

POPULATION DYNAMICS OF GYPSY MOTH IN NORTH AMERICA

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INTRODUCTION

The gypsy moth, *Lymantria dispar*, is a major defoliator of deciduous trees throughout the northern hemisphere. Introduced into eastern Massachusetts from Europe in 1868 or 1869, it has gradually spread south and west and will soon occupy most of the hardwood forests in the eastern United States and Canada. The gypsy moth has been the subject of intensive study by scientists throughout the world, and several reviews exist of the older gypsy moth literature (50, 54, 94). Other reviews that cover more selective topics appear in the proceedings of a recent symposium on the Lymantriidae (173). Here, we provide a summary of current knowledge about the population dynamics of gypsy moth, emphasizing research that has been done since the last major review in 1981 (50). However, we also include some of the earlier studies to provide the appropriate framework for more recent studies. We concentrate on gypsy moth in North America, but we also make comparisons to some of the important studies conducted elsewhere. In preparation for this review, we have drawn from numerous sources including several reference lists (64, 65) and annotated bibliographies (37, 133).

METHODS FOR ESTIMATING DENSITY AND MORTALITY

The proportion of a gypsy moth population found in the canopy of trees compared with that found on tree stems, on understory vegetation, or on the

ground varies with time of day, stage of insect development, and population density. Consequently, the gypsy moth is very difficult to sample. Densities are most frequently expressed as numbers per unit area of ground rather than per unit of foliage. In the last decade, however, new methods for estimating densities and for quantifying mortality during each life stage of the gypsy moth have been developed.

Egg masses are the most frequently and easily sampled life stage of the gypsy moth (191). They are immobile and are present from late summer through early spring of the following year. At high population densities, most egg masses are found on tree stems and branches, but at low densities, a larger proportion of egg masses occur on objects such as rocks and fallen limbs on the forest floor (145). Furthermore, at low to moderate densities, a large proportion of egg masses are concentrated at forest edges and on "man-made objects" (12, 35, 145). A variety of techniques have been used to estimate egg mass densities, such as counting all egg masses found within fixed-radius plots (typically 0.01, 0.05, or 0.061 ha) (78) or using "fixed- and variable-radius plots" (190). With this latter method, egg masses are counted on the forest floor within a fixed-radius plot and on trees that are selected using a prism, a standard device for estimating basal area of trees. The five-minute walk is an indirect measure of egg mass density (51) widely used by gypsy moth managers, but it is too imprecise for most research purposes.

Gypsy moth fecundity varies considerably with population density and quality (26). Because gypsy moth eggs are deposited in a single mass, fecundity can be accurately estimated (23, 25). By collecting eggs in the spring, this technique also can be used to assess egg parasitism and nonviability of eggs. Fecundity can also be estimated from egg mass length (114) and volume (13). Actual numbers of first instars that hatch from egg masses can be determined by letting them emerge in a closed container (21).

Several methods have been used to estimate absolute larval densities. J. R. Gould et al (unpublished) counted all larvae in all habitat strata (litter, tree stems, and canopy) within multiple 2 m × 5 m quadrats. Weseloh (183, 184) estimated larval densities using mark-recapture methods. Liebhold & Elkinton (95, 96) and Campbell (23) used simultaneous measures of frass drop (density of pellets falling from the canopy) and frass yield (number of pellets produced per larva over the same time interval) to estimate late-larval densities. Higashiura (67) estimated densities of successive larval stages by counting the number of head capsules falling per unit area.

Several investigators have used counts of late instars in natural or artificial resting locations, such as under burlap bands, as a relative measure of larval density (23, 30, 31, 36). Regression equations have been developed for predicting larval densities from counts of larvae under bands (183, 185, 175).

Information on causes of mortality and changes in population density over a

generation is typically summarized in a life table that is constructed by computing the number or density of individuals entering each life stage. These numbers differ from the numbers present in each stage at any given moment because stages often overlap in time. Methods used for calculating the numbers entering a stage based on counts of numbers present in sequential samples are reviewed in Southwood (150), but these methods have only rarely been applied to gypsy moth populations because they typically require more frequent data collection than is available in most gypsy moth studies. Only when all individuals are present in a particular stage (such as the gypsy moth egg stage) or the stage leaves identifiable remains, such as counts of gypsy moth head capsules (67) or gypsy moth pupae (160), is it possible to measure numbers entering a stage directly.

Similar problems arise in computing percent mortality caused by specific agents. In order to compare impacts of particular mortality agents between different populations or to enter them into life tables, one needs to calculate stage-specific mortality: the proportion of those individuals that entered the stage that were killed by a given agent (62, 166). Mortality caused by parasitoids is typically estimated by collecting samples of hosts on one or more occasions and calculating from dissections or rearings the proportion attacked (62). However, this proportion is usually a poor estimate of stage-specific parasitism (166). Methods used to calculate percent parasitism from sample percent parasitism include extensions of the method of Southwood & Jepson (151). This method has been applied to gypsy moth (79), but it is subject to severe biases (14). We have proposed an alternate method of calculating mortality based on the numbers dying within specific time intervals rather than stages (62, 63; J. S. Elkinton, unpublished), which includes an approach to quantifying mortality caused by simultaneously acting agents (132), and it expresses mortality in terms of k -values (167).

OVERVIEW OF POPULATION DYNAMICS

In regions of North America where the gypsy moth is well established, populations exist for many years at low densities (innocuous or endemic phase) (27, 33, 172). The release phase, during which the populations expand rapidly into outbreak phase, usually takes place over one or two generations. Both rising and collapsing populations commonly change several orders of magnitude in one year. Similar patterns have been reported in the European literature for many years. The European terms are latency, progradation, culmination, and postgradation, and these correspond respectively to the innocuous, release, outbreak, and decline phases.

Campbell & Sloan (33) hypothesized that gypsy moth populations in North America exhibit bimodal stability; that density-dependent processes maintain

equilibrium densities in both innocuous and outbreak populations for long periods. This model is essentially identical to a more generalized model proposed for many insects by Southwood & Comins (152). On the spatial scale of the stand, outbreak populations usually collapse after one or two years. However, dispersal of first instars between stands can maintain high-density populations on a regional scale for up to a decade (32).

Though outbreaks are recurring events, it is not clear that they occur at regular intervals. Several European studies indicate that some populations are cyclic, with high densities developing every 8–11 years (113); however, there have been no quantitative evaluations of cyclic patterns. Liebhold & Elkinton (97) digitized yearly defoliation maps of Massachusetts and used geostatistical techniques to demonstrate that the timing of outbreaks varied among different portions of the state. We believe that there is little evidence that gypsy moth population densities in North America are cyclic.

The first detailed life-table study of gypsy moth populations in North America was that of Bess (15), who constructed survivorship curves for a population in Freetown, Massachusetts. He found that densities declined dramatically during the fifth and sixth instar. Campbell (23, 25) concluded from quantitative analyses of life-table data collected in Connecticut and New York that variation in late larval survival was the largest source of yearly variation in population density, both for sparse and dense populations. Furthermore, at low population density, mortality during late-larval and pupal stages was density dependent and thus might serve to regulate population growth (34, 36).

Beginning in 1984, we have collected yearly data on gypsy moth survival and density at three sites on Cape Cod that exhibited ranges in density between outbreak and innocuous levels (52). Our findings, to a large extent, agreed with those of Campbell et al. Mortality rates were highest during the late larval stage and were inversely density dependent, a finding consistent with Campbell & Sloan's (33) bimodal stability model. This model predicts inverse density dependence at densities above the hypothetical low density equilibrium that represents the transition between innocuous and expanding populations. We believe, however, that more studies are needed to determine whether low-density populations of gypsy moth are governed by density-dependent equilibrium processes, or whether densities merely fluctuate (52, 63).

SMALL MAMMAL PREDATORS

Bess et al (16) were the first to suggest that predation by small mammals was important to gypsy moth population dynamics in North America. They showed that larval survival was significantly higher on trees inside fences that excluded small mammals. Bess' hypotheses concerning the impact of small

mammal predation on low-density gypsy moth populations were supported by subsequent studies by Campbell and associates (30, 31, 36). Campbell et al found that vertebrate predators, especially the white-footed mouse, *Peromyscus leucopus*, were the major source of late-larval and pupal mortality. Pupae in the litter were less likely to survive to the adult stage than pupae in protected locations on tree stems, even though the majority of individuals pupated in the litter (34). Campbell & Sloan (29) suggested that the behavior of resting in the litter during the day evolved in Europe as an adaptation to avoid mortality caused by avian predators and tachinid parasitoids, which are active in the canopy of trees in daylight hours. They hypothesized that, in contrast to North American populations, these agents cause higher mortality to gypsy moth in Europe than that caused by small mammal predators. The larval resting behavior persists in North America, even though it exposes gypsy moths to higher levels of mortality.

In low-density populations (< 50 egg masses/ha), overall larval mortality and predation rates on pupae were positively correlated with gypsy moth population density (34, 36). These findings support the hypothesis that predation by small mammals is responsible for the regulation of low-density gypsy moth populations. At higher gypsy moth densities, predation by small mammals was much lower (34, 36), presumably because the numerical response of most vertebrate predators is highly constrained (52). Numerical responses of predators to increases in gypsy moth density arise out of aggregative behavior of individual predators or increases in predator reproduction or survival. We are aware of no evidence that gypsy moth populations significantly affect the reproductive success of *P. leucopus* or any other small mammal. Most of the small mammals and birds that feed on gypsy moth are generalists for which gypsy moth is a minor component in their diet (44). Aggregation of predators is limited by the fact that most species occupy distinct home ranges or defend territories. Increases in predation rates, in response to increases in gypsy moth density, would probably be caused by a Type III functional response (69), because predators have switched to gypsy moth from other prey species or learned to forage for gypsy moth as gypsy moth densities increase (52). However, all predators are limited in the number of prey items an individual can consume, so even a Type III functional response is asymptotic and therefore inversely density-dependent at higher prey densities.

