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EFFECTS OF SYNCHRONY WITH HOST PLANT ON POPULATIONS OF A SPRING-FEEDING LEPIDOPTERAN

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Abstract. Comparisons of traits of outbreaking and nonoutbreaking leaf-eating Lepidoptera and Symphyta have shown that spring-feeding species are more likely to have outbreaks than are summer-feeding species. It has been suggested that variable synchrony with host budburst causes the population sizes of spring-feeding species to be more variable primarily because of the negative effects of older leaves on insects. While much evidence exists that leaf age can directly affect survival and reproduction of insects, few studies have looked at the population-level effects of variable phenology, and especially the potential for complex direct and indirect interactions with natural-enemy effects. To examine the consequences of variable phenology for population growth of an outbreaking insect, we manipulated the timing of gypsy moth (*Lymantria dispar*) egg hatch in the field. We released large numbers of gypsy moth larvae into replicate plots in the field at three times relative to budburst. Survival of larvae in protective sleeves was high unless they were released very long before host budburst, and leaf age had a direct negative effect on fecundity: the later the release, the lower was the fecundity of insects reared on white oak and black oak. The later the release, however, the greater was the dispersal by ballooning, which had the effect of reducing local densities. Because the most important natural enemies impose density-dependent mortality, dispersal had the effect of raising survival rate for later release dates. The direct host-plant effect and natural-enemy effects exhibited opposing influences on population processes, because fecundity decreased with release date but survival increased. The survival advantage of the late release outweighed the loss in fecundity, so that the expected population growth rate was highest for the latest release. The net effects of phenology on insect population growth thus depend largely on natural-enemy effects. Very different conclusions would have been drawn had we measured mortality only in protective sleeves and not in the presence of natural enemies. The strong natural-enemy effects may explain the large variability in outcome of plant–herbivore interactions and contribute to the high variability in population size of spring-feeding species.

Key words: dispersal; insect–plant interactions; Lymantria dispar; *Massachusetts; outbreaks, gypsy moth; phenology; population dynamics.*

INTRODUCTION

Forest insect outbreaks are spectacular events that transform forests over both the short term (Thurber et al. 1994) and the long term, affecting forest composition and nutrient cycling (Campbell and Sloan 1977, Mattson and Addy 1975, Loreau 1995, Lovett and Ruesink 1995, Fajvan and Wood 1996). An important contribution to understanding the causes of these outbreaks has been made through comparisons of outbreaking and nonoutbreaking species. Such comparisons have suggested that outbreaking species are more likely to be spring feeders than are nonoutbreaking species (Hunter 1991, 1995*b*, Haack and Mattson 1993, Larsson et al. 1993). One suggested explanation for the importance of spring feeding for defoliator population dynamics is that variable synchrony with host budbreak causes population sizes of spring feeding species to be more variable than those of summer feeding species (Embree 1965, Varley and Gradwell 1968, Holliday 1977, Witter and Waisanen 1978, Nothnagle and Schultz 1987, Hunter 1990, 1991, Watt and McFarlane 1991). This is because insects that emerge from winter dormancy too early risk starving before leaves appear, but insects that emerge too late suffer from poor food quality because older leaves are generally lower in nutritional quality for herbivorous insects (Feeny 1970, Raupp and Denno 1983, Mattson and Scriber 1987). Defoliating insects must therefore synchronize their emergence with this window of opportunity between budburst and the time when foliage quality is too low. This window of opportunity may be variable and unpredictable. Relatively little direct evidence exists to support this hypothesis, beyond the observed decline in foliage quality with leaf age and anecdotal reports that spring feeding insects sometimes have a mismatch with their host and starve. No long-term records of insect emergence and plant emergence exist with which

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to assess the frequency of mismatches or their impact on population sizes. Here we report the results of field experiments designed to test for effects of variability in the timing of insect emergence on population growth rates.

Although the variable synchrony hypothesis has focused solely on the direct effects of foliage quality changes caused by leaf age on insect herbivore performance, natural-enemy effects mediated by timing differences in spring could also be important to dynamics. This includes both direct timing effects such as disruption of synchrony between predator and prey, and indirect effects of the leaf age on susceptibility to natural enemies. The effects of leaf quality on natural enemies of herbivores may be quite large, increasing mortality of herbivores by slowing growth and increasing the duration of exposure to enemies (Lawton and McNeill 1979, Price et al. 1980, Schultz 1983, Benrey and Denno 1997), or by providing host location cues (Benrey and Denno 1997). For example, gypsy moth larvae whose development was slowed by infection with *Bacillus thuringiensis* suffered greater attack rates by the parasitoid *Cotesia melanoscela* (Weseloh and Andreadis 1982), and slow growth on low quality foliage could have a similar effect. Similarly, host leaf age affects susceptibility of gypsy moth to infection with nuclear polyhedrosis virus (Keating et al. 1988) and the success of attacks of *Cotesia melanoscela* on gypsy moth larvae (Werren et al. 1992). On the other hand, leaf quality changes can decrease mortality of herbivores if a chemical defense derived from the host plant increases (Rowell-Rahier and Pasteels 1991).

Here, we are particularly interested in potentially subtle effects of leaf age since we are examining the contribution of variable timing to variability in population sizes. We also sought to examine the population-level effects of all the mortality agents to compare with the effects of leaf age. While a factor like timing may have a seemingly large effect on some component of population growth, such as early mortality or fecundity, it is possible for those effects to be counterbalanced by other effects that act in an opposite direction (as we will show). Thus we sought to evaluate the total effect of changed phenology on the population growth rate.

In short, variation in the degree of synchrony between the time that forest-defoliating insects hatch and the time that their host trees burst their buds can potentially have complex effects. In our experiments, we therefore measured the effects of variation in synchrony on gypsy moth population dynamics due to both natural-enemy effects and foliage quality effects. To do this, we manipulated synchrony by creating large-scale experimental gypsy moth populations in the field at different times relative to the budburst of two important gypsy moth host trees, white and black oak (*Quercus alba* and *Q. velutina*). To see the effects of synchrony, we then quantified the survival, fecundity, and dispersal of the gypsy moths in each population. Direct foliage-age effects on gypsy moth growth, survival, fecundity, and larval ballooning have been extensively documented (Hough and Pimentel 1978, Meyer and Montgomery 1987, Raupp et al. 1988, Sheppard and Friedman 1990, Hunter and Lechowicz 1992, Stoyenoff et al. 1994), but the effects of variable phenology on mortality caused by natural enemies, whether direct or indirect, have seldom been studied. To separate the direct and indirect effects of leaf age, we protected some insects from predators in each release treatment. We measured dispersal because it potentially affects survival directly by exposing larvae to increased chances of mortality (Weseloh 1998), and indirectly by spreading individuals over a larger area, reducing the local density and thus reducing mortality from density-dependent factors.

