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Behavior and development of larval gypsy moth, Lymantria dispar (L.), on trees of the Upper Great Lakes forests

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David Berkeley Roden

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James R. Miller
Major professor
J.R. Miller

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BEHAVIOR AND DEVELOPMENT OF LARVAL GYPSY MOTH, LYMANTRIA DISPAR (L.), ON TREES OF THE UPPER GREAT LAKES FORESTS

By

David Berkeley Roden

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Abstract

BEHAVIOR AND DEVELOPMENT OF LARVAL GYPSY MOTH, LYMANTRIA DISPAR (L.), ON TREES OF THE UPPER GREAT LAKES FORESTS

By

David Berkeley Roden

In laboratory and field experiments, all larval instars of gypsy moth, Lymantria dispar (L.), were influenced by the diameter, height and species of a tree. The degree of larval attraction to an object was positively correlated with the angle presented by the diameter and height. Larval attraction to red oak (Quercus rubra L.) was frequently fifteen-fold greater than to paper birch (Betula papyrifera Marsh.) and trembling aspen (Populus tremuloides Michx.). Diameter, height and tree species may be important considerations for standardizing burlap banding and explaining the gypsy moth "wolf tree" phenomenon.

Pupal weight, developmental time and survival of gypsy moth larvae on three defoliated (60%) and undefoliated tree species were compared for one season. Host species and defoliation both affected female pupal weight, whereas only host species affected male pupal weight. Female and male pupal weights, averaged over defoliation treatment, were 1.43 and 0.49 g, respectively, on trembling aspen, > the 1.13 and 0.40 g on paper birch and > the 0.84 and 0.38 g on red oak. Time of development, averaged over the defoliation treatment, was affected only by tree species: female and male time of development were 46 and 41 days, respectively, on trembling aspen, < the 48 and 44

days on paper birch and < the 50 and 44 days on red oak. Gypsy moth survival was unaffected by defoliation or host species. Better gypsy moth performance on trembling aspen and paper birch was attributed to an imprecise correspondence between host and herbivore that inhibits outbreaks of gypsy moth on these tree species. It is suggested that the gypsy moth nuclear polyhedrosis virus and physical features of the host are responsible for imprecise correspondence.

Gypsy moth larvae were sometimes found to construct silk ladders for climbing on a smooth vertical surface. The use of silk for climbing was six times more frequent in less-fit populations and was common on trembling aspen and paper birch, but absent on red oak. The use of silk for climbing by less-fit larvae in the field may be a result of wound-induced plant defences.

An incandescent and fluorescent lighting system is described that induced a change in feeding behavior between small and large gypsy moth larvae in the laboratory. This change was observed on artificial "tree stems." On the day before pupation began, 85% of the larval population migrated down the artificial tree stems to seek shelter under felt and cardboard "bark flaps."

For Lorne in memory of the years we worked together. Your thoughtfulness and kind and gentle personality were instrumental in my development and provided examples I can only hope to achieve.

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TABLE OF CONTENTS

SUM

REC

APP

LIST

Tab

Tab

Tab

Tab

Tab

Tab

Tab

Tab

Tab

Tab

LIST OF TABLES

Table

Table

Table

Table

Table

Table

Table

Table

Figu

Figu

Figu

Figu

Figu

LIST OF FIGURES

INTRODUCTION

The gypsy moth, Lymantria dispar (L.), is a univoltine defoliator of hardwood trees and is indigenous to Eurasia and the Mediterranean (Mills 1983). It was first introduced to North America by Leopold Trouvelot at Medford, Massachusetts in 1868 or 1869 (Forbush and Fernald 1896). Passive dispersal of life stages, particularly egg masses, via human interaction (McManus and McIntyre 1981), and active dispersal by ballooning of first-instar larvae (Capinera and Barbosa 1976; Cameron et al. 1979; Mason and McManus 1981) have enabled gypsy moth to colonize most of the New England states, as well as areas as far away as California, Michigan and British Columbia (Prittchett 1975; Campbell 1979; Sterner and Davidson 1981).

Many studies in Europe and the United States show that species of trees belonging to the genus Quercus are the preferred gypsy moth host most capable of maintaining populations (Campbell and Sloan 1977; Hough and Pimentel 1978; Barbosa 1978; Barbosa et al. 1979; Houston 1979). However, infestation of the upper Great Lakes basin, which has a tree species composition substantially different from that in the northeastern United States, has raised concern about the utilization of secondary hosts and their potential to support outbreaks of gypsy moth similar to those in the oak forests of New England. Trees such as trembling aspen, Populus tremuloides Michx. and paper birch, Betula papyrifera Marsh., hosts classified as secondary in the forests of the eastern USA , are a major component of the forest in the upper Great Lakes basin and an important sector of the resource base utilized by many forest industries. Studies by Witter et al. (1990) and Roden and Surgeoner (1991) have indicated that gypsy moth larval

development on these hosts may produce more fecund adults in a shorter developmental period than gypsy moth larvae reared on a "traditional" host such as red oak, Quercus rubra (L.). Control of an herbivore and the potential subsequent effect on population dynamics is based on the assumption that the additon or deletion of a particular phase of host-colonization behavior will result in interruption of the host-selection process (Harris and Miller 1991). The objective of the present research was to evaluate the potential of trembling aspen and paper birch in the development of gypsy moth in comparison with that of red oak and investigate the possible influence that the physical features of the host may have on larval behavior.

Chapter one identifies visual stimuli that influence the orientation of gypsy moth larvae and how physical features of a host such as its diameter, height and species influence the larval host-selection process. Chapter two evaluates the potential that trembling aspen and paper birch provide for the development of gypsy moth in the Great Lakes basin compared with red oak and how this potential may be affected when plant defences are evoked by artificial defoliation. Chapter three reports a previously unidentified behavior ("laddering") of gypsy moth larvae that is used for climbing on a smooth vertical surface and the influence of diet on this behavior. Chapter four describes a lighting system for the laboratory that can be used with artificial trees to produce a change in the feeding behavior between small and large larvae and suggests that such a system could be used to further evaluate physical features of a host and how they influence larval behavior.

CHAPTER ONE

Visual Stimuli Influencing Orientation by Larval Gypsy Moth, Lymantria dispar (L.)

Introduction

Host colonization by the gypsy moth, Lymantria dispar (L.), may be influenced by feeding behavior, foraging behavior, or both. Studies of feeding behavior have emphasized either the nutritional suitability of the hosts (Hough and Pimentel 1978; Barbosa and Greenblatt 1979), or the debilitating effects of ingested secondary substances (Keating and Yendol 1987; Meyer and Montgomery 1987; Rossiter and Schultz 1988). Chemical ecologists have suggested that the behavioral response of an insect to a host is mainly a series of simple reactions to chemicals (Thornsteinson 1960; Beck 1965; Shorey 1977). This explanation of insect behavior subscribes to the theory of "labeled lines" (Perkel and Bullock 1968; Dethier 1971, 1982) and implies that a chemical molecule, when it impacts on a chemoreceptor, transmits nonambiguous but severely restricted information that initiates an appropriate behavioral response. The labeled-line model is gradually being replaced by the theory of across-fiber patterning (Dethier 1971, 1982) and across-modality stimulus summation (Miller and Strickler 1984; Miller and Harris 1985). According to these latter concepts, the relative patterns of neuronal action potentials are integrated with sensory patterns from other modalities (i.e., gustatory, olfactory, visual and mechanical) to trigger decision-making interneurons that control behavior. Although there is no doubt that chemical cues play an important

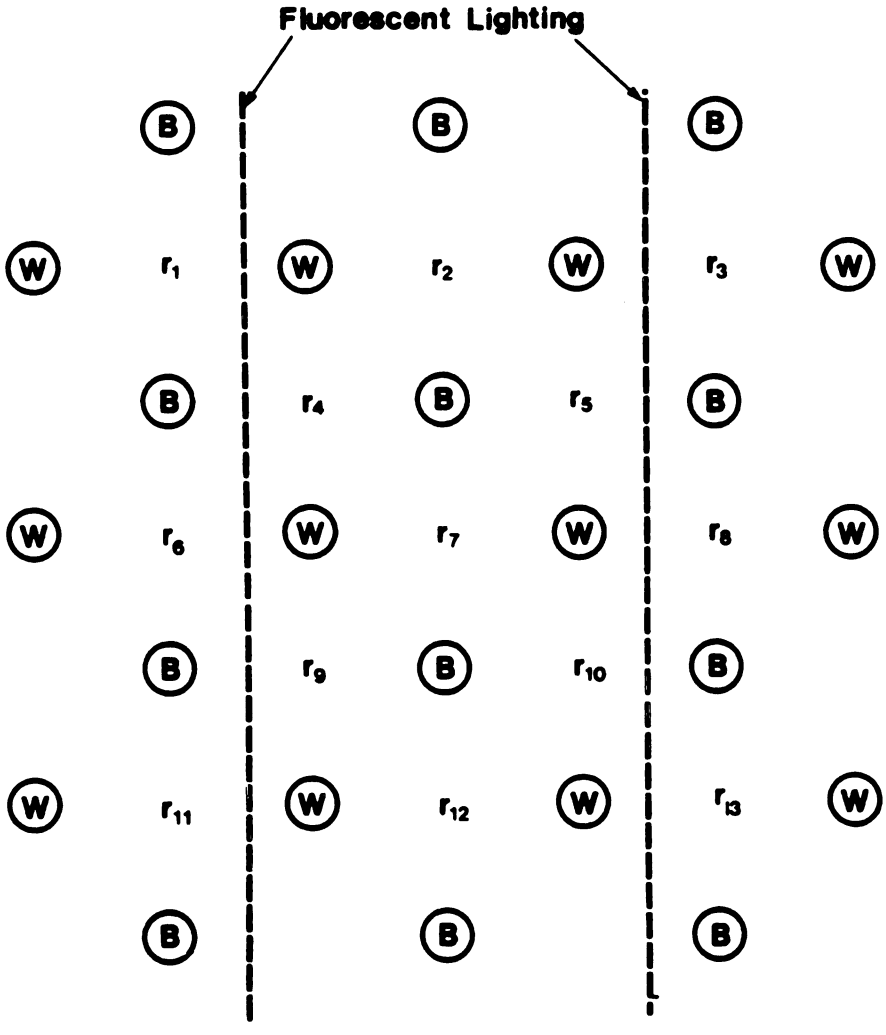
regulatory role in the colonization of hosts by the gypsy moth, the foraging behavior of folivorous insects has received little attention (Schultz 1983; Dethier 1987). Because there is evidence to suggest that the orientation of gypsy moth larvae to hosts in the field is influenced by stimuli from sensory modalities other than chemoreception (Doane and Leonard 1975; Lance and Barbosa 1982), the present study posed the question of how the physical features of a tree influence the host-selection process of larval gypsy moths.

Materials and Methods

Rearing. Behavioral experiments were conducted in the laboratory over a period of 3 years between January and September from 1986 to 1989. Gypsy moth larvae were obtained annually from egg masses collected the preceding October near Kaladar, Ont. ($44^{o}39'N$, $77^{o}07'W$) and held at $5^{o}C$ until diapause was completed. Eggs were then surface sterilized (Shapiro 1977) and incubated, as required, at $22^{o}C \pm 2^{o}C$. No experimental measurements of larval behavior were conducted after 15 September; results from the black-white artificial tree experiment described below indicated that the storage of egg masses each year until 15 September did not affect larval behavior. Larvae used for laboratory experiments were reared individually on artificial diet (Bell et al. 1981) in screened Lab-Tek® 150- by 25-mm plastic Petrie plates at 70% relative humidity with a 16L:8D photoperiod. In 1988, to validate the laboratory results, behavioral studies of fifth- and sixth-instar larvae were repeated in the field at Kaladar with larvae collected from the base of red oak (Quercus rubra L.) trees. These tests were conducted under an overstory of red oak to simulate the lighting conditions experienced by larvae crawling on the forest floor. All larvae tested, whether in the laboratory or the field, were held without food overnight to increase their activity (Leonard 1967; Dethier 1982) and were gently transferred from a Petrie plate with a camel-hair brush to minimize the effects of handling. Each larva was tested only once during an instar.

