DISPERSAL PATTERNS OF GYPSY MOTH LARVAE (*LYMANTRIA DISPAR)*

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Abstract. Population outbreaks of gypsy moths (*Lymantria dispar*) cause serious defoliation of economically and aesthetically valuable forests. Previous studies have shown mice to be the major predator of gypsy moths during low gypsy moth density periods (Schauber 2000). An experimental model employed at the Institute of Ecosystem Studies predicts that if mice and moth populations remain well-mixed, then mice should be able to drive gypsy moths to extinction during these low-density periods (Schauber 2000). Yet, gypsy moth populations continue to persist. The pattern of gypsy moth larval dispersal may provide a mechanism for the persistence of the gypsy moth during these low-density periods. In order to determine the shape and pattern of larval dispersal, six 50-meter radius plots were established on two mixed oak forest grids at the Institute of Ecosystem Studies near Millbrook, New York. Within each grid, a control plot without an egg mass, a single plot with one egg mass, and a multiple egg mass plot were established. An oak tree and non-oak tree (when available) were burlap-banded at five and ten meter intervals along six radial transects with each plot. Larval mortality and instar data were recorded for each band from 25 June to 18 July 2001. Data analyzed using the statistical t-test showed that gypsy moth larvae favor oak over non-oak species. Furthermore, ANOVA analysis demonstrated that compass direction did not have a significant effect on the average number of larvae per tree. When the distribution of larvae within each compass direction was plotted, a bimodal pattern of distribution emerged.

INTRODUCTION

Gypsy moths were introduced from Europe in 1869 (Hunter and Elkinton 2000). During outbreak levels, gypsy moths act as major defoliators of both aesthetically and economically valuable trees. Defoliation may weaken trees by making them more vulnerable to disease and fungal infection (Fajvan and Wood 1996). Furthermore, direct consumption of foliage by gypsy moths disturbs natural ecological processes within forest environments. Forest stand composition may be altered by decreasing the proportion of oaks and other trees greater than one meter in height while increasing the abundance of understory tree species (Fajvan and Wood 1996). In addition, cycling of important nutrients such as nitrogen and carbon may be greatly affected during severe defoliation episodes (Ostfeld et al. 1998).

The gypsy moth progresses through four stages in its life cycle. Adult gypsy moths lay eggs in egg masses in August. The eggs over winter until late-spring or early- summer at which time the eggs hatch into larvae. The larvae grow through six stages called instars. In July, following the sixth instar, the larvae pupate for a period of two weeks before adult moths emerge again in August (Campbell 1975).

Gypsy moth populations exhibit cyclic patterns of density fluctuations over time (Fig. 1). This population cycle is divided into four stages. The first stage is called the release phase during which time gypsy moth population densities undergo a rapid incline. Peak gypsy moth densities are reached during the second stage also known as the outbreak phase. The decline phase follows and is characterized by decreasing gypsy moth densities. The fourth and final stage is called the innocuous phase and is described by very low densities of gypsy moths (Karnosky and Jones 1981).

Previous research at the Institute of Ecosystem Studies has shown the white-footed mouse (*Peromyscus leucopus*) to be a major generalist predator of gypsy moth pupae (Schauber 2000). Although mouse population densities are independent of gypsy moth population densities, research indicates that a strong direct correlation exists between densities of white-footed mice and acorn production (Ostfeld et al. 1998). Periodic masting of oak trees causes high production of acorns (Kelly et al. 2000). The high abundance of acorns combined with favorable winter weather conditions is highly related to increased over winter survival of mice and a subsequent increase in the density of mouse populations the following year (Jones et al. 1998).

Although mouse population densities remain independent of gypsy moth population densities, high mouse densities resulting from periods of oak tree masting may serve to regulate gypsy moth populations during low moth density phases (Elkinton et al. 1998). The inverse density-dependent relationship of moth populations on mouse populations during low moth density phases results from a type II functional response relationship exhibited between the two species (Schauber 2000). With a type II functional response, predation risk from white-footed mice on gypsy moth populations is high during low moth density periods. The type II functional response is determined by the foraging patterns of white-footed mice that suggest gypsy moth pupae serve as a preferred food source for the mice. This type II functional response relationship predicts that mice predation should drive gypsy moth populations to extinction during low gypsy moth density periods (Schauber 2000).

Despite this prediction, gypsy moth populations continue to persist. Figure 2 displays data gathered from IES from twenty fixed area plots, sampled annually for egg masses using visual surveys of all substrate. The figure demonstrates that in 1986, gypsy moth density levels were very low at only 0.1 egg masses per hectare. Yet, gypsy moth populations persisted and the population climbed once again to reach a peak of over 1000 egg masses per hectare in 1990. Moth populations in 1992 were also very low, yet this population also persisted to reach much higher levels by 1994.

Examination of gypsy moth larval dispersal patterns may provide some insight into understanding the causes that underlie gypsy moth persistence during low-density phases despite high mouse predation rates. Many previous studies concerning gypsy moth dispersal have focused upon patterns of early-instar larval dispersal (Campbell 1975 and Mason and McManus 1981). First instar gypsy moth larvae disperse by ballooning out from treetops, often in the direction of the prevailing winds in an area (Weseloh 1997). First instar gypsy moth larvae spin silk strands and rely upon "soaring hairs" to aid them in this first dispersal episode (Deml and Dettner 1995). Wind dispersal may transport first instar larvae up to 21 km from their original point of departure (Weseloh 1998).

