INTERACTIONS AMONG GYPSY MOTHS, WHITE-FOOTED MICE, AND ACORNS[1]

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Abstract. Low-density populations of gypsy moth, *Lymantria dispar*, were studied over a 10-yr period in Massachusetts. Increases in gypsy moth density were associated with declines in density of the white-footed mouse, *Peromyscus leucopus*, a principal predator. Furthermore, changes in density of *P. leucopus* populations were positively correlated with the density of acorn crops, a dominant winter food source for these mice. To demonstrate these effects we used a novel bootstrap regression method that adjusts for spatial and temporal autocorrelation in the time series data. The findings are compatible with a dual equilibrium model of gypsy moth population dynamics, in which low densities are regulated by mice and high densities are regulated by other factors, notably a virus disease.

Key words: acorns; bootstrap; density dependence; insect outbreaks; Lymantria dispar; Peromyscus leucopus; Quercus; *time series analysis.*

INTRODUCTION

The gypsy moth is a major defoliator of deciduous forests throughout the northern hemisphere. It remains at low densities in most years, but it occasionally erupts into outbreak phase. In 1868 it was accidentally introduced into northeastern North America, where outbreaks are frequently synchronized (Liebhold and Elkinton 1989a, Williams and Liebhold 1995a) over large regions. The causes of such outbreaks and their regional synchrony have not been explained (Liebhold and McManus 1991). Earlier research suggested that changes in density of nonoutbreak populations of gypsy moth were determined by survival during late instars (Bess 1961, Campbell 1967). Experimental studies involving mouse exclosures (Bess et al. 1947) and mouse

removal (Campbell and Sloan 1977) indicated that a dominant source of mortality during this period was predation by *P. leucopus*, the white-footed mouse. Here we provide further evidence of the importance of mice as predators of gypsy moths and show, for the first time, that changes in density of gypsy moths and white-footed mice are linked.

Tree seeds, and acorns in particular, are an important part of the diet of *Peromyscus*, and form the bulk of the winter diet (Hamilton 1941, Batzli 1977). Increases in the abundance of *Peromyscus* have been associated with large acorn crops (Hansen and Batzli 1978) and declines have been associated with mast failures (Hansen and Batzli 1979). The mechanisms for population increase following good acorn crops include winter breeding, increased overwinter survival, and earlier onset of breeding in the spring (Hansen and Batzli 1978). Similar relationships have been reported in oak wood-

lands in England for *Apodemus sylvaticus*, whose ecological role is similar to that of *P. leucopus* (Watts 1969, Flowerdew 1972). In most years, the abundance of *Peromyscus* in the spring is positively correlated with seed production during the previous autumn (Gashwiler 1979, Kaufman et al. 1995), but good mast years are not necessarily followed by high spring abundance (Kaufman et al. 1995).

From 1985 to 1987, the numbers of *P. leucopus* declined by about half across the oak forests of central Massachusetts where we were studying gypsy moth populations (Brooks and Healy 1988). We suspected that this decline was associated with annual changes in the size of the acorn crop, and that acorn crops might provide a functional link between gypsy moths and their principal vertebrate predator. We hypothesized that low-density gypsy moth populations escape into outbreak phase during years when densities of *P. leucopus* are low, and that acorn supply is the principal determinant of *P. leucopus* density.

These observations provided the impetus for the current study. Here we show that midsummer white-footed mouse densities are highly correlated with the acorn crop produced the previous autumn. The synchrony of acorn crop densities over large regions (Wentworth et al. 1992) may thus explain the onset of gypsy moth outbreaks.

METHODS

Study area

We conducted our studies within the watershed of the Quabbin Reservoir in Franklin, Hampshire, and Worcester Counties in central Massachusetts. The property is managed by the Metropolitan District Commission to provide water for the Boston municipal area. It contains a 9713-ha reservoir and 22 663 ha of surrounding uplands that are 93% forested. Most of this forest originated naturally after heavy cutting or farmland abandonment in the late 19th and early 20th centuries. Oak cover types occupy 48% of the forested acreage, and northern red oak (*Quercus rubra*), a favored host of gypsy moth, is the most abundant species of oak (Metropolitan District Commission 1995). Gypsy moth populations have been present on the area since before 1910 (Bess et al. 1947). The most recent gypsy moth outbreak occurred in 1981 (Liebhold and Elkinton 1989a), and since then populations have remained at innocuous levels.

Sampling procedures

In 1986 we selected eight stands dominated by northern red oak and established four 1-ha plots separated by at least 100 m within each stand (eight stands, 32 plots). The mean distance between stands was 8 km (range 1–21 km), a distance sufficient that little or no dispersal of either gypsy moths (Liebhold and McManus 1991) or white-footed mice (Batzli 1977) occurred between stands. Starting in 1986, we made annual estimates of gypsy moth and white-footed mouse density on these plots for 10 yr. From 1989 through 1994 we also measured acorn production.