Larval Preference for Black versus White Artificial Trees. Doane and Leonard (1975) reported that larval gypsy moth appeared to orient themselves with respect to vertical objects such as tree trunks. To test these observations and determine if larvae are influenced by contrasting colors, I constructed 24 artificial tree trunks 1 m in height from 7.5-cm ABS plastic pipe. A circular plate, cut from 5-mm Plexiglass® and glued in place with ABS cement, sealed the top of each artificial trunk. The 24 trunks, randomly divided into two groups of 12, were then painted with a mixture of 150 mL of sand (sifted through a 20-mesh screen) and 250 mL of either black or white latex paint (Color Your World, Toronto, Ont. M8W 3R5; paints #5900 and #5920, respectively). Sand was added to the paint to roughen the surface of the tree trunks because previous trials had revealed that larval gypsy moth had difficulty climbing on a smooth surface (Roden, unpublished data). The 24 artificial tree trunks were then arranged in a 4- by 5-m rearing room in a pattern of seven rows and seven columns offset from each other by 0.5 m; trees of the same color were separated by 1 m (Figure 1). Thus, there were four tree trunks, respectively, in each alternating row and column. This arrangement provided a total of 13 release points, one in the center of each square formed by the rows and columns, which were equidistant from the two nearest black (B) and white (W) trunks (Figure 1). These points were used to release 13 larvae for each replication and to compare selection of the tree trunks. The populations tested were classified as neonate larvae. These were unfed, first-instar larvae that had been eclosed from the egg for at least 24 h, but that were less than 48 h old; first-instar larvae (I) that had fed, but that were older than 48 h; separately, second- (II), third- (III) and fourth-instar larvae (IV); collectively, fifth- and sixth-instar larvae (V^{+}); and, collectively field-collected fifth- and sixth-instar larvae (V^{+Field}). In addition to the above, three other tests included first-instar larvae from eggs randomly selected and held until 15 September (I-SEPT); first-instar larvae tested on 122-cm double-density 40-weight kraft paper (Lewis Paper, Toronto, Ont. M9N 2Y8) placed on

Figure 1. The arrangement of black (B) and white (W) artificial tree trunks used to evaluate the attractiveness of vertical objects to gypsy moth larvae. (r_i = points at which larvae were released)


Fluorescent Lighting
B
W
r1
r2
r3
r4
r5
r6
r7
r8
r9
r10
r11
r12
r13

the floor between replications (I-PAP); and third-instar larvae (III-OAK) reared from eclosion on leaves of red oak. Full water content was maintained in excised leaves by placing individual leaves in "water piks" and changing them every other day (Scriber 1977).

A complete randomized block design, blocked by time and with six replications, was used to compare three treatments for each larval population: larvae that oriented toward black artificial tree trunks, white artificial tree trunks and larvae that did not orient to any of the artificial tree trunks within 1 h. In the laboratory, the color of the rows and columns was reversed each time the experiment was replicated to remove the possibility that the arrangement of the fluorescent lights (General Electric F40/C75 lamps with a standard ballast operating at 110/115 V) biased larval choice. Field tests of larvae were conducted with the artificial trees arranged in rows and columns running north-south and east-west on the forest floor; the rows and columns were also reversed between replications. Replication in the field was conducted at 0800, 1200 and 1600 h EST on each of 2 days (7 and 9 July 1988) to allow for a possible effect caused by the change in the position of the sun on larval orientation (Doane and Leonard 1975). In both the laboratory and the field, each larva was released with its head pointed in one of the four cardinal compass directions at the time of release. The order of larval release at the 13 release points and the direction in which they were released were both randomized. One hour after release, the tree trunk to which larvae were attracted was recorded. A Waller-Duncan Bayesian k-ratio Test with $k = 100$ was used for separation of means. A k-ratio of 100 is $\cong$ equivalent to $\alpha=0.05$ (Waller and Duncan 1969; Duncan 1975). Observations of whether or not larvae were attracted to the closest column were made for one larva selected randomly from each replication for neonates and first, second, third, fourth, fifth and sixth instars.

Larval response to contrasting black and white colors while climbing was investigated using a Y-shaped column constructed from 5-cm-diameter ABS plastic pipe. Arms of the "Y", 15 cm in length, were angled at 90^{o} and then glued together with ABS cement before being fastened with a hot-air welder (Leister-Kombi, Type: Triac, purchased from Johnson Industrial Plastics, Toronto, Ont.) to a 5-cm-diameter, 60-cm-tall vertical stem of ABS plastic pipe so that each arm of the Y was at 135^{o} to the vertical stem. Additional support was provided by inserting the bottom of the Y into a 5- by 7-cm coupling. The black paint-sand mixture described previously was then applied to one arm of the Y and the corresponding half of the stem; the other arm and the other half of the stem were painted with a similar mixture of white paint and sand. The larval instars tested were: neonate, first, second, third, fourth, fifth and sixth and, collectively, field-collected fifth- and sixth-instar larvae. When testing larvae, the Y was placed on a table between overhead fluorescent lights so that each color was illuminated equally. Release of larvae onto the column was accomplished by allowing each larva to climb a piece of wooden dowelling positioned at an angle of ca. 30^{o} against the column's black-white interface 25 cm below the Y. Initially, 100 neonate larvae were released; however, the number released for older instars decreased because of mortality. After testing each larva, the column was brushed to remove trails of silk (Leonard 1967) and was wiped with hexane to remove possible pheromone or other chemical substances associated with the silk. Between odd- and even-numbered larva, the Y was also rotated 180^{o} to remove the effect of room lighting, left-right larval preferences, or both. A test was considered completed when a larva had climbed to the top of one arm of the Y; larvae that did not climb to the top within 10 min were not included in the analysis. Sex was determined by rearing larvae until they pupated. Statistical significance for either a black or white surface preference ($p=0.5$) was tested for each instar with a table of values for a two-tailed binomial test (Zar 1984).

Diameter. The influence of the diameter of an artificial tree on larval orientation was investigated using nine 1-m-tall columns with diameters of 3, 6, 12, 25, 50, 100, 150, 200 and 300 mm. Materials used for the 3-mm (steel rod) and the 6- and 12-mm (wood doweling) columns differed from those used for the others (cardboard: Design Tubes, Markham, Ont.) because it was too difficult to obtain a broad range of diameters in one material; however, so that the image and the light reflected by each material was the same, the surface of each column was painted with the black paint-sand mixture described earlier. A randomized complete block design, blocked by time and with five replications, was used to test neonate larvae, first-instar larvae at least 48 h old that had fed, third-instar larvae and, collectively, fifth- and sixth-instar larvae and field-collected fifth- and sixth-instar larvae. The nine test columns, randomly arranged for each replication, were placed along the circumference of a 1-m-diameter circle at 40^{o} intervals; the area within the 1-m circle was the arena used to test larval response. The three smallest columns were supported by nylon fishing line suspended from the ceiling; nylon line was also suspended from the ceiling above each of the larger columns, but was not used for support. For each replication, larvae were released individually with a camel-hair brush from the center of the circle so that the head of each larva was pointed in one of the four cardinal compass directions; the order and direction of each release were both randomized. Each replication was continued until a total of 20 larvae had climbed on a column. Larvae that did not climb on a column within 30 min, or that wandered outside the arena, were also recorded. To remove the possibility that larvae followed a pheromone or silk trail, a piece of 1.2-m-square kraft paper with 15- by 15-cm pencil-drawn grids was placed on the floor for each larva tested. The track of the larval path on a parallel grid and the time required for each larva to reach a column was recorded. Measurements of tortuosity (the number of turns that exceeded 90^{o}) and the time required for larvae to select a column were measured for 20 larvae selected randomly from each instar.

Larval testing in the field was similar to that in the laboratory; however, columns were placed on a 1.2-m-square plywood platform raised ca. 9.0 cm off the forest floor. The smaller-diameter columns (3, 6, 12 and 25 mm) were supported by forcing them through the kraft paper into slightly smaller holes drilled in the plywood; the lengths of these columns were increased to compensate for the distance they were inserted. Three randomly chosen times during the day (0930, 1200 and 1500 h EST) were used to test larval response in the field. Replications 1 and 3 were tested at 0930 and 2 and 4 were tested at 1500 h on separate days; the fifth replication, initiated on a 3rd day, began at 1200 hours. Larval preference for diameter within each respective instar, including the number of larvae that wandered out of the arena and those that did not select a column within 30 min, was ranked for the first 20 larvae tested (Conover and Iman 1981) and then subjected to ANOVA and Waller-Duncan's Bayesian k-ratio Test with k = 100 for separation of means. The perceived angular width of each column (θ) from the center of the arena was also calculated; these were 0.18, 0.36, 0.72, 1.44, 2.84, 5.52, 8.09, 10.45 and 14.82 degrees. The transformed values ($\log_e$) for larvae of each instar (100) that selected columns were tested for normality and regressed against θ. The slopes of each regression equation for each population were compared.

I also investigated the probability that larvae would simply randomly encounter columns when they wandered away from the center of the circle. This was tested with chi-square values by summing and comparing, across instars (because there was no difference between the slopes for each population tested), the number of larvae attracted to columns versus the number of larvae that wandered out of the arena. The expected distribution of larvae attracted to columns was the proportion for θ versus the sum of angles (λ) between columns. A chi-square test was also used to compare the 20 larvae attracted to columns based on an expected proportional distribution of θ. It is conceivable that, although the number of larvae attracted to a column might be significantly

correlated with θ, the proportion of the population attracted to columns with large or small values of θ might be different from what was expected.

Height. Based on the results of the diameter experiment, the effect of height on the choice of a host by L. dispar was investigated by using 150-mm-diameter cardboard columns for the following heights: 20, 40, 80, 160, 320, 640, 1280, 1600 and 2000 mm. Columns were also painted with the black paint-sand mixture. Experimental design and analysis was similar to that for the diameter experiment. The angles (β) from the center of the arena to the top of each column were, respectively, 1.15, 2.29, 4.57, 9.09, 17.75, 32.62, 52.00, 57.99 and 63.44 degrees.

Tree Species. The influence of the species of a tree on gypsy moth larval orientation was investigated using red oak, trembling aspen (Populus tremuloides Michx.) and paper birch (Betula papyrifera Marsh.). The experimental design and the larval instars examined were the same as those in the diameter and height experiments, except that the nine cardboard columns were replaced with three 1-m-tall equal-diameter bolts of each species. These were randomly arranged in a 1-m circle and replaced each time an instar was tested. The number of larvae attracted to each species was analyzed with one-way ANOVA; means were compared with a Waller-Duncan Bayesian k-ratio Test with k = 100.

Statistical Procedures. The Waller-Duncan Bayes test (BLSD) was specifically chosen for means comparisons in this chapter because its ability to detect real differences between means does not depend on the number of means being compared. Consequently, the use of this test to compare the diameter and height means avoids problems assocaited with disagreement in the literature about the use of comparisonwise and experimentwise error rate approaches for means comparisons (Jones 1984; Perry 1986; Day and Quinn

1989). When the BLSD F-value is low (indicating a set of homogeneous means), the test has a conservative characteristic that is typical of an experimentwise error rate approach whereas, when the F-value is high (indicating heterogeneous means), it assumes a comparisonwise error rate approach (Peterson 1985).

Results

Larval Preference for Black versus White Artificial Trees. The color of an artificial tree clearly influenced the orientation of larval gypsy moth crawling on a horizontal plane. All instars (Table 1) significantly preferred black to white artificial trunks (α=0.05); the number of larvae attracted to white trunks and those that left the perimeter of the arena were not significantly different from each other for all instars examined. Most larvae were attracted to the nearest column (Table 2).

