

Forest type affects predation on gypsy moth pupae

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- Abstract**
- 1 Predation by small mammals has previously been shown to be the largest source of mortality in low-density gypsy moth, *Lymantria dispar* (L.), populations in established populations in north-eastern North America. Fluctuations in predation levels are critical in determining changes in population densities.
 - 2 We compared small mammal communities and levels of predation on gypsy moth pupae among five different oak-dominated forest types along this insect's western expanding population front in Wisconsin. Comparisons of predator impact can provide critical information for predicting variation in susceptibility among forest types.
 - 3 The results indicated that small mammals caused more mortality than did invertebrates.
 - 4 Both abundance of *Peromyscus* sp. predators and predation levels were lower in urban and xeric forest types than in mesic sites.
 - 5 These results suggest that, because predation pressures will probably be greater in the mesic sites, gypsy moths may be less likely to develop outbreaks in these habitats, and that defoliation will probably be more frequent in urban and xeric oak-dominated sites.

Keywords Lepidoptera, Lymantriidae, *Lymantria dispar*, *Peromyscus*, predator.

Introduction

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), was introduced to North America, near Boston, Massachusetts, around 1868 and, subsequently, it has been gradually expanding its range (Liebhold *et al.*, 1992). In many parts of the region where this insect has established, populations intermittently erupt to outbreak densities causing extensive forest defoliation. These outbreaks result in a variety of economic and ecological effects. Because the gypsy moth is a polyphagous herbivore, defoliation events may occur in a variety of forest types. However outbreaks are usually concentrated in stands dominated by its primary hosts (e.g. *Quercus*, *Populus* and *Larix*) (Liebhold *et al.*, 1997; Davidson *et al.*, 2001). Numerous studies in the north-eastern portion of the U.S.A. have focused on identifying additional characteristics of highly susceptible stands. These studies suggest that

oak stands growing on dry sites are particularly prone to defoliation (Houston & Valentine, 1977; Valentine & Houston, 1979; Davidson *et al.*, 2001). Unfortunately, these types of studies have been largely limited to the north-eastern U.S.A. and, as the range of the gypsy moth continues to expand southward and westward, more information is needed to identify susceptible forest types in regions where populations are just beginning to colonize. Once populations have been established in these areas for many years, it will be possible to identify forest types where defoliation is most frequent. However, until these data become available, it would be useful to predict those stands that are likely to have the most frequent and intense outbreaks in the future. With such projections in advance of defoliation, land managers can develop and apply appropriate silvicultural approaches to mitigate damage.

The reasons why gypsy moth populations may exist at low densities for many years, but suddenly erupt to outbreak levels, are not entirely clear (Elkinton & Liebhold, 1990; Liebhold *et al.*, 2000). However several studies indicate that predation on late instar larvae and pupae is the largest source of mortality in low-density gypsy moth

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populations and that this mortality is closely associated with temporal trends in low-density populations (Campbell, 1967; Campbell *et al.*, 1977; Elkinton & Liebhold, 1990; Elkinton *et al.*, 1996; Jones *et al.*, 1998). Most of the predation appears to be caused by small mammals, especially by *Peromyscus* spp. (Rodentia: Muridae) (Bess, 1961; Campbell & Sloan, 1977; Grushecky *et al.*, 1998; Liebhold *et al.*, 2000). Furthermore, there is compelling evidence that variation in predator densities and predation rates among forest types may explain differences in susceptibility to gypsy moth outbreaks observed among these same forest types (Smith, 1985; Yahner & Smith, 1991; Cook *et al.*, 1995; Liebhold *et al.*, 1998).

