Population biology of insects

Case study: population regulation and outbreaks of gypsy moths (*Lymantria dispar*) in North America

Setup: Divide the class into groups of three. Everyone will either read a review article plus one of three articles about a more specialized aspect of the problem.

Review paper:

Liebhold A., Elkinton J., and Williams D., 2000. What causes outbreaks of the gypsy moth in North America? Population Ecology 42:257-266.

Specialized articles:

1. Williams, D. W., and Liebhold A. M. 1995. Influence of weather on the synchrony of gypsy moth (Lepidoptera: Lymantriidae) outbreaks in New England. Env. Entomol. 24(5) 987-995.
2. Berryman, A. A., 1991. The gypsy moth in North America: a case of successful biological control? Trends in Ecol. and Evol. 6:110-111. Plus same issue, pages 263-265 (argument and rebuttal).
3. Jones C. G., Ostfeld R. S., Richard M. P., Schauber E. M., and Wolff J. O. 1998. Chain reactions linking Acorns to gypsy moth outbreaks and Lyme disease risk. Science 279(5353) 1023-1026.

The first article deals with the synchrony of the outbreak events over large geographical areas—weather variables affect masting cycles in oak trees, which affect abundance of mice, which in turn controls low density populations of gypsy moths (when mice are abundant), keeping them below outbreak levels. The article only covers the idea that there is geographical synchrony in outbreaks, and this may be caused by weather patterns.

The second article argues that parasitoids control high-density populations of gypsy moths, and then includes arguments by Liebhold and Elkinton against this. This article is good for getting students to think about how natural enemies might control populations and possibly outbreaks, but also points out that it is difficult to demonstrate population control by predators in nature.

This last article deals with both gypsy moths and ticks that spread Lyme disease. Students should concentrate only on the portions of the article that deal with the gypsy moths. This article links Oak tree masting, mice, and gypsy moth population regulation. It does not discuss in depth about regulation of high density populations, or about the effect of weather on these processes, so student discussion will hopefully help them to understand these relationships.

The review article lays out the story more completely, touching all parts of the story. So either we could ask students to read this in addition, to help them figure out the story, which is complicated enough, or we could ask them to each just read one article, and then have them get together and try to figure out the whole story.

I ran the class as a series of small discussions about the series of figures below, presented in order. Thus, I progressively disclosed information about the topic, having students discuss possible relationships between different parts, given what they know at each step. I drew a map of the parts on the board as well, so students could trace possible effects between each part (e.g., between weather variables, oak trees, mouse populations, and gypsy moth populations).

Learning goals:

A. General academic
    1. What factors are involved in regulating populations?
    2. Why are outbreaks important?
    3. What factors might cause population cycles?
B. General practical
    1. How do scientists put together pieces of a large scientific puzzle to get a whole picture?
    2. How to work as a group to figure out the big picture
    3. How to understand difficult information and complex figures, and to summarize important points and explain this to others.
C. Specific academic
    1. Why is the gypsy moth a good model system?
    2. How does this system work (What causes outbreaks? What factors regulate gypsy moth populations?)?
    3. Do you think the gypsy moth system is an especially complicated one?
    4. What do managers need to think about in attempting to control outbreaks of gypsy moths?

Case Study: Simon and the Gypsy Moths

Metro Briefing | New Jersey: Newark: Gypsy Moth Infestation

Biologists fear that thousands of acres of trees in northern New Jersey will die in coming months as victims of gypsy moth larvae, which eat leaves. The bugs are in the third year of a population increase. Usually, their numbers peak about once a decade. A State Department of Agriculture study found that defoliation between April and July was heavy in 140,383 acres across the state, 8,000 more than last year. That is still far less than the 800,000 acres similarly affected in 1981. The damage considered heavy to severe this year occurred mostly in Passaic, Bergen and Morris Counties.

Published: 09-04-2001, New York Times, Late Edition—Final, Section B, Column 5, Page 6.

Simon had lived in cookie-cutter housing all of his life—he only dreamed about walking in woods in his own backyard… When his parents proposed moving to a wooded property in New Jersey, he was dubious at first. Having seen the flame-belching monsters along the turnpike, he couldn't easily believe there was much left of woods in New Jersey. But sure enough, a decent number of acres of forest remained just down the street from their new house. He went exploring immediately.