Fewer studies have been conducted concerning dispersal of late-instar (IV-VI) gypsy moth larvae (Lance and Barbosa 1982 and Weseloh 1997). Late-instar larvae may disperse by crawling from tree to tree (Weseloh 1997). Tree-to-tree movement may be governed by factors such as host tree acceptability and by availability of protective daytime resting spots such as bark flaps (Lance and Barbosa 1982). Data gathered by Weseloh suggests that dispersal of gypsy moth larvae may be limited and that tree-to-tree movement involves only short distances (1985 and 1997).

Limited dispersal may serve as a mechanism for moth population persistence. A limited dispersal pattern would mean that greater numbers of larvae and pupae would be located within a smaller space, and therefore, predation risk by mice would be lower (Weseloh 1997). Furthermore, limited dispersal of gypsy moth larvae may interact with the spatial patterning of mouse foraging to produce a spatially heterogeneous predation risk, therefore enhancing the possibility of moth persistence (Schauber 2000). Assuming that mice forage within home ranges that do not overlap, gaps between such home ranges when predator densities are low may provide areas of refuge against mouse predation for gypsy moth larvae and pupae (Schauber 2000). If gypsy moth dispersal of late-instar larvae is limited, then the possibility of high numbers of larvae occurring within such a refuge or protective area may allow for persistence of moth populations during low moth density phases. The purpose of this research project was to determine the actual shape and pattern of late-instar gypsy moth dispersal.

MATERIALS AND METHODS

Site Description

This research project was conducted at the Institute of Ecosystem Studies near Millbrook, New York (41°50'N, 73°45'W). Three 50-meter radius plots were established on two long-term 150-square meter grids on IES property (Jones et al. 1998 and Ostfeld et al. 1998). Both the Green and Teahouse grids were characterized by a mixed oak forest composition and each grid contained several sloping hills. Compared with the Green grid, the Teahouse grid had a higher amount of fallen and decomposing forest debris such as branches and logs.

Experimental Design

In order to determine the general pattern, distance, and direction of larval dispersal following hatching of gypsy moth larvae from an egg mass, it was necessary to establish a plot on each grid which contained a single egg mass. From knowledge of egg mass locations found during the preliminary survey, a single egg mass plot was created in which the egg mass was made the center point of the plot. From the original survey, the assumption was made that no other egg masses existed within the 50-meter radius area surrounding the central single egg mass.

The possibility that additional egg masses might have existed within the established single egg mass plots (but were missed during the preliminary survey) prompted the creation of a multiple egg mass plot within each grid as well. In this way, unusual larval dispersal patterns caused by missed egg masses within the single egg mass plots could be compared with larval dispersal patterns exhibited on the multiple egg mass plots. Within the multiple egg mass plots, the most central egg mass was made the center point of the plot.

In addition to the single and multiple egg mass plots, a control plot was established on both grids. Based on the preliminary survey, these 50-meter radius plots were believed to be free of egg masses. The control plots were created to determine the background number of gypsy moth larvae in the forest.

The three plot types on each grid were established following a preliminary survey of egg mass density and location. The visual survey was conducted by walking along the ten north/ south and ten east/west gridlines of both the 150-square meter Green and Teahouse grids. When egg masses were located, their location on the grid was recorded.

Within each plot type, three long transects were laid out with sampling points placed at four 5-meter intervals and then three 10-meter intervals. The long transects were laid out in the SW, NE, and SE directions from the center point of the plot (Fig. 3). Data obtained from a long-term environmental monitoring program utilizing a weather station at the Institute of Ecosystem Studies showed that prevailing winds at IES during the first instar ballooning dispersal event (in May) was from the southwest to the northeast. SW and NE transects were established to determine if wind direction had any effect on the distance and direction larvae traveled from the nearest egg mass. Three short transects beginning 30 meters from the center of the plot had sampling points at three 10-meter intervals. These short transects were placed randomly between the long transects in order to account for and to record larval density in the intervening space between the long transects.

Sampling Procedures

Determination of larval presence and density was measured by placing a burlap band around the two trees nearest to each sampling point (usually within one meter). The two-banded trees consisted of an oak and a non-oak tree whenever this condition was present. The burlap-banding procedure involved tying a 30-cm wide strip of burlap

with string around the base of the tree at chest height. The string was placed midway along the width of the burlap so that the top half of the burlap folded over the string to create a flap (Wallner et al. 1990).

Gypsy moth larvae travel down from the tree canopy during the day to rest on tree boles and bark flaps (Weseloh 1985). Burlap banding utilizes this behavior to concentrate the larvae in one location on the tree for counting and estimation of larval density.

From 25 June to 18 July 2001, larvae located on top, between, and underneath the burlap flaps were counted, and larval instar and mortality information was recorded. Furthermore, the distance and direction of each banded tree from the nearest egg mass was determined using a 100-meter tape measure and a compass. Data was pooled so that the average number of larvae per tree was calculated for the entire sampling period.

Several variables concerning larval dispersal were measured in this research project. These variables included differences in larval density on the Green grid compared to the Teahouse grid, the affect of tree species on larval density, as well as the distance and direction that gypsy moth larvae traveled from the nearest egg mass.