We estimated gypsy moth density from counts of overwintering egg masses within five 15-m diameter circles in each 1-ha plot. One circle was at the plot center and the other four were centered on the corners of the square 1-ha plot. Counts were made by teams of 2–4 observers who systematically searched the ground and all tree boles within the circle (Kolodny-Hirsch 1986). Counts were made in late August through October, and they provided the density estimate for the succeeding year. Density estimates for each of the four 1-ha plots were averaged to yield a single estimate for each stand in each year.

Mice were captured in three of the four 1-ha plots in each stand in $8 \times 8 \times 25$ cm Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida) set on a grid with 15-m intervals between traps. Due to limited resources in the early years of the study, we used a 5×5 grid in 1986, a 6×6 grid in 1987 and 1988, and a 7×7 grid from 1989 through 1994. Trapping was conducted for 5-d periods in early August to estimate mouse density at the end of the pupation period for gypsy moths. Traps were set on the morning of the 1st d and checked for the next four consecutive mornings. One trap was set within 1 m of each grid point and covered with leaf litter to protect it from the elements. Traps were baited with a mixture of peanut butter, oatmeal, and bacon fat, and provided with cotton for bedding. Captured mice were marked with uniquely numbered metal ear tags and released at the point of capture.

We used the computer program CAPTURE (Otis et al. 1978, White et al. 1982) to estimate the density of mice on each plot. This program assumes a closed population, tests that assumption, and selects an appropriate estimator from a set of eight models. When the program was unable to select an appropriate estimator, we used the number of individuals caught during the trapping session as the density estimate. This occurred for 11% of 216 estimates of mouse density we made over 9 yr, typically when the densities were very low. Estimates from the three plots were averaged to provide a mean density for each stand each year.

We estimated acorn production by counting acorns falling into funnel traps placed at 40 randomly selected stations on each mammal trapping grid. Traps were constructed of polyethylene sheeting woven on a wire rim, and each had a 0.5-m² collecting area. Traps were supported by two or three stakes with the funnel opening ≈ 1 m above the ground (after Christisen and Kearby 1984). Acorn traps were opened between 8 and 30 August each year and checked periodically until all acorns had fallen (usually mid-November). Acorns were collected at each visit, returned to the laboratory, cut open, examined, and counted. Numbers of sound acorns were summed for all 40 traps on each plot, and

TABLE 1. Hypothesis tests relating change in gypsy moth egg mass density to previous egg mass density and white-footed mouse density (model 1) and change in white-footed mouse density to previous mouse density and acorn production (model 2) along with associated F statistics and conventional and bootstrap P values.

Model	Hypothesis	df	F	Conventional $P > F$	Bootstrap $P > F$
1	H_0: $\gamma_s = 0$, $s = 1-8$ (no mouse effect)	8, 48	3.48	0.003	0.022
1	H_0: $\theta = 0$ (no mouse by egg mass interaction)	1, 47	0.003	0.957	0.97
2	H_0: $\psi = 0$, $\omega = 0$ (no acorn effect)	2, 22	47.24	<0.001	<0.001
2	H_0: $\omega = 0$ (no mouse by acorn interaction)	1, 22	3.78	0.065	0.028

plot totals were averaged to estimate the number of sound acorns per hectare for each stand.

In several years we attempted to experimentally manipulate the density of mice on one or two of the four 1-ha plots in each stand. This was done by removing mice (1989, 1990) or by providing supplemental food during winter months (1987, 1988). These manipulations failed to have the desired effect on mouse density because they were overwhelmed by mouse immigration (Hazzard 1990). For the purposes of the current analyses, we dropped all density estimates for acorns, mice, or gypsy moths for the manipulated plots in the computation of the standwide averages for the year of the manipulation.

An index of predator impact on gypsy moths was obtained by measuring the daily rate of consumption of 300 gypsy moth pupae over 3-d intervals in July 1986–1990 in each plot where we measured small mammal density. The pupae were placed in the forest litter where most naturally occurring pupae are found in low-density populations (Campbell et al. 1975) and were attached in groups of 12 (6 males and 6 females) to burlap-covered boards (Smith 1989). One board was placed at each point in the inner 25 points of the 7 × 7 grid in each ha. Fraction consumed (p) was measured over 3 d and converted to a daily rate: $1 - (1 - p)^{1/3}$, unless loss exceeded 90% on the 1st day. In such cases, the fraction consumed that day was used for the daily rate, because few if any pupae would survive 3 d and any differences between stands would be obscured. The values for the three 1-ha plots were averaged to yield a single value for each of the eight stands in each year. To analyze consumption rates we fit a model (PROC REG, SAS 1989) using suitably defined dummy variables, which allowed a separate linear regression of consumption rate on log(mouse density) in each year and tested whether the average mouse effect was zero.

