SPECIAL FEATURE: REVIEW

Andrew Liebhold · Joseph Elkinton · David Williams
Rose-Marie Muzika

What causes outbreaks of the gypsy moth in North America?

Abstract The gypsy moth has been present in North America for more than 100 years, and in many of the areas where it has become established outbreaks occur with varying degrees of periodicity. There also exists extensive spatial synchrony in the onset of outbreaks over large geographic regions. Density-dependent mortality clearly limits high-density populations, but there is little evidence for strong regulation of low-density populations. Predation by small mammals appears to be the major source of mortality affecting low-density populations, but because these are generalist predators and gypsy moths are a less preferred food item, mammals do not appear to regulate populations in a density-dependent fashion. Instead, predation levels appear to be primarily determined by small mammal abundance, which is in turn closely linked to the production of acorns that are a major source of food for overwintering predator populations. Mast production by host oak trees is typically variable among years, but considerable spatial synchrony in masting exists over large geographic areas. Thus, it appears that the temporal and spatial patterns of mast production may be responsible for the episodic and spatially synchronous behavior of gypsy moth outbreaks in North America. This multitrophic relationship among mast, predators, and gypsy moths represents a very different explanation of forest insect outbreak dynamics than the more widely applied theories based upon predator–prey cycles or feedbacks with host foliage quality.

Key words Lepidoptera · Lymantriidae · Lymantria dispar · Predation · Synchrony · Outbreak

Introduction

The gypsy moth, *Lymantria dispar* (L.), is known to feed on the foliage of several hundred different tree species, and its native range includes most of Europe and Asia. Its most common hosts are *Quercus, Populus*, and *Larix* species. In 1869, the species was accidentally introduced to North America, and it has been slowly expanding its range; currently this insect occupies about one-fourth of its potential range in North America.

The dynamics of gypsy moth populations has been the focus of considerable research in North America, Europe, and Asia, and several reviews of this work currently exist (Leonard 1974; Montgomery and Wallner 1988; Elkinton and Liebhold 1990). Despite this enormous research effort, there remain many unanswered questions about the nature of processes causing yearly fluctuations in gypsy moth abundance. This paper focuses on recent revelations about the mechanisms behind the dynamics of North American gypsy moth populations. Initially, we focus on the patterns of gypsy moth abundance through time and space. The remainder of the article addresses the processes responsible for these patterns.

Temporal patterns

The gypsy moth is an example of an eruptive species in North America. Population densities vary by several orders of magnitude, often reaching epidemic densities that have spectacular effects (i.e., total defoliation of host trees). It is not uncommon for gypsy moth populations to persist for

A. Liebhold
Northeastern Research Station, USDA Forest Service, 180 Canfield St., Morgantown, WV 26505 USA
Tel. +1-304-285-1512; Fax +1-304-285-1505
e-mail: aliebhold@fs.fed.us

J. Elkinton
Department of Entomology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, MA, USA

D. Williams
Northeastern Research Station, USDA Forest Service, PA, USA

R.-M. Muzika
Department of Forestry, University of Missouri, MO, USA

Fig. 1. Historical records of area defoliated by the gypsy moth in five New England states: Maine, Vermont, New Hampshire, Massachusetts, and Rhode Island (1924–1996)
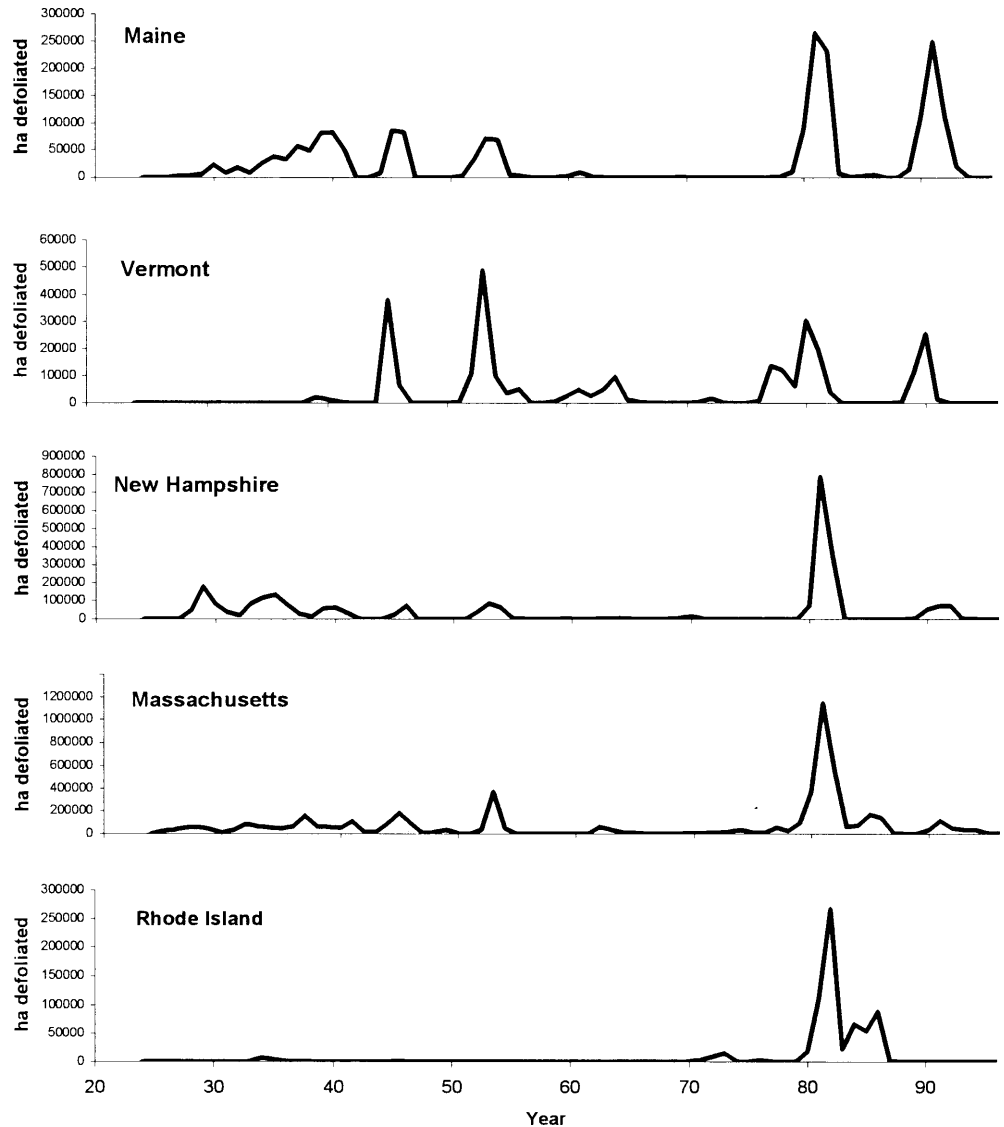
many years at densities so low that it is difficult to detect any life stages. Population densities occasionally increase quickly over several generations, often to defoliating levels >5000 egg masses/ha. Fig. 1 shows the temporal patterns of area defoliated by the gypsy moth in five states in the northeastern United States.