Data Analysis

Data concerning differences in larval density between the two grids and data concerning larval density on oak versus non-oak tree species was measured using the standard statistical t-test. Analysis of variance (ANOVA) was employed to determine the significance of the affect of compass direction on the average number of larvae present per tree. In order to determine the significance that compass direction had on the total distance traveled by larvae away from the nearest egg mass, a hierarchical general linear model was used in which distance traveled by larvae was nested within each compass direction.

RESULTS

Egg Masses

While recording larval instar and density from 25 June to 18 July 2001, several gypsy moth larvae, and subsequently, pupae were discovered on the Green grid's control plot. Following data collection, a second egg mass survey was conducted based upon the location of recorded larval presence in order to locate additional egg masses that were missed during the preliminary survey. One new egg mass was discovered on this control plot. No new egg masses were ever located on either the Green grid's single or multiple egg mass plots.

At the end of the data collection period, an additional egg mass was located on the Teahouse grid's single egg mass plot. No additional egg masses were discovered on the Teahouse grid's multiple egg mass plot. Furthermore, no egg masses were ever found on the Teahouse grid's control plot, and only one larvae was ever recorded as being present on this plot, suggesting low background density levels for gypsy moths in areas devoid of egg masses.

Due to the presence of additional egg masses missed during the preliminary survey on Green grid's control plot and on Teahouse grid's single egg mass plot, data concerning distance and direction to each tree was measured from the egg mass located nearest to each tree rather than from the center of each plot. Data was pooled so that the average number of larvae per tree was calculated for the entire sampling period.

Green vs. Teahouse Grids

An approximately equal number of trees were banded on both Green and Teahouse grids (128 and 141 trees, respectively). However, Figure 4 shows that the mean number of larvae per tree was higher on the Green grid than

on the Teahouse grid (mean = 1.898 and 0.142, respectively). Statistical t-test analysis determined these results to be significant   (P < 0.0001, t = 7.29, df = 135).

Oaks vs. Non-Oaks

Previous research suggests that there is a greater presence of gypsy moth larvae on oak versus non-oak tree species (Campbell 1975, Lance and Barbosa 1982, Weseloh 1998, and Hunter and Elkinton 2000). In order to determine the affect of tree species on the presence of larvae, an oak and a non-oak (when available) tree species was banded within one meter of each sampling point along all transects within all plots. A total of 269 trees were burlap banded during this project (132 oak and 137 non-oak species). Fig. 5 shows that the mean number of larvae on each oak tree was 1.553, while the mean number of larvae per non-oak tree species was 0.423 (Fig. 4). Significant results concerning the difference between mean number of larvae on oak versus non-oak species were obtained using a statistical t-test analysis (P < 0.0001, t = 4.57, df = 173).

Compass Direction

The effect of compass direction on the mean number of larvae per tree was determined to be insignificant using a single factor ANOVA statistical test of the data (F = 3.690, CV = 4.600, P>0.05). However, a few trends concerning the effect of compass direction on the mean number of larvae per tree may be observed from the histogram in Fig. 6. The prevailing winds at IES during the first instar larval dispersal event (May) were from SW to NE. The lowest mean number of larvae per tree occurred in directions upwind (SW) of the nearest egg mass. The highest mean number of larvae per tree was found in the S and W compass directions, occurring along each side of the prevailing wind direction. Furthermore, the mean number of larvae per tree increased downwind (SW to NE) from the nearest egg mass.

Total Larvae vs. Distance

One of the variables measured during this project was the distance traveled by larvae from the nearest egg mass. Fig. 7 displays the mean number of larvae found at increasing distances from the nearest egg mass. As the figure shows, the average number of larvae per tree increased gradually up to a distance of about 72.5 meters. Then, the average number of larvae per tree decreased quite sharply before increasing a final time to reach a final density peak between 95 and 100 meters away from the nearest egg mass.

In order to better represent the effect of distance on the mean number of larvae found per tree, the effect of compass direction was incorporated into the analysis (Fig. 8). Plotting the mean number of larvae per tree versus distance within each compass direction enabled a clearer picture of the distribution of larvae away from the nearest egg mass to emerge.

Considering that the direction of the prevailing winds during the first instar dispersal event was from SW to NE, several observations were made concerning larval distribution away from the nearest egg mass. First, total distance traveled by larvae away from the nearest egg mass increased downwind (N, NE, and E), while total distance traveled by larvae in the upwind (SW) direction decreased. With the exception of the outlier, in the SW direction the distance traveled by larvae was only 35 meters, while the distance traveled by larvae in the NE direction was 80 meters. Total distance traveled by larvae was highest, however, in the S direction, adjacent to the prevailing wind, with a total distance traveled of 100 meters.

In addition to observations concerning total distance traveled by larvae within each compass direction, observations were also made concerning the shape of the larval distribution based upon the mean number of larvae found per tree a set distances away from the nearest egg mass within each compass direction. Three general patterns in the shape of larval distribution were observed among the eight compass directions analyzed.

