FORECASTING GYPSY MOTH EGG-MASS DENSITY

by Robert W. Campbell

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453--145.7 x 18.77 *Porthetria dispar* L.--015.5

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ABSTRACT

Several multiple regression models for gypsy moth egg-mass density were developed from data accumulated in eastern New England between 1911 and 1931. Analysis of these models indicates that: (1) The gypsy moth population system was relatively stable in either the OUTBREAK phase or the INNOCUOUS one; (2) Several naturally occurring processes that could terminate the OUTBREAK phase are represented by the models, but they do not indicate mechanisms sufficient to change the system from the INNOCUOUS phase to the OUTBREAK one. Some of the implications arising from the above conclusions are discussed.

INTRODUCTION

DATA HAVE BEEN accumulating since about 1890 on various aspects of the gypsy moth/forest system in the northeastern United States. Most of these data, unfortunately, are too limited in scope to be of much potential value to us today.

However, one data base may be an exception: data accumulated between 1911 and 1931 by personnel of the now defunct Melrose Highlands, Massachusetts, Gypsy Moth Laboratory, Bureau of Entomology, USDA, and then stored in a variety of places between 1931 and 1970. Some of these records were lost in a fire that destroyed the Northeastern Forest Experiment Station's Forest Insect and Disease Laboratory at New Haven, Connecticut in 1964.

The relatively massive overall scope of the remaining data was re-discovered in 1970. This is a report on some of our efforts to analyze and interpret these old records. In particular, I have attempted to develop preliminary multiple-regression models from these data for forecasting gypsy moth egg-mass density at the start of "next" year (year $n + 1$).

OBJECTIVES

My primary objective was to develop a model from which gypsy moth egg-mass density could be forecast with reasonable accuracy.

A second objective was to use the Melrose data to evaluate as many as possible of the notions about the processes that determine gypsy moth density.

Finally, it was hoped that the models might themselves prove to be useful in expanding our knowledge about the dynamics of this and similar population systems, and that this knowledge might result in new insights about how such population systems should be managed.

PROCEDURES

Source Data

The biological data used here were accumulated by personnel of the old Melrose Highlands Gypsy Moth Laboratory. They established 264 plots in 1911 and 1912. Although about 75 of these plots were dropped within 2 years, 122 were maintained through 1921, and 55 were maintained through the fall of 1931. They were scattered along the seaboard of eastern New England from the landward end of Cape Cod to Kennebunk, Maine *(Campbell 1973)*.

Each plot was circular and 100 feet in diameter. Within each plot the species and dominance class of each tree that was at least 3 inches d.b.h. was recorded. Annual records were kept on gypsy moth egg-mass density *(Campbell 1973)*, defoliation per tree, and tree condition. The diameter of each tree was recorded in 1912 and again in 1921.

The weather data we used were extracted from the records of 31 weather-recording stations in the area of interest. The records were obtained from the U.S. Weather Bureau's archives in Asheville, North Carolina.

Data Processing

The original data set was divided into three decks: the *TREE* deck, the *EGG MASS* deck, and the *WEATHER* deck. The composition of each deck is described below.

The *TREE* deck consisted of 14,266 individual tree records, spanning a maximum of 21 years each. Variables recorded for each tree included plot number, species, diameter class in inches (3-6, 6-9, 9-12, >12), dominance class (dominant, intermediate, suppressed), an annual estimate of tree condition (good, fair, poor, dead), and an annual estimate of defoliation (in 5-percent increments). Tree circumferences were recorded in 1911, and again in 1921 for trees that were still alive and in the plot system.

The *EGG-MASS* deck included plot number, year, egg masses in the plot in years (n — 1), (n), and (n + 1), an index of site soil moisture; the percentage of plots examined in each zone in year (n) that contained (1) more than 500 egg masses per acre, and (2) more than 5,000 egg masses per acre; identification numbers of the closest weather stations and relative distances from these stations to the plot; and approximate elevation of the plot (in feet).

(Dr. David Smith, professor of silviculture at Yale University, who examined the tree records from each plot, was able, in most cases, to place the plot in one of the five site categories. Category 1 represented the driest site, 5 the wettest, and 4 the optimum for tree growth.)

The *WEATHER* deck included the identification number of the weather station, year, monthly precipitation records (in inches), monthly mean spring and summer temperatures, mean minimum winter temperatures, and extreme minimum winter temperature.

The three decks just described were processed to form a *DATA* deck of approximately 2,500 site-years, spanning a 20-year period and representing 190 different stands. (These data will be made available upon request to the author.) Variables in the *DATA* deck were derived as follows:

Total foliage.—First, the basal area, in square feet, was calculated for each living stem in each plot. Second, this value was modified according to tree condition, as measured in the previous fall, by using full basal area for trees rated in good condition, 0.75 basal area for trees rated in fair condition, and 0.5 basal area for trees rated in poor condition. Finally,

these adjusted basal areas were summed across all the trees in each plot to derive an index of total foliage, TFOL.

Overstory components.—Overstory composition was separated into *ROK*; the percentage of the overstory in the red oak group (red oak and black oak and scarlet oak); *WOK*, the percentage of the overstory in the white oak group (white oak and swamp white oak and chestnut oak); *FCA*, the percentage of the overstory in trees favored by the gypsy moth (all oaks and aspen and gray, paper, and river birch, and larch and willow and apple); *FCC*, the percentage of the overstory in trees known to be unacceptable to the insect under most conditions (ash, black locust, pitch and scots pine, all spruces, and red and white cedar); and *FCB*, the percentage of the overstory in all other species. Each of these components was estimated by deriving the adjusted plot basal area in that component and dividing this by *TFOL*.

Dominance of favored food trees.—This variable, *DOM*, is the percentage of the dominant trees on a plot that were favored by the gypsy moth (the FCA trees).

Stand condition.—Each living tree in the *TREE* deck was designated as either in good (1.0), fair (2.0), or poor (3.0) condition for each year. These ranks were averaged for each year for all living trees on the plot to yield an estimate of mean stand condition, *COND*.

Defoliation.—Mean defoliation levels observed on each plot each year were calculated for trees favored by the gypsy moth (DCA); for food class B trees (DCB), and for the whole stand (DEF). These values were easily calculated, since the original tree deck contained an estimate of the percentage of defoliation for each stem on each plot for each year.

Precipitation.—Rainfall on each plot for May and June was estimated from weather-station records. The data from the nearest station were used if the station was within 10 miles of the study plot. If a station was not within this radius, the records from two or three weather stations were interpolated on the basis of distance.

Temperature.—Seasonal temperature estimates, mean temperatures during May and June, the mean minimum temperature during the coldest month of the winter between gypsy moth egg-mass counts for years (n) and (n + 1), and the extreme minimum winter temperature, were interpolated from local weather-station data in a manner similar to the precipitation interpolation. However, differences in elevation between the weather stations and the plot were also taken into account. All weather-station temperature data were transformed to their sea-level equivalents, utilizing the relationship of a 5.4°F. decrease in temperature for every 1,000-foot increase in elevation. The distance interpolation was then performed, and the derived temperature was adjusted to the plot elevation.

The Data Deck

Processed data included an estimate of each of the following variables for every plot in the Melrose system during each year that the plot was examined. Year (n), below, is always the year during which the egg masses designated as MNOW were deposited.

