QUANTIFICATION AND USE OF PHEROMONE-BAITED MILK-CARTON TRAPS TO MONITOR GYPSY MOTH POPULATIONS

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(ABSTRACT)

The goal of this research was to improve the understanding of the dynamics of male gypsy moth-pheromone trap interactions and the ecological factors that influence moth capture in pheromone traps. Defoliation, the most obvious expression of high density gypsy moth populations, may have a significant influence on gypsy moth population dynamics. This research focused on the use of defoliation and defoliation related processes to study moth capture in pheromone traps. Male moth wing length was found to decrease substantially only when defoliation exceeded a threshold level of ca. 40%, resulting in moths with either large or small wings. Moth wing length, determined from moths captured in intensively monitored traps, was found to accurately estimate whether or not defoliation exceeded ca. 40% in the vicinity of the trap. However, for traps serviced less intensively, male wing length provided a poor estimate of defoliation.

Larval development (using degree-days as a physiological measure of time) in sixteen plots was not altered as a result of varying levels of defoliation, but pupal phenology was significantly influenced by the level of defoliation . Despite distinct differences in pupal phenology, there were no differences in male moth capture over time in pheromone traps attributable to defoliation.

A broad relationship between the number of moths captured and egg mass density was developed. The spatial and temporal characteristics of gypsy moth populations were examined using a combination of field studies and defoliation maps. This information, in conjunction with data on wing length and the relationship between moths per trap and egg mass density, was used to develop an algorithm to interpret moth capture in pheromone traps to monitor gypsy moth populations.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1
Introduction

Biology and Ecology. The gypsy moth (Lepidoptera: Lymantriidae Lymantria dispar) is the major insect pest of eastern hardwood forests. First introduced into Massachusetts in 1869, it has spread throughout the northeastern United States and is currently extending its range south and west into Ohio, West Virginia, Virginia, and North Carolina (Fig. 1). The ecology and biology of the gypsy moth have been well studied and there are many excellent publications on the biology, ecology, management, and history of the gypsy moth (Fornbush & Fernald 1896, Bess 1961, Doane and McManus 1981, Smith 1989, Elkinton & Liebhold 1990).

Innovative integrated pest management (IPM) programs currently being developed to manage the gyspy moth will benefit from an effective pheromone trap-based monitoring system. The goal of this research was to improve the understanding of the dynamics of male gypsy moth-pheromone trap interactions. Improving the knowledge of male moth-pheromone trap dynamics will increase the usefulness of pheromone traps used to monitor gypsy moth populations and facilitate development of effective pheromone trap-based monitoring systems.

The southern hardwood forests of the Appalachian mountain and plateau region in Ohio, West Virginia, Virginia, and North Carolina and states further south provide ideal habitat for the gypsy moth. Gypsy moth larvae can feed on over 300 species of trees and shrubs (Lechowicz and Mauffette 1986). Oak species (Quercus) are some of the most preferred hosts and are usually defoliated during population outbreaks. The gypsy moth is univoltine, eggs hatch in mid-April to mid-May in most areas (Fig. 2). The larval stage consists of five instars for males and five or six for females. Following pupation in late June to August, small, gray, nondescript male moths are attracted to the large, flightless, white female moths by the sex pheromone that the females emit. Depending on the level of defoliation experienced by larvae during development, females oviposit a single egg mass consisting of 100 to over 1500 eggs in a protective covering of minute hairs. The buff-colored, oval shaped egg masses are usually deposited in well protected areas such as the underside of over-hanging tree limbs, tree boles, furrows in tree bark, under rocks, and man-made objects.

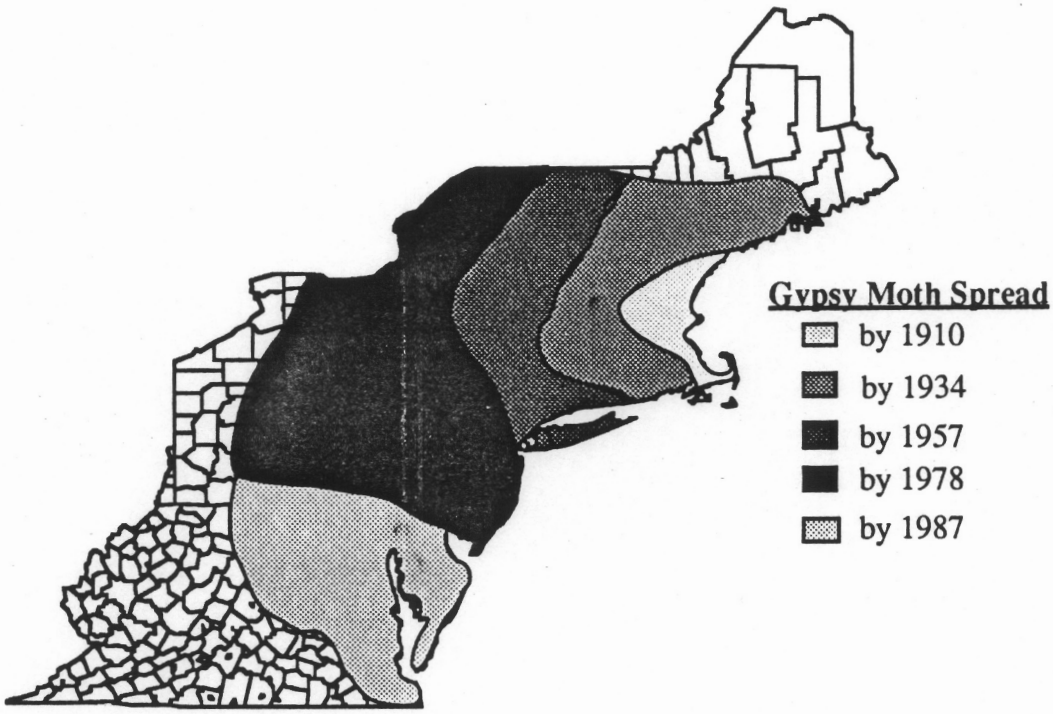

Fig. 1. Map showing spread of the gypsy moth.

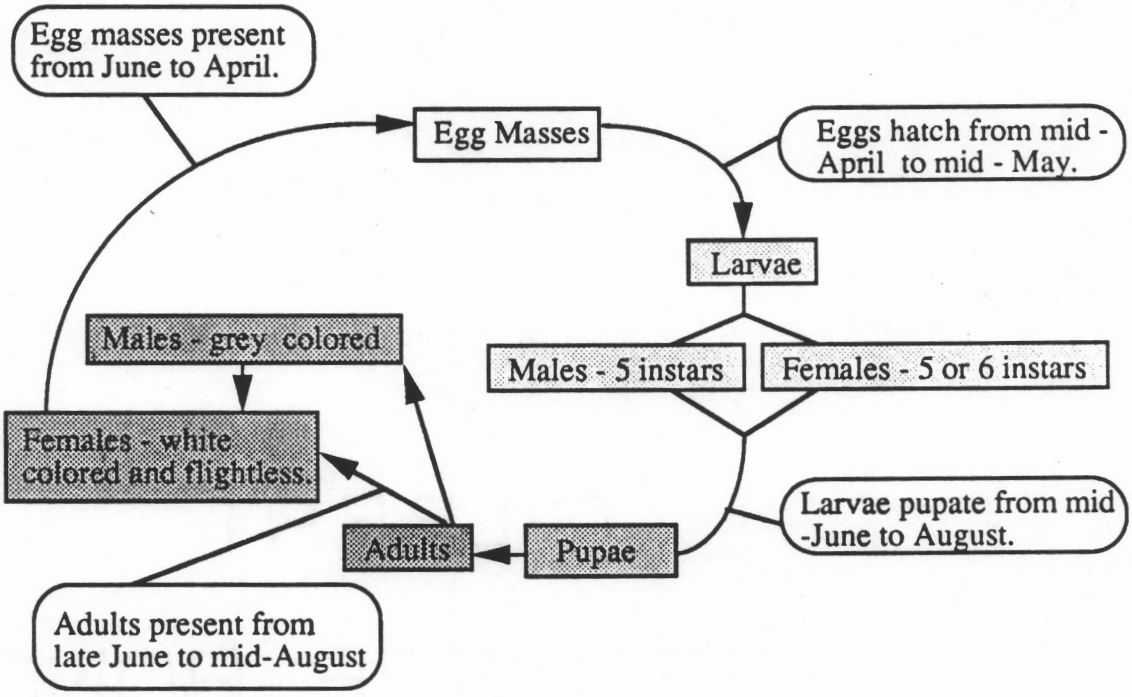

Fig. 2. Gypsy moth life cycle indicating time of occurrence of various lifestages.

Gypsy moth populations[1], in areas where the moth is well established, have been described as numerically bimodal and are characterized by four distinct population phases (innocuous, release, outbreak, and decline) (Fig. 3) (Campbell & Sloan 1978a). Populations may remain at low densities (innocuous phase) for many years. Population density may then increase rapidly during the release phase to reach outbreak densities (outbreak phase). The outbreak phase is characterized by extensive defoliation (Fig. 4a). Outbreak populations may decline with a year or two (decline phase) or they may remain at high population densities for several years. Over large areas, densities among populations may vary widely and populations may influence the dynamics of neighboring populations (Campbell & Sloan 1978b). In the leading edge area[2] , gypsy moth populations tend to reach outbreak levels rapidly (two to three years) after initial infestation and the number of hectares defoliated at a rapid rate (Fig. 4b). Release of populations from an innocuous phase has been hypothesized to be a result of favorable weather conditions, changes in host plant condition, decline of the predator-parasite-pathogen complex, the existence of foci, or an abundance of sheltered pupation sites (Campbell & Sloan 1977, Elkinton & Liebhold 1990). However, the exact reasons why populations increase rapidly to outbreak levels are not well understood. Decline of populations from high density levels is most likely due to the action of pathogens (such as nuclear polyhedrosis virus), food shortages, and/or declines in fecundity.

Since the gypsy moth's introduction into North America, a considerable amount of effort has been directed at attempting to eradicate or control this pest. Early control methods included burning infested trees and shrubs, banding trees, and destroying egg masses. Quarantine practices, quarantine areas, and barrier zones are regulatory practices that have been implemented to slow the spread of the moth (McManus & McIntrye 1981). There is a long history of parasite and pathogen introductions from Europe and Asia (Coulson 1981, Reardon 1981), but the effectiveness of these

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[1] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

[2] The leading edge area is defined as the area newly invaded by the gypsy moth, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time.

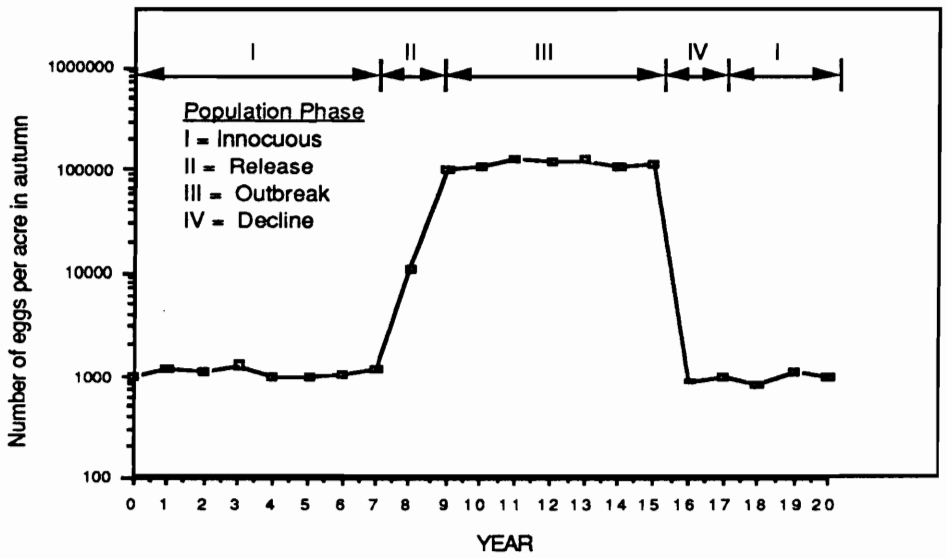
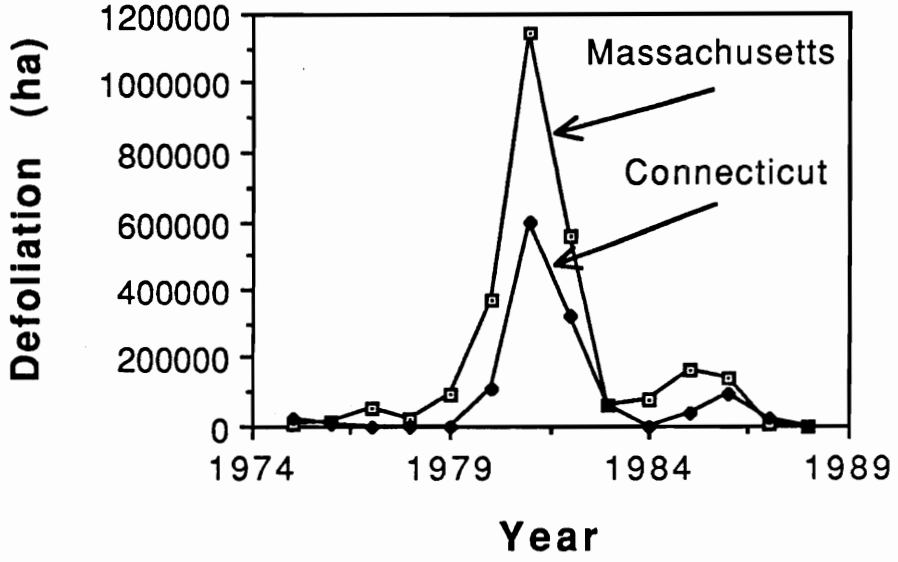


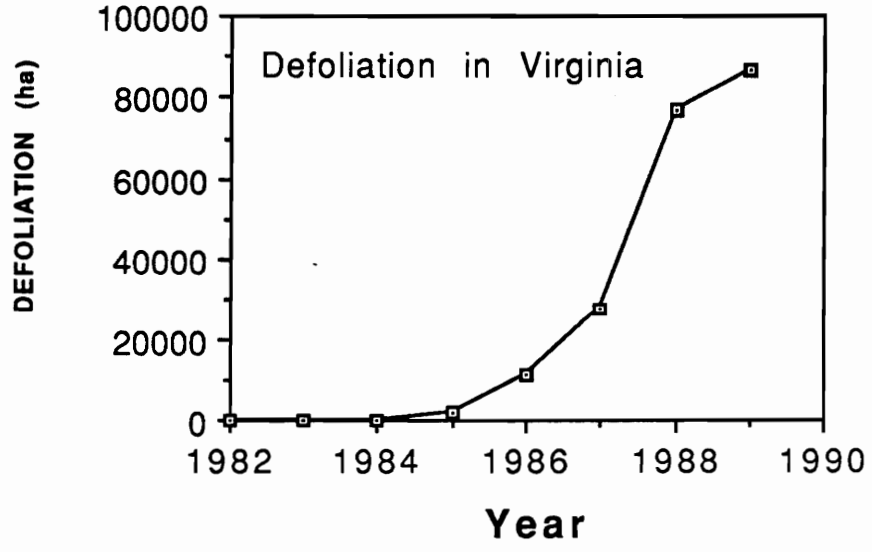
Fig. 3. Hypothetical gypsy moth population indicating population phases. Adapted from Campbell and Sloan (1978a).

introductions has been difficult to determine. Lead arsenate, DDT, carbaryl (Sevin^{R}) are several chemicals that have been used for control. Currently, the most common control practices are no control, or the aerial application of diflubenzuron (Dimilin^{R}) or Bacillus thuriengiensis. Other methods of control have included sterile male release and pheromone disruption. These measures are generally effective only in low density, isolated populations.

Gypsy moth management. Integrated pest management (IPM) is a philosophy of pest management that emphasizes sound environmental practices to control economically damaging pest populations. "An IPM program is comprised of six basic elements: (1) people: the system devisers and pest managers; (2) the knowledge and information necessary to devise the system and make sound management decisions: (3) a program for monitoring the numbers and state of the ecosystem elements--e.g., resource, pest and natural enemies; (4) decision-making levels: the pest densities at which control methods are put into action; (5) IPM methods: the techniques used to manipulate pest populations; and (6) agents and materials; the tools of manipulation" (Flint and van den Bosch 1983). The research presented in this dissertation is concerned with element three, the monitoring component of an IPM program.



A.



B.

Fig. 4. A. Number of hectares defoliated in Massachusetts and Connecticut from 1976 to 1988. The gypsy moth is well established in these states. B. Number of hectares defoliated in Virginia from 1980 to 1988. First recordable defoliation occurred in 1984.

Gypsy moths occur in wooded habitats. These habitats may include small groups of trees in parks or backyards, woodlots with distinct boundaries, or large contiguously forested areas with widely ranging topographical attributes. In all of these habitats the gypsy moth may be a pest. The impact of infestations may not necessarily be related to attributes of the habitat (i.e., the number of trees) or the density of the pest, but to the concerns of the land-owner or land-manager. Regardless of how the severity of an infestation is evaluated, it is important to detect and accurately assess potentially damaging gypsy moth populations so that an appropriate management plan can be implemented.

For the gypsy moth, two sampling techniques are commonly used to monitor populations. These are egg mass counts and pheromone-baited traps for capturing male moths. Egg mass density, the primary criterion for treatment decisions (Ravlin et al. 1987), is assessed through the use of direct egg mass counts, using one of three commonly accepted methods. The fixed radius method involves counting all egg masses within a given area usually a fortieth acre (a hundredth of a hectare) plot, a circle with a radius of 18.6 feet (5.65 m). Fixed radius plots are widely used in gypsy moth management programs. The second method is the fixed and variable radius plot method (Wilson & Fontaine 1978). The variable part of this method involves counting all of the egg masses on trees larger than a specified size, commonly a BAF (basal area factor) of 20 at breast height. These trees are determined from the plot center using a BAF measuring device (i.e., a pyramid). The fixed part of the method involves counting all of the egg mass in a given area, generally a circle of radius eight feet six inches (2.59 m) around the plot center. The fixed and variable radius plot was developed to bias the sampling effort towards larger trees which are more likely to contain a greater percentage of egg masses in an area. The third method utilized to assess egg mass density is timed-walks. This method involves walking a straight line path for a set period of time and counting all egg masses observed. Generally, two individuals make independent counts and the average is used to derive an estimate of egg mass density based on regression equations presented by Eggen & Abrahamson (1983). This method has the advantage of providing a greater spatial coverage, but results can be variable depending on terrain, egg mass density level, and tree size and density. Egg mass sampling is a time and labor intensive activity and, unless many samples are taken or timed-walks are used, provides limited spatial coverage.

Pheromone-baited milk-carton and delta traps (pheromone traps) are used to

delineate gypsy moth populations (Ravlin et al. 1987) and have been used in gypsy moth IPM programs (Appalachian and Maryland IPM Programs). An implicit assumption of the use of pheromone traps is the existence of a relationship between the number of male moths captured and egg mass density. This relationship is assumed to exist for certain ecological conditions, but has not been quantified. Boths changes in trap efficiency as traps fill (Elkinton 1987) and trap saturation (Bellinger et al. 1990) have hampered the development of the relationship between the number of male moths captured and egg mass density. The problem of trap saturation, particularly in areas of low egg mass density, has been hypothesized to be a result of migrant moths. Migrant moths are defined as adult moths that did not develop in the vicinity of the trap, but flew to the trap from distant areas. The capture of migrant moths would, therefore, tend to obscure the relationship between the number of moths captured and the actual egg mass density.

Considerable effort has been invested in the development and testing of the gypsy moth pheromone and pheromone traps (Elkinton and Carde 1981, Mastro 1981, Schwalbe 1981). However, less research (but see Elkinton & Carde 1980, Elkinton 1987) has been conducted to understand the interactions of gypsy moths with pheromone traps and to elucidate the ecological factors that influence the capture of male moths. These factors are complex and may include elevation, wind speed and direction, defoliation, gypsy moth population density, area-wide population dynamics, forest stand density, and forest patchiness. Additional research is required to determine which and to what degree the various factors influence capture of male moths in pheromone traps.

Wing length of male moths. The problem of trap saturation is the result of capturing too many moths; therefore, a technique that would be independent of the number of moths captured in pheromone traps to estimate population density may circumvent this problem. Bellinger et al. (1990) attempted to develop a density index using the wing length of male gypsy moths captured in pheromone traps. The existence of such a relationship between male moth wing length and egg mass density was based on the following premise, "Leonard (1968) reported that there was a relationship between body size and density for the gypsy moth and Hinckley (1970) suggested that male moth size, as measured by wing length, varied inversely with the level of defoliation. It follows that egg mass density should be directly related to larval density, however, the relationship between defoliation and larval density is less direct.

Wilson and Talerico (1981) and Ganser et al. (1985) found a relationship between egg mass density and defoliation but there is a significant amount of variability in these relationships presumably due to population characteristics, site characteristics, and

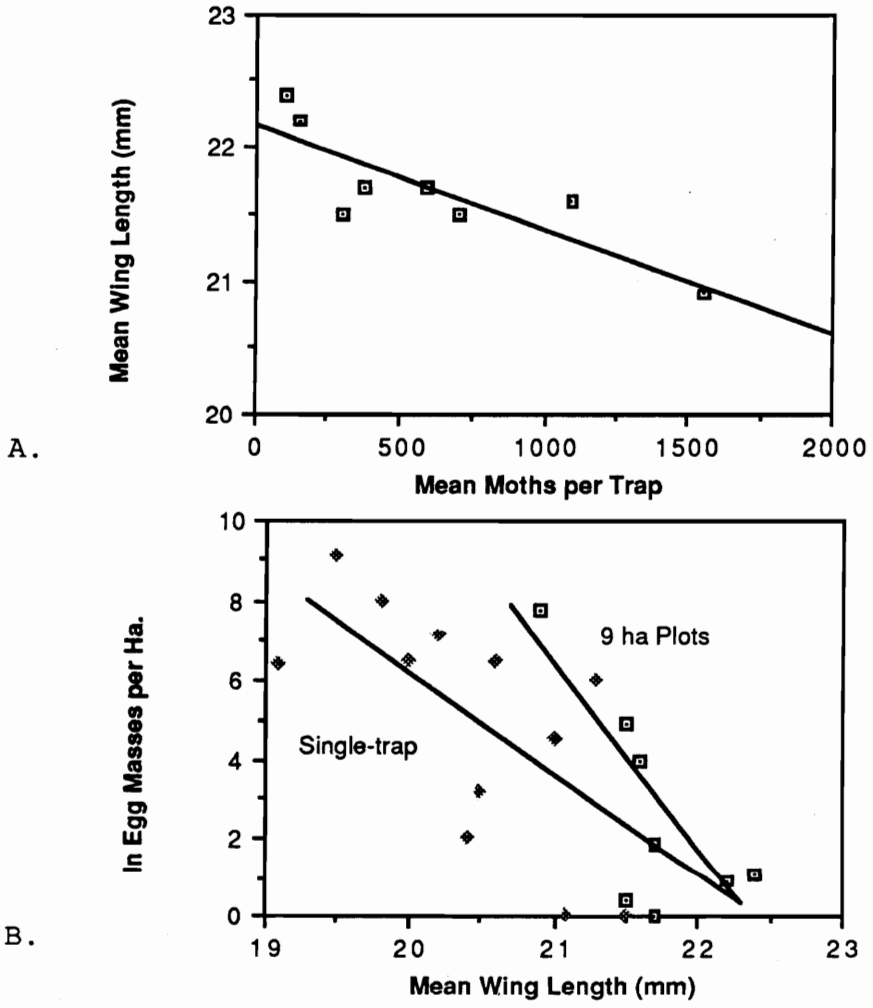


Fig. 5. Relationship between, A. mean number of moths captured per pheromone trap and male moth wing length and B. mean wing length and ln(egg masses per ha). Lines are regression lines. Data from Bellinger et al. (1990).

sample method. Despite the tenuous nature of these relationships we might expect to find a relationship between male moth size and population fecundity based on the assumption that density dependent stress and defoliation will produce populations of smaller individuals." (Bellinger et al. 1990). The results of this research were positive; male wing length was related to the mean number of moths per pheromone trap, egg mass density, and eggs per mass (Fig. 5) (Bellinger et al. 1990). The biological basis for this relationship was not determined, but hypothesized to be density dependent stress factors acting on larval populations as outlined above. Larval density and defoliation are interrelated stress factors that may influence moth size. An inverse relationship between larval density and fecundity has been demonstrated for the gypsy moth (Capinera & Barbosa 1977, Campbell 1978), but the biological basis for this relationship has not been elucidated. Density related changes in food quality alter the normal nocturnal feeding behavior of late instar gypsy moth larvae (Lance et al. 1986) which may alter larval growth. Defoliation is a process that decreases foliage availability and can alter foliage chemistry (Schultz & Baldwin 1982). Changes in foliage quality due to defoliation have been shown to reduce female pupal size and fecundity (Wallner & Walton 1979, Rossiter et al. 1988). However, these studies were conducted using trees on which defoliation was artificially simulated.

Defoliation is a major factor which alters the forest microclimate. Larvae developing in high density populations, and often defoliated areas, may develop faster and pupate earlier than larvae in low density populations (Campbell 1978). The rapid development (as measured in calender days) has been found to be related to changes in microhabitat and temperature (Lance et al. 1987) and not due to density-related stress (larval interaction) (Lance et al. 1986). Defoliation has been suggested as a possible determinant of gypsy moth population quality (Wallner & Walton 1979). In addition the sex ratio of pupae is altered at high population densities (Campbell 1963, Mauffette & Jobin 1985). Despite the recognition of the impact of microclimate and defoliation on gypsy moth biology, there are no quantitative field studies investigating the effects of defoliation (resulting from high larval population densities) on larval and pupal development or on adult gypsy moths.

Defoliation is the most obvious expression of high density gypsy moth populations and may have a significant influence of the dynamics of gypsy moth populations. Population processes related to, or a direct consequence of defoliation, also may have an important influence male moth wing length and the number of moths

captured in pheromone traps. Therefore, this research has focused on using defoliation and defoliation related processes to analyze the relationship between pheromone trap captures (the number and size of male moths) and gypsy moth population characteristics (egg mass density and defoliation).

Research Objectives

The goal of this research was to improve the understanding of the dynamics of male gypsy moth-pheromone trap interactions and the ecological factors that influence the capture of male moths in pheromone traps. An improved knowledge of male moth-pheromone trap dynamics should increase the ability to interpret the captures of male moths in pheromone traps and the usefulness of pheromone traps to monitor gypsy moth populations. Five studies were conducted as part of this research. The objectives of each study are listed below and the results of the studies are presented in the following five chapters.

Chapter 2. *Changes in gypsy moth fecundity and male wing length due to defoliation.* The goal of this research was to investigate the influence of defoliation on gypsy moth fecundity and male moth wing length and the relationship between male moth wing length and egg mass density. The objectives of this study were: 1) to determine if a proportional decrease in fecundity and wing length occurs as defoliation increases; 2) to validate the linear relationship between mean male wing length and egg mass density found by Bellinger et al. (1990); 3) to compare the results with an independent data set presented in Campbell (1978).

Chapter 3. *Dynamics of gypsy moth pheromone-baited milk-carton traps. Part I: Impact of defoliation on gypsy moth phenology and pheromone-baited milk-carton trap capture of male moths.* The objective of this research was to investigate the impact of defoliation on gypsy moth larval development, pupation, the sex ratio of pupae, and the capture of male moths in pheromone traps.