The timing of outbreaks is irregular and difficult to predict, although there is some statistical evidence of a 10- to 11-year cycle in outbreak dynamics. Miller et al. (1989) and Williams and Liebhold (1995a,b) examined autocorrelation functions (ACFs) derived from the data shown in Fig. 1 and interpreted some of them to be indicative of a quasi-periodic behavior (Fig. 2A). The autocorrelation statistic, ρ, quantifies the correlation between values at one point in time with values of the same variable at a lag time unit in the past. The ACF is the set of autocorrelations for a spectrum of increasing time lag values. Damped oscillating patterns in the ACF, as seen in the New Hampshire ACF (Fig. 2A), are characteristic of periodic behavior (Royama 1992).

Williams and Liebhold (1995a,b) observed less evidence of periodicity in data from other regions.

Inference of population processes from time series

Population cycles are a common phenomenon in many species of foliage-feeding insects (Varley et al. 1973; Myers 1988; Berryman 1995). Many explanations have been offered to explain these cycles. A few authors have suggested that they are in some manner caused by cyclic abiotic factors affecting survival and reproduction (Wellington 1954), but most authors argue that they are the result of biotic interactions. Some have suggested that cycles are the result of fluxes in the population genetics and their effects on population quality (Chitty 1967) or the negative effect of population density on maternally transferred traits (Ginzburg and Taneyhill 1994), but most studies have
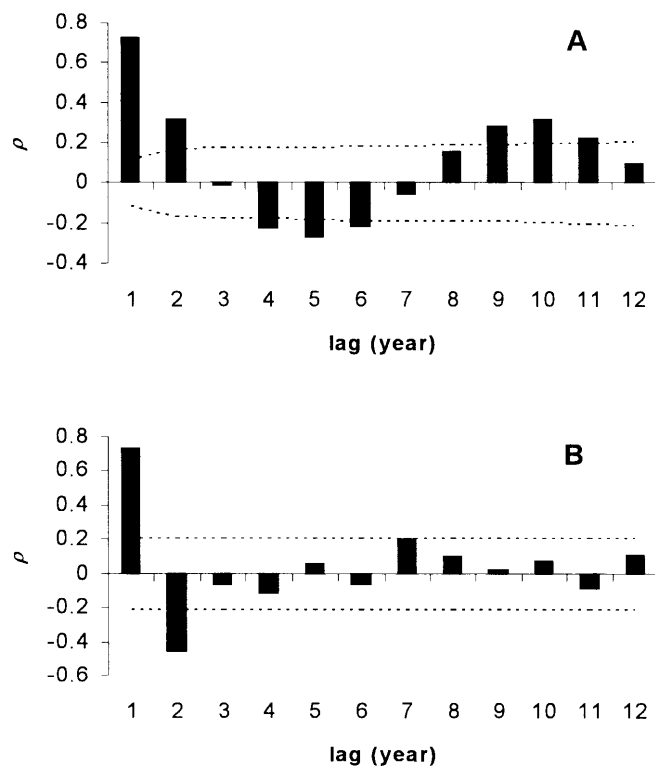
Fig. 2. Time-series statistics for yearly defoliation area from New Hampshire (1924–1996) shown in Fig. 1. **A** Autocorrelation function (ACF). **B** Partial autocorrelation function (PACF)

highlighted the importance of density-dependent mortality caused by parasitoids, specialist predators, and pathogens in generating cycles (Varley et al. 1973; Anderson and May 1981; Myers 1988; Berryman 1995).

Considerable work has focused on the role of natural enemies in the dynamics of gypsy moth populations in North America (Elkinton and Liebhold 1990). It is clear from this work that the most important biotic agents at high population densities are very different from the agents that are important at low densities. At high population densities, the largest and most important source of mortality is a nuclear polyhedrosis virus. This virus operates in a strongly density-dependent fashion and is often the cause of collapse of populations at high densities. At low population densities, predation by small mammals on late-instar larvae and pupae is generally the largest source of mortality. A lesser amount of mortality in low-density populations is also caused by larval and pupal parasitoids (Williams et al. 1992). However, the precise role of these agents in the long-term dynamics of populations is not clear.

What, if anything, can be inferred about the most important processes affecting gypsy moth dynamics by examining the long-term patterns seen in Fig. 2? Williams and Liebhold (1995a,b) examined the partial autocorrelation functions (PACF) from these historical defoliation time series and found that several of these PACFs exhibited a significant inverse correlation at a time lag of 2 years (Fig. 2B). The PACF is functionally similar to the ACF except that autocorrelation in previous lag units are removed when

calculating the PACF for a specific lag time unit. The PACF may be diagnostic of the process generating patterns of abundance (Royama 1992). Turchin (1990) and Berryman (1994) analyzed time series of the abundance of several forest insect species and found that PACFs of many of the series contained a strong negative "spike" at lag(2). They concluded that this type of PACF is indicative of delayed density-dependent mortality, typically caused by a specialist natural enemy (e.g., a parasitoid) whose reproduction is tightly controlled by host abundance.

The data shown in Fig. 2 are of limited value in deducing the ultimate causes of outbreaks because they are only representative of defoliation dynamics, rather than actual population abundance. Unfortunately, there are few long-term data on actual gypsy moth abundance in North America. The largest set of historical data on gypsy moth abundance was collected during the "Melrose Highlands" study from 1910 to 1930. Those data consist of yearly counts of all egg masses in 264 circular (0.07-ha) plots located through much of New England (Campbell 1967; Liebhold 1992). As seen in Fig. 3B, average densities were very high from 1910 to 1921, but populations declined and then partially rebounded in the late 1920s. Campbell and Sloan (1977) interpreted this trend to be indicative of a pattern of dual equilibrium dynamics. According to this concept, which has been widely applied to the dynamics of many insects (Southwood and Comins 1976), two stable equilibria exist at both low and high densities. Populations are regulated about one equilibrium by density-dependent processes unless an extreme event forces populations into the domain of attraction of the other equilibrium. Liebhold (1992) further explored the Melrose data and found that when yearly counts were averaged over the entire area sampled in the Melrose study (spanning about 300 km), the frequency distribution of average density was bimodal and indicative of a dual equilibrium. However, the distribution of counts in individual plots was not bimodal and therefore was not indicative of a dual equilibrium (Fig. 3C). Thus, the appearance of dual equilibrium dynamics was a property emergent only at a large spatial scale.