Independent Variables

PM	= Precipitation in May of year (n), in inches
PJ	= Precipitation in June of year (n), in inches
RM	= Precipitation in May of year (n + 1), in inches
RJ	= Precipitation in June of year (n + 1), in inches
TMN	= Mean minimum temperature (°F.) during the coldest month between years (n) and (n + 1)
TXM	= Absolute minimum temperature (°F.) between years (n) and (n + 1)
TM	= Mean temperature (°F.) in May of year (n + 1)
TJ	= Mean temperature (°F.) in June of year (n + 1)
SSM	= Site soil moisture (driest = 1, . . . , wettest = 5)
COND	= Stand condition (good = 1, fair = 2, poor = 3)

TFOL = An index of total foliage per acre

FCA = Percentage of the total overstory foliage in class A food (all species of oak + gray, paper, and river birch + aspen + larch + willow + apple)

FCC = Percentage of the total overstory foliage in class C food (ash and black locust and pitch and scots pine, all spruces and red and white cedar)

FCB = Percentage of the total overstory foliage in class B food (all species other than FCA and FCC)

ROK = Percentage of the total overstory foliage in the red oak group (red oak and black oak and scarlet oak)

WOK = Percentage of the total overstory foliage in the white oak group (white oak and swamp white oak and chestnut oak)

DOM = Percentage of the dominant trees in the stand that were in food class A (FCA)

DCA(n) = Percentage defoliation of class A trees during year (n)

DCB(n) = Percentage defoliation of class B trees during year (n)

MLSTYR = Egg masses per acre in the fall of year (n − 1). (One egg mass was added to observed per-acre egg-mass density in each plot because in some cases observed egg-mass density was zero.)

MNOW = Egg masses per acre in the fall of year (n)

ZDL = Percentage of acres examined in a zone during year (n) that contained more than 500 egg masses per acre

ZDH = Percentage of acres examined in a zone during year (n) that contained more than 5,000 egg masses per acre

TREND = $\frac{\text{MNOW}}{\text{MLSTYR}}$

DEF(n + 1) = Percentage defoliation of whole stand during year (n + 1)

Dependent Variable

MNXTYR = Egg masses per acre in the fall of year (n + 1). (One egg mass was added to observed per acre egg-mass density in each plot because in some cases observed egg mass was zero.)

Analytical Format

In analyzing these data, I sought primarily to produce a model useful for *predicting* egg-mass density. Although the model may also prove to be useful in *understanding* something of the processes through which particular density levels are determined, this was not intended as its primary function. This distinction, which is discussed elsewhere in more detail *(Campbell 1971)*, has an important bearing on the way the data were anlayzed here.

First, the data were stratified according to overstory composition into *OAK* stands, where more than one-half the total overstory foliage was oak (ROK + WOK), and *POOR FOOD* stands, where less than one-half the total overstory foliage was in tree species favored as food by gypsy moth larvae (FCA). (A third stratum, containing stands where more than one-half of the overstory foliage was in food class A, but where less than one-half was in oak, was set aside for later analysis.)

Second, a variety of multiple regression models, having the general form $Y = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n$, were tested, provisions being made for both non-linear relationships and interactions among the independent variables, after both MNXTYR and MNOW were transformed to their natural logarithms, ln(MNXTYR) and ln(MNOW). In particular, a large number of the unpublished notes and manuscripts (on file at the Forest Insect and Disease Laboratory, USDA Forest Service, Hamden, Connecticut) that reflect the thoughts of some of the Melrose Laboratory personnel on the implications of their data with respect to gypsy moth density proved to be helpful in formulating these models.

RESULTS

The best model for *POOR FOOD* stands, using the criteria of least squares, is presented in table 1. Since 66 percent of the variation in ln (MNXTYR) was associated with variation in the independent variables, this model may prove to be useful for forecasting egg-mass density in such stands. It should be tested as soon as possible.

Two models are presented for ln (MNXTYR) in *OAK* stands (tables 2 and 3). The former model, which includes only independent variables that could be observed by March 1 of year (n + 1), accounted for 67 percent of the variation in ln (MNXTYR) (table 2). The latter model, which incorporates two independent variables that could not be observed directly before a control decision would have to be made, accounted for 74 percent of the variation in ln (MNXTYR) (table 3). Both models should be tested as soon as possible.

Since the models are additive, the contribution of each term to ln (MNXTYR) can be examined separately, and the expected value of egg-mass density itself can be determined by simply transforming ln (MNXTYR) back to MNXTYR. This procedure was followed in developing figures 1 to 18, wherein each independent variable in model three (table 3) is examined with respect to egg-mass density in the fall of year (n + 1). (Since these figures were all derived by using the mean value of each independent variable that was not otherwise specified, these mean values are shown in the appendix.)

Site Density and Zone Density

Changes in gypsy moth density within any specific place were known to be a function of zone density, the general density level of the population system within a larger, spatially defined area, since previous studies had indicated that the Melrose system could be separated into two phases, INNOCUOUS and OUTBREAK, with respect to expected trends in egg-mass density on the basis of zone density *(Campbell 1973)*.

Two measures of zone density were used: ZDL or low zone density, the percentage of the acres examined within any given zone in the fall of year (n) that contained more than 500 egg masses per acre; and ZDH or high zone density, the percentage of the acres examined in the zone that contained more than

Table 1.—Analysis of variance in egg-mass density per acre in year (n + 1) (ln MNXTYR) as a function of the specified independent variables. POOR FOOD stands; N = 1,037.

Source of Variation	DF	MS	F
Regression	14	306.2	143
Residual error	1,022	2.1	—

Intercept = 2.296

Variable	Regression Coefficient	Standard error of coefficient	t ratio on 1,022 d.f.
$(ZDL)^2$	0.00098629	0.00013893	7.1**
$(ZDL)^3$	—.00000734	.00000156	—4.7**
(ZDH)	.28347040	.05245863	5.4**
(ZDL) · (ZDH)	—.00725148	.00161175	—4.5**
$(ZDL)^2$ · (ZDH)	.00004506	.00001197	3.8**
$(PM)^2$	—.14280650	.03367144	—4.2**
$(PM)^3$	.01426990	.00417453	3.4**
(PM) · (lnMNOW)	.04810875	.01454296	3.3**
$(TMN)^2$	—.00307362	.00071851	—4.3**
(TMN) · (lnMNOW)	.01113269	.00301615	3.7**
(FCB) · (lnMNOW)	.00425318	.00125357	3.4**
$(FCB)^2$ · (lnMNOW)	—.00003111	.00001086	—2.9**
(TFOL) · (DOM)	.00016320	.00005453	3.0**
(TFOL) · $(DOM)^2$	—.00000162	.00000080	—2.0*

*Significant at 0.05 probability level.
**Significant at 0.01 probability level.
$R^2 = 0.66$.

Table 2.—Analysis of variance in egg-mass density per acre in year (n + 1) (lnMNXTYR) as a function of the specified independent variables. OAK stands; N = 555.

Source of Variation	DF	MS	F
Regression	17	148.2	72
Residual error	537	2.1	—

Variable	Intercept = 3.409 Regression coefficient	Standard error of coefficient	t ratio on 537 d.f.
$(ZDL)^2$	0.00144493	0.00022818	6.3**
$(ZDL)^3$	—.00001176	.00000259	—4.5**
(ZDL) · (ZDH)	.00539065	.00148093	3.8**
$(ZDL)^2$ · (ZDH)	—.00013696	.00003969	—3.5**
$(ZDL)^3$ · (ZDH)	.00000085	.00000028	3.1**
(TREND) · (lnMNOW)	—.03299060	.01029203	—3.2**
(TREND) · $(lnMNOW)^2$	.01071147	.00291401	3.7**
(TREND) · $(lnMNOW)^3$	—.00083713	.00021198	—3.9**
$(PM)^2$	—.06813522	.02896474	—2.4**
$(PM)^3$	—.00775066	.00426570	1.8[a]
$(TMN)^2$	—.00522347	.00074895	—7.0**
(TMN) · (lnMNOW)	.02198500	.00274274	8.0**
(WOK) · (lnMNOW)	—.00626965	.00183840	—3.4**
(WOK) · $(lnMNOW)^2$	.00073208	.00023822	3.1**
(FCA) · (lnMNOW)	.00163645	.00056021	2.9**
$(FCC)^2$ · (ZDL)	—.00003635	.00001861	—2.0*
(DCA (n)) · (lnMNOW)	—.00156839	.00033867	—4.6**

*Significant at 0.05 probability level.
**Significant at 0.01 probability level.
[a]Significant at 0.10 probability level.
$R^2 = 0.67$.