Chapter 4. *Dynamics of gypsy moth pheromone-baited milk-carton trap. Part II: Use of male moth wing length as a measure of defoliation.* The objective of the research presented in this chapter was to investigate the extent to which the wing length of male moths captured in pheromone traps reflects the wing length of moths collected as pupae in the vicinity of the pheromone trap. A second objective was to develop more general criteria to evaluate wing length of moths captured in pheromone traps. This aspect was addressed by evaluating wing length threshold values. Threshold

values are values to which wing length statistics (i.e. mean wing length) derived from pheromone trap captured moths can be compared. Depending on the level of defoliation in the vicinity of the pheromone trap, the wing length statistics of male moths captured in pheromone traps are expected to be greater or less than threshold values.

Chapter 5. *Spatial and temporal dynamics of leading edge gypsy moth populations*. The goal of this research was to evaluate the usefulness of defoliation data as a source of information to aid in the monitoring of gypsy moth populations. The objectives of this research were to investigate the temporal and spatial dynamics of gypsy moth defoliation in leading edge areas, models for predicting defoliation, and the impact of defoliation on gypsy moth population dynamics.

Chapter 6. *Estimating gypsy moth egg mass density using male moths captured in pheromone-baited milk-carton traps*. The goal of the research presented in this paper was to develop methods to use pheromone traps to monitor gypsy moth populations. Specifically, an attempt was made to quantify the relationship between the number of moths captured in pheromone traps and egg mass density. In addition, an effort was made to determine the precision of estimating defoliation from the wing length of pheromone trap captured moths. Traps in these studies were serviced as they would be in a gypsy moth management program.

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Chapter 2

Changes in gypsy moth fecundity and male wing length due to defoliation.

Pheromone trap-based monitoring systems, used for detection of incipient Douglas-fir tussock moth populations (Daterman 1978, Shepard et al. 1985) and under development for use with the spruce budworm (Allen et al. 1985), would be useful for improving management of the gypsy moth (Lepidoptera: Lymantriidae Lymantria dispar)(Kolodny-Hirsch 1986, Ravlin 1991). However, a relationship between egg mass density, the primary control criterion for gypsy moth (Ravlin et al. 1987) and the number of moths captured in pheromone traps has not been developed. Several problems associated with quantifying this relationship are discussed in Bellinger et al. (1990) and Elkinton (1987). Bellinger et al. (1990) used the wing length of male gypsy moths captured in pheromone traps to estimate egg mass density. Male wing length was related ($r^2 = 0.60$) with the mean number of moths per pheromone trap, egg mass density, and eggs per mass. The biological basis for this relationship was not determined, but was hypothesized to be density-dependent stress factors acting on larval populations[1].

Larval density and defoliation are interrelated stress factors that may influence moth size. An inverse relationship between larval density and fecundity has been demonstrated for the gypsy moth (Capinera & Barbosa 1977, Campbell 1978), but the biological basis for this relationship has not been elucidated. Density-related changes in food quality alters the normal nocturnal feeding behavior of late instar gypsy moth larvae (Lance et al. 1986) which may alter larval growth. Defoliation is a process that decreases foliage quantity and alters foliage quality (Schultz & Baldwin 1982). Changes in foliage quality due to defoliation have been shown to reduce female pupal size and fecundity (Wallner & Walton 1979, Rossiter et al. 1988). However, these studies were conducted using trees on which defoliation was artificially simulated.

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[1] [1] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

The goal of this research was to investigate the influence of defoliation on gypsy moth fecundity and male moth wing length and the relationship between male moth wing length and egg mass density. The objectives of this study were: 1) to determine if a proportional decrease in fecundity and male moth wing length occurs as defoliation increases; 2) to validate the linear relationship between mean male wing length and egg mass density found by Bellinger et al. (1990); 3) to compare these results with an independent data set presented in Campbell (1978).

Materials and Methods

Study Area. Plots were located in the leading edge area of the gypsy moth infestation in Virginia and Maryland. The leading edge area is newly invaded by the gypsy moth, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time. The study plots encompassed both contiguously forested mountainous areas and woodlots located in rolling terrain. The plots were located in the northern and central district of the Shenandoah National Park (Warren, Rappahannock, and Page counties, Virginia) and in Warren, Clarke, Frederick, Prince William, Rockingham, and Faquier Counties, Virginia and in Carroll and Howard counties, Maryland. White, scarlet, red, and chestnut oaks (Quercus species) were the dominant tree species in the plots. After leaf fall, estimates of egg-mass density were obtained from one or more (generally two) fixed and variable - radius plots (20 BAF) (Wilson & Fontaine 1978) located in the area where the pupae or egg masses were collected.

Wing Length - Defoliation Study. Male pupae were collected from 50 field plots during late June to mid-July of 1986, 1987, 1988, and 1989. Two or more collections were made at least one week apart from each plot to sample for possible within-season variation in wing length (Hinckley 1970). Pupae were collected from natural pupation locations or under burlap bands on trees and returned to the laboratory. Following emergence, the length of the left forewing of 2,636 moths were measured to the nearest millimeter. The maximum level of defoliation at each plot was determined visually. Defoliation estimates were made on a whole plot level after larval feeding had ceased and before refoliation occurred. Estimates were made by considering both the number of missing leaves (due to larval feeding) and the amount of leaf area missing from the remaining leaves (Table 1).

Fecundity - Defoliation Study. Twenty or more egg masses, where possible, were collected from 43 field plots in 1986, 1987, 1988, 1989. Gypsy moths

oviposit only one egg mass, so fecundity is total egg production. Fecundity was determined volumetrically for 767 egg masses (Saufley 1972), calibrating for variability in egg volume on each egg mass. Maximum defoliation at each plot was determined subjectively in the same manner as in the wing length - defoliation study.

Analyses. Relationships between the two dependent variables, wing length and eggs per mass, and the two independent variables, percent defoliation and egg mass density, were examined using linear regression (SAS, PROC GLM, SAS Institute, Inc., 1986). To meet the assumption of normality, defoliation data were transformed using an arcsin $\sqrt{x}$ transformation (Zar 1984). Egg masses per ha were transformed to ln(n+1).

Cluster analysis (SAS, PROC CLUSTER, SAS Institute, Inc., 1986) was used to determine if the fecundity and wing length data could be divided into groups based on the level of defoliation. Fecundity and wing length data were standardized on a scale of 0 to 100 prior to analysis. A t-test was used to determine if a significant difference existed between mean wing length or fecundity for the major groups identified by the cluster analysis.

Independent Data Set Analysis. Campbell (1978) reported a curvilinear relationship between the density of fourth instar larvae and fecundity. Campbell did not explicitly quantify defoliation, but did state defoliation rarely exceeded 5 percent unless density was above 10^5 fourth instar larvae per ha. These data were reanalyzed using cluster analysis. Linear regression was used to determine if a relationship existed between larval density and fecundity within the groups identified by the cluster analysis and a t-test was used to determine if fecundity differed between groups.

Results

Cluster Analysis. Results of the cluster analysis indicate that both fecundity and wing length data could be divided into two major groups (Figures 1A and 1B). For the wing length data, the highest level clustering explained ca. 76% of the variation (semipartial $r^2 = 0.7561$). The next highest clustering level explained only ca. 8% of the variation (semipartial $r^2 = 0.0802$). For the fecundity data, the highest level clustering explained ca. 73% of the variation (semipartial $r^2 = 0.7270$). The next highest clustering level explained only ca. 9% of the variation (semipartial $r^2 = 0.0917$). The two groups consisted of either male wing lengths or egg masses from plots with less than forty percent defoliation (referred to as the non-defoliated group) or from plots with more than forty percent defoliation (referred to as the defoliated group).

The mean wing length of moths from the non-defoliated group (mean = 19.89, SEM = 0.524, N = 1,442) was found to be significantly different from the mean wing length of moths from the defoliated groups (mean = 17.94, SEM = 0.037, N = 1584) ($t = 36.9$, $p < 0.0001$) (Figure 2). The mean fecundity from non-defoliated groups (mean = 546.6, SEM = 10.83, N = 460) was found to be significantly different from the mean fecundity from the defoliated group (mean = 262.2, SEM = 7.07, N = 307) ($t = 19.5$, $p < 0.0001$) (Figure 3).

Wing Length - Defoliation Study. Regression analysis indicated a significant relationship exists between wing length and defoliation ($p < 0.0001$), but defoliation explained little of the variation in wing length ($r^2 = 0.20$). A significant relationship was found between wing length and defoliation within each defoliation grouping (non-defoliated plots, $p < 0.0149$; defoliated plots, $p < 0.0001$), but defoliation explained little of the variation in wing length (non-defoliated plots, $r^2 = 0.02$; defoliated plots, $r^2 = 0.02$). Regression equations are listed in Table 2.

Fecundity - Defoliation Study. Regression analysis indicated a significant relationship exists between fecundity and defoliation ($p < 0.0001$), but defoliation explained little of the variation in fecundity ($r^2 = 0.31$). A significant relationship was found between fecundity and defoliation for the non-defoliated group ($p < 0.0001$), but defoliation explained little of the variation in fecundity (non-defoliated plots, $r^2 = 0.05$). The relationship between defoliation and fecundity for the defoliated group was not significant ($p < 0.0800$, $r^2 = 0.01$). Regression equations are listed in Table 2.

Egg mass density - Wing Length. Regression analysis indicated a significant relationship exists between wing length and egg mass density ($p < 0.0376$), but male wing length explained little of the variation in egg mass density ($r^2 = 0.1036$). The equation for this relationship is: ln(egg masses per ha) = 16.44 - 0.4076 * male wing length(mm), SE of the slope = 3.64.

Independent Data Set Analysis. Results of the cluster analysis indicate that Campbell's (1978) fecundity data can be divided into two major groups (Figure 4), approximately divided at 10^5 larvae per ha. The highest level clustering explained ca. 56% of the variation in the data (semipartial $r^2 = 0.5578$). Mean fecundity (mean = 415.71, SEM = 14.55, N = 35) for the group in which larval density was below 10^5 was found to be significantly different ($t = 12.35$, $p < 0.0001$) from the mean fecundity for the group for which larval density exceeded 10^5 (mean = 175.75, SEM = 12.88, N

= 20). Regression analysis indicated a significant relationship exists between larval density and fecundity for data in which density was above ($p < 0.0002$) or below 10^5 4th instar larvae per ha ($p < 0.0035$) (Figure 4). However, larval density explained less than half of the variation in fecundity if density exceeded 10^5 ($r^2 = 0.3844$) or if it did not ($r^2 = 0.3483$).

Discussion

The results of this research indicate that at higher levels of defoliation male wing length is smaller and fecundity is reduced. But the form of the relationship is not linear (i.e., using regression analysis, very little variation in wing length size and fecundity was explained by the level of defoliation). Fecundity and male wing length appear to be substantially influenced by defoliation or processes associated with defoliation only if the level of defoliation exceeds a threshold level of ca. 40%. Changes in defoliation above or below the threshold does not substantially alter male wing length or fecundity. Thus, the effect of defoliation on larval development, as measured by wing length and fecundity, is essentially binomial (i.e., male wing length is either large or small and fecundity is either high or low). These conclusions are based on: 1) the poor relationship between defoliation and the dependent variables for all data (0 to 100% defoliation), 2) the poor relationship between defoliation and the dependent variables within each defoliation group (greater or less than ca. 40%), and 3) identification of only two major groups for the fecundity and wing length data and significant differences between the means of these groups.

The results of this study are consistent with Campbell's (1975) statement that across a broad range of insect density, fecundity will probably be at least 500 and the observation by Campbell (1975) that fecundity drops sharply as a consequence of reduced food supply. Our reanalysis of Campbell's (1978) data also provides strong support for our hypothesis that the effect of defoliation on larval development, as measured by wing length and fecundity, is essentially binomial. In our reanalysis, we found Campbell's (1978) data could be divided into two major groups, with the dividing point at approximately 10^5 larvae per ha. This was the point identified by Campbell (1978) as the larval density below which defoliation was minimal. In addition, we were unable to obtain a strong relationship between larval density and fecundity for larval densities ranging from 10^3 to 10^5, or for larval densities ranging from 10^5 to 10^7. These results indicate there are other factors in addition to larval density, such as defoliation related changes in foliage, that have an important influence

on fecundity. Furthermore, these results indicate that fecundity is substantially influenced by these factors only above some threshold point. Since the ultimate level of defoliation in an area is a function of larval density and the quality and quantity of available foliage, the existence of a relationship between larval density and fecundity is not unexpected. But, increased interactions between larvae (Campbell 1978) that would occur solely as a result of higher larval densities are probably not sufficient to reduce fecundity, particularly at levels of defoliation of ca. 40 to 65%.

Wing length size and fecundity are probably determined by a complex interaction between larval physiology and defoliation related changes in foliage quantity and quality. The total quantity of foliage available to larvae, foliar chemistry (Wallner & Walton 1979, Rossiter et al. 1988), and the extent (localized or systemic) of changes in foliar chemistry (Rossiter et al. 1988) may be altered as a result of defoliation. Larvae are not likely to be foliage limited at defoliation levels of ca. 40 to ca. 65% and at these levels of defoliation, changes in foliar chemistry are probably the major influences on male moth wing length and fecundity. As the level of defoliation increases, the relative importance of foliage quality probably decreases and foliage quantity becomes the limiting factor for larval growth.

This research was conducted in the leading edge area of the gypsy moth infestation. Because gypsy moth related defoliation is occurring for the first time in this area, there may be a set of ecological conditions and biological processes unique to this area that interact to produce the defoliation threshold. However, Campbell (1981) found similarities in fecundity between leading edge populations and some populations in the generally infested area. This suggests that leading edge populations are not completely unique and that a threshold process may exist in the generally infested area. DeGroff (1969) studied gypsy moth populations in New York and suggested that, with respect to egg mass density, two types of populations existed, those with egg masses with more than 300 egg per mass and those less than 300 eggs per mass. Data presented in this study support this hypothesis.

The method of estimating defoliation in this study was subjective, therefore, the use of another rating technique or defoliation scale could result in a different threshold level. However, the general pattern of male size and fecundity obtained in this study would still be apparent. The possibility that the estimates of defoliation may have been biased towards detection of a threshold must also be addressed. Fecundity and wing length data (Figures 1A and 1B) in the range of defoliation levels where this was most

likely to have occurred, 35 to 55%, supports the threshold hypothesis (i.e., data are clearly either large or small). Fecundity and wing length from all plots within and among defoliation levels was variable. This variation may be a result of differences in plot-specific variables or population phase (innocuous, outbreak, or decline) among plots.

The results of this study are not consistent with the hypothesis that male wing length is proportional to egg mass density (Bellinger et al. 1990). We were unable to validate the linear relationship (Bellinger et al. 1990) between egg mass density and male wing length using male gypsy moths collected as pupae. In addition, a relationship between wing length and egg mass density would not be expected given the binomial pattern of male moth wing length. The use of male moths collected from pheromone traps by Bellinger et al. (1990) probably accounts for the discrepancy. Pheromone traps may collect moths from populations distributed over a large area. These populations may have varying levels of defoliation and larval densities. Therefore, moths with different wing lengths (either large or small) may be captured in the same pheromone trap. This would cloud the actual relationship between wing length and egg mass density in the vicinity of the trap. It is probable that the capture of both large and small moths in some of the pheromone traps used in the study by Bellinger et al. (1990) contributed to the strong linear relationship they found between egg mass density and wing length.

Beneficial information could be gained by examining the wing length of moths collected in pheromone traps. Traps capturing moths with wing lengths of predominantly one size (either large or small) would indicate the presence or absence of populations experiencing defoliation greater than ca. 40%. Traps with a mix of wing length sizes (large or small) would indicate that both defoliated and undefoliated patches are located in the vicinity of the trap. This information would be useful for assessing the dynamics of populations being sampled by pheromone traps. Used in conjunction with the number of moths captured, the probability that the populations are at low or high densities, incipient, outbreak, or declining could be determined. This information could then be used in a gypsy moth management program to allocate additional sampling resources (i.e., manpower to conduct egg mass samples) or make control decisions.

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Table 1. Description of percent defoliation used to rate defoliation at each study plot.

Percent Defoliation	Description of defoliation.
0 - 20	Defoliation not noticeable, if present a few holes in leaves.
20 - 30	Holes visible in leaves, but all leaves present.
30 - 40	More holes in leaves, but all leaves present.
40 - 50	Many holes in leaves, often large pieces missing. Some leaves missing.
50 - 60	More leaves missing, most leaves obviously chewed on and large pieces missing.
60 - 75	Many leaves missing, rest of leaves are missing large pieces.
75 - 90	Majority of leaves missing, any remaining are missing large pieces.
90 - 100	All leaves gone.

Table 2. Regression equations, r^2, standard error of the slope for regression of fecundity (FEC) and male (WL) wing on arcsin $\sqrt{\text{percent defoliation}}$ (DEF).

Male Wing Length

Data Category	Equation	r^2	Std. error of slope
All data	WL = 20.09 - 1.54*DEF[1]	0.20	0.06
Non-Defoliated[2] Group	WL = 20.23 - 1.01*DEF	0.02	0.18
Defoliated[3] Group	WL = 17.5 + 0.37*DEF	0.02	0.11

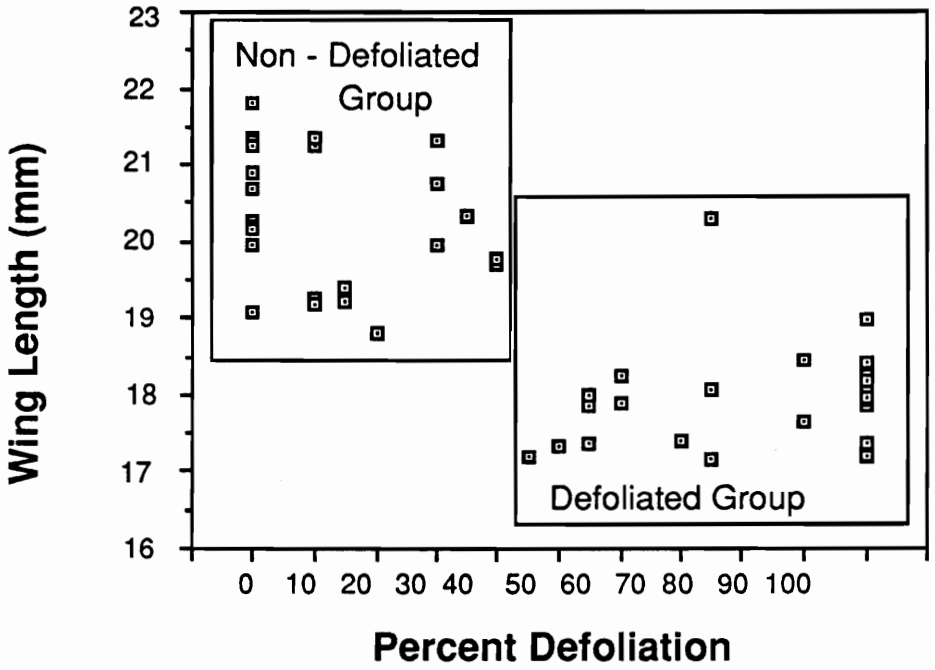
Fecundity

Data Category	Equation	r^2	Std. error of slope
All data	FEC = 586.83 - 248.9*DEF	0.20	13.50
Non-defoliated group	FEC = 589.05 - 162.5*DEF	0.05	34.04
Defoliated	FEC = 308.07 - 39.7*DEF	0.01	22.61

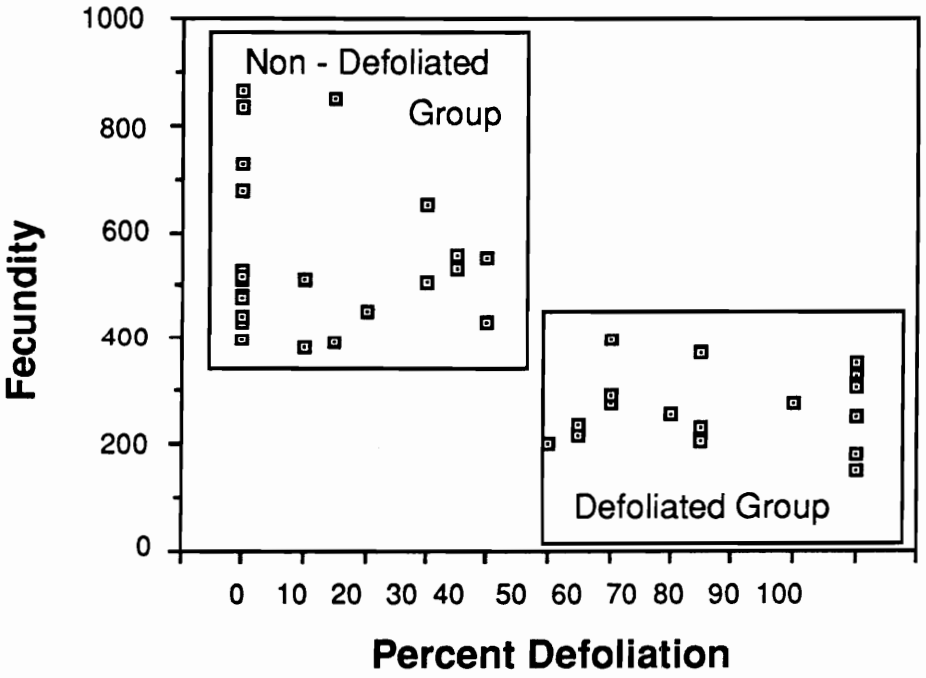
[1] DEF = arcsin $\sqrt{\text{percent defoliation}}$ in radians.

[2] < 40% defoliation

[3] > 40% defoliation



A.



B.

Fig. 1. A) Mean wing length for all plots at each defoliation level; B) Mean fecundity for all plots at each defoliation level.

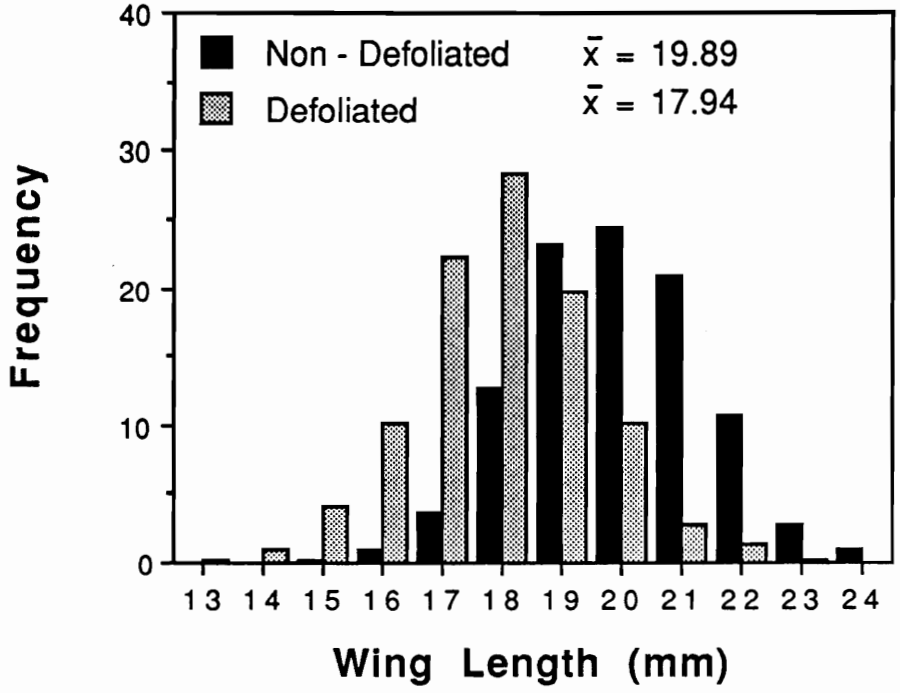


Fig. 2. Frequency distribution of male wing lengths for the defoliated (<40% defoliation) and non-defoliated (>40% defoliation) groups. For the non-defoliated group, mean = 19.89, SEM = 0.524, n = 1442; for the defoliated group, mean = 17.94, SEM = 0.037, n = 1584.

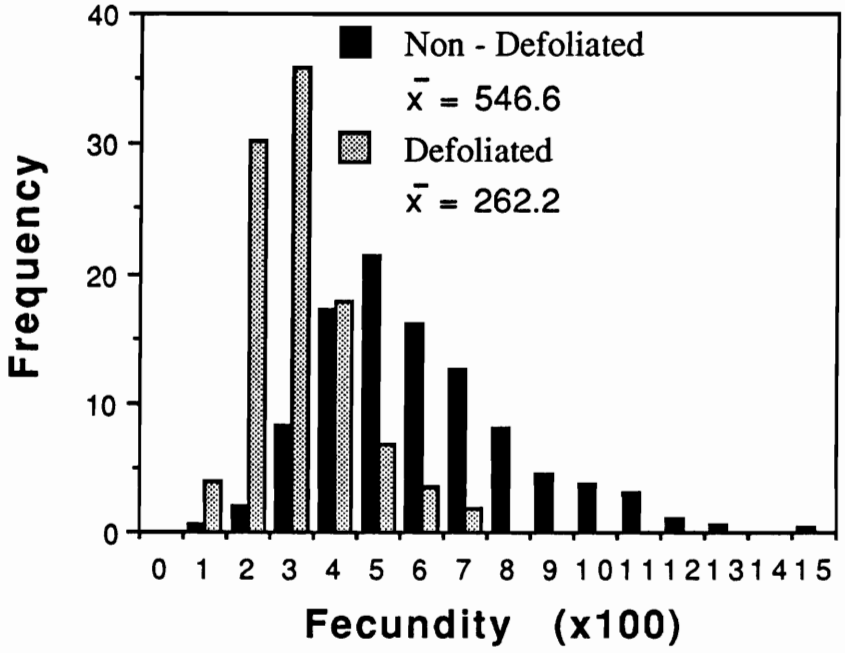


Fig. 3. Frequency distribution of fecundity data for the defoliated (<40% defoliation) and non-defoliated (>40% defoliation) groups. For the non-defoliated group, mean = 546.6, SEM = 10.83, n = 460; for the non-defoliated group, mean = 262.2, SEM = 7.07, n = 307.

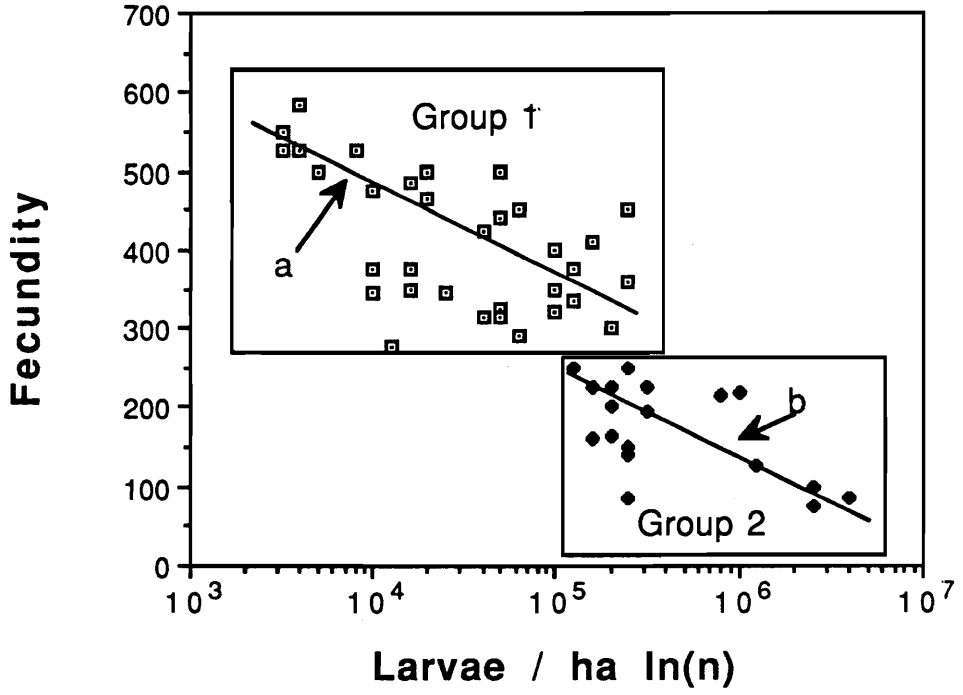


Fig. 4. Relationship of fecundity and defoliation for data from Campbell (1978). Equations are: for line a, eggs per mass = 809.05 - 38.44 * (larvae per ha), r^2 = 0.3483, SEM of slope = 94.41; for line b, eggs per mass = 612.63 - 33.88 * (larvae per ha), r^2 = 0.3844, SE of slope = 130.72.

