TREE SPECIES COMPOSITION, WIND, AND THEIR AFFECTS ON GYPSY MOTH CATERPILLAR DISPERSAL

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Abstract. The gypsy moth (*Lymantria dispar*) is a defoliating, generalist caterpillar that is invasive to North America. It persists at low-density but occasionally has outbreaks, defoliating millions of hectares of forest and increasing the risk of spread. A pattern of local moth dispersal that keeps natal offspring near the original hatch site may be a key factor to their survival. Limited dispersal may create refuges were high pupal densities mitigate against predation, but currently, the nature of lifetime moth dispersal is unknown. In an effort to better understand how gypsy moths distribute themselves in a forest landscape, this experiment measured lifetime larval dispersal from egg masses by counting the number of late instar gypsy moths at different distances from an isolated egg mass. The study measured two factors that may influence dispersal: wind direction and strength during early instar ballooning, and the forest tree species composition encountered by larvae migrating from egg mass to pupation site. Wind did not effect lifetime dispersal, tree species composition did not strongly influence larval migration (even though gypsy moth caterpillars overwhelmingly preferred oak trees), and lifetime gypsy moth dispersal was best described by a decreasing power curve. These findings implied that gypsy moth larvae were found at higher densities near egg masses and were minimally affected by environmental factors such as tree species composition and wind direction.

INTRODUCTION

Since its introduction to North America 130 years ago, the gypsy moth has successfully survived and spread throughout the United States (Forbush and Fernal 1896). Common North American trees have no natural defenses to moth defoliation, and for this reason gypsy moth outbreaks are disastrous to the growth and stability of hardwood forests (Fajavan and Wood 1996). When moth outbreaks occur, they can defoliate large areas of woodland and create a tremendous amount of stress on trees, possibly resulting in death (Campbell and Valentine 1972).

Few biocontrol agents and pathogens for gypsy moths are native to the North American ecosystem. Those that have been introduced specifically to attack the moth have proven affective only at high moth densities (Elkinton and Liebhold 1990). Therefore, at lower population densities, the moth is capable of surviving and initiating further outbreaks, free from any means of control. It is for this reason that low density moth populations should be studied. By characterizing life-time gypsy moth dispersal from an egg mass at low densities and subsequently describing the possible refuge from predation created by this dispersal, we will better understand how gypsy moths survive. Computer models incorporating this information will more accurately predict the environmental conditions necessary for gypsy moth persistence and outbreak. By understanding when, where, and how gypsy moths continue to exist and spread we can better protect the North American ecosystem from the devastation created by gypsy moth defoliation.

To comprehend how gypsy moths continue to exist, we need to first have a basic appreciation of their lifecycle. For much of the larval stage gypsy moths are nocturnal; crawling and feeding in the tree canopy during the night and resting at the base of their host tree during the day (Campbell and Sloan 1976). After the 5th or 6th instar, the caterpillar pupates. During the two week pupal period the caterpillar metamorphoses into a short-lived, reproductively active adult moth. At this adult stage the female gypsy moth is unable to fly. She emits a strong chemical signal which allows chemoreceptive males to travel to her (Lenard 1983). Egg masses are usually laid

by the female near the site of copulation. Therefore, the gypsy moth population, en masse, can only move as far as a female gypsy moth *larva* is capable of dispersing. By studying dispersal potential, we can characterize the distribution capability of the gypsy moth population.

Larval migration occurs in two stages: (1) early instar ballooning and (2) late instar crawling. When ballooning, gypsy moth caterpillars photophilically orient themselves, crawl upward, and release a string of silk to increase their likelihood of being caught and moved by the wind (Lenard 1983). The prevailing winds during the hatch period are likely to be influential in the direction gypsy moth larvae initially travel. The actual distances a gypsy moth is capable of traveling is up to dispute. In this experiment it was assumed that a ballooning caterpillar can move approximately 30 meters (Weseloh 1997). During later instars (IV-VI) gypsy moths are capable of crawling from one host tree to another (Lance and Barbosa 1982). Later instar caterpillars are not considered able to disperse long distances through crawling, but they are cable of frequently redistributing themselves within their local stand (Stoyenoff et al.1994).