Statistical analyses

To assess the potential effects of mice on gypsy moths we fit, using least squares (PROC GLM, SAS 1989), the model, hereafter known as model 1:

$$\log(N_{t+1,s}/N_{ts}) \approx \alpha_s + \beta_s \log(N_{ts}) + \gamma_s \log(M_{ts}) + \epsilon_{ts}, \quad (1)$$

where N_{ts} and M_{ts} represent the respective estimated densities ($+1.0$) of gypsy moth egg masses and mice

in year t and stand s. We used $\log_{10}$ in all calculations. This yielded parameter estimates $\hat\alpha_s$, $\hat\beta_s$, $\hat\gamma_s$, but temporal and spatial correlations in the error term (ϵ_{ts}) would invalidate any estimates of standard errors or hypothesis testing based on standard least squares procedures. This problem is ubiquitous in the analysis of time series data. Our solution to the problem was to use the simple least squares estimates for the parameters but to obtain standard errors and approximate P values to accompany the usual F statistics (Sokal and Rohlf 1981; Eq. 16.14) by employing a bootstrap procedure (Efron and Tibshirani 1993) that accommodated both the temporal and spatial correlations. This procedure, described in detail in the Appendix, is similar in spirit to the bootstrap methodology used by Dennis and Taper (1994) in assessing density dependence. All statistical conclusions that follow involving tests of models 1 or 2, and their variants, are based on this method. For purposes of comparison, however, we present both the bootstrap P value and the conventional least-squares P value associated with each F statistic (Table 1).

The same analytic procedure was used to test for a significant link between white-footed mouse densities and previous years' acorn crops. Here the model, hereafter known as model 2, was:

$$\log(M_{t+1,s}/M_{ts}) \approx \phi_t + \chi_s \log(M_{ts}) + (\psi + \omega \log[M_{ts}]) \log(A_{ts}) + \delta_{ts} \quad (2)$$

where A_{ts} is the estimated density of acorns falling per hectare in year t and stand s, and δ_{ts} is the error term. The model includes an interaction term, the addition of which significantly improved the fit of the model (bootstrap $P = 0.028$, Table 1). We arrived at models 1 and 2 after consideration of several more complicated models based on examination of residuals and hypothesis testing. For example, we considered a version of model 2 with stand-specific acorn coefficients ψ_s, but did not reject the hypothesis that all ψ_s were equal ($F_{1,22} = 0.846$, bootstrap $P = 0.522$).

To test for density dependence in the time series of gypsy moth egg masses and white-footed mice in each stand, we applied the methods of Bulmer (1975), Pollard et al. (1987), and Dennis and Taper (1994). For Bulmer's method we calculated R (see Bulmer 1975 for details) and compared the result to the lower cutoff point R_L. For the randomization test of Pollard et al. (1987), we took 8000 random permutations of the dif-
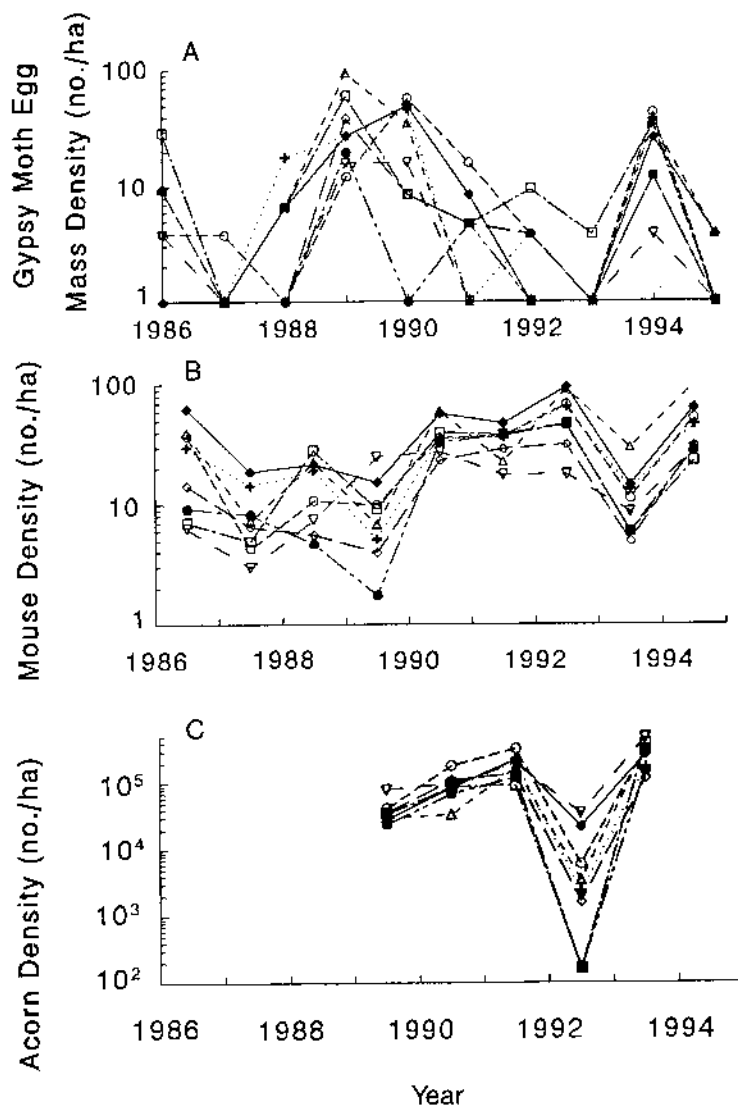
FIG. 1. Yearly estimates from each of eight stands of (A) gypsy moth egg masses per hectare as determined prior to hatch in each year, (B) white-footed mice per hectare, and (C) sound acorns per hectare from each stand beginning in 1989.