Chapter 3

Dynamics of gypsy moth pheromone-baited milk-carton traps. Part I: Impact of defoliation on gypsy moth phenology and pheromone-baited milk-carton trap capture of male moths.

Differences in developmental times, sex ratios, fecundity, and larval behavior have been observed between low and high density gypsy moth (Lepidoptera: Lymantriidae Lymantria dispar) populations[1] (Wallner 1987, Elkinton & Liebhold 1990). Larvae developing in high density populations may develop faster and pupate earlier than larvae in low density populations (Campbell 1978). The rapid development (in calender days) has been found to be related to changes in microhabitat and temperature (Lance et al. 1987) and not due to density-related stress (larval interaction) (Lance et al. 1986). Defoliation is a major factor that may alter the forest microclimate and is largely determined by larval population density (Ganser et al. 1985, Montgomery 1990) and available leaf biomass. Defoliation has been suggested as a possible determinant of gypsy moth population quality (Wallner & Walton 1979) and can have a significant impact on gypsy moth fecundity, male wing length (Chapter 2), and population dynamics (Chapter 5). The sex ratio of pupae also is altered at high population densities (Campbell 1963, Mauffette & Jobin 1985). Despite the recognition of the impact of microclimate and defoliation on gypsy moth biology there are no quantitative field studies that have investigated the effects of defoliation (resulting from high population density) on larval and pupal development.

Pheromone-baited milk-carton traps (pheromone traps) have been used to detect spatially isolated gypsy moth populations (Ravlin et al. 1987) and have been proposed as a integral component of gypsy moth IPM programs (Ravlin 1990). Considerable effort was invested in the development and testing of the gypsy moth pheromone and pheromone traps (Elkinton and Carde 1981). However, less research has been directed toward understanding the interactions of gypsy moths with pheromone traps and to elucidate the ecological factors that influence capture of male moths (Elkinton & Carde 1980, Elkinton 1987). The ecological factors that influence male moth capture are

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[1] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

complex and may include elevation, wind speed and direction, defoliation, gypsy moth population density, area-wide population dynamics, forest stand density, and forest patchiness. The complexity of the gypsy moth - forest system and the lack of research on the dynamics of gypsy moth-pheromone trap interactions have hampered development of a relationship between the number of moths captured in pheromone traps and egg mass density.

The objective of this research was to investigate the impact of defoliation on gypsy moth larval development, pupation, the sex ratio of pupae, and the capture of male moths in pheromone traps.

Methods

Study Plots. Studies were conducted in 1988 and 1989 in sixteen plots located in the leading edge area[2] of the gypsy moth infestation. Plots were located in the Shenandoah Valley area (Warren Co) and the Shenandoah National Park (Warren, Rappahannock, and Page counties) in Virginia (Figure 1). Plots were located over a range of elevation and had a range of egg mass densities, defoliation levels, and forest tract sizes. All but one plot was dominated by oak species (white, scarlet, red, and chestnut oak), but the relative composition of species varied between plots. After leaf fall, egg-mass density estimates were obtained from two fixed and variable - radius plots (20 basal area factor) (Wilson & Fontaine 1978) located in the plot.

Larval Development. Larval development was estimated by collecting frass as an indicator of instar occurrence (Liebhold and Elkinton 1988) and recording field temperatures. Stochastic phenology model (Dennis et al. 1986) parameter sets, which describe larval development, were then computed using this data and compared among all sixteen plots. Details of the methods are discussed below.

Frass collection. A funnel-like frass sampler (Liebhold and Elkinton 1988) and 16 oz. (473 ml) drinking cups were used to collect frass. In 1988, two 40 m^2 grids of frass samplers were used with a single frass sampler located at each 10 m intersection. In 1989, a single 40 by 50 m grid with a pair of frass samplers at each 10 m intersection was used. A total of 40 frass samplers were used in both years. In both years, frass collections were made every four to five days and on each sample date

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[2] The leading edge area is defined as the area newly invaded by gypsy moths, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time.

frass was collected over a ca. 24 hr period. Samples with a low number of pellets (< 100) were counted and measured in entirety, a proportion (one-quarter to one-half, but at least 100 pellets) of samples with a large number of pellets were counted and measured. Pellets were then assigned to a specific instar on the basis of size. For instars 1 to 3 representative frass size was determined from laboratory rearing of larvae on white oak. Frass size of instars 4 and 5 were based on the data presented by Liebhold and Elkinton (1988). Male fifth instar and female fifth and sixth were grouped into the same instar for model development. The rate of frass production during any 24 hr sampling period was assumed to be identical for all instars and a one larvae for one frass pellet relationship was assumed (S. Liebhold pers. comm.). However, because of frass size of late instar larvae (4th and the combined 5th and 6th) tended to overlap, an individual pellet was assigned to each instar for which it was the appropriate size. For each sample date, the percent of the population in each instar was determined by dividing the total number of frass pellets for each instar by the total number of frass pellets and multiplyed by 100. This resulted in a constant population size of 100.

Heat accumulation. Data on heat accumulation (degree-days [DD]) were collected using Campbell Scientific CR-10 dataloggers or Omega model 414 recording thermometers at each plot from the start of egg hatch through the entire sampling period. Accumulated heating DD were calculated using a modified sine wave equation (Allen 1976). A lower threshold of 7.65 °C and upper threshold of 41.0 °C were selected based on values calculated for a comprehensive gypsy moth life system model (Sheehan 1989) and from data in Casagrande et al. (1987). The lower threshold is an average value for male and female larvae and applied to all lifestages in this study. On occasion, temperature data for an individual plot was unavailable due to equipment failure. DD data for the missing interval was determined by comparing total accumulated DD with the closest and most ecologically similar plot.

Model Development. Developmental models for the gypsy moth have been developed by Casangrande et al. (1987) and Shields (1989). A stochastic phenology model (Dennis et al. 1986, Dennis and Kemp 1988) was selected because the methods and associated statistical techniques of the stochastic model were deemed most useful for comparing developmental phenology between plots. Model development and statistical methods are presented in detail in Dennis et al. (1986) and Dennis and Kemp

(1988). Briefly, the proportion of the population (p_{ij}) in stage i present at sampling time j is given by the equations;

for instar 1:

$$p_{ij} = 1/\left\{ 1 + \exp\left[-\left(\frac{(a_i - t_j)}{\sqrt{b^2 t_j}}\right)\right]\right\}$$

for instars 2, 3, and 4:

$$p_{ij} = 1/\left\{ 1 + \exp\left[-\left(\frac{(a_i - t_j)}{\sqrt{b^2 t_j}}\right)\right]\right\} - 1/\left\{ 1 + \exp\left[-\left(\frac{(a_i - t_j)}{\sqrt{b^2 t_j}}\right)\right]\right\}$$

and for instar 5:

$$p_{ij} = 1/\left\{ 1 + \exp\left[\left(\frac{(a_i - t_j)}{\sqrt{b^2 t_j}}\right)\right]\right\}$$

where t_j is measured in degree-days (DD) and is the accumulated DD at the sample time j. The parameters, a_i to a_{i-1}, describe the amount of development (in DD) required to complete the ith stage ($i = 5$ in this study). The parameter b^2 is a positive constant and provides an indication of the influence of factors other than DD on development. Parameter sets (a_i to a_{i-1}, b^2) can be compared statistically using a χ^2 test (Dennis et al. 1986). Parameters were fit to field data and compared using SAS (SAS 1986) as outlined in Dennis et al. (1986). The model was used to calculate accumulated DD and calender days elapsed from from first hatch to selected developmental points. Developmental points were 50% occurrence of first instars, peak occurrence of instars two through four and 50% occurrence of instars five and six.

In addition to the stochastic model, the entire larval developmental period from first hatch to first pupae and 50% pupation were examined by calculating the number of DD, calender days (CD), and DD per calender day (DD/CD) for each plot.

Pupae and Adults. Pupae were collected every three days from beneath burlap bands after the first pupa was observed in a plot. All pupae were removed on each sample date, sexed, and counted. Depending on the larval density in a plot, ten to twenty trees located in each plot were burlaped for collection of pupae. The burlap bands were ca. 20 cm wide and were located at breast height around the boles of the trees. Male moths were collected using pheromone traps hung from a tree located in each plot. In 1988, two pheromone traps placed at least 100 m apart were used and the trap data is the average of the two traps. In 1989, one trap was used. Pheromone traps

were checked every three days after the first moth was captured. For each sample date, all moths were counted.

Analysis. The patterns of male pupation and male moth capture over time (DD) were examined by constructing regression lines and comparing slopes and intercepts of cumulative pupation or male moth capture on DD. Heat units (DD) were accumulated as in the larval development study. Prior to constructing regression lines, DD were transformed to ln(DD). Cumulative percent pupation was transformed using probit analysis. The slopes and intercepts of regression lines were compared using analysis of covariance (SAS 1986). The slopes and intercepts of regression lines of cumulative percent pupation and male moth capture were compared within plots to determine if the capture of male moths through time in pheromone traps is reflective of the occurrence of pupae through time. To determine the extent to which defoliation influenced the pattern of pupation occurrence and male moth capture, the slopes and intercepts of regression lines were compared between plots.

Sex Ratios of Pupae. The sex ratio of hatching larvae has been shown to be 1:1 male:female (ref). The sex ratio of pupae at each plot was assessed by performing X^2 test for goodness of fit to an expected 1:1 male:female sex ratio. Changes in the sex ratio over time were examined visually.

Instar occurrence at the time of maximum defoliation. The estimate of the maximum level of defoliation was made on a whole plot level after larval feeding had ceased and before refoliation occurred. The estimate was made subjectively by considering both the number of missing leaves (due to larval feeding) and the amount of leaf area missing from the remaining leaves. Canopy photographs, taken on the same date as frass samples, were used to determine the date the maximum level of defoliation occurred. Methods used were identical to those used by Liebhold et al. (1988), except prints were made from each photograph. Accumulated DD from hatch to the date of the photograph with the maximum level of defoliation was determined. An estimate of the proportion of each instar on this date (DD) was calculated using the stochastic phenology model. This was done for plots with defoliation reaching or exceeding ca. 35% since the maximum level of defoliation could not be determined in plots with defoliation less than ca. 35%.

Results

Ecological Information. Elevation and valley or mountain plot designation, percent basal area of tree species, egg mass density, peak defoliation, forest tract size, and total moth catch are listed for each plot in Table 1.

Larval Developmental. The stochastic phenology model (Dennis et al. 1986) was fit separately to each of the sixteen study plots. Maximum likelihood parameter estimates (a_i's and b^2) and 95% asymptotic confidence limits (CI's) for the sixteen plots are listed in Table 2. Comparison of all possible pairs of parameter sets indicated all parameter sets were significantly different ($\alpha = 0.05$). Minimal overlap of the 95% (CI's) between plots supports this result. The parameter b^2 tended to be lower (i.e., 5.83 for TG9 verse 13.63 for TG8) in plots experiencing moderate to severe defoliation (> 50% defoliation). However, this trend was not consistent, for example, defoliation in plot LR8 reached ca. 75%, but b^2 was 13.28.

The number of calender days elapsed from hatch to 50% fifth and sixth instar were nearly identical for the two years for all plots (1988, mean = 51.11 calender days; 1989, mean = 51.85 calender days) (Table 3). Plots with higher levels of defoliation (ca. > 40%) tended to reach 50% fifth and sixth instar in fewer calender days (mean = 48.4) than plots with less defoliation (ca < 40%) (mean CD = 53.11). However, defoliation in plot LR8 exceeded 50%, but 56 CD were required to reach 50% fifth and sixth instar. Defoliation in plots MD9 and CG8 was below 40%, but only 49 and 47 CD respectively were required to reach 50% fifth and sixth instar

Total DD, CD, and DD/CD required from first hatch to first pupation and 50% pupation are listed in Table 4. The total DD required for development from hatch to first pupae ranged from 453 to 659 DD and for 50% pupation, 514 to 659 DD. There were no trends, with regard to the level of defoliation, in total DD required to first pupae or 50% pupation. Fewer CD elapsed from hatch to the respective developmental points for three valley plots (MD9, BL9, and ST9) and three severely defoliated (> ca. 70%) plots (TG9, PR8, GR8), but the number of CD was only slightly less than the rest of the plots. For 50% pupation, three severely defoliated (> ca. 70%) plots (TG9, PR8, GR8) developed in fewer CD. The number of DD/CD from hatch to both first pupae and 50% pupation was slightly greater for three severely defoliated (> ca. 70%) plots (TG9, PR8, GR8).

Pupae and Adults. Regression equations, significance levels, and r^2 values for cumulative percent pupation and male moth capture on DD are listed in Table 5.

Regression analysis indicated a significant relationship exists between cumulative percent pupation and male moth capture on DD for all plots. Within-plot comparison of the slopes of cumulative percent pupation and cumulative male moth capture indicated the slopes of the regression lines differed for six plots. Four of the plots (LR8, PR8, GR8, and TG9) were severely defoliated (> ca. 70%) while the other two plots (BL9 and WC8) experienced limited defoliation (< ca. 40%). The p-values for plots BL9 and WC8 indicate that the differences between slopes of the regression lines was far less than the other four, more severely defoliated plots (TG9, PR8, GR8).

Three groups of plots were identified based on between-plot comparisons of cumulative percent pupation (Table 6). Slopes and intercepts of four plots (TG9, PR8, GR8, LR8) were significantly different from a large number of other plots. Slopes and intercepts of two plots (CG9 and BL9) were significantly different from a moderate number of other plots. Plots CG9 and BL9 were significantly different from eight of the same plots. However, the level of defoliation in these two plots (CG9 and BL9) differed considerably. The remaining eight plots were significantly different from a low number of other plots, primarily the four severely defoliated plots (TG9, PR8, GR8, LR8).

For cumulative percent male moth capture, the plots can be divided into three groups, but trends, with respect to defoliation, were less identifiable (Table 7). Two plots (GR9 and PR8) were significantly different from a large number of other plots. Five plots (MD9, WL9, ST8, LR8, GR8) were significantly different from a low number of other plots, primarily GR9 and PR8. Slopes and intercepts of the remaining eight plots were significantly different from a moderate number of other plots. Plots BL9 and ST9 were located in the valley and differed significantly from mountain plots. Five mountain plots (DH9, CG9, TG9, TG8, and CG8) were significantly different from valley plots, including BL9 and ST9. The remaining two plots (CG9 and WC8) of the last group were mountain plots and the slopes and intercepts were significantly different from other mountain plots.

Sex ratio. The sex ratio in all but three plots (CG8, DH9, and WL9) was significantly different from the expected 50:50 male:female sex ratio (Table 8). For only three of the plots (PR8, GR8, and TG9) that differed significantly from the expected sex ratio, the proportion of male pupae exceeded that of female pupae. The change in the sex ratio over time (DD) could be divided into two patterns (Figure 2). Plots TG9, GR8, and PR8 in which most pupae were male and were collected on the

first sampling date is typical of the first pattern. The second pattern is more typical of gypsy moth development. The majority of the pupae collected on early sampling dates were male and on subsequent sampling dates, were predominantly female.

Instar occurrence at the time of maximum defoliation. The maximum level of defoliation at each plot is listed in Table 1. Estimates of the proportion of the population in each instar on the date maximum defoliation occurred are listed in Table 9. The results indicate the proportion of the larval population in instars one to four tended to be greater in plots GR8, PR8, and TG9 when the maximum level of defoliation occurred. The proportion of the larval population in instar five in the remaining plots tended to be greater, regardless of the level of defoliation. For example, in plot TG8 at maximum defoliation (ca. 35%), the percent of the larval population in the first four was 24.6. In plot PR8, at maximum defoliation (ca. 100%), the percent of the larval population in the first four instars was 62.9.

Discussion

There were no apparent trends in larval development related to defoliation as measured by the sets of model parameters and DD required for development to selected developmental points. The lack of trends in larval development related to defoliation is not unexpected since insect development is governed by heat accumulation (Logan 1988) which is described by the model parameters and DD. These results indicate that gypsy moth development is primarily a function of heat accumulation and not density-related factors. This conclusion is consistent with results reached by Lance et al. (1986, 1987). The increased rate of heat accumulation (i.e., more DD per CD) is probably due to increased penetration of solar radiation into the defoliated canopy and changes in larval behavior (Lance et al. 1987). However, the lower b^2 obtained for more defoliated (ca. > 50%) plots indicates that the relative importance of DD (heat accumulation) on development is increased in plots with defoliation > ca. 40%. This suggests that there may be minor influences on development that are more pronounced at low larval densities (e.g., genotypic variation in larval developmental rates, foliage quality). More rapid larval development as measured in CD in plots (TG9, PR8, GR8) with severe defoliation (ca. > 70%) compared to less defoliated (ca. < 70%) plots is consistent with other studies (Campbell 1978, Lance et al. 1987). However, the difference between the number of CD elapsed during the larval development period in the severely defoliated plots and less defoliated plots was not as great as reported in Campbell (1978). The number of elapsed CD during the larvae developmental period

in several plots (MD9, BL9, and ST9) with minimal defoliation (ca. < 25%) was not greatly different than that of the severely defoliated plots. The exact reasons for this are not clear, but may be related to differences in plot specific characteristics, particularly those related to elevational differences.

The failure to identify groups of plots based on sets of model parameters and DD required for larval development indicates the stochastic model is reflective of the gypsy moth larval development. As noted, this indicates development is more related to heat accumulation than other factors. But, given this finding, significant differences between all pair-wise comparisons of model parameters sets should not have been found. Significant differences between all pair-wise comparisons of model parameters may be a result of several factors. First, frass may be a poor indicator of larval occurrence and hence larval phenology was inaccurately estimated. Secondly, the microhabitat or actual thermal environment of larvae may have have been poorly measured. However, if larval occurrence and microhabitat were accurately measured, plot specific characteristic may account for differences in larval phenology. Plot characteristics such as elevation, aspect, host plant species composition, forest structure and intrinsic differences between populations may have contributed to the variability in the data and the differences observed between sets of model parameters. Lastly, a set of model parameters describes the development of all larval instars, but the major impact of the defoliation process probably affects later instar larvae to a greater extent than early instar larvae.

The phenology of male pupae is clearly altered in defoliated (ca. > 40%) plots. Generally, the period of time (DD and CD) over which larvae pupate is reduced. This is probably due to a combination of increased temperature in defoliated plots (Lance et al. 1986) and significantly higher mortality of slower developing male and female larvae. Mortality of female larvae has been shown to be greater in high density plots (Campbell 1967). Higher mortality of female larvae would result in a pupal sex ratio that is male skewed. A pupal sex ratio that is not 1:1 male:female has been reported for high density populations in other studies (Campbell 1963, Mauffette & Jobin 1985). Presumably, these high density populations (Campbell 1963, Mauffette & Jobin 1985) also experienced high levels of defoliation. In this study, the sex ratio of pupae tended not to be 1:1 male:female, but only in three severely defoliated plots (TG9, GR8, PR8) was the sex ratio predominantly male. It was also in these plots (TG9, GR8, PR8) that the maximum level of defoliation occurred while a greater proportion of the larval

population were in instars one to four. These plots (TG9, GR8, PR8) were three of the four plots (TG9, GR8, PR8, LR8) for which the slopes and intercepts of pupae occurrence differed from the majority of other plots. This suggests that not only may the the maximum level of defoliation achieved be important, but the time (at which instar) maximum defoliation occurs may have an important influence on gypsy moth population dynamics.

While it appears that there are characteristics of larval and pupal development related to the level of defoliation in a plot, these characteristics do not appear to be reflected in male moth capture in pheromone traps. If the capture of adult moths were consistent with the phenology of pupae, at least two or possibly three distinct groups of plots should have been identified by comparison of slopes and intercepts. The groupings should be defined on the basis of the level of defoliation, but these groups were not found. This occurred despite the fact the slopes of regression lines of cumulative percent pupation and male moth capture were significantly different only in the more severely defoliated (ca. 70%) plots (LR8, PR8, GR8, TG9). This result indicates that cumulative male moth capture in these more severely defoliated plots (LR8, PR8, GR8, TG9) was similar to the pheromone trap catch of less defoliated plots. This may have been caused by male moth movement between populations with varying biological characteristics, primarily phenology. This would tend to increase the similarity among pheromone trap capture of male moths because moths would be captured over a generally identical interval of time, regardless of the level of defoliation.

The slopes and intercepts of the regression lines of the capture of male moths in pheromone traps over time from two plots (GR9 and PR8) differed from all other plots. The reason why these results were obtained is unclear and underscores the variability observed in pheromone trap captures. The most plausible reason the slopes and intercepts of plots GR9 and PR8 differed from other plots is related to the population density in GR9 and the proximity of PR8 to large undefoliated areas. Plot GR9 had a low larval density and in this plot male moths were collected in pheromone traps prior to collection of the first pupae in the plot. Therefore, many of the moths in the GR9 pheromone trap probably did not develop in the vicinity of the trap. Plot PR8 was severely defoliated, but adjacent to large undefoliated areas with a generally high larval density (this area was defoliated the next year). Substantial numbers of moths from this undefoliated area were probably captured in the PR8 pheromone trap. This likely

altered the pattern of catch. This hypothesis is supported by examination of male moth wing length (Chapter 4) which is indicative of the level of defoliation (Chapter 2).

The failure to detect differences in capture of male gypsy moths, relative to the level of defoliation, is probably the result of a complex interaction between pheromone traps and certain biological attributes of gypsy moth populations in the vicinity of the trap. Pheromone dispersion can be affected by a number of biotic and abiotic conditions including wind speed, temperature, landscape features, pheromone concentration, and receptivity of moths. The dynamics of larval development, adult longevity, and density within each population in the vicinity of the pheromone trap may interact with the pheromone trap and topographical landscape features to produce unique patterns of catch. Trap capacity and changes in efficiency (Elkinton 1987) are also major factors altering male moth capture. The spatial extent of populations and the distance between a population and pheromone trap can influence not only the number of males captured, but when capture occurs. These factors may interact to produce a pool of moths that are available for capture in excess of the time male moths are being produced in any given area. The result is that pheromone trap capture of male moths does not have distinct patterns of capture over time (DD).

Pheromone traps in gypsy moth management programs are serviced once, perhaps two times in a season, whereas traps in this study were emptied every three days. This limits the extrapolation of conclusions concerning pheromone trap data obtained in this study to data that would be collected in a gypsy moth management programs. Despite the intensity of sampling, we were unable to identify characteristics of pheromone trap capture from plots were capture should have been influenced by distinct changes in the incidence of gypsy moth pupae. When combined with the additional problem of changes in trap effeciency (Elkinton 1987) and trap saturation (Bellinger et al. 1990), it is unlikely that the pattern of male moth capture over time, in a pheromone trap used in an operational manner, would closely reflect the pattern of emergence from a single population in the vicinity of the trap. The spatial and temporal variation inherent in gypsy moth populations, the complexity of the forest system, and the topographical variation in the study areas and throughout the southern Appalachians, probably further limits development of a linear model to predict egg mass density from pheromone trap captures. Alternative methods to interpret pheromone traps should be explored. Wing length (Bellinger et al. 1990) has been suggested as one alternative, as has some combination of the number of moths captured

and wing length (Chapter 2). More importantly it may be necessary to reduce the emphasis on evaluating gypsy moth populations on the basis of egg mass density. The attainment of some level of defoliation is assumed in the decision process when using egg mass density as the criteria for control practices. But, the relationship between egg mass density and defoliation is not well understood. Therefore, the use of variables that evaluate the defoliation potential of populations may be more appropriate and useful for management programs. This type of approach to population evaluation would be be more compatible with the types of information that can be obtained from pheromone traps.

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Table 1. Ecological data from research plots.

Plot	Elevation[1]	Percent Basal Area WO	RO	CO	HC	OT	Egg Mass Density Start	End	Peak % Defoliation	Forest Tract Size[2]	Moth Catch[3]
MD9	600 V	17	27	20	4	1	16,968	11,223	20	98	857
BL9	700 V	48	56	13	12	4	12,147	10,495	15	60	1512
ST9	690 V	16	34	0	16	0	13,423	19,425	55	6[4]	1805
WL9	650 V	50	38	28	2	1	4,546	1,276	0	38	2079
ST8	650 V	22	20	1	6	31	621	11,873	15	312	4624
DH9	1700 M	42	16	76	3	5	6,895	12,147	60	10.5	2692
CG9	2540 M	0	32	27	6	5	4,458	42,967	75	171.5	2208
PR9	2700 M	29	39	10	28	3	2,295	14,967	35		1469
GR9	2600 M	21	8	0	58	3	948	359	0		674
TG9	2400 M	31	0	91	1	8	19,816	345	100	23.9	1557
TG8	2400 M	1	43	39	5	14	132	19,816	35		1557
PR8	2700 M	0	50	5	4	14	9,211	2,295	100	1055.8	2449
GR8	2600 M	27	56	1	24	4	2,421	948	90	211.8	1593
WC8	3000 M	15	55	14	13	15	8	8,254	0		1678
LR8	1600 M	3	32	46	9	13	51658	9,398	75	15.7	2212
CG8	2540 M	0	32	27	6	5	4678	4,458	10		1852

[1] Elevation and rating of plot as to valley or mountain location.

[2] For valley plots the size (ha) of the woodlot in which the plot was located. For mountain plots the size (ha) of the defoliated area, otherwise left blank.

[3] Represents the average of two traps for 1988.

[4] Plot located in defoliated area of ca. 2 ha in the middle of a largely undefoliated woodlot.

Table 2. Parameter estimates (±95% asymptotic confidence limits) for the gypsy moth phenology model for sixteen study plot.

	Parameters				
Plot	a_1	a_2	a_3	a_4	b^2
MD9	169.32	241.67	356.69	482.66	9.66
	1.81	2.34	2.60	2.89	0.39
BL9	189.97	261.62	353.69	460.09	12.08
	1.60	1.18	2.42	3.44	0.39
ST9	143.76	215.73	300.56	380.56	7.18
	1.58	2.10	2.45	2.43	0.30
WL9	188.61	257.98	344.64	447.64	18.60
	2.08	2.42	2.71	4.99	0.98
ST8	118.82	237.06	381.53	541.94	11.99
	1.52	1.99	1.26	3.64	0.64
DH9	168.84	241.14	331.12	411.01	4.00
	1.53	1.73	1.65	1.93	0.19
CG9	267.44	347.21	409.86	460.33	2.56
	1.16	2.56	3.26	3.33	0.51
PR9	190.14	272.97	368.16	444.72	4.06
	1.62	.41	2.11	2.40	0.19
GR9	177.11	261.83	402.75	515.53	17.50
	2.3	2.16	2.73	3.63	0.40
TG9	215.99	284.11	397.60	495.08	5.83
	1.64	2.35	2.21	2.71	0.33
TG8	165.30	267.58	354.31	478.86	13.63
	2.23	2.56	2.67	3.13	0.57
PR8	173.34	302.32	400.83	503.91	7.74
	2.26	2.12	2.25	0.23	0.29
GR8	121.59	249.68	374.22	486.31	11.14
	2.3	2.16	2.73	3.63	0.40
WC8	135.58	219.39	307.29	470.83	8.88
	2.21	1.84	1.83	2.84	0.43
LR8	164.00	258.25	334.88	440.96	13.28

	1.94	2.72	2.50	2.85	0.63
CG8	139.36	260.44	340.40	424.24	6.03
	2.3	2.12	0.85	2.5	0.29

Table 3. Accumulated DD (model estimates) and calender days from first hatch of the occurrence of selected developmental points for the gypsy moth.