Berryman (1991, 1999) also examined yearly averages of all Melrose plots and found, at low population densities, that change in population density $R = N_{t+1}/N_t$ was inversely related to lag population density, N_{t-1} (Fig. 3D). Berryman interpreted this result as an indication that delayed density-dependent mortality caused by parasitoids was regulating populations. However, Liebhold and Elkinton (1991) examined the same data and found that in individual plots there was no evidence for a lag correlation in change in population change (Fig. 3D). Thus, the apparent delayed density dependence also was an emergent property of averaging values over a large geographic region and did not appear to be present in the dynamics of individual locations.

The role of parasitoids

What is the evidence to support the claim that parasitoids are regulating gypsy moth populations? In addition to the
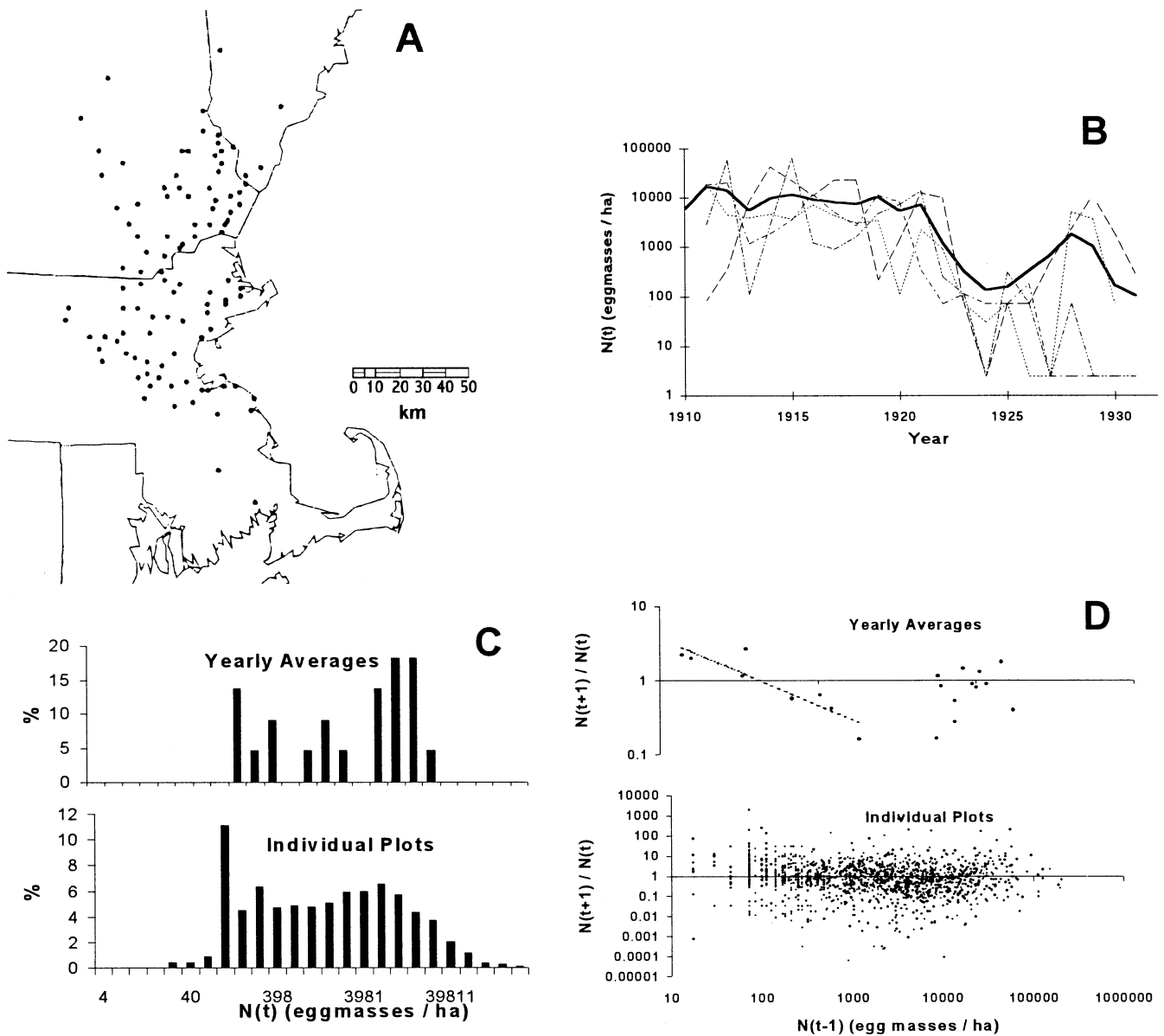
Fig. 3. Melrose Highlands gypsy moth data. **A** Plot locations in northeastern United States. **B** Yearly estimates of gypsy moth eggmass densities 1910–1932. *Heavy, solid line* is mean (of all plots); *light lines* are densities at four arbitrarily selected plots. **C** Histograms showing the frequency distribution of counts per plot. The bottom histogram is the frequency distribution of counts in individual plots in each year. The top histogram is the frequency distribution of averages of all plots in each year. **D** Scatter plots of $r_t = N_{t+1}/N_t$ versus N_{t-1}, where N_t is counts of egg masses in individual plots in year t on the *bottom graph* and in the *upper graph* N_t is the average of all plots in year t. The *broken line* shown in the graph of averages is the regression of $\log(r)$ on $\log(N_{t-1})$ for $N_{t-1} < 1000$ egg masses/ha.

appearance of delayed density dependence (Fig. 3D), Berryman (1991) cited manipulation studies in which increased rates of parasitism by several dipterous and hymenopterous parasitoids were detected following artificial elevation of host gypsy moth populations (Liebhold and Elkinton 1989a; Gould et al. 1990). Berryman (1991) cited this response as evidence that parasitoids were operating in a density. dependent fashion and thus capable of regulating populations. However, there are several problems with this interpretation. First, the spatial gradients in gypsy moth densities created by Gould (1990) and Liebhold and Elkinton (1989a) greatly exceeded any natural spatial variation in densities. Within naturally occurring populations,

density gradients are subtler and there is no evidence for positive spatially density-dependent mortality (Liebhold and Elkinton 1989b). The spatial density dependence observed in these studies thus may have been an artifact of extreme density gradients. Second, even if naturally occurring mortality of gypsy moth populations caused by parasitoids were spatially density dependent, this does not translate into temporal density dependence or population regulation (Hassell 1989). Third, rates of parasitism in North American gypsy moth populations are generally low compared to those of similar defoliator species (Elkinton and Liebhold 1990). Although there are a limited number of studies in which parasitism and host density have been

measured over several generations, results to date indicate a mixture of both inverse and positive density dependence in parasitism (Reardon 1976; Williams et al. 1992). Thus, there is not definitive evidence of density-dependent regulation of the gypsy moth by parasitoids.