In our studies with gypsy moth populations on Cape Cod and in western Massachusetts, substantial mortality in high-density populations was caused by nuclear polyhedrosis virus (NPV), but in low-density populations, parasitism, particularly from *Parasetigena silvestris*, has been a major factor (52). However, viral disease and parasitism have usually accounted for less than 50% of the total mortality during the late larval stage. Losses during this stage appear to be caused mainly by predation (52). At these same sites we estimated small mammal densities and measured the predation rate on pupae

that we deployed in the litter. *P. leucopus* was by far the most abundant small mammal predator captured in our traps, and the rate of pupal predation was highly correlated with *P. leucopus* density. In 1986 we observed a dramatic decline in *P. leucopus* density on plots in western Massachusetts and a concomitant increase in gypsy moth density. Very similar trends have been noted on Bryant Mountain in Vermont (H. R. Smith, personal communication). These findings are consistent with Campbell's & Sloan's hypothesis (30, 31) that variation in predation on pupae and the late-larval stage is the key to whether or not populations remain stable at low density. The occurrence of such simultaneous trends at widely spaced sites suggests that regional changes in small mammal density may account for the region-wide onset of outbreak phase populations of gypsy moth (97).

Recent studies have identified other factors that affect predation by small mammals. Smith (147) showed that an abundance of alternate foods, such as blueberries, can markedly reduce small mammal predation on gypsy moths.

AVIAN PREDATORS

The first study of avian predation on gypsy moth in North America was that of Forbush & Fernald (54), who reported which bird species fed on gypsy moth larvae. More recent studies have shown that many bird species feed on gypsy moth larvae, but they are not a major food item in the diet of any of the most common species (44). Choice tests have shown that most birds prefer hairless caterpillars to gypsy moths (189). Campbell & Sloan (30) concluded that avian predation was important to the dynamics of low-density gypsy moth populations, based on the higher survival in experimental plots in which larvae were protected from birds with poultry netting and burlap bands wrapped around the stems of trees. We do not agree with this conclusion; burlap bands also protect larvae and pupae from ground foraging of small mammal predators (16, 34). We found no evidence for increased density of breeding birds in artificially elevated gypsy moth populations on 1 ha plots (63).

These findings are in marked contrast with those reported in the Japanese literature. Furuta & Koizumi (57) have shown that avian predators aggregate into plots with high densities of gypsy moth larvae and cause density-dependent mortality. Their results suggest that avian predation plays a major role in the regulation of gypsy moth populations in Japan. Similarly, Higashiura (66, 68) has shown high levels of bird predation on gypsy moth egg masses in Japan. In contrast, very little predation seems to occur on egg masses of the gypsy moth in North America (20, 54). In European literature avian predation has been frequently cited as an important influence on population dynamics of *L. dispar*, but few studies exist to prove it.

INVERTEBRATE PREDATORS

Relatively scant attention has been given to the impact of invertebrate predators. Our recent findings (52) support the conclusions of Campbell & Sloan (29) that vertebrate predation on pupae was much greater than that caused by invertebrates. However, Smith & Lautenschlager (148) suggested that some of the mortality attributed to vertebrates by Campbell & Sloan (29) may actually have been due to invertebrates, such as ground beetles (Carabidae) and ants (Formicidae). Weseloh (186) quantified predation on tethered larvae at different heights on trees inside and outside exclosures of different mesh sizes. He found that most invertebrate predation occurred in the litter, whereas larvae tethered on the boles of trees were consumed mostly by vertebrates (presumably small mammals). Very little predation occurred among larvae tethered in the canopy of trees.

Calosoma sycophanta is a large carabid introduced into North America from Europe. Both adult and immature stages feed on gypsy moth larvae or pupae. *C. sycophanta* becomes abundant only in high-density populations of gypsy moth, and peak beetle densities usually lag 1–3 years behind the onset of gypsy moth outbreaks (148, 181). Weseloh (181, 182) used mark-recapture procedures to estimate densities of adult *C. sycophanta*, and he measured their consumption of gypsy moth pupae in outbreak populations. He showed that *C. sycophanta* consumed approximately 75% of pupae on tree stems but a much lower percentage of pupae on leaves and small branches. *C. sycophanta* adults remained abundant the following year even though gypsy moth populations had collapsed to low levels. There has been no study of *C. sycophanta* predation on low-density populations but its impact is thought to be minor (148, 182).

PARASITOIDS

Gypsy moth parasitoids have been widely studied, but most researchers believe that they do not play a major role in the population dynamics of this defoliator in North America. Beginning in 1905, extensive efforts were made to introduce gypsy moth parasitoids from Europe and Asia into North America. Of ca. 40 species that were introduced, ten have become established (155).

The principal egg parasitoids in North America are *Ooencyrtus kuvanae* (Encyrtidae) and *Anastatus disparis* (Eupelmidae). The latter parasitoid is only occasionally a significant source of mortality to gypsy moth on this continent. Brown (18) reviewed the biology and world literature on *O. kuvanae* and showed that it typically attacks from 10 to 40% of eggs per mass. Parasitism by *O. kuvanae* is greater on smaller egg masses, which

characterize high-density or collapsing gypsy moth populations (11, 19). This occurs because *O. kuvanae* attacks only the eggs on the surface of the mass and smaller masses have a higher proportion of eggs near the surface. A recent study by Schaefer et al (134) indicates that parasitism by *O. kuvanae* and other gypsy moth egg parasitoids in Japan and Korea is much lower than levels typically reported for Europe and North America.

The braconid, *Cotesia melanoscela*, attacks early instars and has two generations per year. Numerical responses of this parasitoid are highly constrained by the action of hyperparasitoids, which severely reduce the overwintering generation (180). The impact of this parasitoid is also limited by poor synchronization of the second generation with its host (178). Second generation, adult *C. melanoscela* females actively search for hosts in gypsy moth populations that have advanced to late instars which this parasitoid does not readily accept. Factors that prolong the development of early instar gypsy moths, such as ingestion of sublethal doses of *Bacillus thuringiensis*, result in much higher parasitism by *C. melanoscela* (187).

Parasetigena silvestris is a univoltine, oligophagous tachinid that oviposits large macrotype eggs on the integument of larvae. It is most active during daylight hours, and it concentrates attacks on larvae on the stems of trees, particularly when the larvae are moving between the canopy and daytime resting locations at dawn or in the evening (121, 124, 177, 179). *P. silvestris* often causes more mortality than any other parasitoid, and peak parasitism typically occurs after gypsy moth populations decline from high density (52, 126, 159). In European populations, parasitism by *P. silvestris* sometimes exceeds 95% (17). It appears to exhibit a classic delayed density-dependence which may account for the regular cycles of gypsy moth evident in some European populations (113, 143, 144).

The tachinid, *Blepharipa pratensis*, is another oligophagous parasitoid that attacks gypsy moth larvae. It is a major source of mortality in intermediate density gypsy moth populations (159). In European populations *B. pratensis* attains peak parasitism after gypsy moth populations have declined from high density (113, 144). It lays microtype eggs on foliage; these eggs hatch after they are consumed by gypsy moth larvae. *B. pratensis* aggregates to and oviposits on leaves damaged by gypsy moth (60, 122). Laboratory studies indicate that many larvae that are parasitized by *B. pratensis* and *P. silvestris* die without yielding adult parasitoids (61).

Brachymeria intermedia (Chalcididae), a polyphagous parasitoid of gypsy moth pupae, was introduced to North America in 1908 but was not recovered again until 1942. By 1971 it was quite abundant (49). It causes high levels of mortality in dense gypsy moth populations in Pennsylvania (159) and on Cape Cod (52). However, it appears to be very scarce in low-density populations. Therefore, *B. intermedia* is probably unimportant to the maintenance of gypsy

moth populations at innocuous levels, even though it evidently causes density-dependent mortality at higher densities.

The tachinid, *Compsilura concinnata*, is a multivoltine parasitoid of gypsy moth larvae with a wide host range (45). Because it depends on alternate hosts, *C. concinnata* would not be expected to exhibit strong numerical responses between generations of gypsy moths. On the other hand, unlike parasitoids that specialize on gypsy moth, it can remain abundant when gypsy moth populations are very sparse. Consequently, *C. concinnata* often causes higher mortality than any other parasitoid, when gypsy moth populations are at low density (8). Most theoretical treatments of host-parasitoid dynamics have focused on specialist parasitoids, so the role of generalists in the maintenance of many insect species at low density may have been generally underestimated (117).

We have conducted a series of experiments to explore the response of parasitoids to artificially elevated densities of gypsy moth larvae on 1 ha plots (63, 98). We found that *C. concinnata* and, to a lesser extent, *P. silvestris* caused mortality that was spatially density dependent; this mortality resulted in the collapse of such artificial populations. Similar results have been obtained in Vermont (S. Wilmot et al, unpublished) and Pennsylvania (T. M. ODell, unpublished). We suspect that these parasitoids may play an important role in suppressing incipient outbreak populations but that such population declines may go unnoticed. Assuming that this density-dependent response is a result of aggregation of these parasitoids into stands with high host density, then the response may not occur if gypsy moth populations rise simultaneously over large areas. This may explain why the levels of parasitism that occurred on our 1 ha plots with artificially elevated densities on Cape Cod were far higher than those we recorded in naturally occurring populations, which tend to fluctuate on a larger spatial scale (98).