Larval preference for a black or a white surface while climbing vertically varied with instar (Table 3). Neonate larvae preferred white (α=0.1) whereas first-, second-, third- and fourth-instar larvae did not discriminate (α=0.1). However, laboratory-reared fifth- and sixth-instar larvae and field-collected fifth- and sixth-instar larvae preferred black (α=0.05). These results were not influenced by sex, except for neonate larvae (α=0.1); neonate females had no significant color preference but males preferred white (the ratio B:W was 20:21 for females and 14:26 for males).

When climbing onto the Y, fifth- and sixth-instar larvae consistently oriented klinotactically to the black-white interface of the column; larvae paused at the interface between colors and would repeatedly swing the anterior portion of their body (head, thorax and the first two abdominal segments) back and forth between the black and white colors before making a choice. It was also not uncommon to observe larvae climbing

Table 1. Attraction of gypsy moth larvae on a horizontal surface to black versus white columns.

Instar*	Mean number of larvae recovered**			
	Black	White	Other++	MSE***
Neonate	12.3a	0.5b	0.2b	0.6
I	13.0a	0.0b	0.0b	0.0
II	11.7a	1.2b	0.2b	2.7
III	12.0a	0.5b	0.5b	1.9
IV	12.2a	0.8b	0.0b	0.6
V^{+}	11.0a	1.7b	0.3b	1.9
V^{+Field}	11.8a	0.8 b	0.3b	1.3
I-SEPT	11.0a	1.0b	0.7b	1.7
I-PAP	12.0a	0.5b	0.5b	0.7
III-OAK	13.0a	0.0b	0.0b	0.0

* Neonate to V^{+} = larval instars reared on artificial diet in the laboratory; V^{+Field} = field-collected fifth- and sixth-instar larvae tested in the field; I-SEPT = first-instar larvae from eggs randomly selected and held until 15 Sept.; I-PAP = first-instar larvae tested on the floor, with new kraft paper between each replication; III-OAK = third-instar larvae reared on leaves of red oak from eclosion.

** Total possible was 13. Within a row, values followed by the same letter are not significantly different (Waller-Duncan k-ratio test, k=100).

++ Other represents the number of larvae that either did not climb on a column within 1 h or that wandered outside the arena.

***MSE = mean squared error.

Table 2. Numbers of gypsy moth larvae of various instars that were attracted to adjacent versus non-adjacent black or white columns in the laboratory.

Instar*	Adjacent**	Non-adjacent**
Neonate	6	0
I	6	0
II	5	1
III	5	1
IV	5	1
V+	4	2

* Larval instars are designated as in Table 1.

** Adjacent and non-adjacent values total to 6 because only 1 larva was observed for each replication.

Table 3. Influence of instar on larval gypsy moth choice of the black versus the white arm of a Y after climbing 25 cm up a 5-cm-diameter column.

Instar*	n	% larvae selecting black#
Neonate	100	*40
I	94	51
II	46	38
III	76	54
IV	78	53
V	80	**70
VI	34	**71
V^{+Field}	50	**80

* Larval instars are designated as in Table 1. All larvae were reared on red oak (Quercus rubra) in the laboratory except instar V^{+Field}; these were field-collected larvae from the base of red oak trees from Kaladar, Ontario.

Significance determined by a two-tailed binomial test with $p = 0.5$, $\alpha^{*} = 0.1$, $\alpha^{**} = 0.05$.

along the interface at the top of the Y after initially selecting white and walking for 2 to 3 cm on this arm, pausing, apparently looking back at the black arm and then turning around and proceeding to the top on the black surface.

Diameter. The number of larvae attracted to a column was strongly influenced by column diameter (Figure 2). The ranked number of larvae that did not orient to a column within the allotted time, or that wandered out of the arena, was always significantly less than the number of larvae attracted to the larger columns and was small compared with the total number of larvae tested for each population. Larval tracks (Figure 3) for neonate, third-instar and field-collected fifth- and sixth-instar larvae revealed that older instars oriented to a column more quickly and turned less frequently (Table 4) than did early instars.

Regression analysis of the $\log_e$ transformation of the number of larvae attracted to a column against θ yielded similar slopes and elevations for each population, each of which was significantly different from zero (α=0.05); the equation for the combined regressions was: $\text{Log}_e\ Y = 0.13x + 0.14$ (n=225). The proportions of the variation explained by the regression of $\mu_{y/x}$ for the combined instars (r^2=0.58) were, for neonate, I, III, V^+ and $V^{+\text{Field}}$, 0.52, 0.51, 0.61, 0.55 and 0.71, respectively. There was very little difference among instars in the total number of larvae attracted to each column as a function of θ (Figure 4a). I tested the possibility that more larvae might have randomly encountered larger columns as they left the center of the circle simply because the probability of encountering a larger column was greater than that of encountering a smaller one. This probability was defined by the proportions $\Sigma\theta_i$ and $\Sigma\lambda_j$, where i represents the angle of the ith column and j represents the jth angle between columns for θ and for λ (Figure 5). Summed values for the angles θ and λ were θ=44.42° and λ=315.58°. Therefore, by definition, the expected distribution of larvae attracted to

Figure 2. The ranked position, by instar, of the number of gypsy moth larvae attracted to columns of different diameters. Columns A to I, respectively, represent the smallest to the largest-diameter columns; X and Z, respectively, represent larvae that exceeded the 30-min test period and larvae that wandered out of the arena. Numbers for columns above the same horizontal line are not significantly different (Waller-Duncan k-ratio test, k=100). Numbers below each column are the mean ranked numbers of the first 20 larvae attracted. Numbers within brackets are the total number of larvae attracted to each column. (TLT = total larvae tested for each instar until 20 larvae oriented to a column; instars tested = neonate, I, III, V^{+} and V^{+Field}).

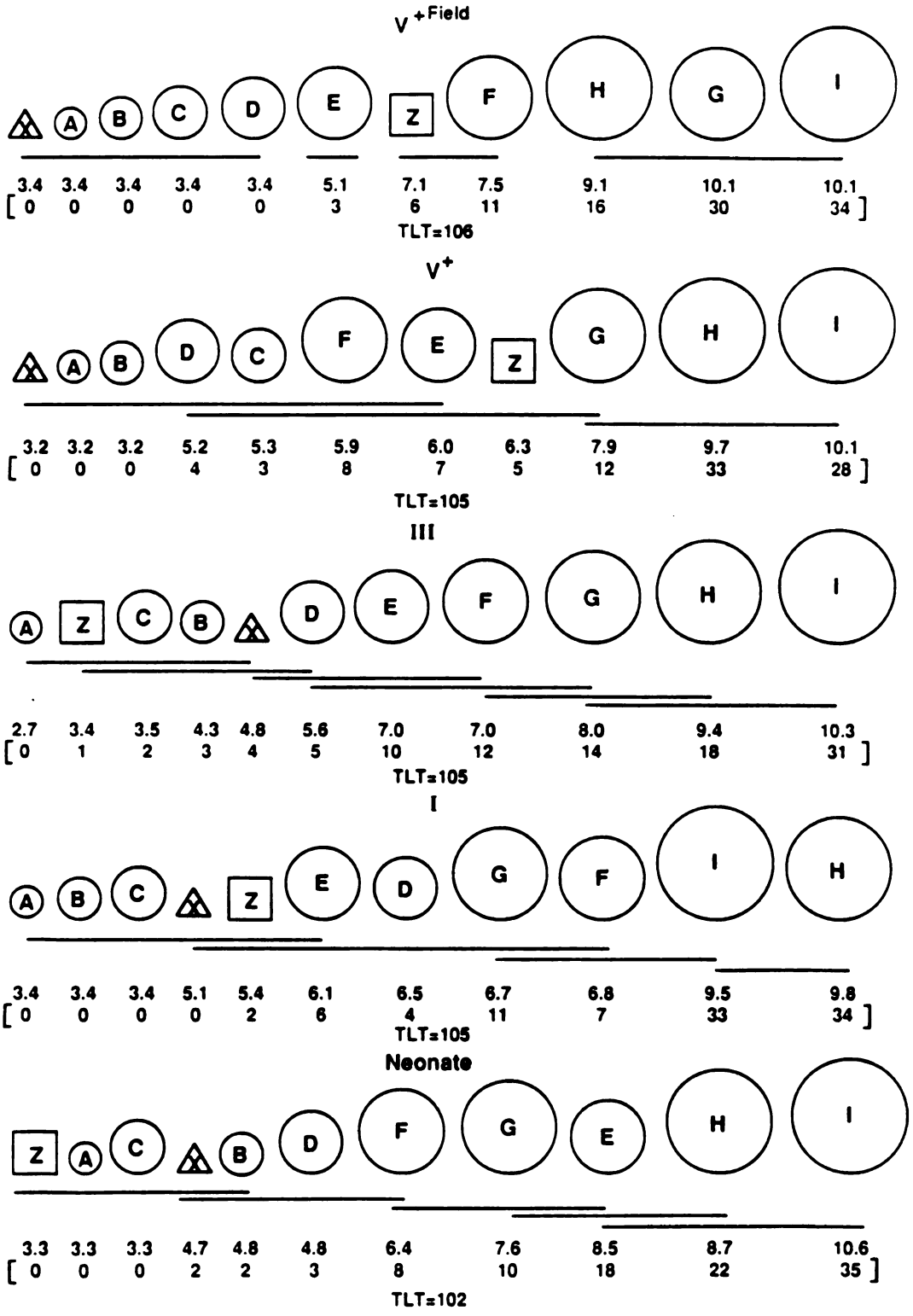
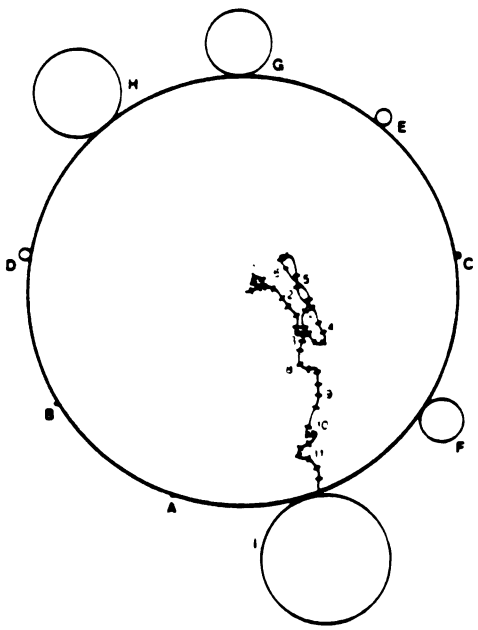
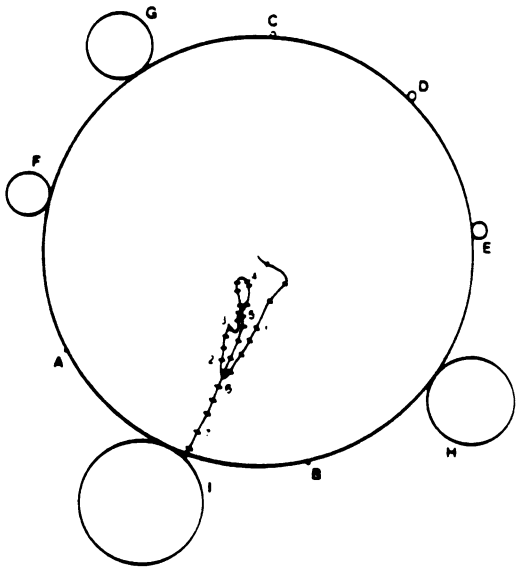