Study organism

The gypsy moth is a typical outbreaking, spring-feeding species: it spends the winter as an egg, females are flightless so that most dispersal is by larval ballooning, large numbers of eggs are laid in a single mass, and it feeds on diverse host tree species. These traits are shared by many spring-feeding species (Nothnagle and Schultz 1987, Barbosa et al. 1989, Hunter 1991, 1995*a, b,* Haack and Mattson 1993, Larsson et al. 1993). Gypsy moth has outbreaks both in northeastern North America, where it was introduced in 1869, and in Eurasia, where it is native. The gypsy moth has a very broad host range but prefers to feed on oak species.

Gypsy moth egg hatch occurs at about the time of budburst of red and black oaks (Hunter 1993). Larval ballooning occurs only in a brief period after egg hatch (Leonard 1971). Larvae are too heavy to balloon once they have begun feeding, so we can quantify dispersal in experimental populations at the end of the first instar when ballooning is complete. Early instar larvae feed mostly during the day and stay in the tree canopy. In the late fourth instar, however, they feed at night and descend the trees to find hiding places during the day. Larvae move among trees at this stage, but accumulate on trees with good hiding places (Liebhold et al. 1986). We exploited this behavior to estimate relative late instar density in our experimental populations by providing hiding places (burlap skirts stapled to trees). Pupation also often occurs in these sheltered locations, and egg masses are laid nearby by flightless females. Since the females cannot disperse, larval ballooning and the intertree movements of late instar larvae are the only natural dispersal mechanisms for gypsy moths.

Study site

We carried out our experiments on the Otis Air Force Base, Cape Cod, Massachusetts in 1995 and 1996. Although densities of gypsy moth larvae were very low, <5 egg masses/ha in both years of the study, this site is highly suitable for the gypsy moth. Outbreaks have

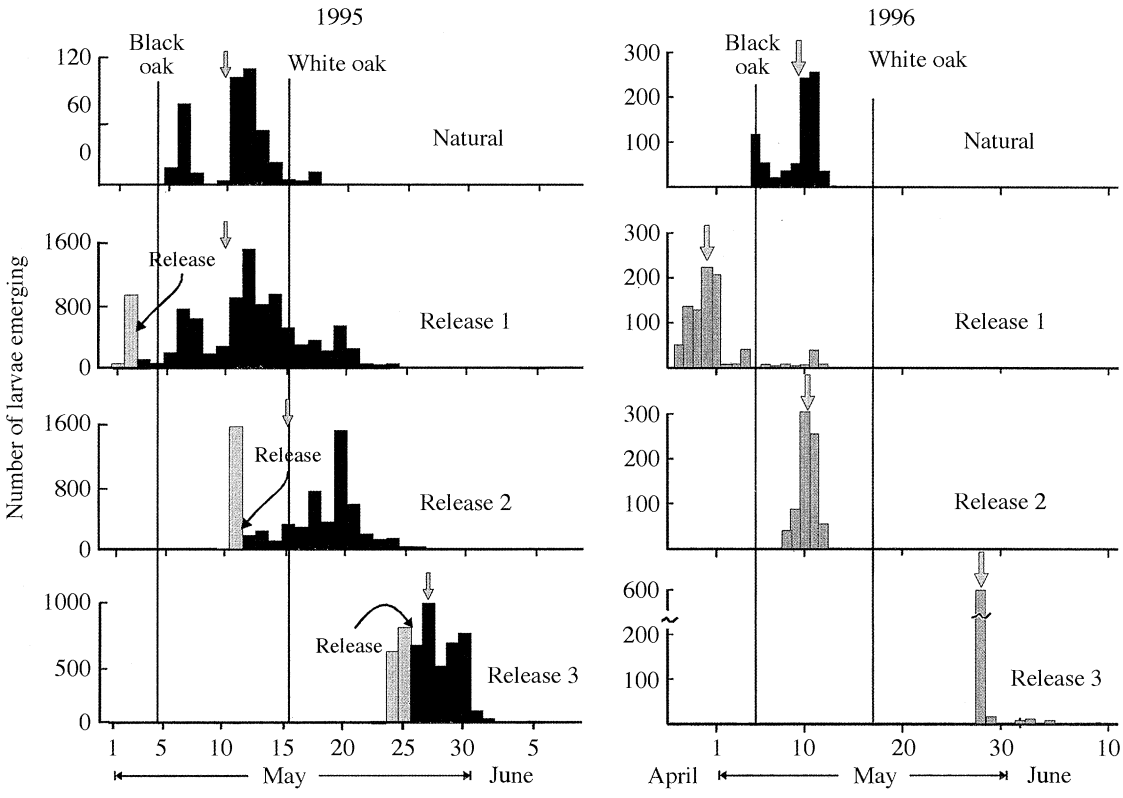

FIG. 1. Time of hatching of natural egg masses (1995) or of laboratory-reared egg masses placed outdoors in February (1996), and of the three experimental releases. Vertical lines indicate budburst dates of black oak and white oak. Vertical arrows indicate mean hatch dates of each release. In 1995, eggs were warmed indoors until they began hatching (gray), then released (black). In 1996, larvae were released daily, and eggs were returned indoors for warming overnight until over 70% had hatched (gray), at which time eggs were released (black).

occurred on Cape Cod more frequently than anywhere else in Massachusetts (Liebhold and Elkinton 1989). The preferred gypsy moth hosts, black oak (*Quercus velutina*) (70% of stems >2.45 cm dbh), and white oak (*Quercus alba*) (12% of stems) dominate the forest, with pitch pine (*Pinus rigida*) (9% of stems) and red maple (*Acer rubrum*) (6% of stems) comprising most of the remainder. Blueberry (*Vaccinium* sp.) dominates the understory. Trees in these stands are relatively short, ~6–8 m high, so the canopy can be readily sampled with pole pruners. The Air National Guard collects weather data at Otis Air Base.

Gypsy moth eggs

We used slightly different release protocols in 1995 and 1996 because different egg sources were available in the two years, and because we wanted to reduce the variance in hatching time in 1996. In 1995 we obtained eggs from the U.S.D.A. Animal and Plant Health Inspection Service Methods Development Center at Otis Air Base. These insects have been reared in laboratory conditions for 42 generations, but have the same survival rate, development rate, and pupal body mass as the wild type when reared on black oak (Keena and Odell 1994). In 1996 we collected eggs from outbreak populations in West Virginia in midwinter. Populations have only recently spread to West Virginia and probably have not adapted to the local phenology. Only a small number of gypsy moths was introduced to North America initially, and populations have low genetic variation (Harrison et al. 1983), which further decreases the chance of local adaptation to phenology.