At low densities, there are considerable distances between egg masses. Biocontrol agents, such as specialized viruses and insects that prey on the moth have difficulty encountering host or victim gypsy moth under these low densities. One of the only control agents capable of finding gypsy moths under almost any condition is the white-footed mouse (*Peromyscus leucopus*). The white-footed mouse is a largely indiscriminant forager that will readily consume gypsy moth pupae encountered while foraging (Campbell and Sloan 1977, Gould et al. 1990). The white-footed mouse is common and wide spread in North American forests, and because of this it is able to eat a great number of gypsy moth pupae, even when the population is at low density. As shown by Jones et al. (1996), if a gypsy moth pupates in a mouse homerange it generally lasts no more than 3 days, while the average amount of time need for successful pupation is well over 2 weeks (Jones et al. 1996). It seems dubious that the gypsy moth population would survive at all, especially at low-density levels, with the presence of white-footed mice.

But after being in North America for over one hundred years, gypsy moth populations are still flourishing. For this reason, we hypothesized that gypsy moths disperse in such a way that they overwhelm mouse predation, creating isolated areas of locally dense pupae. This hypothesis would only hold true if dispersal distances tended to be short, allowing the concentration of offspring around the natal egg mass to function as a refuge that protected moths from the threat of white-footed mice. The main question that this study addressed was, how do moths, at low-density, disperse? More specifically, what does the larval dispersal kernel (a curve which represents the density of gypsy moths around an egg mass) look like within a forest landscape? It was expected that the density of gypsy moth larva would be high near the egg mass and decline at greater distances away from the egg mass. With these questions in mind, this study also examined both how prevailing winds during the early instar activity, along with tree species composition around an egg mass, affected lifetime larval dispersal. It was hypothesized that wind direction would push moth dispersal in one direction, downwind. It was also hypothesized that moths would be less likely to migrate, or disperse, if they were ballooning and crawling through a forest stand that contained preferable hosts.

METHODS

The experiment was conducted on five sites at the Institute of Ecosystem Studies grounds near Millbrook, New York. Each of the five sites consisted of secondary forests with a mixture of mature trees and saplings. Most of the mature stand was oak (*Quercus* spp.), with a minority of maple (*Acer* spp.) and pine (*Pinus strobu*s) mixed with hickory (*Carya* spp.), birch (*Betula* spp.), and hemlock (*Tsuga canadensis*). The topography was primarily flat, but some sites straddled hilltops. Each site was heavily forested and centered on an egg mass.

To quantify the presence of and the direction moved by gypsy moth caterpillars near the egg masses, three transects were laid out in specific directions. Transects were placed north and south to account for local up and down wind trends during the gypsy moth hatching period. For 2002, this window of time most likely occurred

between May 1 and May 14, where the mean windward direction was 356.8° (Daily wind direction data provided by IES weather station, IES Environmental Monitoring Program, 2002). A third eastern transect acted as a control for direct wind affect (Figure 1).

Each transect consisted of ten sampling plots located every 12 meters for a total transect length of 108 meters. To account for the linear increase in the sampling area away from the egg mass, the area of the sample plots increased with distance from the egg mass by maintaining a fixed width of 5 meters and increasing the length by 3.2 meters. The first plot of each of the three transects was centered on the egg mass and was 5 meters wide and 5 meters in length. The dimensions of the last sampling plot was 5 meters by 35 meters. Each transect, with all its sampling plots, sampled 715 m² of forest area.

Any tree within a sample plot with a diameter breast height (DBH) $\geq$ 10 cm was banded. Banding is a common and effective way of measuring the presence of gypsy moth larva (Weseloh 1985). A single band was a 1 meter by 0.25 meter strip of burlap which would be wrapped around a tree lengthwise. The burlap band was stapled onto the tree and then cut into segments to enable easy access underneath. In total, 481 trees were banded.