Table 3.—Analysis of variance in egg-mass density per acre in year (n + 1) (lnMNXTYR) as a function of the specified independent variables, including precipitation in June of year (n + 1) and defoliation in year (n + 1). OAK stands; N = 533.

Source of variation	DF	MS	F
Regression	22	112.1	65
Residual error	510	1.7	—

Variable	Intercept = 3.53 Regression coefficient	Standard error of coefficient	t ratio on 510 d.f.
$(ZDL)^2$	0.00203155	0.00024235	8.4**
$(ZDL)^3$	—.00001862	.00000280	—6.6**
(ZDL) · (ZDH)	.00502920	.00130149	3.9**
$(ZDL)^2$ · (ZDH)	—.00013631	.00003681	—3.7**
$(ZDL)^3$ · (ZDH)	.00000088	.00000026	3.4**
(TREND) · (lnMNOW)	.11396300	.04357555	2.6**
(TREND) · $(lnMNOW)^2$	—.26747010	.01086141	—2.5*
(TREND) · $(lnMNOW)^3$	.00148031	.00060085	2.2*
$(PM)^2$	—.06666974	.02820550	—2.4*
$(PM)^3$	.00879564	.00413062	2.1*
(RJ) · (ZDL)	—.00961119	.00211648	—4.5**
(RJ) · $(ZDL)^2$	.00009795	.00002789	3.5**
$(TMN)^2$	—.00522493	.00069087	—7.6**
(TMN) · (lnMNOW)	.02789139	.00247935	11.2**
(WOK) · (lnMNOW)	—.00573563	.00178512	—3.2**
(WOK) · $(lnMNOW)^2$	.00079620	.00022758	3.5**
(WOK) · (ROK)	—.00053924	.00022538	—2.4*
(WOK) · $(ROK)^2$	.00000924	.00000391	2.4*
$(FCC)^2$ · (ZDL)	—.00003377	.00001700	—2.0*
(DCA (n)) · (lnMNOW)	—.00184766	.00032763	—5.6**
(DEF (n+1)) · (lnMNOW)	.00926943	.00114017	8.1**
(DEF (n+1))^2· (lnMNOW)	—.00011429	.00001395	—8.2**

*Significant at 0.05 probability level.
**Significant at 0.01 probability level.
$R^2 = 0.74$.

5,000 egg masses per acre. Since high zone density was usually zero until low zone density reached 40 percent, changes in egg-mass density are shown in figure 1 for low zone densities ranging from zero to 40 percent, with high zone density set at zero. Both low zone density and high zone density were allowed to vary in figure 2, for the egg-mass density values shown.

Density in the fall of year (n + 1) is shown in figure 1 for three values of current egg-mass density (MNOW). These values (50, 250, and 500 egg masses per acre) were also held constant at these same values in the fall of year (n — 1) (MLSTYR). About 50 egg masses per acre could be expected to decrease to about 40 egg masses per acre when low density was less than 20 percent, but it might increase to about 150 egg masses per acre when low zone density reached 40 percent. Five hundred egg masses per acre, on the other hand, could be expected to decrease to about 125 egg masses per acre when low zone density was less than 20 percent, and would still decrease slightly (to about 450 egg masses per acre) even when low zone density reached 40 percent. All densities could also be expected to be slightly lower in year (n + 1) when low zone density was 10 percent than when it was zero.

The results (fig. 1) indicate that isolated high-density populations could be expected to return to low, innocuous densities within a year or so, and that sparse populations could be expected to remain stable at low density levels as long as their neighboring populations were at low levels.

Five levels for high zone density (0, 10, 20, 30 and 40 percent) are shown (fig. 2) for all

Figure 1.—Relationships between egg-mass density per acre in the fall of year (n + 1) (MNXTYR), egg mass densities per acre in the fall of years (n — 1) and (n) (MLSTYR and MNOW), and the percentage of the plots in the zone containing more than 500 egg masses per acre in the fall of year (n). All other independent variables have been held constant at their mean values.

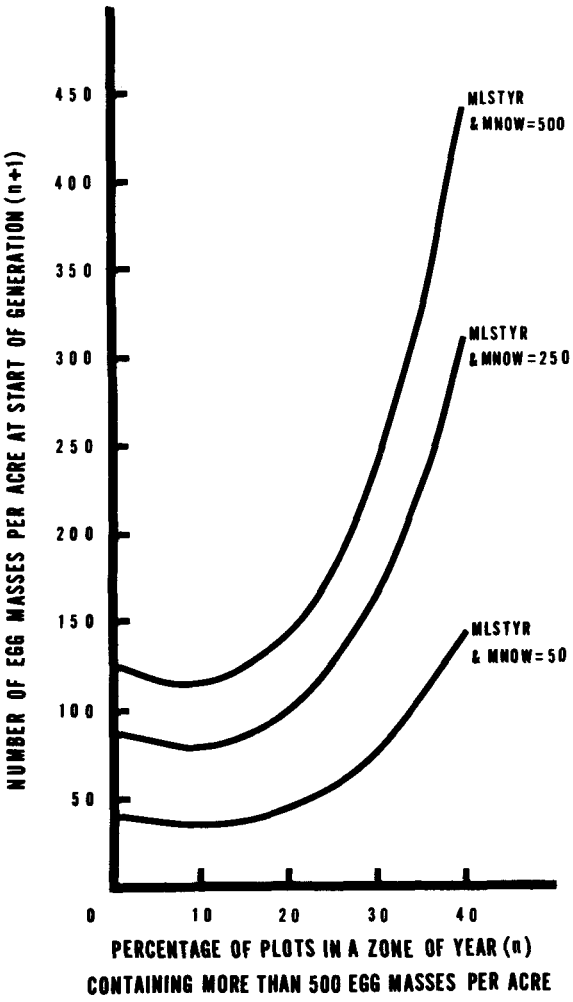
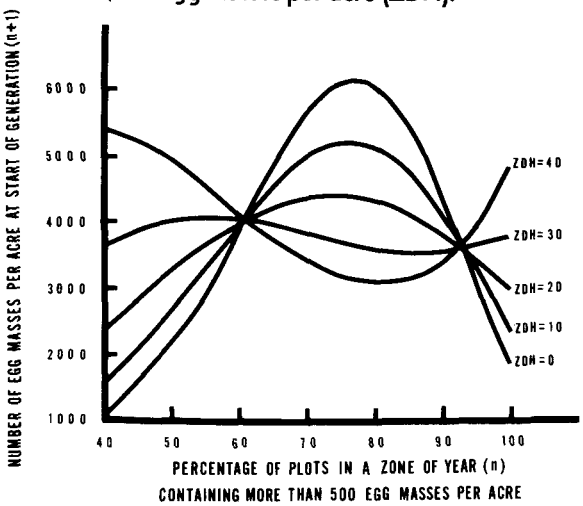


Figure 2.—Relationships between egg-mass density per acre in the fall of year (n + 1), and the percentages of the acres in the zone in the fall of year (n) containing: (a) more than 500 egg masses per acre (ZDL), and (b) more than 5,000 egg masses per acre (ZDH).