V+Field
A B C D E Z F H G I
3.4 3.4 3.4 3.4 3.4 5.1 7.1 7.5 9.1 10.1 10.1
[0 0 0 0 0 3 6 11 16 30 34]
TLT=106
V+
A B D C F E Z G H I
3.2 3.2 3.2 5.2 5.3 5.9 6.0 6.3 7.9 9.7 10.1
[0 0 0 4 3 8 7 5 12 33 28]
TLT=105
III
A Z C B D E F G H I
2.7 3.4 3.5 4.3 4.8 5.6 7.0 7.0 8.0 9.4 10.3
[0 1 2 3 4 5 10 12 14 18 31]
TLT=105
I
A B C Z E D G F I H
3.4 3.4 3.4 5.1 5.4 6.1 6.5 6.7 6.8 9.5 9.8
[0 0 0 0 2 6 4 11 7 33 34]
TLT=105
Neonate
Z A C B D F G E H I
3.3 3.3 3.3 4.7 4.8 4.8 6.4 7.6 8.5 8.7 10.6
[0 0 0 2 2 3 8 10 18 22 35]
TLT=102

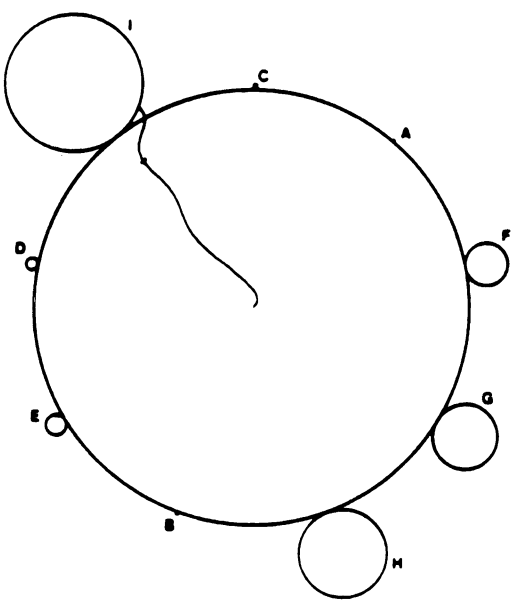
Figure 3. Tracing of gypsy moth larval tracks from the diameter experiment for (a) neonate, (b) third-instar and (c) field-collected fifth- and sixth-instar larvae. Ticks perpendicular to a trace show the posterior position of the larva every 15 sec.



a



b



c

Table 4. Orientation time and accuracy in response to columns, as influenced by instar.**

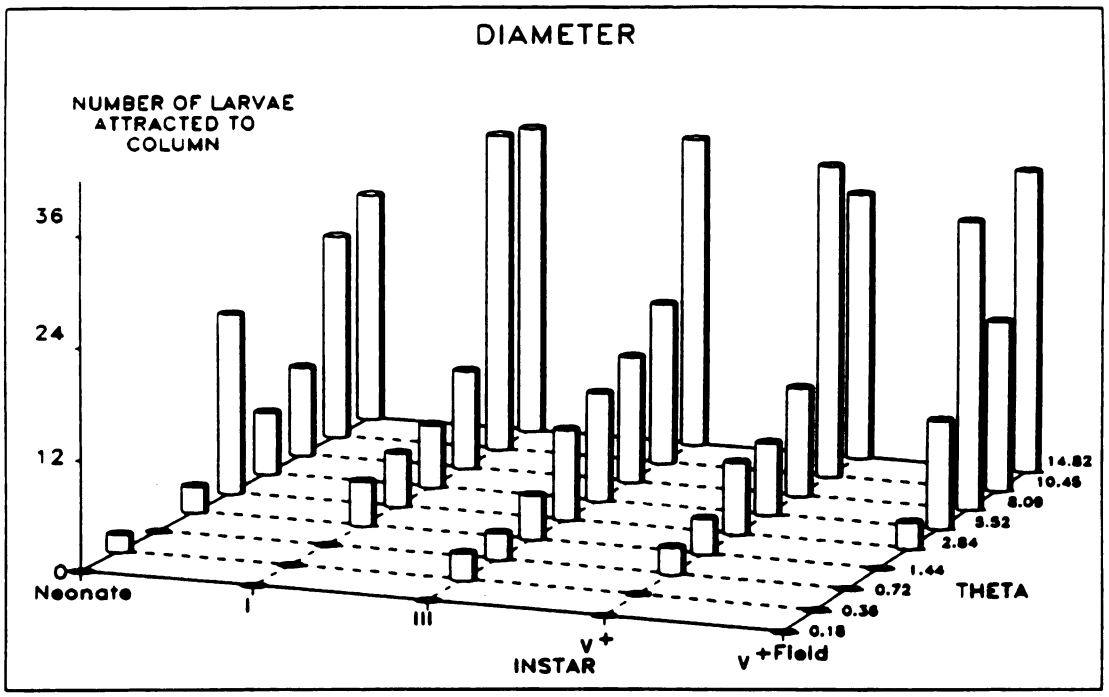
Instar*	Time#	No. turns ≥ 90° #
Neonate	12.4a	12.7a
I	11.2ab	9.1b
III	7.8b	5.7c
V^{+}	3.7c	2.1d
V^{+Field}	0.4c	0.3d

* Larval instars are designated as in Table 1.

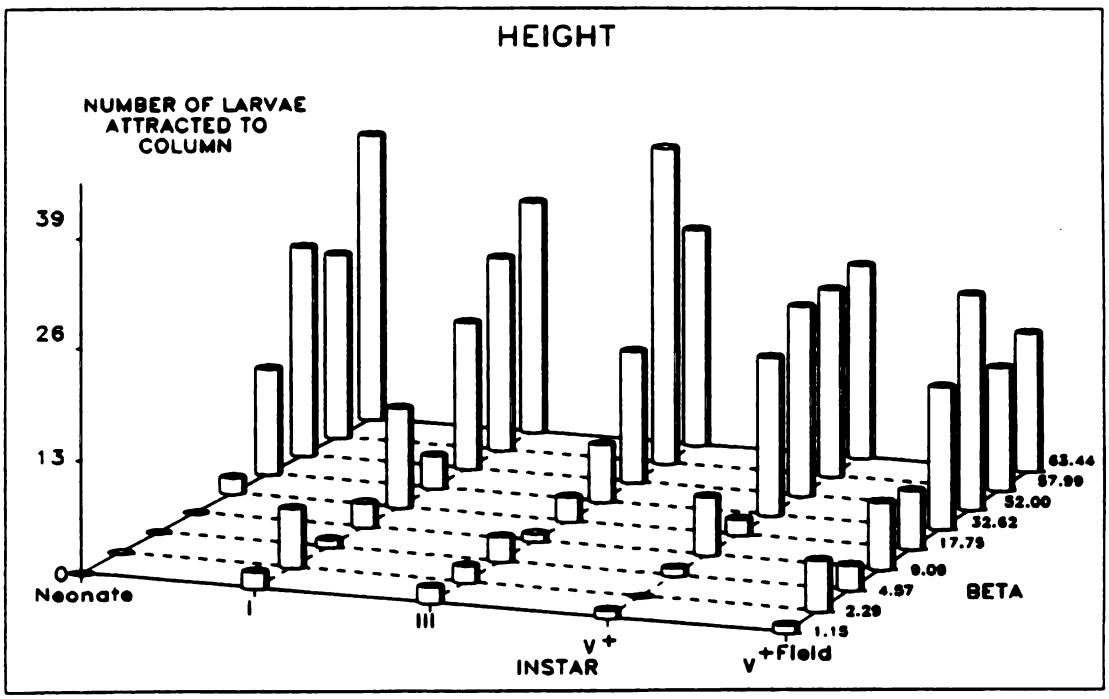
** Data based on the tracks of 20 gypsy moth larvae randomly selected from each instar tested in the diameter experiment.

Within columns, means followed by the same letter are not significantly different (Waller-Duncan k-ratio test, k=100; mean squared errors for time and turns = 34.3 and 25.4, respectively).

Figure 4. Numbers of each instar attracted to columns of (a) different diameters and the same height and (b) different heights and the same diameter, as a function of the angles θ and β, respectively, as subtended by a column from the center of the arena where larvae were released.

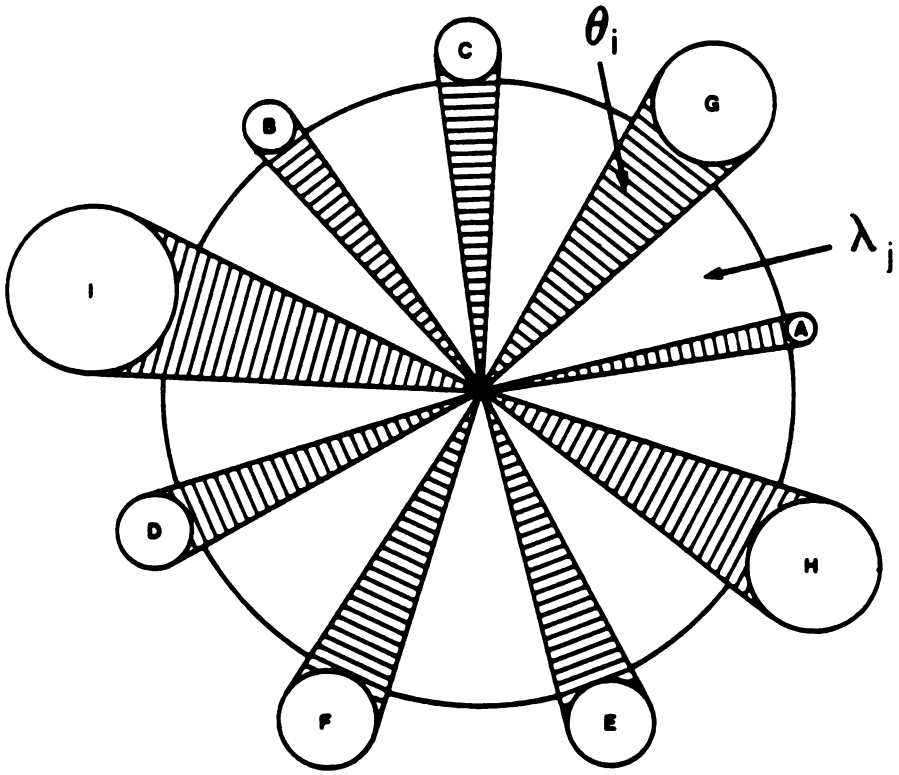

DIAMETER
NUMBER OF LARVAE ATTRACTED TO COLUMN
36
24
12
0
Neonate
I
III
V+
INSTAR
V+Field
14.82
10.45
8.09
5.52
2.84
1.44
0.72
0.36
0.18
THETA

a


HEIGHT
NUMBER OF LARVAE ATTRACTED TO COLUMN
39
26
13
0
Neonate
I
III
V+
INSTAR
V+Field
63.44
57.99
52.00
32.62
17.79
9.08
4.57
2.29
1.15
BETA

b

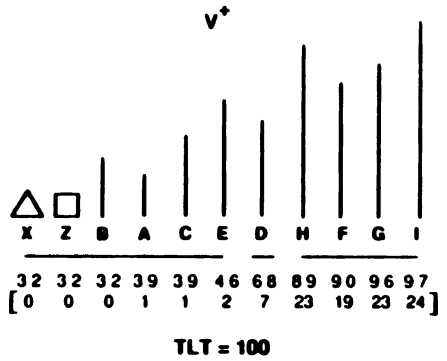
Figure 5. An illustration of the angles θ and λ used to calculate the expected proportion of larvae attracted to the different columns or open spaces between columns.

