ASSESSING THE MOVEMENT OF LATE-INSTAR GYPSY MOTHS, LYMANTRIA DISPAR, IN A SECONDARY OAK FOREST

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Abstract. The invasive gypsy moth, *Lymantria dispar* (L.) has been the cause of massive defoliation in northeastern United States. Research toward management of this pest has contributed to a growing body of knowledge on the ecology of the gypsy moth, including the web of interactions in which they participate within oak forests. Gypsy moths introduce a complex feedback dynamic into the donor-controlled system of oak trees, acorns, white-footed mice, deer, ticks, and Lyme disease. The persistence of the gypsy moth, a rare prey, in the face of intense predation by the white-footed mouse, a generalist predator, maintains this feedback. The synergistic effect of two factors—moth lifetime dispersal and spatially heterogeneous predation risk—is thought to be responsible for moth persistence at scales where extinction would be expected. To better understand lifetime dispersal, the movement of gypsy moth larvae in the 4th to 6th instars was measured by marking 300 caterpillars recruited by burlap bands across 69 different trees with unique color codes and observing them over 18 consecutive days of sampling. In a total of 650 caterpillar observations, only 14 movement events were recorded. It is concluded that late instar movement does not contribute significantly to lifetime dispersal of the gypsy moth, and that future research concerning moth persistence can utilize the simple "seed shadow" model of silking early instar larvae to predict lifetime dispersal.

Keywords: gypsy moth; Lymantria dispar; invasive species; rare prey; predation risk.

INTRODUCTION

Understanding the specifics of lifetime dispersal patterns of the gypsy moth (*Lymantria dispar*) is essential to understanding how this pest is able to persist in the face intense predation by white-footed mice (*Peromyscus leucopus*). It is thought that persistence is due to the synergistic effects of limited moth dispersal and spatially heterogeneous predation risk. Moth persistence has implications for the ecology of the oak forests they inhabit, Lyme disease incidence, and pest management. This study focuses on the gypsy moth dispersal aspect of persistence, with its findings contributing a definitive picture of what moth dispersal in the late instar stages looks like.

Native to Asia and Europe, the gypsy moth was brought to North America in 1868 by Etienne Trouvelot, who had hopes of cross-breeding it with the silk moth to generate a silk-producing crossbreed that could survive the harsher climate of northern United States (Forbush and Fernald 1896). His hopes went unrealized, and over the next century escaped insects spread to populate the entire Northeastern United States, as far south as Virginia and as far west as Minnesota (McManus and McIntyre 1981). Though often thought of as just a pest, because of the intense defoliation and even death it can cause to oak trees (*Quercus* spp.) when its population is at outbreak levels, the gypsy moth is also an important player in a web of interactions that takes place within oak forests.

Gypsy moths in their pupal life-stage are preyed upon in oak forests primarily by white-footed mice (Campbell et al. 1977; Elkinton et al. 1996; Jones et al. 1998; Ostfeld et al. 1996). The moths, in turn, feed on the foliage of oak trees as larvae (Elkinton *et al.* 1996). The acorns of oak trees provide the primary food source for white-footed mice, which are also a primary host of *Ixodes scapularis*, the black-legged tick (Jones *et al.* 1998). The black-legged tick is a vector for the bacterial spirochete (*Borrelia burgdorferi*) that causes Lyme disease in human hosts

(Jones *et al.* 1998). Every two to six years, mouse population levels rise the summer after oaks produce a mast crop. After a two-year time lag, due to the tick life cycle, there is a subsequent rise in the incidence of Lyme disease (Jones *et al.* 1998). Gypsy moths also experience a kind of periodicity, in which their numbers reach outbreak levels roughly every ten years (in which moth numbers are several orders of magnitude higher than in non-outbreak populations). In outbreak years, gypsy moths can defoliate, even kill, oak trees over large areas, giving them the power to indirectly affect mouse densities—at very high moth population numbers, tree damage can result in a lowered acorn crop, and a subsequent decline in the mouse population for want of enough food (Jones *et al.* 1998). This characteristic of the gypsy moth is what has made it of such great interest to the general public and the government as an invasive species. As a result, a great deal of time and money has been spent on gypsy moth research in the time since their invasion began.