ferences of the observed log densities in successive years and computed the r_{dx} statistic (see Pollard et al. 1987 for details). The method of Dennis and Taper (1994) first involved deciding which of two alternative models to use: the Gompertz model (Dennis and Taper: Eq. 5) or the stochastic logistic (Dennis and Taper 1994: Eq. 23). We used the Gompertz model, because it gave a better fit to the data. The Gompertz model is identical to models 1 and 2 without the terms for mice in model 1 or acorns in model 2 and is the same model that underlies the procedure of Pollard et al. (1987). Under the null model we generated 8000 bootstrap samples and calculated the T_{12} statistic (Dennis and Taper 1994). To look for evidence of delayed density dependence in these time series we used PROC ARIMA (SAS 1993) to compute the partial autocorrelation functions

(Turchin 1990) and examined the resulting plots for evidence of significant lag 2 or higher effects.

We measured the degree of synchrony among the eight stands in the density estimates of acorns, white-footed mice, and gypsy moth egg masses. This was done using the method of Hanski and Woiwod (1993), which involved fitting the Gompertz model to the data separately for each stand (PROC REG, SAS 1989) and computing the pairwise correlation coefficients among stands of the yearly model residuals (PROC CORR, SAS 1990).

RESULTS

Over the 10-yr period, gypsy moths fluctuated between 0 and 100 egg masses per hectare (Fig. 1A). These densities are characteristic of nonoutbreak pop-
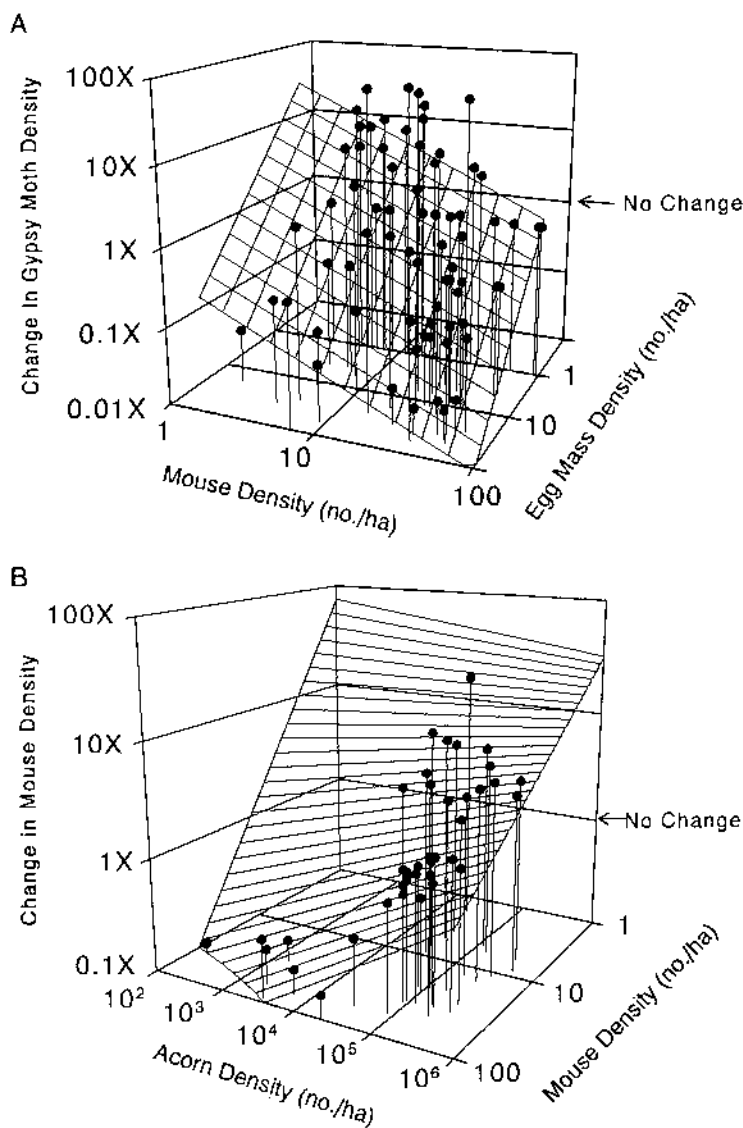
A

B

Fig. 2. (A) Change in gypsy moth egg mass density (N_{t+1}/N_t) as a function of white-footed mouse density (per hectare) and previous egg mass density. Surface corresponds to the fitted model 1 using mean values for stand-specific coefficients: $\alpha = 1.87$, $\beta = -1.08$, $\gamma = -0.86$. (B) Change in density of white-footed mice (M_{t+1}/M_t) as a function of mouse density (M_t) and the density of the acorn crop the previous autumn. Surface corresponds to the fitted model 2 using mean values for stand-specific coefficients: $\phi = 2.04$, $\chi = -2.26$, $\psi = -0.088$, $\omega = 0.254$.

ulations, an order of magnitude lower than those that cause noticeable defoliation (Ganser et al. 1985). Increases in gypsy moth density occurred in years when densities of white-footed mice were low (Figs. 1A, B and Fig. 2A). The effect of mice was statistically significant (bootstrap $P = 0.022$, Table 1), as determined by a test of the model in Eq. 1 for no mice effects.