Simon roamed "his" woods very often during the next year, quickly becoming familiar with many of the animals and plants there. Watching sadly as other tracts of forest in his town disappeared in the wake of development, he took comfort thinking that at least his forest was left relatively intact. Then, during his second summer in his new house, even this changed…

He went to the woods, one sunny summer afternoon, and sensed something was wrong. The majestic oaks usually thickened the canopy all summer with their broad leaves, but that day he could see several patches of sky through the trees. Even more disturbing was the noise—not the shrill call of cicadas he usually heard, but something like a rustling—like rain! On a sunny day? It certainly wasn't rain… it was black, and grainy, like small pellets, or… poop… poop was falling from the sky—from the trees—like rain! He guessed there must be thousands of insects up there, destroying his trees…

Then he saw the caterpillars—large, fuzzy caterpillars, that seemed to be on every leaf he could see. What were they doing in his forest? Why hadn't he seen them last summer? Would they be here from now on? When he asked his parents about it, they didn't know, but they had heard something about gypsy moths on NPR news. He decided to look on the internet for himself, and came upon this web site:

http://www.dnr.state.wi.us/org/caer/ce/eek/critter/insect/moth.htm

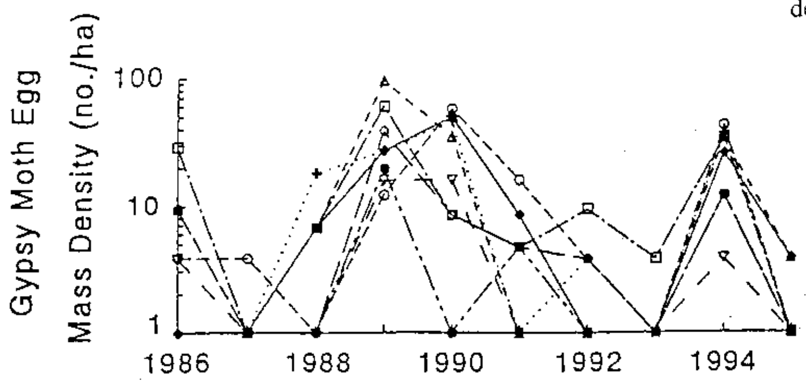
Check it out for yourself, in addition to reading the following journal article before coming to class tomorrow

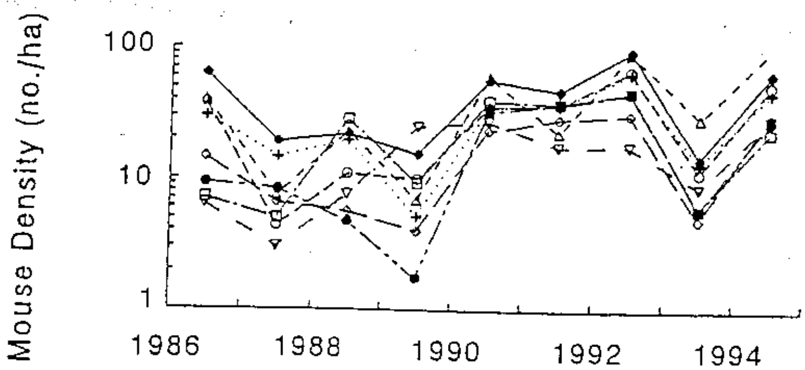
Study # 1a. Elkinton J. S., Healy, W. M., Buonaccorsi, J. P., Boettner, G. H., Hazzard, A. M., Smith, H. R., and Liebhold, A. M. 1996. Ecology 77(8):2332-2342.