Placing burlap bands around the base of a tree imitates bark flaps which gypsy moth larva use as refuges during the day. The burlap bands were likely to be chosen by a gypsy moth larva caterpillar as a site of diurnal refuge, but only if that caterpillar had already selected the tree as a host. It has been shown that gypsy moth larvae prefer trees with good refuges (Stoyenoff et al. 1994), and it was assumed that the bands were put up too late (the week before most of the caterpillars' last instars) to influence host selection. The number of gypsy moth caterpillar, under these bands allowed us to estimate gypsy moth larval densities. Because the bands were placed on trees in plots at increasing distances from an egg mass, the distance that larvae traveled from its hatch point could be evaluated.

The comparison between the frequency of larval presence and the various distances sampled created a *density curve*. This curve was analyzed for a best fit with the following curves: linear regression, 2nd order polynomial, 3rd order polynomial, rational function, power and exponential.

The third and final section of this experiment was the test of tree species composition on migration distances. First, it was necessary to find which tree species gypsy moth caterpillars preferred. The technique used to calculate gypsy moth preference for a tree species should not merely account for the presence of an individual tree, but rather, each tree's *basal area*. Basal area indicates a tree's influence and size within the forest canopy, thereby corresponding to the likelihood of being chosen as a prospective host by a ballooning or crawling gypsy moth. Second, it was necessary to determine the likelihood of a ballooning or crawling gypsy moth to encounter a certain tree species during its path of migration. This can be simply accessed by adding and comparing the basal areas of all the tree species in the sampling plots that came before the sampling plot which contained a late instar larva.

Because of the low densities of the gypsy moth population, it can be assumed that most of the moth larvae found under the burlap bands originated from the closest known egg mass. We will use the idea of "migration stoppage", defined as the distance that a moth migrated before it settled upon permanent host, as an indicator of how tree species affects gypsy moth larva movement. The idea of "migration stoppage" assumes that all caterpillars travel in a straight line and that very late instar caterpillars have finished migrating. To ensure that the caterpillars recorded had stopped migrating, this experiment only recorded the presence of caterpillars in instar stages just before pupation, either 5th or 6th. Late instar caterpillars are likely to remain with the same host because during late instar phases, caterpillars begin to follow their own silk trail, which is likely to lead them up and down the same host tree until they pupate (Lenard, 1983).

The presence of moths underneath burlap bands was recorded starting July 2, 2002, and continued until July 11, 2002. Plots were checked in the brightest part of the day (early afternoon), and never checked after heavy rain. It

took two days to check all the bands and each band was visited three separate times. All live, late instar caterpillars and their host's details (such as sampling plot, species of tree, basal area) were recorded. If a same-instar caterpillar was found multiple times on a concurrent host, it was not recorded multiple times.

RESULTS

Examining the presence of live, late instar caterpillars (V and VI), oak trees were overwhelmingly chosen as hosts (95% of all caterpillars were found on oaks; Fig. 2B) even though just over half of the basal area of the trees on the sampling plots were oak (Fig. 2A). Caterpillars chose oaks more then would be expected by the natural abundance of the tree species ($\chi^2 = 15.5$, p < 0.001, df = 1).

Transect direction had no effect on gypsy moth caterpillar density across all 5 egg masses (2-factor ANOVA, *F = 1.167, p = 0.315*) suggesting that wind direction did not affect lifelong larval dispersal. However, caterpillar densities did differ significantly between the various experimental plots with CG2 being significantly lower (2-Factor ANOVA, *F = 3.743, p = 0.0063* followed by Scheffe's Test to pinpoint CG2). The density for experimental plot CG2 was so low (only 2 caterpillars found), that we collected and analyzed the egg mass itself. Through dissection, the egg mass was found to have a low fecundity and contain a large amount of un-hatched eggs (500% more unhatched eggs than other egg masses). The data collected from CG2 was disregarded.

After all the gypsy moth migration data was combined it was found that the tendency of larval dispersal was best represented by a power curve (Figure 4). Other curves, such as the linear regression, 2nd order polynomial, 3rd order polynomial, rational function, and exponential all yielded lower R squared-values compared to the power curve (Table 1).