Changes in population densities of white-footed mice and gypsy moth, and in acorn production, were all partially synchronized among stands across the study region (Fig. 1). Quantitatively, we can express synchrony as the pairwise spatial correlation in density between stands after removing the effects of local dy-

namics as described by Hanski and Woiwod (1993). The mean correlations were 0.75 (range: 0.52–0.95) for gypsy moth egg masses, 0.69 (range: 0.05–0.96) for white-footed mice, and 0.83 (range: 0.34–1.0) for acorns.

We evaluated a version of the model in Eq. 1 with an interaction term $[\theta \log(M_a) \times \log(N_a)]$, but we did not include it because we did not reject H_0: $\theta = 0$ (bootstrap $P = 0.97$, Table 1). This implies that the rate of predation by white-footed mice for a given mouse density did not depend on gypsy moth density, i.e., it was not density dependent. The pronounced decline in gypsy moth density change with increases in

TABLE 2. Tests for density dependence in time series of estimated density per hectare of (A) gypsy moth egg masses and (B) white-footed mice based upon Bulmer's R (Bulmer 1975), the randomization test of Pollard et al. (1987), and the parametric bootstrap method of Dennis and Taper (1994).

Stand	Bulmer's R	Pollard et al.		Dennis and Taper	
		T[†]	P	T_{12}[‡]	P
A) Gypsy moths					
1	0.695	−0.62	0.35	−2.11	0.24
2	0.601	−0.66	0.27	−2.33	0.19
3	0.520§	−0.74	0.13	−2.91	0.08
4	0.460§	−0.79	0.06	−3.39	0.04
5	0.404§	−0.84	0.02	−4.16	0.02
6	0.338§	−0.89	0.01	−5.25	0.01
7	0.645	−0.66	0.28	−2.29	0.19
8	0.537§	−0.72	0.31	−2.77	0.09
B) White-footed mice					
1	0.515	−0.69	0.29	−3.25	0.05
2	0.459	−0.67	0.32	−2.66	0.12
3	0.608	−0.62	0.47	−2.40	0.17
4	0.550	−0.68	0.31	−2.72	0.11
5	0.608	−0.74	0.18	−2.68	0.12
6	0.769	−0.65	0.35	−2.00	0.28
7	1.232	−0.39	0.72	−1.43	0.47
8	0.794	−0.69	0.27	−2.15	0.24

[†] $T = r_{dx}$ statistic from Pollard et al. (1987:2050).
[‡] One-sided T_{12} statistic from the Gompertz model (see Dennis and Taper 1994: Eq. 8).
§ Significantly density dependent ($R < R_L = 0.542$ for gypsy moths and $R < R_L = 0.470$ for white-footed mice).

gypsy moth density (Fig. 2A) might be interpreted as evidence for just such a negative feedback in gypsy moth population trends. A similar decline is evident for white-footed mice (Fig. 2B). However, the nonindependence of axes in plots of $\log(N_{t+1}/N_t)$ vs. $\log(N_t)$ causes negative slopes to occur even if there is no density dependence present (Royama 1992: 31). Consequently, we used the methods of Bulmer (1975), Pollard et al. (1987), and Dennis and Taper (1994) to apply explicit tests for density dependence (Table 2) in the time series of gypsy moth egg masses and white-footed mice. Bulmer's test revealed significant density dependence among gypsy moths in five of eight stands (Table 2). Three of these five stands were density dependent with the Dennis and Taper test at $P < 0.05$, and all five were density dependent at $P < 0.10$. The tests of Pollard et al. (1987) revealed significant density dependence in two of the eight stands (Table 2). These comparisons control the per-stand error rate and not the experimentwise error rate. For white-footed mice, significant density dependence ($P < 0.05$) was detected in only one stand and only with the Dennis and Taper test (Table 2). None of the estimated partial autocorrelation functions (PROC ARIMA, SAS 1993) indicated the existence of delayed density dependence in the time series of gypsy moths or white-footed mice. We recognize, however, the limited statistical power of this procedure for time series as short as 10 generations.

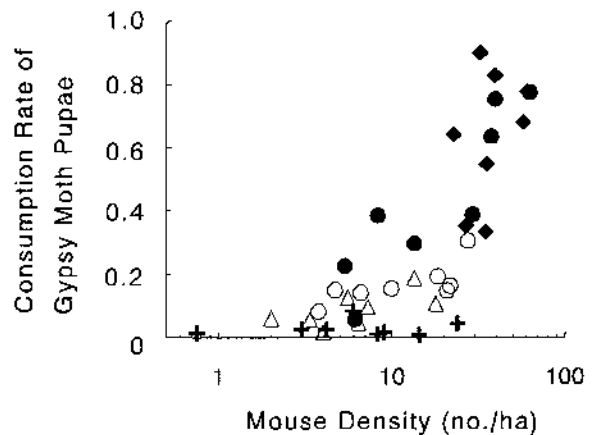Consumption rates by all predators, including mice,

FIG. 3. Density of white-footed mice plotted against the mean daily proportion of 300 gypsy moth pupae deployed on each plot that were consumed by all predators including mice over a 3-d test period. Symbols indicate different years: 1986, ●; 1987, △; 1988, ○; 1989, +; 1990, ◆.

of the experimentally deployed gypsy moth pupae were positively correlated with white-footed mouse densities (Fig. 3, $F_{1,30} = 14.13$, $P = 0.007$), suggesting that white-footed mice were indeed the dominant source of predation on these pupae.