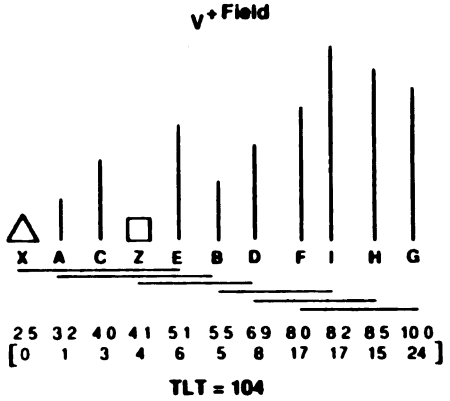

θi
λj
C
G
B
I
A
D
H
F
E

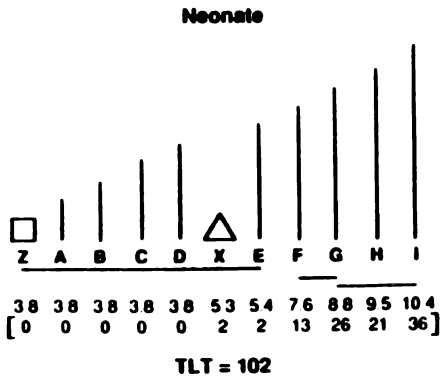
columns versus those that wandered out of the arena, if columns had no influence, was, respectively, 13 and 87 out of every 100 larvae tested. The chi-square test comparing these values left little doubt that the attraction of larvae to a column was not random; observed and expected values for the Chi-square were 486/65 and 14/435, respectively. The chi-square value (χ^2=13.89; α=0.05) comparing the expected number of larvae attracted to each column with the expected distribution of larvae based on the proportional distribution of θ for each column was not significantly different from a χ^2 with 8 df and α=0.05. The observed and expected values were, respectively: 1 versus 2, 5 versus 4, 6 versus 8, 17 versus 16, 46 versus 32, 47 versus 62, 79 versus 91, 130 versus 118 and 169 versus 167.

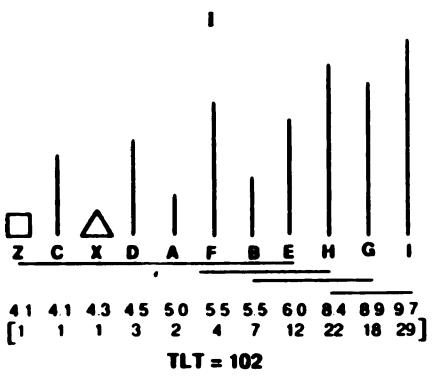
Height. The height of a column also influenced the orientation behavior of L. dispar larvae. The ranked number of larvae attracted to columns with different heights compared with larvae that wandered out of the arena and those that did not respond within the specified time period (Figure 6) closely paralleled the observations in the diameter experiment (Figure 2). Regression analysis of the height relationships also yielded similar slopes and elevations for each population, each of which was significantly different from zero (α=0.05); the equation for the combined regressions was $Log_eY = 0.25x + 0.16$ (n=225). The values of r^2 for the height regressions, for the same instars as those tested in the diameter experiment, were, respectively, 0.73, 0.38, 0.73, 0.57 and 0.33; the r^2 value for the combined populations was 0.55. Columns that presented the largest angle (the tallest columns) consistently attracted more larvae (Figure 4b). The numbers of larvae attracted to a column, expressed as the expected larval distribution based on the proportional distribution of β for the height of each column, were significantly different from a χ^2 with 8 df and α=0.05. Observed and expected values, respectively, were 6 versus 2, 12 versus 5, 8 versus 10, 19 versus 19, 26 versus 37, 63

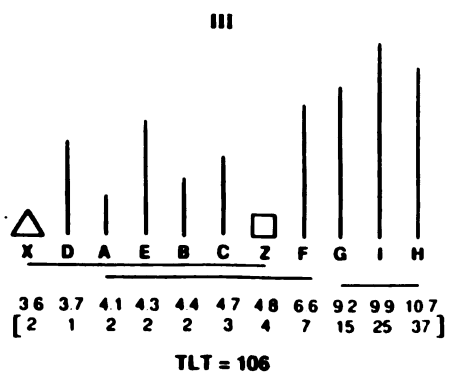
Figure 6. The ranked position, by instar, of the number of gypsy moth larvae attracted to columns with different heights. Columns A to I, respectively, represent the shortest to tallest columns; X and Z, respectively, represent larvae that exceeded the 30-min test period and larvae that wandered out of the arena. Numbers for columns above the same horizontal line are not significantly different (Waller-Duncan k-ratio test, k=100). Numbers below each column are the mean ranked numbers of the first 20 larvae attracted. Numbers within brackets are the total number of larvae attracted to each column. (TLT = total larvae tested for each instar until 20 larvae oriented to a column; instars tested = neonate, I, III, V^{+} and V^{+Field}).


V+
X Z B A C E D H F G I
32 32 32 39 39 46 68 89 90 96 97
[0 0 0 1 1 2 7 23 19 23 24]
TLT = 100


V+ Field
X A C Z E B D F I H G
25 32 40 41 51 55 69 80 82 85 100
[0 1 3 4 6 5 8 17 17 15 24]
TLT = 104


Neonate
Z A B C D X E F G H I
38 38 38 38 38 53 54 76 88 95 104
[0 0 0 0 0 2 2 13 26 21 36]
TLT = 102


I
Z C X D A F B E H G I
41 41 43 45 50 55 55 60 84 89 97
[1 1 1 3 2 4 7 12 22 18 29]
TLT = 102


III
X D A E B C Z F G I H
36 37 41 43 44 47 48 66 92 99 107
[2 1 2 2 2 3 4 7 15 25 37]
TLT = 106

versus 68, 109 versus 108, 124 versus 120 and 133 versus 132, which produced a chi-square value of 22.35.

Species of Tree. The numbers of larvae attracted to bolts of authentic tree trunks were noticeably affected by the species of tree (Table 5). Consistently more larvae (α=0.05) were attracted to bolts of red oak than to bolts of either trembling aspen or paper birch, for each instar tested. The numbers of larvae that wandered out of the arena or that exceeded the allowed time period were significantly less than the number attracted to red oak for each population (α=0.05). As might be expected from previous diameter and height results, the youngest larvae (neonates) exceeded the 30-min time period most frequently. However, the numbers that exceeded the time period or that wandered out of the arena were also small compared with the total numbers of larvae tested. The results were almost identical for laboratory-reared instars. Red oak was also preferred by field-collected fifth- and sixth-instar larvae (α =0.05); however, trembling aspen and paper birch were selected second and third in order of preference and the preference for each was significantly different from that for red oak and each other.

Discussion

Larval Preference for Black versus White Artificial Trees. The results in Table 1 clearly demonstrate the strong attraction of all gypsy moth larval instars crawling on a horizontal surface for a black vertical column. In my experiments, this behavior was not affected by the storage of egg masses for several months or the use of artificial diet. First-instar larvae that emerged from eggs held until 15 September (I-SEPT) and larvae reared to the third instar on red oak (III-OAK) showed the same preference for black columns as did other populations. The choice of larvae on kraft paper on the floor (I-PAP) for black columns suggests that larvae do not depend on silk trails, pheromones

Table 5. Larval gypsy moth response, by instar, to vertically positioned bolts 13.8 ± 3.1 cm wide by 1 m long, from three naturally occurring host tree species.

	Mean number of larvae recovered*				
Treatment	Neonate	I	III	V^{+}	V^{+Field}
red oak	15.2a	16.6a	15.2a	18.0a	7.6a
trembling aspen	1.0c	0.6b	2.4b	1.0b	5.4b
paper birch	0.2c	0.8b	1.6bc	0.8b	2.6c
exceeded time limit**	3.6b	1.2b	1.2bc	0.0b	0.0d
exited arena	0.2c	0.8b	0.4c	0.0b	5.0b

* Instars are identified as in Table 1. Within a column, means followed by the same letter are not significantly different (Waller-Duncan k-ratio test, k=100; Mean squared error, respectively, for each larval population: Neonate = 1.09, I = 1.68, III = 2.69, V^{+} = 0.83 and V^{+Field} = 1.25)

**30 min.

chemical substances associated with silk for orientation; these are important cues that influence the larval behavior of other lepidoptera (Fitzgerald and Peterson 1988). However, my experiments do not rule out the possibility that silk trails, pheromones and possible kairomones of the host do not complement host finding and larval orientation. Liebhold et al. (1986) found that when they removed silk trails from trees by scrubbing them with a brush, they were unable to eliminate the possibility that larvae used pheromones or possible chemical substances associated with the trails to find burlap bands in which to rest.

While climbing on the vertical surface of the Y, significant numbers of laboratory-reared and field-collected fifth- and sixth-instar larvae selected the black side of the column (α=0.05), whereas first, second, third and fourth instars showed no preference for either color (α=0.1) and neonate larvae preferred white (α=0.1). The differences between larval behavior on a horizontal plane (Table 1) and that on a vertical surface (Table 3) could be explained by several hypotheses. For example, the selection of black columns by all larval instars on a horizontal surface suggest that larvae orient to dark objects contrasted against light backgrounds. This scenario occurred both in the laboratory and the field, where black columns were contrasted against either light beige walls or the background of sky light. In the field, tree trunks would also be contrasted against sky light, but it is also possible that larvae discriminate between objects that present contrasting images in infrared or ultraviolet light. In the laboratory, Hundertmark (1937a) found that first-instar larvae of the nun moth, Lymantria monacha (L.), never approached posts whose color was the same as the background. Irrespective of the mechanism employed, the ability to identify dark columns (tree trunks) by dispersing first-instar gypsy moth that land on the forest floor (Leonard 1981), late-instar larvae moving between trees (Barbosa 1978; Liebhold et al. 1986), or larvae accidently

dislodged from a tree, is highly advantageous for survival because it allows displaced larvae to find a prospective host quickly and effectively.

The examination of black versus white preferences of larval gypsy moth was initiated as a preliminary investigation of field observations of fifth- and sixth-instar larvae on paper birch and trembling aspen. Observations indicated that late-larval instars selected dark areas on the bole of these trees as resting locations during the day. This behavior is indiscernible on trees with dark bark (red oak) or trees with uniformly colored bark on which larvae resting locations do not contrast with the adjacent bark. A possible hypothesis that explains the selection of a dark color by climbing fifth- and sixth-instar larvae (Table 3) is a behavioral response designed to camouflage late-instar larvae from predators that hunt visually on lightly colored trees or trees without protective bark flaps. In one study (Campbell et al. 1975a,b), ≅90% of the late-larval instars died, but only 7.5% of the mortality could be attributed to parasites and disease. It was suggested that predators that hunt visually were the principal mortality factor; larval survival was attributed to the selection of protected resting locations (Campbell and Sloan 1976).

The selection of dark areas by late instars may also be influenced by temperature; caterpillars, especially dark-colored ones such as those of gypsy moth, are susceptible to heat prostration and desiccation (Doane and Leonard 1975; Dethier 1989). However, Knapp and Casey (1986) presented a strong argument that gypsy moth caterpillars do not regulate their body temperature. Further studies would be useful to evaluate how temperature influences the choice of resting locations by gypsy moth.

The attraction of a significant number of neonate larvae (α=0.1) to a white surface while climbing was not exhibited by first-instar larvae that had been fed, or by

any of the other instars tested. Neonate larvae are positively phototropic and negatively geotropic (Leonard 1981; Weseloh 1989); after leaving an egg mass, they climb to the top of a tree to disperse before feeding (McManus 1973). It is possible that the attraction of neonate larvae to white is a response to higher levels of reflected ultraviolet light from a white surface. In a forest stand, the intensity of ultraviolet light above the forest canopy would be greater than within the stand and would attract larvae to the canopy for dispersal. However, larval attraction to the forest canopy may be suppressed by feeding, as when satiated first instars become too heavy to disperse effectively and it is more important for larvae to prepare a mat of silk to ameliorate molting (Leonard 1967). The indifference to either color by other larval instars (second, third and fourth) while climbing is also possibly a result of feeding. In a study that investigated larval orientation reactions in response to stimulation by light, Wellington (1948) found that third-instar spruce budworm, Choristoneura fumiferana (Clem.), larvae did not respond to light when starved. Satiation may induce a similar behavioral response in gypsy moth. However, this does not explain the indifference of fourth-instar larvae to either color and the difference in preference for black among fourth, fifth and sixth instars. These instars migrate down trees in the morning to select resting locations for the day and move back into the crown at night to resume feeding (Leonard 1981; Roden et al. 1990). The fourth instar of gypsy moth larvae may represent a transitional period before genes that control the selection of dark areas on a tree by fifth and sixth instars are activated. It is also possible that the preference of fifth- and sixth-instar larvae for black is influenced by diet. Lance et al. (1986a) suggested that changes in the feeding-rhythm behavior of late-instar gypsy moth larvae may be influenced by defoliation-induced changes in leaf quality.