What then is the cause of the apparent delayed density-dependent mortality that is only evident at large spatial scales (Fig. 3D)? Royama (1992) and Williams and Liebhold (1995b) demonstrated that there are problems with the analytical methods proposed by Turchin (1990) and applied by Berryman (1991) to detect delayed density dependence and infer the importance of a reproductively linked mortality such as a specialist parasitoid in the dynamics of gypsy moth populations. They showed that any autocorrelation in an exogenous mortality factor can create the same inverse lag correlations that are used to diagnose delayed density dependence in these tests. It is conceivable that an exogenous factor such as weather may have a temporally autocorrelated effect on populations and may thus be the cause of these patterns. However, most weather variables are at best weakly autocorrelated among successive years (Burroughs 1992). Alternatively, it is possible that a generalist predator or parasite could exhibit first-order density-dependent growth in its own populations and that this would result in autocorrelated mortality in host populations. The autocorrelated mortality caused by a generalist predator could explain the appearance of delayed density dependence detected by Berryman (1991) and evident in Fig. 3D.

The role of predators

The fact that small mammals are generalist predators and that they cause a large amount of mortality in low-density gypsy moth populations makes them good candidates to explain the apparent delayed density dependence in populations. Predation has been recognized as the major cause of mortality in low-density gypsy moth populations (Bess et al. 1947; Campbell 1975). Furthermore, there is good evidence that most of this predation is caused by small mammals (Bess et al. 1947; Campbell et al. 1977; Weseloh 1988, 1990; Smith 1989; Elkinton et al. 1989, 1996; Grushecky et al. 1998). Most animal populations exhibit first-order autocorrelation in abundance because of their reproductive inertia, and small mammals are no exception (Lewellen and Vessey 1998).

Predation plays an important role in gypsy moth dynamics, not only because it is a large source of mortality but also because it explains a large amount of the variation in yearly changes in gypsy moth abundance. Analysis of partial life tables for low-density gypsy moth populations indicated that predation was negatively correlated with changes in gypsy moth abundance (Campbell 1976; Campbell and Sloan 1977). More recent studies indicated a strong inverse correlation between changes in densities of natural gypsy moth populations and predation on tethered gypsy moth pupae (Elkinton et al. 1989, 1996; Grushecky et al. 1998).

Measurement of predation on tethered pupae may provide a biased estimate of absolute predation levels, but it can be used effectively to compare predation levels among locations and years (Smith 1985, 1989). These studies also indicate that predation on tethered pupae is highly correlated to densities of small mammal populations. This hypothesis was experimentally tested by Elkinton (unpublished data), who supplemented the overwintering food supply of small mammals and observed increased levels of predation in the spring as a result of increased predator abundance. Similarly, Jones et al. (1998) artificially decreased small mammal populations using traps and observed a decrease in rates of predation on gypsy moth pupae and an increase in gypsy moth populations.

Do small mammals regulate gypsy moth populations? The term regulation implies some form of negative feedback or positive density dependence that acts to stabilize populations (Turchin 1995). Campbell (1975) argued that predation by small mammals on gypsy moth populations was density dependent and therefore responsible for regulation of low-density populations. Although there is considerable evidence of density-dependent predation by small mammals on other forest insects (Holling 1965), Campbell's evidence for density dependence was weak. Elkinton et al. (1989) studied low-density populations and found no evidence for positive density dependence. They suggested that, even though small mammals cause high levels of mortality in low-density gypsy moth populations, they are not responsible for regulation. More recently, Elkinton et al. (1996) confirmed that variation in rates of predation by small mammals was a major determinant of intergenerational changes in the density of low-density populations. However, predation rate was mostly determined by variation in predator densities, not gypsy moth densities.

The apparent lack of positive density dependence in predation on the gypsy moth is in stark contrast with several classical studies of the functional response of vertebrate predators to prey densities. Because generalist predators by definition have many hosts, the numerical response of predators to populations of individual prey species may be limited or nonexistent (Hanski 1990). Therefore, if generalist predators regulate prey populations, this must occur via the functional response to prey density (Holling 1965). Indeed, it was Holling's (1959) classic work with small mammal predation on European pine sawflies that inspired his differentiation among types of functional responses. He recognized that for some predator–prey systems the proportion of prey consumed declined continuously with prey density; he referred to this as a type II functional response. In other systems, the proportion of prey consumed increased with host densities up to a maximum level and then declined again at higher densities. This type of response, termed a type III functional response, has been recognized as capable of regulating prey populations via negative feedback (Holling 1965; Murdoch and Oaten 1975; Hassell 1978).

It is relatively easy to manipulate the densities of gypsy moth pupae by deploying laboratory-reared individuals over a range of densities. Using this approach, studies indi-

cate that predation by small mammals on gypsy moths is characteristic of a type II functional response in which the proportion of the population killed declines through the entire range of densities (Elkinton et al. 1989, 1996). A likely explanation of this type II response of mammals to gypsy moths but a type III response to other species is that gypsy moth pupae and larvae are of low palatability to predators compared with other prey items (Liebhold, unpublished data). Holling (1965) reported that the functional response of predation to prey density can be modified both by the palatability of the prey item relative to alternative items and by the abundance of alternative items. This modification means that, for gypsy moth populations, predation is generally inversely density dependent and therefore does not stabilize abundance. Furthermore, Smith and Lautenschlager (1981) found that when a highly preferred alternate prey was abundant, predation on gypsy moth populations was greatly diminished.