The species composition (in this case, the measure of the amount of oak) of individual transects did not effect the distance moved by gypsy moth larvae (Fig. 5; linear regression *F = 0.986, p = 0.325*). Though gypsy moth larvae overwhelmingly preferred oak trees, forest tree species composition had no measurable effect on the distance caterpillars chose to migrate in order to find a suitable host. This analysis assumes that all the gypsy moths found originally came from the egg mass in question and traveled directly from the egg mass to the banded tree it was found upon.

DISCUSSION

Understanding the migration of gypsy moth larvae is the first step in proving that gypsy moth dispersal forms refuges. As Elkington and Liebhold point out in their overview paper on gypsy moth population dynamics (1990), the traveling distance of a caterpillar is still subject to controversy among scientists. Experiments by Mason and McManus (1981) show larvae sporadically dispersing hundreds of meters while Taylor and Reling (1986) have shown distances to be even longer (19 kilometers). But, as Elkington and Liebhold further explain, it is generally accepted that gypsy moth populations advance slowly from specific population sites called "focal areas" or "refugia". Two studies in 1985 and 1997 by Weseloh have shown a tendency of gypsy moth populations to stay near their egg mass and for their population to decrease in density away from their egg masses. These studies offer an explanation to the propensity of moth populations to advance slowly. Weseloh's studies also hint at the creation of refuges, which could play a factor in moth persistence in the presence of white-footed mice.

This study's data indicates that moth populations do in fact create concentrated dispersal kernels, which is illustrated by the best-fit power curve (Fig. 4). Moths are therefore likely to advance slowly from discrete population concentrations, and this agrees with Elkington and Liebhold's observation. To determine how tree species composition shapes this kernel, we measured the moth's preference for oak against the distance moth's traveled. The data suggests that moths highly prefer oak trees (Fig. 2), but their migration is not strongly influenced by the tree species composition of the forest area that they encounter (Fig. 5). It was anticipated that moths would display a preference for oak because multiple studies have recorded such phenomena (Elkinton and

Leiebhold 1990, Gross et al. 1990, Lance and Barbosa 1982). With the gypsy moth's predilection for oak it was expected that dispersal would be affected by the presence of oak trees in their dispersing area. However, using this study's data, it is necessary to reject the hypothesis that tree species composition (specifically percentage oak) of the forest that a gypsy moth caterpillar disperses through can influence that dispersal. As seen in Figure 5, migration distance versus percent oak was not significantly correlated.

This discrepancy may be clarified for two separate reasons. First, this study may have been too small. With only four viable egg masses to measure the parameters of moth dispersal, a great deal of error may have resulted in comparing the trends between the experimental plots. Increasing the sample size of isolated egg masses might clarify the relationship between forest composition and moth dispersal curves. The second, which is more theoretically based, is that the migration tendency of the gypsy moth is to form tightly-packed refuges, ultimately ignoring the tree species composition. It is possible that the creation of refuges is an integral link to gypsy moth population survival in the presence of white-footed mice. Staying close and overwhelming foraging mice may be the crucial factor thwart extinction. If this were the case, it would not be evolutionarily sound for the moth population to adjust their dispersal pattern, and thereby shift their dispersal kernel, for more preferable hosts (such as oak trees).

The conclusions of this study illustrate the possible importance of the dispersal kernel and the importance of understanding gypsy moth behavior to understanding the species' population dynamics. If concurrent experiments agree with this study's data it will be apparent that moth populations manage to persist and continue to have outbreaks with deleterious consequences because of innate ballooning and crawling activities which cannot be prohibited by biocontrol agents or humans alike. More extensive and rigorous research may reveal the information that is necessary to stop the gypsy moth population from spreading across the whole of North America and continuing to eat its way through this country's ecosystem.