First, a bimodal larval distribution pattern was observed within the N, NW, W, S, and SE compass directions. In these bimodal distributions, the mean number of larvae per tree increased away from the nearest egg mass, then declined before reaching the highest final peak of mean larval densities per tree, usually between 50 and 55 meters away from the nearest egg mass. The second type of distribution pattern occurred in the upwind compass direction. The mean number of larvae per tree experienced a general decline away from the nearest egg mass in the upwind (SW) direction. The third type of larval distribution pattern was exhibited in the NE and E compass directions and was characterized by a very gradual increase in the mean number of larvae per tree with increasing distance from the nearest egg mass.

DISCUSSION

Green vs. Teahouse Grids

Three possible reasons might have accounted for the difference in the total number of larvae on the Green grid compared to the Teahouse grid. First, more oak tree species were banded on the Green grid compared to the Teahouse grid. Previous research strongly indicates that gypsy moth larvae prefer oak to non-oak tree species (Campbell 1975, Lance and Barbosa 1982, Weseloh 1998, and Hunter and Elkinton 2000). Weseloh explains that when gypsy moths encounter less suitable tree species, they are more likely to disperse in search of more favorable hosts upon which to feed and rest (1998). The greater the amount of time spent dispersing and crawling along the forest floor, the higher the probability that larvae will be attacked by predators, such as small vertebrates like the white-footed mouse. Densities may have been lower on the Teahouse grid because of the possibility of increased dispersal movement away from non-oak banded tree species. Increased dispersal may have also led to increased mortality from small vertebrate predators within the Teahouse grid.

Second, the sampling time may have had an influence on the number of larvae found and recorded on each grid. Data collection from the Teahouse grid began one week following the beginning of data collection from the Green grid. Because mortality due to predation, starvation, and disease increases with the amount of time that gypsy moth larvae are exposed to such dangers, sampling one week later on the Teahouse grid compared to the Green grid may have accounted for decreased recorded densities (Sharov and Colbert 1994). Furthermore, Campbell explains that gypsy moths undergo various patterns of vertical movement according to their developmental stage (1975). For example, in Campbell's study, just prior to the fifth instar, about 45% of larvae were located between the forest floor and six feet high. However, this number declined to 10% when larvae began to pupate, while the amount of larvae in the litter increased from 10% to 30% with the onset of pupation (Campbell 1975). Because sampling was conducted a week later on the Teahouse grid, more larvae on the grid that were about to enter the pupa stage may have descended to the forest floor and would not have been recorded from the bands.

Finally, rain occurred on two sampling days at the Teahouse grid. In a 1985 study by Weseloh, he describes that fewer numbers of larvae are to be found under burlap bands during rainy weather conditions. The fact that sampling occurred on two rainy days may account for some of the density differences between the Green and Teahouse grids.

Oaks vs. Non-Oaks

Data gathered during this research project supports previous research that suggested that gypsy moth larvae prefer oak to non-oak tree species (Campell 1975, Lance and Barbosa 1982, Weseloh 1998, and Hunter and Elkinton 2000). Host tree acceptability and suitability for gypsy moths depends upon at least two major factors: food quality and availability of daytime resting locations (Lance and Barbosa 1982). Oak trees serve as better host trees for gypsy moth larvae compared to other tree species such as maples as evidenced by the larger size and fecundity of gypsy moths feeding on this preferred host species (Lance and Barbosa 1982). Furthermore, oak trees provide more suitable daytime resting spots, such as bark flaps, for developing larvae (Weseloh 1998). Lance and Barbosa also include tree size as a related factor leading oak trees to be a preferred host for gypsy moths (1982). A larger

tree will provide more foliage to eat and more resting spots for protection for gypsy moth populations. As discussed in the previous section, species composition of a forest may, therefore, affect gypsy moth dispersal patterns.

Compass Direction

In this study, compass direction did not have a significant affect on the mean number of larvae found per tree, suggesting that larval distribution is random in space. These results support research completed by Weseloh describing a random distribution as related to compass direction (1985). However, Weseloh did mention prevailing wind direction to be an important consideration when analyzing larval distribution in space (1985). The prevailing wind may help to push first instar ballooning larvae in directions downwind (Weseloh 1997). This, in turn, would lead to higher numbers of larvae in the downwind direction and lower numbers of larvae in the upwind direction. The possibility that higher numbers of larvae may exist downwind implies that moth persistence in the downwind compass direction may be greater because a smaller proportion of the total moth population is likely to be attacked by small vertebrate predators when moth numbers are higher (Schauber 2000).

Furthermore, prevailing winds may be a factor causing migration of larvae into new territories, thus helping to stabilize moth populations (Sharov and Colbert, 1994).

Total Larvae vs. Distance

When looking at the total number of larvae as a function of distance alone, a general increase in the mean number of larvae occurred with increasing distance from the nearest egg mass. This trend contradicts results obtained by Weseloh in his 1985 and 1997 studies which described a limited pattern of gypsy moth dispersal with decreasing densities of larvae away from the nearest egg mass.

The differences in the results obtained from the research conducted at IES and the results obtained by Weseloh may be due to the different methods used in each study. This study involved burlap banding and larval sampling based upon known locations of egg masses within the study areas, while Weseloh utilized manipulation experiments involving the release of larvae from introduced egg masses and mark and recapture techniques. Differences may also have been due to the presence of additional egg masses not previously located during the original visual surveys of all substrate. Extra-unidentified egg masses may have affected the larval distribution patterns observed. In addition, immigration and emigration of larvae into the study areas may have altered true distribution patterns.