The role of mast

Because predation appears to be a major determinant of yearly fluctuations in gypsy moth abundance, it is important to understand what factors affect variation in predation rates among years. As stated earlier, it is likely that predation rates can be affected by the abundance of alternative prey items that are present during the same portion of the season as gypsy moth larvae and pupae (e.g., other foliage-feeding insects, berries) (Smith and Lautenschlager 1981). However, it is also clear that predation levels are strongly related to small mammal abundance and thus year-to-year variation in predator abundance is a major determinant of changes in gypsy moth densities (Elkinton et al. 1989, 1996). The dynamics of small mammal populations, most notably *Peromyscus* spp., have been the object of considerable study over many years (King 1968; Stenseth 1985; Kaufman et al. 1995). Several of these studies (Wolff 1996) indicate that survival of overwintering mammal populations is critical in determining yearly trends in abundance and that overwintering survival is closely tied to the abundance of food such as mast. Elkinton et al. (1996) measured mast abundance, small mammal abundance, predation levels, and gypsy moth densities at eight sites over 5 years and found a strong relationship between mast abundance and change in mouse densities, which were in turn inversely correlated with change in gypsy moth abundance. Jones et al. (1998) confirmed this relationship by experimentally elevating overwintering mast abundance and observing increases in small mammal densities.

Most of the forests where gypsy moth outbreaks occur in North America are dominated by oaks. In these stands, acorns are thus the major source of mast to sustain overwintering small mammal populations. Mast production is affected by physiological factors that cause cyclic patterns of acorn production and by abiotic (weather) factors that cause deviations from the cycles (Sork et al. 1993). The period of an acorn production cycle varies from 2 to 4 years
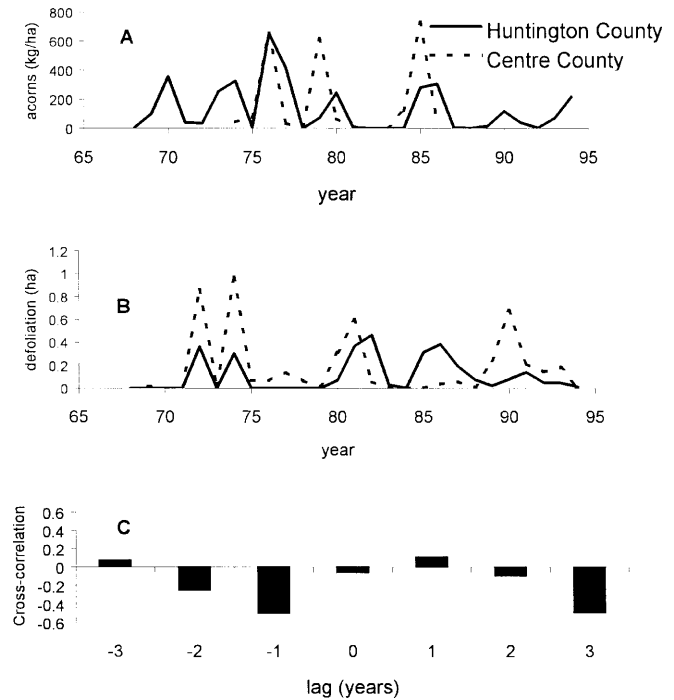

Fig. 4. Temporal patterns of acorn fall and gypsy moth dynamics in two counties in Pennsylvania (USA). **A** Measurements of acorn fall (all oak species) in Centre County (from Drake 1995) and Huntington County (Cogan 1995), Pennsylvania. **B** Historical records of defoliation in Centre and Huntington Counties (*right axis*) and total defoliation over all of Pennsylvania (*left axis*). **C** Cross-correlogram of defoliation and acorn fall in Huntington County

among different oak species. In mixed-oak stands, mast "failures" occur for all species in some years, and it is likely that in those years small mammal populations would be greatly diminished. Elkinton et al. (1996) and Jones et al. (1998) hypothesized that in years of general mast failure gypsy moth populations may be released from low densities and outbreaks may ensue (Fig. 4). There is considerable variation among stands in the relative dominance of different oak species. For this reason, specific years of mast failure may vary considerably among stands. Whether this explains part of the variation in gypsy moth dynamics that is seen among nearby stands remains to be determined.

Elkinton et al. (1996) is the only study to date in which naturally occurring mast, mouse, and gypsy moth densities have been recorded simultaneously, but even that study is limited by the inclusion of only 5 years of mast data. Data collected over such a short interval are clearly not representative of mast dynamics over an entire gypsy moth outbreak cycle. We present, in Fig. 4, a longer set of data representing records of mast abundance (Fig. 4A) and gypsy moth defoliation (Fig. 4B) recorded as part of separate state forest and game management programs. Acorn fall was recorded annually at two separate plots in Centre and Huntington Counties, located in central Pennsylvania (USA) (Drake 1997; Cogan 1995). Defoliation records were derived from historical aerial sketch map data, and annual proportions of each county defoliated were extracted using a geographic information system (Liebhold et al. 1994).

There appeared to be considerable synchrony between the Huntington and Centre County sites in both acorn production and defoliation (Fig. 4A,B) even though they were separated by about 50 km. Defoliation data (Fig. 4B) indicate the occurrence of major outbreaks in the two counties in the years 1972–1974, 1981–1982, 1985–1986, and 1990. In most cases, these outbreaks were preceded by general mast failures occurring in 1968, 1978, 1982–1983, and 1987–1988. There were some exceptions to this association (e.g., mast failure in Huntington Co. in 1975 did not result in a gypsy moth outbreak). A cross-correlogram between defoliation and acorn fall in Huntington Co. (Fig. 4C) indicated a negative association between acorn fall and gypsy moth defoliation at time lags of −1 and +3 years. We hypothesize that the lag +3 inverse correlation is caused by the lagged effect of acorn failures that caused a decline in predator populations, resulting in increased gypsy moth growth and abundance. The 3-year lag would result from the time required for population growth from low densities to outbreak levels. The lag −1 inverse correlation may reflect the negative effect of defoliation on acorn production (Gottschalk 1990). We are aware that serial dependence in these data results in a lack of statistical independence among samples (Buonacorsi et al. 2000), and therefore we did not attempt a rigorous statistical test of cross-correlation between acorn abundance and gypsy moth outbreaks. Nevertheless, these results indicate that acorn failure may precede gypsy moth outbreaks by 2–4 years and thus support the theory that acorn failure is causally linked with the onset of gypsy moth outbreaks.

Outbreak synchrony

Deviations from average weather conditions tend to extend over considerable distances, and these deviations have been hypothesized to cause large-scale synchrony in mast cycles over large geographic regions (Sork et al. 1993; Kelly 1994; Crawley and Long 1995; Koenig and Knops 1998). Any spatial synchrony in mast failures would likely create large-scale synchrony in small mammal abundance, although the evidence for synchrony in small mammal populations is minimal (Krohne 1997).