PATHOGENS

High-density populations of the gypsy moth eventually collapse owing primarily to the action of pathogens, especially the gypsy moth nuclear polyhedrosis virus (NPV). Mortality from NPV usually peaks during late-larval instars. Early investigators believed that gypsy moth NPV and other baculoviruses existed in a latent form within the host insect and that epizootics were triggered by environmental stresses (153). Wallis (169) indicated that NPV epizootics could be triggered by high relative humidity. Campbell's analyses (23) indicated that the collapse of high-density populations often was associated with years of heavy rainfall in June. Doane (48), however, proposed an alternate theory based on density-dependent transmission of virus particles on the foliage consumed by larvae. He demonstrated that gypsy moth

neonates acquired lethal doses of virus by ingesting egg chorions following hatch. Doane suggested that NPV from the cadavers of these neonates provides the inoculum that caused late larval mortality. Woods & Elkinton (192) provided support for this hypothesis. They showed that NPV-induced mortality in high- and low-density populations followed a bimodal pattern: an early wave of mortality beginning a week or two after egg hatch, and a second wave of mortality culminating in the last larval instar. This bimodal pattern is matched by a concomitant pattern of foliage contamination with NPV as determined by bioassay of field-collected leaves. The same pattern was demonstrated in laboratory experiments (192) and in a simulation model (H. T. Valentine, unpublished).

Doane (47) showed that virtually all mortality caused by NPV among larvae hatched from field-collected egg masses could be eliminated by surface-treating the egg mass with chlorine bleach. This finding indicated that the viral inoculum resided on the surface of the mass rather than within the egg. Doane (47) assumed that this inoculum was derived from the infected female parent via transovum transmission. Laboratory experiments indicate that females which ingest sublethal doses of NPV during the larval stage produce some offspring that die from NPV (138). Murray & Elkinton (118) have shown, however, that most of the viral inoculum on the egg mass is acquired from the contaminated surface on which it is laid. In addition, neonates can acquire lethal doses of virus from contaminated bark or from pupal mats after the larvae leave the egg mass (188, 193). Particles of NPV remain viable in protected locations under bark flaps for up to a year following an epizootic (123).

Although horizontal transmission via environmental sources of virus appears to be the principal means of transmission between generations of gypsy moth, the passage of latent infections from females to their offspring remains a possible but unproven method of transmission for gypsy moth NPV. Indeed, Evans (53) concluded that the existence of latent virus has not been proven for any Lepidoptera. Mortality from gypsy moth NPV can be induced with chemical stressors (194) or by foreign viruses (100). These findings constitute circumstantial evidence for the existence of latent virus. However, increased susceptibility to background contamination of NPV is a possible alternate explanation of these results. If NPV exists in a latent form, it may be important as a means of transmission between gypsy moth generations when population densities are very low and environmental contamination with NPV is extremely sparse.

There is an interaction between foliage chemistry and susceptibility of larvae to NPV. Gypsy moth larvae ingesting NPV on leaves of aspen (*Populus* spp.) have higher rates of mortality from the virus than do larvae fed on red oak, (*Quercus rubra*) (75). Furthermore, larvae fed leaves from trees with

high tannin content had reduced susceptibility to NPV (76). Tannins apparently bind with viral particles in the gut, inhibiting passage through the peritrophic membrane (77). Foliage chemistry also affects midgut pH (136), which, in turn, affects dissolution rates of the protein matrix (occlusion body) in which the virus particles are imbedded.

Isolates of NPV from different populations differ in virulence (139, 168). Gypsy moths from different locations also vary in susceptibility to a given viral isolate (129, 146). Myers (119) has speculated that short-term genetic changes in susceptibility to pathogens may account for the cyclic pattern of population densities of many forest insects, although there is no direct evidence for this.

Several other pathogens play important roles in gypsy moth population dynamics in other continents. In the Soviet Union, microsporidia are a major source of mortality in high-density gypsy moth populations and cause longer development times and lower fecundity (109, 195). Epizootics of the fungus *Entomophaga maimaiga* often decimate high density gypsy moth populations in Japan, but only under very humid conditions (142, 149). Recently, there have been efforts to introduce *E. maimaiga* and several European species of microsporidia to North America (72, 73, 109, 149). In 1989 an epizootic of *Entomophaga* decimated gypsy moth populations throughout New England (Hajek, unpublished). Bacteria such as *Streptococcus faecalis* (48) reportedly caused high levels of mortality in some gypsy moth populations in North America. Finally, "unknown mortality" is often the predominant mortality factor affecting gypsy moth in many population studies (28). We do not know if such mortality is due to unknown pathogens or other causes.

DISPERSAL

Female gypsy moths in North America are generally incapable of flight, and move an average of only 1–2 m between sites of eclosion and oviposition (120). Second and third instars move within a tree but rarely between trees (183, 184). Most early instars remain in the lower canopy or in the understory of the forest throughout the day (158). In contrast, late instars are very mobile. The diurnal behavior by which late instars from endemic populations seek resting sites in the litter often results in larvae moving from one tree to another (82, 99, 170). Such behavior is of considerable importance in the host switching process. Most first instars successfully become established mainly on primary hosts (*Quercus*, *Populus*, etc), but between-tree movement of late instars causes a net outflux of larvae from these hosts to less-preferred species (*Pinus*, *Acer*, etc) (82, 107, 130, 170). This behavior also causes larvae to accumulate on trees and in areas with a large number of above-ground resting sites (e.g. bark flaps) (99). This may help explain reports of high egg mass

densities in areas that previously were attributed entirely to the high survival of late instars in such resting sites.

Newly hatched larvae descend on silk threads and are subsequently transported by winds. Passive movement of first instars is unquestionably the major mode of gypsy moth dispersal, though the distance traveled is a matter of some controversy. Collins (43) trapped larvae on sticky panels and speculated that they may have originated up to 40 km away. Mason & McManus (106) constructed a Gaussian plume model of first instar dispersal and verified it experimentally by releasing neonates in the field. They confirmed the model predictions that a relatively small proportion of insects would disperse beyond 100 m. More recently, Taylor & Reling (157) proposed that extensive long-range dispersal (up to 19 km) may result from horizontal movement of atmospheric convection cells, but their atmospheric samples above a dense population did not demonstrate that this occurred. Mason & McManus (106) point out that if dispersal is extensive, then the rate of expansion of the generally infested region would have been much greater.

Historical defoliation maps show that defoliation often radiates progressively outward from specific sites, typically referred to as "focal areas" or foci. These terms are synonymous with the terms "primary foci," "epicenters," and "refugia" in the European and Canadian literature (97, 172). Foci are characterized by forest stands that are growing on xeric sites such as ridgetops or on sandy soils (71). Several studies have assigned a causal connection between the initiation of outbreaks in focal areas and their expansion to surrounding areas (42, 164, 171, 172). It is hypothesized that the large numbers of larvae emigrating from these focal areas upset the assumed endemic equilibrium of local populations, causing them to enter outbreak phase. However, the relatively low dispersal rates reported by Mason & McManus (106) suggest that dispersal is unlikely to cause this large-scale spread of defoliation.

BEHAVIOR AND POPULATION QUALITY

Changes in behavior and other qualitative differences have long been noted between gypsy moths from innocuous low-density populations versus high-density or collapsing populations. Gypsy moths from high density or collapsing populations have shorter development times (26), male-biased sex ratios, (22) and smaller pupal or adult body weights; they may also lay fewer eggs (26). It has been suggested that first instars from high-density populations are more likely to disperse than larvae from low-density populations (137, 23), although, in our opinion, few data exist to support this conclusion. Leonard (91) showed that the last-laid eggs in an egg mass tend to be smaller than the first-laid eggs. Furthermore, the smaller eggs were more likely to yield larvae

which have extra instars. Such larvae occurred more frequently among individuals reared under crowded (90) or starvation (92) conditions and had a longer duration first stadium. Starved larvae are more active than unstarved larvae (89). Leonard theorized that these traits represented behavioral adaptations that make dispersal more likely in high-density populations, enabling individuals to escape the near-certain death from disease or starvation that occurs in such populations (91).

Capinera & Barbosa (38) showed that small eggs yielded larvae that were less likely to disperse in laboratory tests than larvae from large eggs. Larvae from small eggs had lower yolk supply (40) and therefore lower energy reserves from which to produce silk. Smaller eggs were produced by females reared on less preferred host trees. Also, females reared from small eggs produced small eggs themselves; thus, egg size may be heritable. However, there was no correlation between egg size and population density (39, 127). Egg masses collected from high-density populations had fewer but not smaller eggs. Further studies showed that neonates are more likely to disperse from nonpreferred than from preferred hosts (6, 38, 81). In our opinion, however, the hypothesis that population density influences the dispersive behavior of neonates has not been conclusively demonstrated.

High-density populations of gypsy moth mature more rapidly and attain the adult stage 2–3 weeks ahead of adjacent low-density populations. Leonard (90) found that larvae reared in the laboratory under crowded conditions developed more quickly than larvae reared individually, but the differences averaged ca. 3 days and were not consistent among replicates. Laboratory studies by Lance et al (83) found no effects due to crowding, partial starvation, sublethal doses of NPV, or exposure to larval silk on the developmental times of gypsy moth larvae. Field studies in high- and low-density populations showed that on sunny days, larvae from high-density populations were 2–6°C warmer than larvae from low-density populations (83). These differences occurred because larvae in high-density populations remained in the canopy of trees during the day where they were exposed to more solar radiation than were larvae from low-density populations that sought daytime resting locations in the litter. Also, solar radiation penetrates defoliated stands much more than nondefoliated stands. Furthermore, when reared in the laboratory under the same diurnal temperature regimes that were measured in the high- versus low-density populations, larvae differed in developmental time to the pupal stage by 1–2 weeks. Thus, it seems that differences in body temperature account for the differences in developmental rates between high- and low-density populations.