A larval distribution with increasing larval densities away from the nearest egg mass as found in this study would imply that gypsy moth larvae would be spread over a wide distance. Because larval numbers would not be concentrated within a small radius near the egg mass (limited dispersal), predation risk would be higher. Since larvae would be spread out over a greater distance, the proportion of moths consumed by predators such as the white-footed mouse would be higher (Schauber 2000).

Because compass direction may have been an important consideration in determining larval distribution patterns, it was combined with distance traveled by larvae to reveal several interesting patterns. The total distance traveled by larvae increased downwind from a distance of 35 meters to a distance of 80 meters. This suggests that the pattern laid down by the effect of wind direction on first instar ballooning dispersal was preserved in the overall pattern of larval distribution throughout the entire larval period. In other words, data from this research may suggest that larvae will be found at a greater distance in directions downwind.

Although only one compass direction (SW) exhibited a limited pattern of dispersal with a higher mean number of larvae per tree occurring nearest to the egg mass, five compass directions exhibited a bimodal larval distribution. The bimodal distribution downwind might reflect the possibility of two dispersal episodes. The first dispersal

might have developed with the first instar ballooning episode. Larvae would have dispersed out and away from the treetops by gliding with the wind (Weseloh 1997). Previous research suggests that wind dispersal usually transports larvae only a short distance (~30m) away from their original egg mass (Weseloh 1985). However, some later instar larvae may disperse by crawling on the ground with the purpose of locating suitable host trees for food and resting spots (Lance and Barbosa 1982). This method of dispersal may account for the second peak in the larval distributions.

Such bimodality in larval distribution demonstrates that moth populations may exhibit spatially heterogeneous patterns of existence within their forest environment. Spatially heterogeneous moth populations may interact with spatially heterogeneous predator populations (such as the white-footed mice) to produce refuges or areas of lower predation risk for the gypsy moth. If a population of gypsy moth larvae exhibiting a spatially heterogeneous distribution is located in an area with a low predator density, this situation may allow for the persistence of gypsy moth populations despite the predicted outcome of extinction due to a type II functional response relationship between mice and moths.

Further research utilizing mark and recapture methods and larval sampling from introduced egg masses would be important in determining the actual patterns of gypsy moth larval distribution in space. Evidence for limited and bimodal dispersal patterns resulting in spatial heterogeneity of populations would help to further explain the possible mechanisms allowing for the persistence of gypsy moth populations during low-density periods.

LITERATURE CITED

Campbell, R. W., D. L. Hubbard, and R. J. Sloan. 1975. Patterns of gypsy moth occurrence within a sparse and numerically stable population. Environmental Entomology **4**:535-542.

Deml, R., and K. Dettner. 1995. "Balloon hairs" of gypsy moth larvae (Lep., Lymantriidae): morphology and comparative chemistry. Comp. Biochemistry Physiology. **112B**:673-681.Elkinton, J. S., W. M. Healy, J. P.

Buonaccorsi, G. Boettner, H. R. Smith, and A. M. Liebhold. 1998. Gypsy moths, mice, and acorns. Pages 25-33 in M.L. McManus and A.M. Liebhold, editors. Proceedings: population dynamics, impacts, and integrated pest management of forest defoliating insects. U.S. Department of Agriculture Forest Service General Technical Report NE-247.

Fajvan, M. A., and J. M. Wood. 1996. Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. Forest Ecology and Management **89**: 79-88.

Hunter, A. F., and J. S. Elkinton. 2000. Effects of synchrony with host plant on populations of spring-feeding Lepidopteran. Ecology **81**:1248-1261.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science **279**:1023-1026

Karnosky, D. F., and C. G. Jones. 1981. Living with the gypsy moth. Garden: May-June.

Kelly, D., A. L. Harrison, W. G. Lee, I. J. Payton, P. R. Wilson, and E. M. Schauber. 2000. Predator satiation and extreme mast seeding in 11 species of Chionochloa (Poaceae). Oikos **90**:477-488.

Lance, D., and P. Barbosa. 1982. Host tree influences on the dispersal of late instar gypsy moths, Lymantria dispar. Oikos **38**:1-7.

Mason, C. J., and M. L. McManus. 1981. Larval dispersal of the gypsy moth. Pages 161-202 in C. C. Doane and M. L. McManus, editors. The gypsy moth: research toward integrated pest management. U.S. Department of Agriculture Technical Bulletin 1584.

Ostfeld, R. S., F. Keesing, C. G. Jones, C. D. Canham, and G. M. Lovett. 1998. Integrative ecology and the dynamics of species in oak forests. Integrative Biology **1**:178-186.

Schauber, E. M. 2000. Models of mast seeding and its ecological effects on gypsy moth populations and Lyme disease risk. Thesis. University of Connecticut.

Sharov, A. A. and J. J. Colbert. 1996. A model for testing hypotheses of gypsy moth, Lymantria dispar L., population dynamics. Ecological Modeling **84**:31-51.

Wallner, W. E., C. G. Jones, J. S. Elkinton, and B. L. Parker. 1990. Sampling low-density gypsy moth populations. U.S. Department of Agriculture Forest Service-Northeastern Forest Experimental Station General Technical Report NE-146:40-44.