Plot	50% instar 1	Peak instar 2	Peak instar 3	Peak instar 4	50% instar 5 & 6
Plots with limited defoliation (ca. < 40%).					
MD9	170[1]	196	290	410	483
	29[2]	31	37	44	49
BL9	190	214	296	395	461
	32	34	41	48	53
WL9	189	206	284	378	448
	33	35	42	48	55
SN8	119	166	297	450	542
	21	26	41	56	62
PR9	191	228	317	403	445
	31	33	41	49	53
TG8	166	203	298	403	479
	28	31	39	49	56
CG8	140	193	295	377	425
	19	25	35	44	47
WC8	136	169	255	380	471
	16	20	31	43	50
GR9	178	203	315	442	516
	30	33	41	49	53
Plots with more severe defoliation (ca.> 40%).					
SS9	144	173	251	334	381
	28	30	37	43	46
DH9	169	201	283	368	412
	29	32	40	45	49
CG9	268	305	377	433	461
	33	35	40	45	49
TG9	216	245	335	441	496
	27	29	35	43	47

PR8	174	230	344	445	504
	17	22	32	40	44
GR8	122	174	301	420	487
	17	23	35	44	48
LR8	165	198	284	375	441
	27	30	41	50	56

[1] DD from model estimates.

[2] Calender days from model estimates.

Table 4. Calender days (CD), degree-days (DD), and DD/CD from hatch to first pupae and 50% pupation.

	First Pupae			50% Pupation		
PLOT	CD	DD	DD/CD	CD	DD	DD/CD
MD9	49	487	9.94	57	619	10.86
BL9	55	483	8.78	60	544	9.07
ST9	52	453	8.71	57	514	9.02
WL9	58	485	8.36	61	521	8.54
ST8	61	528	8.66	66	600	9.84
DH9	57	504	8.84	63	582	9.24
CG9	57	592	10.39	61	659	10.80
PR9	60	493	8.22	64	546	8.53
GR9	63	574	9.11	66	613	9.29
TG9	51	550	10.78	55	605	11.00
TG8	61	562	9.21	61	568	9.31
PR8	53	659	12.43	53	659	12.43
GR8	56	614	10.96	56	614	10.96
WC8	58	562	9.68	63	651	10.33
LR8	61	527	8.64	61	528	8.65
CG8	57	566	9.93	58	576	9.93

Table 5. Regression equations and statistics for cumulative percent pupation and cumulative percent pheromone trap capture over time.

Plot	Plot type	Equation	r^2	Significance[1] of slope	Significance[1] of slope comparison
MD9	P[2]	$y^3 = -57.45 + 8.92*DD^4$	0.92	0.0006	0.3906
	PT[5]	y = -66.67 + 9.76*DD	0.99	0.0001	
BL9	P	y = -74.02 + 11.69*DD	0.95	0.0011	0.0324
	PT	y = -55.91 + 8.37*DD	0.95	0.0001	
ST9	P	y = -61.67 + 9.79*DD	0.90	0.0003	0.4702
	PT	y = -58.25 + 8.70*DD	0.93	0.0001	
WL9	P	y = -69.21 + 11.02*DD	0.96	0.0033	0.3976
	PT	y = -63.96 + 9.70*DD	0.97	0.0001	
ST8	P	y = -54.70 + 8.56*DD	0.99	0.0001	0.2634
	PT	y = -61.63 + 9.21*DD	0.98	0.0001	
DH9	P	y = -68.59 + 10.77*DD	0.97	0.0017	0.8545
	PT	y = -72.97 + 11.00*DD	0.98	0.0001	
CG9	P	y = -84.93 + 13.10*DD	0.98	0.0008	0.4519
	PT	y = -79.23 + 11.67*DD	0.96	0.0001	
PR9	P	y = -61.03 + 9.71*DD	0.97	0.0016	0.3903
	PT	y = -55.81 + 8.45*DD	0.96	0.0001	
GR9	P	y = -76.92 + 11.97*DD	.0.95	0.0231	0.1136
	PT	y = -42.50 + 6.39*DD	0.90	0.0001	
TG9	P	y = -146.95 + 22.97*DD	0.99	0.0305	0.0028
	PT	y = -77.75 + 11.55*DD	0.97	0.0001	
TG8	P	y = -53.82 + 8.48*DD	0.98	0.0001	0.0915
	PT	y = -68.84 + 10.32*DD	0.98	0.0001	
PR8	P	y = -26.93 + 4.41*DD	0.99	0.0029	0.0070
	PT	y = -96.72 + 14.22*DD	0.97	0.0001	
GR8	P	y = -30.49 + 4.90*DD	0.99	0.0004	0.0072
	PT	y = -68.67 + 10.33*DD	0.95	0.0001	

WC8	P	y = -65.84 + 10.16*DD	0.99	0.0001	0.0236
	PT	y = -56.91 + 8.42*DD	0.98	0.0001	
LR8	P	y = -30.64 + 4.89*DD	0.95	0.0001	0.0001
	PT	y = -65.30 + 9.75*DD	0.96	0.0001	
CG8	P	y = -49.40 + 7.78*DD	0.99	0.0001	0.1976
	PT	y = -69.75 + 10.49*DD	0.93	0.0001	

[1] p - value

[2] Pupae

[3] Probit cumulative percent.

[4] Ln(DD)

[5] Pheromone Traps

Table 6. Slope and intercept comparisons for pupae. Slopes comparison are lower left of matrix and intercepts are upper right of matrix. Plots that differed significantly are indicated by bold capital S. Total number of S's for each plot are listed at the bottom for slope comparisons and on the right for intercept comparisons.

	MD9	BL9	ST9	WL9	ST8	DH9	CG9	PR9	GR9	TG9	TG8	PR8	GR8	WC8	LR8	CG8	
MD9		S	n	n	n	n	S	n	n	S	n	S	S	n	S	n	6
BL9	S		n	n	S	n	n	n	n	S	S	S	S	n	S	S	8
ST9	n	n		n	n	n	S	n	n	S	n	S	S	n	S	n	5
WL9	n	n	n		n	n	n	n	n	S	n	S	S	n	S	n	4
ST8	n	S	n	n		n	S	n	n	S	n	n	S	n	S	n	5
DH9	n	n	n	n	n		n	n	n	S	n	S	S	n	S	n	4
CG9	S	n	S	n	S	n		n	n	S	S	S	S	n	S	S	9
PR9	n	n	n	n	n	n	n		n	S	n	S	S	n	S	n	4
GR9	n	n	n	n	n	n	n	n		S	n	S	S	n	S	n	4
TG9	S	S	S	S	S	S	S	S	S		S	S	S	S	S	S	15
TG8	n	S	n	n	n	n	S	n	n	S		n	S	n	S	n	5
PR8	S	S	S	S	n	S	S	S	S	S	n		n	S	n	n	10
GR8	S	S	S	S	S	S	S	S	S	S	S	n		S	n	n	12
WC8	n	n	n	n	n	n	n	n	n	S	n	S	S		S	n	4
LR8	S	S	S	S	S	S	S	S	S	S	S	n	n	S		S	13
CG8	n	S	n	n	n	n	S	n	n	S	n	n	n	n	S		4
	6	8	5	4	5	4	9	4	4	15	5	10	12	4	13	4	

Table 7. Slope and intercept comparisons for pheromone traps. Slopes comparison are lower left of matrix and intercepts are upper right of matrix. Plots that differed significantly are indicated by bold capital S. Total number of S's for each plot are listed at the bottom for slope comparisons and on the right for intercept comparisons.

	MD9	BL9	ST9	WL9	ST8	DH9	CG9	PR9	GR9	TG9	TG8	PR8	GR8	WC8	LR8	CG8	
MD9		n	n	n	n	n	n	n	S	n	n	S	n	n	n	n	2
BL9	n		n	n	n	S	S	n	S	S	S	S	S	n	n	S	8
ST9	n	n		n	n	S	S	n	S	S	S	S	n	n	n	S	7
WL9	n	n	n		n	n	S	n	S	S	n	S	n	n	n	n	4
ST8	n	n	n	n		n	S	n	S	S	n	S	n	n	n	n	4
DH9	n	S	S	n	n		n	S	S	n	n	S	n	S	n	n	6
CG9	n	S	S	S	S	n		S	S	n	n	S	n	S	S	n	9
PR9	n	n	n	n	n	S	S		S	S	S	S	n	n	n	S	7
GR9	S	S	S	S	S	S	S	S		S	S	S	S	S	S	S	15
TG9	n	S	S	S	S	n	n	S	S		n	S	n	S	n	n	8
TG8	n	S	S	n	n	n	n	S	S	n		S	n	S	n	n	6
PR8	S	S	S	S	S	S	S	S	S	S	S		S	S	S	S	15
GR8	n	S	n	n	n	n	n	n	S	n	n	S		S	n	n	4
WC8	n	n	n	n	n	S	S	n	S	S	S	S	S		n	S	8
LR8	n	n	n	n	n	n	n	n	S	n	n	S	n	n		n	3
CG8	n	S	S	n	n	n	n	S	S	n	n	S	n	S	n		6
	2	8	7	4	4	6	8	7	15	8	6	15	4	8	2	6	

Table 8. Total number of pupae collected, sex ratio, and significance value for X^2 for test of deviation from expected 1:1 male:female sex ratio.

Plot	Pupae	% male	% female	Significance value (p)
MD9	168	0.29	0.71	0.0001
BL9	382	0.28	0.72	0.0001
ST9	387	0.38	0.62	0.0001
WL9	111	0.41	0.59	0.0628
ST8	2469	0.36	0.64	0.0001
DH9	88	0.41	0.69	0.1286
CG9	247	0.32	0.68	0.0001
PR9	131	0.37	0.63	0.0036
GR9	52	0.25	0.75	0.0001
TG9	97	0.89	0.11	0.0001
TG8	1827	0.40	0.60	0.0001
PR8	2228	0.80	0.20	0.0001
GR8	992	0.66	0.34	0.0001
WC8	1272	0.37	0.63	0.0001
LR8	1464	0.29	0.71	0.0001
CG8	312	0.53	0.47	0.3370

Table 9. Proportion of five instars in the population of plots with defoliation reaching or exceeding ca. 35%.

	Instar				
Plot	1	2	3	4	5 & 6
ST9	0.4	0.9	4.2	13.5	80.9
DH9	0.0	0.0	0.3	1.2	98.5
CG9	0.0	0.1	0.3	0.8	98.8
PR9	0.1	0.5	3.8	15.5	80.1
TG9	0.7	1.7	15.0	39.7	42.9
TG8	0.9	2.0	4.5	17.2	75.3
PR8	0.7	5.0	17.9	39.3	37.1
GR8	1.7	9.4	34.4	36.7	17.8
LR8	0.8	1.4	2.8	9.8	85.2

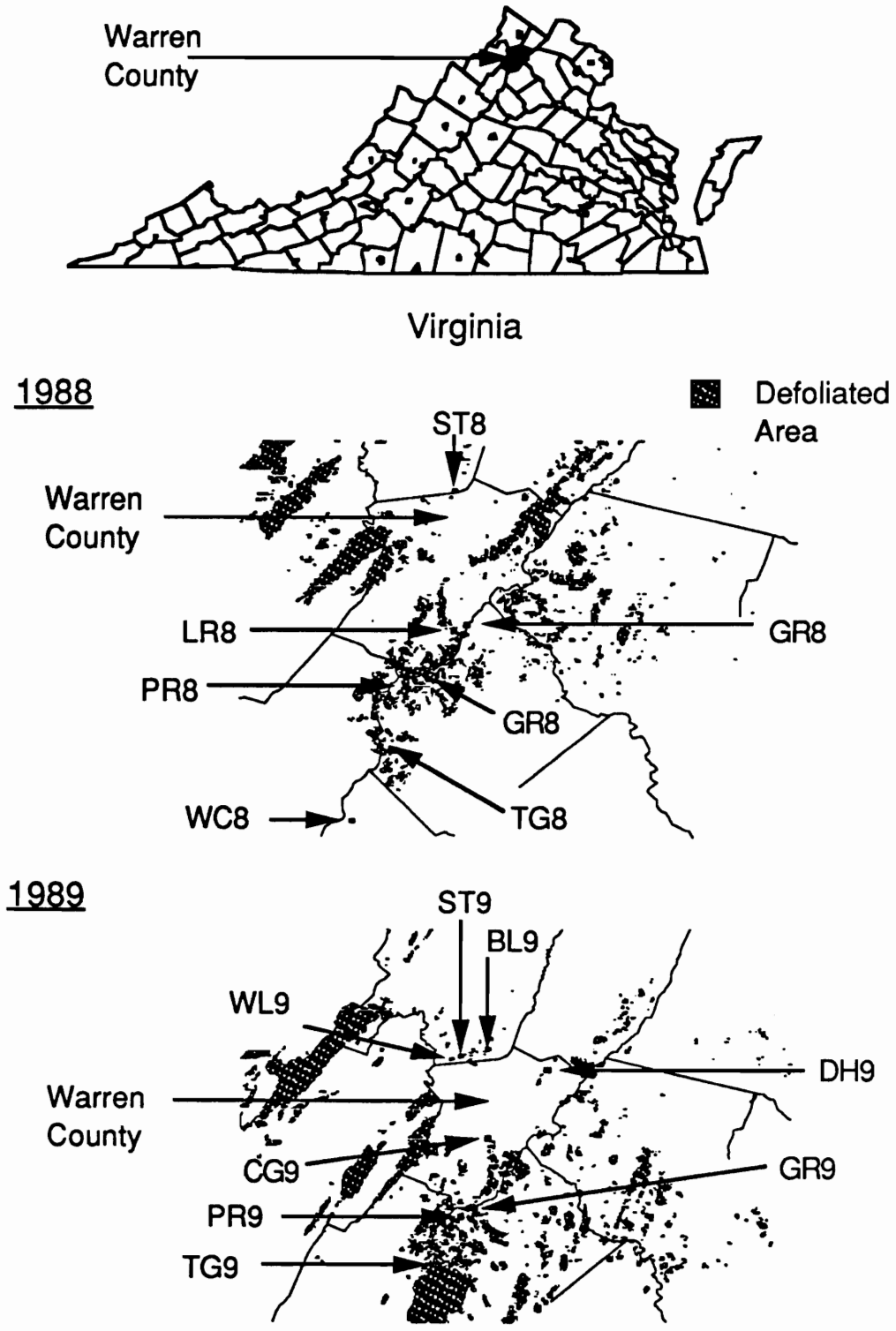

Fig. 1. Location of plots used in the study indicating location of defoliated areas in Virginia.

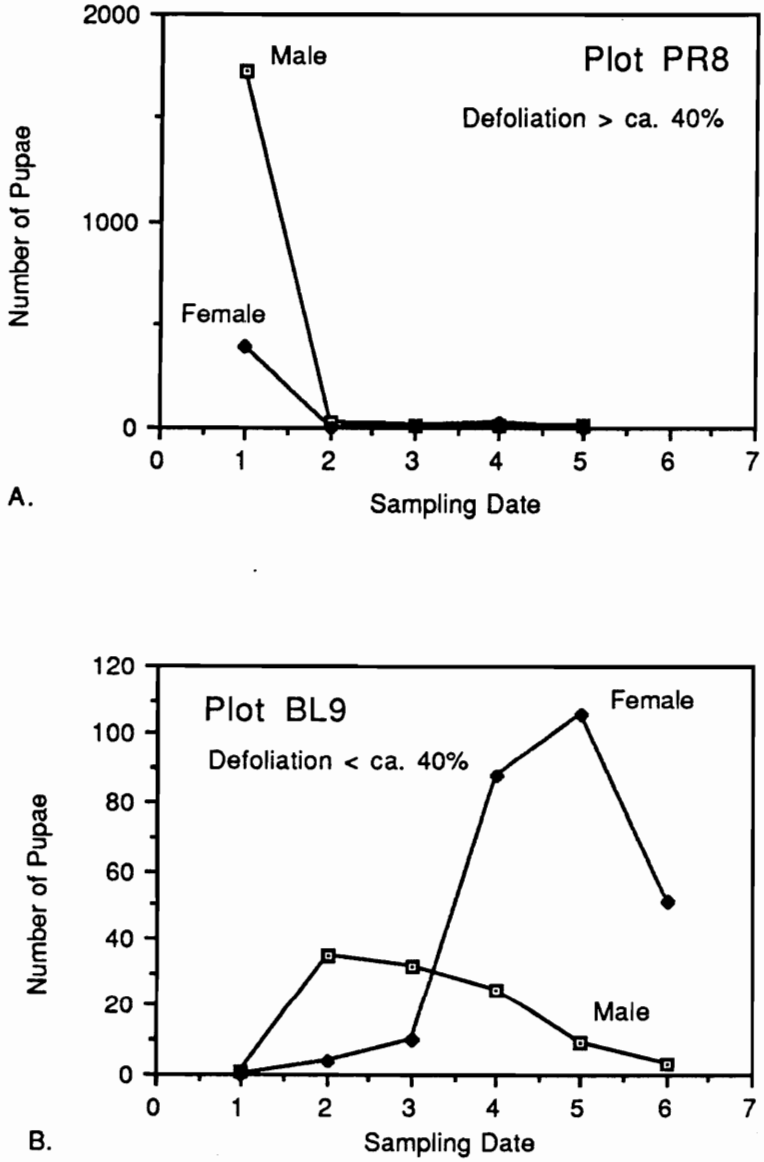

Fig. 2. Example of collection over time of male and female pupae for A) a severely defoliated (> ca. 70%) plot (PR8) and B) a plot with limited defoliation (< ca. 25%) (BL9).

Chapter 4

Dynamics of gypsy moth pheromone-baited milk-carton traps. Part II: Use of male moth wing length as a measure of defoliation.

Pheromone-baited milk-carton traps (pheromone traps) have been widely used for detection and monitoring of gypsy moth populations. They have been employed extensively to monitor populations in two large scale gypsy moth (Lepidoptera: Lymantriidae Lymantria dispar) IPM programs (Maryland IPM and Appalachian Gypsy Moth IPM programs). Despite this use, relatively little research (but see Elkinton & Carde 1980, Elkinton 1987) has been conducted to understand the underlying factors that influence the capture of male gypsy moths in pheromone traps. Factors such as elevation, wind speed and direction, defoliation, gypsy moth population[1] density, and area-wide population dynamics may influence male moth capture in pheromone traps. In a study (Chapter 3) designed to investigate some of the underlying factors influencing pheromone traps, the pattern of male moth capture in pheromone traps over time was found not to be related to the level of defoliation in the vicinity of the trap. However, identifiable trends in larval and pupal development could be related to the level of defoliation in a plot. This fact suggested that the capture of male moths in pheromone traps is not necessarily indicative of larval population dynamics or egg mass density in the vicinity of the trap.

Male moth wing length is a variable obtainable from moths captured in pheromone traps that may have utility to aid in interpreting pheromone trap catch. The use of wing length to estimate egg mass density was proposed by Bellinger et al. (1990). Bellinger et al. (1990) found a correlation ($r^2 = 0.60$) between egg mass density and male wing length. However, additional studies (Chapter 2) determined that the pattern of wing length size of moths collected as pupae is essentially binomial (i.e., wing length is either small or large) and dependent upon whether or not larvae experience defoliation in excess of ca. 40%. The size of wing lengths was found to be either large (> 19.89 mm), if defoliation was less than ca. 40%, or small (< 17.94 mm) if defoliation was greater than ca. 40%. This finding suggested that the linear

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[1] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

relationship between wing length and egg mass density found by Bellinger et. al. (1990) may be spurious and, in fact, was not validated in the latter study (Chapter 2). The results of the this study (Chapter 2) also indicated that criteria to evaluate male wing length, if they are to be used to monitor gypsy moth populations, should be based on the threshold wing length values (i.e., large moths (> 19.89 mm); small moths (< 17.94 mm)). However, because mean wing length from individual plots may deviate from these values (listed above), development of more general criteria for evaluating the wing length of moths captured in pheromone trap may be required.

The objective of the research presented in this chapter was to investigate the extent to which the wing length of male moths captured in pheromone traps reflects the wing length of moths collected as pupae in the vicinity of the pheromone trap. A second objective was to develop more general criteria to evaluate wing length of moths captured in pheromone traps. This aspect was addressed by evaluating wing length threshold values. Threshold values are values to which wing length statistics (i.e. mean wing length) derived from pheromone trap captured moths can be compared. Depending on the level of defoliation in the vicinity of the pheromone trap, the wing length statistics of male moths captured in pheromone traps are expected to be greater or less than threshold values.

Methods

Study Plots. Studies were conducted in 1988 and 1989 in sixteen plots located in the leading edge area[2] of the gypsy moth infestation. Plots were located in the Shenandoah Valley area (Warren Co) and the Shenandoah National Park (Warren, Rappahannock, and Page counties) in Virginia (Figure 1). Plots were located over a range of elevation and had a range of egg mass densities, defoliation levels, and forest tract sizes. All but one plot was dominated by oak species (white, scarlet, red, and chestnut oak), but the relative composition of species varied between plots. After leaf fall, egg-mass density estimates were obtained from two fixed and variable - radius plots (20 basal area factor) (Wilson & Fontaine 1978) located in the plot. Study plots and plot names are the same as those described in Chapter 3.

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[2] The leading edge area is defined as the area newly invaded by gypsy moths, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time.

Degree-Day Accumulation. Data on heat accumulation (degree-days [DD]) were collected using Campbell Scientific CR-10 dataloggers or Omega model 414 recording thermometers at each plot from the start of egg hatch through the entire sampling period. Accumulated heating DD were calculated using a modified sine wave equation (Allen 1976). A lower threshold of 7.65 °C and upper threshold of 41.0 °C were selected based on values calculated for a comprehensive gypsy moth life system model (Sheehan 1989) and from data in Casagrande et al. (1987). The lower threshold is an average value for male and female larvae and applied to all lifestages in this study. On occasion, temperature data for an individual plot was unavailable due to equipment failure. DD data for the missing interval was determined by comparing total accumulated DD with the closest and most ecologically similar plot.

Male Moth Wing Length. Pupae were collected every three days from beneath burlap bands after the first pupa was observed in a plot. Depending on the larval density in a plot, ten to twenty trees located in each plot were burlaped for collection of pupae. The burlap bands were ca. 20 cm wide and were located at breast height around the boles of the trees. All pupae were removed on each sample date, sexed, and counted. The left forewing length of emerged male moths collected as pupae (MMCAP) was measured using a standard mm rule.

Male moths were collected using pheromone traps hung from a tree located in each plot (male moths captured in pheromone traps, MMCPT). In 1988, two pheromone traps placed at least 100 m apart were used and the trap data is the average of the two traps. In 1989, one trap was used. Pheromone traps were checked every three days after the first moth was captured. For each sample date, all moths were removed from the trap and the left forewing of up to twenty moths were measured. .

Analysis. Wing length of MMCAP was used directly in the analysis. For MMCPT, wing length was calculated by multiplying the percent of moths in each mm class (i.e., 13, 14,..., 25 mm) from each sampling date by the total number of moths captured on that sampling date. Wing length statistics where calculated from the derived data for each sampling date or for the entire season as appropriate. Two data sets for MMCPT were developed for the analyses. One data set consisted of all the MMCPT data. The second data set (reduced data set) consisted of MMCPT that were collected on sampling dates with more accumulated DD than the first date (in DD) on which MMCAP adult emergence from the same plot first occurred. The MMCPT sampling date immediately preceding the date (in DD) of first adult MMCAP emergence

was included. The second data set was only calculated for plots in which first MMCPT capture preceded first MMCAP adult emergence. For each plot and data set, the wing length of MMCAP and MMCPT (both data sets) were compared using the Wilcoxon rank sum test (SAS 1986). Data were ranked using PROC Rank Percent option in SAS (SAS 1986). Wing length of MMCAP and MMCPT (full data set only) were compared separately using ANOVA and Duncans multiple range test (SAS 1986).

Variation in wing length may be important for interpreting pheromone trap captures. One standard deviation ($\pm$ 1 SD) around the mean was calculated as a measure of the variation of wing length. Expected threshold values for mean wing length and mean wing length $\pm$ 1 SD were based on data in Chapter 2 and from observation of the data. The threshold values were assumed to be indications of the level of defoliation experienced by larvae in a plot. Expected threshold wing length values of mean wing length > 19.0 for MMCAP and > 19.5 for MMCPT and mean wing length $\pm$ 1 SD values of 17.0 and 21.0 mm for MMCAP and 18.0 and 21.0 mm for MMCPT. The MMCAP and MMCPT wing length statistics and threshold values were compared to these threshold values. For these comparisons, wing length statistics for plots experiencing limited defoliation (ca. < 40%) were expected to exceed the threshold values. Wing length statistics for plots with more severe defoliation (ca. > 40%) should be less than the expected threshold values.

Pheromone traps in gypsy moth management programs are generally serviced once at the end of male moth flight. To simulate this, twenty sets of twenty moths each were randomly selected from the MMCPT full data set for each plot. The mean and standard deviation for each set of twenty moths were calculated. Using the twenty sets of statistics a single mean and standard deviation were calculated for each plot. The threshold values (mean $\pm$ 1 SD) for each plot were determined.

The change in mean wing length over time (DD) for MMCAP and MMCPT were examined using regression analysis. DD for MMCAP is the sum of field DD accumulated from hatch to the pupal collection date plus the accumulated laboratory DD from the pupal collection date to the date of emergence. To facilitate comparison of wing length between MMCAP and MMCPT, each sampling date was standardized on a 0 to 1 scale. The first date moths from each plot emerged from pupae or were collected from pheromone traps being 0 and the last 1. Wing length was estimated at 0.1 to 0.9 by linear interpolation, using the mean wing length of the two closest sampling dates. For 0 and 1 the actual mean wing length value was used. This procedure for MMCAP

essentially extends the life of each moth and simulates pheromone trap capture of male moths. Because pheromone traps were sampled every three days, daily variation inherent in the MMCAP data does not occur in the MMCPT data. Variation in the MMCAP data was eliminted by grouping the wing length data into five groups consisting of the standardized DD dates: Group 1, 0.0 and 0.1; Group 2, 0.2 and 0.3; Group 3, 0.4, 0.5, and 0.6; Group 4, 0.7 and 0.8; and Group 5, 0.9 and 1.0. Regression equations of mean wing length for the five groups on standardized sampling dates were calculated. Two sets of regression equations were calculated for MMCPT using the full data set and the reduced data set.

Results

Ecological Information. Elevation and valley or mountain plot designation, percent basal area of tree species, egg mass density, peak defoliation, forest tract sizes, and total moth catch are listed for each plot in Table 1. The location of the study plots used in this study are presented in Figure 1.

Wing length. Pupae were collected from the sixteen plots over a 15 to 30 day period. Male moths were collected in pheromone traps over a 30 days to 45 day period. Mean wing length, mean wing length $\pm$ 1 SD, and the results of the Wilcoxon rank sum test are listed in Table 2. Generally, the mean wing length of MMCAP was less than that of the corresponding MMCPT (full or reduced data set). Male wing length of MMCAP and MMCPT was significantly different for only one plot (DH9) in the full data set and two plots (CG9 and GR9) in the reduced data set. Analysis of variance indicated significant differences between plots for wing length of MMCAP ($F = 67.67$, $p > F = 0.0$, $N = 1502$) and MMCPT ($F = 1263.84$, $p > F = 0.0$, $N = 47844$) (Table 3). Wing length of MMCAP of only one plot (MD9) that experienced limited defoliation (ca. < 40%) was not significantly different from more severely defoliated (ca. > 40%) plots (Table 1).