The preferences of larvae on vertical and horizontal surfaces were unaffected by their sex except for female neonate larvae. It is possible that this discrepancy can be attributed to the subsequent random mortality of neonate females that chose white and

the reduced sample size for comparison that resulted from dividing the initial population by two when identifying sex.

Diameter, Height and Species of Tree. There was no observed difference among larval instars for response to either the horizontal or vertical angles presented by a column. A nonsignificant chi-square value for the proportion of larvae attracted to a given diameter as a function of θ confirms that attraction to a column (and, presumably, to tree trunks) is a direct function of the angle. That is, when all other stimuli are equal, larvae will be attracted to the host with a diameter that presents the largest angle. Of course, the angle will vary depending on the distance between the caterpillar and the host and where there are two hosts with equal diameters, the nearest host will present the largest angle and, hence, be more attractive. Laboratory observations of larval attraction to the nearest column support this (Table 2).

The chi-square value for height was significantly different (α=0.05) for the expected larval distribution as a function of β (Figure 4b). Differences between the observed and expected values for the two shortest columns contributed 17.8 units to the chi-square value of 22.35 and indicate that proportionally more larvae were attracted to the two smallest columns than would have been expected. There are several possible explanations why the attraction of larvae to the different column heights is not distributed as a function of β. For example, field-collected larvae accounted for 6 out of the 12 larvae attracted to the 40-mm column. It is possible that this disagreement can simply be attributed to a type II statistical error. Hungry, field-collected fifth- and sixth-instar larvae not accustomed to being restrained may have been agitated by being confined overnight in a Petrie plate. These larvae were the most active and spent the least time in the arena before choosing a column (Table 4). Alternatively, the efficiency of finding a host may have been adversely affected because the upper portion of larger columns

disappeared against the background of the forest canopy and, hence, they did not appear much taller than shorter columns. It is also possible that the sensitivity of larvae to vertical angles (height) is less than it is for horizontal angles (diameter) and that height, as a stimulus, may be less important than diameter for host colonization. Nevertheless, observations about diameter and height confirm that the horizontal and vertical visual angles subtended by an object are both important linear dimensions that strongly influence orientation of larva of L. dispar. Similar findings of crude form perception have been reported. Saxena and Khattar (1977) reported that larvae of Papilio demoleus L. recognized differences in the vertical and horizontal angles subtended by vertical sheets of Citrus leaves. Hundertmark (1937b) also observed that larvae of L. monacha L. show a greater response to larger objects than to smaller ones offered together at the same distance and, when larvae were presented with objects of different heights set at different distances so that the visual angles were the same, almost all larvae showed equal preferences for the objects.

A significant preference by all larval instars for red oak bolts compared with trembling aspen and paper birch bolts (Table 5) suggests that gypsy moth larvae discriminate among different tree species based on color because other studies indicate that it is unlikely that the olfactory range of caterpillars exceeds a distance of 1 cm (Saxena and Khattar 1977; Cain et al. 1983). Hundertmark (1937a) found that larvae of the nun moth distinguished between colors. From preliminary behavioral experiments I have conducted (unpublished data), it appears that larval gypsy moth can also detect different wavelengths of light.

The ability of gypsy moth caterpillars to distinguish between vertical and horizontal linear dimensions and the possibility that contrasting images or the wavelength of light presented by an image, or both, influence larval behavior has important

implications for the colonization of many species of trees and may influence the population dynamics of gypsy moth. For example, species of trees with light bark that is not strongly contrasted against skylight, or trees with bark that reflects different wavelengths of light may be less attractive than preferred species (i.e., oak) with darker trunks, which may be correlated with high-quality food resources. Since significantly more larvae in my experiment were attracted to red oak than to either paper birch or trembling aspen (Table 5), it is likely that proportionally more red oak would be colonized in northern hardwood forests in which red oak, paper birch and trembling aspen are commonly found together. Where low winter temperatures do not inhibit overwinter survival (Sullivan and Wallace 1972), gypsy moth larvae at non-outbreak population levels may colonize red oak in mixed stands, not only because these trees provide superior nutritional suitability and palatability (Hough and Pimentel 1978; Barbosa and Greenblatt 1979) and leaves with a lower pH, which enhances survival (Keating and Yendol 1987), but because red oaks are also frequently the tallest, darkest and largest-diameter trees found in a forest. Further, since gypsy moth larvae are attracted to the largest-diameter and tallest objects, it is likely that the identification of these stimuli may also explain why "wolf trees" sustain high population levels of gypsy moth for several seasons. Mason and McManus (1981) speculated that high larval population levels were maintained on "wolf trees" (a large-diameter branching white oak, Quercus alba L.,) because the fractured silk threads of dispersing first-instar larvae became entangled with the many branches on this type of tree and first-instar larvae did not become dislodged during dispersal. In addition, I suggest that this phenomenon also occurs because these trees are the tallest and largest-diameter trees in a forest and, hence, attract more larvae than other trees and, because of their size and microclimates (i.e., under bark flaps), which enhance survival (Mason and McManus 1981; Lance and Barbosa 1982), support large populations.

How increasing the distance from a host will affect larval behavior and the relative efficiency of finding a host at different distances is unknown. All my measurements of the stimuli that affect gypsy moth visual foraging behavior were made at distances of 0.5 m. Dethier (1989) suggested that the effective distance for crude form perception in caterpillars is not likely to exceed 30 cm, and cited work by Ichikawa and Tateda (1982) to support this contention. The distance reference cited by Ichikawa and Tateda was quoted from Hundertmark (1937b) and is the distance at which Hundertmark found that caterpillars could no longer distinguish between differences in height of 1 cm for columns with widths between 13 and 19 cm. A distance of 30 cm, however, should not be considered the maximum distance at which caterpillars can perceive different crude shapes. Fifth- and sixth-instar larvae in my experiments directly approached columns from distances of 0.5 m (Figure 3c) and Doane and Leonard (1975) found that larval gypsy moth are attracted equally to vertical objects at distances of 1 and 2 m; in their experiment, approximately one-quarter of the larvae tested responded at 3 m, but no response was obtained from larvae at 4 m. Differences of 1 cm in the height of an object, or in the angle presented by this difference, are probably not significant in the field. It is more likely that an optimal height-diameter ratio exists for a perceived object and that the combination of height and diameter has a synergistic effect, but this ratio and the distance for effective perception of differences in horizontal and vertical angles by gypsy moth larvae must be quantified by further research. Such synergistic effects have been noted for adult Diptera (Moericke et al. 1975; Miller and Harris 1985).

My study suggests that host selection by L. dispar larvae involves information from different sensory modalities. The suggestion that selection of a host by gypsy moth can be best explained by an inverse relationship between foliage quality and the frequency of dispersal (Lance 1983) is too naive. The experiments in this chapter clearly demonstrate that visual cues are important stimuli for this herbivore. Visual and chemi

cues may complement each other and influence host selection either simultaneously or sequentially, or both; however, the mechanism for this is unknown. For example, L. dispar may respond to olfactory stimuli (kairomones) emanating from the host in conjunction with visual stimuli and, on reaching the host, initiate feeding in the presence of chemotactile stimuli that influence larval acceptance or rejection. Alternatively, only visual stimuli from the host may be responsible for larval orientation and, on reaching the host, chemotactile stimuli determine if the host is rejected or accepted. The identification of visual stimuli that influence host colonization by larval gypsy moth has important implications for the use of burlap bands in monitoring gypsy moth larval and pupal populations. Because larvae are influenced by the species, diameter and height of the host, these variables may be important considerations for standardizing burlap banding in operational monitoring systems. The color of the burlap material used should also be considered.

The foraging repertoire and the ecological responsiveness of the gypsy moth is richer than previously envisioned. In addition to chemical cues, visual cues are important stimuli that influence host colonization by this herbivore.

CHAPTER TWO

Influence of Current Defoliation and Different Tree Species on Gypsy Moth, Lymantria dispar (L.), Growth and Development

Introduction

Insect injuries can often elicit physiological changes in plants that render them less suitable for future herbivore generations (Haukioja and Niemela 1977; Niemela et al. 1979; McClure 1977, 1979, 1980). It may also increase within- (Way and Cammell 1970; Whitham 1983) and between-plant variation (Schultz 1983) in nutritional and defensive chemistry, which can affect herbivore feeding and host acceptance (Feeny 1970; Raupp and Denno 1983; Meyer and Montgomery 1987). Such changes have been described as rapid induced resistance (RIR) and delayed induced resistance (DIR). However, their adverse effects on insect populations are far from clear (Wratten et al. 1990). It has been suggested that RIR may stabilize insects densities (Haukioja 1990), whereas DIR contributes to population cycles and the decline of outbreaks (Haukioja et al. 1988). In contrast, some studies have reported negligible effects (Fowler and Lawton 1985), or even improved growth and survival on trees which have been previously damaged (Niemela et al. 1984; Haukioja et al. 1990).

Several studies have investigated the relationship between the gypsy moth, Lymantria dispar (L), defoliation and host plant quality (Wallner and Walton 1979;

Schultz and Baldwin 1982; Valentine et al. 1983; Rossiter et al. 1988; Barbosa et al. 1990a, 1990b). Without exception, they have established that tree species common to the forests of New England, such as red oak, Quercus rubra L., produce defensive plant chemicals that can adversely affect larval development. However, little is known about trembling aspen, Populus tremuloides Michx., and paper birch, Betula papyrifera Marsh., two very abundent trees in the Great Lakes basin. It has been reported (Witter et al. 1990; Roden and Surgeoner 1991) that trembling aspen produces more fecund pupae faster than red oak. It has also been suggested that outbreaks of gypsy moth have occurred in stands of trembling aspen (Leonard 1981; Witter et al. 1990). However, the outbreak potential of less preferred hosts, such as trembling aspen and paper birch (Houston 1979), has never been investigated. It is not only important to identify those species of trees in the forests of the Great Lakes which provide the greatest nutritional potential as hosts for the development of gypsy moth, but also to determine if damage-induced changes in plant chemistry occur, and if so, how these host changes affect larval development and growth. In this study I compared survival, development and fecundity of gypsy moth larvae reared on trembling aspen and paper birch to those of larvae reared on red oak, at two levels of defoliation designed to simulate hosts with and without RIR.

Materials and Methods

In 1986 I selected a 2-ha site situated 10 km northeast of Arden, Ontario (44°43'N, 76°56'W) which was typical of sites where gypsy moth would be expected to do well (Houston and Valentine 1977; Houston 1979). The site consisted of saplings that had reestablished on abandoned farmland and were inspected in 1986 and 1987 to insure that they had not been defoliated or infested with other herbivores. In 1987, numerous forest tent caterpillar, Malacosoma disstria Hbn., eggs were found on several trees. These were removed by hand from experimental trees in the spring of 1988 and then the bas

each tree was coated with Stickum® (Seabright Enterprises, 4026 Harlan St., Emeryville, CA) to prevent inter-tree herbivore movement. Study trees were dispersed throughout the stand; the mean diameter and height were 5.51 ± 0.18 cm and 5.9 ± 0.08 m, respectively. Each tree was selected so that it had full exposure to the sun because shading may decrease concentrations of carbon-based secondary metabolites such as phenolics (Larsson et al. 1986; Mole et al. 1988).