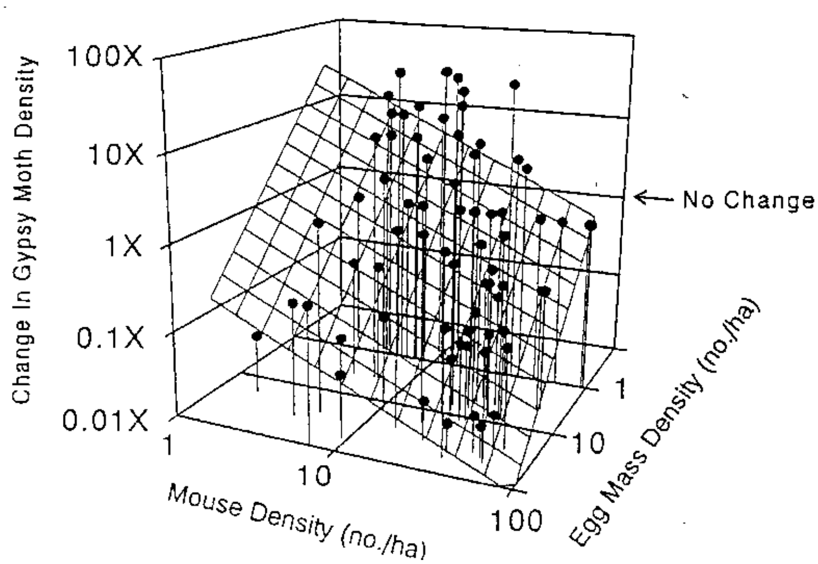
White-footed mice feed on gypsy moth pupae. The authors made estimates of gypsy moth egg mass density (an index of gypsy moth density) and density of white-footed mice in four 1-hectare plots in each of eight sites (32 total plots) in oak forests of Massachusetts. They made the same measurements in these plots for ten years (1986-1995). During these years, gypsy moths were not at outbreak levels. They tested whether changes in gypsy moth egg mass density were correlated with white-footed mouse density. Interpret the graphs of their results below and explain what conclusions, if any you can draw from them.

In addition, the authors placed 300 gypsy moth pupae in 1-2 plots within each of the eight sites, and measured rate of predation on (removal of) pupae. Interpret the graph of their results—how does this fit in with the information in the previous two graphs? Why was it important for the authors to demonstrate this?

In this figure, the different symbols refer to different sites where the scientists made density estimates.