LITERATURE CITED

Campbell, R.W., and R. J. Sloan. 1976. Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. Environmental Entomology **5**:1211-1217

Campbell, R.W., and R.J. Sloan. 1977. Natural regulation of innocuous gypsy moth populations. Environmental Entomology **6**:315-322

Campbell, R.W., and H.T. Valentine. 1972. Tree condition and mortality following defoliation by the gypsy moth. USDA Forest Service Research Paper NE-236. Washington DC: USDA Forest Service.

Elkinton, J.S., W.M. Healy, J.P. Buonaccorsi, G.H. Boettner, A.M. Hazzard, H. R. Smith, A.M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. Ecology **77**(8):2332-2342

Elkinton, J.S., A.M. Liebhold. 1990. Population dynamics of gypsy moth in North America. Annul Review of Entomology. **35**:571-596

Fajavan, 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

Forbush, E.H., and C.H. Fernald. 1896. The Gypsy Moth. Wright and Potter, Boston, Massachusetts USA.

Gould, J.R., and J.S. Elkinton, and W.E. Wallner. 1990. Density-dependent suppression of experimentally created gypsy moth, Lymantria dispar, populations by natural enemies. Journal of Animal Ecology **59**:213-233

Gross, P., Montgomery, M.D., and Barbosa, P. 1990. Within and Amount Site Variability in Gypsy Moth (Lepidoptera: Lymantriidae) Performance on Five Tree Species. Environmental Entomology **19(5)**:1344-1355

Institute of Ecosystem Studies, Environmental Monitoring Program. 2002. Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, www.ecostudeis.org

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

Jones, C.G., R.S. Ostfeld, J.O. Wolff. 1996. Of mice and mast. Bioscience **46**:323-334

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

Lenard, D.E. 1983. The gypsy moth research toward intergraded pest management technical bulletin 1584. US Department of Agriculture. ed. Doane, C.C., M.L. McMaus. Pages 9-29

Mason, C.J. and McManus, M.L. 1981. Larval dispersal of the gypsy moth. USDA Forest Service Technical Bulletin. 1584.

Stoyenoff, J.L., J.A. Witter, M.E. Motgomery. 1994. Nutritioal indices in the gypsy moth (Lymantria dispar L.)under field conditions and host switching situations. Oecologia **97**:158-170

Taylor, R.A.J. and Reling, D. 1986. Density/height profile and long-range dispersal of first instar pysy moth (Lepidoptera: Lymantriidae). Environmental Entomology. **15**:431-435

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), larvae determined by releases and mark-recapture studies. Annals of the Entomological Society of America **78**:728-735
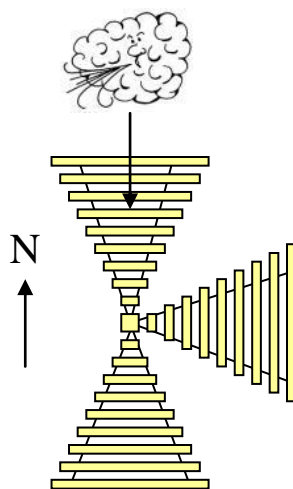
APPENDIX

FIGURE 1: Representation of three transects radiating from a centrally located egg mass. Each rectangle represents the area of experimentation. Windward due north, as indicated.
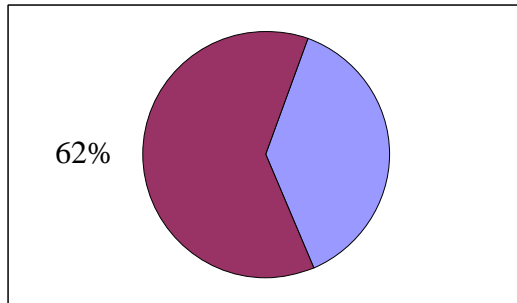
FIGURE 2A: Total basal area of all banded trees. Sight majority is oak (red), while hickory, birch, pine, and maple made up the rest (blue).
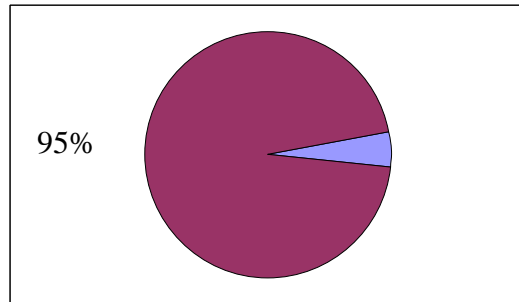

FIGURE 2B: Tree species that gypsy moths were found on . Red is oak, blue is other.