The duration of chilling of eggs can affect the rate of larval emergence (Masaki 1956). Eggs for each release were produced at different dates in 1995, so that they received similar amounts of chilling: First release, 181 d; Second release, 168 d; Third release, 168 d. We held each batch of eggs in cold storage (4°C) until needed, and then warmed them at room temperature (24°C) until hatching began (Fig. 1). In 1996, the wild eggs from West Virginia were all laid at the same time so the duration of their chilling differed. To see whether the chilling duration affected larval survival, we compared larvae from the different release treatments by rearing 200 insects from each of the three releases individually in 30-mL cups with 15 mL of a diet based on wheat germ, enough for a larva to complete development. We placed these larvae in an outdoor insectary

so that they experienced the same chilling duration and temperatures as the released insects. This allowed us to quantify the combined effects of different chilling durations and temperatures during the larval period on survival. We compared the proportions surviving using the normal approximation to the binomial test (Zar 1984: 395).

After removing eggs from cold storage, we sterilized them in 10% formaldehyde for 1 h, then rinsed them under running water for 1 h. This treatment kills virus on egg surfaces (virus commonly occurs in high density populations). The fungus *Entomophaga maimaiga* does not appear to be transported on egg masses (Yerger and Rossiter 1996). In both years, the hatching phenology and percentage hatch were obtained by counting numbers emerging, out of the 1000 eggs per release date, subdivided into 10 subsamples of 100 eggs each. We held the samples at the same temperature as the rest of the eggs, and counted numbers of larvae emerging each day.

Release methods and timing

To manipulate the synchrony of hatch of our experimental populations relative to budburst, we released gypsy moths in each year into field plots at three different times relative to the date of black oak budburst. We replicated each release phenology in four plots in each year. All plots received 450 g of eggs, yielding $n = 5 \times 10^5$ larvae per plot. Plots were separated by $\geq$300 m so that dispersal of larval insects between plots was negligible. In 1995 we released eggs evenly in each plot on oak tree boles in a 20 $\times$ 20 m square, in open-topped pockets made of burlap. In 1996 we released larvae on the 20 oak trees closest to the central tree within 7 m of the center of the release area.

In 1995, we released eggs on 2 May ("First release"), 10 May ("Second release"), and 25 May ("Third release") (Fig. 1). Eggs placed outdoors in the First release in 1995, however, hatched slowly during periods of cool temperatures before 10 May (Fig. 1), and did not hatch as early as we desired. To achieve more control, in 1996 we released newly hatched larvae instead of eggs. To do this, we placed eggs in hardware-cloth packets that allow larvae to emerge while retaining eggs. We placed 5 g of eggs in each packet, and stored them at 4°C until needed. To stimulate hatching, we then warmed the packets at room temperature (24°C) in paper bags. When $\geq$30% of eggs had hatched in subsamples, we released the larvae into the field. We gently brushed the emerging larvae from the packets onto the paper bags, stapled the bags to trees, and then returned the hardware-cloth packets to the laboratory to continue warming overnight. When >70% of larvae had emerged, the packets were stapled to the trees and the subsamples were placed in an outdoor insectary. These releases were begun on 28 April ("First"), 12 May ("Second"), and 28 May ("Third") (Fig. 1).

For purposes of comparison, in each year we estimated the timing of natural egg hatch by holding egg masses in the insectary and counting the number of larvae emerging each day. In 1995, we collected a few naturally occurring egg masses for this purpose, but in 1996 natural densities were extremely low and we were unable to find egg masses. In 1996 we therefore placed several laboratory-colony egg masses in the outdoor insectary in February, and then monitored their hatch. Tree phenology was gauged by visual estimates of the proportion of leaves emerged on 15 trees of each species. Budbreak is markedly synchronous at this site, probably because the topography is level and temperatures are strongly influenced by coastal air masses.

Direct foliage age effects on survival and growth

To measure the direct effects of foliage age on survival and growth independently of dispersal and natural-enemy mortality, we placed newly hatched larvae on oak branches in spun polyester sleeves (Reemay) at each release date in 1996. Doubled sleeves protect larvae from predators and parasitoids (Turchin and Kareiva 1989). On each release date, we placed 40 larvae in each of 20 sleeves: 10 on white oaks and 10 on black oaks. Larvae were carefully transferred from sterile plastic containers onto the foliage and the inner surface of the sleeve, with sterile, fine paintbrushes. In the third instar (when we first counted survivors) we split the remaining larvae into groups of $\leq$10 individuals per sleeve. After that we moved sleeves as often as necessary to ensure that larvae had ample foliage. Each sleeve was placed on a different tree, and trees were not re-used. We weighed pupae, then held them in the insectary until adults emerged. Males and females were then paired and the eggs laid by the females were counted.

These experiments were analyzed separately for the two oak species due to interactions between the effects of species and of release dates. The arcsine square-root transformed proportion of larvae surviving to the third instar was compared among release dates for each host species in a one-way analysis of variance (ANOVA). Fecundity was compared in a one-way ANOVA with sleeve effects nested within the release treatments.

Larval dispersal by ballooning

To examine the effect of phenology on larval dispersal by ballooning, we measured the overall displacement of larvae from the center of each release area. As all larval dispersal by ballooning occurs early in the first instar, we assessed total population dispersal at the end of the first instar. Growth stage was determined by finding 25 larvae in each plot every 2–3 d and measuring the relative sizes of bodies and head capsules. Just prior to molting, the head capsule appears very small relative to the diameter of the body; just after molting the head capsule is larger in diameter than the body. This made it easy to determine when the larvae were at the end of the first instar.

To quantify larval dispersal, we clipped foliage from the canopy at 5-m intervals along transects radiating from the center of the plot in the directions N, NE, E, SE, S, SW, W, and NW. At this time of year the prevailing winds on Cape Cod are from the SW, so most of the observed spread is towards the NE. Accordingly, in 1996 we ran additional transects in the NNE and ENE directions. In both years we extended transects in each direction until no larvae could be found. Foliage was dropped onto tarpaulins, gypsy moth larvae were counted and removed, and all the leaves were collected so they could be counted later. We collected ~100 leaves at each sampling point (essentially trees) (average = 102 leaves, range = 41–283 leaves). The nearest black oaks were sampled at all points, and a white oak was sampled if there was one within a 1.5-m radius of the sampling point.