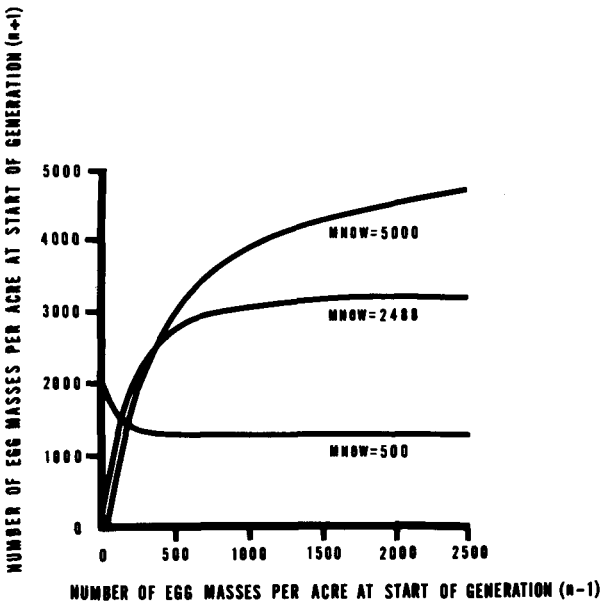


values of low zone density from 40 to 100 percent. In this case, both prior egg-mass density (MLSTYR) and current egg-mass density (MNOW) were set at their mean values, 2,705 and 2,488 egg masses per acre.

Relationships between low zone density (ZDL), high zone density (ZDH), and egg-mass density per acre within any specific place in the fall of year (n + 1) (MNXTYR) reversed twice within the range of low zone densities shown. When ZDL was near 40 percent or 100 percent, a much higher density could be expected in any given place when ZDH was high than when it was low, but when ZDL was between 65 and 90 percent, higher densities could be expected in any given place when ZDH was low than when it was high.

These results suggest that this system contained internal mechanisms for maintaining itself within the OUTBREAK phase for an indefinitely long period of time; that internal mechanisms existed for constraining this phase so that it neither collapsed nor increased without bounds.

Figure 3.—Relationships between egg-mass density per acre in the fall of year (n + 1), and egg-mass densities per acre in the fall of years (n — 1) and (n) (MLSTYR and MNOW). Outbreak conditions.



Site Density Under Outbreak Conditions

Figures 3 to 10 represent expected values of gypsy moth egg-mass density under OUTBREAK conditions. Both low zone density and high zone density were set at their mean values (53 percent and 14 percent) in these figures.

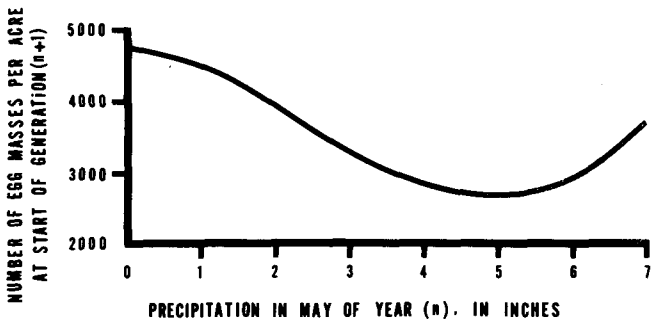
Egg-mass densities (MLSTYR) and (MNOW).—Egg-mass density per acre in the fall of year (n + 1) (MNXTYR) is shown in fig. 3 as a function of current density (MNOW) and density in the fall of year (n + 1) (MLSTYR).

Individual populations that had been stable at about 5,000 egg masses per acre for 2 years running tended to maintain high densities for a third year, while populations that had increased dramatically from a lower density in year (n — 1) to 5,000 egg masses per acre in year (n) tended to decrease. No plausible mechanisms can be suggested at this time through which the first of these results might have been determined, but one mechanism that might have been involved in determining the second sort of outcome is suggested below.

Suppose current density had been reached through a dramatic increase from year (n — 1) to (n). Density continued to increase greatly from year (n) to (n — 1) when year (n) density was 500 egg masses per acre, but greatly from year (n) to (n + 1) when year year (n) density was 5,000. Both populations may have temporarily expanded beyond the ability of their natural enemies to prevent further increase, but the former population may have been more likely than the latter to reach a density level where food exhaustion and physiological stress, leading to population collapse, were likely to occur.

Precipitation in May of year (n) (PM).—The relationship between precipitation in May of year (n) and gypsy moth egg mass density in the fall of year (n + 1) indicates that density decreased as precipitation in May of year (n) increased from zero to about 5 inches, but that density tended to increase in year (n + 1) as precipitation in this month increased above 5 inches (fig. 4). These re-

Figure 4.—Relationship between egg-mass density per acre in the fall of year (n + 1) and precipitation in May of year (n) (PM). Outbreak conditions.



sults may indicate that disease incidence increased and reduced population density in year (n + 1) as a function of increasingly high precipitation in May of year (n), but they also suggest that precipitation levels above about 5 inches in May of year (n) may reflect the operation of a hitherto unsuspected mechanism, which was influenced in some way by exceptionally high precipitation levels in May of year (n), through which the physiological state of the insect is altered in year (n + 1).

Precipitation in June of year (n + 1) (RJ.) —Relationships between ZDL, the percentage of the acres examined in a zone that contained more than 500 egg masses per acre in the fall of year (n), RJ, the number of inches of rainfall in June of year (n + 1), and MNXTYR, egg-mass density per acre in the fall of year (n + 1), are shown in figure 5. June precipitation in year (n + 1) bore a particularly close relationship to subsequent egg-mass density *(Campbell 1967a)*. This close statistical relationship probably reflects both the underlying relationship between precipitation and disease incidence among instar IV to VI larvae, and the importance of variation in the survival rate during this particular age interval to variation in egg density in the fall of the year *(Campbell 1967a)*.

The results (fig. 5) support the notion that exceptionally heavy precipitation levels in June of year (n + 1), if they are sufficiently widespread, may indicate the abrupt collapse of the OUTBREAK phase.

Mean minimum winter temperature (TMN).—Gypsy moth eggs cannot survive at temperatures below about —20°F., which is probably reflected (fig. 6) in relationships between the mean minimum temperature during the coldest month between year (n) and (n + 1) (TMN), current egg-mass density (MNOW), and egg-mass density in the fall of year (n + 1) (MNXTYR). Egg-mass density in year (n + 1) was usually reduced to an innocuous level when the mean minimum winter temperature was about zero °F., another naturally occurring mechanism through which the OUTBREAK phase could be reduced to the INNOCUOUS one.

Egg-mass density in year (n + 1) was somewhat lower when the mean minimum temperature was exceptionally high than when it was close to its mean value (14°F.), and the

Figure 5.—Relationships between egg-mass density per acre in the fall of year (n + 1), precipitation in June of year (n + 1) (RJ), and percentage of the acres in the zone in the fall of year (n) containing more than 500 egg masses per acre (ZDL). Outbreak conditions.

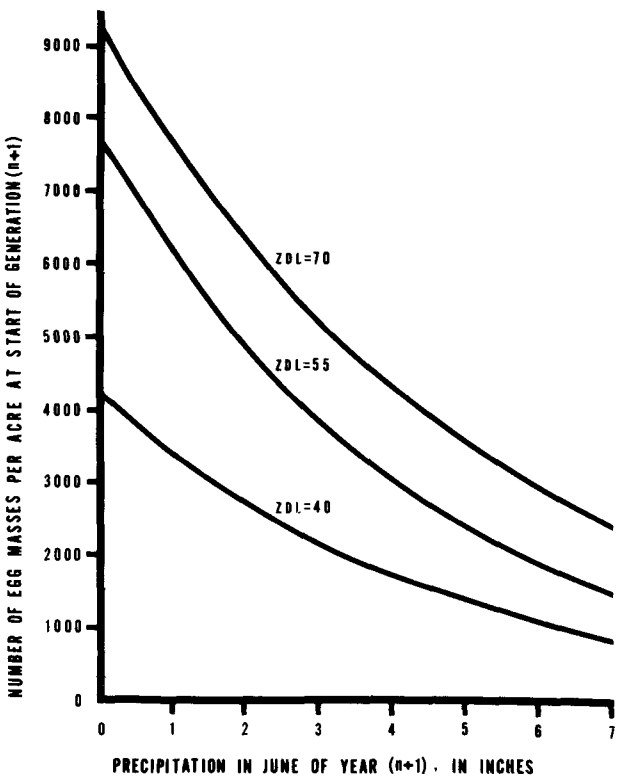
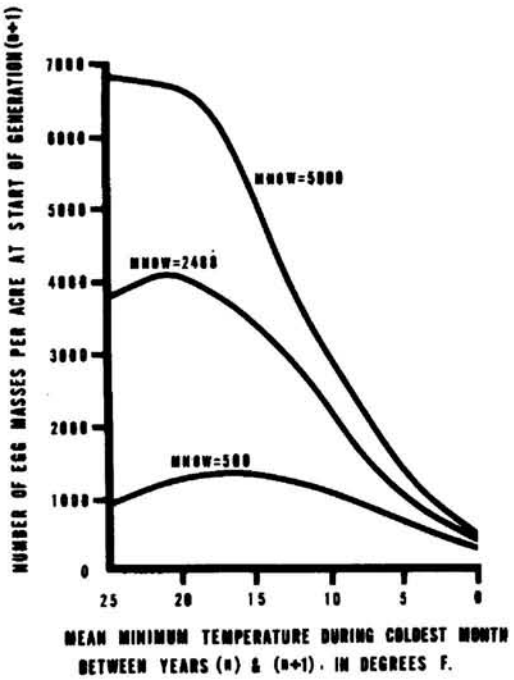