Weseloh, R. M. 1985. Dispersal, survival, and population abundance of gypsy moth, Lymantria dispar (Lepidoptera: Lymantriidae), larvae determined by releases and mark-recapture studies. Annals of the Entomological Society of America **78**:728-735.

Weseloh, R. M. 1997. Evidence for limited dispersal of larval gypsy moth, Lymantria dispar L. (Lepidoptera: Lymantriidae). The Canadian Entomologist **129**:355-361.

Weseloh, R. M. 1998. Modeling the influence of forest characteristics and ant (Formicidae: Hymenoptera) predation on dispersal and survival of neonate gypsy moths (Lymantriidae: Lepidoptera). Environmental Entomology **27**:288-296
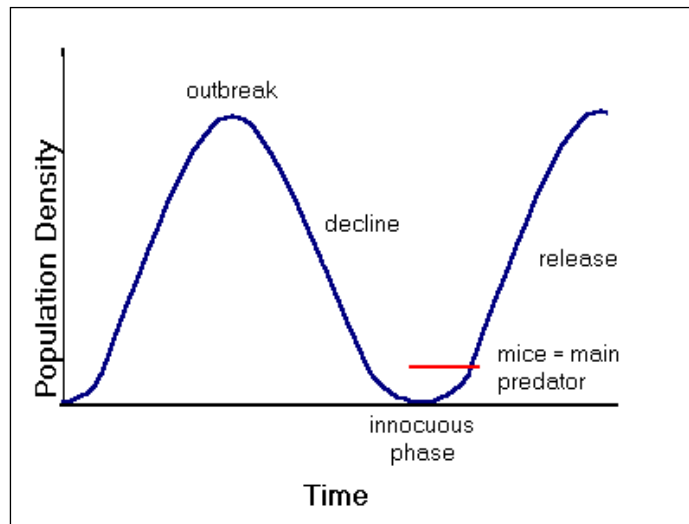
APPENDIX

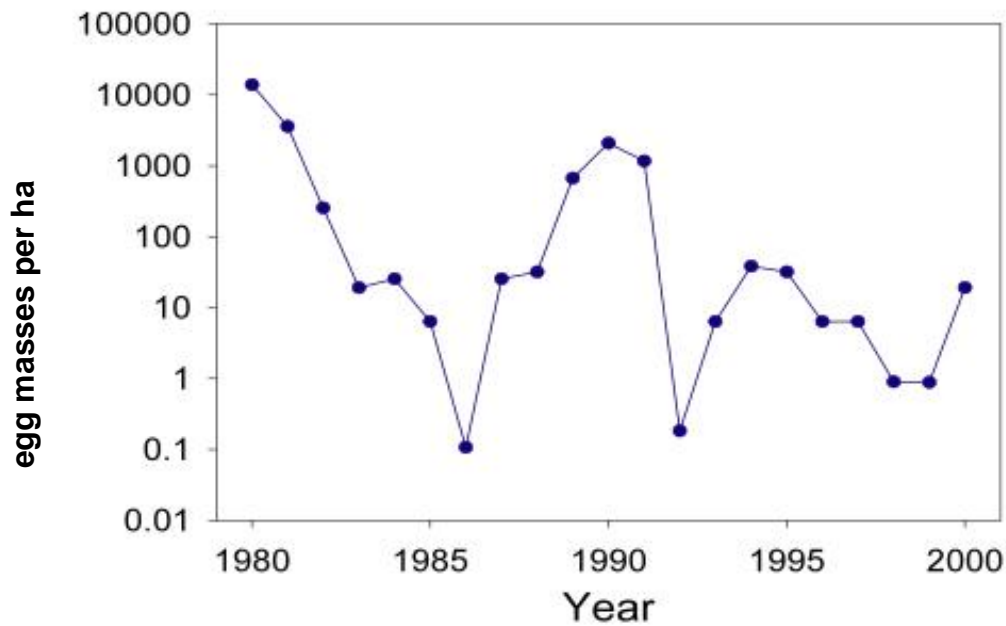**FIGURE 1.** Gypsy moth population cycles exhibit four stages.

FIGURE 2. Egg mass densities per hectare determined annually (1980-2000) from visual surveys of 20 fixed area plots at IES near Millbrook, NY, demonstrate the persistence of gypsy moth populations despite two severe declines in population densities in 1986 and 1992.
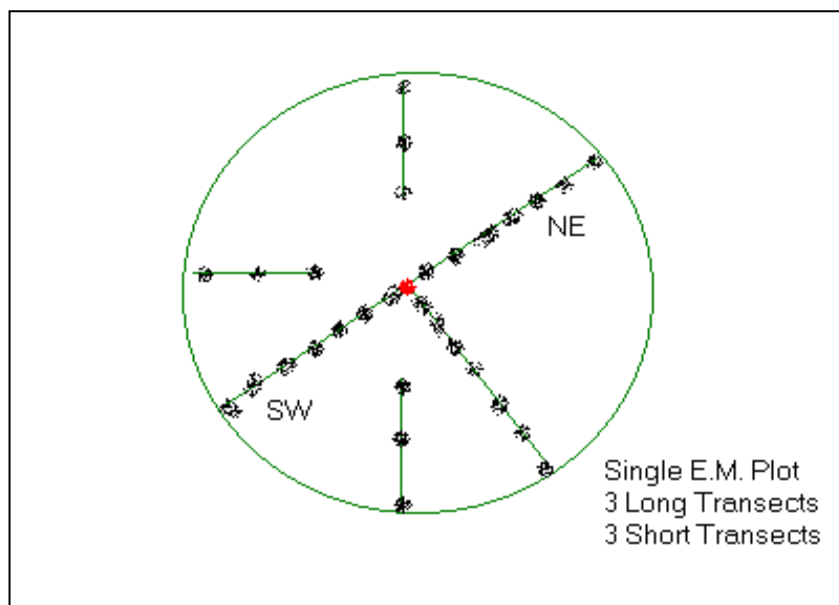