To compare the relative displacement of larvae, we pooled data from the four replicates within each treatment. We estimated the center of the resulting three-dimensional surface using the nonlinear procedure (NLIN) of SAS, under the assumption of a bivariate normal distribution of larvae. Although differences in wind could potentially account for any differences in dispersal, a comparison of wind speeds between the date of releases and the date the samples from the canopy were taken, showed that differences among the releases in wind speed were slight.

Since black oak leaves emerge much earlier than white oak leaves, we expected that gypsy moth larvae would at first prefer black oak over the closed buds of white oak. At the late release, when black oak leaves were much older than white oak leaves, we expected a preference for white oak. We compared larval densities on adjacent white and black oak trees at each release in 1996 using paired differences in an analysis of variance. This pairing of adjacent trees controlled for distance from the release area.

Sources of mortality: pathogens and parasitoids

To measure the contributions of pathogens and parasitoids to gypsy moth mortality, we collected larvae from each plot at weekly intervals after the releases. Larvae were placed directly into plastic cups containing wheat-germ-based diet. We scored the larval instar, and held larvae for 1 wk in an outdoor insectary. Larvae that died in this week were held for at least two additional days to allow for the emergence of parasitoids, and then were autopsied under a light microscope at 400× to check for pathogens. First instar larvae suffer little mortality, so more (50 individuals per replicate plot) were collected. In the later instars, only 30 larvae were collected from each replicate. In 1996, we increased collections to 100 first instar and 50 later instar larvae per replicate. Larval mortality was expressed as marginal rates (Elkinton et al. 1992), converted to k values, and compared among release dates with ANOVA. Since the three releases in each year do not represent the same relative phenologies, the years were analyzed separately.

The most common parasitoids of gypsy moth in this area are the specialist braconid wasp *Cotesia melanoscela* and the generalist tachinid fly *Compsilura concinnata*. The fungus *Entomophaga maimaiga* and a nuclear polyhedrosis virus (NPV) are common pathogens but little virus was detected in our samples. NPV is usually rare in low density populations such as we had in these years, and the surface sterilization of eggs prevented the transfer of NPV from the high density source populations in 1996.

Mortality in the field: burlap counts and predation

As described above, late fourth instar and older gypsy moth larvae seek daytime resting locations where they are concealed from some predators. In 1996 we provided burlap skirts on the boles of trees at 5-m intervals (≤40 m from the center of the release area) along transects in the main compass directions in the release plots (i.e., 65 trees per plot). We counted the number of larvae and pupae under or near the burlaps four times for each release, at roughly weekly intervals, and we made a final count of egg masses in August. We followed standard procedure in calculating k values for total mortality in the field ($-\log_{10}$(survival), Varley et al. [1973]).

Population growth rate estimates

To integrate the opposing effects of host plant quality and mortality from natural enemies, we calculated the population growth rates based on survival and fecundity. Given the sampling schemes described in *Methods: Sources of mortality . . .*, we were able to estimate larval survival in each stage as follows. First, the subsamples of eggs that we used to quantify hatch also allowed us to estimate the fraction of eggs that hatched. We then estimated survival from hatch to the second instar using our estimates of density obtained from our canopy samples, in the following way. First we fit a bivariate normal curve to the canopy data. Integrating under this curve then gave the number of larvae per unit leaf area (A. F. Hunter and J. S. Elkinton, *personal observation*). We then converted from larvae per unit leaf area to total number of larvae by multiplying by the leaf area in each plot, as estimated previously in our laboratory (Liebhold et al. 1988) and measured again in 1997 with a LI-COR leaf area meter to find the total number of second instar larvae in each plot. Next, we estimated survival from the second to fourth instars from the count of live plus dead larvae at the first count under burlap. Finally, we estimated survival from the fourth instar to adulthood by comparing counts of larvae under the burlap bands at the end of the fourth instar and at adulthood.

To estimate overall population growth, we combined these estimates of survival with estimates of fecundity. We assumed that larval distribution matched the pro-

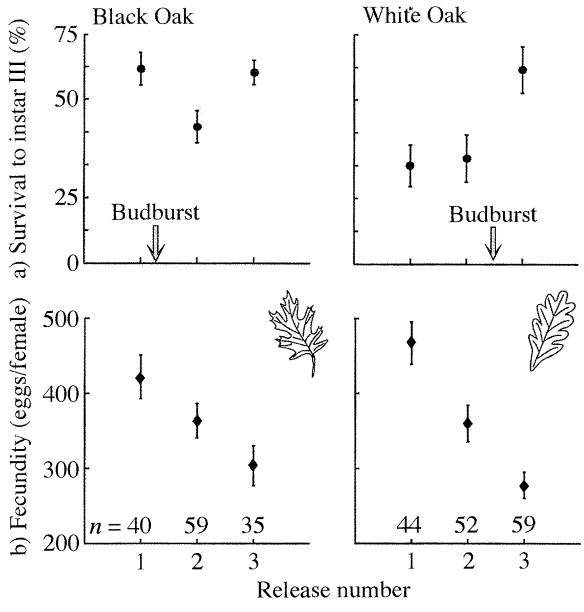

FIG. 2. (a) Survival of larvae (mean ± 1 SE) in protective sleeves from hatch until third instar in 1996. Larvae were put in the sleeves at the same time as the releases in Fig. 1. (b) Fecundity (mean ± 1 SE) of females raised in protective sleeves from each of the release dates until pupation in 1996. Sample sizes (no. surviving females) are indicated below each data point.

portion of trees of the hosts, so that 70% of larvae were on black oak and 30% were on white oak. We assumed a sex ratio of 1 : 1, as is appropriate for most gypsy moth populations.

RESULTS

Timing of egg hatch vs. budburst

In 1995, the manipulation of phenology was successful in that the timing of egg hatch differed substantially among the three treatments (Fig. 1). However, the hatch times of eggs in the "First" treatment and natural eggs were less different than expected, because of difficulties with the experimental protocol. The average hatch time of the first release was thus approximately synchronous with that of natural egg masses, and the variance in hatch date was large.

Black oak buds began to emerge around 4 May in 1995 (1 SD = 0.85 d, n = 15 trees) (Fig. 1). By the time of the Second release, most black oak leaves had emerged from the buds, and the expansion of leaves of the canopy was ~5% complete. White oak budburst began on 15 May (1 SD = 0.65 d, n = 15 trees), so that at the time of the Third release, black oak canopy expansion was ~50% complete and white oak expansion was only 5% complete.

In 1996, by releasing larvae instead of eggs, we had greater success at controlling phenology of gypsy moth, and we were able to reduce the differences in variance among releases (Fig. 1). Black oak again burst buds on 5 May (1 SD = 0.93 d), and white oak on 17 May (1 SD = 0.65 d; n = 15 trees for both species). The First release was thus largely complete 4 d before black oak budburst, the Second release was synchronous with natural hatch, and the Third release was 10 d after white oak budburst.