Midsummer white-footed mouse densities declined or remained at low levels when acorn production was low the previous autumn and increased or remained at high levels following large acorn crops (Figs. 1B, C and 2B). A test for no acorn effect in the model of Eq. 2 was rejected at bootstrap $P < 0.001$ (Table 1). The model includes a significant mouse-by-acorn interaction term (bootstrap $P = 0.028$, Table 1), which causes the surface in Fig. 2B to twist (i.e., it is not a plane). The interpretation is that the relationship between acorns and change in mouse density was weakest at the lowest mouse densities. The coefficient ψ for acorns in the model of Eq. 2 is negative (-0.088), but this is counteracted by the larger positive value (0.254) of the interaction coefficient ω so that the model predicts that change in mouse density will increase with increasing acorn density (see Fig. 2B) for all except mouse densities <2.2 mice per ha. This value is lower than all except one of our estimated mouse densities from these stands.

DISCUSSION

Our findings are compatible with the general synoptic model for outbreak insects proposed by Southwood and Comins (1976), in which low-density populations are maintained by predators or parasitoids with constrained abilities to respond to increases in the density of their prey. Such constraints are pronounced in the case of polyphagous predators, whose densities are weakly linked to those of their prey. A specific model of this type was proposed for gypsy moth by Campbell (1975) and Campbell and Sloan (1977). According to

Campbell's model, low densities are maintained near equilibrium by predators, whereas high densities are limited by other factors, notably a virus disease (Doane 1970, 1976). The low-density equilibrium constitutes a threshold density above which the predator consumes a declining fraction of the gypsy moth population, which thereupon expands exponentially to outbreak phase. The low-density threshold thus determines the onset, but not the cessation, of outbreaks. Our data suggest that the threshold density of gypsy moth is governed by variation in the density of white-footed mice.

The synoptic model proposes that the generalist predator or parasitoid stabilizes the prey populations at low density by way of a negative feedback (positive density dependence) between prey density and predation rates. Our tests for density dependence (Table 1) provided only equivocal evidence for density dependence in the egg mass time series from some stands. Although recent analyses have identified these tests as the most statistically powerful available, all three procedures have low power for time series as short as 10 generations (Holyoak 1993, Dennis and Taper 1994). Dennis and Taper (1994) showed that their test was more powerful than that of Pollard et al. (1987), which may explain why there was no evidence for density dependence with the latter test. It is clear that unequivocal conclusions regarding the presence or absence of density dependence in these population systems will require analyses of further data.

For white-footed mice, it would seem that density-dependent constraints on population growth are a foregone conclusion, because, in contrast to gypsy moths, their populations fluctuate over a narrow range of densities despite a high reproductive rate (Ostfeld 1988). The multiple generations of mice that elapsed between our annual mouse censuses may help explain why the tests failed to detect density dependence in mice. On the other hand, simulations by Holyoak (1994) indicate that such gaps in a time series do not compromise these tests for direct density dependence.

Of course, the analyses of our time series data reveal correlations and not causation. It is certainly possible that other factors correlated with acorn crops, presumably weather related, may cause the observed fluctuations of mice or gypsy moths. However, our experimental demonstration of a link between mouse densities and predation rates on gypsy moth pupae (Fig. 3), coupled with the experimental results of earlier researchers (Bess et al. 1947, Campbell and Sloan 1978a), strongly supports the conclusion that changes in mouse density are responsible for fluctuations in gypsy moth density. Similarly, our results, along with previous studies that demonstrate that acorns are an important overwintering food for *P. leucopus* (Hansen and Batzli 1978, 1979, Kaufman et al. 1995), suggest that variation in the size of acorn crops is the cause of fluctuations in mouse density.

For gypsy moth, high-density populations are constrained by virus diseases (Doane 1970, 1976) and other density-dependent factors, including competition for food, but for low-density populations, the existence of density-dependent regulation is debatable. Evidence in favor of density dependence was presented by Campbell (1967), who analyzed gypsy moth life table data and found that mortality of late instars increased with density at the lowest densities. Campbell and Sloan (1978a) analyzed the Melrose Highlands data, a 22-yr time series of gypsy moth egg mass densities, and concluded that populations were stabilized at low density based on the fit of nonlinear regression models relating rate of growth [log (N_{t+1}/N_t)] to log density. In contrast, however, Liebhold (1992) analyzed the same data with different analytical techniques and concluded that there was little evidence for low-density regulation. Elkinton et al. (1989) argued that it is possible for mice to exert a large influence on low-density gypsy moth populations without causing density-dependent mortality. The low-density equilibrium of gypsy moth populations either may not exist or may be caused by other factors. What is needed are experiments to determine whether predation by mice on gypsy moths is density dependent.