While most early research concerning gypsy moths focused on pest management, the latter part of the twentieth century saw a shift from research purely for control or eradication purposes to an interest in the ecology of the gypsy moth. Research by Elkinton *et al.* (1996) over a ten-year period, and Ostfeld *et al.* (1996) over a fifteen-year period elucidated key linkages in the acorn-mouse-moth web. There was found to be a direct relationship between the acorn crop density and mouse density, and an inverse relationship between mouse and moth densities. This general model was proposed by Campbell (1975) and Campbell and Sloan (1977), and highlights the importance of mice in the control of nonoutbreak populations of the moths, and speculated on the effects a gypsy moth outbreak can have on mast and mice densities. Jones *et al.* (1998) experimentally demonstrated the acorn-mouse-moth connections and further linked gypsy moth outbreaks to Lyme disease risk, though this assertion has been contested (Randolph 1998). The persistence of the moths in spite of high predation risk becomes of interest, and has been studied with an eye toward population ecology, conservation and pest management.

Recent work has determined that mice show a type-II functional response to moth pupae, meaning that risk of predation increases with decreasing pupal density (Schauber 2000). This would suggest that moth populations of low-density will frequently be driven to extinction locally. But while field data show this to be the case in areas of one hectare or less, they do not show this to be the case for areas as small as 10 ha (Goodwin *et al.*, in press). It has been hypothesized that a combination of moth dispersal and spatially heterogeneous predation risk contribute to moth persistence where extinction would otherwise be expected (Goodwin *et al.*, in press). Researchers are now trying to use empirical data to create simulation models which will test the relative importance of these two factors, and allow derivation of some general hypotheses about the scales of risk and refuge in space. This is done by measuring predator density, foraging activity, attacks on moth pupae, and lifetime moth dispersal.

Weseloh (1985) evaluated late instar dispersal of the gypsy moth in a study that included the measuring of actual distance traveled by a small number (n=9; n=23) of lab-reared, individually marked and recaptured larvae. Weseloh stated that caterpillars, "generally did not move more than 15 m between captures," but no actual distances were reported (Weseloh 1985). Additionally, there is some indication that the marking method used led to increased mortality of the caterpillars. A study of late instar movement conducted by Liebhold *et al.* (1986) in a forest composed almost entirely of young, dense oak species, at generally high moth densities, arrived at approximately 5 m for late instar dispersal distance, but lacked the lifetime dispersal data necessary to draw conclusions about relative importance of ambulatory versus airborne to total dispersal.

My study broke moth lifetime dispersal down into its component parts and studied the ambulatory gypsy moth movement of the late instar stages. Determination of whether late instar movement contributes significantly to lifetime dispersal will aid in the continual development of computer simulations modeling spatial and temporal risk and refuge to gypsy moths by predating mice. While the models are currently concerned only with lifetime dispersal, a breakdown of dispersal patterns will allow the pieces to be pulled apart, and a more accurate model based on empirical data to be developed. The results of this study contribute to the body of knowledge being used to explain moth persistence by addressing how far gypsy moths move in their late instar stages.

METHODS

Study site and Set-up

Monitoring of larval gypsy moths took place on the grounds of the Institute of Ecosystem Studies (IES) in Millbrook, New York, where moths are currently at low densities (3-4 egg masses /ha). Observations were made and measurements taken on five adjacent 2.25-ha secondary forest plots that consist primarily of oak and maple trees (*Acer* spp.). Four radial 120 m transects were set up on each plot, originating from egg masses discovered during plot censuses in 2003 for part of a larger study. Sub-plots were created perpendicular to the transect every 15 m along each transect (9 sub-plots per transect), and were uniformly 5 m in width. Length of plots increased with increasing distance from egg mass, to account for the increasing area over which larvae can disperse (9m at the 30 m mark, 14 m at 45 m along the transect, and 19 m long at a distance of 60 m). Burlap bands, frequently used to detect and monitor moths since they are experienced as the bark crevices gypsy moths typically rest in during the day, were doubled over, wrapped, and stapled at breast height to all trees greater than 10 cm in diameter at breast height within the sub-plots (McManus *et al.* 1980; McManus and Smith 1984).

Monitoring and Measuring

Intensive monitoring of gypsy moth larvae began with the appearance of the first fourth instars within the plots (June 17, 2004). When found, a larva's exact position (by tree) was recorded, as well as its instar stage. To track larvae from one day to the next during the data collection phase, each larvae was marked with a specific three-dot color code on its dorsal surface using nine colors of acrylic paints, allowing the marking of 300 unique larvae without a combination being used twice (Wallner 1983). Monitoring took place along set transects and sub-plots, as well as surrounding trees and leaf litter when a marked caterpillar could not be located within the sub-plot. Repeated observations of marked larvae allowed determination of late instar movement patterns.

Data analysis

Mark/recapture data were analyzed by comparing the number of movement to non-movement events among larvae that were seen again after initial marking.