Although the initial numbers of eggs were the same in the three releases, the hatching success varied so that the number of larvae released differed slightly between the releases. In 1995 the numbers per plot were 5.0×10^5, 5.7×10^5, and 4.6×10^5 larvae in the First, Second, and Third releases respectively. In 1996 estimated numbers released were 4.1×10^5, 5.1×10^5 and 3.8×10^5 larvae in the First, Second, and Third releases respectively.

The survival rate of larvae reared on artificial diet in 1996 was high: 79% in the First release, and 84% in the Second and Third releases. Most importantly, the duration of chilling in winter and temperature during larval growth did not affect the survival of larvae on diet (t_2 = 1.41, $P > 0.05$).

Direct effects on survival and fecundity

Larval survival in protective sleeves was affected both by release date and host tree species (Fig. 2a, Table 2a). Because of interactions between the effects of species and release dates, data were analyzed separately for the two host species. Such interactions are expected

TABLE 1. Comparisons of two gypsy moth (*Lymantria dispar*) population statistics among the three release dates (ANOVA).

	Black oak			White oak		
Source of variation	df	*F*	*P*	df	*F*	*P*
a) Survival to instar III						
Release date	2	4.97	0.016	2	5.84	0.008
Error	26			26		
b) Fecundity						
Release date	2	16.6	<0.001	2	4.28	0.017
Sleeve(Release)	39	1.0	0.46	42	1.05	0.42
Error	114			80		

Notes: (a) Proportion surviving to the third instar in protective sleeves. Proportions were arcsine square-root transformed before analysis. (b) Fecundity of females raised in protective sleeves. Sleeve effects were nested within release treatments. Note that there were more sleeves because in the third instar we split up large groups.

TABLE 2. Comparisons of gypsy moth mortality among the three release dates.

Source of variation	1995			1996		
	df	*F*	*P*	df	*F*	*P*
a) Total mortality	2, 9	10.2	0.005	2, 9	6.49	0.02
b) *Entomophaga maimaiga*	2, 9	10.3	0.005	2, 9	3.67	0.068
c) *Cotesia melanoscela*	2, 9	24.0	<0.001	2, 9	0.89	0.44
d) *Compsilura concinnata*	2, 9	1.03	0.40	2, 9	2.64	0.13
e) Unknown causes	2, 9	2.18	0.17	2, 9	4.12	0.054

Notes: (a) total mortality rates in weekly collections of larvae, (b) mortality from the fungus *Entomophaga maimaiga,* (c) mortality from the braconid wasp *Cotesia melanoscela,* (d) mortality from the tachinid fly *Compsilura concinnata,* and (e) mortality from unknown causes.

because of the very different leaf emergence phenologies of the two oak species (e.g., the Second release does not represent the same leaf age for both species). Specifically, leaf emergence in black oak occurred very soon after the first release, resulting in a generally high survival rate in gypsy moth (Fig. 2a, Table 2a). White oak buds, in contrast, had not burst at either of the first two release dates, so gypsy moth survival was much lower at these dates than at the final release. After the third instar, survival in sleeves was >90% for all releases.

Fecundity strongly decreased with later release dates (Fig. 2b, Table 2b), no matter which oak species larvae fed on. Females in the earliest release produced on average 100 more eggs than females from the latest release.

Larval dispersal by ballooning

The overall dispersal by ballooning increased from the First to the Third release in both years (Figs. 3 and 4). The center of all of the postdispersal distributions shifted in a northeasterly direction, as expected from the prevailing wind (Fig. 3). The earlier the release relative to black oak budburst, the smaller the overall displacement of the new center of the larval distribution from the center of the release area (Fig. 4).

The wind speeds differed among the three releases (1995: $F_{2,433} = 3.34$, $P = 0.036$; 1996: $F_{2,474} = 5.17$, $P = 0.006$), but the third releases had lower wind speeds than did the second release in both years (1995: mean wind speeds 5.7, 5.6, and 4.9 m/s at the First, Second, and Third dispersal periods, respectively, and 1996: 4.4, 5.0, and 4.1 m/s). Wind speed therefore cannot explain the greater dispersal of larvae in the third releases in each year.

As expected, larvae preferred black oak over white oak in the early releases, but with the last release they shifted to the less-advanced white oak ($F_{2,118} = 8.07$, $P = 0.001$). There were five more larvae per 100 leaves on black oak than on adjacent white oaks at the First release, and four more at the Second release, but one fewer at the Third release.

Mortality

Mortality from parasitoids and diseases differed substantially among treatments (Table 2a). In each year, mortality from parasitoids and diseases was greatest in the Second release. Also in each year, the fungus *Entomophaga maimaiga* caused the most mortality in the First and Second releases, while the Third release had significantly lower mortality from fungus (Fig. 6, Table 2b). Mortality from the parasitoid wasp *Cotesia melanoscela* increased from the early to late releases in 1995, but in 1996 did not differ significantly among the releases (Fig. 5, Table 2c). Mortality from the fly *Compsilura concinnata* did not differ among treatments (Fig. 5, Table 2d). Unknown causes of mortality did not vary among treatments in 1995 but were slightly higher in the early releases in 1996 (Fig. 5, Table 2e). Mortality from virus was very low (<0.1%) in both years, as we expected, because we decontaminated the eggs before release.

Survival under burlaps

In 1996 the number of live larvae found under burlap bands at the beginning of the fourth instar decreased with increasing release date ($F_{2,9} = 11.2$, $P = 0.004$). Larval mortality between the second and the final burlap census increased with increasing density at the first census (Fig. 6). This mortality was most strongly correlated with mortality from *E. maimaiga* in the weekly collections over the same period ($r = 0.85$, $P < 0.001$, df = 10). This density dependence is confounded by the release treatment in that the lowest initial densities and k values were all from the third release (Fig. 6).

We also related the mortality in the weekly collections with the density in the first burlap count, to show that only the fungus ($r = 0.74$, $P = 0.006$, df =10) and unknown sources ($r = 0.67$, $P = 0.016$, df = 10) were density dependent. The unknown sources may include some mortality from fungus because the stage producing conidia is of short duration and relatively difficult to diagnose.

Population growth rates

Since fecundity decreased with the later release date but overall survival rate increased, the net effect of release date can only be estimated from the population growth rate (Fig. 7). All populations were shrinking as we found very few adults in any of the release areas. The second release had the lowest growth rate and the third release the highest population growth rate (Fig.