Wing length statistics (mean wing length and mean wing length $\pm$ 1 SD) generally exceeded threshold values if defoliation was less than ca. 40% and were below threshold values if defoliation exceeded ca. 40% (Table 2). There were only a few exceptions to this result. The mean wing length and wing length + 1 SD of MMCAP from plot MD9 for which defoliation was less than ca. 40% did not exceed the threshold value; however, the mean wing length - 1 SD did exceed the threshold value. The MMCPT wing length statistics for plot MD9 exceeded the threshold values as was expected. The MMCAP wing length statistics of plots DH9 and ST9 did not

exceed the threshold values as was expected based on the level of defoliation (> ca. 40%) in these plots. But, the wing length statistics for MMCPT exceeded the threshold values. For plot CG9, the three wing length statistics for both MMCAP and MMCPT exceeded the threshold values. This was not expected given the level of defoliation (> ca. 70%) in plot CG9.

The wing length of moths from the data set calculated to simulate pheromone traps serviced only once was generally more similar to the wing length of MMCAP than to the wing length of moths from the two MMCPT data sets (Table 2). The SD of simulated wing length was generally greater than the SD of MMCAP and MMCPT. Therefore, the mean wing length $\pm$ 1 SD statistics were either greater or less than the same statistics for moths from the MMCAP and MMCPT data sets. Based on the threshold values for MMCAP, the mean + 1 SD statistic was below the threshold for MD9, ST8, BL9 and ST9. The mean wing length and mean wing length - 1 SD for PR8 were greater than the thresholds.

Moths were collected in pheromone traps from nine plots, primarily mountain plots, substantially earlier than the first MMCAP emerged (Figure 2). The first moths captured in pheromone traps and MMCAP emergence in the remaining plots was relatively coincident. Except for TG9, these plots were valley plots or lower elevation mountain plots (LR8 and DH9). One plot (MD9) in the valley had an unusually early single MMCAP emergence.

The slopes of the majority of regression equations of mean wing length on standardized sampling dates for both data sets were not significant (Table 4). Additional analyses (i.e., homogeneity of slope comparisons) were not conducted for this reason. For those regression equations with significant slopes, the slopes were generally negative indicating wing length generally declined from the earliest sampling dates to later sampling dates. This trend is apparent in the data (Figure 3).

Discussion

The results of this study indicate that the wing length of male moths captured in pheromone traps is in most cases similar to the wing length of males collected as pupae in the vicinity of the trap. Mean wing length of MMCAP and MMCPT were significantly different for only one plot. The use of threshold values to evaluate wing length of male moths appears to be a valid technique. The mean wing length and mean wing length $\pm$ 1 SD statistics for MMCAP and MMCPT were generally consistent with the level of defoliation in the plot (i.e., the mean wing length or mean wing length $\pm$ 1

SD values were either above or below the threshold value as predicted based on the level of defoliation in the plot). Exceptions to this result occurred in only four plots. In two of these plots (DH9 and ST9), the mean wing length and mean wing length $\pm$ 1 SD of MMCAP were consistent with the level of defoliation (> ca. 40%) in the plot, but the MMCPT statistics exceeded the threshold values. The size of the defoliated patch in which these plots were located was small and surrounded by large undefoliated areas. Apparently, large moths from outside the defoliated patch contributed significantly to total moth catch in the pheromone trap. The wing length statistics for MMCAP from plot MD9 were lower than expected and for plot CG9 MMCAP and MMCPT statistics were greater than expected. The reason the wing length statistics for plot MD9 and CG9 were not consistent with the level of defoliation is not clear, but may related to a previous years defoliation impact on tree quality and larval development. Greater than expected values for plot PR8 were obtained for the simulated pheromone trap catch. In this plot (PR8), maximum defoliation occurred while a large proportion of the larval population were early larval instars (Chapter 3). This probably increased larval mortality and reduced the number of male moths available for capture (plot PR8). The proximity of plot PR8 to areas with limited defoliation and a high larval density (these areas were defoliated the next year) also may have resulted in many larger moths being captured.

The slopes of regression lines of wing length on DD for most plots were not different from zero, suggesting the change in wing length over time is relatively constant throughout the adult period. The negative slope of most regression lines and observation of the data indicates there is a slight decrease in size from first to last emergence or capture. Moths captured in pheromone traps prior to emergence of MMCAP, primarily in mountain plots, altered the the slope of the regression line. It is likely that plots in lower elevations captured moths from higher elevations late in the adult season and beyond the time when moths from the vicinity of the trap were available for capture. However, it is impossible to detect when this occurred and the removal of these late season migrants was not possible. Pheromone traps capturing moths early were almost entirely at higher elevations. The early capture of moth in pheromone traps located at higher elevations indicates movement of moths from lower elevations where hatch and larval development occurs earlier in the year.

The pattern of moth capture in pheromone traps was generally found not to differ from the pattern of occurrence of pupae in the research plots (Chapter 3). The

pattern of occurrence of pupae tended to be related to the level of defoliation in the plot. However, based on the patterns of pheromone trap catch over time (DD), plots could not be grouped according to the level of defoliation in the plot (Chapter 3). Since the wing length of MMCAP and MMCPT in each plot were similar, the inability to detect differences in the pattern of capture of male moth in pheromone traps was probably due to slight differences in larval and pupal phenology with in populations with approximately the same level of defoliation. It is likely however, that moths from areas with different levels of defoliation may influence the pattern of male moth capture over time. In these cases, the number of moths from areas with different levels of defoliation (and presumably a different size moth) was not sufficient to alter the wing length statistics of the trap. The spatial array and size of defoliated or non-defoliated patches are certainly contributing factors to the characteristics of pheromone trap capture. The capture of large numbers of moths due to movement of moths between areas has been considered one of the major problems associated with pheromone traps. The distance from which moths were being collected was not quantified and several factors such as elevation, the array of spatially distinct populations, and differences in population dynamics make this impossible.

It must be emphasized that pheromone traps were not sampled as would traps in an operational gypsy moth management program. The three measures (mean wing length and mean wing length $\pm$ 1 SD) used in this research should be applied to trap captures that are collected as in an operational management program. The results of the simulated wing length analysis indicate that the use of threshold values would be a valid technique for evaluating pheromone traps serviced only once. Development of a relationship between egg mass density and moths per trap has been difficult. The approach to predicting egg mass density from pheromone trap catch that will be most successful is one that relies on a number of different types of information. Obviously, the number of moths captured is one type of information that could be used. Male wing length is a second type of information that could be employed. Wing length is an indicator of whether or not defoliation exceeded a critical threshold, therefore, wing length could be used as a flag to limit repeated episodes of defoliation. In addition, there is evidence to suggest that defoliation can be used as a measure of mortality factors (e.g., increased parasitism, higher incidence of nuclear polyhedrosis virus, increased overwintering mortality) that reduce larval populations in subsequent generations (Chapter 5). Depending on the size of moths, as a measure of the level of

defoliation, and the number of moths captured, areas could be prioritized for egg mass sampling. While density is not directly estimated in the prioritization process, an implicit decision is made to sample those areas where preventing high density populations is most important and these are often areas with a high egg mass density. However, there may be more effective, less costly alternatives to pheromone trapping with regard to measuring the location and extent of defoliation. Use of aerially obtained defoliation maps in a geographic information system may be an alternative.

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Table 1. Ecological data of research plots.

Plot	Elevation[1]	Percent Basal Area WO	RO	CO	HC	OT	Egg Mass Density Start	End	Peak % Defoliation	Forest Tract Size[2]	Moth Catch[3]
MD9	600 V	17	27	20	4	1	16,968	11,223	20	98	857
BL9	700 V	48	56	13	12	4	12,147	10,495	15	60	1512
ST9	690 V	16	34	0	16	0	13,423	19,425	55	6[4]	1805
WL9	650 V	50	38	28	2	1	4,546	1,276	0	38	2079
ST8	650 V	22	20	1	6	31	621	11,873	15	312	4624
DH9	1700 M	42	16	76	3	5	6,895	12,147	60	10.5	2692
CG9	2540 M	0	32	27	6	5	4,458	42,967	75	171.5	2208
PR9	2700 M	29	39	10	28	3	2,295	14,967	35		1469
GR9	2600 M	21	8	0	58	3	948	359	0		674
TG9	2400 M	31	0	91	1	8	19,816	345	100	23.9	1557
TG8	2400 M	1	43	39	5	14	132	19,816	35		1557
PR8	2700 M	0	50	5	4	14	9,211	2,295	100	1055.8	2449
GR8	2600 M	27	56	1	24	4	2,421	948	90	211.8	1593
WC8	3000 M	15	55	14	13	15	8	8,254	0		1678
LR8	1600 M	3	32	46	9	13	51658	9,398	75	15.7	2212
CG8	2540 M	0	32	27	6	5	4678	4,458	10		1852

[1] Elevation and rating of plot as to valley or mountain location.

[2] For valley plots the size (ha) of the woodlot in which the plot was located. For mountain plots the size (ha) of the defoliated area, otherwise left blank.

[3] Plot located in defoliated area of ca. 2 ha in the middle of a largely undefoliated woodlot.

[4] Represents the average of two traps for 1988.

Table 2. Statistics for male moth wing length and t-test comparison. Comparisons are between MMCAP and MMCPT full data set and the data set without data sampling dates prior to first MMCPT emergence.

Plot	Plot Type	Mean	N	SEM	Wing Lengths +1 SD	Wing Lengths -1 SD	Wing Length t test p > t
MD9	P[1]	18.81	36	0.16	19.79	17.83	
	PTF[2]	19.65	847	0.05	20.99	18.32	1.2304
	PTS[3]	19.10	20		21.29	16.91	
BL9	P	19.26	80	0.12	20.30	18.22	
	PTF	19.64	1504	0.03	20.84	18.44	0.0646
	PTS	19.20	20		20.85	17.55	
ST9	P	18.90	88	0.13	19.18	16.82	
	PTF	19.53	1791	0.03	20.94	18.13	0.5500
	PTS	19.02	20		20.81	17.23	
WL9	P	19.09	34	0.25	20.55	17.62	
	PTF	19.77	2071	0.03	21.06	18.49	0.2681
	PTR[4]	19.76	2061	0.03	21.05	18.47	0.2681
	PTS	19.55	20		21.19	17.91	
ST8	P	19.30	484	0.16	20.66	17.95	
	PTF	19.65	9241	0.01	20.92	18.38	0.8396
	PTR	19.65	9218	0.01	20.91	18.39	0.8396
	PTS	19.29	20		20.97	17.61	
DH9	P	17.89	19	0.36	19.45	16.34	
	PTF	19.89	2684	0.03	21.40	18.38	0.0401
	PTR	19.90	2656	0.03	21.40	18.4	
	PTS	18.93	20		20.87	16.99	
CG9	P	20.31	54	0.20	21.75	18.88	
	PTF	20.72	2187	0.03	21.94	19.50	0.5621
	PTR	20.74	2136	0.03	21.94	19.54	0.0402
	PTS	20.14	20		21.57	18.71	

PR9	P	20.33	27	0.24	21.60	19.06	
	PTF	20.96	1453	0.04	22.30	18.32	0.4568
	PTR	21.02	1351	0.04	22.34	19.70	0.4336
	PTS	20.47	20		22.13	18.81	
GR9	P	21.33	9	0.53	22.91	19.75	
	PTF	20.30	665	0.06	22.53	19.33	0.2280
	PTR	21.37	483	0.06	22.71	20.03	0.0409
	PTS	20.26	20		21.88	18.64	
TG9	P	17.97	39	0.23	20.71	14.34	
	PTF	19.06	1551	0.03	20.35	17.77	0.1648
	PTS	18.46	20		20.11	16.81	
TG8	P	19.88	115	0.12	21.18	18.57	
	PTF	20.86	6226	0.02	22.19	19.52	0.2702
	PTR	20.86	6119	0.02	22.17	19.55	0.2418
	PTS	20.25	20		21.99	18.51	
PR8	P	18.20	52	0.19	19.55	16.83	
	PTF	19.27	4887	0.02	20.61	17.92	0.2718
	PTR	19.27	4860	0.02	20.61	17.93	0.2718
	PTS	19.02	20		20.56	17.48	
GR8	P	18.18	61	0.16	19.40	16.96	
	PTF	19.22	3178	0.03	20.77	17.68	0.4929
	PTR	19.35	2433	0.03	20.77	17.93	0.3303
	PTS	18.67	20		20.35	16.99	
WC8	P	20.32	84	0.13	21.51	19.14	
	PT	21.09	3319	0.02	22.24	19.71	0.4038
	PTR	21.09	3236	0.02	22.45	19.73	0.3993
	PTS	20.67	20		22.23	19.11	
LR8	P	17.25	256	0.09	18.75	15.75	
	PTF	18.19	4410	0.02	19.66	16.74	0.3270
	PTS	18.37	20		20.22	16.52	
CG8	P	21.24	65	0.15	22.45	20.05	
	PTF	21.03	1831	0.03	22.35	19.70	0.8105
	PTR	21.03	1818	0.03	22.35	19.71	0.7804
	PTS	19.90	20		22.14	17.66	

[1] Wing length data form male collected as pupae (MMCAP).

[2] Pheromone traps with full data set.

[3] Simulated wing length data using MMCPT full data set.

[4] Pheromone traps with reduced data set.

Table 3. Comparison of mean wing length of adults collected as pupae and adults collected in pheromone traps.

Pupae				Pheromone Traps			
Plot	Mean	N		Plot	Mean	N	
GR9	21.33	9	a[1]	WC8	21.08	3319	a
CG8	21.24	65	a	CG8	21.03	1831	ab
PR9	20.33	27	b	PR9	20.96	1453	bc
WC8	20.32	84	b	GR9	20.93	665	dc
CG9	20.31	54	b	TG8	20.86	6226	d
TG8	19.89	115	cb	CG9	20.71	2187	e
ST8	19.30	484	cd	DH9	19.88	2684	f
BL9	19.26	80	cd	WL9	19.77	2071	g
WL9	19.09	34	d	MD9	19.65	847	h
MD9	18.81	36	ed	ST9	19.65	9241	h
PR8	18.20	52	ef	BL9	19.64	1504	h
GR8	18.18	61	ef	ST8	19.53	1791	i
ST9	18.00	88	f	PR8	19.27	4887	j
TG9	17.97	39	f	GR8	19.22	3178	j
DH9	17.89	19	f	TG9	19.06	1551	k
LR8	17.25	256	g	LR8	18.19	4410	l

[1] Plots followed by the same letter are not significantly different.

Table 4. Regression equations, r^2, and slope significance level for regression of normalized wing length on standardized time.

Plot	Plot Type	Equation	r^2	Slope Significance[1]
MD9	P[2]	y = 18.93 - 0.16*NDD[4]	0.91	0.4568
	PT[3]	y = 19.16 + 005*NDD	0.00	0.9810
BL9	P	y = 19.89 - 0.29*NDD	0.32	0.3173
	PT	y = 20.79 - 0.58*NDD	0.77	0.0505
ST9	P	y = 19.13 - 0.40*NDD	0.43	0.2282
	PT	y = 20.50 - 0.48*NDD	0.82	0.0351
WL9	P	y = 18.59 - 0.31*NDD	0.62	0.1152
	PT	y = 20.60 - 0.45*NDD	0.61	0.1188
	PT	y = 20.65 - 0.45*NDD	0.62	0.1108
ST8	P	y = 20.24 - 0.46*NDD	0.85	0.0269
	PT	y = 19.97 - 0.25*NDD	0.35	0.2912
	PT	y = 19.96 - 0.25*NDD	0.35	0.2913
DH9	P	y = 19.70 - 0.65*NDD	0.98	0.0015
	PT	y = 20.56 - 0.49*NDD	0.46	0.2097
	PT	y = 20.65 - 0.46*NDD	0.39	0.2571
CG9	P	y = 22.00 - 0.74*NDD	0.88	0.0195
	PT	y = 21.45 - 0.46*NDD	0.66	0.0961
	PT	y = 20.44 - 0.19*NDD	0.13	0.5508
PR9	P	y = 20.97 - 0.20*NDD	0.16	0.5084
	PT	y = 21.90 - 0.47*NDD	0.70	0.0479
	PT	y = 21.18 - 0.28*NDD	0.27	0.3744
GR9	P	y = 21.55 - 0.05*NDD	0.09	0.6232
	PT	y = 21.76 - 0.47*NDD	0.75	0.0581
	PT	y = 19.58 - 0.11*NDD	0.05	0.7231
TG9	P	y = 18.71 - 0.16*NDD	0.20	0.4496
	PT	y = 20.28 - 0.51*NDD	0.87	0.0204
TG8	P	y = 21.10 - 0.47*NDD	0.77	0.0510

	PT	y = 22.13 - 0.71*NDD	0.96	0.0038
	PT	y = 20.45 - 0.24*NDD	0.16	0.5750
PR8	P	y = 19.10 - 0.31*NDD	0.37	0.2755
	PT	y = 19.78 - 0.26*NDD	0.62	0.1123
	PT	y = 19.09 - 0.06*NDD	0.06	0.6907
GR8	P	y = 16.66 - 0.62*NDD	0.64	0.1045
	PT	y = 19.02 - 0.29*NDD	0.40	0.2488
WC8	P	y = 22.24 - 0.56*NDD	0.50	0.1839
	PT	y = 22.29 - 0.14*NDD	0.83	0.0304
	PT	y = 21.59 - 0.35*NDD	0.30	0.3418
LR8	P	y = 17.22 - 0.11*NDD	0.03	0.7722
	PT	y = 18.19 + 0.10*NDD	0.18	0.4655
CG8	P	y = 22.14 - 0.50*NDD	0.67	0.0905
	PT	y = 22.63 - 0.77*NDD	0.77	0.0511
	PT	y = 19.65 - 0.01*NDD	0.00	0.9755

[1] p-value

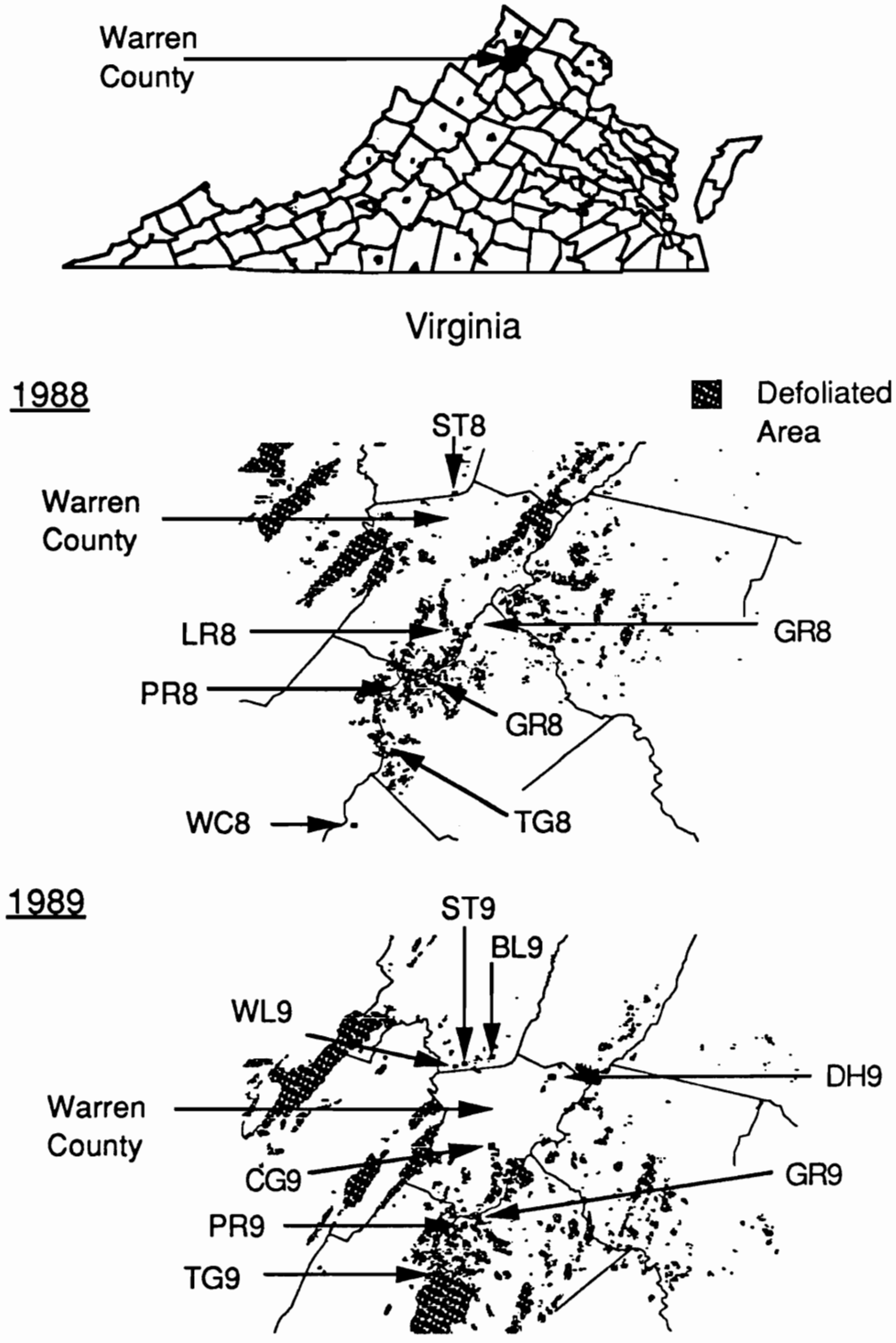

Fig. 1. Location of plots used in the study indicating location of defoliated areas in Virginia.

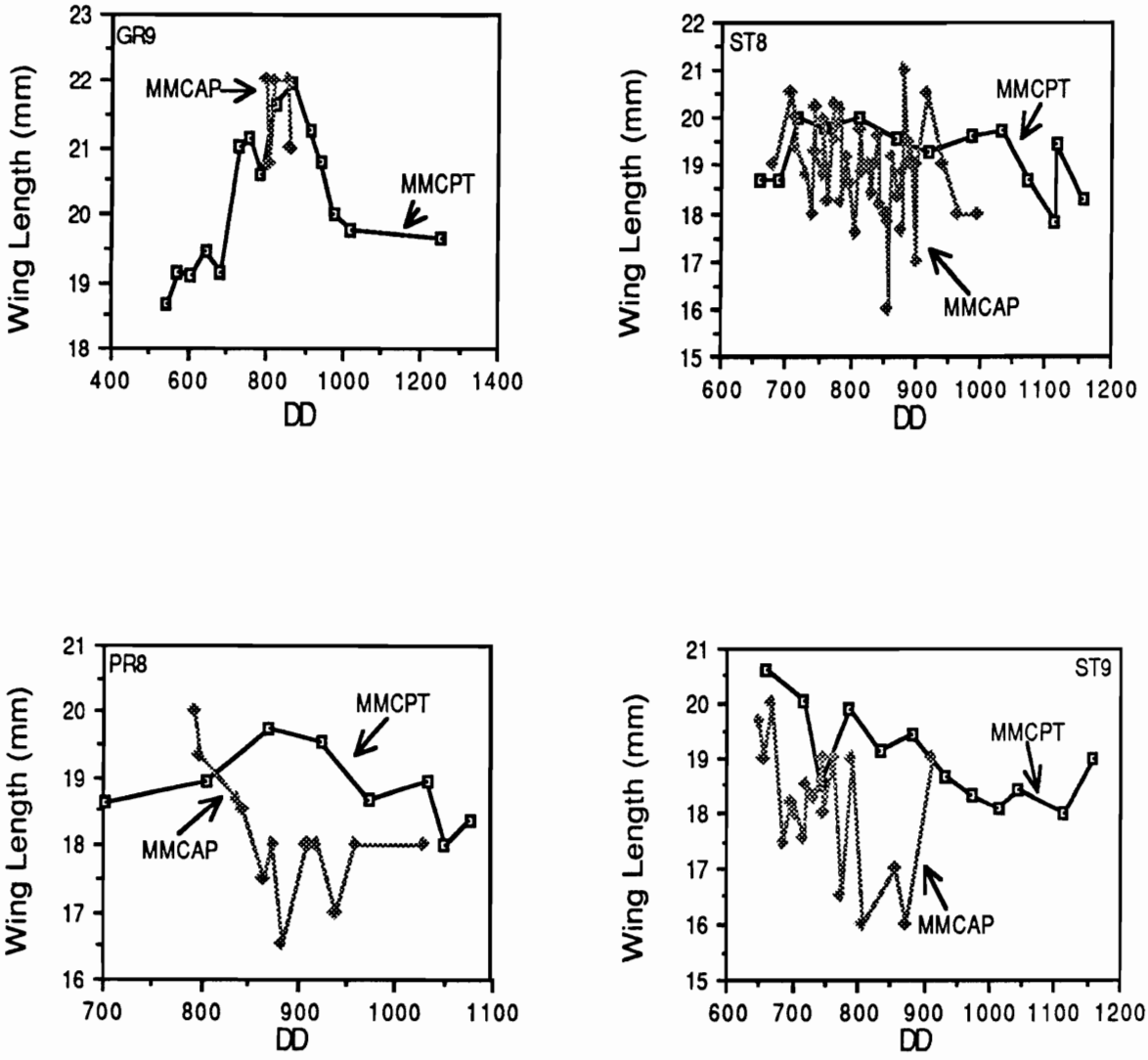

Fig. 2. Examples of changes in wing length over time for male moths collected as pupae (MMCAP) and male moths captured in pheromone traps (MMCPT).

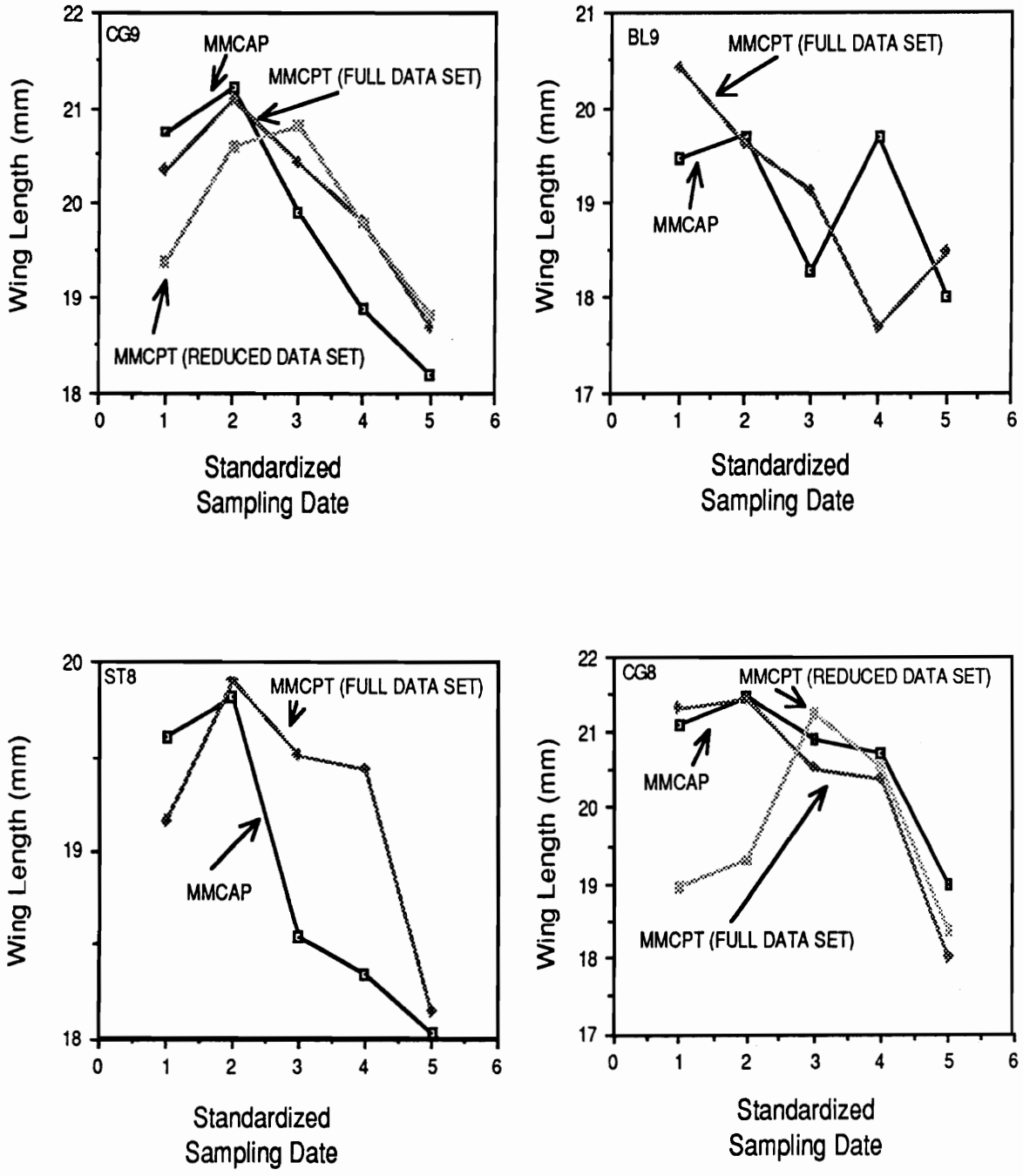

Fig. 3. Examples of grouped mean wing length on standardized time. For all figures, the open square is male moths collected as pupae (MMCAP), the diamond is male moths captured in pheromone traps (MMCPT) full data set, and the closed square is MMCPT reduced data set.