North American studies of variation in predator communities and associated predation on gypsy moth populations have been limited to New England, the Appalachian Mountains and the mid-Atlantic coastal plain regions. Virtually nothing is known about how predation varies among different forest types in the Great Lakes region. As the gypsy moth expands its range into this area, outbreaks are likely to occur in new forest types, about which little is known on their susceptibility (Biging *et al.*, 1980; Witter *et al.*, 1992; Kruse & Raffa, 1997). In the present study, we compared both small mammal predator communities and rates of predation on gypsy moth pupae among a variety of forest types in Wisconsin where known gypsy moth hosts occur. Our objective in undertaking this study was to use the observed variation in predation levels to extrapolate susceptibility to gypsy moth outbreaks once this region becomes entirely colonized.

Methods

Study areas

Predator communities and predation pressure were compared among five different forest types where gypsy moth hosts were abundant and would therefore be expected to support populations. These forest types were: pin oak, bur oak, upland oak, swamp bottomland and urban. Pin oak stands were dominated by *Quercus palustris*, *Quercus alba*, *Quercus rubra* and *Pinus resinosa*. Bur oak types were dominated by *Quercus macrocarpa* and *Q. alba*. Upland oak stands were dominated by *Q. palustris* and *Q. rubra*. Swamp bottomland sites were dominated by *Acer saccharinum*, *Populus tremuloides* and *Fraxinus nigra*. These forest types represent a continuum from highly xeric (Pin oak sites) to highly mesic (swamp bottomland) conditions (Kotar *et al.*, 1988; Kotar & Burger, 1996). The urban sites were dominated by large *Quercus* and *Acer* spp. with cultivated turf as a ground cover. For each forest type, three replicate 10-ha sites were located in separate woodlots in Wisconsin, U.S.A. (Table 1). At each site, species composition was assessed using measurements with a 20 BAF prism (Ben Meadows Co., Jamesville, Wisconsin) at eight plots.

Small mammal census

We evaluated the small mammal communities at 12 of the 15 sites via trapping (populations in the three 'urban oak' forest type sites were not censused due to the high likelihood of vandalism there). Small mammals were sampled using a grid of 49 Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida) set on a grid with 15-m intervals between traps. Populations were sampled for one night each in July and August (this coincides approximately with the timing of gypsy moth pupal development in Wisconsin), both in 1998 and 1999. Trapping was not conducted over successive nights to avoid 'learning' by raccoons, which might disturb traps. Traps were baited with peanut butter and provided with cotton for bedding. Captured mice were marked with uniquely numbered metal ear tags and released at the point of capture. Records of captures and recaptures for each season were used to calculate 'minimum number animals known alive' (Krebs, 1998) for each species at each site. A repeated measures analysis of variance (Sokal & Rohlf, 1995) was applied to log transformed yearly totals of each small mammal species trapped at each site to test the significance of differences in mammal abundance among forest types.

Measurement of predation

Predation rates were measured in July 1999 and 2000 at each of the 15 study sites, by monitoring the disappearance of 75 deployed gypsy moth pupae in the field. Laboratory-reared pupae were glued individually to 15 × 15 cm burlap squares with melted beeswax. To avoid accidental colonization of sites that were not currently infested with resident gypsy moth populations, irradiated pupae (Mastro *et al.*, 1981) were used at all locations (in a preliminary test in which freeze-dried pupae were deployed, there was almost 100% predation after one night at all sites and freeze-dried pupae were therefore not used in further tests). Burlap squares were fixed to the forest floor with a small steel stake on transects distributed uniformly through the study site, with 10–20 m between each pupa. Over each of the next 3 days, each burlap square was visited and the condition of each pupa was recorded. Condition was recorded as intact, partially eaten or completely missing, based on protocols used in previous studies (Smith, 1985; Cook *et al.*, 1995; Elkinton *et al.*, 1996; Grushecky *et al.*, 1998). A repeated measures analysis of variance (Sokal & Rohlf, 1995) was applied to arcsine square root-transformed yearly proportions of pupae predated (partially or completely missing) at each site to test the significance of differences in predation among forest types.