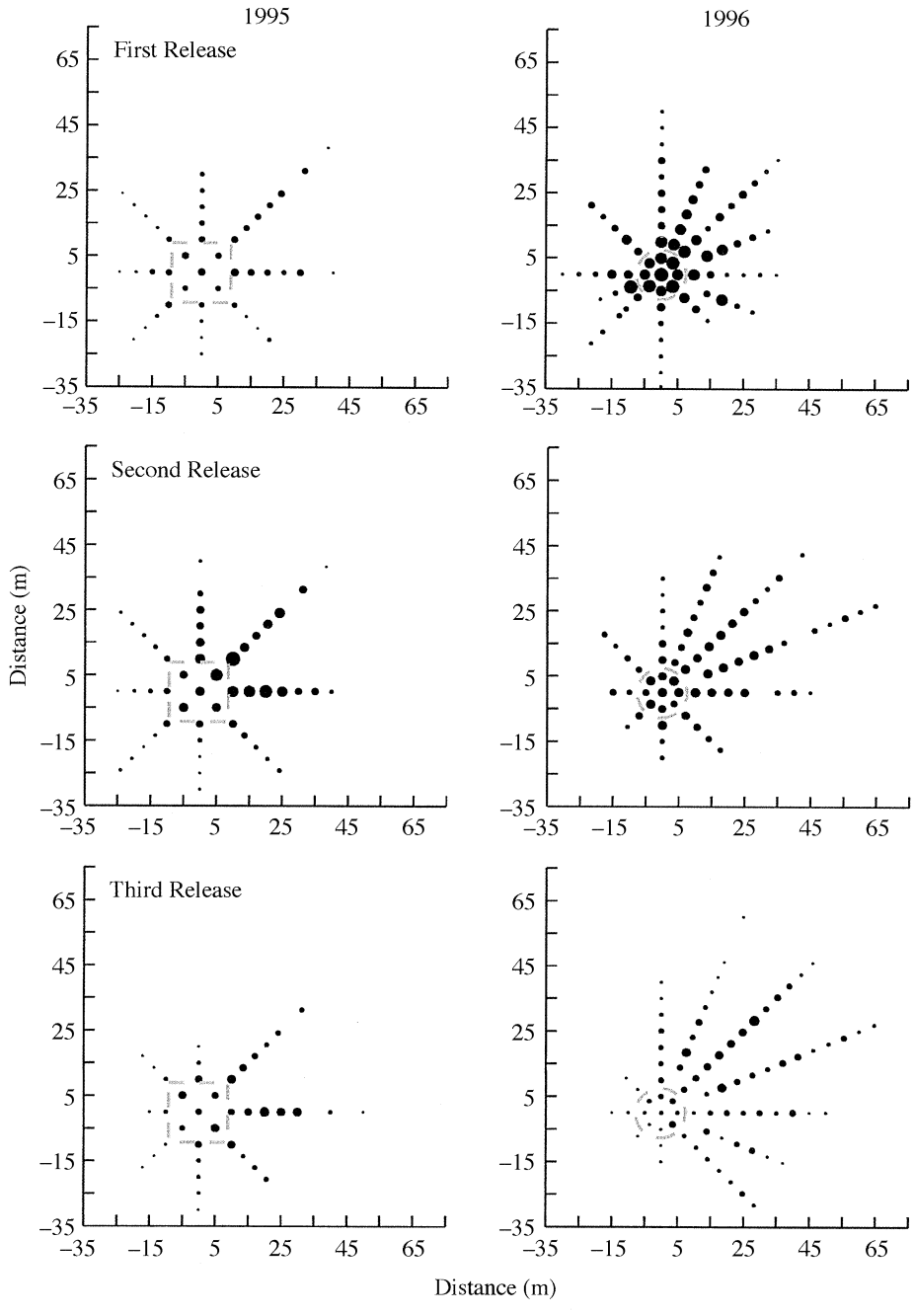

FIG. 3. Distribution of larvae at the end of the first instar. The size of the solid circles is proportional to the number of larvae per 100 leaves, averaged across the four replicate releases at each date. The horizontal axis is east and west; the vertical axis is north and south.

7; $F_{2,9} = 9.03$, $P = 0.007$). Although the fecundity of moths from the late release was much lower, the higher survival in the late instar and pupal stages offset this cost.

DISCUSSION

The classical model of the effects of timing of emergence on spring-feeding insects holds that insects emerging too early will starve, while insects emerging too late will suffer from decreased foliage quality. We found support for this model in that early hatching gypsy moth larvae that were protected from natural enemies starved, and fecundity decreased with leaf age over the three weeks between release dates. Larvae that emerged after budburst had high survival and this survival rate was little affected by time of emergence, in

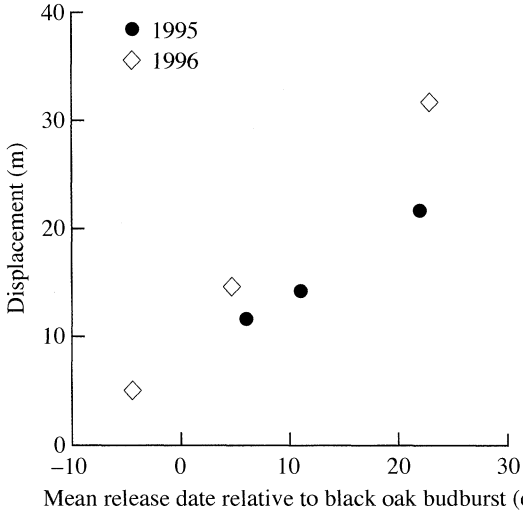

FIG. 4. Mean displacement of larvae from the center of the release area, vs. difference between the mean dates of hatch of the experimental populations and the date of black oak budburst in 1995 (circles) and 1996 (diamonds).

the absence of natural enemies. However, experiments that allowed for natural-enemy effects gave radically different results. In the presence of enemies, larval survival was much higher in the late release so the final, adult density was higher than in the early releases. Also, the higher fecundity in the early releases did not offset the lower final densities, so the overall effect was that early releases had much lower population growth rates. This result suggests a need for caution in predicting the impact of timing on population dynamics when some factors are excluded from consideration.