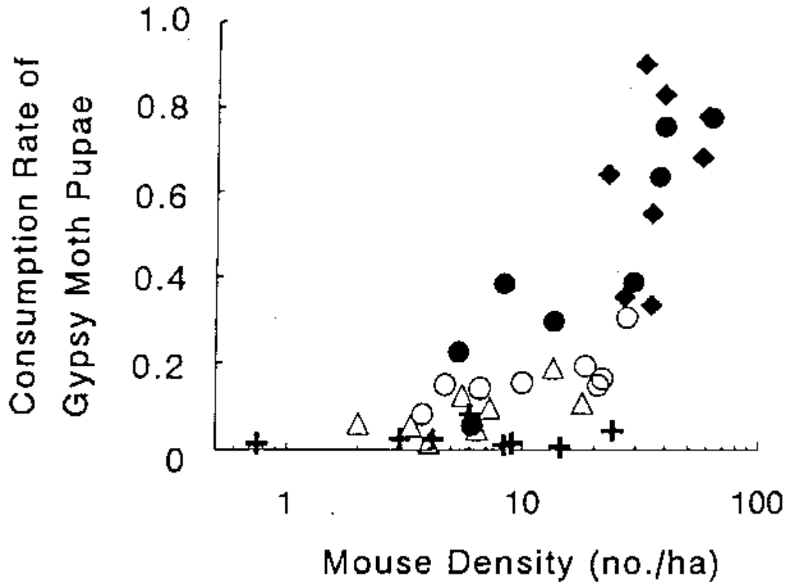
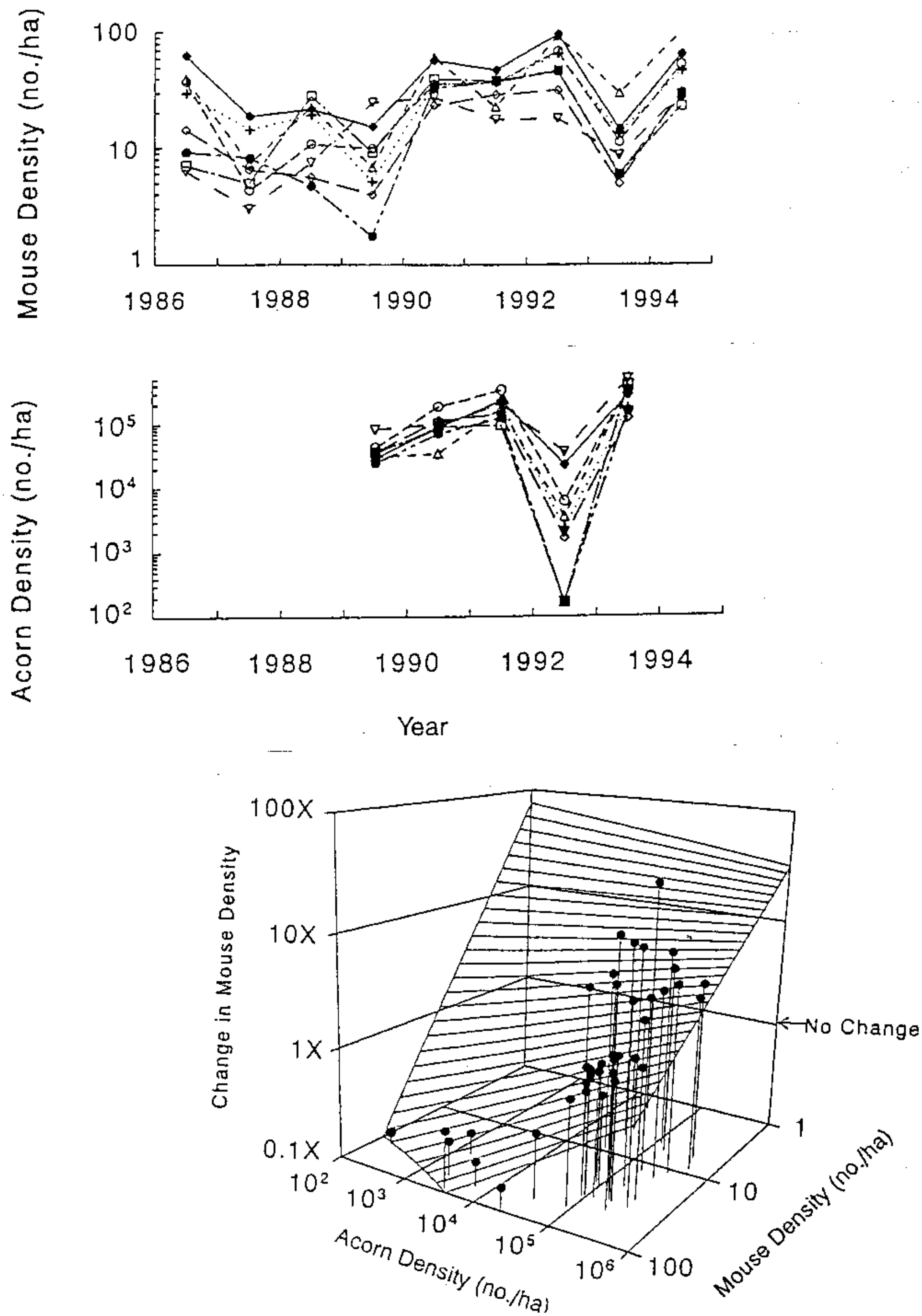


FIG. 3. Density of white-footed mice plotted against the mean daily proportion of 300 gypsy moth pupae deployed on each plot that were consumed by all predators including mice over a 3-d test period. Symbols indicate different years: 1986, ●; 1987, △; 1988, ○; 1989, ✚; 1990, ◆.

Study # 1b. Elkinton J. S., Healy, W. M., Buonaccorsi, J. P., Boettner, G. H., Hazzard, A. M., Smith, H. R., and Liebhold, A. M. 1996. Ecology 77(8):2332-2342.

These same authors also made estimates of acorn production by oaks during the same years of the study. They then tested whether the changes in mouse density were correlated with acorn density. Interpret the graphs of their results below and explain what conclusions, if any you can draw from them. How might this fit into the larger picture of gypsy moth population regulation?

In this figure, the different symbols refer to different sites where the scientists made density estimates.



Study # 2a. Sork, V. L., Bramble, J., and Sexton, O. 1993. Ecology 74(2):528-541.

Study # 2b. Crawley, M. J. and Long, C. R. 1995. J. of Ecol. 83:683-696.

In these studies, authors measured acorn density in one or several areas over several years. In the study 2a, authors tested whether acorn density was correlated with each of several weather-related variables. Interpret the graphs and tables below. How might this explain the Moran effect on gypsy moth outbreaks? i.e., What might explain why gypsy moth outbreaks are synchronized over large regions?