Figure 6.—Relationships between egg-mass density in the fall of year (n + 1), egg-mass density per acre in the fall of year (n) (MNOW), and the mean minimum temperature during the coldest month between years (n) and (n + 1) (TMN). Outbreak conditions.

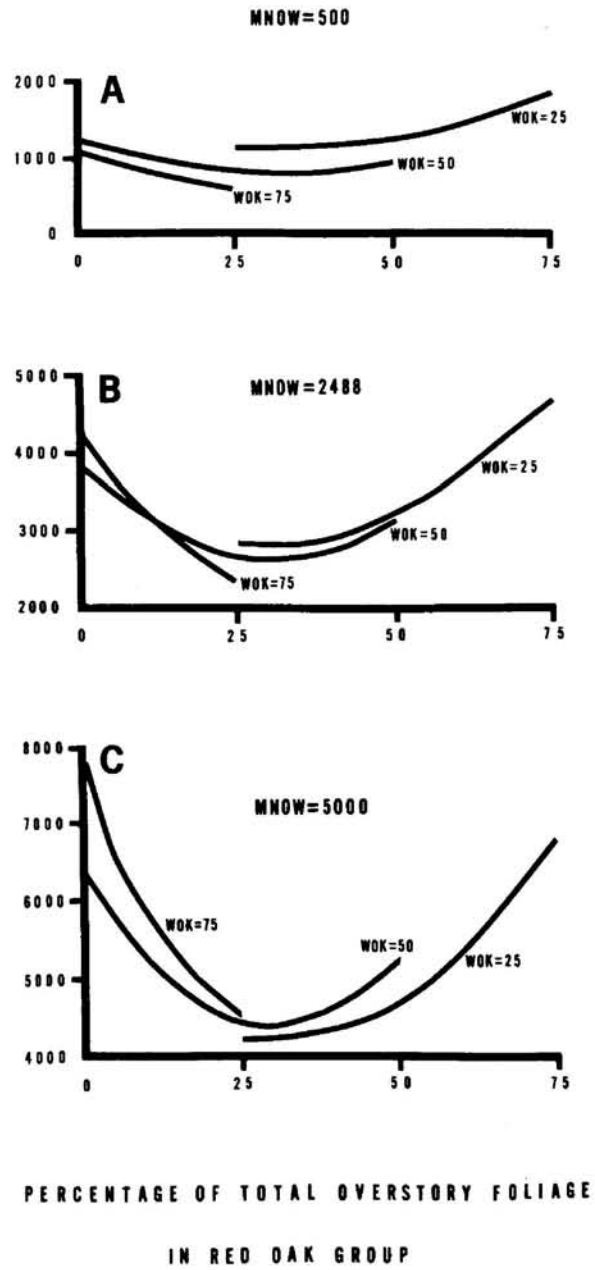


optimum mean minimum temperature for the gypsy moth apparently varied as a function of current egg-mass density. Both these relationships may imply that mechanisms similar to those described by Wellington *(1965)* for the western tent caterpillar, *Malascosoma pluviale* (Dyar), and by Morris *(1969)* for the fall webworm, *Hyphantria cunea*, may also be operative in the dynamics of gypsy moth populations. This possibility should be explored.

White oak (WOK), red oak (ROK), and current density (MNOW).—Relationships between WOK, the percentage of the total overstory foliage in the white oak group; ROK, the percentage in the red oak group; and MNOW, current egg-mass density, are shown in figure 7. (At least one-half of the total overstory foliage had to be in oak for a stand to be within this stratum, and this figure reflects this constraint.)

Higher egg-mass densities could be expected in stands composed primarily of red oak than

Figure 7.—Relationship between egg-mass density in the fall of year (n + 1) (MNXTYR) and the percentages of the total overstory foliage in the red oak group (ROK) and the white oak group (WOK). A, Relationship between MNXTYR, ROK, and WOK when egg-mass density per acre in the fall of year (n), (MNOW) is held constant at 500 egg masses per acre. B, Relationships between MNXTYR, ROK, and WOK when MNOW is held constant at 2,488 egg masses per acre. C, Relationships between MNXTYR, ROK, and WOK when MNOW is held constant at 5,000 egg masses per acre. Outbreak conditions.



in those composed primarily of white oak when current density was about 500 egg masses per acre (fig. 7A), but this relationship reversed when current density was about 5,000 egg masses per acre (fig. 7C). A transition stage is shown between these two extremes, when current density was about 2,500 egg masses per acre (fig. 7B).

In the first case, stands composed primarily of trees in the red oak group may have provided a larger number of resting locations for gypsy moth larvae where these insects were relatively safe from predators than did their counterparts in the white oak group.

When current egg-mass density reached 5,000 egg masses per acre, gypsy moth egg-mass density tended to be higher in year (n + 1) in stands composed primarily of white oaks than in those composed primarily of the red oak group. One reason for this may be that the insect tends to complete its development somewhat more rapidly, within any given field population, on white oak than on red oak, at least when population density is high *(Campbell 1961)*. This differential development rate could have been critically important in determining generation survivorship, especially when defoliation by the insect approached 100 percent.

Food class C (FCC).—Egg-mass density was reduced as FCC, the percentage of the overstory foliage that is usually unpalatable to gypsy moth larvae, increased (fig. 8). This result is in complete accord with many previous observations in this country, going back to those summarized by Mosher *(1915)*.

Defoliation of food class A in year (n) (DCA(n)).—Density decreased in the fall of year (n + 1) as defoliation of the favored food trees increased in the preceding summer (fig. 9). This relationship probably reflects the reduction in the average number of eggs in each egg mass in the fall of year (n) as defoliation increased during the summer of that same year. It may also reflect on the physiological state of the larvae issuing in the spring of year (n + 1).

Overall defoliation in year (n + 1) (DEF(n + 1)).—Relationships between egg-mass density in the fall of year (n), subsequent defoliation in the summer of year (n +

Figure 8.—Relationships between egg-mass density in the fall of year (n + 1), the percentage of the total overstory in class C food, (FCC), and the percentage of the acres in the zone in the fall of year (n) containing more than 500 egg masses per acre (ZDL). Outbreak conditions.