I used larvae from gypsy moth egg masses that I collected randomly on 10 April 1988 at the edge of a new infestation at Kaladar, Ontario (44°39'N, 77°07'W). These were surface-sterilized (Shapiro 1977) and then held a $^{+}5^{o}C$ until incubation so that larval emergence could be synchronized with gypsy moth emergence in the field. A randomized complete block design, with a two by three factorial arrangement of treatments, was used to compare gypsy moth survival, pupal weight and the period of time required by larvae to pupate. The two experimental factors, level of defoliation (0 and 50%) and tree species (trembling aspen, paper birch and red oak), were each replicated five times. Gypsy moth larvae, reared on artificial diet (Bell et al. 1981) in the laboratory until the second instar, were held at 10°C until there were sufficient larvae for each replication. Five larvae were then selected at random and enclosed with foliage from a terminal branch in four 50- by 30-cm nylon mesh bags on each tree. During the larval feeding period, which lasted from 26 of May to 17 July, nylon bags secured around the opening with fabric ties, were randomly dispersed throughout the crown of each tree and were moved to new terminal shoots weekly. Foliage in a bag was always sufficient to insure that larvae never consumed more than 50% of the available food. Shoots that were used as feeding sites were identified with flagging tape and were not used again. Light transmission through the nylon bag, measured with a light meter, was reduced by ≅ 15%. The placement of larvae on the trees was synchronized with second-instar larval development in the field; replications 1 to 5 were placed on trees on 26, 27, 28, and 30

May and on 3 June, respectively. To reduce experimental variation, defoliated and undefoliated trees within each replication were grouped together by the proximity of their location within the stand, their diameter and height, the day that second-instar larvae were placed on them and the date leaves were torn in an attempt to simulate defoliation. The mean initial second-instar larval weight (measured on the day larvae were placed on the tree and after they had been removed from storage for 12 h) was used as a covariate. Pupae were collected from the nylon bags and weighed within 24 h of pupation.

I simulated gypsy moth defoliation by tearing leaves by hand (parallel to the leaf mid-rid) throughout the canopy of each tree on 3 occasions (6-10 June, 15 June and 22 June) at defoliation levels that closely corresponded to the amount of foliage removed by gypsy moth on trees in a nearby infestation. For the first two tearings, every 10th leaf was torn in half (5% defoliation); this coincided to the damage that occurred when the majority of larvae reached third- and fourth-instar development in the field. On the final tearing date, every remaining leaf was torn (50% cumulative defoliation) coincident with fifth- and sixth-instar larval development. The tearing of foliage for the first defoliation was completed at the rate of one replication per day; for the last two tearings, all replications were completed within a day. Tukey's test ($\alpha = 0.05$) was used for separation of the means for gypsy moth pupal weight, development time and survival. Data from the fifth replication were excluded from the analysis because of high larval mortality.

Results

Pupal weight. Both defoliation and tree species affected female pupal weight, but their interaction was not significant (Table 6). Female gypsy moth larvae that fed on defoliated trees produced pupae that weighed ca. 12% less than females that fed on

Table 6. Analysis of variance of gypsy moth pupal weights, as influenced by defoliation and tree species.

Source	Female			Male		
	df	MSE	F	df	MSE	F
Total Corrected	35			63		
Replication	3	0.072	3.58*	3	0.044	7.45**
Defoliation	1	0.186	9.91**	1	0.004	0.78
Tree species	2	0.826	41.16***	2	0.059	10.04**
Defoliation X Tree species	2	0.040	2.01	2	0.002	0.43
Covariate (mean L_2 weight/cage)	1	0.148	7.37*	1	0.038	6.46*
Experimental error (variance between trees)	9	0.020	0.77	14	0.005	2.18*
Sampling error (variance between cages)	17	0.026		40	0.002	

* Significant at α=0.05

** Significant at α=0.01

*** Significant at α=0.001

undefoliated trees (Table 7). The smallest female pupae (0.849 g) came from red oak (Table 8); these were significantly smaller than pupae from females feeding on paper birch (1.13 g), which were intermediate and significantly smaller than pupae from females feeding on trembling aspen (1.43 g). Tree species was the only factor that affected male pupal weight: oak < paper birch < trembling aspen (Table 7 and 8). Interestingly, the covariate (mean initial second-instar larval weight) was significant for both female and male pupal weights (Table 6). This, implies that small differences in initial size among early instars are still significant and expressed after weeks of feeding on their host plant.

Development Time and Survival. The number of days required by both male and female larvae for development from second-instar to pupation was not affected by defoliation, only by host species (Table 9). Female larvae that fed on trembling aspen required 4 fewer days to complete development than did females reared on red oak. Female larval development time on paper birch was intermediate, but not significantly different from times on either trembling aspen or red oak (Table 10). Similarly, male larvae that fed on trembling aspen developed about 4 days faster than larvae that fed on either paper birch or red oak (Table 10).

Gypsy moth mortality, observed bi-weekly, was apparently unaffected by either defoliation or tree species (Table 11). However, it may have been masked by severe larval mortality that resulted from Podisus placidus Uhl. (Pentatomidae), which attacked larvae through the nylon screening as they crawled on the interior surface of the bag. The number of larvae that escaped from cages in the experiment or that died as a result of nuclear polyhedrosis virus (NPV) infections was negligible (Table 12).

Table 7. Mean pupal weight for gypsy moth larvae reared on undefoliated and defoliated trees, averaged over host species. Mean standard errors for females and males = 0.02 and 0.005, respectively.

	Mean pupal weight (g)*	
Treatment	Female	Male
Undefoliated	1.144a	0.433a
Defoliated	0.999b	0.423a

* values in a column followed by different letters are significantly different ($P<0.05$, Tukey's honestly significant difference test).

Table 8. Mean pupal weight for gypsy moth larvae reared on trees of three host species, averaged over defoliated and undefoliated treatments. Mean standard errors for females and males = 8.86 and 7.13, respectively.

	Mean pupal weight (g)*	
Treatment	Female*	Male*
Trembling aspen	1.429 a	0.494a
Paper birch	1.130b	0.404b
Red oak	0.840c	0.386b

* values in a column followed by different letters are significantly different ($P<0.05$. Tukey's honestly significant difference test).

Table 9. Analysis of variance for gypsy moth development time, as influenced by defoliation and tree species.

	Female			Male		
Source	df	MSE	F	df	MSE	F
Total Corrected	35			63		
Replication	3	126.11	14.24**	3	84.27	11.81**
Defoliation	1	20.30	2.29	1	4.68	0.66
Tree species	2	40.10	4.53*	2	47.08	6.60**
Defoliation X Tree species	2	8.83	1.00	2	0.30	0.04
Covariate (mean L_2 weight/cage)	1	2.30	0.26	1	20.33	2.85
Experimental error (variance between trees)	9	8.86	2.07	14	7.13	1.84
Sampling error (variance between cages)	17	4.27		40	3.87	

* Significant at α=0.05

** Significant at α=0.01

Table 10. Mean development time (days) for female and male gypsy moth larvae, as influenced by host species averaged over defoliated and undefoliated treatments. Mean standard errors = 8.86 and 7.13, respectively.

	Mean development time (days)	
Treatment	Female*	Male*
Trembling aspen	46.1a	40.8a
Paper birch	48.4ab	43.6b
Red oak	50.4bc	44.0b

* values in a column followed by different letters are significantly different ($P<0.05$, Tukey's honestly significant difference test).

Table 11. Analysis of variance for gypsy moth survival, as influenced by defoliation and tree species. No results were significant at α=0.05.

	Female			Male		
Source	df	MSE	F	df	MSE	F
Total Corrected	35			63		
Replication	3	0.747	0.77	3	0.684	0.43
Defoliation	1	0.012	0.01	1	0.459	0.29
Tree species	2	0.970	1.00	2	0.585	0.37
Defoliation X Tree species	2	0.761	0.79	2	1.319	0.83
Covariate (mean L_2 weight/cage)	1	1.724	1.78	1	0.001	0.00
Experimental error (variance between trees)	9	0.969	1.45	14	1.584	1.37
Sampling error (variance between cages)	17	0.669		40	1.153	

Table 12. Source of mortality and number of larvae surviving from second-instar to adult eclosion for female and male gypsy moth larvae reared on defoliated and undefoliated host species.

		Deaths from		Survivors	
Treatment	n	NPV*	P. placidus	Female	Male
Undefoliated trees	240	0	141	27	62
Defoliated trees	240	2	134	29	70

*nuclear polyhedrosis virus

Discussion

The primary focus of this study was to determine if two of the most common deciduous trees found in the forests of the Great Lakes region respond to defoliation with an immediate or rapid induced response (RIR) that impairs the development of gypsy moth larvae. At the same time, I also wanted to compare the nutritional suitability of these species in the field with that of red oak. In the laboratory, Roden and Surgeoner (1991) reported that trembling aspen and paper birch hosts were superior to red oak for gypsy moth.

Other studies besides have shown that the nutritional quality of food for gypsy moth declines after severe defoliation (Wallner and Walton 1979; Schultz and Baldwin 1982; Rossiter et al. 1988). There is evidence that leaf damage occurring in the spring has a much more detrimental effect on herbivore growth and development than damage later in the season (Wratten et al. 1984). Moreover, insect-caused damage may elict a stronger defensive reaction than artificial damage (Hartley and Lawton 1990; Wratten et al. 1990). Finally, all three tree species used in the present study are hosts that are characterized by leaf chemistry comprised mostly of phenolics (Barbosa and Krischik 1987), which have been shown to vary inversely with gypsy moth pupal weight and fecundity (Rossiter et al. 1988). Thus, differences that occurred in the present study can only be attributed to differences in foliage quality that resulted because of defoliation or that were characteristic of the host species.

Mean pupal weights for female and male gypsy moth larvae reared on undefoliated red oak in this experiment fell within the range reported by Wallner and Walton (1979) for female and male L. dispar reared on undefoliated black oak, Quercus velutina Lam., 0.90 and 0.41 g versus a range of ≅ 0.75 to 1.05 and ≅ 0.34 to 0.42 g,

respectively. Male pupal weights from larvae fed on defoliated oaks in both studies were also comparable (0.36 g in this study versus an range of ≅ 0.32 to 0.36 g in their study). However, the mean female pupal weight (0.68 g) of larvae fed on defoliated red oak in this study was less than the lowest female pupal weight (range 0.69 to 0.81 g) from larvae fed on comparable black oak and noticeably less than the ≅ mean (0.76 g) for the different sites reported by Wallner and Walton.

Male pupal weights (a range of ≅ 0.35 to 0.42 g) on undefoliated grey birch, Betula populifolia Marsh, in Wallner and Walton (1979) were comparable to those on undefoliated paper birch in my study (0.41 g). Mean male pupal weight on defoliated paper birch trees was ca 20% higher than that on defoliated grey birch (0.40 g in my study versus a range of ≅ 0.32 to 0.34 g). Pupal weights of female larvae that fed on undefoliated and defoliated paper birch in my study were both consistently higher than those of larvae that fed on gray birch (1.17 and 1.07 g versus a range of ≅ 0.69 to 1.05 and 0.63 to 0.87 g, respectively). Thus, although there are small differences between female pupal weights among different studies on oak and birch, the male pupal were very similar on all trees. There are several possible explanations for this.