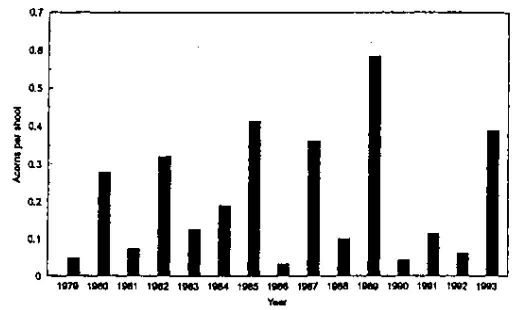


Fig. 1 Acorn production by *Quercus robur* in Silwood Park, Berkshire, England over the 15-year period 1979–93. Acorn production is recorded as the mean number of acorns (including acorns galled by the cynipid wasp Andricus *quercus*calicis) per shoot averaged over 30 trees. Notice that acorn production during the 'high' years is extremely variable, and that there were two consecutive 'low' years in 1983 and 1984 (see text for details). Different trees were used for the periods 1979–81 and 1982–93.

Table 1 Acorn production at various sites in south eastern England for the period 1980–83. Data show the number of *Quercus robur* out of 30 trees which produced high (H) acorn crops (more than about 0.2 acorns per shoot) and low (L) acorn crops (less than about 0.02 acorns per shoot) in a given year. Trees with intermediate acorn crops are not shown, but they number 30-H-L for each site. These data established that there was a broad pattern of synchrony in fruiting by *Q. robur* for the peaks (years, $\chi^2_3 = 237.8$; sites, $\chi^2_7 = 6.712$, NS; interaction years by sites, $\chi^2_{21} = 24.43$, NS) and the troughs (years, $\chi^2_3 = 178.4$; sites, $\chi^2_7 = 16.86$, $P < 0.025$; interaction years by sites, $\chi^2_{21} = 15.60$, NS) in this part of southern England. Data from Sunningdale and Windsor Great Park were gathered for the entire study period (for 1984–93; see Table 4)

Site	Grid Reference	1980		1981		1982		1983	
		H	L	H	L	H	L	H	L
Silwood Park	41/945686	23	3	2	14	19	5	4	11
Sunningdale	41/948660	18	6	0	21	22	3	3	18
Chobham	41/973618	25	5	3	25	18	5	2	22
Windsor Great Park	41/962692	19	10	4	20	24	1	5	19
Virginia Water	41/990677	11	2	3	22	11	4	6	21
Windlesham	41/931640	22	8	0	27	18	4	1	25
Hartley Wintney	41/771574	24	4	1	26	19	5	2	25
Richmond Park	51/205733	17	9	2	25	21	8	3	26

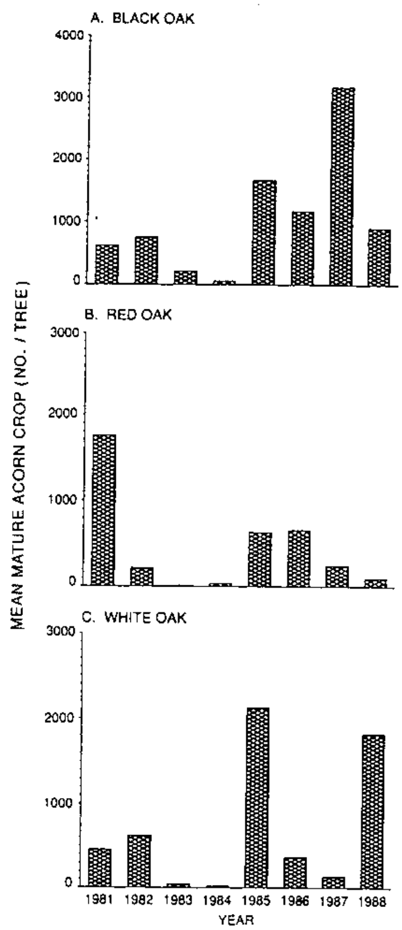


FIG. 1. Annual mean mature acorn production for black oak (n = 13 trees), red oak (n = 12 trees), and white oak (n = 15 trees) sampled at Tyson Research Center, St. Louis County, Missouri, from 1981 to 1988.

