Preoutbreak Dynamics of a Recently Established Invasive Herbivore: Roles of Natural Enemies and Habitat Structure in Stage-Specific Performance of Gypsy Moth (Lepidoptera: Lymantriidae) Populations in Northeastern Wisconsin

REBECCA HOFFMAN GRAY,[1,2] CRAIG G. LORIMER,[3] PATRICK C. TOBIN,[4] AND KENNETH F. RAFFA[1]

Environ. Entomol. 37(5): 1174–1184 (2008)

ABSTRACT A major challenge to addressing biological invasions is that the need for emergency responses often precludes opportunities to analyze the dynamics between initial establishment and population eruption. Thus, a broader understanding of underlying processes and management opportunities is often lacking. We examined the effects of habitat structure and natural enemies on recently established preeruptive gypsy moth, *Lymantria dispar* L., populations over 4 yr in northeastern Wisconsin. Forty-five sites were established across a range of habitat structures in oak-dominated northern hardwood forests. The number of egg masses was positively related to percent composition of oaks and other favored species. Other life stages were not related to habitat structure variables. Abundance of each life stage can predict the subsequent life stage with variable degrees of accuracy, but male moth densities were only a weak predictor of egg mass or larval densities the following year. The parasitic fly *Compsilura concinnata* (Meigen), an introduced generalist with deleterious nontarget effects, caused the highest mortality to larvae. The specialist pathogens *Entomophaga maimaiga* and nucleopolyhedrosis virus were widely distributed but caused less mortality than reported in the northeastern United States, where gypsy moth has been established much longer. Small mammals are the major predators of pupae as elsewhere, but invertebrates seem less important along the western than southern advancing front of gypsy moth. Overall habitat structure did not influence natural enemy populations. These results suggest that the pre-eruptive phase is distinct from the pre-establishment phase by high mating success and from the eruptive phase by the prominent role of generalist natural enemies. Improved understanding of these dynamics can help guide silvicultural and biocontrol strategies in newly invaded regions of the Midwest and provide general insight into invasive forest defoliators.

KEY WORDS *Lymantria dispar*, habitat structure, invasive species, natural enemies, forest insects

Invasive species have negatively affected the productivity, biodiversity, and socioeconomic values of North American forest ecosystems (Liebhold et al. 1995, Niemelä and Mattson 1996). In particular, the rate of introduction of nonindigenous insects has intensified with increased global trade and international travel (Vitousek et al. 1996, Sala et al. 2000, Leung et al. 2005, Work et al. 2005, McCullough et al. 2006). More than 360 species of nonindigenous insects have now become established in North America, and 30% are considered serious pests (Niemelä and Mattson 1996, Liebhold et al. 1995b, Pimentel et al. 2000, Mattson et al. 2007). In the United States, the economic and environmental costs caused by nonindigenous invasive insects may approach $120 billion annually (Pimentel et al. 2005). A major difficulty in developing strategies for contending with biological invasions is that the need for rapid response under emergency conditions often precludes opportunities for the development of the basic information needed for process-based management guidelines. Consequently, there are few examples where substantial baseline information was generated in advance of population eruptions, leaving us with little quantitative and qualitative understanding of long-term impacts and remedial tactics (Jenkins et al. 1999).

One of the most damaging invasive forest insects in the United States is the gypsy moth, *Lymantria dispar* L., which defoliates a broad range of deciduous and coniferous host trees. State and federal governments spend $10–14 million annually to mitigate outbreaks

[1] Department of Entomology, University of Wisconsin-Madison, 345 Russell Laboratories, 1630 Linden Dr., Madison, WI 53706.
[2] Corresponding author: Wisconsin Department of Agriculture, Trade and Consumer Protection, 2811 Agriculture Dr., Madison, WI 53718 (e-mail: rahoffma@yahoo.com).
[3] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 113 Russell Labs, 1630 Linden Dr., Madison, WI 53706.
[4] Forest Service, U.S. Department of Agriculture, Northern Research Station, 180 Canfield Street, Morgantown, WV 26505.

0046-225X/08/1174–1184$04.00/0

and reduce its spread into uninfested areas (Tobin and Blackburn 2007, Gypsy Moth Digest 2008). The gypsy moth is now well established over much of the northeastern United States and is currently spreading south through North Carolina and west through Wisconsin at a variable rate of ≈6–18 km/yr (Tobin et al. 2007a). The gypsy moth was first detected in Wisconsin in 1988 and is now established in most of the eastern half of the state; the western half remains sporadically infested.

Defoliation by the gypsy moth can reduce tree growth, vigor, and resistance to other stresses and cause direct mortality to host trees (Kulman 1971, Herrick and Gansner 1987, Naidoo and Lechowicz 2001). Damaging outbreaks adversely affect forest productivity, esthetic quality, recreational values, and residential values (Liebhold et al. 1995b, Leuschner et al. 1996). Although the gypsy moth can feed on >300 host species, populations grow to particularly high levels in stands dominated by *Quercus*, *Salix*, *Populus*, and *Larix* species and can cause extensive damage in xeric sites where host trees tend to be under greater environmental stress (Liebhold et al. 1995a, Muzika and Liebhold 2000). Outbreaks have typically developed in areas where at least 20% of the trees were represented by preferred species (Herrick and Gansner 1986).

Gypsy moth population dynamics can be complex (Doane and McManus 1981, Elkinton and Liebhold 1990), and there are numerous natural enemies that can be important in either maintaining low population densities or diminishing outbreak populations. At low population levels, small mammals such as *Peromyscus* spp. are considered to be the most important natural enemies (Bess et al. 1947, Campbell and Sloan 1978, Hastings et al. 2002b, Elkinton et al. 2004), with their populations influenced by mast dynamics (Elkinton et al. 1996, Jones et al. 1998). The parasitoid *Compsilura concinnata* (Meigen) (Diptera: Tachinidae) can exert spatially density-dependent control (Gould et al. 1990, Liebhold and Elkinton 1989), but this generalist species has caused pronounced nontarget impacts (Boettner et al. 2000, Strong and Pemberton 2000, Kellogg et al. 2003). Other important introduced enemies include the egg parasitoid *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), the larval parasitoids *Cotesia melanoscela* (Ratzeberg) (Hymenoptera: Braconidae), *Parasetigena silvestris* (Robineau-Desvoidy) (Diptera: Tachinidae) and *Blepharipa pratensis* (Meigen) (Diptera: Tachinidae), the pupal parasitoid *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae), and the predator *Calosoma sycophanta* (Linneaus) (Coleoptera: Carabidae) (Brown and Cameron 1982, Weseloh 1985, Elikinton and Liebhold 1990, Skinner et al. 1993, Grushecky et al. 1998, Hastings et al. 2002a, Liebhold et al. 2005). At outbreak densities, populations tend to be regulated by two host specific entomopathogens (Doane 1970, Dwyer et al. 2004). The fungal entomopathogen *Entomophaga maimaiga*, introduced from Eurasia, and a nucleopolyhedrosis virus (LdMNPV) that arrived with the founding gypsy moth population are widely distributed and are usually the principal biotic agents causing the decline of outbreaks (Elkinton and Liebhold 1990). *E. maimaiga* has had a particularly strong impact in regions in which gypsy moth has been established for long periods and underwent outbreaks (Hajek 1997, 1999, Dwyer et al. 1998).