Superficial examination of defoliation totals in Fig. 1 suggests the existence of outbreak synchrony in disjunct gypsy moth populations. Williams and Liebhold (1995a) examined these time series and identified significant spatial synchrony among all populations. The existence of spatial synchrony over large geographic regions is a common feature of many animal populations ranging from butterflies to sheep (Ranta et al. 1995; Grenfell et al. 1998; Hudson and Cattadori 1999). Two principal mechanisms have been proposed to explain spatial synchrony in animal abundance: dispersal and regional stochasticity. Under both hypotheses the assumption is made that some endogenous process (e.g., density-dependent mortality caused by a predator, parasite, or pathogen) dominates the dynamics of the species and results in population cycles, limit cycles, or some other

nonlinear behavior. Under the dispersal hypothesis, it can be shown using theoretical models that a relatively small amount of dispersal among disjunct populations will serve to synchronize the timing of outbreaks (Barbour 1990). The regional stochasticity hypothesis is also referred to as the "Moran effect" because it was originally proposed by Moran (1953) to explain synchronous fluctuations of Canadian lynx populations. Under this hypothesis, some exogenous factor (most likely a weather condition that affects reproduction or survival) acts synchronously over a large geographic area. Moran (1953) showed that even if the effect is relatively minor it may quickly bring population fluctuations in disjunct areas into synchrony (Moran 1953; Royama 1992; Ranta et al. 1997; Myers 1998).

Williams and Liebhold (1995a) pointed out that North American gypsy moth populations lack a long-distance dispersal mechanism (females are flightless) and thus the observed synchrony is most likely caused by the Moran effect. They found that certain synchronous weather patterns were correlated with deviations from autoregressive (endogenous) models fit to the series, and thus weather may explain the observed synchrony in disjunct gypsy moth populations. However, Williams and Liebhold (1995a) did not identify what mechanism(s) were involved by which the synchronous weather deviations might affect gypsy moth survival or reproduction. We propose here that a likely mechanism by which weather synchronizes gypsy moth populations is via effects on acorn crop oscillations. Acorn dynamics is driven by endogenous physiologically based processes that generate cycles (Sork et al. 1993; Kelly 1994). These cycles tend to be highly synchronized over large regions (Crawley and Long 1995; Koenig and Knops 1998). This synchrony is most likely a result of the Moran effect because masting can be influenced by weather. The interval between large mast years varies among different oak species. For example, Olson (1974) listed a 4- to 10-year interval between mast crops for white oak, *Quercus alba*, but a 3- to 5-year interval for red oak, *Q. rubra*. Total mast failures would result when low mast years "line up" for all species present in a stand. Spatial synchrony in masting observed within each species would thus result in spatially synchronous total acorn failure over large regions; this would likely cause synchronous declines in small mammal populations and synchronous release of gypsy moth populations from low densities to outbreak levels (Fig. 5). It is likely that the Moran effect may also synchronize gypsy moth populations via direct effects of weather on gypsy moth survival. For example, cold winter temperatures can kill eggs (Smitley et al. 1998), or cool spring temperatures can result in poor synchrony between larval populations and host plant development (Hunter and Elkinton 2000).

Conclusions

Our new knowledge of gypsy moth dynamics suggests that organisms at different trophic levels interact in more complex ways than previously conceived. Early concepts of the
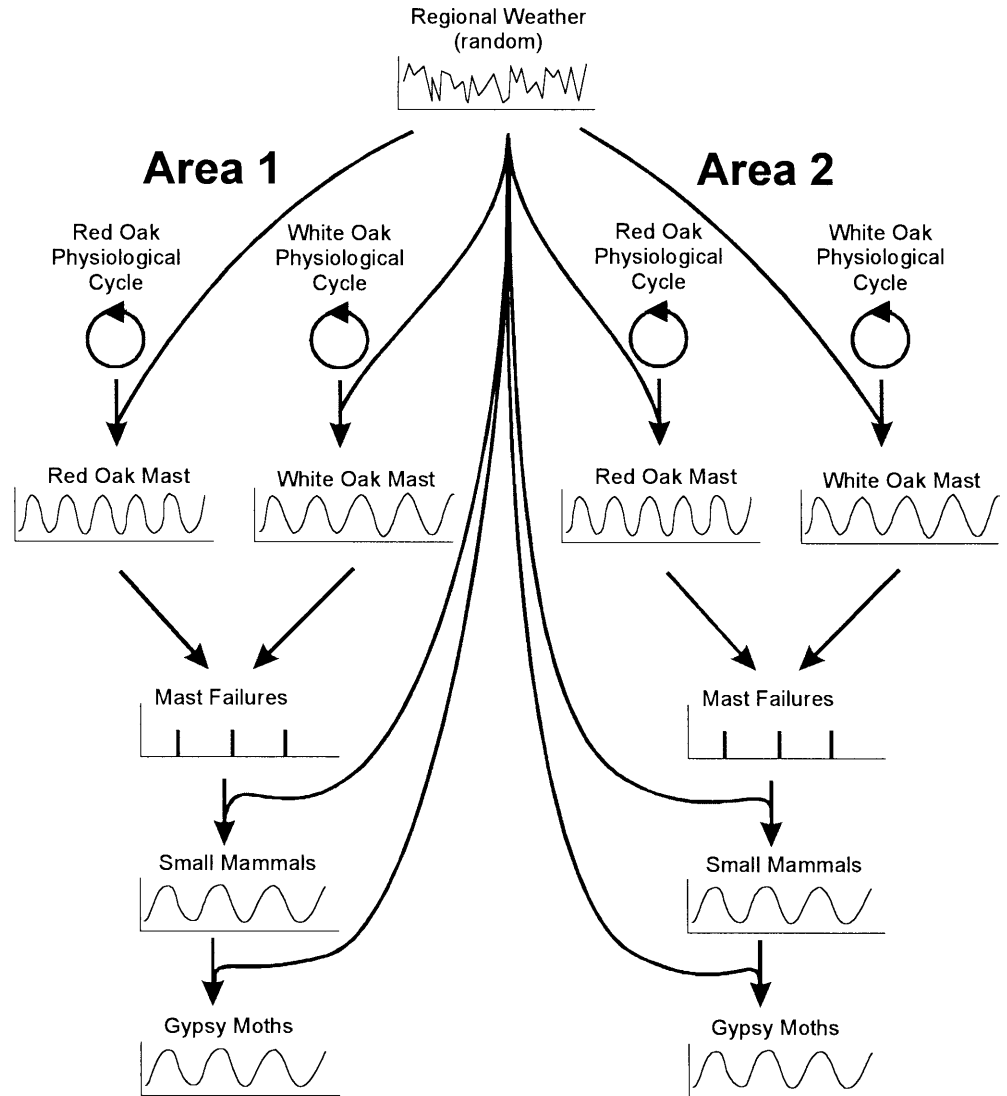
regulation of insect populations focused on mechanisms by which density-dependent mortality regulated populations about equilibrium levels (Varley et al. 1973). Although it is clear that density-dependent regulation of gypsy moth populations may occur at high densities, any density-dependent regulation at low densities by higher or lower trophic levels is weak. Predators and parasitoids may affect populations, but they do not appear to be linked in a strong negative feedback mechanism with their hosts. Thus, it does not appear that the periodicity in gypsy moth outbreaks in Fig. 1 is the result of density-dependent regulation. It is more likely that oscillations in mast production are at least partially responsible for the episodic nature of gypsy moth outbreaks (see Fig. 4). Further evaluation of this hypothesis will only be possible after more data are collected over several regional outbreak cycles.