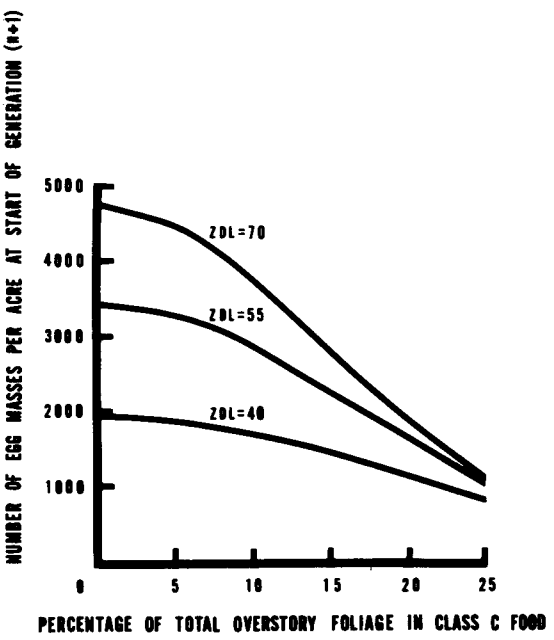


Figure 9.—Relationships between egg-mass density in the fall of year (n + 1), egg-mass density per acre in the fall of year (n) (MNOW), and percentage defoliation of class A food trees during year (n) (DCA(n)). Outbreak conditions.

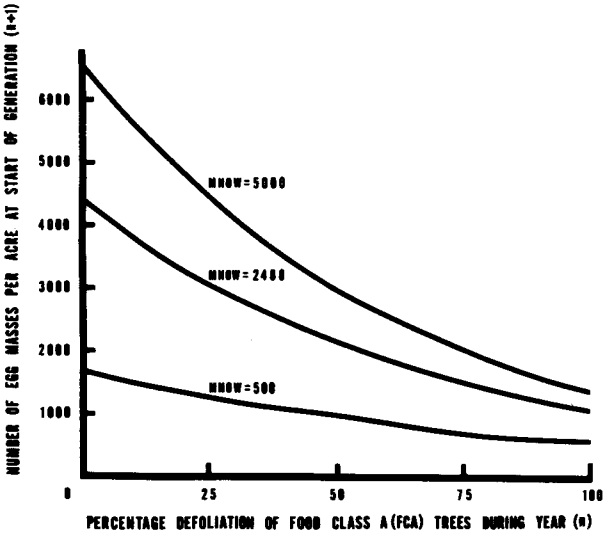
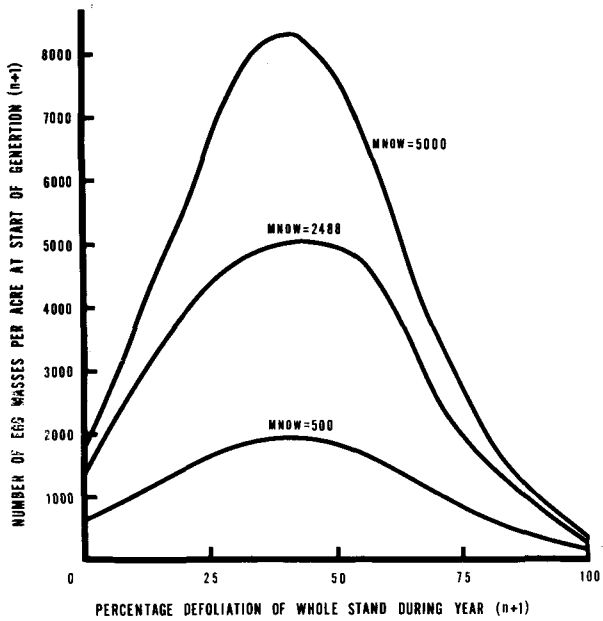


Figure 10.—Relationships between egg-mass density in the fall of year (n + 1), egg-mass density per acre in the fall of year (n) (MNOW), and percentage defoliation of the whole stand during the summer of year (n + 1), (DEF (n + 1). Outbreak conditions.



1), and egg-mass density in the fall of year (n + 1) are shown in figure 10. Although density clearly tended to decrease dramatically as defoliation approached 100 percent, it also tended to decrease as defoliation approached zero.

Density undoubtedly tended to decrease as defoliation approached 100 percent not only because the insect was exhausting its food base, but also because the incidence of disease, desiccation, and stinging by ichneumonid wasps all tend to increase dramatically under these conditions *(Campbell 1963a and (1963b)*; and since all these mortality factors also tend to kill more female than male insects, their real effects would be magnified even more. This mechanism could reduce an OUTBREAK phase to an INNOCUOUS one, although widespread and extremely heavy defoliation would both be prerequisites.

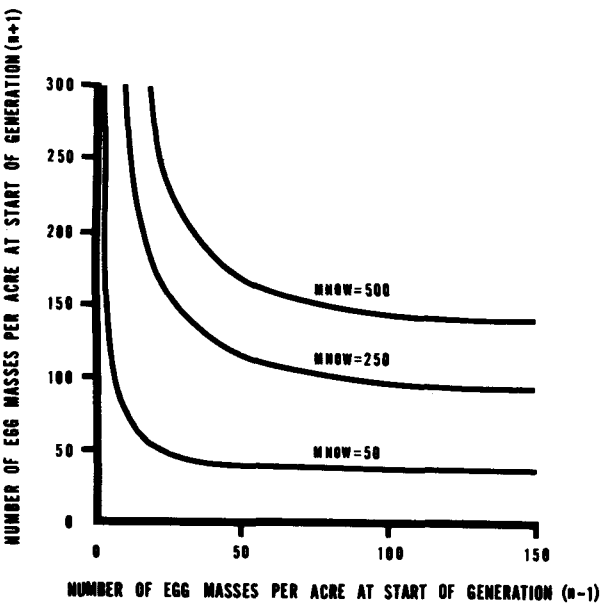
Finally, why should population density have tended to decrease as defoliation approached zero? Although this phenomenon appears to be relatively common, it has been mentioned only briefly in the literature, and no mechanisms have been proposed that might account for it. Here is a problem that should be examined as soon as possible.

Site Density Under INNOCUOUS Conditions

Figures 11 to 18 represent expected values of gypsy moth egg-mass density under INNOCUOUS conditions, wherein both low zone density and high zone density are set at zero; prior egg-mass density (MLSTYR) is set at 50 egg masses per acre unless otherwise specified; and the other independent variables are allowed to vary.

Egg-mass densities (MLSTYR) and (MNOW).—Egg-mass density in the fall of year (n + 1) (MNXTYR) is shown as a function of current density (MNOW) and density in the fall of year (n — 1) (MLSTYR) in figure 11. Density only tended to increase from year (n) to (n + 1) if it had already increased several fold from year (n — 1) to (n) and population density, in general, tended to stabilize at less than 50 egg masses per acre under these INNOCUOUS conditions. Recent stud-

Figure 11.—Relationships between egg-mass density per acre in the fall of year (n + 1), and egg-mass densities per acre in the fall of year (n — 1) and (n) (MLSTYR and MNOW). Innocuous conditions.



ies suggest that this low-level stability may have been achieved largely through the activities of vertebrate predators *(Campbell 1967b)*.

Precipitation in May of year (n) (PM).—The relationship between precipitation in May of year (n) and egg-mass density in the fall of year (n + 1) is shown in figure 12, with both prior and current densities held at 50 egg masses per acre. Even when no rainfall occurred in May of year (n), only about 60 egg masses could be expected per acre in the fall of year (n + 1), so this relationship was probably not biologically significant during the INNOCUOUS phase.

Figure 12.—Relationships between egg-mass density in the fall of year (n + 1) and precipitation in May of year (n) (PM). Innocuous conditions.

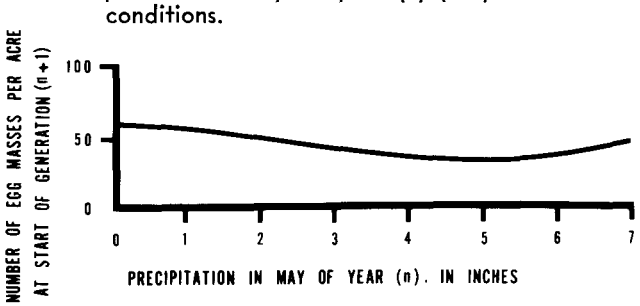


Figure 13.—Relationships between egg-mass density in the fall of year (n + 1), precipitation in June of year (n + 1) (RJ), and the percentage of the acres in the zone in the fall of year (n) containing more than 500 egg masses per acre (ZDL). Innocuous conditions.