Another important result of our experiments was that the amount of ballooning by first instar larvae increased as the foliage aged. While this effect was known from small-scale laboratory experiments (Hunter and Lechowicz 1992), we have presented the first large scale measurement of phenological effects on ballooning in the field. We infer that the increase in dispersal occurs not just because greater temperatures at the late release increase larval activity, but also because of changing foliage quality and because larvae showed a shift in host use towards greater use of the younger white oak

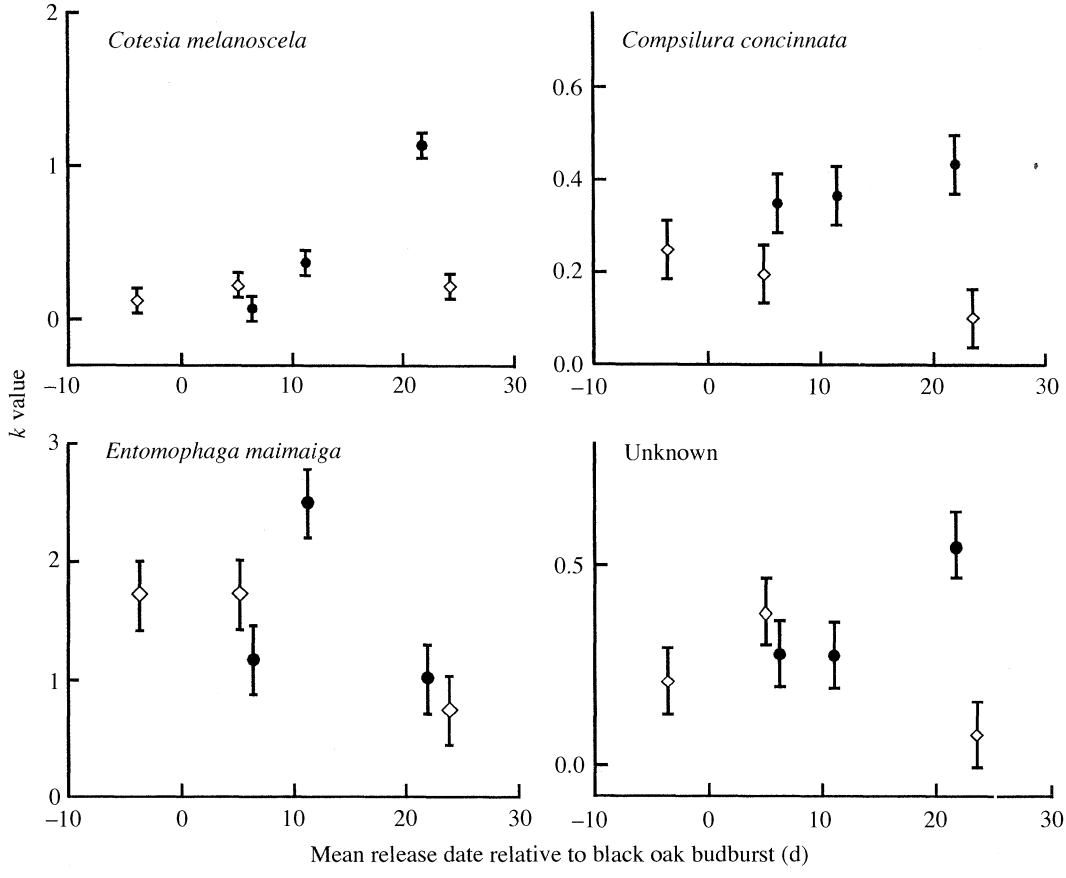

FIG. 5. Average k values from each release date and each source of mortality in 1995 (circles) and 1996 (diamonds) (mean ± 1 SE), from larvae collected each week. Note the different scales. *Entomophaga maimaiga* was usually the most important cause of mortality.

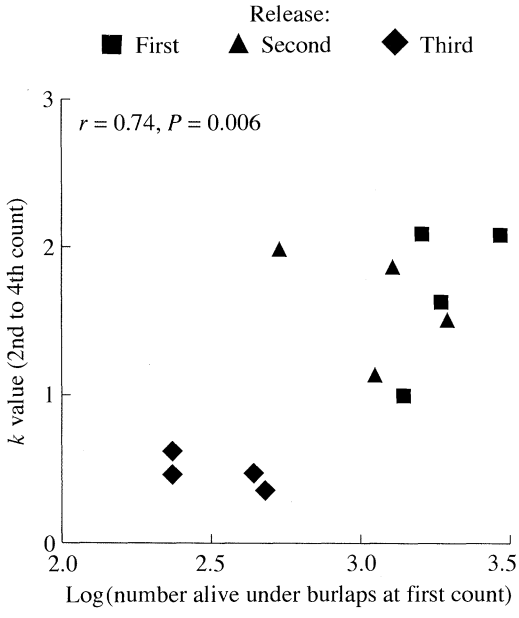

FIG. 6. Mortality k value from second to final burlap count vs. density at the first count of larvae under burlap. Each count is of the total number of live larvae on 65 trees per release plot.

foliage. The greater dispersal is not caused by temperature differences experienced by the eggs because such temperature differences do not affect dispersal rates (Diss 1996), nor was greater dispersal at later release dates due to differences in wind speed between the release dates. Instead, it appears that the greater dispersal was caused by the reduction in foliage quality of the hosts as the leaves aged (Hunter and Lechowicz 1992). Ballooning behavior reduces the impact of variable synchrony with leaf emergence by allowing larvae to locate hosts that are in a more favorable phenological stage.

An additional important consequence of dispersal in this type of experiment is its effect on density. Apparently because of their higher dispersal in the first instar, the late-released insects had lower densities at the time of the first burlap count and lower mortality in the final instars because of the density-dependent response of the fungal pathogen. The early mortality was not due to the decline in foliage quality because the survival of insects protected from predators was high in the late release. It was also not due to parasitoids or disease because mortality of unprotected insects was lower for the late release than for the two earlier releases during the early instars. Predation mortality was presumably much more important in the latest release. Thus the most important effect of leaf age was the effect on dispersal, which in turn affected natural-enemy mortality rates via density effects.