Identification of agents causing predation

Previous studies in North America indicate that a complex of species, including birds, small mammals and invertebrates, prey on gypsy moth larvae and pupae (Smith, 1981, 1985). To estimate the amount of mortality caused by small mammals, we compared predation levels inside of

Table 1 Location and forest composition (basal area, m²/ha) at the 15 study sites

	Urban			Pin oak			Bur oak			Upland oak			Swamp bottomland		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Latitude	43°N 01° 03'	44°N 28° 18'	43°N 03° 29'	44°N 23° 00'	44°N 16° 56'	44°N 20° 53'	42°N 56° 36'	42°N 50° 40'	42°N 51° 48'	45°N 22° 44'	45°N 21° 22'	45°N 21° 22'	44°N 38° 56'	44°N 40° 36'	44°N 40° 36'
Longitude	89°W 24° 45'	88°W 02° 24'	88°W 01° 48'	89°W 15° 11'	89°W 15° 34'	89°W 23° 04'	88°W 27° 21'	88°W 36° 18'	88°W 32° 22'	88°W 22° 35'	88°W 26° 26'	88°W 26° 09'	87°W 31° 31'	87°W 32° 21'	87°W 32° 24'
<i>Quercus alba</i>	16.5	12.6	5.7	5.7		4.0	8.8	2.7	14.9						
<i>Quercus macrocarpa</i>	22.9	15.3	12.0	3.1			3.1	5.7	3.4						
<i>Quercus palustris</i>	22.9			6.9	8.0	4.6	1.1	0.8		11.1	4.6	6.1			
<i>Quercus rubra</i>			1.7	5.3	5.2		1.9		2.3	12.6	10.6	12.2			
<i>Pinus resinosa</i>				4.6	3.1	9.2						2.3			
<i>Pinus strobus</i>				3.1	4.6										
<i>Pinus banksiana</i>					2.3										
<i>Ulmus americana</i>				4.6											
<i>Acer rubrum</i>				2.3							5.0	2.9			
<i>Acer saccharinum</i>	22.9	2.3											8.0	9.6	10.7
<i>Prunus serotina</i>				2.3	3.4										
<i>Betula alleghaniensis</i>													3.4	5.0	3.1
<i>Betula papyrifera</i>												2.3	3.4		
<i>Populus tremuloides</i>			1.7										5.3	2.9	4.0
<i>Fraxinus nigra</i>													6.5	8.8	6.9
<i>Carya ovata</i>		3.4					1.5	1.1							
<i>Aesculus hippocastanum</i>		2.3													
<i>Tilia americana</i>	16.5	12.6	5.7	5.7		4.0	8.8	2.7	14.9						

cages (1.27 cm = 1/4 steel mesh) that excluded small mammals with predation on pupae with no exclosures. This method for differentiating among predation caused by various groups of gypsy moth predator species has been used in several previous studies (Campbell & Sloan, 1977; Weseloh, 1990; Grushecky *et al.*, 1998). Comparisons of predation on pupae using exclosures was conducted at 11 of the 15 study sites during 1999.

Data on total mortality of deployed pupae were expressed as a k factor [$-\log(\text{survival})$] (Varley *et al.*, 1973; Grushecky *et al.*, 1998). Total predation can be partitioned into mortality caused by mammals and invertebrates:

$$k_{\text{total}} = k_{\text{mammal}} + k_{\text{invertebrate}} \quad (1)$$

Predation in control (no exclosure) pupae was the same as total mortality:

$$k_{\text{control}} = k_{\text{mammal}} + k_{\text{invertebrate}} \quad (2)$$

We based our further calculations on the assumption that the wire mesh excluded all mammals (but not invertebrates) and thus all mortality was due to invertebrates:

$$k_{\text{invertebrate}} = k_{\text{exclosure}} \quad (3)$$

It was then possible to estimate predation by small mammals:

$$k_{\text{mammal}} = k_{\text{control}} - k_{\text{exclosure}} \quad (4)$$

Results and discussion

Numbers of small mammals trapped at the 12 study sites are shown in Table 2. *Peromyscus* was generally the predominant small mammal trapped at all locations. However, there is probably some variation among small mammal species in their tendency to enter traps and these frequencies thus may not precisely reflect relative densities among

species. For example, *Sorex* spp. tend not to enter Sherman live traps; thus, they may be relatively more dominant than indicated by Table 2. It is not clear why 22 *Sorex* spp. were trapped in 1998 but none were trapped in 1999, although this difference could have been due to varying environmental conditions (e.g. weather) in those years. Furthermore, the minimum number known alive generally provides an under-estimate of true densities (Krebs, 1998), but the use of more complex estimators was precluded by the limitation of mammal-sampling to two nights per year. Despite these limitations, mammal-sampling was adequate for differentiating small mammal communities among different forest types (see below).

Mean numbers of *Peromyscus* spp. trapped per site varied significantly among the four forest types tested ($F = 21.48$, $P = 0.0003$) (Table 2). The rank order of mean abundance (over all years and sites) was lowest in the Pin Oak type ($\bar{X} = 13.8$), larger in the Bur Oak type ($\bar{X} = 24.7$), larger yet in the Upland Oak type ($\bar{X} = 26.2$) and largest in the Swamp Bottomland type ($\bar{X} = 31.4$). This order generally paralleled the known order of soil moisture conditions, with the Pin Oak stands being the driest and the swamp bottomlands being the most mesic (Kotar *et al.*, 1988; Kotar & Burger, 1996). These results are similar to comparisons of *Peromyscus* among oak-dominated sites in New England and elsewhere in the north east: densities are typically lowest on dry sites (e.g. ridge tops) and highest in the more mesic sites (e.g. mid-slope) (Smith, 1985).

Repeated measures analysis of variance indicated a significant effect of forest type on percent mortality of deployed pupae after 3 days ($F = 3.48$, $P = 0.0498$). Similar to the trend observed for *Peromyscus* abundance, mortality was lowest at the Pin Oak sites, followed by the Bur Oak Sites, followed by the Upland Oak sites (Fig. 1).

Table 2 Number of small mammals trapped at 12 forested sites in Wisconsin during July and August, 1998–99

Site	Year	Pin oak			Bur oak			Upland oak			Swamp bottomland		
		1	2	3	1	2	3	1	2	3	1	2	3
<i>Blarina brevicauda</i>	1998							14		1	1	1	2
	1999	2	2			1					1	2	
<i>Tamias striatus</i>	1998					1				1			
	1999		4	5		3	4	10	5	10			
<i>Zapus hudsonius</i>	1998												
	1999									5			
<i>Mustela nivalis</i>	1998												1
	1999												1
<i>Peromyscus</i> spp.	1998	8	4	6	17	15	17	17	36	10	33	39	26
	1999	16	27	22	23	25	51	27	25	42	33	21	37
<i>Clethrionomys gapperi</i>	1998					2						3	1
	1999		1	2				1	2	1	3	3	
<i>Synaptomys cooperi</i>	1998												5
	1999												
<i>Glaucomys volans</i>	1998									1			
	1999		1					1					
<i>Sorex</i> spp.	1998					7		6		4	1	2	2
	1999												