Late-larval instars from low-density populations feed only at night and seek daytime resting sites in the litter or in protected locations on the stems of trees. In high-density populations, late instars feed both day and night and

remain in the canopy of trees (16, 54). Lance et al (84, 86) have shown that such larvae from high-density populations consume no more foliage than larvae from low-density populations, even though they are feeding over a much longer period each day. Feeding bouts on foliage of individuals from high-density populations are of shorter duration than feeding bouts from low-density populations. Changes in foliage chemistry may explain the shift away from feeding only at night in high-density populations (84). Larvae hatched from field-collected eggs and reared on foliage from a site experiencing heavy defoliation showed no diurnal feeding rhythm. In contrast, larvae reared on foliage from a site with little or no defoliation showed a marked diurnal feeding rhythm. Similar results were produced in the laboratory by incorporating tannic acid into artificial diet (84). Larvae reared on normal diet exhibited the diurnal rhythm, whereas larvae reared on a diet containing tannins, at concentrations comparable to that of leaves from defoliated trees, exhibited no diurnal rhythm. These findings support the growing body of knowledge indicating that foliage chemistry has an important impact on quality and behavior of gypsy moths. These impacts include reductions in body size and fecundity, which are among the most important changes associated with dense populations of gypsy moth (131).

HOST TREE SPECIES AND FOLIAGE CHEMISTRY

Tree species composition has a major impact on the susceptibility of forest stands to gypsy moth. Gypsy moth has a very wide host range, although some tree species (notably *Quercus*, *Populus*, and *Salix* spp.) are clearly more preferred than others (104, 116). Outbreaks rarely occur in stands dominated by nonpreferred host species (16, 58, 71).

In recent years, much research has concentrated on quantifying gypsy moth host preferences in the field (3, 4, 88, 107, 108, 130). These studies have shown that different gypsy moth stages differ markedly in their host preferences. First instars are the most specific, late instars are more catholic in their preferences, and pupae are often most common on tree species that are unsuitable hosts for early instars. Rossiter (130) proposed that this exploitation of nonpreferred hosts by late instars represents an adaptation by which larvae avoid high levels of density-dependent mortality (such as starvation and NPV) on preferred species. Generally, there is almost complete congruence in the relative acceptability (measured in laboratory feeding trials with first instars) of various host species and their suitability (measured by weight gain and developmental time) (9, 104). Furthermore, a good correspondence exists between the performance of larvae on a given host species (as measured by developmental time and pupal weight) and its preference (as measured in both feeding trials and by the distribution of larvae in the field) (3, 5, 70).

The chemical basis of this host preference is poorly understood. No single factor alone (such as tannin or nutritional content) explains the performance or preference of gypsy moth on a particular species; instead, the preference for a given species probably results from a complex interaction of the allelochemical, nutritional, and physical properties of its foliage (87). Barbosa & Krischik (7) argued that alkaloid content is a major determinant of foliage acceptability to gypsy moth. Several recent studies have examined preferences for various tree species from regions not yet infested with gypsy moths (10, 46, 111a).

Even among stands dominated by preferred hosts, there is considerable variation in susceptibility (16, 71). Montgomery (112) has shown that some differences in foliage quality (measured by foliage chemistry and larval performance) exist between trees of a given species located in resistant and susceptible sites.

Defoliation induces changes in host leaves that cause qualitative changes in gypsy moths, such as changes in pupal weight, developmental time, and survival (174). Schultz & Baldwin (135) suggested that these changes may be due to increases in hydrolyzable and condensed tannins, increased total phenolics, higher tanning coefficients, and increased leaf toughness. Valentine et al (165) showed that defoliation induced a decrease in free sugar levels, and they found that these levels were inversely correlated with pupal weight. Rossiter et al (131) experimentally defoliated trees and demonstrated that defoliation induced increased levels of total phenolics and hydrolyzable tannins, and increased protein-binding capacities, but there was no effect on condensed tannin levels. Furthermore, these induced changes occurred only in leaves adjacent to the defoliation and not throughout the tree.

Baldwin & Schultz (2) reported on laboratory tests in which defoliation induced elevated phenolic levels both in trees that were defoliated and in nearby undefoliated trees. Under the so-called "talking trees" hypothesis, hypothetical pheromones are released by defoliated trees and these pheromones induce phytochemical reactions in other trees. Fowler & Lawton (55) rejected the "talking tree" hypothesis, partially because of statistical problems in the Baldwin & Schultz (2) article. The hypothesis has not been subsequently substantiated.

Schultz & Baldwin (135) proposed that variation in foliage quality may cause both the initiation and collapse of gypsy moth outbreaks. While host relationships are important, their role is still uncertain due to the complexity of their effect. Unquestionably, interspecific and intraspecific variation in foliage chemistry has an impact on fecundity (70, 112), but no evidence exists to support the theory that host-induced increases in fecundity cause the release of innocuous populations to outbreak densities. Host foliage affects susceptibility of larvae to mortality caused by NPV (75) and parasitism (J.

Werren, unpublished data), but the significance of these effects to the overall dynamics remains unclear.

The phenology of bud-break and leaf development on host trees relative to gypsy moth phenology can have a dramatic effect on larval survival and growth (125, 162). For many tree species the growth rate and survival of gypsy moth declines with leaf age (70, 125). With cottonwood, *Populus deltoides*, however, gypsy moth grows better on older leaves (110). In Morocco, defoliated cork oaks, *Quercus suber*, do not put out new leaves the following spring, thus forcing gypsy moths to feed on old leaves. This greatly reduces gypsy moth fecundity and survival and results in a population decline (56).

WEATHER

Weather affects all of the dynamical interactions of forest insect populations, although the mechanisms are often obscure and complex. Several studies have addressed the gross relationship between yearly weather patterns and gypsy moth outbreak development. The results of these analyses are not entirely consistent, though warm, dry weather does recur as a factor associated with outbreaks. Watt (176) found that the rate of increase in yearly North American defoliation area was positively correlated with late summer temperatures. Miller et al (111) found that New England state defoliation totals were positively correlated with minimum temperature from mid-April to mid-May of the current and the previous years. Defoliation was inversely correlated with maximum temperatures in early April and precipitation in October of the previous year. Earlier analyses of the same data revealed that the area defoliated was positively correlated with maximum November temperature and minimum January temperature, and was inversely correlated with mean December temperature (59); however, these relationships were not significant in all states. Campbell (24) related changes in egg mass density to precipitation in May of the previous year. Declines in density were correlated with low winter temperatures and heavy precipitation in June of the same year (23, 24). Skaller (145) reported increases in gypsy moth density were correlated with warm, dry conditions in May and June. Kono (80) related gypsy moth outbreaks to sunspot activity. The lack of any consistent relationship among these various studies highlights the inadequacy of correlation analyses and the difficulty in elucidating weather effects (103). Perhaps, a variety of weather patterns promote outbreaks.

Ultimately, an understanding of the complex mechanisms by which weather affects gypsy moth populations will be required before accurate predictions can be made. For instance, we know that exposure of egg masses to very cold winter temperatures ($< -25^{\circ}\text{C}$) causes high mortality (59, 101,

102, 105) and that a snow cover over egg masses can provide sufficient insulation to prevent this mortality (93, 101).

SIMULATION MODELS

Various simulation models (recently reviewed by Sheehan—141) synthesize the large volume of information on gypsy moth biology and ecology. Campbell (24) developed a series of regression models for forecasting future egg mass densities based on current densities, stand composition, and meteorological conditions. Valentine (161) developed a series of differential equations that describe the effects of foliage availability (starvation), reproduction, and NPV-caused mortality on the dynamics of gypsy moth populations. Valentine (163) devised a more complex differential equations model that incorporated induced changes in foliage quality. In both models, he was able to produce regular cycles in gypsy moth densities. Morse & Simmons (115) developed a simulation model that incorporated the net impact of gypsy moth pathogens and natural enemies, as well as foliage availability; depending on parameter values, the model predicted regular outbreak cycles or behaved chaotically. Brown et al (20a) developed a simulation model of the impact of *O. kuvanae* on gypsy moth populations. The Gypsy Moth Life System Model (140) is a very large simulation model developed by the US Forest Service that simulates detailed interactions between gypsy moth populations, their host trees, and natural enemies.

Models of growth as a function of temperature are fundamental components of most population simulations for poikilothermic animals like gypsy moths. Casagrande et al (41) developed a nonlinear, temperature-dependent growth model for gypsy moth larvae and pupae. Such models can be used to make predictions of developmental times for populations in the field, but a major limitation is the usual assumption that the temperature of the animal is the same as air temperature. Gypsy moth larvae often deviate from air temperature by several °C, and populations in adjacent stands with nearly identical air temperature can differ in developmental times to the pupal stage by 2–3 weeks (85). Anderson et al (1) have developed a simulation of microclimate within and beneath the forest canopy that predicts gypsy moth temperatures from basic weather data. Other models have been developed that predict the timing of egg hatch (74, 168a). These models address only the incubation of eggs, and their use assumes that the timing of diapause termination is known. Chilling is required to terminate diapause, but it is a gradual process (156) with complex and not fully understood interactions among chilling temperature, chilling time, average incubation time, and variance in incubation time (59, 105, 196). Valentine (162) modeled the phenology of leaf expansion of host trees relative to gypsy moth larval development and showed that the

timing of gypsy moth life stages relative to host leaves may be important in determining the extent of foliage depletion (and subsequent starvation).

SUMMARY AND CONCLUSION

Recent studies (52) support the earlier conclusions of Bess et al (16) and Campbell & Sloan (30, 31) that gypsy moth populations are maintained at low densities primarily by the action of small mammal predators. Spatially density-dependent parasitism by tachinids such as *C. concinnata* may also be important in suppressing incipient outbreaks (63). The reasons such factors fail in certain years and allow gypsy moth populations to escape into outbreak phase have not been elucidated. Factors that affect small mammal population density such as overwintering food supply are important possible causes of population release. Other factors that affect predation rates by small mammals such as berry crops which compete with gypsy moth as a food item (147) may also be important. However, changes in factors that affect fecundity or survival of early instars may in certain years result in densities of late instar larvae or pupae that approach the satiation points of predators. The synchronous behavior of gypsy moth populations over fairly large regions suggests that weather conditions drive the system in some manner, but the mechanisms remain obscure. It is entirely possible that different weather events and the failure of different mortality agents are responsible for the onset of outbreak phase in different years.