In recent years, silvicultural approaches to managing gypsy moth populations have been considered (Gottschalk 1993, Liebhold et al. 1998). Trees with vigorous crowns and of dominant or codominant crown class seem more tolerant to repeated years of defoliation (Gottschalk 1993). Research has also been conducted to study the effects of forest type, habitat structure, and/or thinning on the performance of gypsy moth natural enemies, but these relationships are only partially understood (Weseloh 1995, Liebhold et al. 1997, Grushecky et al. 1998, Hastings et al. 2002b, Muzika et al. 2004).

As the gypsy moth continues to spread into new areas, it is unclear how trophic interactions, coupled with differences in forest composition, will influence its dynamics, particularly its transition from the newly established to eruptive phases. Management strategies are uniformly applied along the invasion front through the Slow-the-Spread Program coordinated at the federal level (Sharov et al. 2002, Tobin and Blackburn 2007), but recent evidence has shown that gypsy moth establishment and spread dynamics are quite different along the leading edge (Whitmire and Tobin 2006, Tobin et al. 2007a, b, Tobin and Blackburn 2008), and the underlying mechanisms remain unclear. We studied relationships among gypsy moth, forest composition, stand architecture, and natural enemies in northern hardwood forests in Wisconsin. Our specific objectives were to (1) determine effects of habitat structure on stage-specific performance of the gypsy moth, (2) identify the major natural enemies affecting each life stage and their relative importance, and (3) establish baseline information, in advance of the first major defoliation, for long-term studies on how habitat structure affects the transition of gypsy moth from establishment to outbreak dynamics.

Materials and Methods

Field Sites. Forty-five sites were established in Oconto County in northeastern Wisconsin within the Lakewood/Laona Ranger district of the Chequamegon-Nicolet National Forest over an area of ≈29 km^2 (Fig. 1). All sites were classified as the *Acer/Viburnum* habitat type (Kotar et al. 2002) in oak-dominated northern hardwood stands. The climate is characterized by an average temperature range of 12–20°C, annual frost-free period of 113 d, and 810 mm of precipitation (National Oceanic and Atmospheric Administration 2008). Northern red oak (*Quercus rubra* L.), a highly preferred host of gypsy moth (Liebhold et al. 1995a), was the predominant tree species in all stands. Other common trees included the favored host species of witch hazel (*Hamamelis virginiana* L.), ironwood [*Ostrya virginiana* (Miller) K. Koch], quaking aspen (*Populus tremuloides* Michaux), paper birch

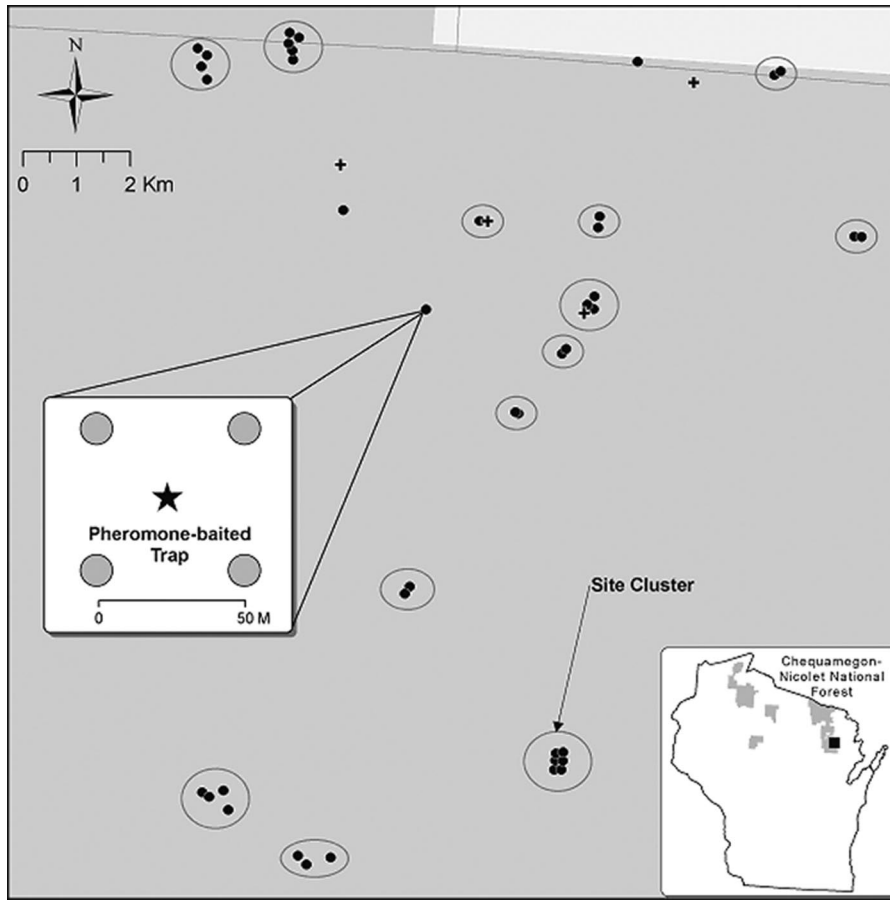

Fig. 1. Study sites located on portions of the Chequamegon-Nicolet National Forest in northwestern Oconto County in northeastern Wisconsin. Each site contained four 100-m^2 plots separated by 50 m, and a central pheromone-baited trap (inset). Sites denoted by a cross indicate those removed from the study at the end of 2004. Sites in close proximity were clustered together for additional correlation analyses (cf. Table 2).

(*Betula papyrifera* Marshall), and American basswood (*Tilia americana* L.), as well as the less or nonpreferred host species of white ash (*Fraxinus americana* L.), beech (*Fagus americana* Sweet), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* L.) (Liebhold et al. 1995a, Hoffman 2006). The first male gypsy moths were captured in Oconto county in 1995, which may or may not indicate establishment, and this region was placed under quarantine in 1999 after repeated and increasing trap catches (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45).