The synoptic model contrasts with previous descriptions of the dynamics of gypsy moth populations in Yugoslavia, which appear to be regulated by parasitoids (Sisojevic 1975, Montgomery and Wallner 1988) and exhibit delayed density dependence (Turchin 1990). Such a system exhibits regular cycles around a single equilibrium density, whereas the synoptic model proposes two equilibria maintained by different factors at high and low density. In North America, 10 species of specialist and generalist parasitoids have been introduced and established, but their role in gypsy moth population dynamics is ambiguous. Several studies have shown that parasitoids can decimate experimentally created populations of gypsy moth with a marked spatially density-dependent parasitism (Liebhold and Elkinton 1989b, Gould et al. 1990). Most studies of natural populations in North America, however, have indicated little or no evidence for direct or delayed density-dependent parasitism and rates of parasitism that are much lower at all gypsy moth densities (Liebhold and Elkinton 1989b, Williams et al. 1992), than those reported for European populations (Sisojevic 1975, Montgomery and Wallner 1988).

A general model for outbreak insects has been proposed by Ginzburg and Taneyhill (1994) driven by delayed density dependence in fecundity. These authors cite evidence for such maternal effects in gypsy moth (Rossiter 1991) in support of their model. The fluctuation of low-density gypsy moth populations evident in Fig. 1A is not compatible with the Ginzburg and Taneyhill model, which predicts a steady exponential increase in low-density populations following the collapse of an outbreak. Similar predictions are made by

simple models of insect diseases, which appear to predict the frequency of outbreaks of some forest insects (Anderson and May 1981). It is well established that outbreaks of gypsy moth are usually terminated by epizootics of a nuclear polyhedrosis virus (Doane 1970, 1976). Foster et al. (1992) have proposed a modified Anderson–May model of this virus to explain the long-term dynamics of gypsy moth. Mortality from this pathogen is negligible at the densities reported in this study (Doane 1970), and we have observed very few larvae dying from it among those we have collected from our plots, even in years (1990, 1991) when densities declined dramatically. Our data suggest that such simple models are inadequate and that gypsy moth populations are maintained by different factors at high and low density, as in the synoptic model (Southwood and Comins 1976).

Mouse densities explain only a part of the overall variation in gypsy moth density change (Fig. 2A). Some of the unexplained variation is due to measurement error (not explicitly modeled here), especially in our low-density estimates of egg masses per hectare. Additional variation is undoubtedly caused by other sources of gypsy moth mortality, including other predators, parasitoids, and disease. In particular, in 1989, the first recorded epizootic of the fungal pathogen *Entomophaga maimaiga* decimated gypsy moth throughout the northeastern United States (Hajek et al. 1990). Despite larval mortality from *E. maimaiga* of 60–90% on our plots (Hajek et al. 1990), we saw little consistent change in gypsy moth egg mass density in that year (Fig. 1A). We believe this occurred because densities of white-footed mice across the region were low in 1989. In subsequent years, *E. maimaiga* caused substantially lower mortality on our plots.

The link we have established between gypsy moths and white-footed mice, both of which are autocorrelated systems (density in any year is a function of density in previous years), complicates the interpretation of findings of significant direct (Bulmer 1975, Pollard et al. 1987, Dennis and Taper 1994) and delayed density dependence (Turchin 1990) based on time series analysis. Tests of direct density dependence for gypsy moths entail fitting model 1, or a variant of model 1, without the term involving mice, the effect of which is incorporated into the error term. The resulting autocorrelated error may lead to spurious positive tests for density dependence (Solow 1990), at least with Bulmer's test. Such autocorrelated errors will also result in findings of spurious delayed density dependence (Royama 1992, Williams and Liebhold 1995b) with time series analysis (Turchin 1990). Thus, findings of significant delayed density dependence do not necessarily imply the action of agents such as specialist parasitoids, whose densities lag behind that of their hosts by one or more generations.

Our findings that changes in white-footed mouse density are related to the acorn crop the previous autumn confirm earlier studies that link mouse densities to the overwintering food supply. In our data, the biggest effect occurred when the mouse densities declined from high levels following a bad acorn year (Fig. 2B). In years of abundant acorns, mouse densities did not always increase, a finding consistent with the conclusion of Kaufman et al. (1995), and presumably the cause of the significant mouse-by-acorn interaction term (model 2) as illustrated by the bend in the fitted surface (Fig. 2B). It is the synchronous decline in density in white-footed mice that is most important to the regional onset of gypsy moth outbreaks. In contrast to acorns, late-instar gypsy moths are an ephemeral food resource for white-footed mice that occur when other foods are abundant (Smith 1989). Thus, gypsy moths should have little or no impact on mouse density.