To determine whether results were consistent over the greater gypsy moth population, data collected by the Jones lab field crew (Institute of Ecosystem Studies, Millbrook, NY) were analyzed for movement events. Data collection utilized the same method of burlap band recruitment described above; but, as it assessed gypsy moths on the population level, larvae were marked with a single dot of acrylic paint, rather than being treated as individuals. To determine movement events in the population, the appearance of a larvae on a tree where there were none previously recorded (or of three where there were two, etc.) was taken as a definitive movement event. The caveat of this method is that all movement events would not be detected. Consequently, the proportion of movement to non-movement events would be expected to be lower than that obtained from the study of individually marked larvae. Nonetheless, proportions of movement to non-movement events on the population and individual levels were compared.

RESULTS

Over the course of three weeks, between June 17, 2004 and July 04, 2004, a total of 300 individual larvae were marked on 69 different trees. 213 out of 300 (71%) were "recaptured," or observed again after the initial marking. 148 of 300 (48%) were observed three or more times. This yielded a total of 650 recapture events, 2.2% (14) of which were definitive movement events, and 636 represented non-movement events, in which a caterpillar was seen in the same location on subsequent days of observation. Of the 14 movement events, 4 represented movement between trees that were banded separately, but that shared a trunk, and thus had a great deal of canopy

overlap. Of the remaining 10 movement events, half were the multiple movements of a single gypsy moth larvae between three different trees no more than 5 m apart, over the sampling period. 4 of the movement events were to neighbouring trees, and constituted a displacement of less than 1 m. Finally, a single movement event represented displacement of roughly 5 m. 39 of the 300 larvae died over the course of sampling, either by predation, nucleopolyhedrosis virus, or the fungal pathogen *Entomophaga maimaiga*; 13 molted and left behind exuvia on which the acrylic markings were still evident.

Data collected on the population level yielded 1711 observations of already-marked caterpillars over sampling from June 16, 2004 to July 8, 2004. Of the 1711 observations, 33 represented definitive movement events (2.0%).

DISCUSSION

Lifetime dispersal data for gypsy moths is unknown, as are the relative importance of early instar ballooning versus late instar ambulation. The data obtained in this study suggest that gypsy moths do not disperse to any great extent in the late larval instar stages under the low densities (3-4 egg masses/hectare) that they are currently seen. The population data, with a nearly identical incidence of movement events (2.0%, compared with 2.2% for individually marked larvae), offer another line of evidence that supports this conclusion.

This straightforward result—that late instar ambulatory movement does not contribute significantly to lifetime dispersal—will be useful in work done on moth dispersal. The component of moth lifetime dispersal critical to understanding why moths persist in the face of intense predation by the white-footed mouse, even at densities where extinction would be expected, can now be boiled down to early instar dispersal by silking. Tree composition and density, canopy cover, and other factors thought to affect gypsy moth behavior in the larval stages, and thus important if late instar dispersal is significant, no longer need to be taken into account, which somewhat simplifies experimental modeling. In the early (first through third) instar stages, the gypsy moth disperses by floating on silk strands it weaves, and relies upon the wind. In later instar stages (fourth through sixth), the caterpillar disperses by walking (Wilson 1981). Given the difficulties associated with doing so accurately, larval dispersal by ballooning is rarely studied, though a model for early instar dispersal has been developed by Weseloh (1985).

Weseloh's conclusion that late instar larvae do not generally disperse more than 15 m is upheld by this study, while these data would further specify that late instars rarely travel, and any generalization made would state that they travel in general less than *five* meters (Weseloh 1985). My results do not support Liebhold's (1986) conclusion that average late instar dispersal is roughly 5 m. The difference between study sites may be responsible for this difference in results. The site for Liebhold's observations, near the coast in Massachusetts, is windy and composed of trees of a smaller average size than those at the site of this study (Liebhold 1986).

The next step to be taken in follow-up study will be to compare moth dispersal curves generated by Weseloh's early instar model against lifetime dispersal curves, using data generated by the Institute of Ecosystem Studies. If the curves for early instar dispersal fit the lifetime dispersal curves, the conclusion reached herein will be further confirmed.

Understanding moth persistence allows us to draw conclusions about rare invasive prey species and mouse-moth interactions, especially how they affect—and will affect in the future—the oak forest system in which they operate, and to make decisions about pest management. Experimental models utilizing data on gypsy moth lifetime dispersal and spatially heterogeneous predation risk are constantly being reworked. With better data on each component of dispersal—early instar silking and late instar ambulation—more accurate models can be formed and predictions as to the fate of the gypsy moth made. This study contributes to this body of work by clearly showing that late instar ambulation has little to no affect on total lifetime dispersal of the gypsy moth.

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