Each site consisted of four circular 100-m^2 plots (5.67-m radius). The plots were 50 m apart in a square configuration (Fig. 1). Plot center coordinates were recorded using GPS. The diameter at breast height (dbh), species, and condition of all trees >5.08 cm dbh in each plot were recorded. Basal area within each plot was calculated and used to determine the percentage of oak and favored host species (which includes oak) for each plot. Stand basal area (m^2/ha) of each plot was estimated using a 10 factor prism. We also calculated the stocking percent, which is an integrated measure of tree density, stand basal area, and mean tree diameter, in each plot using the stocking chart of McGill et al. (1991) and the methods of Gingrich (1967). Stocking is generally a more biologically meaningful index of crowding than stand basal area alone because stands with the same basal area but widely different mean diameters can have much different levels of competition. Stocking percent is calculated as the ratio of observed plot basal area to maximum basal area of oak stands on the chart with the same mean diameter and multiplied by 100. The basal area, stocking percent, and percentage of oak and favored host species for each of the 45 sites were determined by averaging the respective values from the four adjacent plots. Based on the distribution of basal area on a site level, which ranged from 18.4 to 35.6 m^2/ha (Table 1), we pooled sites into five categories (18.9–21.0, 21.1–23.4, 23.5–25.4, 25.5–27.5, and >27.5 m^2/ha) and randomly chose three sites from each category for more intensive sampling and experimentation. Hereafter, these 15 sites, comprised of 60 plots, are referred to as "intensive," whereas the re-

Table 1. Summary of habitat structure variables of study sites in oak-dominated northern hardwood stands in northeastern Wisconsin

	Basal area		Stocking % (site)	Site host species composition (%)[a]			
	Plot (m^2/ha)	Site (m^2/ha)		Oak	Favored hosts	Intermediate hosts	Unfavored hosts
Mean± SEM	24.0 ± 0.2	24.0 ± 0.6	67.9 ± 1.9	67.7 ± 2.8	77.3 ± 2.3	21.3 ± 2.3	1.3 ± 0.5
Maximum	43.6	35.6	50.0	100.0	100	63.7	17.8
Minimum	9.2	18.4	100.0	9.4	36.1	0.0	0.0

[a] Details in Hoffman (2006).

maining 30 sites (120 plots) are referred to as "extensive."

Field Sampling and Analysis. At all plots, we counted gypsy moth eggs, larvae, and adults each year from 2004 to 2007 and pupae in 2004 and 2005. Egg masses were counted by direct observation in April, with binoculars when necessary (Buss et al. 1999). All egg masses on the trees and ground within a plot were independently counted by at least two observers. All egg masses within 2 m of the ground were evaluated as to whether they were new (i.e., viable) or old (i.e., hatched during previous years). Larvae were sampled twice, 7 d apart, in late June of 2004 and 2005 and once in 2006 and 2007. In each plot, each tree ≥8 cm dbh was wrapped with a burlap band to measure larval density (Naidoo and Lechowicz 1999). The larvae were directly counted from under the burlap bands and the stadium (L1–L6) of each larva was noted. In 2004 and 2005, the two larval counts were averaged to provide a single value for comparison with 2006 and 2007. Pupae were counted in late July from under the same burlap bands used to sample larvae. Adult males were sampled using pheromone-baited traps. One milk carton trap baited with 500 mg of (+) disparlure in twine dispensers was placed at the center of each site in early July and remained in the field until mid-September. Each trap also contained a kill strip (10% 2,2-dichlorovinyl dimethyl phosphate; Hercon Environmental, Emigsville, PA). In 2004, the intensive traps were emptied twice before takedown to estimate flight period, and thereafter all the traps were emptied twice before takedown.

The total number of egg masses, larvae, pupae, and adult males per year and site was estimated by averaging the respective values from each plot. Counts were transformed using the $\log_{10} + 1$ transformation. We measured the correlation, using the Pearson correlation coefficient (R Development Core Team 2008), among gypsy moth stages within a year to determine stage-to-stage relationships in abundance. We also measured the correlation between adult males and the density of egg masses and larvae in the following year to determine the relationship in abundance between successive generations. Because some sites were in close proximity to each other, we also performed the same correlation analysis based on clusters of neighboring sites to account for differences of scale between flying adult males and all other, flightless, stages (Fig. 1). These clusters were on average at least 7.3 km (SE = 0.4) apart, and ranged from 1.0 to 16.4 km apart, which was sufficient separation because adult males generally do not disperse >800 m, and the majority disperse <400 m (Elkinton and Cardé 1988). For each year and on a site level, we examined the fixed effects of basal area, stocking percent, percentage of oak trees, and percentage of host tree species favored by gypsy moth (using the classification of Liebhold et al. 1995a) on life stage abundance (using $\log_{10}$-transformed + 1 counts). Regression analyses were performed in R (R Development Core Team 2008).

Field Experiments on the Roles of Natural Enemies. We conducted direct field experiments on our 15 intensive sites. These experiments were aimed at estimating the major sources of mortality affecting each life stage, the relative survival of each life stage, and the relationships of specific natural enemy impacts and gypsy moth survival rates to habitat features such as basal area, stocking percent, and tree species composition. In 2004 and 2005, various life stages of gypsy moths were reared under laboratory conditions for deployment in field experiments.

Egg masses were obtained from the New Jersey Standard Strain culture maintained at the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Pest Survey, Detection and Exclusion Laboratory, Otis ANGB, MA. Egg masses were placed in petri dishes and either used directly in experiments or reared to larvae or pupae in an environmental chamber under a photoperiod of 16:8 (L:D) h at 25°C. Neonates, in groups of 100–150, were provided with ≈2 1-cm^3 cubes of artificial diet (USDA, Hamden formula), which was replaced as needed until the larvae were used for either field experiments or left to pupate. Full details on rearing and handling are provided in Hoffman (2006).

Egg masses were assayed in the field in August 2005 by placing one mass in the center of a white 15 by 15-cm sticky card that was tacked to two trees per plot 2 m above the ground (eight egg masses per site), using a modified method of Weseloh (1972a, b). Egg masses were left in the field for 1 mo and returned to the laboratory and individually held for 3 wk in a 1-oz diet cup at 24°C, 50% RH, and 16:8 (L:D) h, during which time they were observed for parasitoid emergence.

Larvae were brought to the field in June 2004 and 2005 to measure infection rates by *E. maimaiga* and LdMNPV (Hajek et al. 2000) and the rate of larval parasitism. Five larvae per plot were exposed to the soil on the forest floor (20 larvae per site). We used mid-third instars to ensure that they molted to the

fourth instar during the experiment (Hajek et al. 2000). Larvae were enclosed in a cage, made of PVC pipe and window screen, containing a cube of diet, and the cage was secured to the forest floor by pole barn nails (20.3 cm long, 0.64 cm wide). A layer of hardware cloth was added the second year to reduce destruction by animals. After 7 d of exposure, larvae were transferred to individual 1-oz diet cups containing a cube of diet and held under laboratory conditions at 20°C and a photoperiod of 14:10 (L:D) h. Larvae were observed daily for 14 d, and cadavers were assessed to determine the presence or absence of *E. maimaiga* and LdMNPV (Hajek et al. 2000). In 2005, this procedure of exposing laboratory-reared larvae in the field was supplemented with the sampling of field larvae. Burlap bands were placed on an additional five trees just outside of each plot (20 trees per site), and larvae were collected from beneath these bands and reared in the laboratory to determine infection by *E. maimaiga* or LdMNPV. The rate of larval parasitism and the identities of larval parasitoids were determined. The binary response variable of infected versus not infected, examined separately for *E. maimaiga* and LdMNPV, was subjected to logistic regression analysis to determine the site-level effects of basal area, stocking percent, percentage of oak trees, and percentage of gypsy moth favored host tree species. Significance was based on the likelihood ratio χ^2 (G^2) (R Development Core Team 2008).