The factors controlling outbreak populations are better understood. In recent years major advances have occurred in our understanding of NPV epizootiology and the influence of changes in foliage chemistry and other determinants of population quality. The role of other diseases and the causes of "unknown mortality" remain to be elucidated. Important advances have been seen in methods for estimating gypsy moth density and quantifying mortality, but extreme difficulties remain in collecting adequate measures of the important variables, particularly at low population density. Thus, we should not be surprised if future studies lead to a very different understanding of the dynamics of this population system.

ACKNOWLEDGMENTS

We are grateful to C. Boettner, G. Boettner, D. Leonard, M. Montgomery, R. Mazzocchi, and J. Wells for help in assembling references. We thank K. Conlan, J. Gould, D. Jennings, D. Lance, D. Leonard, M. McManus, M. Montgomery, K. Murray, T. Odell, M. Peters and R. Weseloh for helpful reviews of an earlier draft of this manuscript.

Literature Cited

1. Anderson, D. E., Miller, D. R., Wallner, W. E., Taigen, T. L., Schwartz, J. J. 1987. A numerical simulation of the microclimate of gypsy moth caterpillars in forest canopies. *Proc. 8th Conf. Aero and Bio-Met. AMS, Purdue Univ., W. Lafayette, Ind.*, Sept. 14-18, pp. 353-55
2. Baldwin, I. T., Schultz, J. C. 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221:277-79
3. Barbosa, P. 1978. Host plant exploitation by the gypsy moth, *Lymantria dispar*. *Entomol. Exp. Appl.* 24:28-37
4. Barbosa, P. 1978. Distribution of an endemic larval gypsy moth population among various tree species. *Environ. Entomol.* 7:526-27
5. Barbosa, P., Capinera, J. L. 1977. The influence of food on developmental characteristics of the gypsy moth, *Lymantria dispar* (L.). *Can. J. Zool.* 55:1424-29
6. Barbosa, P., Greenblatt, J. 1979. Suitability, digestibility and assimilation of various host plants of the gypsy moth *Lymantria dispar* L. *Oecologia* 43:111-19
7. Barbosa, P., Krischik, V. A. 1987. Influence of alkaloids on feeding preference of eastern deciduous forest trees by the gypsy moth *Lymantria dispar*. *Am. Nat.* 130:53-69
8. Barbosa, P., Capinera, J. L., Harrington, E. A. 1975. The gypsy moth parasitoid complex in western Massachusetts: a study of parasitoids in areas of high and low density. *Environ. Entomol.* 4:842-46
9. Barbosa, P., Greenblatt, J., Withers, W., Cranshaw, W., Harrington, E. A. 1979. Host-plant preferences and their induction in larvae of the gypsy moth, *Lymantria dispar*. *Entomol. Exp. Appl.* 26:180-88
10. Barbosa, P., Waldvogel, M., Martinat, P., Douglass, L. W. 1983. Developmental and reproductive performance of the gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), on selected hosts common to mid-Atlantic and southern forests. *Environ. Entomol.* 12:1858-62
11. Bellinger, R. G., Ravlin, F. W., McManus, M. L. 1988. Host plant species and parasitism of gypsy moth (Lepidoptera: Lymantriidae) egg masses by *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae). *Environ. Entomol.* 17(6): 936-40
12. Bellinger, R. G., Ravlin, F. W., McManus, M. L. 1989. Forest edge effects and their influence on gypsy moth (Lepidoptera: Lymantriidae) egg mass distribution. *Environ. Entomol.* 18:840-43
13. Bellinger, R. G., Roberts, E. A., Ravlin, F. W. 1989. Validation of volumetric counts of gypsy moth *Lymantria dispar* L. (Lepidoptera: Lymantriidae) eggs for field and laboratory populations. *J. Econ. Entomol.* In press
14. Bellows, T. S., Van Driesche, R. G., Elkinton, J. S. 1989. Extensions to Southwood and Jepson's graphical method of estimating numbers entering a stage for calculating losses to parasitism. *Res. Popul. Ecol.* In press
15. Bess, H. A. 1961. Population ecology of the gypsy moth *Porthetria dispar* L. (Lepidoptera: Lymantriidae). New Haven: *Conn. Agric. Exp. Sta. Bull.* 646. 43 pp.
16. Bess, H. A., Spurr, S. H., Littlefield, E. W. 1947. Forest site conditions and the gypsy moth. *Harv. For. Bull.* 22. 56 pp.
17. Bogenschütz, H., Maier, K., Trzebitzky, C. 1989. Gypsy moth outbreak and control in southwest Germany, 1984-96. See Ref. 173, pp. 89-99
18. Brown, M. W. 1984. Literature review of *Ooencyrtus kuvanae* (Hym.: Encyrtidae), an egg parasite of *Lymantria dispar* (Lep.: Lymantriidae). *Entomophaga* 29:249-65
19. Brown, M. W., Cameron, E. A. 1979. Effects of disparture and egg mass size on parasitism by the gypsy moth egg parasite, *Ooencyrtus kuvanae*. *Environ. Entomol.* 8:77-80
20. Brown, M. W., Cameron, E. A. 1982. Natural enemies of *Lymantria dispar* (Lep.: Lymantriidae) eggs in central Pennsylvania, U.S.A. and a review of the world literature on natural enemies of *L. dispar* eggs. *Entomophaga* 27: 311-22
- 20a. Brown, M. W., Williams, F. M., Cameron, E. A. 1983. Simulations on the role of the egg parasite, *Ooencyrtus kuvanae* (Howard), in the population dynamics of the gypsy moth. *Ecol. Model.* 18:253-68
21. Buonaccorsi, J. P., Liebhold, A. M. 1988. Statistical methods for estimating ratios and products in ecological studies. *Environ. Entomol.* 17:572-80
22. Campbell, R. W. 1963. Some factors that distort the sex ratio of the gypsy

- moth *Porthetria dispar* (L.) (Lepidoptera: Lymantriidae). *Can. Entomol.* 95:465-74
23. Campbell, R. W. 1967. The analysis of numerical change in gypsy moth populations. *For. Sci. Monogr.* 15:1-33
 24. Campbell, R. W. 1973. Forecasting gypsy moth egg-mass densities. *USDA For. Serv. Res. Pap. NE-268.* 17 pp.
 25. Campbell, R. W. 1976. Comparative analysis of numerically stable and violently fluctuating gypsy moth populations. *Environ. Entomol.* 5:1218-24
 26. Campbell, R. W. 1978. Some effects of gypsy moth density on rate of development, pupation time and fecundity. *Ann. Entomol. Soc. Am.* 71:442-48
 27. Campbell, R. W. 1981. Historical review. See Ref. 50, pp. 65-86
 28. Campbell, R. W., Podgwaite, J. D. 1971. The disease complex of the gypsy moth: I. Major components. *J. Invertebr. Pathol.* 18:101-7
 29. Campbell, R. W., Sloan, R. J. 1976. Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. *Environ. Entomol.* 5:1211-17
 30. Campbell, R. W., Sloan, R. J. 1977. Natural regulation of innocuous gypsy moth populations. *Environ. Entomol.* 6:315-22
 31. Campbell, R. W., Sloan, R. J. 1977. Release of gypsy moth populations from innocuous levels. *Environ. Entomol.* 6:323-30
 32. Campbell, R. W., Sloan, R. J. 1978. Natural maintenance and decline of gypsy moth outbreaks. *Environ. Entomol.* 7:389-95
 33. Campbell, R. W., Sloan, R. J. 1978. Numerical bimodality among North American gypsy moth populations. *Environ. Entomol.* 7:641-46
 34. Campbell, R. W., Hubbard, D. L., Sloan, R. J. 1975. Location of gypsy moth pupae and subsequent pupal survival in sparse, stable populations. *Environ. Entomol.* 4:597-600
 35. Campbell, R. W., Miller, M. G., Duda, E. J., Biazak, C. E., Sloan, R. J. 1976. Man's activities and subsequent gypsy moth egg-mass density along the forest edge. *Environ. Entomol.* 5:273-76
 36. Campbell, R. W., Sloan, R. J., Biazak, C. E. 1977. Sources of mortality among late instar gypsy moth larvae in sparse populations. *Environ. Entomol.* 6:865-71
 37. Campbell, R. W., Levitan, L. C., Sobocki, E. R., Tardiff, M. F. 1978. Population dynamics of the gypsy moth: an annotated bibliography. *USDA For. Serv. Gen. Tech. Rep. NE-48.* 124 pp.
 38. Capinera, J. L., Barbosa, P. 1976. Dispersal of first-instar gypsy moth larvae in relation to population quality. *Oecologia* 26:53-64
 39. Capinera, J. L., Barbosa, P. 1977. Influence of natural diets and larval density on gypsy moth, *Lymantria dispar* (Lepidoptera: Orgyiidae), egg mass characteristics. *Can. Entomol.* 109: 1313-18
 40. Capinera, J. L., Barbosa, P., Hagedorn, H. H. 1977. Yolk and yolk depletion of gypsy moth eggs: implications for population quality. *Ann. Entomol. Soc. Am.* 70:40-42
 41. Casagrande, R. A., Logan, P. A., Wallner, W. E. 1987. Phenological model for gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae and pupae. *Environ. Entomol.* 16:556-62
 42. Chuginin, Ya. 1949. Focal periodicity of gypsy moth outbreaks. *Zool. Zh.* 28:431-48
 43. Collins, C. W. 1917. Methods used in determining wind dispersion of the gypsy moth and some other insects. *J. Econ. Entomol.* 10:170-77
 44. Cooper, R. J. 1988. *Dietary relationships among insectivorous birds of an eastern deciduous forest.* PhD thesis. West Va. Univ., Morgantown. 193 pp.
 45. Culver, J. J. 1919. A study of *Compilura concinnata*, an imported tachinid parasite of the gypsy moth and the brown-tail moth. *USDA Bull.* 776. 26 pp.
 46. Daterman, G. E., Miller, J. C., Hanson, P. E. 1985. Potential for gypsy moth problems in southwest Oregon. In *Forest Pest Management in Southwest Oregon, Workshop Proc.*, Aug. pp. 37-40, Corvallis: Oregon State University
 47. Doane, C. C. 1969. Trans-ovum transmission of a nuclear-polyhedrosis virus in the gypsy moth and inducement of virus susceptibility. *J. Invertebr. Pathol.* 14:199-210
 48. Doane, C. C. 1970. Primary pathogens and their role in the development of an epizootic in the gypsy moth. *J. Invertebr. Pathol.* 15:21-33
 49. Doane, C. C. 1971. A high rate of parasitization by *Brachymeria intermedia* (Hymenoptera: Chalcididae) on the gypsy moth. *Ann. Entomol. Soc. Am.* 64:753-54
 50. Doane, C. C., McManus, M. L., eds. 1981. The gypsy moth: research toward integrated pest management. *USDA For. Serv. Tech. Bull.* 1584. 757 pp.
 51. Eggen, D. A., Abrahamson, L. P. 1983. Estimating gypsy moth egg mass densi-