FIGURE 3. The experimental design of this research project consisted of three plot types (single egg mass, multiple egg masses, and no egg masses) within both the Green and Teahouse grids at IES. This figure displays a representative setup of transects within a single egg mass plot.
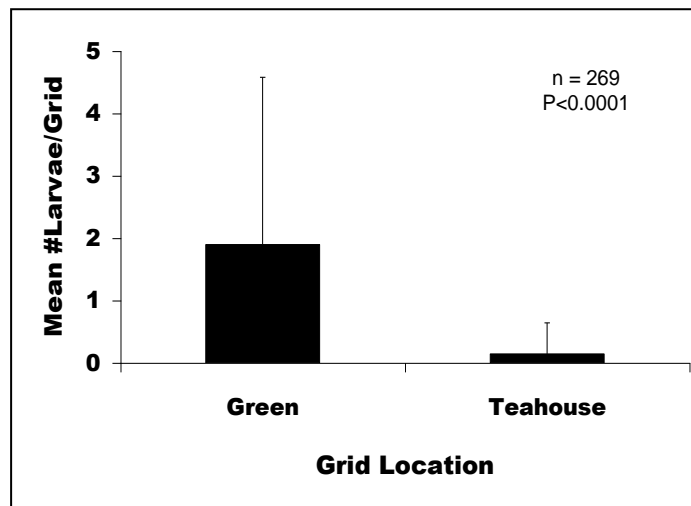
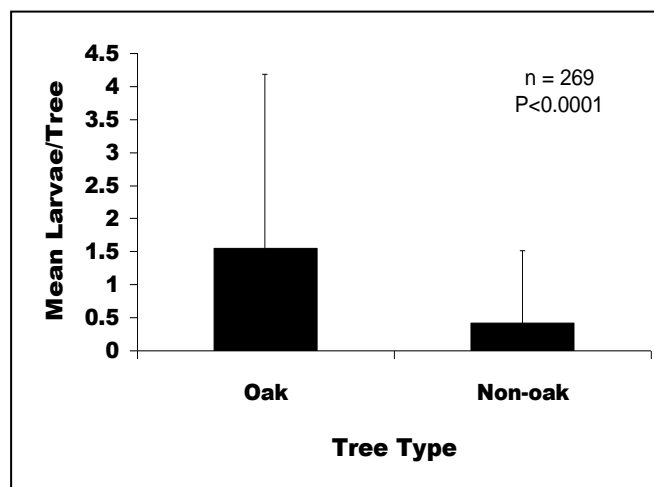**FIGURE 4.** The mean number of larvae per tree was significantly higher on the Green grid than on the Teahouse grid.

FIGURE 5. The mean number of larvae per tree was significantly higher on oak trees species than on non-oak tree species.
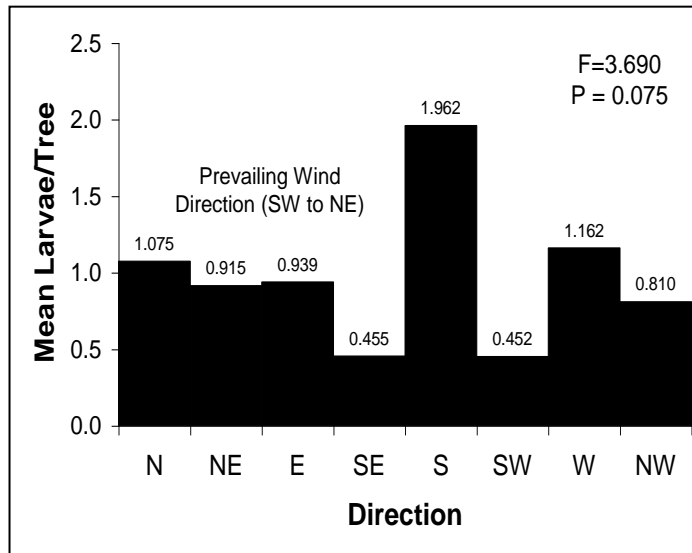
FIGURE 6. Each category in this figure represents a compass direction from the nearest egg mass. The mean number of larvae per tree within each compass direction was calculated. The effect of compass direction on the mean number of larvae per tree was determined to be insignificant using ANOVA statistical analysis.
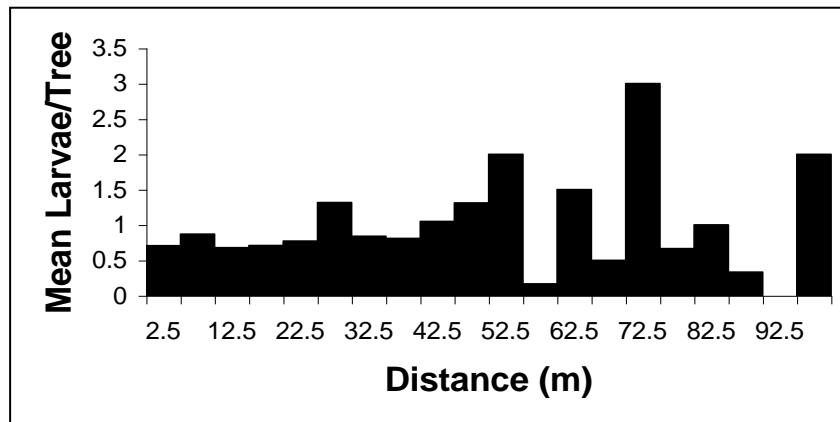