Chapter 5

Spatial and temporal dynamics of defoliation in leading edge[1] gypsy moth populations.

Egg mass density is the primary criterion used to make gypsy moth (Lepidoptera: Lymantriidae Lymantria dispar) control decisions (Ravlin et al. 1987). Egg mass sampling is a costly activity and many samples must be taken to accurately determine the egg mass density in a large forested area. An implicit relationship between egg mass density and the expectation of attaining some level of defoliation is assumed when egg mass density is used as the criterion. However, the relationship between egg mass density and defoliation is not well understood. Several studies (Campbell 1966, Campbell & Standaert 1974, Wilson & Talerico 1981, Ganser et al. 1985, Montgomery 1991) have attempted to define this relationship, but have been only moderately effective. In addition, the accuracy of extrapolating an egg mass density estimate over a large areas is not known.

Some gypsy moth integrated pest management (IPM) programs rely on data from pheromone-baited milk-carton traps (pheromone traps) and information obtained from landowners and land managers to locate egg mass density samples. While pheromone traps are widely used for detection purposes (Ravlin 1987), problems with changes in trap efficiency as traps fill (Elkinton 1987), trap saturation, and a lack of a good relationship between male moth capture and egg mass density limit their use for predictive purposes. Egg mass density surveys may not provide sufficient information to properly evaluate all gypsy moth populations[2]. This leads to situations where high density populations may go undetected until visible defoliation occurs. It is, therefore, important to increase, and then effectively interpret all sources of information to evaluate gypsy moth populations in order to efficiently allocate resources to conduct

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[1] The leading edge area is defined as the area newly invaded by gypsy moths, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time.

[2] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

egg mass surveys. Most importantly, it is desirable to increase the probability of sampling areas with high egg mass density and limiting visits to areas with a low egg mass density.

The goal of this research was to evaluate the usefulness of defoliation data as a source of information to aid in the monitoring of gypsy moth populations. The objectives of this research were to investigate the temporal and spatial dynamics of gypsy moth defoliation in leading edge areas, models for predicting defoliation, and the impact of defoliation on gypsy moth population dynamics.

Materials and Methods

Study Area. The Northern District (ND) of the Shenandoah National Park (SNP) and the State of Virginia were used as study areas in this research. The SNP is primarily oak forested and except in special cases, gypsy moth populations have not been controlled with pesticides. The SNP lies on the Blue Ridge Mountains and is bordered by the Shenandoah Valley on the west and the piedmont physiographic region of Virginia on the east. Recordable defoliation in the SNP first occurred in 1986. For the State of Virginia, recordable defoliation first occurred in 1984. Virginia has applied pesticides since the gypsy moth was found in the state. Therefore, recordable defoliation could have been greater than has been recorded and the occurrence of defoliation in time and space has probably been altered. Virginia and the SNP are on the leading edge of gypsy moth populations.

Defoliation. Defoliation data from the SNP were provided by the Natural Resources Office of the Shenandoah National Park and were available for the years 1984 to 1989. Data were derived from interpretation of 9 by 9 in. format aerial photographs. Defoliation data for Virginia were provided by the United States Forest Service and derived from a combination of high altitude optical bar photography, 9 in. by 9 format aerial photographs, and aerial sketch map surveys. The defoliation data used in this study was binary (i.e., defoliation occurred or it did not).

Analyses. Defoliation data were provided in a geographic information system (GIS) compatible format. Maps of defoliation were produced and the defoliation data analyzed using two GIS's, ARC/INFO (1989) and IDRISI (1989). ARC/INFO was used for all analyses except those requiring raster format data in which case IDRISI was used. Statistics on the total ha defoliated and mean size of defoliation patches were calculated for each year. For consecutive years, the total ha defoliated and the mean defoliation patch size of areas defoliated in both years were calculated for the SNP data

and only total ha for the Virginia defoliation data. ARC/INFO was used to calculate these statistics.

Spatial autocorrelation has been used to characterize patterns of gypsy moth defoliation by Liebhold & Elkinton (1989) and an excellent explanation of this statistical technique is given. Spatial autocorrelation analysis was performed to describe spatial variation exhibited by the response surface of the defoliation data. This analysis provides a method to quantify the degree of association a response variable (defoliation) has with spatially adjacent points (Sokal & Oden 1978, Liebhold et al. 1989). Space-time autocorrelation (Cliff & Ord 1973) was conducted to determine the degree to which defoliation in one year was spatially dependent on defoliation the previous year. Space-time autocorrelation is similar to spatial autocorrelation, except that the degree of association a response variable (defoliation) has with adjacent points is determined in both space (point to point) and time (year to year). Results of the analyses are expressed as standard normal deviates. For both the spatial and space-time autocorrelation analyses, the Rook's move of adjacency and ten distance classes were used (Figure 1). Vector coverages in ARC/INFO were converted to raster images with 250 m^2 cells for use in IDRISI in order to perform the analyses.

The spatial extent of defoliation in a year was predicted on the basis of previous year's defoliation were . Defoliation patches equal to or less than the mean patch size for each year were selected and a 1000 and 2000 m buffer was created around the patch center. The buffered data was overlaid with the next years defoliation data to determine how much defoliation was predicted in the following year. ARC/INFO was used to perform this analysis.

Estimating Defoliation. As a corollary to estimating the location and spatial extent of defoliation using defoliation maps, defoliation at single plots was estimated using three methods. Defoliation estimates were made using (1) a mechanistic model based on total larval leaf biomass consumption and available leaf biomass, (2) estimates using the equation presented in Ganser et al. (1985), and (3) using the estimates from method 2, but correcting the estimate based on the previous years defoliation. For all methods the accuracy of the defoliation estimate was determined by comparing the predicted level of defoliation with the actual level. Only two categories, greater or less than 60%, were used in the comparison.

For the mechanistic model of defoliation, available dry weight leaf biomass was calculated using the diameter at breast height (DBH) of oak species with a DBH greater

than 25 mm. Thirteen 1650 m^2 oak dominant plots were used. The total number of leaves for white, red, and chestnut oak species were computed using equations or computed from data in Kittredge (1944). Total dry weight of leaves for each plot was computed by multiplying the total number of leaves by the dry weight of a leaf (Valentine & Talerico 1983). Gypsy moth larvae are inefficient feeders, but estimates of the actual dry weight of leaves consumed by larvae are not available. Observations indicated that only 55 to 70% of a leaf may actually be consumed. This was accounted for by multiplying the total available leaf biomass by 62.5%. This value was assumed to acccurately represent total available leaf dry weight. Average available dry weight was subtracted from larval consumption. Larval consumption was based on the total consumption required for development of one larvae (Valentine & Talerico 1980) multiplied by the total number of larvae that hatch. The number of larvae at hatch was computed by multiplying egg mass density by eggs per egg mass and assuming no mortality. Eggs per mass was assigned a value of 546 depending if defoliation was below ca. 40% of a value of 262 if defoliation was above ca. 40% in the plot the previous summer. Eggs per egg mass values are taken from Chapter 2.

The second method used the equation in Ganser et al. (1985) to estimate defoliation using egg mass density data. Egg mass density data were collected as in previous studies. For the third method, the defoliation estimates were also made using the equation in Ganser et al. (1985), but were corrected for the level of defoliation the previous year at the site where the egg mass density data was collected. Observations indicated that the year following defoliation in excess ca. 40% defoliation did not occur or was limited. If defoliation the previous year exceeded ca. 40%, the estimate of defoliation (from the equation in Ganser et al. (1985)) was assigned a value of 0.0.

Plot data. Egg mass density, fecundity, defoliation and gross mortality were monitored in six plots in the SNP. The number of years each plot was monitored varied, ranging from three to five years. Egg mass density was determined after leaf fall from one or more fixed and variable - radius plots (20 basal area factor) (Wilson and Fontaine 1978). I attempted to obtain at least twenty egg masses per plot to estimate fecundity. If fecundity data was not available for a plot, fecundity was estimated from later years data if the level of defoliation was similar between years or estimated from data presented in Chapter 2. For those sites were egg masses were obtained, fecundity was determined volumetrically (Saufley 1972), calibrating for variability in egg volume

on each egg mass. The maximum level of defoliation at each plot was determined visually.

Defoliation estimates were made on a whole plot level after larval feeding had ceased and before refoliation occurred. These estimates were made subjectively by considering both the number of missing leaves (due to larval feeding) and the amount of leaf area missing from the remaining leaves. Estimates were determined to be consistent by comparing estimates made by several field workers. Sources of larval mortality were not determined in this study. However, gross mortality rates for each plot were estimated by dividing egg masses per ha at the end of the generation by the the number of eggs per ha at the beginning of the generation. All eggs were assumed to be viable and the sex ratio was assumed to be 50:50 male:female.

Modeling Changes in Population Density. To predict increases in egg mass density from year to year, egg mass density data from the field plots were fit to an exponential model:

$$\text{egg mass density}_{(t)} = \text{egg mass density}_{(t-1)} * \exp^{(b*\text{year})}$$

Egg mass density is (egg masses density + 1) and time (t) was based on years from the first sampling year (i.e., the first sampling year = year 1). The exponential model and the conceptual double equilibrium model of Campbell and Sloan (1978) predict a rapid increase in egg mass density from low to high density levels. To determine if a rapid increase in egg mass density occurred in Virginia, egg mass density data collected during 1986, 1987, 1988, and 1989 were examined to determine if this data is randomly distributed among low (< 1237), moderate (1237 to 2774) and high (> 2774) density levels (egg mass/ha). A test for randomness was conducted using X^2 analysis.

Results

Defoliation. Defoliation in the SNP (Figure 2) increased each year after defoliation was first recorded (Table 1). Visual inspection of the defoliation maps shows that the first year extensive defoliation occurred (1987), it was generally concentrated in the northern part of the ND. Defoliation generally occurred farther south in 1988 with with most defoliation occurring in the central part of the ND. In 1989 significant defoliation occurred in the southern and northern part of the ND (Figure 2). Except for 1986, the majority of the area defoliated in one year was not defoliated a second consecutive year (Table 1, Figure 2). Mean patch size within a year (range = 23.10 to 72.34 ha, mean = 38.67 ha) was greater than for patches defoliated for two consecutive years (range = 5.4 to 15.0 ha, mean = 10.2 ha) (Table 1). The size

of small and large defoliation patches are defined by the size of patches defoliated two consecutive years for small patches and by the size of defoliated patches within a year for large patches.

Spatial autocorrelation analysis indicated defoliation patches were significantly autocorrelated for all years and lag distances (Figure 3). Results of the space-time autocorrelation suggests defoliation between consecutive years are dependent on the previous year's defoliation.

Notable defoliation first occurred in Virginia in 1984 (Table 1). From 1984 to 1988 the number of ha defoliated increased dramatically, followed by a smaller increase from 1988 to 1989. Most of the defoliation occurred in the northwestern part of the state and has moved south in subsequent years. The largest patches of defoliation have been recorded on the mountains surrounding the Shenandoah valley, the Blue Ridge Mountains to the east and the Appalachians Mountains on the west. Except for two years (1984 and 1987) most of the area defoliated the previous year was not defoliated in the current year.

Predicting the spatial extent of defoliation. The percent area (ha) of 1987 defoliation predicted from 1986 defoliation was 36 and 62% (Table 2). for the 1000 and 2000 buffer (Table 2). In 1988, 43.5 and 80.3% of defoliation was predicted from 1987 defoliation and, for 1989, 63.9 and 88.2% of defoliation was predicted from 1988 defoliation. However, for all years the number of ha predicted to be defoliated greatly exceeded the area that was actually defoliated.

Estimating Defoliation. Fifty-eight plots were used in this study. Twenty of these plots had not been defoliated previously. Based on larval consumption and available leaf biomass, the model correctly predicted defoliation would be above or below the 60% threshold 75% percent of the time. Separating those plots that had been previously defoliated, the model correctly predicted 71% of the time for previously defoliated plots and 85% of the time for plots not previously defoliated. Using the equation in Ganser et al. (1985), the model predicted the level of defoliaiton correctly only 55% of the time for all plots, 44% of the time for previously defoliated plots and 75% of the time for previously undefoliated plots. Using the equation in Ganser et al. (1985), and correcting for the previous years defoliation the level of defoliation, was predicted correctly 100% of the time.

Plot data. Egg mass density tended to increase rapidly to high density levels (Figure 4). For those sites in which data on low density levels were not available, the

spatial distribution in the SNP of defoliating populations suggests that these populations also increased rapidly from low density levels. Defoliation tended be very high and most severe (ca. 100%) the year following attainment of maximum egg mass density. Defoliation greater than ca. 50% did not occur in two consecutive years in any plot. Fecundity dropped sharply in the year defoliation peaked. Gypsy moth larval mortality generally exceeded 99.5% and mean mortality was 99.8% for plots in which defoliation was greater than ca. 40% (Table 3). Larval mortality in plots with limited defoliation (> ca. 40%) ranged from 0.0% to 99.7%. Mean mortality was 81.1% excluding the three plots with 0.0% mortality and 63.2% including these plots.

Modeling Changes in Population Density. The exponential model was successfully fit ($r^2 = 0.899$) to the egg mass density data (Figure 5). The egg mass data collected over four years were found not to be randomly distributed ($\chi^2 = 69.87$, D.F. = 2, .005 > p) among low (< 1235 egg mass/ha), moderate (1236 to 2471 egg mass/ha) and high (> 2471 egg mass/ha) densities.

Discussion

Based on past research results and the complexity of the gypsy moth-forest system it is unlikely that absolute answers will be obtained to all gypsy moth research and management problems. Factors such as varying management objectives, forest species composition, ever changing population densities, geographic locations of populations, and population phases (innocuous, outbreak, or decline) severely limit our ability to derive all of the answers. Even if satisfactory research answers are obtained and would be valuable for management, the required sampling procedures may be prohibitively costly or too limited in spatial extent to be employed in a gypsy moth management program. Given this situation, the best approach to management will be to maximize the probability of deriving the best solution from available information. Ideally, this information will be easily obtained. Egg mass density, fecundity, and defoliation data are examples of this type of information. Prediction of population fluctuations would be improved if some measure of the factors that influence gypsy moth dynamics could be obtained in an easily measured piece of information, such as defoliation.

Several important attributes of defoliation are ideally suited for making management decisions. It is the most obvious expression of high density gypsy moth populations. Defoliation is easily measured at single locations and over large areas and the occurrence of defoliation has predictable properties. The spatial autocorrelation

analysis indicates defoliation patches do not occur randomly and are dependent on the location of defoliation patches in the previous year. Commonly, the first episode of spatially extensive defoliation is severe and is followed by limited defoliation in the second year. The same pattern of limited defoliation the year following severe defoliation is apparent in data presented by Campbell (1966). Subsequent episodes of defoliation tend to be less severe (Campbell & Standaert 1974) or populations decrease from high density levels (Elkinton & Liebhold 1990). Therefore, it may be most important to predict and control the first episode of severe (ca. > 60%) spatially extensive defoliation. Small defoliation patches (defined by the size of SNP patches defoliated two consecutive years) tend to precede the next year's spatially extensive defoliation patches and can be considered as patches that are one year ahead of surrounding areas in terms of defoliation dynamics. These small defoliated patches could be used to predict the location of defoliation the following years.

Predicting the location and spatial extent of defoliation based on previous year's defoliation patches was moderately successful. Over-estimating the total area that could be potentially defoliated is problematic. Using additional coverages (maps containing information) in a GIS may improve the accuracy of this method. Coverages related to the 1) physical environment (i.e., elevation), 2) biologically relevant themes such as forest species composition, 3) sampling themes, including egg mass density and numbers of moths captured in pheromone-baited traps, and 4) gypsy moth management zones would be relevant. Gypsy moth management zones would be areas where specific management objectives are set and are related to tolerable high density population impact, acceptable intervention practices, and economic, social, and political value. Overlay and interpretation of these coverages using geographic information systems, coupled with expert systems, will allow land managers to most effectively allocate sampling resources to areas where the impact of gypsy moth populations would be most detrimental. Lastly, the algorithm used for this study is circular, alteration of the algorithm to a shape (i.e., oval) that more closely reflects the north-south ridge and valley topography typical of the southern Appalachians may greatly improve the technique's accuracy.

Preventing defoliation in excess of 60% is important (Ganser et al. 1985), because defoliation in excess of this level force trees to refoliate. Refoliation requires expenditure of energy reserves, weakening a tree, and making it more susceptible to secondary mortality sources. However, defoliation often occurs over large areas of

uninhabited forest, where preventing all defoliation is either unjustifiably costly or logistically impossible. Therefore, preventing defoliation in excess of ca. 60% may be a highly reasonable management objective. For areas where political and social pressures dictate defoliation be minimized, the 60%, defoliation threshold is unrealistic.

The three methods of predicting defoliation worked moderately well for defoliation in excess of ca. 60%. The use of egg mass density alone may not be suitable for estimating defoliation in many cases: for those areas where fecundity is low, a rule can be used modify the prediction. The rule is to reduce the level of defoliation to 0.0% if defoliation exceeded ca. 40% the previous year. Since reduced fecundity is a result of defoliation in excess of ca. 40% (Chapter 2), it would also be possible to implement this rule, if only fecundity could be determined. The mechanistic model presented here is not entirely biologically reasonable since the continuous cumulative process of leaf growth and feeding by larvae are ignored. However, the results underscore the need to consider fecundity in predicting defoliation. Measuring the available leaf biomass is unrealistic for a management program, but using an average value for oak-dominant plots may be feasible. While the three methods used in this study estimated defoliation well, defoliation may be more effectively estimated using heuristic methods. A simple rule-based model was developed and based on the information presented in this paper and in Ganser et al. (1985) (Fig. 6). This rule-based model incorporates much of the information presented in the paper and provides an ability to predict defoliation over large spatial areas when used in conjunction with defoliation maps.

The study of the spatial dynamics of defoliation provides minimal insight into the mechanisms that influence population fluctuations. The plot data presented in this paper indicate changes in egg mass density and fecundity occur as a result of high defoliation. Gross mortality is also increased as a result of defoliation. The extent to which a reduction in egg mass density and fecundity, relative to other sources of mortality, are responsible for limiting defoliation the year following severe defoliation were not determined. Obviously, fewer egg masses and reduced fecundity will reduce the potential number of larvae in the next generation. But, egg mass density alone can be a poor indicator of the potential for populations that have experienced defoliation to cause defoliation, because it fails to consider changes in fecundity. Fecundity drops sharply when larvae develop in areas where defoliation exceeds ca. 40% (Chapter 2). A reduction in the total egg population at the end of a generation, however, is probably

not the sole factor suppressing populations following an episode of severe defoliation. A complex relationship between reduced larval populations and mortality factors (i.e., increased winter mortality, egg parasites, nuclear polyhedrosis virus (NPV), and host effects) ultimately govern the level of defoliation in the next year. Occurrence of NPV in populations has been identified as a primary mortality source and a major factor in the collapse of high density populations (Elkinton and Liebhold 1990, Podgwaite 1981, Campbell 1967). Occurrence of NPV also tends to be related to high density gypsy moth populations, as does defoliation.

It may be possible to assess the potential of a gypsy moth population to cause additional defoliation by examining the previous episodes of defoliation experienced by that population. Determining fecundity and the size of the defoliated area created by a population essentially accomplishes this task. Fecundity is not a quantitative indication of population density, but seems to be correlated with the potential of a gypsy moth population to cause defoliation.

Estimating or modeling increases in population density prior to defoliation has proven difficult. Complex simulation and statistical models have been developed (Valentine and Campbell 1975), but not implemented. The exponential model presented in this paper predicts a rapid increase in egg mass density. The predicted rapid increase in egg mass density from low levels was verified by the analysis of randomly collected egg mass densities. The rapid increase in population density is apparent in areas of building populations, particularly leading edge areas. Here, there is a tendency for first time defoliation to be either minimal (0 - 20%) or severe (> 60%). Assuming that a direct relationship between egg mass density and defoliation exists, severe first time defoliation would be expected based on the rapid increase in egg mass density observed in this research. The exponential model would provide a simple method to estimate egg mass density in subsequent years. However, this equation is probably appropriate for leading edge areas and areas where area-wide density is increasing. Coupled with defoliation maps and possibly pheromone trap catch data, the exponential equation could be used to help monitor gypsy moth populations. It would be particularly useful for areas where egg mass sampling is conducted sporadically.

The research presented in this paper will be valuable when considered in the context of an integrated information management system for gypsy moth management. The complexity of the gypsy moth-forest system has prevented the successful application of simulation models (i.e., Gypsy Moth Life System Model) and numerous

statistical models (Sheehan 1989) to the management of the gypsy moth. The rapidly developing field of information management using knowledge-based systems (Stone 1989) may provide a solution to the problem of integrating disparate sources of information into a usable management model for the gypsy moth. The results of the research presented in this paper could be incorporated into a knowledge-based management model for the gypsy moths.

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Table 1. Defoliation for four years in Shenandoah National Park and for four years in Virginia.

SNP

Year	ha Defoliated	Patch Size	Defoliation in Previous Year ha	%	Patch Size
1986	543.60	25.89			
1987	2,376.95	23.10	390.60	72.0	
1988	5,497.76	72.34	548.71	23.1	5.4
1989	6,003.85	33.35	2,105.55	38.2	15.0
		Virginia			
1984	98.4	32.8			
1985	2425.2	43.3	61.8	62.9	
1986	10,762.9	59.8	782.2	32.2	
1987	26,880.4	90.8	4047.8	37.6	
1988	79,847.4	89.8	15,954.4	59.3	
1989	88,567.7	98.4		25.2	

Table 2. Statistics on ha of defoliation predicted from defoliated patches from the previous years defoliation.

Year	Total ha Predicted to be Defoliated		Predicted ha Actually Defoliated in Next Year		% Actually Defoliated in Next Year - Predicted to be Defoliated	
	Buffer Size (m)					
	1000	2000	1000	2000	1000	2000
1986	3498	9408	869	1472	36.0	62.0
1987	11608	22182	3515	4847	63.9	88.2
1988	9817	23627	2610	4821	43.5	80.3

Table 3. Percent mortality in 20 plots recorded from 1985 to 1989.

Percent Mortality	
Plots with defoliation > ca. 40%	Plots with defoliation < ca. 40%
99.9	95.7
99.9	43.0
99.9	70.1
99.8	99.7
99.7	99.4
99.2	29.0
99.9	99.8
	98.0
	96.2
	90.2
	0.0
	0.0
	0.0
$\bar{x}$ = 99.8	$\bar{x}$ = 82.1 without plots with mortality of 0
	$\bar{x}$ = 63.1 with plots with mortality of 0.0 included.

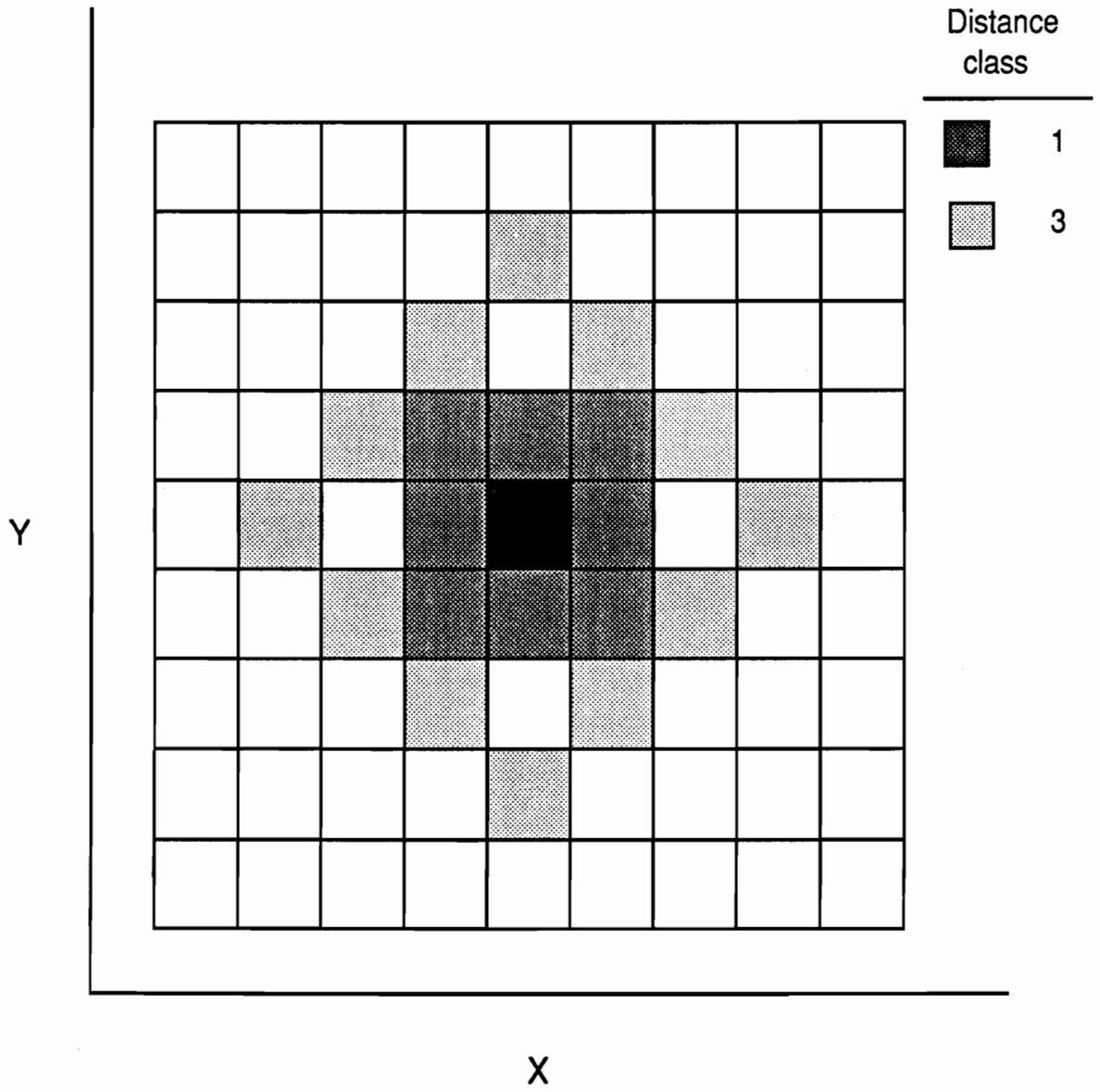

Fig. 1. Example of Rook's definition of adjacency and distance classes of 1 and 3.

