014	-0.008
Small mammal k	0.073	0.037	-0.013	0.128	0.041	0.005
Bird k	0.123	0.042	0.011	0.104	-0.005	0.009

Predation rates recorded within enclosures were used to estimate k values.

(k value = 0.08) stands. The interaction between the height of enclosure and the size of enclosure also influenced the proportion of larvae surviving predation ($F = 6.70$; $df = 4,320$; $P = 0.0001$). At ground and trunk heights, significantly fewer larvae were destroyed in 1.27-cm versus 2.54-cm and reference enclosures (Table 4).

Enclosure data indicated that invertebrates were the most active larval predators on the ground and trunk, followed by birds and small mammals. Both invertebrates and birds had similar impact on larval survival in the foliage; small mammals had a very minimal presence in foliage (Table 5).

When survival rates of gypsy moth larvae at ground and trunk heights in reference enclosures were regressed on gypsy moth egg mass density and total small mammal abundance, only egg mass density explained a significant amount of the variation in the proportion of larvae surviving predation (Table 6). These results were similar to those found when larval survival was regressed on gypsy moth egg mass density and *Peromyscus* spp. abundance, and egg mass density and *S. cinereus* abundance. Estimated coefficients indicated that larval survival tended to decrease with increasing gypsy moth density (Table 6).

Gypsy moth density did not explain a large amount of variation in larval survival when only small mammal predators were considered. However, *Peromyscus* spp. abundance accounted for a significant amount of variation in larval survival (Table 7). As *Peromyscus* spp. predation increased, survival of larvae decreased.

A significant amount of the variation in gypsy moth populations at time $T+1$ was explained by total small mammal abundance and *S. cinereus* abundance at time T ; however, survival rates of larvae, when only small mammal predators were considered at time T , did not

partition a significant amount of variation in gypsy moth populations at time $T+1$ (Table 8). Avian predation on larvae had no influence on gypsy moth populations the following year. Likewise, predation on larvae by invertebrates did not explain a significant amount of the variation in egg mass densities at time $T+1$ (Table 8).

Pupal Studies. Of the 4,762 pupae deployed after thinning, 75% were not predated. The overall survival rate of the artificially placed pupae (1989–1992) was 78%.

Neither thinning nor defoliation had an effect on the proportion of gypsy moth pupae surviving predation ($F = 1.91$; $df = 3,12$; $P = 0.1822$). However, differences were found in the proportion of pupae surviving among years ($F = 7.36$; $df = 2,24$; $P = 0.0032$). The survival rate of pupae in 1992 was greater than that found in 1991 and 1990. Pupal survival rates, when only small mammal predators were considered, were not different among treatments ($F = 0.52$; $df = 3,36$; $P = 0.6693$) or years ($F = 2.44$; $df = 2,36$; $P = 0.1011$).

Placement height of enclosure ($F = 96.77$; $df = 2,352$; $P = 0.0001$) and size of enclosure ($F = 28.69$; $df = 2,352$; $P = 0.0001$) also had an effect on survival rates of pupae. Fewer pupae survived on the ground than on the trunk, and on the trunk than in the foliage (Table 9). Survival rates were lower in reference versus 2.54-cm-mesh and 2.54-cm-versus 1.27-cm-mesh enclosures (Table 9).

The interaction between enclosure size and height also influenced survival rates ($F = 17.04$; $df = 4,352$; $P = 0.0001$). Significantly fewer pupae survived predation on the ground in reference enclosures than in 2.54-cm-mesh and in 2.54-cm versus 1.27-cm-mesh enclosures (Table 9). On the trunk, significantly fewer

Table 6. Gypsy moth larval and pupal k values in reference enclosures as dependent variable, gypsy moth egg mass density and small mammal abundances as independent variables

Source ^a	Larvae			Pupae		
	t^b	P	Coefficient ^c	t^b	P	Coefficient ^c
Gypsy moth density	-2.07	0.0434	-0.0367	0.13	0.9006	0.0019
Total small mammal abundance	1.38	0.1727	0.1372	4.35	0.0001	0.3813
Gypsy moth density	-1.95	0.0563	-0.0356	0.35	0.7292	0.0057
<i>Peromyscus</i> abundance	0.68	0.5019	0.0828	2.40	0.0194	0.2786
Gypsy moth density	-2.31	0.0248	-0.0419	-0.58	0.5623	-0.0088
<i>Sorex cinereus</i> abundance	1.23	0.2235	0.1322	4.13	0.0001	0.3978

^a Results from 3 separate regressions. Dependent variable is the k value for larvae-pupae on the ground and trunk in control enclosures for each model.

^b Null hypothesis that the parameter is equivalent to 0.

^c Estimated coefficients of regression model.