Pupal predation rates were estimated using the method of Liebhold et al. (2005). In 2004, pupae were brought to the field and adhered to 15 by 15-cm burlap squares with melted beeswax. Seven pupae were deployed in each plot (28 pupae per site). The burlap squares were placed randomly within each plot and secured to the forest floor with marking flags, left in the field for 48 h, after which they were recorded as intact or attacked by predators. At randomly chosen sites, the first plot was checked nondestructively after 24 h to obtain an estimate of the predation time frame (Liebhold et al. 2005). All pupae were returned to the laboratory and reared to evaluate the presence of parasitoids. This experiment was expanded in 2005 to compare rates of predation on the ground versus on the tree and by vertebrates versus invertebrates. Preliminary experiments indicated that beeswax did not securely hold pupae onto burlap on trees. Therefore, larvae were placed in petri dishes with a square of fabric and allowed to adhere themselves naturally to the fabric before pupating, which provided a more secure attachment. Fourteen pupae were deployed per plot (56 per site): seven each on trees and ground. One fabric square was stapled to each trunk 2 m above ground level. If less than seven adequately sized trees were available in a plot, multiple squares were attached to randomly chosen trees. The remaining seven squares were fixed to the forest floor with pole barn nails (Hastings et al. 2002b). An additional 14 pupae per plot were deployed at 3 of our 15 intensive sites in three 2-mm hardware cloth cages to exclude vertebrate predators. One half of these were on trees and one half were on the ground. The total number of deployed pupae was 1,008 (uncaged on ground: 420; caged on ground: 84; uncaged on tree: 420; caged on tree: 84). After 48 h, pupae were collected, their conditions were recorded, and they were returned to the laboratory for rearing and observation of parasitoid emergence. The binary response variable of a pupa being attacked or not attacked by predators was subjected to logistic regression analysis to determine the effect of ground or tree deployment, and caged (i.e., invertebrate) or uncaged (i.e., vertebrate) predation. This variable was also assessed with respect to the site-level effects of basal area, stocking percent, percentage of oak trees, and percentage of gypsy moth favored host tree species (using uncaged, ground pupae only, which were deployed over two years). Significance was based on the likelihood ratio χ^2 (G^2) (R Development Core Team 2008).

The mating success of adult females was measured in mid-August 2004. Six virgin females, each within 4 d after emergence, were deployed in the center of each intensive site. The females were tethered with a 10–15 cm length of cotton thread tied at the base of a front wing. Each female was deployed ≥15 m apart, and each was attached to an oak tree 1.5 m above ground level with a pushpin. After 24 h, females and any egg masses they had oviposited were collected and returned to the laboratory to determine fertilization by analysis of egg embryonation (Sharov et al. 1995) and test for egg parasitism. Each site's pheromone trap (cf. Fig. 1) was removed during the 24-h period during which females were deployed.

Results

A total of 1,247 and 1,155 trees across all sites and plots were sampled in 2004 and for each year from 2005 to 2007, respectively. The most numerically dominant species overall were northern red oak (426 trees), red maple (333 trees), and sugar maple (186 trees). In terms of basal area, northern red oak and other gypsy moth–favored host tree species were the most dominant. Unfavored hosts (mainly white ash) were far less abundant. Details of the basal area, stocking percent, and percent gypsy moth hosts (favored, intermediate, and unfavored) are presented in Table 1, and complete details are in Hoffman (2006).

The time series of the site-level counts of gypsy moth life stages are presented in Fig. 2. Egg mass densities were relatively consistent during the first 2 yr but dropped sharply in 2006 and remained low in 2007. The highest egg mass density at any one site was observed in 2004 (816 egg masses, which corresponds to 3,302.4 egg masses/ha). Larval and pupal counts (Fig. 2B) were highest in 2004. Adult males were initially high and declined in 2005 and 2006 but rebounded in 2007, suggesting the population is again rising, males are immigrating into the sites, or both (Fig. 2C).

There were significant correlations between several life stages of the gypsy moth. The most consistent were those from one stage to the immediate next stage (Table 2). Egg masses were not correlated with the

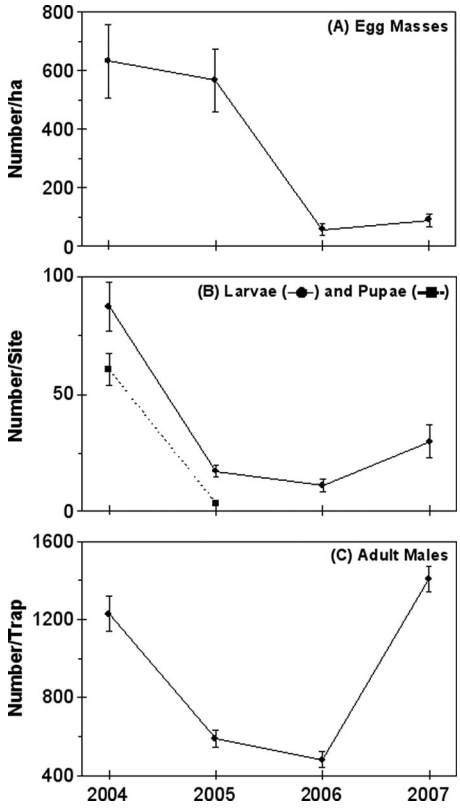

Fig. 2. Mean (±SE) numbers of egg masses (extrapolated to numbers per hectare) (A), larvae and pupae per site (B), and male moths recorded from pheromone-baited traps per site (C), 2004–2007.

number of male moths at either the site or clustered-site level and only correlated with larval densities on a site level. Larval densities were a significant predictor of subsequent pupal densities, and pupal densities were a significant predictor of subsequent male moths (Table 2). Adult male densities were only weakly correlated with subsequent egg mass or larval densities in the following year (Table 2). Overall, the clustering of sites to a larger scale did not improve the correlations between life stages. The most consistently positive association was between larvae and pupae (Table 2). It should be noted that for these two stages, the sampling design was identical (i.e., tree banding), whereas eggs and adults were sampled using stage-specific methods.