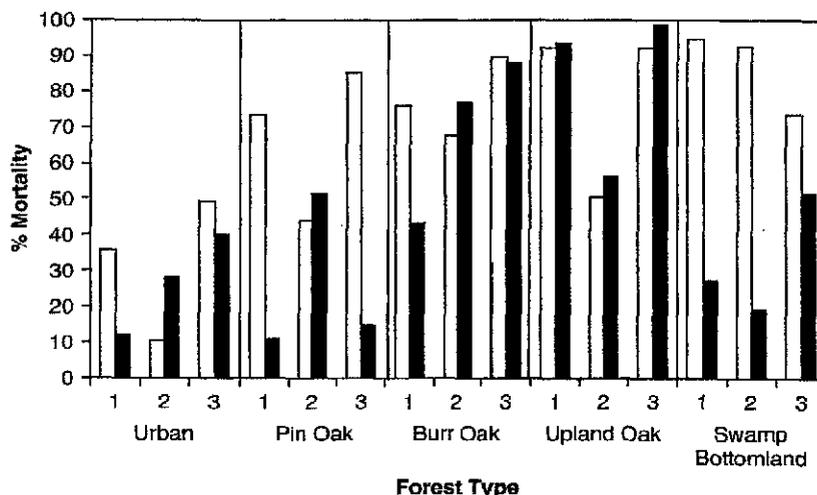


Figure 1 Percent predation (day 3) on deployed pupae at 15 sites in 1999 (□) and 2000 (■).

Mortality was very high at the swamp bottomland sites in 1999 but low in 2000. Extensive precipitation occurred during the period of pupal deployment in 2000 and many pupae in these sites were observed either completely surrounded by standing water or the burlap squares were themselves floating. This may explain why predation levels were so low at these sites in 2000. Predation at the urban sites was generally as low as, or lower than, that at the pin oak stands.

The only year for which data on both *Peromyscus* abundance and predation were both available was 1999. When counts of *Peromyscus* were paired with day 3 mortality rates from the same site, the correlation coefficient was positive (0.302) but not significant ($P = 0.340$, $n = 12$). Several other studies in which more data were available found a significant association between *Peromyscus* abundance and predation levels (Elkinton *et al.*, 1989; Elkinton

et al., 1996; Grushecky *et al.*, 1998). The lack of significance in the present study may be largely attributed to the relatively small number of observations.

Pooling enclosure data among all sites, the predation rate of pupae outside of enclosures was 81.6% but was 33.4% for pupae inside of enclosures. The mean k_{mammal} over all plots was 0.780 and the mean $k_{\text{invertebrate}}$ was 0.175. Most mortality was apparently caused by small mammals at all sites (Fig. 2). This trend is generally in agreement with similar studies conducted in the north-eastern U.S.A. (Smith, 1985; Grushecky *et al.*, 1998). Studies in the south-eastern U.S.A. also found high pupal mortality by small mammals when present, but relatively high pupal mortality by invertebrates when small mammals were not present (Cook *et al.*, 1995; Hastings *et al.*, 2002). As observed for the more extensive pupal mortality experiments without enclosures (Fig. 1), the data from the

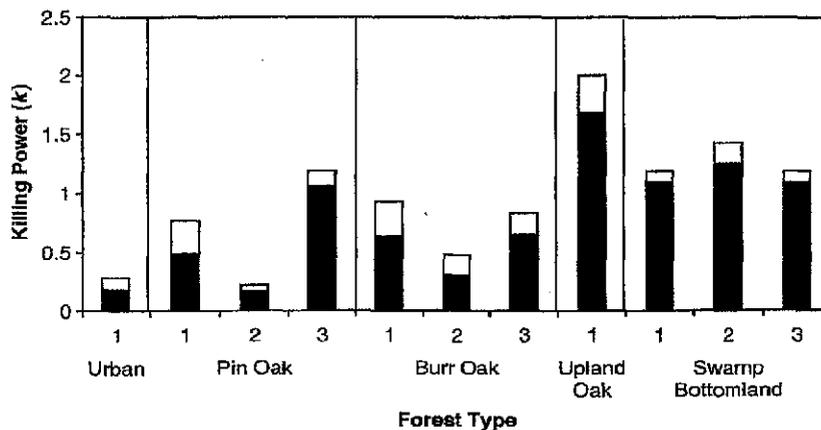


Figure 2 Killing power (k) of predation caused by small mammals (■; calculated from Eq. (4)) and invertebrates (□; calculated from Eq. (3)) estimated from survival of deployed pupae inside and outside of enclosures after three nights at 11 sites in 1999.

enclosure study (Fig. 2) indicated that mortality was generally lowest in the urban and xeric (Pin Oak and Bur Oak) sites and highest in the more mesic sites (Upland Oak and Swamp bottomland).