The determinants of acorn production are complex, involving both genetics and weather-related factors (Olson and Boyce 1971). Each oak species tends to produce large acorn crops at certain intervals, but weather effects are superimposed on these inherent tendencies and explain much of the yearly variation in acorn crop size (Sork et al. 1993). In our research area, and indeed over much of the northeastern United States, red oak is by far the most abundant oak species (Brooks et al. 1993). Good and poor acorn crops have been reported for relatively large areas (Downs and McQuilkin 1944, Goodrum et al. 1971, Christisen and Kearby 1984, Wentworth et al. 1992). Good mast years result from exceptional production from one species, or coincident fair to good production among several species. Poor production by one species is often offset by good production from another (Beck 1977, Christisen and Kearby 1984). Although complete mast failures are considered rare, synchronous poor production among species has been reported frequently within stands (Burns et al. 1954, Beck 1977, Rogers et al. 1990, Sork et al. 1993), and occasionally over large areas (Uhlig and Wilson 1952, Wentworth et al. 1992). Weather effects, such as those of late spring frosts on acorn crops (Goodrum et al. 1971), and the synchrony of such crops over regions of at least 1000 km² (Christisen and Kearby 1984) may explain the synchronous fluctuation of gypsy moth and white-footed mice evident in our data. These findings may thus explain the regional synchrony of gypsy moth outbreaks reported in previous studies (Williams and Liebhold 1995a, Liebhold and Elkinton 1989a, Liebhold and McManus 1991) and the regional onset of gypsy moth outbreaks.

The interactions described here are complicated by the fact that gypsy moths can influence acorn crops. Previous studies have shown that acorn production is severely reduced following defoliation by gypsy moth (Gottschalk 1989). However, these effects last for 1 or 2 yr after gypsy moth outbreaks collapse and would have little influence during the long periods between outbreaks, such as those reported here. Defoliation from gypsy moth last occurred on our study sites in

1981, 5 yr prior to the beginning of our study. The suppression of acorn crops during gypsy moth outbreaks and the consequent decline of mouse populations may explain why gypsy moths sometimes rebound to outbreak phase within 1 or 2 yr following a virus-induced collapse of high-density populations (Campbell and Sloan 1978b). More typically, however, gypsy moth populations remain at low density following a collapse. Doane (1976) has shown that mortality from virus remains high in the year following the collapse because of high amounts of viral inoculum in the environment.

Acorns have been implicated as important foods that influence the densities of several mammalian species including white-tailed deer, *Odocoileus virginianus* (Wentworth et al. 1992, McShea and Schwede 1993). *Peromyscus* spp. are the most abundant small mammals in forests throughout North America, and prey on many forest insects (Smith 1989). The white-footed mouse is also a principal reservoir of Lyme disease (Mather et al. 1989). The links we have described among acorns, white-footed mice, and gypsy moths may thus extend to other species and are a dominant feature of the food web that comprises the oak forests that cover much of eastern North America.

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APPENDIX

Conventional least squares analyses assume that the errors are uncorrelated and are independent of any regressors (independent variables) used in the model. The use of lagged variables [e.g., $\log(N_{ts})$ in Eq. 1] violates the latter assumption, while the former can be negated by either temporal correlations that are typical of time series data or spatial correlations that arise when random factors within a year influence response variables on all plots. A full discussion of this topic is beyond the scope of this paper. Our solution to these problems was to model the error term ϵ_{ts} in Eq. 1 as: $\epsilon_{ts} = \rho_s\epsilon_{t-1,s} + u_{ts}$ where ρ_s describes an autocorrelation in the errors for stand s and u_{ts} represents other errors specific to stand s in year t, which were allowed to vary and to be correlated between stands. For stand s the autocorrelation ρ_s was estimated by: $\hat{\rho}_s = \sum_{t=2}^{T} r_{ts}r_{t-1,s}/\sum_{t=2}^{T} r_{t-1,s}^2$ where r_{ts} are the residuals from least squares and u_{ts} was estimated by $\hat{u}_{ts} = r_{ts} - \hat{\rho}_s r_{t-1,s}$.

Because, for a given stand, the $\hat{u}$ do not necessarily average to zero, we used a centered version (Efron and Tibshirani 1993: 95): $e_{ts} = \hat{u}_{ts} - \sum_{t=1}^{T} \hat{u}_{ts}/(T - 1)$ for bootstrapping. We then generated 500 bootstrap estimates of the 10-yr time series from each stand based on model 1 using, as input, the least squares parameter values ($\hat{\alpha}_s, \hat{\beta}_s, \hat{\gamma}_s$), the observed density of mice (M_{ts}) and the 1st yr's density of gypsy moths (N_{1s}). The error term $\hat{e}_{ts}$ for each successive year was calculated as follows: for $t = 2$ we selected an integer k at random from 1 to T and set $\hat{e}_{2s} = r_{ks}$. For $t > 2$, we selected an integer k from 2 to T and set $\hat{e}_{ts} = \hat{\rho}_s\hat{e}_{t-1,s} + e_{ks}$. For each bootstrap time series we recalculated $\hat{\alpha}_s, \hat{\beta}_s, \hat{\gamma}_s$, thus obtaining a distribution of these parameters from which we calculated standard errors (Efron and Tibshirani 1993). For hypothesis testing we bootstrapped under the null model.