Table 7. Gypsy moth larval and pupal *k* values when only predation from small mammal predators was included as dependent variable, gypsy moth egg mass density and small mammal abundances as independent variables

Source ^a	Larvae			Pupae		
	t ^b	P	Coefficient ^c	t ^b	P	Coefficient ^c
Gypsy moth density	0.88	0.3852	0.1242	-0.30	0.7676	-0.0037
Total small mammal abundance	1.99	0.0515	0.1578	1.96	0.0549	0.1450
Gypsy moth density	1.42	0.1620	0.0192	0.02	0.9813	0.0002
<i>Peromyscus</i> abundance	3.46	0.0010	0.3140	3.30	0.0016	0.2805
Gypsy moth density	0.67	0.5064	0.0099	-0.34	0.7346	-0.0044
Masked shrew abundance	0.51	0.6098	0.0453	0.29	0.7697	0.0244

^a Results from 3 separate regressions. Dependent variable is the *k* value for larvae-pupae on the ground and trunk in control enclosures for each model.

^b Null hypothesis that the parameter is equivalent to 0.

^c Estimated coefficients of regression model.

pupae survived in reference and 2.54-cm enclosures than in 1.27-cm-mesh enclosures (Table 9).

As in larval studies, there was a significant interaction between treatment and the height of enclosures ($F = 3.32$, $df = 6,352$; $P = 0.0035$). On the ground, significantly fewer larvae survived in thinned (*k* value = 0.20) and control (*k* value = 0.19) stands than in thinned and defoliated (*k* value = 0.13) and defoliated (*k* value = 0.11) stands. Pupae placed in the foliage had significantly lower survival rates in thinned (*k* value = 0.02) stands than in control (*k* value = 0.01), defoliated (*k* value = 0.001), and thinned and defoliated (*k* value = 0.002) stands. Survival rates were similar on tree trunks across all treatments.

Enclosures data indicated that small mammals were the most active predator of pupae on the ground and trunk, followed by birds on the ground and inverte-

brates on the tree bole. Results also indicated that birds were the most active pupal predators in the foliage, followed by small mammals and invertebrates, respectively (Table 5).

When the survival rates of gypsy moth pupae at ground and trunk heights in reference enclosures were regressed on gypsy moth egg mass density and total small mammal abundance, only total small mammal abundance explained a significant amount of the variation in the proportion of pupae surviving predation (Table 6). Likewise, when survival rates of pupae were regressed on both gypsy moth density and *Peromyscus* spp. abundance, and egg mass density and *S. cinereus* abundance, only *Peromyscus* spp. and *S. cinereus* abundance explained a significant amount of the variation in the pupae survival (Table 6).

Relationships with pupal survival when only small mammal predators were considered were similar to those with larval survival; gypsy moth egg mass density did not explain a large amount of variation in pupal survival. However, only *Peromyscus* spp. abundance accounted for a significant amount of variation in survival rates (Table 7). This relationship was positive—as *Peromyscus* spp. abundance increased, predation also increased.

Survival rates of pupae when only small mammal predators were considered did not explain a significant amount of variation in gypsy moth populations at time *T*+1 (Table 8). Likewise, avian-caused mortality did not explain a significant amount of variation in egg mass density at time *T*+1 (Table 8). Pupal survival rates when only invertebrate predation was consid-

Table 8. Results from regression analysis on gypsy moth egg mass densities found on the West Virginia University Forest. Gypsy moth egg mass density at time *T*+1, as the dependent variable; gypsy moth egg mass density at time *T*, small mammal abundances, and survival of pupae and larvae when only small mammal, bird, or invertebrate predators were the independent variables

Source ^a	t ^b	P	Coefficient ^c
Gypsy moth density (time <i>T</i>)	3.03	0.0036	0.2913
Total small mammal abund.	-3.64	0.0006	-2.0744
Gypsy moth density (time <i>T</i>)	2.73	0.0084	0.2904
<i>Peromyscus</i> abundance	-0.21	0.8329	-0.1611
Gypsy moth density (time <i>T</i>)	4.10	0.0001	0.3691
Masked shrew abundance	-5.10	0.0001	-2.9160
Gypsy moth density	1.58	0.1199	0.1763
Larval-mammal <i>k</i> value ^d	-0.47	0.6416	-0.4691
Gypsy moth density	2.75	0.0079	0.2897
Pupal-mammal <i>k</i> value ^d	-0.73	0.4655	-0.7714
Gypsy moth density	1.51	0.1359	0.1692
Larval-bird <i>k</i> value ^d	-0.15	0.8820	-0.1609
Gypsy moth density	2.86	0.0058	0.2940
Pupae-bird <i>k</i> value ^d	-1.93	0.0587	-2.677
Gypsy moth density	1.02	0.3117	0.1200
Larval-invertebrate <i>k</i> value ^d	-1.21	0.2314	-1.326
Gypsy moth density	3.03	0.0036	0.3088
Pupal-invertebrate <i>k</i> value ^d	-2.32	0.0240	-3.2949

^a Table shows results from 5 separate regressions. Dependent variable is gypsy moth egg mass density at time *T*+1 for each model (eg. gypsy moth density in 1990 versus small mammal abundance in 1989).