When assessing the significance of the main effects of basal area, stocking percent, percentage of oak, and percentage of favored host species on life stage densities, we did not observe a significant interaction between main effects and year of study (all $P > 0.30$); thus, analyses were conducted across time. None of the main effects were significant predictors of the density of larvae, pupae, or adults (all $P > 0.24$). We did observe a significant effect of the percentage of oak ($F = 22.45$; df = 1,166; $P < 0.01$) and percentage of favored gypsy moth host species ($F = 28.96$; df = 1,166; $P < 0.01$) on egg mass densities but no significant effect of basal area ($F = 0.05$; df = 1,166; $P = 0.77$; Fig. 3). We initially observed a significant effect of stocking percent on egg mass densities, but stocking percent was significantly inversely correlated with the percentage of oak ($\rho = -0.48$; df = 47; $P < 0.01$; Fig. 3B inset) and to a lesser extent, with the percentage of favored host species. After controlling for oak composition, there was no significant effect between stocking percent and egg mass density ($F = 2.46$; df = 1,166; $P = 0.12$), whereas the inverse (i.e., effect of percent oak when controlling for stocking percent) was still significant ($F = 9.81$; df = 1,166; $P < 0.01$), as was the interaction between oak and stocking percent ($F = 6.41$; df = 1,166; $P = 0.01$).

The estimated mortality of each life stage attributable to natural enemies and the mating success of deployed females are shown in Table 3. No egg parasitoids emerged from the 72 field-collected or 120 deployed egg masses. Also, no parasitoids were found on any of the 120 sticky cards. The presence of *E. maimaiga* was observed at 87% of the 15 sites in 2004, and this is likely an underestimate as some sites experienced loss of deployed larvae because of animals. The presence of LdMNPV was observed at all of the sites in 2004. Pupal predation was high in 2004 and 2005, particularly when left uncaged, and the nature of pupal damage was indicative of attack by small mammals, such as presence of rodent feces on some of the

Table 2. Pairwise correlation coefficients (*P* values) between densities of gypsy moth life stages at the site and clustered site level (see Fig. 1) over 4 yr[a] in northeastern Wisconsin

	Larvae	Pupae[a]	Adult males	Egg masses-following year	Larvae-following year
Site level					
Egg masses	0.20 (≤0.01)	−0.14 (0.21)	0.12 (0.14)	—	—
Larvae	—	0.79 (≤0.01)	0.38 (≤0.01)	—	—
Pupae	—	—	0.52 (≤0.01)	—	—
Adult males	—	—	—	−0.15 (0.09)	0.17 (0.06)
Clustered site level					
Egg masses	0.24 (0.06)	−0.15 (0.39)	0.22 (0.07)	—	
Larvae	—	0.82 (≤0.01)	0.51 (≤0.01)	—	
Pupae	—	—	0.71 (≤0.01)	—	
Adult males	—	—	—	−0.10 (0.49)	0.25 (0.09)

[a] Pupae measured in 2004 and 2005 only.

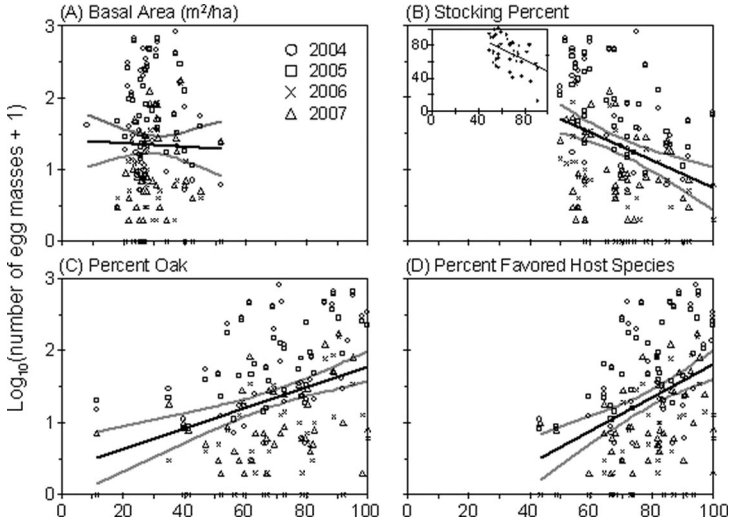

Fig. 3. Relationship between site-level basal area (A), stocking percent (B), percent oak (C), and percent favored host tree species (D) on gypsy moth egg mass densities, 2004–2007. The inset graph in B shows the relationship between stocking percent (x-axis) and percent oak (y-axis); thus, after controlling for oak composition, there was no significant effect of stocking percent on egg mass densities.

burlap squares (Table 3). Ants were observed on these pupae but seemed to be secondary predators or scavengers. Pupal predation was significantly higher on the ground than on trees ($G^2 = 16.9$; df = 1; $P < 0.01$), and when exposed to vertebrates than when caged ($G^2 = 203.2$; df = 1; $P < 0.01$; Fig. 4). Overall, pupae were 1.7 times more likely to succumb to predation when deployed on the ground than on trees, and 25.8 times more likely to succumb to predation when left uncaged. No parasites were found among the 475 pupae returned to the laboratory (Table 3). The percentage of females successfully mated and laying viable egg masses was high (Table 3), and site-level female mating success ranged from 50 to 100%.

There were some consistent relationships between mortality exerted by natural enemies and features of stand architecture. In both years, pupal predation (uncaged only) was negatively correlated with basal area (2004: $G^2 = 12.9$; df = 1; $P < 0.01$; 2005: $G^2 = 5.9$; df = 1; $P = 0.02$) and to the percentage of favored host trees in the stand (2004: $G^2 = 46.4$; df = 1; $P < 0.01$; 2005: $G^2 = 9.2$; df = 1; $P = 0.01$), but not to stocking percent or the percentage of oak trees (all $P > 0.05$). Mortality rates caused by entomopathogens were also not related to a site's basal area, stocking percent, percent oak trees, or percent favored hosts (all $P > 0.05$).

Discussion

Habitat structure influenced the numbers of gypsy moth egg masses in preoutbreak conditions in northern hardwood stands. The number of egg masses across all 4 yr showed a consistently positive relationship with percent oak and percent favored hosts. However, densities of larvae and pupae were not significantly related to habitat structure variables. Adult male density likewise could not be attributed to any habitat structure variable. This is not likely because of male moth dispersal, because evaluating these rela-

Table 3. Estimation of mean percentage ± SEM gypsy moth mortality sources and mating success in oak-dominated northern hardwood stands in northeastern Wisconsin

Life stage	Mortality source	Method	2004	2005
Egg	Parasitism	Deployed females	0.0%	—
		Sticky cards	—	0.0%
Larva	*C. concinnata*	Field collected	—	32.9 ± 4.4%
	C. melanoscela	Field collected	—	0.0%
	E. maimaiga	Deployed	9.0 (1.6)%	—
		Field collected	—	5.5 ± 1.4%
	LdMNPV	Deployed	21.9 (3.4)%	—
		Field collected	—	16.9 ± 3.2%
Pupa	Predation	Deployed-Uncaged	69.0 (5.7)%	62.0 ± 3.3%
		Deployed-Caged	—	6.0 ± 3.3%
	Parasitism	Deployed	0.0%	0.0%
Mating success	NA	Deployed	86.7 (0.03)%	—

NA, not available.