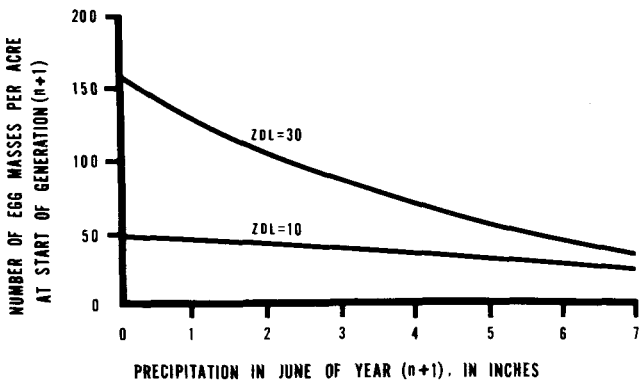
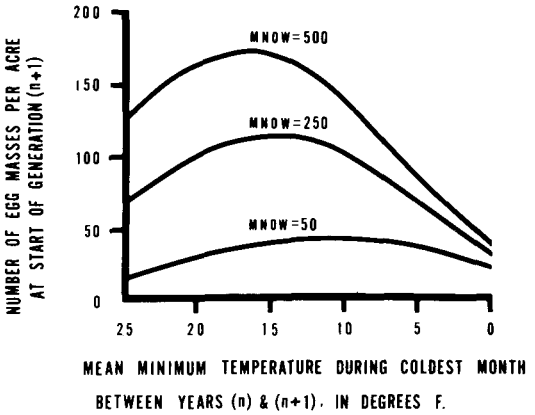


Figure 14.—Relationships between egg-mass density in the fall of year (n) (MNOW), and the mean minimum temperature during the coldest month between years (n) and (n + 1) (TMN). Innocuous conditions.



Precipitation in June of year (n + 1) (RJ).—Relationships between precipitation in June of year (n + 1), low zone density in the fall of year (n), and subsequent egg-mass density in the fall of year (n + 1) are shown in figure 13. Apparently this precipitation variable, like precipitation in May of year (n), was not biologically significant within the INNOCUOUS range.

Mean minimum winter temperature (TMN).—Gypsy moth density in year (n + 1) was not particularly responsive to variation in the mean minimum winter temperature during the coldest month between year (n) and (n + 1) (fig. 14). Thus this variable, like precipitation, was probably not biologically significant within the INNOCUOUS range, except when exceptionally low temperature regimes were maintained.

White oak (WOK), red oak (ROK), and current density (MNOW).—Relationships between the percentage of the total overstory foliage in the white oak group (WOK), the percentage of this total in the red oak group (ROK), the current number of egg masses per acre (MNOW), and the number of egg masses per acre in the fall of year (n + 1) (MNXTYR) are shown in figure 15. Although stands composed primarily of red oak group trees consistently tended to produce higher

Figure 15.—Relationships between egg-mass density in the fall of year (n + 1) (MNXTYR) and the percentages of the total overstory foliage in: (a) the red oak group (ROK) and (b) the white oak group (WOK). A, Relationships between MNXTYR, ROK, and WOK when egg-mass density per acre in the fall of year (n) (MNOW) is held constant at 50 egg masses per acre. B, Relationships between MNXTYR, ROK, and WOK when MNOW is held constant at 250 egg masses per acre. C, Relationships between MNXTYR, ROK, and WOK when MNOW is held constant at 500 egg masses per acre. Innocuous conditions.

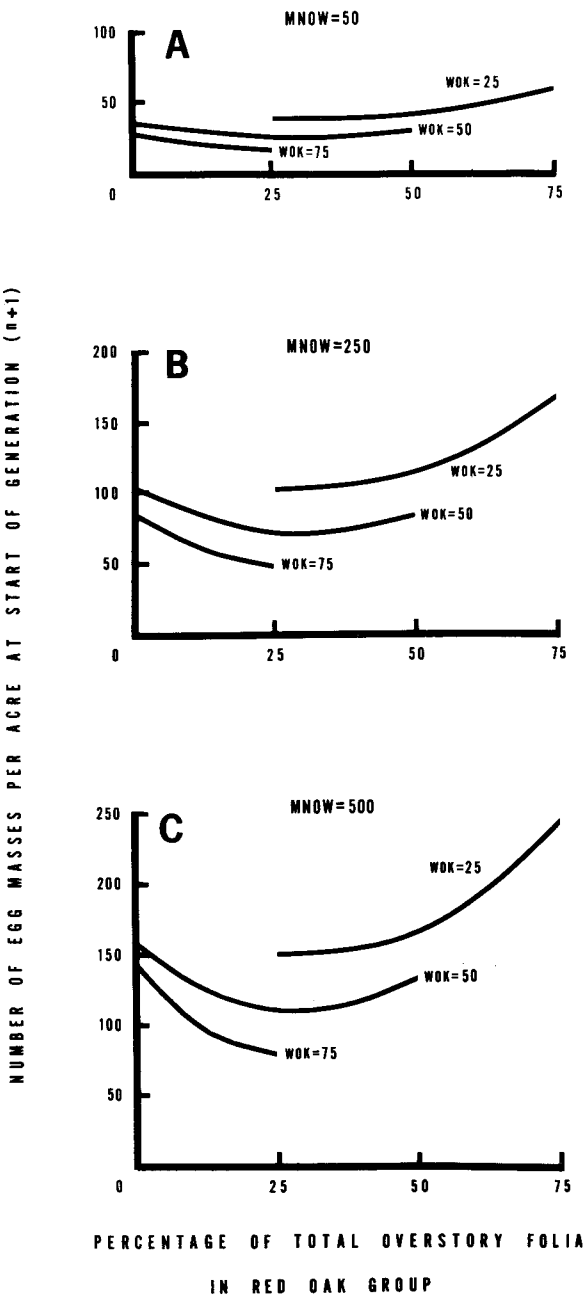
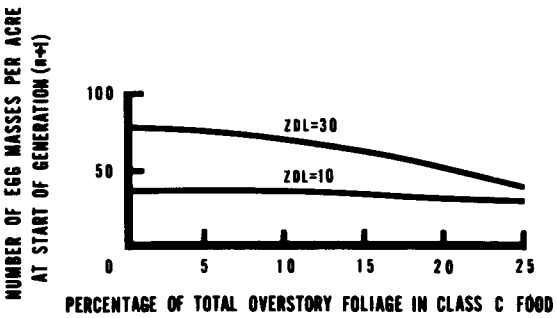


Figure 16.—Relationships between egg-mass density in the fall of year (n + 1), the percentage of the total overstory in class C food (FCC), and the percentage of the acres in the zone in the fall of year (n) containing more than 500 egg masses per acre (ZDL). Innocuous conditions.



egg-mass densities than those composed primarily of trees from the white oak group, egg-mass densities tended to be reduced from year (n) to (n + 1) under any combination of these overstory variables if they had chanced to reach 250 or more egg masses per acre in the fall of year (n). Thus variation in the overstory composition does not appear to include a mechanism through which the population system could reach the OUTBREAK-phase.

Food class C (FCC).—Variation in the amount of class C food bore almost no relationship to egg-mass density in the fall of year (n + 1) under INNOCUOUS conditions (fig. 16).

Defoliation of food class A in year (n) (DCA(n)).—Relationships between defoliation of class A food in year (n) and egg-mass density in the fall of year (n + 1) are shown in figure 17. The relationship shown indicates that egg-mass density could not be expected to increase out of the INNOCUOUS range under any previous defoliation regime.