Although the limitations of the data presented here preclude any detailed conclusions about the complete numerical relationships between small mammal populations and gypsy moth dynamics, it is possible to make some important predictions about how small mammal populations may influence gypsy moth dynamics in these forest types, once this insect becomes established there. First, these data indicate that levels of predation on gypsy moth pupae by small mammals are high and comparable to levels observed for gypsy moth populations elsewhere in North America and the world (Cook *et al.*, 1995; Elkinton *et al.*, 1996; Grushecky *et al.*, 1998; Liebhold *et al.*, 1998; Hastings *et al.*, 2002). Thus, we can expect that once gypsy moth becomes established in this region, small mammals are likely to play an important role in the dynamics of low-density populations. Furthermore, extrapolating from these data, we might expect gypsy moth outbreaks to be more common in these types of stands because predation levels (and *Peromyscus* populations) tend to be lower in urban and xeric oak stands than in mesic oak stands. This conclusion is supported by studies in the north-eastern U.S.A. indicating that gypsy moth outbreaks are often chronic in xeric stands that support lower mouse densities and consequently predation levels are lower (Smith, 1985; Yahner & Smith, 1991). Similarly, our finding that mouse populations were highest (and predation pressure was highest) in mesic oak stands is consistent with similar findings in New England states.

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References

- Bess, H.-A. (1961) Population ecology of the gypsy moth *Porthetria Dispar* L. (Lepidoptera: Lymantriidae). *Bulletin 43*. New Haven Connecticut Agricultural Experiment Station, New Haven, Connecticut.
- Björing, G.S., Giese, R.L. & Nordheim, E.V. (1980) Gypsy moth population simulation for Wisconsin. *Forest Science*, **26**, 710–724.
- Campbell, R.W. (1967) The analysis of numerical change in gypsy moth populations. *Forest Science Monographs*, **15**, 33.
- Campbell, R.W. & Sloan, R.J. (1977) Natural regulation of innocuous gypsy moth populations. *Environmental Entomology*, **6**, 315–322.
- Campbell, R.W., Sloan, R.J. & Biazak, C.E. (1977) Sources of mortality among late instar gypsy moth [*Lymantria dispar*] larvae in sparse populations. *Environmental Entomology*, **6**, 865–871.
- Cook, S.P., Smith, H.R., Hain, F.P. & Hastings, F.L. (1995) Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae by invertebrates at low small mammal population densities. *Environmental Entomology*, **24**, 1234–1238.
- Davidson, C.B., Gottschalk, K.W. & Johnson, J.E. (2001) European gypsy moth (*Lymantria dispar* L.) outbreaks: a review of the literature. *US Department of Agriculture, Forest Service, General Technical Report*, **278**, 1–15.
- Elkinton, J.S., Gould, J.R., Liebhold, A.M., Smith, H.R. & Wallner, W.E. (1989) Are gypsy moth populations in North America regulated at low density? *Proceedings, Lymantriidae: A comparison of features of New and Old World tussock moths*, (ed. by W.E. Wallner and K.A. McManus), pp. 233–249. US Dept. Agric. Forest Service, Radnor, Pennsylvania.
- Elkinton, J.S. & Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–596.
- Elkinton, J.S., Healy, W.M., Buonaccorsi, J.P., Boettner, G.H., Hazzard, A.M., Smith, H.R. & Liebhold, A.M. (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecology*, **77**, 2332–2342.
- Grushecky, S.T., Liebhold, A.M., Greer, R. & Smith, R.L. (1998) Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantriidae) larvae and pupae. *Environmental Entomology*, **27**, 268–276.
- Hastings, F.L., Hain, F.P., Smith, H.R., Cook, S.P. & Monahan, J.F. (2002) Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae in three ecosystems along the southern edge of infestation. *Environmental Entomology*, **31**, 668–675.
- Houston, D.R. & Valentine, H.T. (1977) Comparing and predicting forest stand susceptibility to gypsy moth [*Lymantria dispar*]. *Canadian Journal of Forest Research*, **7**, 447–461.
- Jones, C.G., Ostfeld, R.S., Richard, M.P., Schaubcr, E.M. & Wolff, J.O. (1998) Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science*, **279**, 1023–1026.
- Kotar, J. & Burger, T.L. (1996) *A Guide to Forest Communities and Habitat Types of Central and Southern Wisconsin*. Department of Forestry, University of Wisconsin, Madison, Wisconsin.
- Kotar, J., Kovach, J.A. & Locey, C.T. (1988) *Field Guide to Forest Habitat Types of Northern Wisconsin*. Department of Forestry, University of Wisconsin, Madison, Wisconsin.
- Krebs, C.J. (1998) *Ecological Methodology*, 2nd edn. Benjamin Cummings, San Francisco, California.
- Krusc, J.J. & Raffa, K.F. (1997) Effects of selected midwestern larval host plants on performance by two strains of the gypsy moth (Lepidoptera: Lymantriidae) parasitoid *Cotesia melanoscela* (Hymenoptera: Braconidae). *Environmental Entomology*, **26**, 1155–1166.
- Liebhold, A.M., Halverson, J.A. & Elmes, G.A. (1992) Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography*, **19**, 513–520.
- Liebhold, A.M., Gottschalk, K.W., Mason, D.A. & Bush, R.R. (1997) Evaluation of forest susceptibility to the gypsy moth across the conterminous United States. *Journal of Forestry*, **95**, 20–24.
- Liebhold, A.M., Higashiura, Y. & Unno, A. (1998) Forest type affects predation on gypsy moth (Lepidoptera: Lymantriidae) pupae in Japan. *Environmental Entomology*, **27**, 858–862.
- Liebhold, A., Elkinton, J., Williams, D. & Muzika, R.M. (2000) What causes outbreaks of the gypsy moth in North America? *Population Ecology*, **42**, 257–266.