Considerable work in the past has also focused on "bottom-up" effects on gypsy moth dynamics, and this work has suggested that induced responses by host plants may have

important effects on gypsy moth dynamics (Schultz and Baldwin 1982; Rossiter 1994). However, despite considerable attention to these interactions, there is still a lack of evidence that naturally occurring variation in gypsy moth survival and reproduction is directly affected by hosts in a manner that significantly affects changes in densities among generations (Myers et al. 1998; D'Amico et al. 1998). Instead of these direct effects, lower trophic levels (plants) may affect gypsy moth populations mostly via indirect interactions (e.g., effects of mast abundance on predator populations).

Our studies of gypsy moth dynamics also illustrate that many important population processes are only emergent at large spatial scales. Traditionally, population dynamics research has focused on collection of life table statistics and other data from populations located in specific forest stands. Although important processes can be observed at these spatial scales, other processes can only be observed at larger spatial scales. We have seen that characteristics such

as bimodal dynamics, population cycles, second-order lag correlations (i.e., apparent delayed density dependence), and spatial synchrony are features of gypsy moth population dynamics that are only evident when examining the dynamics of populations over large regions. This result stresses that future studies of insect dynamics should examine population processes operating at several different spatial scales.

References

Anderson RM, May RM (1981) Infectious diseases and population cycles of forest insects. Science 210:658–661

Barbour DA (1990) Synchronous fluctuations in spatially separated populations of cyclic forest insects. In: Watt AD, Leather SR, Hunter MD, Kidd NA (eds) Population dynamics of forest insects. Intercept, Andover, pp 339–346

Berryman AA (1991) The gypsy moth in North America: a case of successful biological control? Trends Ecol Evol 6:110–111

Berryman AA (1994) Population dynamics: forecasting and diagnosis from time-series. In: Watt AD, Leather SR, Hunter MD, Kidd NA (eds) Population dynamics of forest insects. Intercept, Andover, pp 119–128

Berryman AA (1995) What causes population cycles of forest lepidoptera? Trends Ecol Evol 11:28–32

Berryman AA (1999) Principles of population dynamics. Stanley Thornes, Cheltenham

Bess HA, Spurr SH, Littlefield EW (1947) Forest site conditions and the gypsy moth. Harv For Bull 22

Buonaccorsi JP, Elkinton JS, Evans SR, Liebhold AM (2000) Assessing spatial synchrony: issues in measurement and analysis. Ecology (in press)

Burroughs WJ (1992) Weather cycles: real or imaginary? Cambridge University Press, Cambridge

Campbell RW (1975) The gypsy moth and its natural enemies. Agric Inf Bull 381. U.S. Department of Agriculture, Washington, DC

Campbell RW (1976) Comparative analysis of numerically stable and violently fluctuating gypsy moth populations. Environ Entomol 5:1218–1224

Campbell RW, Sloan RJ (1977) Natural regulation of innocuous gypsy moth populations. Environ Entomol 6:315–322

Campbell RW, Sloan RJ, Biazak CE (1977) Sources of mortality among late instar gypsy moth larvae in sparse populations. Environ Entomol 6:865–871

Chitty D (1967) The natural selection of self-regulatory behaviour in animal populations. Proc Ecol Soc Aust 2:51–78

Cogan RD (1995) Project annual job report: acorn production study. Pennsylvania Game Commission, Harrisburg

Crawley MJ, Long CR (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. J Ecol 83:683–696

D'Amico V, Elkinton JS, Dwyer G, Willis RB, Montgomery ME (1998) Foliage damage does not affect within-season transmission of an insect virus. Ecology 79:1104–1110

Drake WE (1995) Evaluation of an approach to improve acorn production during thinning. In: Edwards MB (ed) Proceedings of the eighth biennial southern silvicultural research conference. For Serv Gen Tech Rep SRS-1. U.S. Department of Agriculture, Washington, DC, pp 429–441

Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. Annu Rev Entomol 35:571–596

Elkinton JS, Gould JR, Liebhold AM, Smith HR, Wallner WE (1989) Are gypsy moth populations regulated at low density? In: Wallner WE, McManus KA (eds) Lymantriidae: a comparison of features of New and Old World tussock moths. For Serv Gen Tech Rep NE-123. U.S. Department of Agriculture, Washington, DC, pp 233–249

Elkinton JS, Healy WM, Buonaccorsi JP, Boettner GH, Hazzard AM, Smith HR, Liebhold AM (1996) Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77:2332–2342

Ginzburg LR, Taneyhill DE (1994) Population cycles of forest Lepidoptera: a maternal effect hypothesis. J Anim Ecol 63:79–92

Gottschalk KW (1990) Gypsy moth effects on mast production. In: McGee CE (ed) Proceedings of the workshop: southern Appalachian mast management. University of Tennessee, Knoxville, pp 42–50

Gould JR, Elkinton JS, Wallner WE (1990) Density dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. J Anim Ecol 59:213–233

Grenfell BT, Wilson K, Finkerstädt BF, Coulson TN, Murray S, Albon SD, Pemberton JM, Clutton-Brock TH, Crawley MJ (1998) Noise and determinism in synchronized sheep dynamics. Nature (Lond) 394:674–677

Grushecky ST, Liebhold AM, Greer R, Smith RL (1998) Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantriidae) larvae and pupae? Environ Entomol 27:268–276

Hanski I (1990) Small mammal predation and the population dynamics of *Neodiprion sertifer*. In: Watt AD, Leather SR, Hunter MD, Kidd NAC (eds) Population dynamics of forest insects. Intercept, London, pp 253–264