^b Null hypothesis that the parameter is equivalent to 0.

^c Estimated coefficients of regression model.

^d *k* value of larvae and pupae when only small mammal, bird, or invertebrate predators were included.

Table 9. Gypsy moth pupal *k* values found at all heights, enclosures, and height-enclosure combinations during the summers of 1990-1992 in the West Virginia University Forest

Enclosure size, cm	Enclosure location			
	Ground	Trunk	Foliage	Total
Reference	0.29	0.07	0.02	0.11a
2.54 cm.	0.17*	0.07	0.003	0.08b
1.27 cm.	0.06*	0.03*	0.001	0.03c
Total	0.17a	0.05b	0.007c	0.07

* significant increase in pupal survival by enclosure size.

Values with the same letter are not significantly different (Duncan multiple range test).

ered explained a significant amount of the variation in egg mass densities at time $T+1$ (Table 8).

Discussion

Buckner (1966) found that the beneficial qualities of vertebrate predators could be maximized by manipulating their habitat, thus increasing its carrying capacity. *Peromyscus* populations have been enhanced successfully by providing nest boxes and supplemental food (Smith 1975); however, there was no evidence of higher gypsy moth pupal mortality. We found results similar to that of Smith (1975). Although the abundance of small mammal predators increased significantly in the silviculturally manipulated stands (Grushecky 1995), the proportion of gypsy moth larvae and pupae surviving predation was similar in both thinned and reference stands. The finding that larval survival was significantly higher in stands that were defoliated, regardless of any silvicultural manipulation, may be a result of over saturation of predators with gypsy moth larvae. As larval populations climbed to defoliating levels, predators may have been satiated, allowing a greater percentage of gypsy moth larvae to survive.

The silvicultural manipulations did not influence the effectiveness of small mammal predators because larval and pupal survival, when only small mammal predators were considered, did not differ between stands that were thinned or defoliated. Increased complexity of understory vegetation and slash cover following timber harvests could have benefited population growth of small mammal predators, but, at the same time, decreased the vulnerability of gypsy moth larvae and pupae to predation. Increased heterogeneity of vegetation has been found to hinder mammalian predators of ground-nesting birds (Bowman and Harris 1980, Yahner and Cypher 1987, Martin 1988). Thus, because of an increase in searching time, proportionally fewer gypsy moth larvae and pupae may have been killed, even though the number of small mammal predators in the thinned stands increased. Moreover, the changes in understory vegetation may have provided small mammals with an abundance of alternate foods, which can markedly reduce their effectiveness as gypsy moth predators (Smith 1989). It also is possible that complex vegetation at the ground level may have provided gypsy moth larvae and pupae with safer resting and pupating locations.

The proportion of larvae and pupae surviving predation was found to differ between the 3 enclosure positions. It has been shown previously that the survival rate of gypsy moth larvae is related to the resting site they choose (Campbell et al 1975a,b; Campbell et al 1977; Weseloh 1988). The survival rate of tethered larvae placed in the litter was lower than that found at other heights within the forest strata. These results are similar to those found by other researchers (Bess et al. 1947; Bess 1961; Campbell and Sloan 1976; Weseloh 1988, 1990). Because small mammal predators spend the majority of their foraging time in the litter, larvae

resting in the litter are more likely to be preyed upon (Campbell and Sloan 1976). The proportion of larvae killed declined as enclosure height increased, which provides further evidence supporting the concentration of predators in the litter. Although predated larvae have been found at least 35 ft above the ground (Campbell 1975), most research has shown that larval mortality decreases as the height of resting location increases (Smith 1985, Weseloh 1988).

The effect of enclosure size on predation rates provides additional insight on the identity of gypsy moth larval predators. Similar to the results of past larval enclosure studies (Campbell and Sloan 1977a, Weseloh 1988), there was a decline in the proportion of larvae killed on the ground and trunk when birds were excluded (2.54-cm mesh) and when both avian and small mammal predators were excluded (1.27-cm mesh). Enclosure results (Table 5) indicated that invertebrate predators were destroying the greatest number of gypsy moth larvae on the ground and the trunk. Likewise, Weseloh (1988) determined that invertebrate predators accounted for most of the predation of large larvae in the litter. However, he also found that vertebrate predators caused most of the larval predation found on tree trunks, which contradicts our results.