- ties. *State Univ. NY Sch. For. Misc. Publ. 1 (ESF 83-002)*. 30 pp.
52. 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?. See Ref. 173, pp. 233-49
 53. Evans, H. F. 1986. Ecology and epizootiology of baculoviruses. In *The Biology of Baculoviruses*, ed. R. R. Granados, B. A. Federici, 2:89-132. Boca Raton, FL: CRC
 54. Forbush, E. H., Fernald, C. H. 1896. *The Gypsy Moth*. Boston: Wright & Potter. 495 pp.
 55. Fowler, S. V., Lawton, J. H. 1985. Rapidly induced defenses and talking trees: the devil's advocate position. *Am. Nat.* 126:181-95
 56. Fraval, A. 1984. Influence de la qualite et de la quantite de l'alimentation sur les fluctuations des populations de *Lymantria dispar* L. (Lep: Lymantriidae) en foret de la Mamora (Maroc). *Agronomie* 4:819-28
 57. Furuta, K., Koizumi, C. 1975. The mortality factors of experimental populations of *Lymantria dispar* in a larch plantation and natural forest. *J. Jpn. For. Soc.* 57:432-35
 58. Ganser, D. A., Herrick, O. W., Mason, G. N., Gottschalk, K. W. 1987. Coping with gypsy moth on new frontiers of infestation. *South. J. Appl. For.* 11: 201-9
 59. Giese, R. L., Casagrande, R. A. 1981. Egg development and diapause. See Ref. 50, pp. 145-50
 60. Godwin, P. A., O'Dell, T. M. 1981. Intensive laboratory and field evaluations of individual species: *Blepharipa pratensis* (Meigen) (Diptera: Tachinidae). See Ref. 50, pp. 375-93
 61. Godwin, P. A., O'Dell, T. M. 1984. Laboratory study of competition between *Blepharipa pratensis* and *Parasetigena silvestris* (Diptera: Tachinidae), in *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 13: 1059-63
 62. Gould, J. R., Van Driesche, R. G., Elkinton, J. S., O'Dell, T. M. 1989. A review of techniques for measuring the impact of parasitoids of lymantriids. See Ref. 173, pp. 517-31
 63. Gould, J. R., Elkinton, J. S., Wallner, W. E. 1989. Density dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. *J. Anim. Ecol.* In press
 64. Griffiths, K. J. 1976. The parasites and predators of the gypsy moth: a review of the world literature with special application to Canada. *Can. For. Serv. Gt. Lakes For. Res. Cent. Rep. O-X-243*. 92 pp.
 65. Griffiths, K. J. 1980. A bibliography of gypsy moth literature. *Can. For. Serv. Gt. Lakes For. Res. Cent. Rep. O-X-312*. 350 pp.
 66. Higashiura, Y. 1980. Analysis of factors affecting bird predation on gypsy moth egg masses by using Holling's dis-equation. *Res. Popul. Ecol.* 22:147-62
 67. Higashiura, Y. 1987. Larval densities and a life-table for the gypsy moth, *Lymantria dispar*, estimated using the head-capsule collection method. *Ecol. Entomol.* 12:25-30
 68. Higashiura, Y. 1989. Survival of eggs in the gypsy moth *Lymantria dispar*: I. Predation by birds. *J. Anim. Ecol.* 58:403-12
 69. Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:5-60
 70. Hough, J. A., Pimentel, D. 1978. Influence of host foliage on development, survival and fecundity of the gypsy moth. *Environ. Entomol.* 7:97-102
 71. Houston, D. R., Valentine, H. T. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. *Can. J. For. Res.* 7:447-61
 72. Jeffords, M. R., Maddox, J. V., McManus, M. L., Webb, R. E., Wieber, A. 1988. Egg contamination as a method for the inoculative release of exotic microsporidia of the gypsy moth. *J. Invertebr. Pathol.* 51:190-96
 73. Jeffords, M. R., Maddox, J. V., McManus, M. L., Webb, R. E., Wieber, A. 1989. Evaluation of overwintering success of two European microsporidia inoculatively released into gypsy moth populations in Maryland. *J. Invertebr. Pathol.* 53:235-40
 74. Johnson, P. C., Mason, D. P., Radke, S. L., Tracewski, K. T. 1983. Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. *Environ. Entomol.* 12:929-32
 75. Keating, S. T., Yendol, W. G. 1987. Influence of selected host plants on gypsy moth (Lepidoptera: Lymantriidae) larval mortality caused by a baculovirus. *Environ. Entomol.* 16:459-62
 76. Keating, S. T., Yendol, W. G., Schultz, J. C. 1988. Relationship between susceptibility of gypsy moth larvae (Lepidoptera: Lymantriidae) to a baculovirus

- and host plant foliage constituents. *Environ. Entomol.* 17:952-58
77. Kcating, S. T., Hunter, M. D., Schultz, J. C. 1989. Leaf phenolic inhibition of gypsy moth nuclear polyhedrosis virus: the role of polyhedral inclusion body aggregation. *J. Chem. Ecol.* In press
 78. Kolodny-Hirsch, D. M. 1986. Evaluation of methods for sampling gypsy moth (Lepidoptera:Lymantriidae) egg mass populations and development of sequential sampling plans. *Environ. Entomol.* 15:122-27
 79. Kolodny-Hirsch, D. M., Reardon, R. C., Thorpe, K. W., Raupp, M. J. 1988. Evaluating the impact of sequential releases of *Cotesia melanoscela* (Hymenoptera: Braconidae) on *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 17:403-8
 80. Kono, H. 1938. Relationship between the number of sunspots and outbreaks of gypsy moth in Japan. *Jpn. J. Appl. Zool.* 10:146-48
 81. Lance, D. R., Barbosa, P. 1981. Host tree influences on the dispersal of first instar gypsy moths, *Lymantria dispar* (L.). *Ecol. Entomol.* 6:411-16
 82. Lance, D. R., Barbosa, P. 1982. Host tree influences on the dispersal of late instar gypsy moths, *Lymantria dispar*. *Oikos* 38:1-7
 83. Lance, D. R., Elkinton, J. S., Schwalbe, C. P. 1986. Components of density-related stress as potential determinants of population quality in the gypsy moth, (Lepidoptera: Lymantriidae). *Environ. Entomol.* 15:914-18
 84. Lance, D. R., Elkinton, J. S., Schwalbe, C. P. 1986. Feeding rhythms of gypsy moth larvae: effect of food quality during outbreaks. *Ecology* 67: 1650-54
 85. Lance, D. R., Elkinton, J. S., Schwalbe, C. P. 1987. Microhabitat and temperature effects explain accelerated gypsy moth development during outbreaks of the gypsy moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 16: 202-5
 86. Lance, D. R., Elkinton, J. S., Schwalbe, C. P. 1987. Behaviour of late-instar gypsy moth larvae in high and low density populations. *Ecol. Entomol.* 12:267-73
 87. Lechowicz, M. J. 1983. Leaf quality and the host preferences of gypsy moth in the northern deciduous forest. See Ref. 154, pp. 67-82
 88. Lechowicz, M. J., Jobin, L. 1983. Estimating the susceptibility of tree species to attack by the gypsy moth, *Lymantria dispar*. *Ecol. Entomol.* 8:171-83
 89. Leonard, D. E. 1967. Silking behavior of the gypsy moth *Porthetria dispar* (L.). *Can. Entomol.* 99:1145-49
 90. Leonard, D. E. 1968. Effects of density of larvae on the biology of the gypsy moth, *Porthetria dispar* (L.) *Entomol. Exp. Appl.* 11:291-304
 91. Leonard, D. E. 1970. Intrinsic factors causing qualitative changes in populations of the gypsy moth. *Can. Entomol.* 102:239-49
 92. Leonard, D. E. 1970. Effects of starvation on behaviour, number of larval instars, and developmental rate of *Porthetria dispar*. *J. Insect Physiol.* 16:25-31
 93. Leonard, D. E. 1972. Survival in a gypsy moth population exposed to low winter temperatures. *Environ. Entomol.* 1: 549-54
 94. Leonard, D. E. 1974. Recent developments in ecology and control of the gypsy moth. *Annu. Rev. Entomol.* 19:197-229
 95. Liebhold, A. M., Elkinton, J. S. 1988. Techniques for estimating the density of late instar gypsy moth (Lepidoptera: Lymantriidae), populations using frass drop and frass production measurement. *Environ. Entomol.* 17:381-84
 96. Liebhold, A. M., Elkinton, J. S. 1988. Estimating the density of larval gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae), using frass drop and frass production measurement. Sources of variation and sample size. *Environ. Entomol.* 17:385-90
 97. Liebhold, A. M., Elkinton, J. S. 1989. Characterizing spatial patterns of gypsy moth regional defoliation. *For. Sci.* 35:557-68
 98. Liebhold, A. M., Elkinton, J. S. 1989. Elevated parasitism in artificially augmented gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations. *Environ. Entomol.* In press
 99. Liebhold, A. M., Elkinton, J. S., Wallner, W. E. 1986. Effect of burlap bands on between-tree movement of late-instar gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 15:373-79
 100. Longworth, J. F., Cunningham, J. C. 1968. The activation of occult nuclear polyhedrosis viruses by foreign nuclear polyhedra. *J. Invertebr. Pathol.* 10:361-67
 101. Madrid, F. J., Stewart, R. K. 1981. The influence of some environmental factors on the development and behavior of the gypsy moth (*Lymantria dispar* L.) in Quebec. *Ann. Soc. Entomol. Quebec* 26:191-211
 102. Maksimovic, M. 1958. Experimental re-