Hassell MP (1978) The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton

Hassell MP (1989) Seeing the wood for the trees: detecting density dependence from existing life-table studies J Anim Ecol 58:883–892

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320

Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. Mem Entomol Soc Can 45:1–60

Hudson PJ, Cattadori IM (1999) The Moran effect: a cause of population synchrony. Trends Ecol Evol 14:1–2

Hunter AF, Elkinton JS (2000) Complex effects of synchrony with the host plant on population growth of a spring-feeding lepidopteran. Ecology 81:1248–1261

Jones CG, Ostfeld RS, Richard MP, Schauber EM, Wolff JO (1998) Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279:1023–1026

Kaufman DW, Kaufman GA, Finck EJ (1995) Temporal variation in abundance of *Peromyscus leucopus* in wooded habitats of eastern Kansas. Am Midl Nat 133:7–17

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9:465–470

King JA (ed) (1968) Biology of *Peromyscus* (Rodentia). American Society of Mammalogists, Provo, UT

Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. Nature (Lond) 396:225–226

Krohne DT (1997) Dynamics of metapopulations of small mammals. J Mammal 78:1014–1026

Leonard DE (1974) Recent developments in ecology and control of the gypsy moth. Annu Rev Entomol 19:197–229

Lewellen RH, Vessey SH (1998) Modeling biotic and abiotic influences on population size in small mammals. Oecologia (Berl) 113:210–218

Liebhold AM, Elkinton JS (1989a) Elevated parasitism in artificially augmented gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations. Environ Entomol 18:986–995

Liebhold AM, Elkinton JS (1989b) Use of multi-dimensional life tables for studying insect population dynamics. In: McDonald L, Manly B, Lockwood J, Logan J (eds) Estimation and analysis of insect populations. Springer, Berlin, pp 360–369

Liebhold AM, Elkinton JS (1991) Reply to Allan Berryman. Trends Ecol Evol 6:263–264

Liebhold AM, Halverson JA, Elmes GA, Quimby J (1994) Landscape characterization of gypsy moth susceptibility. For Sci 40:18–29

Miller DR, Mo TK, Wallner WE (1989) Influence of climate on gypsy moth defoliation in southern New England. Environ Entomol 18:646–650

Montgomery ME, Wallner WE (1988) The gypsy moth, a westward migrant. In: Berryman AA (ed) Dynamics of forest insect populations. Plenum, New York, pp 353–375

Moran PAP (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. Aust J Zool 1:291–298

Murdoch WW, Oaten A (1975) Predation and population stability. Adv Ecol Res 9:1–131

Myers J (1988) Can a general hypothesis explain population cycles in forest Lepidoptera? Adv Ecol Res 18:179–242

Myers JH (1998) Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran efect. Ecology 79:1111–1117

Myers JH, Boettner G, Elkinton J (1998) Maternal effects in gypsy moth: only sex ratio varies with population density. Ecology 79:305–314

Olson DF (1974) *Quercus* L. oak. In: Schopmeyer CS (ed) Seeds of woody plants in the United States. Agriculture Handbook 450. U.S. Department of Agriculture, Washington, DC, pp 692–703

Ranta E, Lindstrom J, Lindén H (1995) Synchrony in population dynamics. Proc R Soc Lond B 262:113–118

Ranta E, Kaitala V, Lindström J (1997) The Moran effect and synchrony in population dynamics. Oikos 78:136–142

Reardon RC (1976) Parasite incidence and ecological relationships in field populations of gypsy moth larvae and pupate. Environ Entomol 5:981–987

Rossiter MC (1994) Maternal effects hypothesis of herbivore outbreak. Bioscience 44:752–763

Royama T (1992) Analytical population dynamics. Chapman & Hall, London

Schultz JC, Baldwin IT (1982) Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217:149–150

Smith HR (1985) Wildlife and the gypsy moth. Wildl Soc Bull 13:166–174

Smith HR (1989) Predation: its influence on population dynamics and adaptive changes in morphology and behaviour of the Lymantriidae. In: Wallner WE, McManus KA (eds) Lymantriidae: a comparison of features of New and Old World tussock moths. For Serv Gen Tech Rep NE-123. U.S. Department of Agriculture, Washington, DC, pp 469–488

Smith HR, Lautenschlager RA (1981) Gypsy moth predators. In: Doane CC, McManus ML (eds) The gypsy moth: research toward integrated pest management. Tech Bull 1584. U.S. Department of Agriculture, Washington, DC, pp 96–124

Smitley D, Andresen J, Priest R, Mech R, McCullough D (1998) Winter mortality of gypsy moth (Lepidoptera: Lymantriidae) eggs in Michigan. Environ Entomol 27:700–708

Sork VL, Bramble J, Sexton O (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74:528–541

Southwood TRE, Comins HN (1976) A synoptic population model. J Anim Ecol 45:949–965

Stenseth NC (1985) Mathematical models of microtine cycles: models and the real world. Acta Zool Fenn 173:7–12

Turchin P (1990) Rarity of density dependence or population regulation with lags? Nature (Lond) 34:660–663

Turchin P (1995) Population regulation: old arguments and a new synthesis. In: Cappuccino N, Price PW (eds) Population dynamics: new approaches and synthesis. Academic Press, San Diego, pp 19–40

Varley GC, Gradwell GR, Hassell MP (1973) Insect population ecology. Blackwell, Oxford

Wellington WG (1954) Weather and climate in forest entomology. Meteorol Monogr 2:11–18

Weseloh RM (1988) Effects of microhabitat, time of day, and weather on predation of gypsy moth larvae. Oecologia (Berl) 77:250–254

Weseloh RM (1990) Estimation of predation rates of gypsy moth larvae by exposure of tethered caterpillars. Environ Entomol 19:448–455

Williams DW, Liebhold AM (1995a) Influence of weather on the synchrony of gypsy moth (Lepidoptera: Lymantriidae) outbreaks in New England. Environ Entomol 24:987–995

Williams DW, Liebhold AM (1995b) Detection of delayed density dependence: effects of autocorrelation in an exogenous factor. Ecology 76:1005–1008

Williams DW, Fuester RW, Metterhouse WW, Balaam RJ, Bullock RH, Chianese RJ, Reardon RC (1992) Incidence and ecological relationships of parasitism in larval populations of *Lymantria dispar* (Lepidoptera: Lymantriidae). Biol Control 2:35–43

Wolff JO (1996) Population fluctuations of mast-eating rodents are correlated with production of acorns. J Mammaal 77:850–856