Results obtained from regression analyses provide further information on the identity of predators of tethered larvae. No relationships were found between the proportion of larvae surviving on the ground and trunk and small mammal predator abundance. If small mammals were the primary predator of larvae in the litter, mortality rates would be expected to increase as small mammal abundance increased. The actual relationship between small mammals and larval predation rates is difficult to ascertain, particularly since alternate foods may dilute their response (Holling 1959, Buckner 1966, Smith 1989). Nevertheless, we found a significant relationship between *Peromyscus* spp. abundance and larval survival rates when only small mammal predators were included in regressions (Table 7). Therefore, it can be concluded that the predation by small mammal predators was indeed attributable to small mammals.

There was an inverse relationship between total predation rates and gypsy moth egg mass density (Table 6). This supports previous findings that predation on gypsy moth is inversely density dependent (Campbell and Sloan 1978, Elkinton et al. 1989, Gould et al. 1990).

Predation rates of tethered caterpillars may not accurately reflect predation on field populations, because of the inability of tethered larvae to escape predators. Weseloh (1990) found that tethered larvae are preyed upon to a greater extent than are free-ranging larvae. Actual larvae in field populations may find more cryptic resting sites than tethered larvae. It also is possible that missing caterpillars, which were recorded as predated, may have actually escaped from their tethers. Therefore, larval predation rates observed in this study may be much higher than those that would be expected in field populations.

Overall survival rates of pupae were higher than those found by previous researchers (i.e., Campbell and Torgersen 1983, Smith 1985, Cook et al. 1994); $\approx 39\%$ of the pupae deployed on the ground were killed. Predation was more intense in the litter than at other heights within the forest strata (Table 9). This result is closely aligned with the results obtained with larvae (Table 4) and with previous studies (Campbell et al. 1975a; Campbell and Sloan 1976; Smith 1985, 1989; Elkinton and Liebhold 1990; Cook et al. 1994). Similar to the results of Campbell et al. (1975a), Smith (1985), and Cook et al. (1994), pupal survival increased with increasing height within the forest strata. Small mammals have been found to prey heavily upon pupae on the ground (Smith 1985, 1989; Elkinton and Liebhold 1990; Cook et al. 1994). Therefore, pupae in sheltered locations above the ground may be less likely to be found by foraging predators, particularly small mammals.

Based on evidence from the enclosure study (Table 5), predators larger than invertebrates were responsible for a majority of the predation of pupae in the litter. However, predator specific k values computed for the different enclosure heights imply that small mammals were destroying the most pupae on the ground and bole, but not in the foliage: k values computed for birds in the foliage were higher than those calculated for small mammal predators. Previous research has shown that small mammals destroy more pupae than do avian predators. Likewise, Campbell and Torgersen (1983) found that pupal predation by small mammals compensated for avian predation, but avian predation did not compensate for small mammal predation. The combined effect of birds and small mammals may be important in maintaining low gypsy moth densities; however, it appears that avian predators feed mainly upon gypsy moth larvae (Campbell 1975, Campbell and Sloan 1976, Campbell et al. 1977, Smith 1989).

Alone, the enclosure studies provided information on the identity of predators feeding on pupae; however, examination of the relationship between survival and small mammal abundance provided additional information on these identities. Of the small mammal predator species sampled on our site, only the abundance of *Peromyscus* spp. were closely correlated with the level of predation by small mammal predators (Table 7). However, the effectiveness of *Peromyscus* spp. in maintaining low gypsy moth populations was not evidenced in this study. Predation on larvae and pupae by small mammal predators did not explain a significant portion of the variation in gypsy moth egg mass densities (Table 8), even though there was a significant inverse relationship between total small mammal abundance and *S. cinereus* (Kerr) abundance at time T and gypsy moth egg mass densities at time $T+1$. The relationship between small mammal abundance and gypsy moth egg mass densities the following year does not imply that small mammal predation on pupae in our study was density dependent. Moreover, we found no relationship between the proportion of pupae killed and gypsy moth egg mass density, which

may have indicated some form of a density dependent response (Table 7).

The importance of small mammals as gypsy moth predators has been well documented. However, one cannot expect to influence survival rates of gypsy moth larvae or pupae by managing predator habitat alone. Predation by small mammals on gypsy moth has previously been found to be inversely density dependent (Campbell and Sloan 1978, Elkinton et al. 1989, Gould et al. 1990), although we did not find this relationship. Thus as gypsy moth densities increase, the effect of small mammals on reducing populations may diminish. Increasing small mammal populations may increase their effectiveness as gypsy moth predators; however, if larvae and pupae are able to escape predation, or if alternative foods become more plentiful, larvae and pupae survival would increase. Although thinning may increase predator abundance, this apparently does not translate into increased rates of predation. Liebhold et al. (1998b) reported in a parallel study that thinning had no observable effect on rates of parasitism or disease in gypsy moth populations. Thus, it appears that thinning may cause gypsy moth populations to decline by decreasing the quantity of host foliage but it has little effect on other processes affecting gypsy moth dynamics.

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