FIGURE 7. The mean number of larvae per tree increased with increasing distance from the nearest egg mass up to a distance of about 72.5 meters before declining and then rising again at a distance of about 95-100 meters.

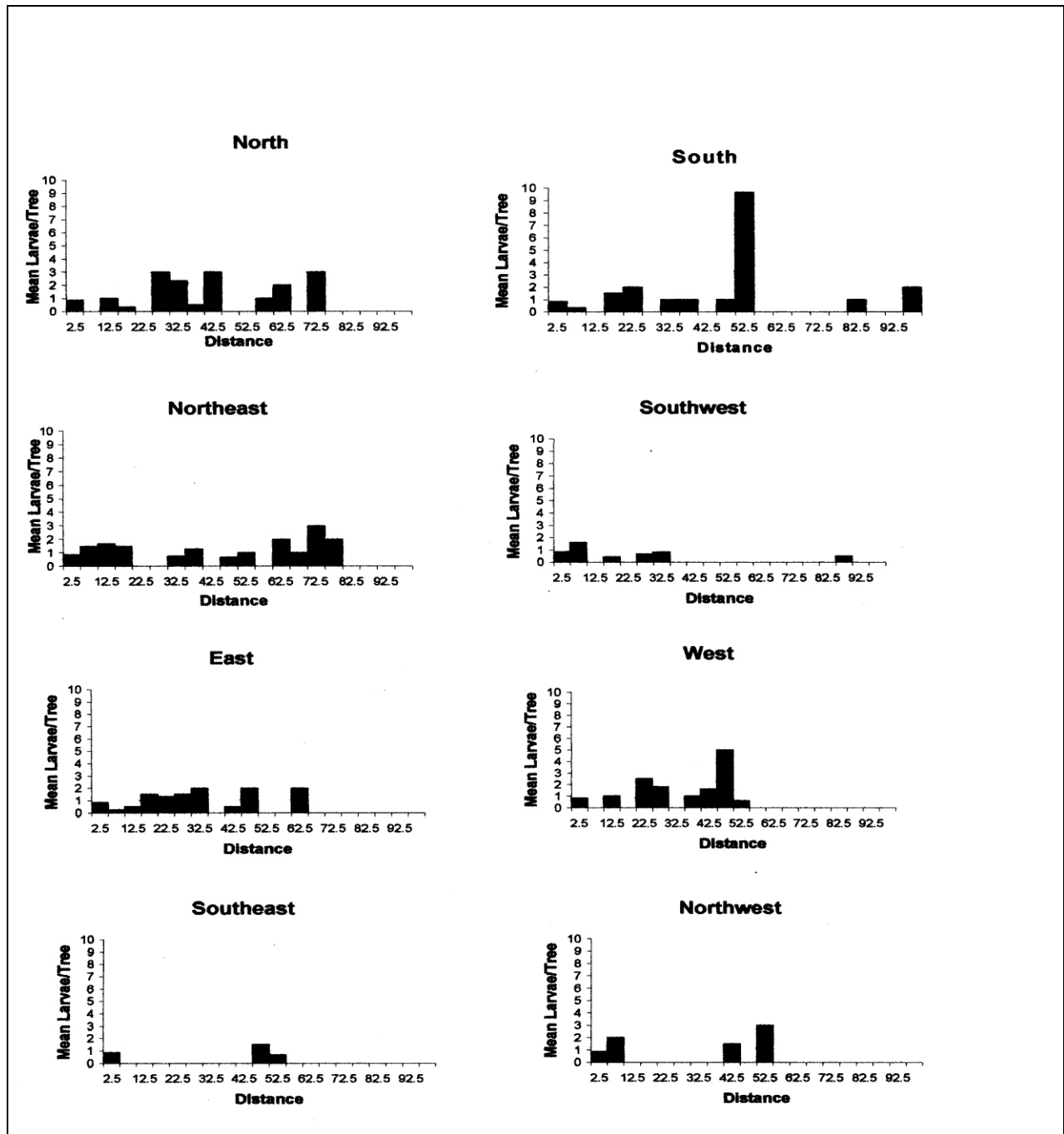**Total Larvae vs. Distance in each Compass Direction**

FIGURE 8. In order to determine the significance that compass direction had on the total distance traveled by larvae, a hierarchical general linear model was used in which distance traveled by larvae was nested within each compass direction. Bimodal patterns of distribution emerged in the N, NW, W, S, and SE directions. Limited dispersal occurred in the upwind (SW) direction, while patterns of increasing density away from the nearest egg mass occurred in the NE and E directions.