These density-related effects constitute indirect effects of phenology on natural enemies through effects on density. Direct effects of timing on mortality could also have occurred and could have contributed to the patterns of survival. Phenology could have affected mortality from *Entomophaga maimaiga* and *Cotesia melanoscela*, as follows. The fungal pathogen *E. maimaiga* is the most important source of mortality in the two earlier releases, and has a temperature optimum for development at ~20°C (Hajek et al. 1990). *E. maimaiga* may have been able to multiply faster in the cooler early releases, and so build to higher abundance. *E. maimaiga* is unlikely to show the same pattern every year, however, because spore germination rates and production of infective conidia depend on high humidity and rainfall (Hajek et al. 1990, Weseloh and Andreadis 1992*a*). Leaf age does not affect the susceptibility of gypsy moth larvae to infection by *E. maimaiga* (Hajek et al. 1995). The timing and amount of rainfall are also important (Weseloh and Andreadis

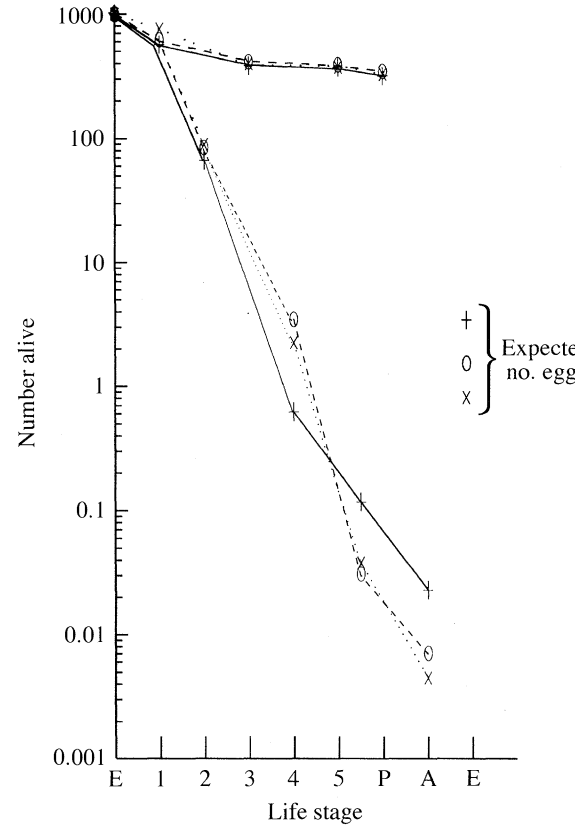

FIG. 7. Estimated average cohort survivorship of the three releases (lower three lines) and of the insects in protective sleeves on black oak (upper three lines) in 1996. First release, circles and dashed lines; second release, × and dotted lines; third release, + and solid lines. The final three data points (above right-hand "E") indicate the expected egg production of each of the three releases, on the same scale as the survivorship curves, assuming that the sex ratio was 50:50 and that 70% of individuals feed on black oak, and 30% on white oak.

1992*b*, Elkinton et al. 1991), making *E. maimaiga* dynamics unpredictable.

The parasitoid wasp *Cotesia melanoscela* is also directly affected by phenology in two ways. The second generation of *Cotesia melanoscela* typically emerges when gypsy moth populations have reached late instars, which female wasps can not easily parasitize (Weseloh 1976). In our experiments, the Third release provided younger hosts that were more suitable for oviposition by the second generation of *Cotesia melanoscela,* which is probably why mortality from *Cotesia melanoscela* was so high at the Third release in 1995. Counterpoised with these timing effects is the direct effect of leaf age on *Cotesia* survival; for *Cotesia* developing in gypsy moth larvae of similar age but feeding on leaves of different ages, *Cotesia* survival decreases with leaf age in the 16-d period after budbreak (Werren et al. 1992). This may help explain why the impact of *Cotesia melanoscela* on the Late release in 1996 was not as high as in 1995.

To fully understand the effects of density and phenology in our experiments, it is important to realize that the effects of late-instar density and phenology were unintentionally confounded. That is, the late release had the lowest late-instar density and thus the lowest mortality rate, so we cannot tell whether the lower mortality of the late release was due to its lower density, or to the effects of phenology on mortality agents. Nevertheless, in additional experiments we crossed density and phenology treatments to separate these effects and discovered that *both* density and phenology contribute to the mortality difference between early and late releases (Hunter and Elkinton 1999).

Why don't gypsy moths emerge later since there was a net benefit to late emergence in our study? First of all, the most important source of mortality in the early releases, *E. maimaiga,*. is a new natural enemy in this system since 1989 (Andreadis and Weseloh 1990), and the gypsy moth probably has not had time to adjust its phenology in response to it. Gypsy moth populations in North America have low genetic variation (Harrison et al. 1983), which can limit their evolutionary response. Also, the mortality from *E. maimaiga* and the other natural enemies varies substantially and unpredictably among years. The fecundity effect, in contrast, is apparently consistent among years, and so exerts consistent selection pressure for early emergence.

Although our experiments were carried out at a much larger scale than most ecological field experiments (Kareiva and Andersen 1988), the spatial scale was necessarily much smaller than the typical 10–100-km^2 scale typical of natural gypsy moth outbreaks. In such naturally occurring outbreaks, dispersal by ballooning might not decrease local densities, because increased ballooning in our experiments did not appear to increase mortality. In natural populations, the indirect effect of phenology via increased dispersal may therefore disappear. The direct effects of higher temperatures decreasing *E. maimaiga* success and delayed phenology increasing the impact of the second generation of *Cotesia melanoscela,* would remain.

In summary, there is a complex interaction between host plant phenology effects and natural-enemy mortality for the gypsy moth. Timing effects on natural-enemy mortality are clearly an important contributor to among-year variability in gypsy moth population growth rates. Mortality rates from particular natural enemies varied unpredictably, and such variation may contribute to explaining why population sizes of spring-feeding species are more variable than those of summer-feeding species. Similar effects probably occur for many other spring-feeding species. In winter moth, for example, both host plant phenology and predation contribute to variation in population densities among years, and predation explains twice as much of the variation as does plant phenology (Hunter et al. 1997). Our experiments with gypsy moth provide several messages for ecologists. First, the outcome of the treatments was very different when natural-enemy mortality was included than when it was excluded. Second, the most important effect of phenological changes in host quality was to increase dispersal, thereby spreading larvae over a greater area and reducing density-dependent mortality from natural enemies. This indirect effect of host quality was in this case more important than direct effects. Third, there was great variability among years in the amounts of mortality from different natural enemies, and since enemies were more important than host effects, the overall effects of release date on population growth probably vary greatly among years. A consistent negative impact of leaf age on fecundity occurred as well, but in our studies the positive impact of leaf age on survival in the presence of natural enemies was stronger.

Laboratory studies with gypsy moth and other spring-feeding Lepidoptera have almost always shown that younger foliage is a higher quality resource. The results of field studies, however, have been far more equivocal, probably because of the presence of natural enemies. Some field studies have reported that younger foliage is better for Lepidoptera (Futuyma and Wasserman 1980, Phillipson and Thomson 1983, Hunter 1992, Quiring 1992, Shepherd 1992, 1994, Mopper and Simberloff 1995), while other field studies have found little effect of foliage age (Crawley and Achteruzzaman 1988, Hunter et al. 1991, Watt and McFarlane 1991, Myers 1992, Connor et al. 1994). The inclusion of natural enemies in a study can thus have a profound impact on the population-level effects of phenology, suggesting that a major source of variation in the effects of budburst phenology is due to mortality caused by natural enemies and its interaction with phenology.

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