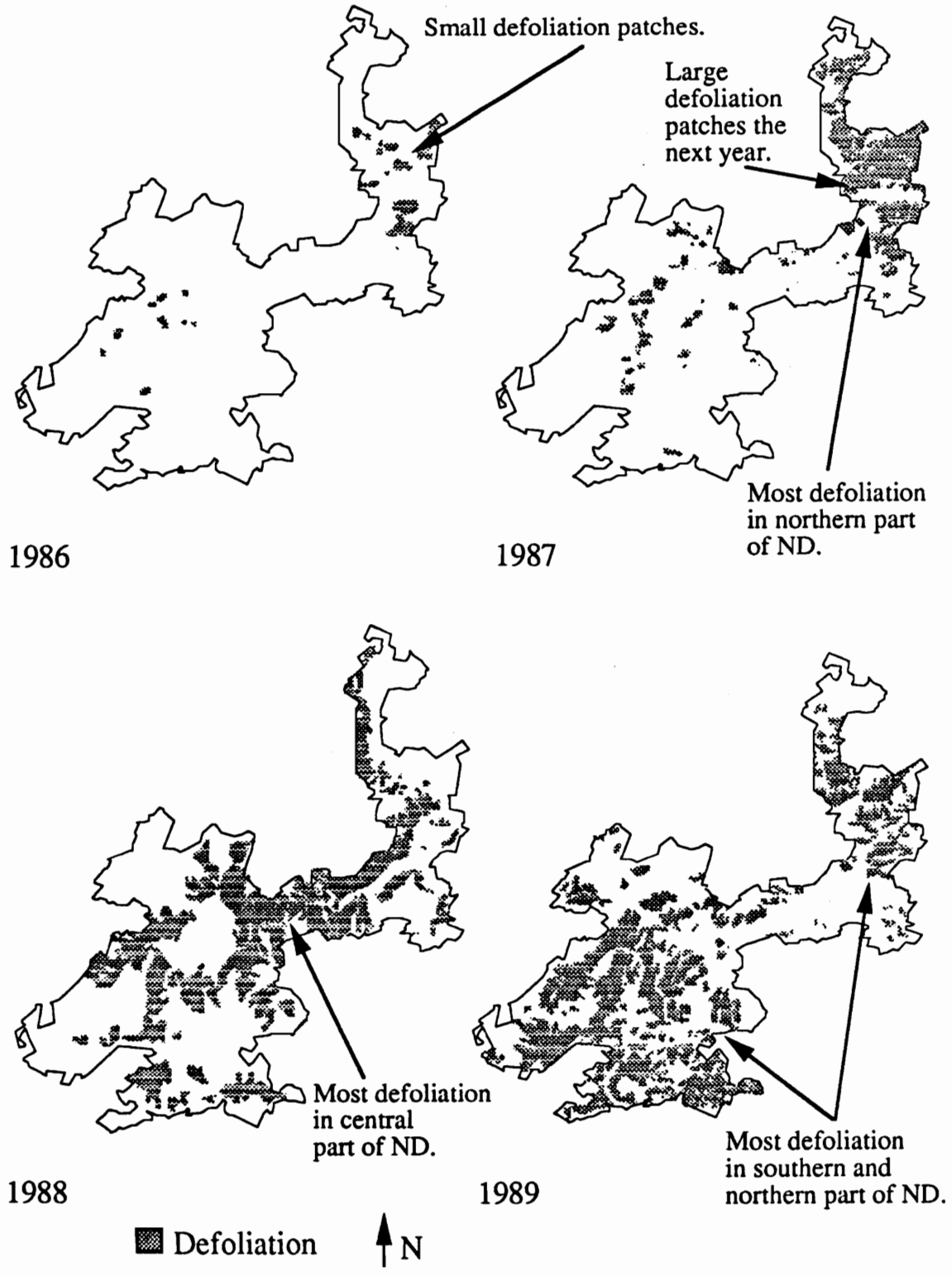

Fig. 2. Defoliation in the SNP for 1986 to 1989.

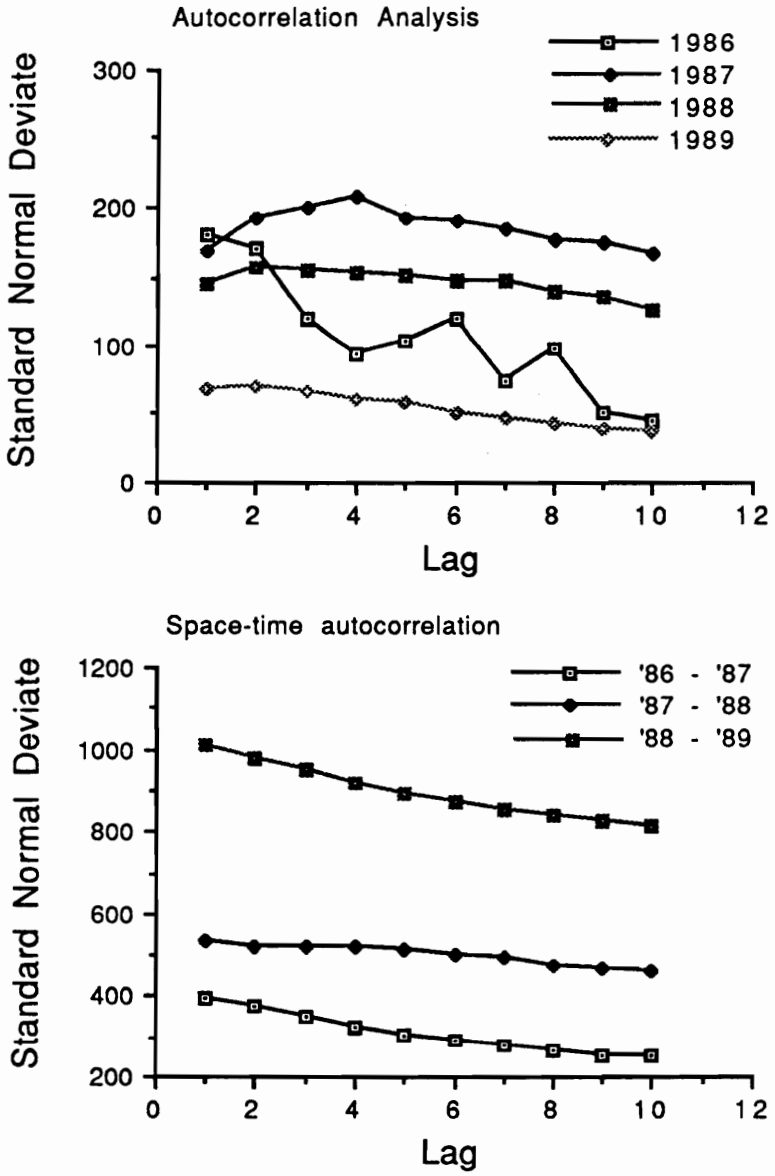

Fig. 3. Spatial and space-time autocorrelation for the Shenandoah National Park.

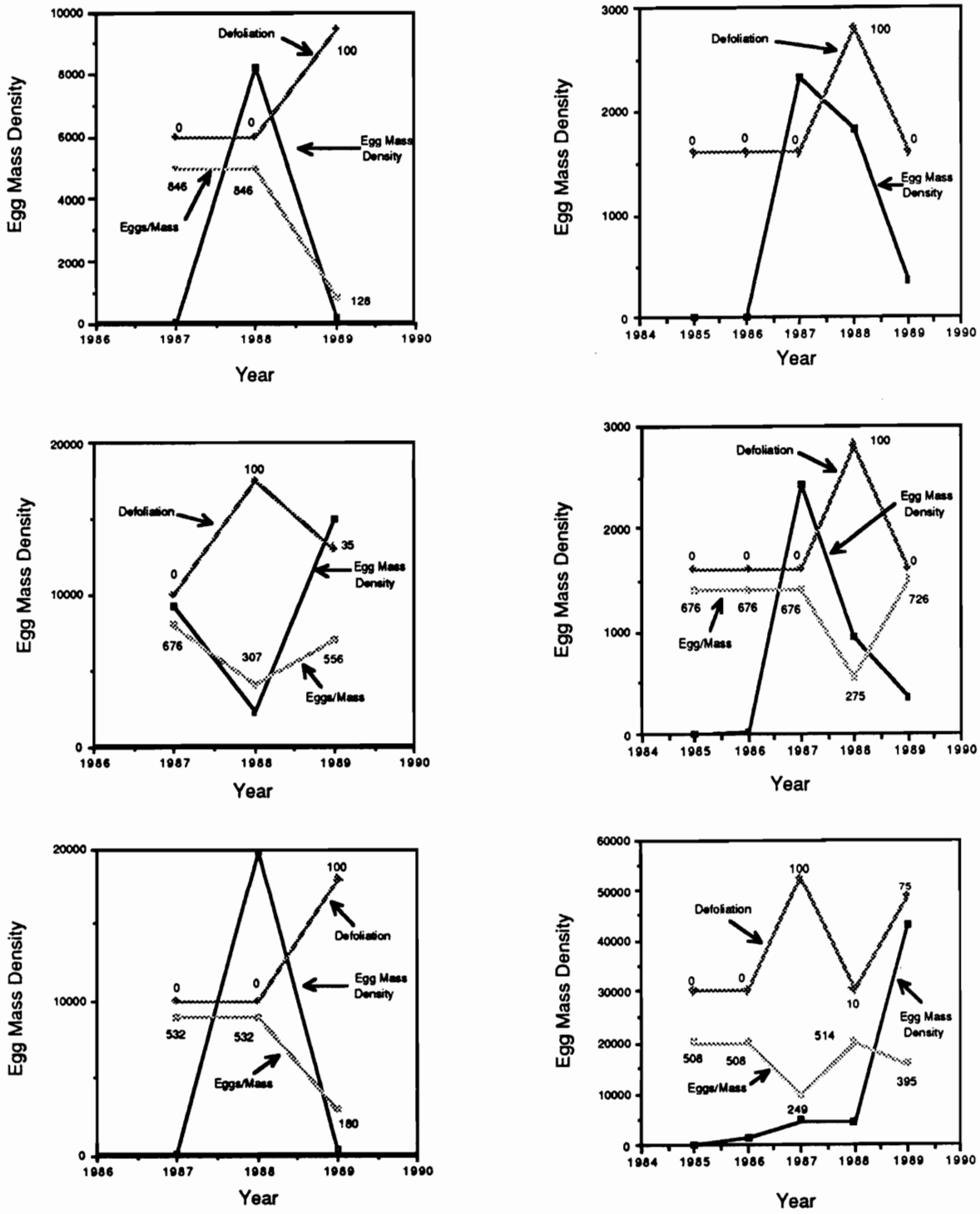

Fig. 4. Egg mass density, fecundity, and defoliation for six plots in the Shenandoah National Park.

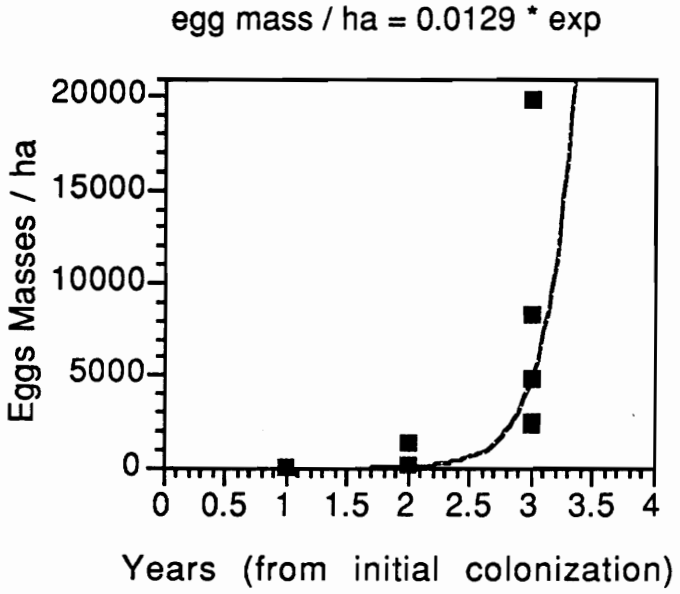

Fig. 5. Exponential fit of egg mass density data over time (years).

Rule 1: If area was defoliated last year and

eggs per mass is < 300 and

area is not a small patch (patch size range = 5.4 to 15.0 ha, mean = 10.2 ha),

then defoliation will not occur or will be minimal (0 - 20%).

Explanation: Defoliation is limited in areas experiencing defoliation the previous year. Small egg masses are an indication of the previous years defoliation. Large patch (patch size range = 23.10 to 72.34 ha, mean = 38.67 ha) dynamics limit the possibility of defoliation due to larval movement or undetected high egg mass density spots.

Rule 2: If defoliation did not occur last year and

area is not adjacent to a small defoliated patch,

then defoliation (DEF) is predicted from the equation,

$$DEF = 100[1.0 + 7.248(0.3680)^{00173x}]^{-1} \quad (1)$$

where x = egg mass density (ha plot) (from Ganser et al. 1985)

Explanation: The larvae population is not likely to be increased by adjacent high density populations.

Rule 3: If area was defoliated last year and

area is a small patch and

egg mass density in adjacent areas is high,

then defoliation will be severe and spatially extensive.

Explanation: The small patch and surrounding high egg mass density is indicative of a large patch in which defoliation will exceed defoliation predictions based on equation 1 due to the a high area-wide larval population..

Rule 4: If area was defoliated last year and

area is a small patch and

egg mass density in adjacent areas is low,

then defoliation will be high, but localized.

Explanation: Egg mass density in the patch is likely to be high, but the defoliation will not be influenced by adjacent high density populations.

Fig. 6. A rule-based heuristic model to predict defoliation.

Chapter 6

Estimating gypsy moth egg mass density using male moths captured in pheromone-baited milk-carton traps.

A basic tenant of the integrated pest management (IPM) philosophy is the detection and accurate assessment of potentially damaging pest populations[1]. For the gypsy moth (Lepidoptera: Lymantriidae lymantria dispar), two sampling techniques are commonly used to monitor populations. Egg mass density (EMASD), the primary criterion for treatment decisions, is assessed through the use of direct egg mass counts (Ravlin 1987). This is a time and labor intensive activity and provides limited spatial coverage. Pheromone-baited milk-carton traps (pheromone traps) are used to delineate gypsy moth populations, and are currently used in gypsy moth IPM programs (Ravlin 1987). An implicit assumption of the use of pheromone traps is the existence of a relationship between the number of male moths captured and EMASD. This relationship is assumed to exist for certain ecological conditions, but it has not been quantified.

Bellinger et al. (1990) attempted to develop a density index which would be independent of the number of moths captured in pheromone traps. This technique used the mean wing length of male gypsy moths captured in pheromone traps to estimate egg mass density. The validity of estimating EMASD using male wing length is questionable (Chapter 2), but the use of wing length to monitor other characteristics of gypsy moth populations may have potential. In Chapter 4, three statistics were presented which describe the wing length of pheromone trap captured male moths that could be used to assess the level of defoliation experienced by developing larvae. This research (Chapter 4) was conducted using pheromone traps monitored on a three day basis. The level of defoliation (0 to 100%) and the spatial properties of defoliated patches can have an important influence on gypsy moth population dynamics (Chapter 5). Therefore, male moth wing length could be useful as an index of the biological

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[1] Population or deme, in this case refers to the gypsy moths that occur in a distinct geographical location.

potential of gypsy moth populations to cause defoliation. Here, the biological potential of gypsy moth populations is defined as the potential for a population to exceed larval densities sufficient for moderate to severe defoliation (> ca. 40%). Defoliation is thought to be an index of the biological processes such as nuclear polhydrosis virus infection, parasitism, egg mortality, and reduced fecundity that suppress high density populations (Chapter 5).

The goal of the research presented in this paper was to develop methods to use pheromone traps to monitor gypsy moth populations. Specifically, an attempt was made to quantify the relationship between the number of moths captured in pheromone traps and egg mass density. In addition, an effort was made to determine the precision of estimating defoliation from the wing length of pheromone trap captured moths. Traps in these studies were serviced as they would be in a gypsy moth management program.

Materials and Methods

This research was conducted in northwest Virginia and northeastern West Virginia. These areas are in the leading edge[2] area of gypsy moth populations. Populations were in all population phases (innocuous, release, outbreak, and decline). For all studies, standard USDA milk-carton type pheromone-baited traps were used.

Moths per trap - egg mass density. Data for this study were collected over a four year period from 1986 to 1989. Following cessation of male moth flight, traps were collected and all moths counted. After leaf fall, EMASD estimates were obtained from fixed and variable - radius plots (20 basal area factor) (Wilson & Fontaine 1978) located in the vicinity of each trap.

Regression analysis and a moth catch-EMASD contingency table were used to examine the relationship between male moths captured in pheromone traps and EMASD. The objective of constructing the moth catch-EMASD contingency tables was to determine the probability of finding a given level of EMASD in the vicinity of a pheromone trap given the capture of a specific number of moths. This was accomplished by categorizing moths captured and EMASD into broad categories (i.e., 0 to 500 moths or EMASD). For each moth and EMASD category the frequency and

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[2] The leading edge area is defined as the area newly invaded by gypsy moths, but contiguous with generally infested areas to the north and east. Leading edge areas are experiencing gypsy moth related defoliation for the first time.

percentage of plots in each category were determined. The moth categories used in this analysis consisted of 0 - 250, 251 - 500, 501 - 1000, and 1001 or more moths. EMASD categories were 0 - 1235, 1236 - 2471, and 2472 or more egg masses/ha. The regression analysis and moth catch-EMASD contingency table were conducted using SAS, PROC GLM and PROC FREQ respectively (SAS Institute, Inc., 1986).

Validation of the wing length statistics to estimate defoliation. A total of fourteen grids of pheromone traps consisting of 9 to 16 traps were set in two years (1988 and 1989). Traps were located ca. 1 k apart. Following cessation of male moth flight, traps were collected and all moths counted. The left forewing length of 20 male moths was measured using a standard mm rule. The level of defoliation (defoliated or not-defoliated) in the immediate vicinity of each pheromone trap (referred to as the patch) was determined by examination of defoliation maps produced using a geographic information system (ARC/INFO 4.1, 1989). Defoliation maps for Virginia and West Virginia were provided by the United States Forest Service and derived from a combination of high altitude optical bar photography, 9 by 9 format aerial photographs and aerial sketch map surveys. The actual level of defoliation (0 to 100%) in patches recorded as defoliated was impossible to assess from the defoliation maps. However, in the study area, defoliation was often either severe (ca. > 70%) or barely noticeable (ca. 0 to 20%). After leaf fall, EMASD estimates were obtained from fixed and variable - radius plots (20 basal area factor) (Wilson & Fontaine 1978) located in the vicinity of a trap. Not all trap locations were sampled for egg masses.

A wing length index for each trap was developed using the mean wing length, the mean wing length + 1 standard deviation, and the mean wing length - 1 standard deviation (mean wing length $\pm$ 1 SD). This index was used to rate the moths in the trap as either large or small moths. This was accomplished by individually comparing each of the three statistics to expected wing length values. Expected values were assumed to be indications of the level of defoliation (either > or < ca. 40%) experienced by larvae and reflected in the wing length of male moths. The expected values were based on data from Chapter 2 and are same as used in Chapter 4. The expected values were for the mean, 19.5 mm; for the mean - 1 SD, 18.0 mm, and for the mean + 1 SD, 21.0 mm. If the mean wing length, mean wing length + 1 SD, or mean wing length - 1 SD from the trap equaled or exceeded the expected value, the index was incriminated by one, otherwise the index was not incriminated. The index could therefore, range from

0 to 3. Moths from traps with an index equal to or greater than 2 were rated as large, moths from traps with an index below 2 were rated as small moths.

The analysis consisted of comparing the wing length rating (large or small) with the level of defoliation (defoliated or not defoliated) in the patch where the pheromone trap was located. This was done to determine if the rating was indicative of the level of defoliation in the patch. Also, sites where EMASD was available, data were categorized on the basis of the wing length rating (large or small) and by EMASD to determine if a broad relationship between wing length and EMASD existed. EMASD was categorized into two levels, greater or less than 2471 egg masses/ha. This EMASD was selected because areas with densities greater than 2471 egg masses/ha are often considered for control measures. Additionally, this EMASD is slightly greater than the EMASD which will result in defoliation exceeding ca. 40% (Ganser et al. 1985). Lastly, as EMASD increases above 2471 egg masses/ha a point (ca. 60% defoliation) is reached above which trees refoliate. This can reduce energy reserves and increase tree mortality.

Results

Moths per trap - egg mass density. Pheromone traps and EMASD determined at 391 sites over the four year period. Regression analysis indicated a significant relationship exists between moths per trap and egg mass density ($p < 0.0001$), but moths per trap explained little of the variation in egg mass density ($r^2 = 0.3023$). The regression equation was: EMASD = -1241.99 + 4.61*(number of moths captured). The moth catch-EMASD contingency table (Table 1) indicates there is a broad relationship between moths captured and EMASD. Generally, the more moths captured the greater the probability of finding a higher EMASD. For example, if a trap captures less than 250 moths the probability of finding a EMASD of 0 to 1235 is 0.9688, if more than 1000 moths are captured the probability of finding an EMASD of greater than 2472 is 0.6029.

Validation of the wing length statistics to estimate defoliation. The total number of traps used in this study was 179; 91 traps were set in 1988 and 88 traps in 1989. A majority of the traps (86%) were located in patches that were not defoliated. Area-wide defoliation in the vicinity of the pheromone traps tended to be greater in 1988, however, total defoliation in Virginia (1988: 79,847 ha; 1989: 88,567 ha) and West Virginia 1988: 29,095 ha; 1989: 35,050 ha) was greater in 1989. Considerable differences exist in the total number of moths captured in each year of the

study. The mean number of moths captured for all categories in 1988 exceeded the mean number of moths captured in 1989 (Table 2). Small moths were captured in many traps that were located in non-defoliated patches (58% of traps in 1988, 35% traps in 1989, and 45% of traps for both years combined for traps located in non-defoliated areas). Small moths were captured primarily in traps that were located in defoliated patches (91% of traps in 1988, 100% of traps in 1989, and 92% of traps for both years combined for traps located in defoliated patches).

For sites in which an EMASD was available, the number of moths captured was greater in sites with small moths which had a high EMASD than sites with small moths which had a low EMASD (Table 3). The number of traps that had small moths that were actually in defoliated patches was low (i.e. 4 of 12 in 1988 for high EMASD; 0 of 20 in 1989 for low EMASD). However, of those traps with small moths and not in defoliated patches, several were within 1 k of defoliated patches. For 1988, traps that captured large moths and had a high EMASD had a total catch greater than that of sites with large moths and a low EMASD. This trend was reversed in 1989.

Discussion

The focus of this research was to examine information obtainable from moths captured in pheromone traps that could be used to monitor gypsy moth populations. The goal was to develop an accurate and cost effective means to estimate egg mass density, or at least to aid in prioritizing areas that might require egg mass sampling. The results of this research indicate it is possible to determine the probability of finding a given EMASD in the vicinity of a pheromone trap, given the capture of a specific number of moths in that trap. These probabilities tended to change in a predictable manner with the capture of more moths resulting a higher probability of finding a greater EMASD. Therefore, within large categories, the numbers of moths captured in a trap appears to be related to EMASD.

The best use of this technique will be to evaluate an area for potential egg mass sampling on the basis of finding some level of EMASD given the capture of a specific umber of moths. Gypsy moth managers can evaluate the risk of failing to detect high EMASDs with the need to optimally allocate sampling resources. The availability of additional information concerning the areas under consideration would aid in the decision making process. Land-use data, economic value, probability of tree mortality, and the social-political value of the land could also be considered. This type of data, in conjunction with the probability of finding a given EMASD, could be used to prioritize

areas on the basis of greatest risk (i.e., biological, economic, or social-political) due to the presence of gypsy moths. Areas with the highest priority could then be directly sampled for egg masses.

A linear relationship exists between the number of moths captured and EMASD. This is not unexpected given the results of the moth catch-EMASD contingency tables. However, the precision of the linear regression model is not great. The reasons for the inability to estimate EMASD from moths captured using linear regression are complex. Trap capacity, changes in trap efficiency (Elkinton 1987), and trap saturation (Bellinger et al. 1990) are three reasons, but more likely the underlying cause is related to the location of a trap relative to areas with varying larval densities and the movement of male moths. The number of adults produced in an area, and the location of the different populations relative to the pheromone traps, influences the potential number of moths that can be captured. In addition, widely varying topographical and ecological conditions associated with individual traps limits ones ability to identify the factors that influence male moth catch. A direct result of the heterogeneity of these site-specific conditions is that the relationship between moths captured and EMASD is obscured. The moth catch-EMASD frequency analysis approach reduces the heterogeneity associated with the site-specific variables by grouping the number of moths captured and EMASD.

Wing length is not a reliable indicator of whether or not defoliation occurred. While traps located in defoliated patches yielded, in most cases, small moths, a large number of trap sites in non-defoliated areas also produced small moths. Failure to detect and record patches on defoliation maps with defoliation in excess of ca. 40% may account for the capture of small moths in non-defoliated patches. However, field observations indicate this did not occur. The capture of small moths in areas with a low EMASD supports the validity of the field observations. Small moths are the result of defoliation in excess of ca. 40% (Chapter 2) and defoliation is a direct consequence of high larval densities. High larval densities generally lead to high EMASD. The capture of small moths in areas of low EMASD could be a result of a population that has crashed, but knowledge of the trap locations suggests this only occurred once.

A second possibility is that the capture of small moths in non-defoliated areas is the result of movement of small moths from defoliated areas. Capture of a low number of large moths in the vicinity of the trap would allow relatively few small migrant moths to influence the wing length statistics determined for the trap. The low EMASD in the

vicinity of the trap supports the contention that there were few larvae and subsequently few large adults available to be captured. Because small moths are the result of defoliation, which generally occurs at high larval densities, there should be a large number of moths captured in the trap. This however, did not occur in non-defoliated trap sites with small moths relative to defoliated trap sites. This re-enforces the hypothesis that small moths in non-defoliated areas are migrant moths. The exception to this may be non-defoliated sites that are less than 1 k to defoliated patches.

The converse situation, capture of large moths in defoliated areas is an anomaly. This should only occur in small defoliated patches surrounded by non-defoliated areas with a relatively high EMASD (Chapter 4). These results suggest male wing length could be used to qualify or remove traps from subsequent analysis. Primarily, traps with small moths in non-defoliated areas are not likely to accurately represent the EMASD in the vicinity of the trap. These traps may not warrant further consideration or should be carefully evaluated with regard to location relative to defoliated areas. The dynamics of defoliated patches is such that it also may not be necessary to consider traps that were in defoliated areas (Chapter 5). Traps located in small defoliated patches or near large defoliated patches, regardless of the size of moths, probably should be considered in deciding where to conduct egg mass sampling. Patch size of small (patch size range = 5.4 to 15.0 ha, mean = 10.2 ha) and large (patch size range = 23.10 to 72.34 ha, mean = 38.67 ha) defoliation patches were determined from the study of defoliation in the Shenandoah National Park, Virginia (Chapter 5).

An algorithm to interpret pheromone traps is presented in Figure 1. Trap interpretation involves the use of male wing length, the number of moths captured, and defoliation maps. The decision making process can be divided in two steps. The first step focuses on deciding which traps will be selected for inclusion in subsequent analyses. This is accomplished by examining male wing length and the defoliation maps. Traps with small moths which are located in non-defoliated areas are eliminated from consideration. The capture of small moths in non-defoliated patches indicates the moths are migrants and that the actual EMASD may be low. These trap sites may be considered for sampling after areas with a greater probability of having a high EMASD are sampled. The exception would be traps capturing small moths, but located in sites that are within 1 k of a defoliated patch. Traps with small moths in defoliated areas can also be eliminated if the defoliated patch is extensive. Traps located in small defoliated patches, regardless of moths size, are included in the next analysis. The remaining

traps are those with large moths located in non-defoliated patches. These traps are included in the next analysis. The number of moths captured in these traps is then evaluated using Table 1 or 2 to obtain the probability of finding a given EMASD. Combined with other information, as previously mentioned, an area can be prioritized for egg mass sampling.