- Mastro, V.C., Schwalbe, C.P. & O'Dell, T.M. (1981) Sterile-male technique. *The Gypsy Moth: Research Toward Integrated Pest Management*, vol. 1584 (ed. by C.C. Doane and M.A. McManus), pp. 669–679. US Dept. of Agriculture, Washington, DC.
- Smith, H.R. (1981) *The Gypsy Moth: Research Toward Integrated Pest Management*, vol. 1584 (ed. by C.C. Doane and M.L. McManus), pp. 96–124. US Dept. of Agriculture, Washington, DC.
- Smith, H.R. (1985) Wildlife and the gypsy moth. *Wildlife Society Bulletin*, **13**, 166–174.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. W.H. Freeman, New York, New York.
- Valentine, H.T. & Houston, D.R. (1979) A discriminant function for identifying mixed-oak stand susceptibility to gypsy moth *Lymantria dispar* defoliation. *Forest Science*, **25**, 468–474.
- Varley, G.C., Gradwell, G.R. & Hassell, M.P. (1973) *Insect Population Ecology: An Analytical Approach*. Blackwell Scientific, U.K.
- Weseloh, R.M. (1990) Estimation of predation rates of gypsy moth larvae by exposure of tethered caterpillars. *Environmental Entomology*, **19**, 448–455.
- Witter, J.A., Stoycnoff, J.L. & Sapio, F. (1992) Impacts of the gypsy moth in Michigan. *Michigan Academician*, **25**, 67–90.
- Yahner, R.H. & Smith, H.R. (1991) Small mammal abundance and habitat relationships on deciduous forested sites with different susceptibility to gypsy moth defoliation. *Environmental Management*, **15**, 113–120.

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