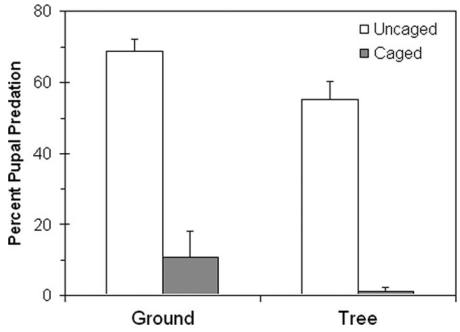

Fig. 4. Effect of location and mammal exclusion on predation of gypsy moth pupae.

tionships at a larger scale (i.e., clustered site analysis; Fig. 1) did not affect this pattern.

Oak forests in northeastern Wisconsin seem to have an incompletely established complex of natural enemies. We found no evidence of egg parasitism despite the widespread distribution of *O. kuvanae* in southern Wisconsin. The introduced tachinid, *C. concinnata*, seems to be the most important natural enemy of gypsy moth larvae in northeastern Wisconsin. Unfortunately, this generalist exerts harmful nontarget effects on native Lepidoptera (Strong and Pemberton 2000, Kellogg et al. 2003, Elkinton et al. 2006). *Cotesia melanoscela* is an important parasite of the gypsy moth along the southern leading edge (Hastings et al. 2002a) and was released in northeastern Wisconsin in 1998, but we found no evidence of its establishment.

Past work in regions in which gypsy moth is well established suggests that epizootics by *E. maimaiga* require a substantial larval population, suitable weather, and a period of inoculum buildup (Hajek 1997, 1999, Dwyer et al. 1998). Although both *E. maimaiga*, and LdMNPV are widely distributed throughout Wisconsin, rates of pathogen infection in field-collected larvae in our sites (Table 3) was substantially lower than those observed in New York (Hajek et al. 2000). We cannot distinguish whether this was caused by regional differences such as climate and habitat or differences in the duration of establishment. For example, the first counties in Wisconsin were quarantined in 1998 versus 1945 in New York (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45).

Small mammals seem to be the main predators of gypsy moth pupae in northeastern Wisconsin. Because pupae were ≈26 times more likely to be attacked when left uncaged than when caged in screening, this predation can be attributed mostly to small mammals. Moreover, Liebhold et al. (2005) found that pupal predation was correlated with the number of rodents trapped. The only invertebrates excluded by these cages are *Calosoma* spp. However, in an extensive study of ground-occurring beetles in neighboring sites in northeastern Wisconsin and the southern upper peninsula of Michigan, Werner and Raffa (2000) found no *C. sycophanta* among >65,000 beetles trapped, and the only *Calosoma* species obtained, *C. frigidum* Kirby, occurs too early (peak, 7–18 June) to impact gypsy moth pupae in the area of our study sites (Werner and Raffa 2003). Thus, invertebrates seem to play a much smaller role in pupal predation in Wisconsin than along the gypsy moth's southern leading edge, where predation by invertebrates equaled predation by vertebrates at 42% of sites (Hastings et al. 2002b). Pupal predation was higher at ground than tree level in both Wisconsin (Fig. 4) and in the south (Hastings et al. 2002b). The pupal parasitoid *B. intermedia*, which parasitizes an average of ≈8% of the pupae in the northeastern United States and can have a much higher impact during outbreaks (Elkinton and Liebhold 1990, Kerguelen and Cardé 1996), was not recovered from any of the pupae we assayed in northeastern Wisconsin.

Mating success and survivorship of adult females were high across all sites and habitat structures. This suggests an important distinction between the pre-establishment and pre-eruptive phases of gypsy moth and between its western and southern advancing fronts. Inability to find mates at very low densities seems to be the primary cause of an Allee effect (Courchamp et al. 1999) in newly establishing gypsy moth populations (Liebhold and Bascompte 2003, Whitmire and Tobin 2006). However, it does not seem to affect population dynamics during the postestablishment pre-eruptive phase, at least in northeastern (Table 3) or southeastern (Tcheslavskaia et al. 2002) Wisconsin. Furthermore, an Allee effect caused by low mating success seems to extend across a broader range of population densities along the southern than western leading edges of gypsy moth, perhaps because of differences in topography and natural enemies (Tcheslavskaia et al. 2002, Tobin et al. 2007b). There are similar distinctions between the pre-eruptive and eruptive phases. In particular, the major sources of mortality to the former seem to be generalists, including both mammalian predators and dipteran parasitoids (Table 3). In contrast, the most important mortality agents during eruptions are usually host-specific entomopathogens (Hajek et al. 2000). Thus, as gypsy moth populations in northeastern Wisconsin progress from the postestablishment, pre-eruptive stage to the outbreak stage, the importance of various natural enemies, and hence the roles of various habitat features, are likely to change. Availability of suitable hosts is an important component across all phases of invasion (Elkinton and Liebhold 1990, Kleiner and Montgomery 1994).

Each life stage can be used to predict the subsequent stage with variable degrees of accuracy (Table 2), and therefore can be incorporated into population models to improve long-term analysis. However, counts of males from pheromone-baited traps, the least labor-intensive method, was not a good predictor of the next season's abundance of larvae, which as the damaging stage is of primary interest for management. Therefore, monitoring tactics such as trapping male moths or counting egg masses may be useful for predicting the incidence of resident populations but not the quantity of larval feeding, at least within this range

of population densities. Future research should emphasize improving these predictive capabilities.

The lack of a relationship between gypsy moth population densities with either basal area or stocking percent has implications for forest management. Our results do not indicate that reducing stand basal area by thinning will reduce gypsy moth populations, either directly or indirectly by supporting more natural enemies. The latter result is consistent with previous findings that forest thinning does not seem to affect gypsy moth mortality (Grushecky et al. 1998; Liebhold et al. 1998). Stand tolerance to defoliation, however, may increase after thinning (Liebhold et al. 1998), and selective removal of preferred species or stressed trees may reduce mortality (Kleiner and Montgomery 1994). In our study sites, defoliation has not yet occurred, so ongoing studies throughout the course of infestation will help separate components of population dynamics, habitat structure, tree tolerance, and stand impact of this invasive defoliator.

These results provide baseline information on the effects of habitat structure on preoutbreak populations of an invasive forest insect. Subsequent research extending the time frame and applying controlled manipulations could further elucidate important aspects of the overall process of invasion. Additional information is needed to determine how well our results apply to other forest types, especially when comparing western and southern leading edges of the gypsy moth population front. There is also a need to study underlying mechanisms of why invertebrates cause less pupal predation, why some key parasitoids are not effective, in Wisconsin as elsewhere, and how habitat structure affects gypsy moth population dynamics. Understanding these more general relationships may assist resource managers in contending with gypsy moth and other invasive forest insects, particularly in estimating expected intervals during the postestablishment, pre-eruptive phase.