FIGURE 2: Compares the basal area of oak trees that made up the whole of trees sampled, and the frequency of oak chosen as a host by gypsy moths.
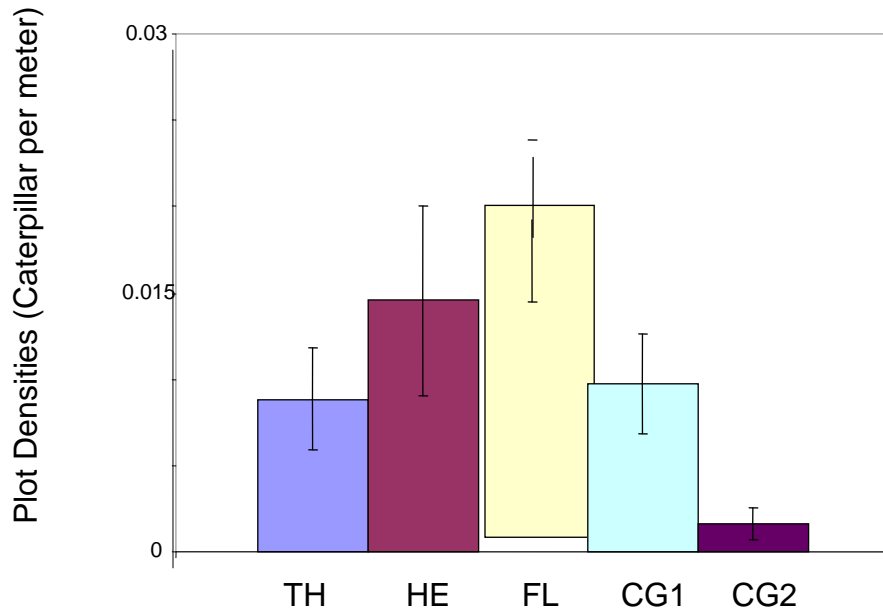
FIGURE 3: Mean gypsy moth density on the different plots. The error bars represent standard error. TH - Tea House; HE - Henry Experimental; FL - Field Lab; CG1 and CG2 - both located on Canoe Gap 1&2.
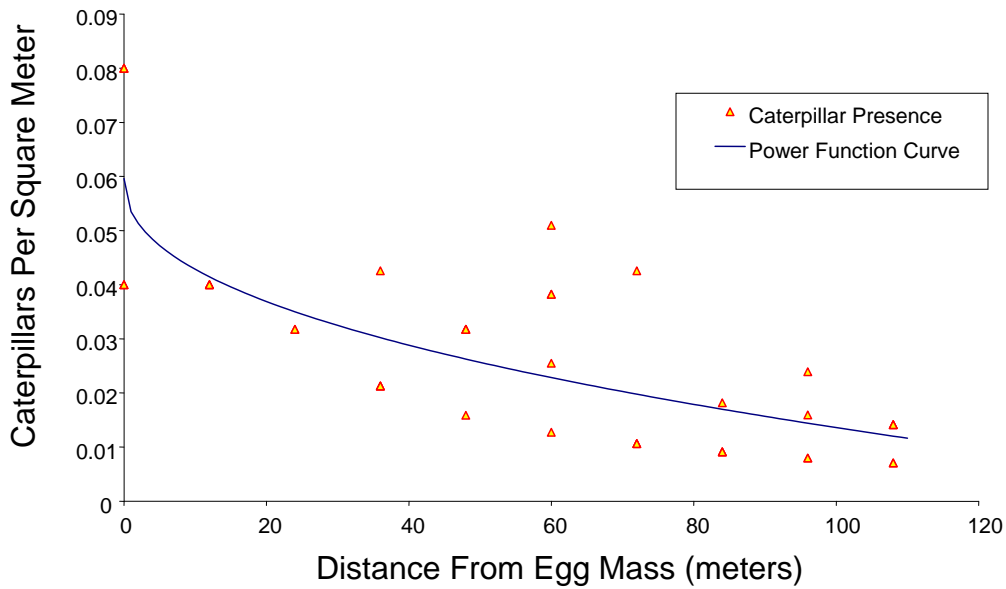