This approach to estimating EMASD is based on the probability of detecting some EMASD given characteristics of pheromone trap capture. The probabilities were derived from the results of relatively limited pheromone trapping and EMASD determination study. The addition of more data will certainly improve the reliability of this method and encompass a wider range of gypsy moth related ecological conditions. Secondly, the moths per trap-EMASD relationship was not developed using traps that had been qualified using wing length. This should be done to improve the predictive power of this approach. Lastly, this technique is designed for areas where defoliation of ca. < 60% can be tolerated which often occurs at the 2471 egg masses/ha density level. Areas where minimal defoliation or the presence of any larvae is not acceptable may be more effectively monitored in other ways than pheromone traps. Economic considerations are often secondary to social and political considerations in these areas and the chance of failure to detect high density populations is not acceptable. Direct egg mass counts are probably more appropriate in these situations.

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Table 1. Probability (P) of finding an EMASD (egg masses/ha) given the capture of some number of moths following into four categories and the number of traps (N) in each category.

	Moths/Trap							
	0 - 250		250 - 500		500 - 1000		1000 +	
EMASD	P	N	P	N	P	N	P	N
0 - 1235	0.9688	93	0.8200	82	0.7165	91	0.2059	14
1236 - 2471	0.0104	1	0.0500	5	0.0945	12	0.1912	13
2472 +	0.0208	2	0.1300	13	0.1890	24	0.6029	41

Table 2. Number of traps, percent of total traps in defoliation category, and mean number ($\bar{x}$) of moths captured in defoliated and non-defoliated patches.

	Large moths			Small moths		
Year	Number of traps	Percent	$\bar{x}$	Number of traps	Percent	$\bar{x}$
			Not-defoliated Areas			
1988	29	42	1119.9	40	58	1211.5
1989	56	65	535.0	30	35	419.6
Both	85	55	700.5	70	45	785.2
			Defoliated Areas			
1988	2	9	1204.5	20	91	1340.4
1989	0	0	0.0	2	100	663.0
Both	2	8	1204.5	24	92	1278.8

Table 3. Number of traps grouped by male moth wing length rating, EMASD (egg masses/ha), and year.

	Small Moths					Large Moths	
	# traps	ND[1]	D[2]	C[3]	# moths	# traps	# moths
				1988			
Low EMASD	3	1	2	0	1313	2	1566
High EMASD	12	4	8	3	1738	3	1208
				1989			
Low EMASD	20	0	20	4	340	38	501
High EMASD	7	2	5	3	591	13	680
				1988 and 1989			
Low EMASD	23	1	22	4	467	40	554
High EMASD	19	6	13	6	1316	16	779

[1] Not defoliated

[2] Defoliated

[3] Within 1 K of a defoliated area.

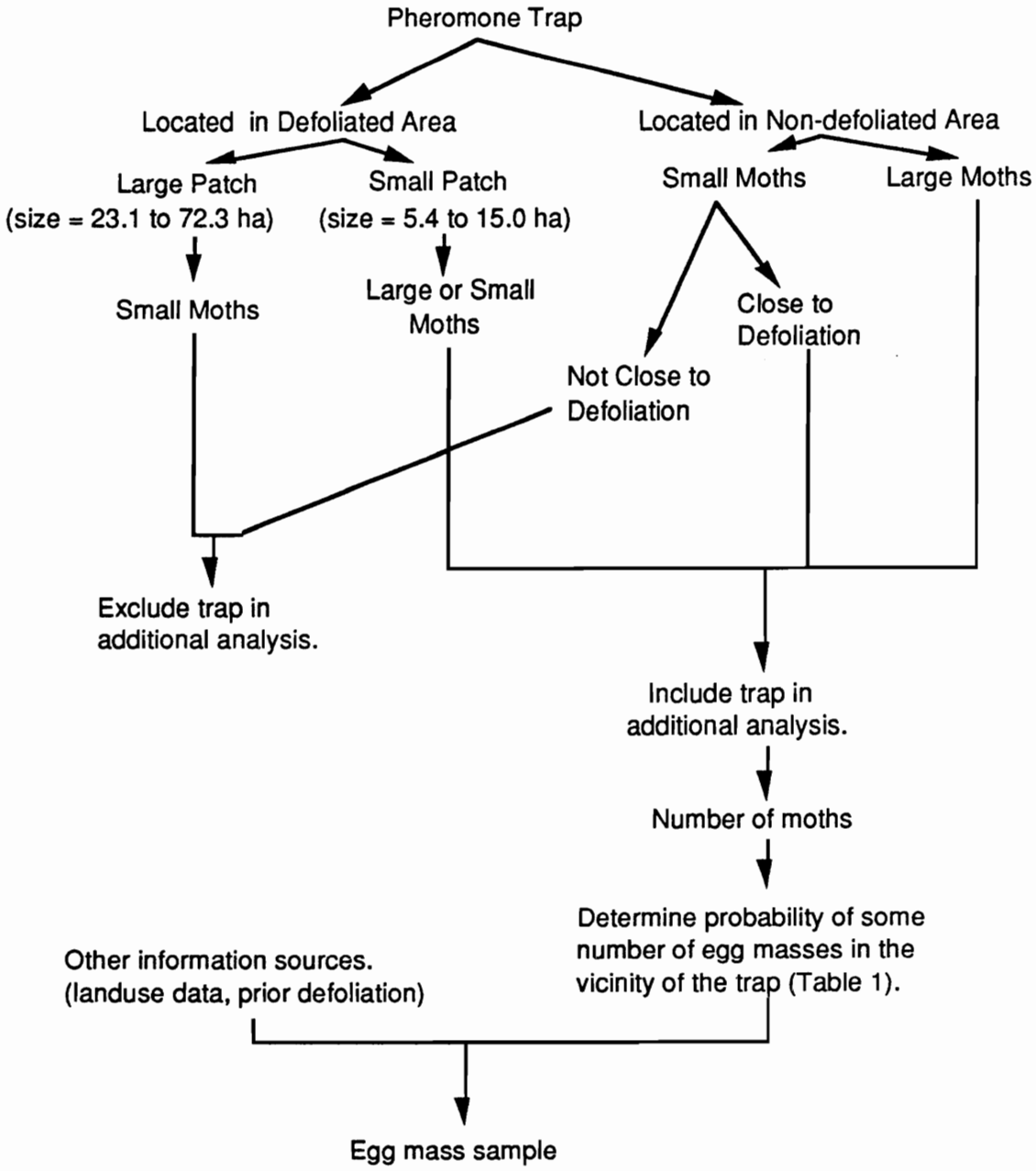


Fig. 1. Flow chart to prioritize areas for egg mass sampling based on pheromone trap catch.

Chapter 7

Summary

The goal of this research was to improve the understanding of the dynamics of male gypsy moth-pheromone trap interactions and the ecological factors that influence the capture of male moths in pheromone traps. The general approach of this research focused on the impact of defoliation on the capture of male moths in pheromone traps. Pheromone traps are tools to monitor gypsy moth (Lepidoptera:Lymantriidae Lymantria dispar) populations, preferably as a means to estimate population density. By knowing population density, the potential for defoliation can be assessed and, if necessary, the larval population can be reduced to acceptable levels. The capture of moths in pheromone traps is influenced by many interrelated factors including gypsy moth population dynamics, defoliation, and population density (Figure 1). The same factors that influence trap catch are themselves interrelated. Defoliation is primarily a function of the number of larvae and available leaf biomass. Defoliation alters foliage availability and foliage quality (Schultz & Baldwin 1982). Defoliation and the larval mortality factors associated with it can impact larval density and subsequently, egg mass density and population dynamics in the next generation. Defoliation can also influence the characteristics of pheromone trap catch. The impact on the larval population occurs through both a reduction in the number of larvae and the size of the resulting adults. Smaller female moths are less fecund and produce egg masses with fewer eggs. Male moths are smaller at higher levels of defoliation. With regard to pheromone traps, larval density is a major factor influencing the number of moths captured.

Density-dependent mortality factors, of which nuclear polyhedrosis virus (NPV) may be one of the most important, are expressed at high population densities and can have a significant influence on gypsy moth population dynamics. Higher rates of mortality reduce the number of egg masses laid and NPV contamination of the environment may lead to increased larval mortality in the following year. In addition, mortality of over-wintering eggs, higher rates of egg parasitism, and reduced fecundity due to high levels of defoliation may also contribute to suppressing the following year's larval populations. This can lead to over-estimation of expected defoliation expected

based on egg mass density. Therefore, it is difficult to study any aspect of pheromone trap

dynamics without placing a substantial emphasis on gypsy moth population dynamics. The following discussion focuses on the major findings of this research project as they relate to pheromone traps and dynamics of the gypsy moth populations.

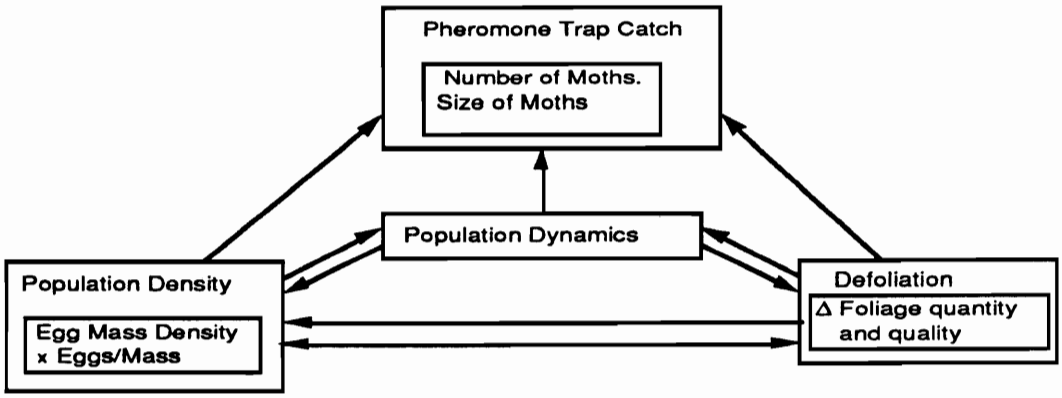
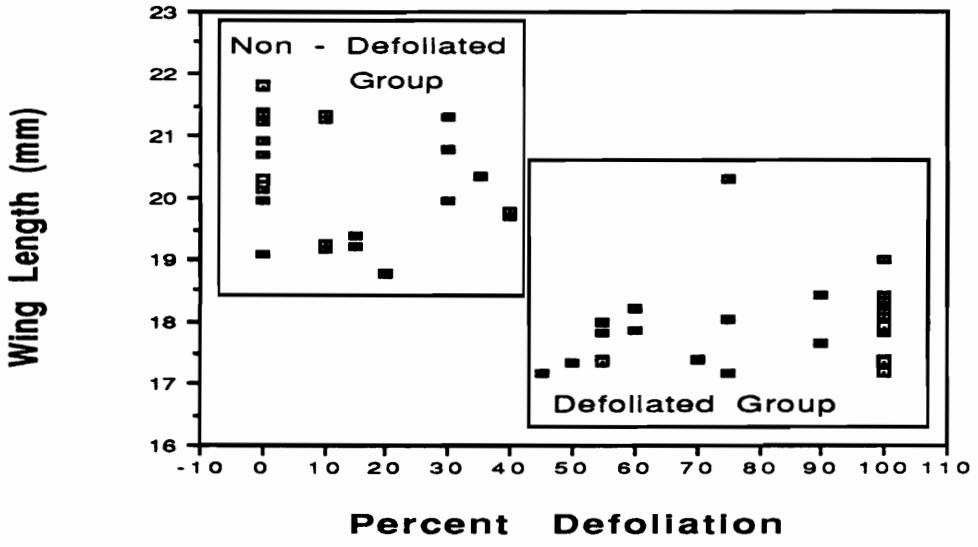


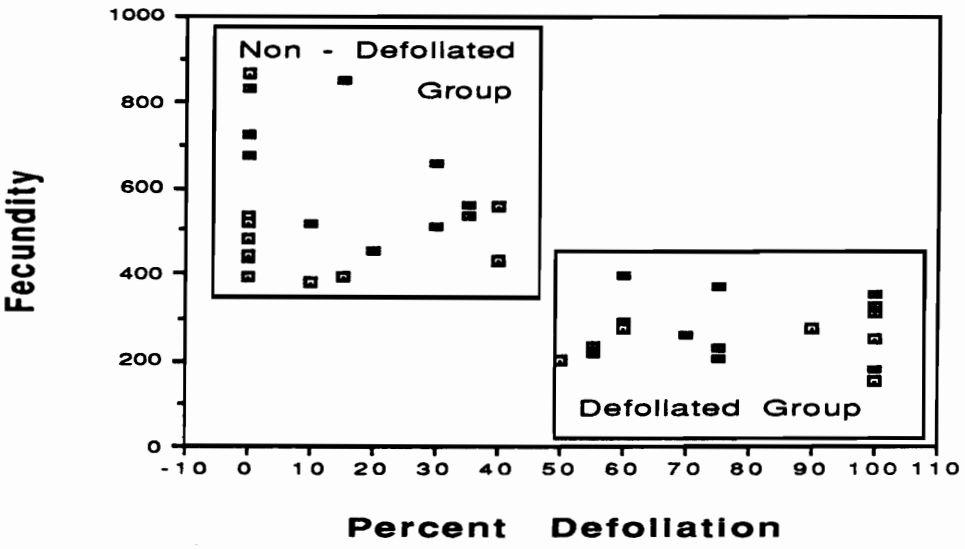
Fig. 1. The relationship between pheromone trap catch, populations dynamics, population density, and defoliation.

Research on pheromone traps. The objective of the first study (Chapter 2) was to investigate the influence of defoliation on gypsy moth fecundity and male moth wing length. The results of this study indicate that at higher levels of defoliation male wing length is smaller and fecundity reduced. But the form of the relationship is not linear. Fecundity and male wing length appear to be substantially influenced by defoliation only if defoliation exceeds ca. 40%. The result is either large or small male moths and high or low fecundity (Chapter 2) (Figure 2). In this study, it was not possible to validate the linear relationship found by Bellinger et al. (1990) between egg mass density and male wing length. In the second study (Chapter 3), differences were detected between plots for larval and pupal development that are related to the level of defoliation in a plot. These differences were not apparent in the number of male moths captured over time in pheromone traps (Chapter 3). However, the wing length of male moths captured in these pheromone traps was, in most cases, similar to the wing length of males collected as pupae in the vicinity of traps (Chapter 5). The inability to detect differences between plots for the number of moths captured through time is probably due to slight differences in larval and pupal phenology among populations with approximately the same level of defoliation (either > ca. 40% or < ca. 40%). It is

probable that moths from patches with different levels of defoliation may have influenced the pattern of male moth capture over time. In these cases though, the number of moths from patches with different levels of defoliation (and presumably a different size moth) was not sufficient to alter the wing length statistics (mean wing



A.



B.

Fig. 2. A) Wing length and B) fecundity for plots at defoliation levels from 0 to 100% indicating the threshold response to defoliation.

length and mean length ± 1 standard deviation). Only for plots located in small defoliated patches which were surrounded by a large non-defoliated patch were the wing length statistics of moths from pheromone traps not consistent with the level of defoliation. This strongly suggests that the spatial array and size of defoliated or non-defoliated patches are important factors influencing the capture of male moths in pheromone traps. Patch size of small (patch size range = 5.4 to 15.0 ha, mean = 10.2 ha) and large (patch size range = 23.10 to 72.34 ha, mean = 38.67 ha) defoliation patches were determined from the study of defoliation in the Shenandoah National Park, Virginia (Chapter 5).

As a means to estimate the level of defoliation (either < ca. 40% or > ca. 40%) using male moth wing length, the use of threshold values was investigated. Threshold values are values to which wing length statistics (mean wing length and mean wing length ± 1 standard deviation) derived from pheromone trap captured moths can be compared. Depending on the level of defoliation in the vicinity of the pheromone trap, wing length statistics of male moths were expected to be either greater or less than the threshold values. The use of threshold values as a criterion to evaluate wing length statistics was generally successful and appeared to be a valid technique. The level of defoliation in study plots was in most cases correctly estimated using threshold values to evaluate wing length statistics (Chapter 4).

In a latter study (Chapter 6) using threshold values to evaluate the wing length of male moths, it was found that wing length is apparently not a reliable indicator of whether or not defoliation occurred (Chapter 6). Traps located in defoliated patches yielded, in most cases, small moths, but a large number of traps in non-defoliated patches also produced small moths. However, the capture of small moths in non-defoliated areas may be the result of movement of small moths (migrant moths) from defoliated areas. The discrepancy between the results (the ability to estimate the level of defoliation using male moths wing length statistics) obtained in Chapter 4 and those in Chapter 6 can probably be attributed primarily related to differences between ecological conditions existing in and around the study plots. The plots selected for the research reported in Chapter 4 did not include one that had a relatively low egg mass density at both the beginning and end of the gypsy moth season and was not in close proximity to high density populations. Many of the the pheromone traps used in the research reported in Chapter 6 that captured small moths were located in large, undefoliated patches that had a relatively low egg mass density. Only one of the plots (GR9) used in

the research reported on in Chapter 4 had a relatively low egg mass density at the end of the gypsy moth season and was in the middle of a patch in which the density was apparently low. It was in this plot (GR9) that capture of moths over time in pheromone traps was noticeably different from all but one other plot (Chapter 3). The results of the among plot comparisons for moth capture over time in pheromone traps suggests that migrant moths may have significantly altered the catch pattern of moths in plot GR9 (Chapter 3, Chapter 4).

While wing length may not necessarily be indicative of defoliation in the vicinity of the trap, the results suggested male wing length could be used to qualify or remove traps from subsequent analysis. A method to interpret pheromone traps was developed using the wing length information (Figure 3). This method incorporates wing length information, the number of moths captured, and data from defoliation maps. Wing length data and defoliation coverages are used to determine if a trap should be included in the final analysis for estimating the probability of finding a specified egg mass density in the vicinity of a pheromone trap. The number of moths captured is then used to estimate this probability. This approach to estimating the probability of finding some egg mass density given the capture of a specific number of moths was found to be moderately successful (Chapter 6). In conjunction with other types of information (i.e., land-use data, economic value, or probability of tree mortality) the probability of finding an egg mass density could be used to prioritize areas on the basis of greatest risk (i.e., biological, economic, or social-political). Areas with the highest priority could then be directly sampled for egg masses.

This monitoring and assessment approach was designed for areas where defoliation of ca. 60% can be tolerated. Areas where minimal defoliation or the presence of any larvae is not acceptable, often in urban areas, may be more effectively monitored in other ways than pheromone traps. Economic considerations are often secondary to social and political considerations in these areas and the chance of failure to detect high density populations is not acceptable. Direct egg mass counting is probably more appropriate in these situations.

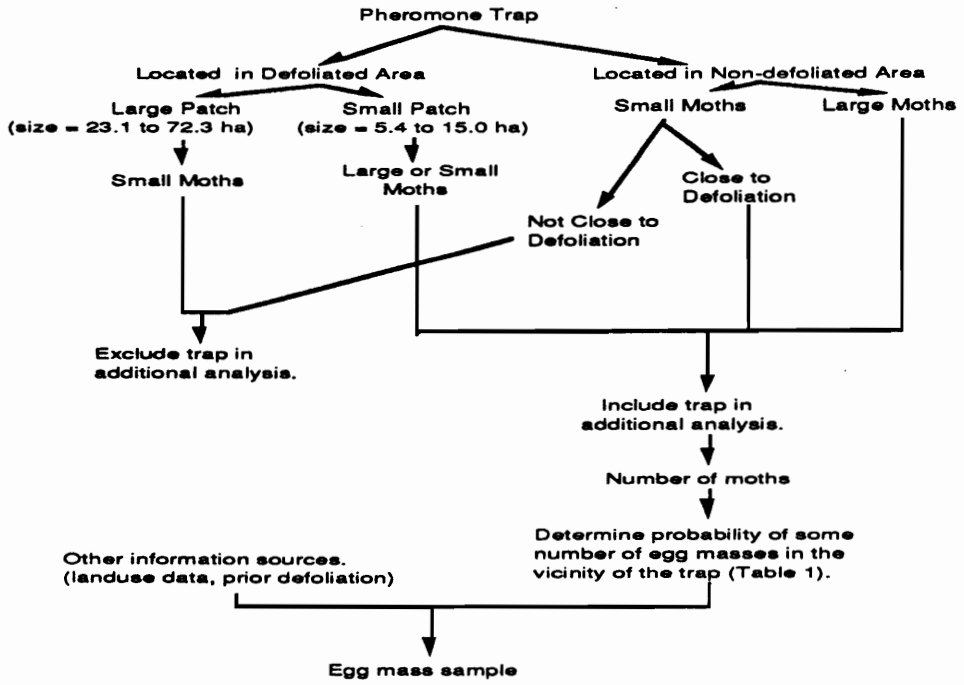


Fig. 3. Flow chart to prioritize areas for egg mass sampling based on pheromone trap catch.

Influence of Defoliation on Populations Dynamics. A reduction in fecundity can have a significant impact on population dynamics by reducing the potential number of larvae in the next generation. Fecundity was significantly reduced by defoliation only if defoliation exceeded ca. 40%. This is probably related to an interaction between foliage availability, changes in foliar chemistry, and the extent (localized or systemic) of the changes in foliar chemistry due to feeding by the gypsy moth (Rossiter et al. 1988). Larvae are probably not foliage limited at defoliation levels of ca. 40 to 75%. At these levels, changes in foliar chemistry are probably the major influence on male moth wing length and fecundity. As the level of defoliation increases (i.e., > ca. 75%), the relative importance of food quality may decrease and foliage quantity may become the limiting factor for larval growth.

There were no apparent trends in larval development related to defoliation as measured by sets of stochastic phenology model parameters and degree-days required for development. These results indicate that gypsy moth development is primarily a function of heat accumulation and not density-related factors. The phenology of male pupae is altered in defoliated (> ca. 40%) plots, but more so in patches in which defoliation was severe (> ca. 70%). Generally, the period of time (degree-days and julian days) over which larvae pupate is reduced. This may be due to increased

temperature in the defoliated plots or significantly higher mortality of slower developing larvae of which the majority are females. In three plots with defoliation in excess of ca. 70%, the maximum level of defoliation occurred while the greatest proportion of the larval population were in instars one to four. In these plots, the sex also ratio was found to be significantly male skewed. This suggests that defoliation above ca. 40% has an impact on gypsy moth population rates of increase (reduced fecundity), but probably not until foliage becomes limiting (ca. > 70% defoliation) is the impact drastic (significantly higher larval mortality).

In addition, the time at which the maximum level of defoliation occurs may have important implications for larval survival. The causes of larval mortality were not determined in these studies, but the dynamics of NPV transmission is such that greater numbers of early instar larvae in the higher density plots (plots with defoliation in excess of ca. 70%) would likely speed the spread of NPV infection. The higher levels of defoliation may also increase mortality due to starvation.

Small defoliated patches tend to precede spatially extensive defoliation patches by a year. These small patches can be considered to be areas that are one year ahead of surrounding areas in terms of defoliation dynamics. While the level of defoliation of a large number of small patches was not directly assessed, observations and data from chapters three and four indicate that defoliation in these patches was above ca. 40% but below ca. 70%. Areas with severe defoliation (ca. > 70%) tended to be larger patches. Therefore, even if fecundity in these small patches is reduced, there is a high probability the surrounding area will contain many large egg masses. The patterns of defoliation from year to year indicate that egg mass density in areas surrounding the defoliated patch is, in fact, often high (at least above levels that will cause defoliation). Most of the area defoliated in any year generally occurs in large patches and is not defoliated the next year. Clearly then, there is an interaction between the level of defoliation, the size of the defoliated patch, and the population dynamics within these defoliated areas. Based on this information, it may be possible to assess the potential of a gypsy moth population to cause additional defoliation by examining the previous episodes of defoliation. A rule-based model embodies the defoliation, patch size, and population dynamics triad (Figure 4).

Conclusion. The level of defoliation, the size of the defoliated patches, population density, and the population dynamics within these patches can have significant effects on both pheromone trap catch and area-wide gypsy moth population

dynamics. Sole reliance on the number of moths captured in pheromone traps to monitor gypsy moth populations with widely varying spatial and density characteristics will probably not provide satisfactory results. Innovative methods to intepret pheromone traps and basic information concerning the biology of the gypsy moth must be considered when interpreting pheromone trap catch. The temporal and spatial dynamics of gypsy moth populations and the dynamics of pheromone traps are too complex and intertwined to rely on a single measure (i.e., the number of moths) to relate pheromone trap catch to egg mass density or defoliation in the next generation. An approach that incorporates several measures may require more investment of time by field workers, supervisors, and data analysis technicians, but if the the accuracy of predicting where to conduct egg mass samples is improved, the investment is certainly justified. The number of moths captured, the wing length of captured moths, and defoliation maps are the three variables identified in this study that will allow more accurate estimation of egg mass density or to prioritize areas for egg mass sampling. The use of defoliation maps provides information on the location of certain types of gypsy moth populations (high density populations). Defoliated areas, in many cases, can be detected using the wing length of moths captured in pheromone traps. In addition, the fact that defoliation occurred provides information on the probability of defoliation in subsequent years. Pheromone trap catches that deviate from expected values (i.e., small moths in non-defoliated areas) can be more carefully evaluated to determine the accuracy of the information provided by both the number and size of moths in the trap. This evaluation can lead to an assessment of the need to conduct egg mass sampling.

This research only provides a direction; more effort must be put forth to determine the value of the methods outlined in this dissertation. The methods outlined, to a great extent, rely on the probability of certain events occurring, obtaining a specified number of moths, or capturing moths of a specific size given a set of ecological conditions. To be confident that the probabilities are correct, considerably more data of the type used in this dissertation should be gathered and utilized. Specifically, data on the number and size of male moths captured in pheromone traps, egg mass density in the vicinity of the traps, the number of eggs per mass, the defoliation level in the area of the trap, and data from defoliation maps should be gathered and analyzed to determine it usefulness for monitoring gypsy moth populations and predicting population trends.

Rule 1: If area was defoliated last year and
eggs per mass is < 300 and
area is not a small patch (patch size range = 5.4 to 15.0 ha, mean = 10.2 ha),
then defoliation will not occur or will be minimal (0 - 20%).

Explanation: Defoliation is limited in areas experiencing defoliation the previous year. Small egg masses are an indication of the previous years defoliation. Large patch (patch size range = 23.10 to 72.34 ha, mean = 38.67 ha) dynamics limit the possibility of defoliation due to larval movement or undetected high egg mass density spots.

Rule 2: If defoliation did not occur last year and
area is not adjacent to a small defoliated patch,
then defoliation (DEF) is predicted from the equation,

$$DEF = 100[1.0 + 7.248(0.3680)^{00173x}]^{-1} \quad (1)$$

where x = egg mass density (ha plot) (from Ganser et al. 1985)

Explanation: The larvae population is not likely to be increased by adjacent high density populations.

Rule 3: If area was defoliated last year and
area is a small patch and
egg mass density in adjacent areas is high,
then defoliation will be severe and spatially extensive.

Explanation: The small patch and surrounding high egg mass density is indicative of a large patch in which defoliation will exceed defoliation predictions based on equation 1 due to the a high area-wide larval population..

Rule 4: If area was defoliated last year and
area is a small patch and
egg mass density in adjacent areas is low,
then defoliation will be high, but localized.

Explanation: Egg mass density in the patch is likely to be high, but the defoliation will not be influenced by adjacent high density populations.

Fig. 4. A rule-based heuristic model to predict defoliation.

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VITAE

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