Acknowledgments

We thank K. Gottschalk, A. Liebhold, and L. Blackburn (U.S. Forest Service, Morgantown, WV), and S. Katovich (U.S. Forest Service, St. Paul, MN) for technical assistance and valuable input. The Wisconsin Department of Agriculture, Trade and Consumer Protection supplied pheromone lures and kill strips. J. Lampereur at the Lakewood/Laona Ranger District, assisted in site location. K. Kromm, M. Stienstra, E. Whalen, G. Richards, S. Eastwood, K. Herning, M. Preston (Department of Entomology, UW-Madison) E. Lund, S. Lorenz, B. Matuszak, and E. Larson (Department of Forestry, UW-Stevens Point) helped with field work and rearing. We thank S. Krauth (Insect Research Collection, UW-Madison) for insect identification and M. Allington for field cage construction (Department of Entomology, UW-Madison). We thank D. Mahr and C. Gratton (Department of Entomology, UW-Madison) for input on experimental design and manuscript review. J. Zhu (Department of Statistics, UW-Madison) and B. Aukema (Department of Entomology, UW-Madison) provided valuable statistical advice. This study was funded by a Research Joint Venture Agreement from the U.S. Forest Service-Northern Research Station (06-JV-11242300-047) and by a Cooperative Agreement from the Forest Service Special Technology Development Program (Project NA-2002-03). The critical reviews by the journal referees are greatly appreciated.

References Cited

Bess, H. A., S. H. Spurr, and E. W. Littlefield. 1947. Forest site conditions and the gypsy moth. Harv. For. Bull. 22: 1–56.

Boettner, G. H., J. S. Elkinton, and C. J. Boettner. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conserv. Biol. 14: 1798–1806.

Brown, M. W., and E. A. Cameron. 1982. Spatial distribution of adults of *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae), an egg parasite of *Lymantria dispar* (Lepidoptera: Lymantriidae). Can. Entomol. 114: 1109–1120.

Buss, L., D. G. McCullough, and C. Ramm. 1999. Comparison of three egg mass survey methods to gypsy moth (Lepidoptera: Lymantriidae) defoliation in Michigan. Environ. Entomol. 28: 485–495.

Campbell, R. W., and R. J. Sloan. 1978. Numerical bimodality among North American gypsy moth populations. Environ. Entomol. 7: 641–646.

Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. 14: 405–410.

Doane, C. C. 1970. Primary pathogens and their role in development of an epizootic in gypsy moth. J. Invertebr. Pathol. 15: 21–27.

Doane, C. C., and M. E. McManus. 1981. The gypsy moth: research toward integrated pest management. U.S. Dep. Agric. For. Serv. Gen. Tech. Bull. 1584.

Dwyer, G., J. S. Elkinton, and A. E. Hajek. 1998. Spatial scale and the spread of a fungal pathogen of gypsy moth. Am. Nat. 152: 485–494.

Dwyer, G., J. Dushoff, and S. H. Yee. 2004. The combined effects of pathogens and predators on insect outbreaks. Nature (Lond.) 430: 341–345.

Elkinton, J. S., and R. T. Cardé. 1988. Effects of intertrap distance and wind direction on the interaction of gypsy moth (Lepidoptera: Lymantriidae) pheromone-baited traps. Environ. Entomol. 17: 764–769.

Elkinton, J. S., and A. M. Liebhold. 1990. Population dynamics of gypsy moth in North America. Annu. Rev. Entomol. 35: 571–596.

Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. Hazzard, A. M. Liebhold, and H. R. Smith. 1996. Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77: 2332–2342.

Elkinton, J. S., A. M. Liebhold, and R. M. Muzika. 2004. Effects of alternative prey on predation by small mammals on gypsy moth pupae. Popul. Ecol. 46: 171–178.

Elkinton, J. S., D. Parry, and G. H. Boettner. 2006. Implicating an introduced generalist parasitoid in the invasive browntail moth's enigmatic demise. Ecology 87: 2664–2672.

Gingrich, S. F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. For. Sci. 13: 38–53.

Gottschalk, K. W. 1993. Silvicultural guidelines for forest stands threatened by the gypsy moth. U.S. For. Serv. Gen. Tech. Rep. NE-171.

Gould, J. R., J. S. Elkinton, and W. E. Wallner. 1990. Density-dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera, Lymantriidae), populations by natural enemies. J. Anim. Ecol. 59: 213–233.

Grushecky, S. T., A. M. Liebhold, R. Greer, and R. L. Smith. 1998. Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantriidae) larvae and pupae? Environ. Entomol. 27: 268–276.

Gypsy Moth Digest. 2008. http://na.fs.fed.us/fhp/gm/.

Hajek, A. E. 1997. Ecology of terrestrial fungal entomopathogens. Adv. Microb. Ecol. 15: 193–249.

Hajek, A. E. 1999. Pathology and epizootiology of Entomophaga maimaiga infections in forest Lepidoptera. Microbiol. Mol. Biol. Rev. 63: 814–835.

Hajek, A. E., L. Butler, J. K. Liebherr, and M. M. Wheeler. 2000. Risk of infection by the fungal pathogen *Entomophaga maimaiga* among Lepidoptera on the forest floor. Environ. Entomol. 29: 645–650.

Hastings, F. L., F. P. Hain, and T. M. Odell. 2002a. A survey of parasitoids and other organisms affecting gypsy moth (Lepidoptera: *Lymantria dispar* L.) along the leading edge of its southward movement. J. Entomol. Sci. 37: 207–209.

Hastings, F. L., F. P. Hain, H. R. Smith, S. P. Cook, and J. F. Monahan. 2002b. Predation of gypsy moth pupae (Lepidoptera: Lymantriidae) in three ecosystems along the southern edge of infestation. Environ. Entomol. 31: 668–675.

Herrick, O. W., and D. A. Gansner. 1986. Rating forest stands for gypsy moth defoliation. U.S. For. Serv. Res. Pap. NE-583.

Herrick, O. W., and D. A. Gansner. 1987. Gypsy moth on a new frontier: forest tree defoliation and mortality. North. J. Appl. For. 4: 128–133.

Hoffman, R. 2006. Life history parameters of recently established gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations in relation to stand density of Wisconsin oak forests. MS thesis, University of Wisconsin-Madison, Madison, WI.

Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can. J. For. Res. 29: 630–645.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279: 1023–1026.

Kellogg, S. K., L. S. Fink, and L. P. Brower. 2003. Parasitism of native luna moths, Actias luna (L.) (Lepidoptera : Saturniidae) by the introduced *Compsilura concinnata* (Meigen) (Diptera : Tachinidae) in central Virginia, and their hyperparasitism by trigonalid wasps (Hymenoptera : Trigonalidae). Environ. Entomol. 32: 1019–1027.

Kerguelen, V., and R. T. Cardé. 1996. Increased host acceptance in experienced females of the parasitoid *Brachymeria intermedia:* which types of oviposition behaviour contribute to experience? Entomol. Exp. Appl. 78: 95–103.