- search on the influence of temperature on the development and the population dynamics of the gypsy moth (*Liparis dispar*). *Posebna Izd. Biol. Inst. NR Srb. Beograd* 3:1-115
103. Martinat, P. J. 1987. The role of climatic variation and weather in forest insect outbreaks. In *Insect Outbreaks*, ed. P. Barbosa, J. Schultz, pp. 241-68. New York: Academic
 104. Martinat, P. J., Barbosa, P. 1987. Relationship between host-plant acceptability and suitability in newly enclosed first-instar gypsy moths, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). *Ann. Entomol. Soc. Am.* 80: 141-47
 105. Masaki, S. 1956. The effect of temperature on the termination of diapause in the eggs of *Lymantria dispar* Linne. *Jpn. J. Appl. Zool.* 21:148-57
 106. Mason, C. J., McManus, M. L. 1981. Larval dispersal of the gypsy moth. See Ref. 50, pp. 161-202
 107. Mauffette, Y., Lechowicz, M. J. 1984. Differences in the utilization of tree species as larval hosts and pupation sites by the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). *Can. Entomol.* 116:685-90
 108. Mauffette, Y., Lechowicz, M. J., Jobin, L. 1983. Host preferences of the gypsy moth, *Lymantria dispar* (L.) in southern Quebec. *Can. J. For. Res.* 13:53-60
 109. McManus, M. L., Maddox, J. V., Jeffords, M. R., Webb, R. E. 1989. Evaluation and selection of candidate European microsporidia for introduction into U.S. gypsy moth populations. See Ref. 173, pp. 455-68
 110. Meyers, G. A., Montgomery, M. E. 1987. Relationships between leaf age and the food quality of cottonwood foliage for the gypsy moth, *Lymantria dispar*. *Oecologia* 72:527-32
 111. Miller, D. R., Mo, T. K., Wallner, W. E. 1989. Climate influences on gypsy moth defoliation in southern New England. *Environ. Entomol.* 18:646-50
 - 111a. Miller, J. C., Hanson, P. E. 1989. Laboratory studies on development of the gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae on foliage of gymnosperms. *Can. Entomol.* 121:425-29
 112. Montgomery, M. E. 1986. Gypsy moth host plant relationships and population dynamics. *Proc. 18th IUFRO World Congr., Div. 2*, 2:743-53
 113. Montgomery, M. E., Wallner, W. E. 1988. The gypsy moth, a westward migrant. In *Dynamics of Forest Insect Populations*, ed. A. A. Berryman, pp. 353-75. New York: Plenum
 114. Moore, K. E. B., Jones, C. G. 1987. Field estimation of fecundity of gypsy moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 16:165-67
 115. Morse, J. G., Simmons, G. A. 1979. Simulation model of gypsy moth introduced into Michigan Forests. *Environ. Entomol.* 8:293-39
 116. Mosher, F. H. 1915. Food plants of the gypsy moth in America. *USDA Bull.* 250. 39 pp.
 117. Murdoch, W. W., Chesson, J., Chesson, P. L. 1985. Biological control in theory and practice. *Am. Nat.* 125:344-68
 118. Murray, K. D., Elkinton, J. S. 1989. Environmental contamination of egg masses as a major component of trans-generational transmission of gypsy moth nuclear polyhedrosis virus (LdMNPV). *J. Invertebr. Pathol.* 53:324-34
 119. Myers, J. H. 1988. Can a general hypothesis explain population cycles of forest Lepidoptera? *Adv. Ecol. Res.* 18:179-242
 120. ODell, T. M., Mastro, V. C. 1980. Crepuscular activity of gypsy moth adults. (*Lymantria dispar*). *Environ. Entomol.* 9:613-17
 121. ODell, T. M., Godwin, P. A. 1979. Attack behavior of *Parasetigena sylvestris* in relation to host density and behavior. *Ann. Entomol. Soc. Am.* 72: 281-86
 122. ODell, T. M., Godwin, P. A. 1984. Host selection by *Blepharipa pratensis* (Meigen), a tachinid parasite of the gypsy moth, *Lymantria dispar* L. *J. Chem. Ecol.* 10:311-20
 123. Podgwaite, J. D., Shields, K. S., Zerillo, R. T., Bruen, R. B. 1979. Environmental persistence of the nucleopolyhedrosis virus of the gypsy moth, *Lymantria dispar*. *Environ. Entomol.* 8:528-36
 124. Prell, H. 1915. Zur biologie der tachinen *Parasetigena segregat* Rdi. und *Parizeria rudis* Fall. *Z. Angew. Entomol.* 2:57-148
 125. Raupp, M. J., Werren, J. H., Sadof, C. S. 1988. Effects of short-term phenological changes in leaf suitability on the survivorship, growth and development of gypsy moth (Lepidoptera: Lymantriidae) larvae. *Environ. Entomol.* 17:316-19
 126. Reardon, R. C. 1976. Parasite incidence and ecological relationships in field populations of gypsy moth larvae and pupae. *Environ. Entomol.* 5:981-87
 127. Richerson, J. V., Cameron, E. A.,

- White, D. E., Walsh, M. 1978. Egg parameters as a measure of population quality of the gypsy moth, *Lymantria dispar*. *Ann. Entomol. Soc. Am.* 71:60-64
129. Rollinson, W. D., Lewis, F. B. 1973. Susceptibility of gypsy moth larvae to *Lymantria* spp. nuclear and cytoplasmic polyhedrosis virus. *Zast. Bilja* 24:163-68
130. Rossiter, M. C. 1987. Use of a secondary host by non-outbreak populations of the gypsy moth. *Ecology* 68:857-68
131. Rossiter, M., Schultz, J. C., Baldwin, I. T. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69:267-77
132. Royama, T. 1981. Evaluation of mortality factors in insect life table analysis. *Ecol. Monogr.* 5:495-505
133. Schaefer, P. W., Idebe, K., Higashiura, Y. 1988. Gypsy moth, *Lymantria dispar* (L.), and its natural enemies in the far east (especially Japan). *Del. Agric. Exp. Stn. Bull.* 476. 160 pp.
134. Schaefer, P. W., Kanamitsu, K., Lee, H-P. 1988. Egg parasitism in *Lymantria dispar* (Lepidoptera: Lymantriidae) in Japan and South Korea. *Kontyu, Tokyo* 56:430-44
135. Schultz, J. C., Baldwin, I. T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217:149-50
136. Schultz, J. C., Lechowicz, M. J. 1986. Host plant, larval age and feeding behavior influence midgut pH in the gypsy moth (*Lymantria dispar*). *Oecologia* 71:133-37
137. Semevsky, F. N. 1971. Optimization of caterpillar behavior in the gypsy moth (*Porthetria dispar* L.) in relation to their distribution in the crown. *Zh. Obshch. Biol.* 32:312-16
138. Shapiro, M., Robertson, J. L. 1987. Yield and activity of gypsy moth (Lepidoptera: Lymantriidae) nucleopolyhedrosis virus recovered from survivors of viral challenge. *J. Econ. Entomol.* 80: 901-5
139. Shapiro, M., Robertson, J. L., Injac, M. G., Katagiri, K., Bell, R. A. 1984. Comparative infectivities of gypsy moth (Lepidoptera: Lymantriidae) nucleopolyhedrosis virus isolates from North America, Europe and Asia. *J. Econ. Entomol.* 77:153-56
140. Sheehan, K. A. 1985. Gypsy moths and northeastern forests: modeling a complex biological system. In *Symposium on Systems Analysis in Forest Resources*, ed. P. E. Dress, R. C. Field, pp. 444-54. *Soc. Am. For. Publ. No. SAF 86-03*
141. Sheehan, K. A. 1989. Models for the population dynamics of *Lymantria dispar*. See Ref. 173, pp. 533-47
142. Shimazu, M., Soper, R. S. 1986. Pathogenicity and sporulation of *Entomophaga maimaiga* Humber, Shimazu, Soper and Hajek (Entomophthorales: Entomophthoraceae) on larvae of the gypsy moth *Lymantria dispar* L. (Lepidoptera: Lymantriidae). *Appl. Entomol. Zool.* 21:589-96
143. Sisojevic, P. 1975. Population dynamics of tachinid parasites of the gypsy moth (*Lymantria dispar* L.) during a gradation period (in Serbo Croatian). *Zast. Bilja.* 206:97-170
144. Sisojevic, P. 1979. Interactions in the host-parasite system, with special reference to the gypsy moth tachinids (*Lymantria dispar* L.-Tachinidae). In *Pap. 6th Interbalcanic Plant Protection Conf., Izmir, Turkey*, pp. 108-11. Turkish Minist. Food, Agric., Anim. Husb., Res. Sect. 13
145. Skaller, P. M. 1985. Patterns in the distribution of gypsy moth (*Lymantria dispar*) (Lepidoptera: Lymantriidae) egg masses over an 11-year population cycle. *Environ. Entomol.* 14:106-17
146. Skatulla, V. U. 1987. On the susceptibility of *Lymantria dispar* larvae of different geographical regions to an NPV-virus. *Anz. Schadlingskd. Pflanz. Umweltschutz* 60:15-18
147. Smith, H. R. 1989. Predation: its influence on population dynamics and adaptive changes in morphology and behavior of the Lymantriidae. See Ref. 173, pp. 469-88
148. Smith, H. R., Lautenschlager, R. A. 1978. Predators of the gypsy moth. *USDA Agric. Handb.* 534. 72 pp.
149. Soper, R. S., Shimazu, M., Humber, R. A., Ramos, M. E., Hajek, A. E. 1988. Isolation and characterization of *Entomophaga maimaiga* sp. nov., a fungal pathogen of gypsy moth, *Lymantria dispar*, from Japan. *J. Invert. Pathol.* 51:229-41
150. Southwood, T. R. E. 1978. *Ecological methods with particular reference to the study of insect populations*. London/New York: Chapman & Hall. 524 pp. 2nd ed.
151. Southwood, T. R. E., Jepson, W. F. 1962. Studies on the populations of *Oscinella frit* L. (Diptera: Chloropidae) in the oat crop. *J. Anim. Ecol.* 31:481-95
152. Southwood, T. R. E., Coffins, H. N.