Overall defoliation in year (n + 1 — (DEF(n = 1)).—Finally, relationships between defoliation in the summer of year (n + 1) and egg-mass density in the fall of that year are shown in figure 18. Although egg-mass density tended to be highest in year (n + 1) following defoliation of about 40 percent of the overstory, the model indicates that even

Figure 17.—Relationships between egg-mass density in the fall of year (n + 1), egg-mass density per acre in the fall of year (n) (MNOW), and percentage defoliation of class A trees during year (n) (DCA(n)). Innocuous conditions.

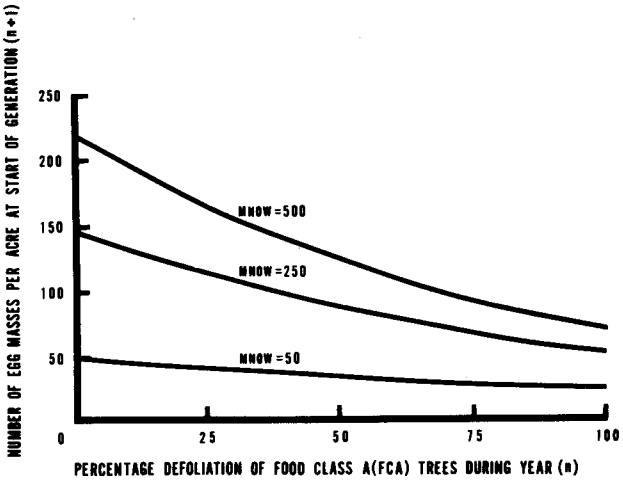
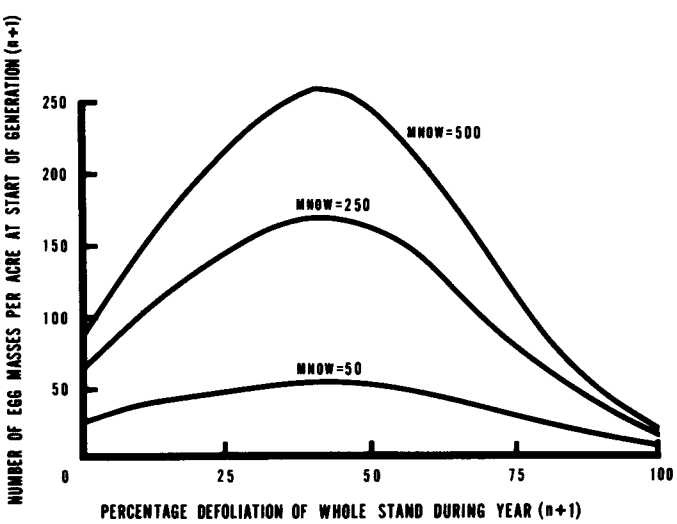


Figure 18.—Relationships between egg-mass density in the fall of year (n + 1), egg-mass density per acre in the fall of year (n) (MNOW), and percentage defoliation of the whole stand during the summer of year (n + 1) (DEF (n + 1). Innocuous conditions.



this highest density represented about a two-fold reduction in egg-mass density from year (n) to (n+ 1) if about 500 egg masses were present per acre in the fall of year (n).

DISCUSSION

The model just described leads toward four general conclusions about the behavior of the gypsy moth population system between 1911 and 1931 in eastern New England.

First, once the system reached a sufficiently high overall density, a massive outbreak could be expected to continue for many years.

Second, almost any woodland environment, regardless of its inherent capacity to maintain gypsy moth populations within a sparse range, would probably have been characterized, at times, by a high density resident gypsy moth population, if it were located in the vicinity of a massive outbreak.

Third, the system was relatively stable in either the OUTBREAK phase or the INNOCUOUS one, but it showed no tendency toward, or capacity for, stability within any intermediate phase. Local isolated outbreaks were much more likely to subside within a year or two to the INNOCUOUS phase than to expand to the OUTBREAK phase, while isolated low-density populations tended to increase rapidly to high density levels during the OUTBREAK phase.

Fourth, this model does not indicate mechanisms sufficient to change the system from the INNOCUOUS phase to the OUTBREAK one. Both a raitonale for each of the above conclusions and the implications arising from each one are described below.

Conclusions one and two are truly alarming, because they imply that a massive outbreak by this insect, left alone, may not only persist for many years, but also will probably expand in size.

This conclusion is difficult to verify or deny, because man has seldom left massive woodland outbreaks by this pest untreated, yet the population system that was studied in Glenville, New York, between 1958 and 1964 remained in the OUTBREAK phase for about 8 years and tended to expand during this time. A similar situation, on a truly massive scale, may also have developed in southern Connecticut, southern New York state, New Jersey, and eastern Pennsylvania in recent years.

Both the model and the experience of specialists in the management of this pest indicate that treatment applied piecemeal to ex-

ceptionally high-density populations does not cope with the underlying problem during the OUTBREAK phase. Such spot treatments can usually be relied upon to save foliage and to keep trees alive that might otherwise be lost, but that is *all* they can be relied upon to accomplish. Indeed, many spots can be found within any massive outbreak that have been treated several times—at intervals ranging from 2 to 5 years.

Options for coping with a massive outbreak of this pest are limited.

(1) We can do nothing, and hope that one of the following naturally occurring processes will terminate the OUTBREAK phase:

- Populations will increase explosively to extremely high levels from year (n — 1) to (n) and then recede abruptly to innocuous levels in year (n + 1).
- The area covered by the entire OUTBREAK system will be virtually stripped of its foliage in the summer of year (n + 1), and subsequent density levels will return to the INNOCUOUS phase.
- Precipitation will be extremely high in June of year (n + 1) across the entire area.
- The mean minimum winter temperature during the coldest month between years (n) and (n + 1) will approach zero °F. across the entire area.

(2) Or we can continue to treat places where the values threatened by the insect are known to exceed both the known direct cost and estimated indirect costs of control, in the knowledge that such treatments will not solve the underlying problem.

Clearly, what is really needed here is an environmentally acceptable treatment that could be applied *effectively* to the entire massive outbreak, but no such treatment is now available.

The fact that we are dealing with an apparently two-phase system, INNOCUOUS or OUTBREAK, is encouraging. This implies that both research and control work can be planned to cope with one phase or the other, with the knowledge beforehand that this system will transit rapidly to one phase or the other even if it happens to be in a transient state when work is initiated. Further, the model implies that the state of the system in year (n + 1) could have been forecast accurately between 1911 and 1931 just by knowing zone density in year (n).

Finally, the model failed to indicate a mechanism through which the INNOCUOUS phase might be transformed to the OUTBREAK one, except through increasing the general density level of the system, presumably through an overlap between areas in the OUTBREAK and INNOCUOUS phases. This is unfortunate because the ideal way to manage this population system would be to prevent outbreaks from occurring, but we can only hope to specify strategies through which this management goal could be achieved after these mechanisms have been discovered. A clue to the physical whereabouts of one such mechanism may be attributed to Forbush and Fernald *(1896)*, who wrote that:

> The study of the infested territory made in 1891 showed that the most densely infested areas were very nearly coincident with the centers of [human] population. In other words the moth colonies were larger and more numerous in or near thickly populated districts.

In short, one answer to this puzzle may be found literally in our own backyards, and we are now establishing a plot system in suburban areas to evaluate this possibility.

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APPENDIX

Mean values of the independent variables used to calculate figures 1 to 18.

Variable	*Mean value*
Current egg-mass density (MNOW)	2,448 egg masses per acre
Prior egg-mass density (MLSTYR)	2,705 egg masses per acre
Low zone density (ZDL)	53 percent
High zone density (ZDH)	14 percent
Precipitation in May of year (n) (PM)	3.17 inches
Precipitation in June of year (n + 1) (RJ)	3.59 inches
Mean minimum winter temperature (TMN)	14°F
White oak group (WOK)	24 percent
Red oak group (ROK)	51 percent
Food class C (FCC)	0.4 percent
Prior defoliation (DCA(n))	22 percent
Current defoliation (DEF (n + 1))	16 percent

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