Kleiner, K. W., and M. E. Montgomery. 1994. Forest stand susceptibility to the gypsy moth (Lepidoptera, Lymantriidae): species and site effects on foliage quality to larvae. Environ. Entomol. 23: 699–711.

Kotar, J., J. A. Kovach, and T. L. Burger. 2002. A guide to forest communities and habitat types of northern Wisconsin. University of Wisconsin-Madison, Department of Forest Ecology and Management, Madison, WI.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16: 289–324.

Leung, B., D. Finnoff, J. F. Shogren, and D. Lodge. 2005. Managing invasive species: rules of thumb for rapid assessment. Ecol. Econ. 55: 24–36.

Leuschner, W. A., J. A. Young, S. A. Walden, and F. W. Ravlin. 1996. Potential benefits of slowing the gypsy moth's spread. South. J. Appl. For. 20: 65–73.

Liebhold, A. M., and J. S. Elkinton. 1989. Elevated parasitism in artificially augmented populations of *Lymantria dispar* (Lepidoptera: Lymantriidae). Environ. Entomol. 18: 986–995.

Liebhold, A. M., K. W. Gottschalk, R. M. Muzika, M. E. Montgomery, R. Young, K. O'Day, and B. Kelley. 1995a. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. U.S. For. Serv. Gen. Tech. Rep. NE-211.

Liebhold, A. M., W. L. Macdonald, D. Bergdahl, and V. C. Mastro. 1995b. Invasion by exotic forest pests: a threat to forest ecosystems. For. Sci. Monogr. 30: 1–49.

Liebhold, A. M., K. W. Gottschalk, D. A. Mason, and R. R. Bush. 1997. Evaluation of forest susceptibility to the gypsy moth across the conterminous United States. J. For. 95: 20–24.

Liebhold, A. M., R. M. Muzika, and K. W. Gottschalk. 1998. Does thinning affect gypsy moth dynamics? For. Sci. 44: 239–245.

Liebhold, A. M., K. F. Raffa, and A. Diss. 2005. Forest type affects predation on gypsy moth pupae in Wisconsin. Agric. For. Entomol. 7: 179–185.

Mattson, W. J., H. Vanhanen, T. Veteli, S. Sivonen, and P. Niemelä. 2007. Few immigrant phytophagous insects on woody plants in Europe: legacy of the European crucible? Biol. Invas. 9: 957–974.

McCullough, D. G., T. T. Work, J. F. Cavey, A. M. Liebhold, and D. Marshall. 2006. Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol. Invas. 8: 1573–1464.

McGill, D., R. Rogers, A. J. Martin, and P. S. Johnson. 1991. New stocking charts for northern red oak in Wisconsin. University of Wisconsin For. Res. Notes 277: 1–8.

Muzika, R. M., and A. M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. Agric. For. Entomol. 2: 97–105.

Muzika, R. M., S. T. Grushecky, A. M. Liebhold, and R. L. Smith. 2004. Using thinning as a management tool for gypsy moth: the influence on small mammal abundance. For. Ecol. Manag. 192: 349–359.

Naidoo, R., and M. J. Lechowicz. 1999. Radial growth losses in preferred and avoided tree species during gypsy moth outbreaks. North. J. Appl. For. 16: 11–18.

Naidoo, R., and M. J. Lechowicz. 2001. Effects of gypsy moth on radial growth of deciduous trees. For. Sci. 47: 338–348.

National Oceanic and Atmospheric Administration. 2008. http://www.nws.noaa.gov.

Niemelä, P, and W. J. Mattson. 1996. Invasion of North American forests by European phytophagous insects. BioScience 46: 741–753.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50: 53–65.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52: 273–288.

R Development Core Team. 2008. http://www.r-project.org.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiver-

sity—global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Sharov, A. A., A. M. Liebhold, and W. F. Ravlin. 1995. Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. Environ. Entomol. 24: 1239–1244.

Sharov, A. A., D. Leonard, A. M. Liebhold, E. A. Roberts, and W. Dickerson. 2002. "Slow the spread": a national program to contain the gypsy moth. J. For. 100: 30–35.

Skinner, M., B. L. Parker, W. E. Wallner, T. M. Odell, D. Howard, and J. Aleong. 1993. Parasitoids in low-level populations of *Lymantria dispar* [Lep, Lymantriidae] in different forest physiographic zones. Entomophaga 38: 15–29.

Strong, D. R., and R. W. Pemberton. 2000. Biological control of invading species—risk and reform. Science 288: 1969–1970.

Tcheslavskaia, K., C. C. Brewster, and A. A. Sharov. 2002. Mating success of gypsy moth (Lepidoptera: Lymantriidae) females in southern Wisconsin. Great Lakes Entomol. 35: 1–7.

Tobin, P. C., and L. M. Blackburn. 2007. Slow the spread: a national program to manage the gypsy moth. U.S. For. Serv. Gen. Tech. Rep. NRS-6.

Tobin, P. C., and L. M. Blackburn. 2008. Long-distance dispersal of the gypsy moth (Lepidoptera: Lymantriidae) facilitated its initial invasion of Wisconsin. Environ. Entomol. 37: 87–93.

Tobin, P. C., A. M. Liebhold, and E. A. Roberts. 2007a. Comparison of methods for estimating the spread of a nonindigenous species. J. Biogeogr. 34: 305–312.

Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjørnstad, and A. M. 2007b. Invasion speed is affected by geographic variation in the strength of Allee effects. Ecol. Lett. 10: 36–43.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. Am. Sci. 84: 468–478.

Werner, S. M., and K. F. Raffa. 2000. Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. For. Ecol. Manag. 139: 135–155.

Werner, S. M., and K. F. Raffa. 2003. Seasonal activity of adult, ground-occurring beetles (Coleoptera) in forests of northeastern Wisconsin and the Upper Peninsula of Michigan. Am. Mid. Nat. 149: 121–133.

Weseloh, R. M. 1972a. Field responses of gypsy moths and some parasitoids to colored surfaces. Ann. Entomol. Soc. Am. 65: 742–746.

Weseloh, R. M. 1972b. Spatial distribution of the gypsy moth (Lepidoptera: Lymantriidae) and some of its parasitoids within the forest environment. Entomophaga 17: 339–351.

Weseloh, R. M. 1985. Predation by *Calosoma sycophanta* L. (Coleoptera: Carabidae): Evidence for a large impact on gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), pupae. Can. Entomol. 117: 1117–1126.

Weseloh, R. M. 1995. Forest characteristics associated with abundance of foraging ants (Hymenoptera: Formicidae) in Connecticut. Environ. Entomol. 24: 1453–1457.

Whitmire, S. L., and P. C. Tobin. 2006. Persistence of invading gypsy moth colonies in the United States. Oecologia (Berl.) 147: 230–237.

Work, T. T., D. G. McCullough, J. F. Cavey, and R. Komsa. 2005. Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol. Invas. 7: 323–332.

Received 29 February 2008; accepted 5 June 2008.