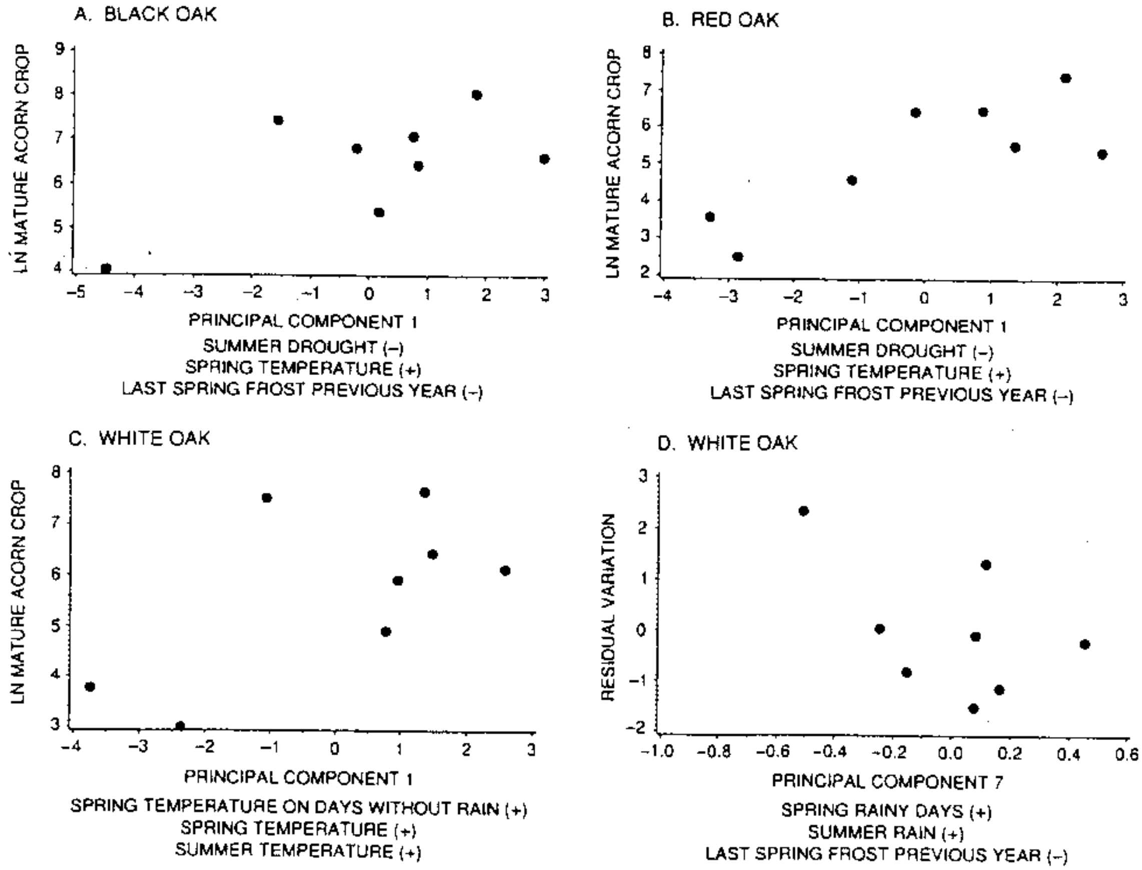


FIG. 3. Mean annual Mature Acorn Crop per tree (log transformed) plotted against the most significant principal component for each oak species. The three weather variables that are highly correlated with this principal component are given beneath each graph, with the sign of the correlation. (A) Black oak: $r = 0.552$, df = 1,6, $F = 7.4$, $P < .05$. (B) Red oak: $r = 0.894$, df = 1,6, $F = 50.5$, $P < .001$). (C, D) White oak, the first principal component and its residual variation plotted against the seventh principal component: overall model $R^2 = 0.771$, df = 1,6, $F = 8.4$, $P < .05$.

Study # 3. Jones C. G., Ostfeld R. S., Richard M. P., Schauber E. M., and Wolff J. O. 1998. Science 279(5353):1023-1026.

The previous articles test for population-level correlations among participants in this complicated system of species interactions. Do these correlations demonstrate that masting in oaks is driving low-density population regulation in gypsy moths? Why or why not?