FIGURE 4: Gypsy moth dispersal is fit best by a power function curve (density = 0.0596-(0.0061)*distance$^{0.4387}$, $R^2 = 0.636$). Each point can represent the presence of multiple caterpillars
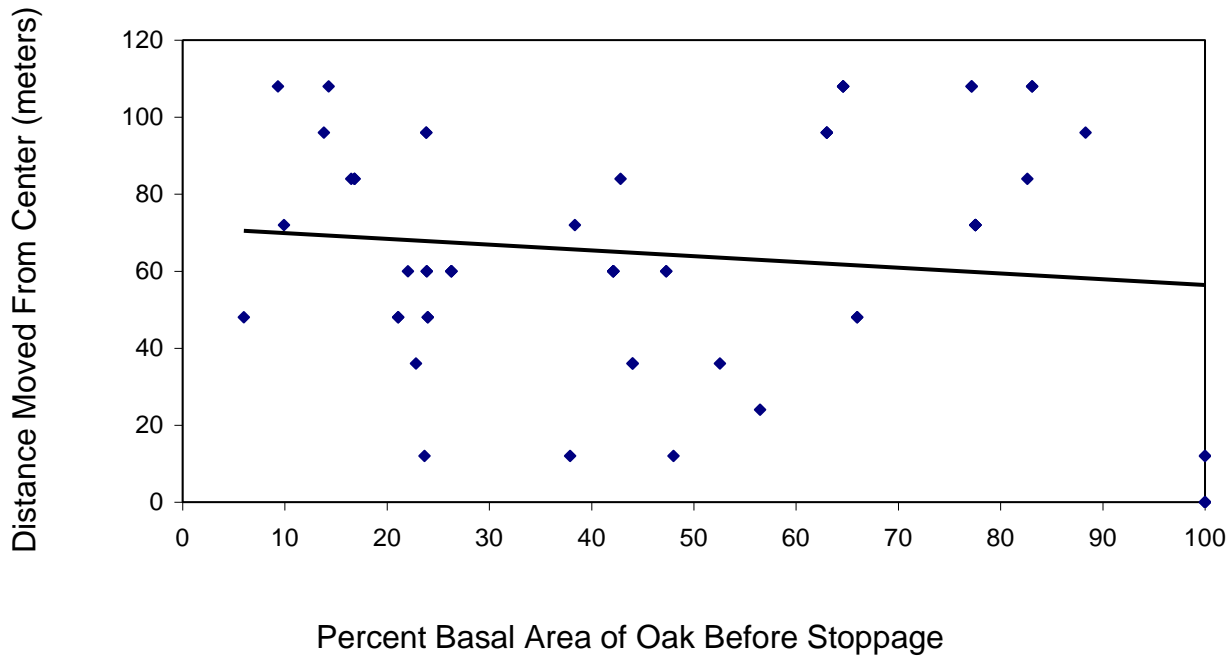
FIGURE 5: Percent basal area of oak before stoppage indicates the amount of tree area oak represented within a single transect that a gypsy moth, starting from the known egg mass, would have encountered during its migration to its chosen host. The linear regression line is fit to the data (y = -0.1503x + 71.404, R^2 = 0.017).

TABLE 1: The types of curves fitted to the gypsy moth larvae dispersal pattern. The value with the highest R squared-value indicates the curve that fits the data best. The power curve indicates that the majority of larvae were likely to be found within 35 meters of the egg mass.

Curve Name	R squared-value
Power curve	0.636
Linear regression	0.573
2nd order polynomial	0.604
3rd order polynomial	0.622
Rational function	0.466
Exponential	0.610