1976. A synoptic population model. *J. Anim. Ecol.* 45:949-65
153. Steinhaus, E. A. 1958. Crowding as a possible factor in insect disease. *Ecology* 39:503-14
154. Talerico, R. L., Montgomery, M., eds. 1983. Proceedings forest defoliator—host interactions: a comparison between gypsy moth and spruce budworms. *USDA For. Serv. Gen. Tech. Rep. NE-85*. 141 pp.
155. Tallamy, D. W. 1983. Equilibrium biogeography and its application to insect host-parasite systems. *Am. Nat.* 121:244-54
156. Tauber, M. J., Tauber, C. A. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annu. Rev. Entomol.* 21:81-107
157. Taylor, R. A. J., Reling, D. 1986. Density/height profile and long-range dispersal of first instar gypsy moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 15:431-35
158. Ticehurst, M., Yendol, W. G. 1989. Distribution and abundance of early instar gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae) in forests during day and night. *Environ. Entomol.* 18:459-464
159. Ticehurst, M., Fusco, R. A., Kling, R. P., Unger, J. 1978. Observations on parasites of gypsy moth in first cycle infestations in Pennsylvania from 1974-1977. *Environ. Entomol.* 7:355-58
160. Tigner, T. C. 1974. Gypsy moth parasitism in New York State: A manual for field personnel. *Appl. For. Res. Inst. Rep.* 20. 34 pp.
161. Valentine, H. T. 1981. A model of oak forest growth under gypsy moth influence. See Ref. 50, pp. 50-61
162. Valentine, H. T. 1983. Budbreak and leaf growth functions for modeling herbivory in some gypsy moth hosts. *For. Sci.* 29:607-17
163. Valentine, H. T. 1983. The influence of herbivory on the net rate of increase of gypsy moth abundance: a modeling analysis. See Ref. 154, pp. 105-11
164. Valentine, H. T., Houston, D. R. 1979. A discriminant function for identifying mixed-oak stand susceptibility to gypsy moth defoliation. *For. Sci.* 25:468-74
165. Valentine, H. T., Wallner, W. E., Wargo, P. M. 1983. Nutritional changes in host foliage during and after defoliation, and their relation to the weight of gypsy moth pupae. *Oecologia* 57:298-302
166. Van Driesche, R. G. 1983. The meaning of "percent parasitism" in studies of insect parasitoids. *Environ. Entomol.* 12: 1611-22
167. Varley, G. C., Gradwell, G. R. 1960. Key factors in population studies. *J. Anim. Ecol.* 29:399-401
168. Vasiljevic, L., Injac, M. 1973. A study of gypsy moth viruses originating from different geographical regions. *Zast. Bilja* 24:169-86
- 168a. Waggoner, P. E. 1984. The hatching of gypsy moth eggs, a phenological model. *Agric. For. Meteorol.* 33:53-65
169. Wallis, R. C. 1957. Incidence of polyhedrosis of gypsy moth larvae and the influence of relative humidity. *J. Econ. Entomol.* 50:580-83
170. Wallner, W. E. 1983. Gypsy moth host interactions: a concept of room and board. See Ref. 154, pp. 5-8
171. Wallner, W. E. 1986. Susceptible forest sites: their perceived role in gypsy moth population dynamics. In *Proc. 1986 Natl. Gypsy Moth Rev.*, pp. 175-78.
172. Wallner, W. E. 1987. Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annu. Rev. Entomol.* 32:317-40
173. Wallner, W. E., ed. 1989. The Lymantriidae: a comparison of features of new and old world tussock moths. *USDA For. Serv. Gen. Tech. Rep. NE-123*. 554 pp.
174. Wallner, W. E., Walton, G. S. 1979. Host defoliation: a possible determinant of gypsy moth population quality. *Ann. Entomol. Soc. Am.* 72:62-67
175. Wallner, W. E., Zarnack, S., Devito, A. 1989. Regression estimators for late-instar gypsy moth larvae at low population density. *For. Sci.* 35:789-800
176. Watt, K. E. F. 1968. *Ecology and Resource Management*. New York: McGraw-Hill. 450 pp.
177. Weseloh, R. M. 1974. Host-related microhabitat preferences of the gypsy moth larval parasitoid *Parasetigena agilis*. *Environ. Entomol.* 3:363-64
178. Weseloh, R. M. 1976. Reduced effectiveness of the gypsy moth parasite, *Apanteles melanoscelus* in Connecticut due to poor seasonal synchronization with its host. *Environ. Entomol.* 5:743-46
179. Weseloh, R. M. 1976. Diel periodicity and host selection as measured by ovipositional behavior of the gypsy moth parasite *Parasetigena silvestris* in Connecticut woodlands. *Environ. Entomol.* 5:514-16
180. Weseloh, R. M. 1983. Population sam-

- pling method for cocoons of the gypsy moth (Lepidoptera: Lymantriidae) parasite, *Apanteles melanoscela* (Hymenoptera: Braconidae), and relationship of its population levels to predator- and hyperparasite-induced mortality. *Environ. Entomol.* 12:1228-31
181. Weseloh, R. M. 1985. Changes in population size, dispersal behavior, and reproduction of *Calosoma sycophanta* (Coleoptera: Carabidae), associated with changes in gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), abundance. *Environ. Entomol.* 14:370-77
182. Weseloh, R. M. 1985. Predation by *Calosoma sycophanta* (Coleoptera: Carabidae): evidence for a large impact on gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), pupae. *Can. Entomol.* 117:1117-26
183. Weseloh, R. M. 1985. Dispersal, survival and population abundance of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), larvae determined by releases and mark-recapture studies. *Ann. Entomol. Soc. Am.* 78:728-35
184. Weseloh, R. M. 1987. Dispersal and survival of gypsy moth larvae. *Can. J. Zool.* 65:1720-23
185. Weseloh, R. M. 1987. Accuracy of gypsy moth (Lepidoptera: Lymantriidae) population estimates based on counts of larvae in artificial resting sites. *Ann. Entomol. Soc. Am.* 80:361-66
186. Weseloh, R. M. 1988. Effects of microhabitat, time of day and weather on predation of gypsy moth larvae. *Oecologia* 77:250-54
187. Weseloh, R. M., Andreadis, T. G. 1982. Possible mechanism for synergism between *Bacillus thuringiensis* and the gypsy moth (Lepidoptera: Lymantriidae) parasitoid, *Apanteles melanoscelus* (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Am.* 75:435-38
188. Weseloh, R. M., Andreadis, T. G. 1986. Laboratory assessment of forest microhabitat substrates as sources of the gypsy moth nuclear polyhedrosis virus. *J. Invertebr. Pathol.* 48:27-33
189. Whelan, C. J., Holmes, R. T., Smith, H. R. 1989. Bird predation on gypsy moth (Lepidoptera: Lymantriidae) larvae: an aviary study. *Environ. Entomol.* 18:43-45
190. Wilson, R. W. Jr., Fontaine, G. A. 1978. Gypsy moth egg mass sampling with fixed-and-variable-radius plots. *USDA Agric. Handb.* 523. 46 pp.
191. Wilson, R. W., Ivanowsky, S. M., Talerico, R. L. 1981. Direct evaluation. See Ref. 50, pp. 34-38
192. Woods, S. A., Elkinton, J. S. 1987. Bimodal patterns of mortality from nuclear polyhedrosis virus in gypsy moth (*Lymantria dispar*) populations. *J. Invertebr. Pathol.* 50:151-57
193. Woods, S. A., Elkinton, J. S., Podgwaite, J. D. 1989. Acquisition of nuclear polyhedrosis virus from tree stems by newly emerged gypsy moth (Lepidoptera: Lymantriidae) larvae. *Environ. Entomol.* 18:298-301
194. Yadava, R. L. 1971. On the chemical stressors of nuclear-polyhedrosis virus of gypsy moth, *Lymantria dispar* L. *Z. Angew. Entomol.* 69:303-11
195. Zelinskaya, L. M. 1980. Role of microsporidia in the abundance dynamics of the gypsy moth, *Porthetria dispar*, in forest plantings along the lower Dnieper river (Ukrainian Republic, USSR) *Vestn. Zool.* 1:57-62
196. Zlotin, A. Z., Tremli', A. G. 1964. Development of the gypsy moth (*Ocneria dispar*) under laboratory conditions. *Zool. Zh.* 43:287-90