The authors of study # 3 sought to experimentally demonstrate that masting in oaks could affect mouse populations, which could in turn affect gypsy moth populations. To do this, they set aside several plots, with one of three treatments. In one treatment type, mice were removed from the plots, and in another, large numbers of acorns were added to the plots. The third treatment served as a control.

Interpret the following figures. What do they show? For what two reasons is the first graph of mouse density over time necessary to their argument?

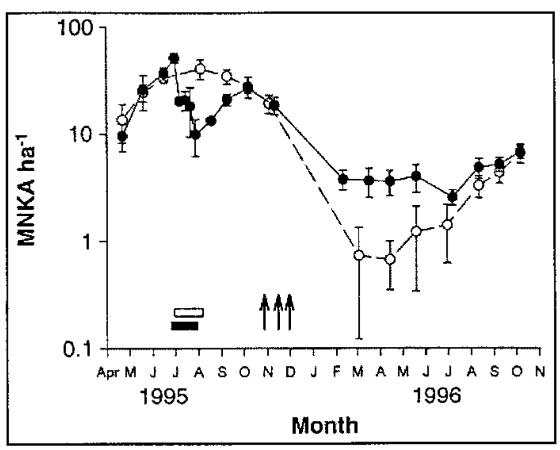


Figure 1. White-footed mouse densities on three control (○) and three experimental (●) grids as mean (±SE) MNKA ha^{-1}, April 1995-October 1996, showing (i) 1995 densities before, during, and after the period of mouse removal from experimental grids (black bar) at the time of native female gypsy moth pupation (white bar); (ii) 1995 densities before and during acorn additions (arrows) to experimental grids, October-November 1995, when there were very low numbers of acorns produced on control grids; and (iii) 1996 densities after acorn additions to experimental grids in 1995. High 1995 mouse densities were associated with autumn 1994 masting, and mouse densities typically decline during winter (1).

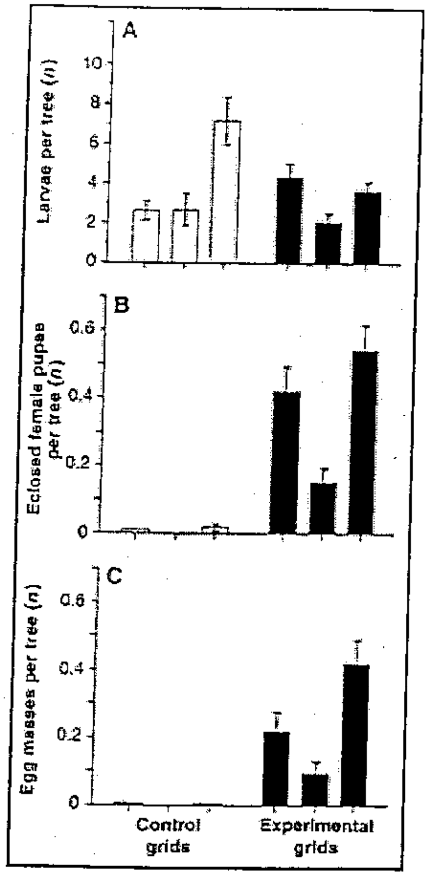


Fig. 2. Densities of gypsy moth life stages on or under burlap bands on trees on control grids (open bars) versus experimental grids (solid bars) where mice were removed. The bars show grid means and within-grid SEs. Across-grid control and experimental means (±SE) and statistical comparisons are also shown for each graph. (**A**) Number of living late-stage larvae per tree just before mouse removal. Control grids, 4.17 (±1.51); experimental grids, 3.36 (±0.68); $P = 0.83$, Mann-Whitney U test. (**B**) Number of female pupae per tree successfully eclosing to adults after mouse removal. Control grids, 0.008 (±0.005); experimental grids, 0.370 (±0.115); $P = 0.02$, one-tailed Mann-Whitney U test. (**C**) Number of egg masses per tree after mouse removal. Control grids, 0.006 (±0.003); experimental grids, 0.245 (±0.095); $P = 0.02$, one-tailed Mann-Whitney U test.

Assignment (to hand in for next class):

Discuss, in one paragraph (or a few short paragraphs), a detailed chain of events that could lead to an outbreak of gypsy moths, beginning with the weather and ending with an outbreak.