Because male larvae have only five instars compared to the six of females, it is possible that the shorter development time, and hence the lower consumption of defoliated foliage, does not affect male development to the same degree as female development in the first year of defoliation. A second year of subsequent defoliation might have exposed male larvae in my study to increased levels of plant phenolics and other qualitative changes in foliage that may trigger developmental abnormalities and reduced pupal weight. In the second year of the Wallner and Walton (1979) experiment, male pupal weight was significantly affected by defoliation whereas female pupal weight was not. Another possible explanation is that female development may be affected mor-

by a nutrient or water imbalance than male development. It has been demonstrated that slower growth and less efficient utilization of plant material and nitrogen may be attributed to reduced leaf water content (Scriber 1977; Mattson and Scriber 1987). However, it is also conceivable that differences between my study and that of Wallner and Walton could be attributable to disparities between the way trees were defoliated. The defoliation treatment in my experiment was applied similarily to all species while the one used by Wallner and Walton was different for oak and birch. This discrepancy may also explain the absence of a defoliation X tree species interaction in my experiment, which implies that RIR occurred in a parallel way in the tree species examined; whereas, the presences of a defoliation X tree species interaction in Wallner and Walton suggests RIR does not occur similarly in all trees species.

The time required for larval development in my study was not affected by defoliation; however, host species strongly influenced the time required for development (Table 9). Larvae always developed slower on red oak than on trembling aspen and paper birch (Table 10). These results differ somewhat from those of Wallner and Walton (1979), who found that defoliation of oak prolonged larval development; the development of larvae on grey birch was not affected by defoliation, and this agrees with my observations on paper birch. My observed development time on red oak for both sexes was ≅ 10% less than that reported by Wallner and Walton for gypsy moth larval development on black oak. The times required for female and male larval development on paper birch were 23 and 20% less than larvae developing on grey birch. Shorter developmental periods for northern strains of gypsy moth have been reported by Leonard (1966), who found that gypsy moth from Quebec developed faster than those from Connecticut. He attributed these differences to the adaptation of larvae to a northern climate.

Pupal weights and development times on undefoliated hosts in this study are ≅ 25 and 32% less, respectively, than the pupal weights and development times reported by Roden and Surgeoner (1991) for larvae reared on excised foliage of the same hosts in the laboratory at constant temperature and humidity. Male and female pupal weights of larvae reared on undefoliated trembling aspen and red oak in my study were ≅ 43 and 44% and 30 and 16% heavier, respectively, than pupal weights of gypsy moth larvae reared on the same tree species in lower Michigan in 1988. Witter et al. (1990) found that pupal weight varied significantly by year, site, tree species and trembling aspen clone. Observation of these sources of variation would explain differences in pupal weight between their study and ours for larvae reared on the same tree species. They would also explain differences in pupal weight and development time between my study and those reported by others (Wallner and Walton 1979; Roden and Surgeoner 1991). Disparities may have occurred because of differences in rainfall, temperature and geographic location that affected the insects, the trees or both; although, possible differences between field and laboratory studies that result from laboratory rearings at constant temperature and humidity should not be discounted.

Close correspondence of my pupal weights with those of Wallner and Walton (1979), comparable pupal weights with those reported by Maksimovic (1958) and observation about gypsy moth development on trembling aspen that are similar to those reported by others (Witter et al. 1990; Roden and Surgeoner 1991) or studies that have reported that gypsy moth development on oak does not always yield the most fecund pupae (Barbosa 1978; Lance and Barbosa 1982; M.E. Montgomery and J.C. Schultz, personal communication), impart confidence to my findings and reinforce my belief that the results I obtained would parallel unfretted larval development in the field. It is noteworthy, however, that all studies of gypsy moth development on trembling aspen share one particular finding: pupal weights of larvae fed on trembling aspen, a host not

traditionally associated with outbreaks of gypsy moth, are heavier than pupal weights of larvae that fed on red oak, a traditional host of L. dispar. Since gypsy moth development on trembling aspen produced potentially more fecund pupae in a shorter development time than larvae reared on red oak, an immediate question is whether pure stands of trembling aspen, paper birch or both will (or can) support outbreaks of gypsy moth in the forests of the upper Great Lakes.

Survivorship, development and reproductive success of an insect depends in part on its ability to select appropriate sources of nutrition. Consequently, an insect's host preference is normally closely correlated with the most nutritionally suitable host in its environment (Tabashnik 1986). Nevertheless, mismatches between host preference and nutritional suitability may occur. For example, imprecise correspondence between host preference and nutritional suitability has been attributed to ecological factors such as parasitism and predation (Smiley 1978; Price et al. 1980) which can make the most nutritious host inappropriate, or host finding and acceptance behavior that is not directly related to host suitability because suitable habitats are avoided (Singer 1971; Chew 1981). I suggest that the imprecise correspondence between gypsy moth and hosts that have been identified as potentially more nutritious exists because gypsy moth development and potential population increases are restricted on these hosts due to the effectiveness of NPV and to physical features of the host that affect larval behavior.

The primary natural regulator of North American gypsy moth populations is NPV (Podgwaite 1981). Gypsy moth survival in my study was not affected by tree species or defoliation (Table 11); however, these results should be viewed conservatively. Egg masses used in my study were sterilized to reduce larval mortality as a result of NPV; only 2 larvae (< 0.05%) showed symptoms that could be attributed to NPV (Table 12). In naturally infested stands, a much higher percentage of the gypsy moth population wou1

be infected. Reports of gypsy moth NPV mortality that average 36% are not uncommon and some estimates are as high as 56% (Podgwaite 1981). Gypsy moth susceptibility to NPV is influenced, among other things, by the pH of the leaf tissue consumed (Keating and Yendol 1987). The lower foliage pH of traditional gypsy moth hosts, such as red oak, is thought to buffer the high midgut pH of gypsy moth (Schultz and Lechowicz 1986) and make larvae less susceptible to the polhyhedral inclusion bodies (PIB) of NPV, which require alkaline conditions for solubility and infection (Keating and Yendol 1987). Hydrogen or covalent bonding, or both between phenolic compounds and viral proteins are thought to be responsible for inhibition of NPV (Keating et al. 1988; Keating et al. 1990). Schultz et al. (1990) found that the high LD_{50} value for gypsy moth from ingested PIBs in stands of oak with high hydrolyzable tannin contents was primarily associated with reduced NPV effectiveness compared to condensed tannins, but small compared with the LD_{50} for ingested PIBs on tree species like trembling aspen. For this reason, I believe that the success of gypsy moth in the Great Lakes basin will be limited in stands dominated by trembling aspen and paper birch, not only because of the demonstrated effectiveness of NPV on such hosts, but also because larvae are highly attracted to oak because of its darker color and its larger diameter and height (Roden et al. 1992). Gypsy moth may invade trembling aspen strands, and population growth may occur, but I expect that the incidence of NPV will increase rapidly in these populations and that they will collapse quickly.

The effectiveness of NPV on these populations may also be enhanced by tremulacin, a phenolic glycoside found in trembling aspen foliage. Lindroth and Hemming (1990) indicated that increased concentrations of tremulacin in association with increased levels of defoliation may overload the esterase detoxification capacity of gypsy moth larvae and lead to impaired survival, growth or both. Although Leonard (1981) reported that gypsy moth has established and maintained populations on trembl

aspen in the boreal forest where oaks are less common, specific occurrences were not cited. Witter et al. (1990) also reported outbreaks of gypsy moth in stands of trembling aspen, but these were either in stands of aspen mixed with oak or were transient infestations and support my contention. The lack of reports of gypsy moth outbreaks in stands of trembling aspen in Maine, where infestations should probably have occurred by now because of the state's proximity to the North American introduction point for gypsy moth, or in Ontario, further support my contention. In mixed stands, where species other than oak are common, larvae will be attracted after first-instar dispersal to species with darker trunks (Roden et al. 1992), such as maple (Acer); several studies have shown that species of maple are not optimal hosts for gypsy moth (Hough and Pimentel 1978; Lance and Barbosa 1982; Roden and Surgeoner 1991), therefore, larval development will be impaired. In mixed stands that contain trembling aspen and oak, it is still too early to forecast about the magnitude of the potential threat from gypsy moth. At low population levels, research suggests that most larvae will be attracted to species of oak (Roden et al. 1992); however, further research is required to clarify this issue for several reasons.

First, Meyer and Montgomery (1987) reported that cottonwood, Populus deltoides Marsh., an indeterminate species, concentrates its defenses in young leaves, whereas species of oak, a determinate species, retain one set of heavily defended leaves over the entire growing season. However, the production of defensive chemicals and their association with age-related characteristics are poorly understood (Mooney et al. 1983; Meyer and Montgomery 1987). A tree that can replace leaf area lost to herbivory throughout the season may be less affected by damage than one that cannot (Coley et al. 1985). Second, Schultz et al. (1990) speculated that NPV is likely to play a major regulatory role for L. dispar in stands dominated by weakly inhibitory trees and a minor role in stands comprised mainly of tree species that are inhibitory. They suggested that the ratio between condensed and hydrolyzable tannins was responsible for the influenc

of gypsy moth NPV in such stands. Third, the ratio between condensed and hydrolyzable tannins may influence or may be influenced by the type of defence response employed by the tree (i.e., RIR versus DIR). All species in the present study evoked plant defences that retarded gypsy moth development, and all species are characterized by a leaf chemistry that is comprised mostly of phenolics (Barbosa and Krischik 1987). To better understand the potential for gypsy moth development in forest stands that contain these species, the ratio between condensed and hydrolyzable tannins should be established, including how this relationship varies within and between tree species and how it is influenced by defoliation and resistance. In addition, the manner in which visual stimuli interact and influence inter-tree larval behavior should be assessed. I lost ≅ 60% of the larvae in my experiment to attacks by P. placidus (Table 12); therefore, the potential of this predator should also be investigated in terms of its influence on gypsy moth populations in the Great Lakes basin.

CHAPTER THREE

Laddering: A Climbing Behavior of the Gypsy Moth, Lymantria dispar (L.)

Introduction

While investigating the potential use of ABS plastic pipe as artificial trees in a study of the movement of gypsy moth, Lymantria dispar (L.), larvae, Roden et al. (1990, 1992), I noticed that many larvae had difficulty climbing vertically on a smooth surface. Some larvae, however, experienced no difficulty, although their rate of climb was slow because they would pause frequently and move their head from side to side. Close examination revealed that the larvae were spinning 1- to 2-cm-long sequential strands of silk and using these like the rungs of a ladder to ascend the "tree". Although healthy gypsy moth larvae are known to trail a single silk thread (Leonard 1967, McManus and Smith 1972), descriptions of the use of silk as a mechanism for gaining a foothold (Balfour-Browne 1925; Dethier 1980) are not well documented quantitatively or experimentally. This chapter reports on laboratory experiments to describe the climbing behavior, here termed "laddering".

Materials and Methods

In my study I used several populations of gypsy moth between January and September from 1987 to 1989 to investigate the possibility that gypsy moth larvae were

using silk to construct a "ladder" to assist climbing on a smooth surface. Gypsy moth larvae were obtained from egg masses collected annually in October near Kaladar, Ontario (44°39'N, 77°07'W), and held at $^{+}5^{\circ}C$ until diapause was completed, then were surface sterilized (Shapiro 1977) and incubated at 22°C. Larvae were reared individually on artificial diet (ICN Biochemicals, Cleveland, OH 44128) in 150- by 25-mm screened plastic Lab-Tek Petrie plates at 70% RH with a 16L:8D photoperiod. To investigate the frequency of laddering and how it was affected by the surface being climbed, a randomized complete block design, blocked by time with five replications of 10 larvae each, was used to observe larval climbing behavior on two 50-cm pieces of 5-cm-diameter ABS plastic pipe. A mixture of 250 mL of black paint (Color Your World, Toronto, Ontario M8W 3R5; paint # 5900) and 150 mL of sand sifted through a 20-mesh screen was applied to one piece of pipe to provide a rough surface; the other piece of pipe was covered with the same paint but without sand. The populations tested were: neonate larvae 24 to 48 h old; fed first-instar larvae older than 48 h; second-, third-, and fourth-instar larvae; and pooled fifth- and sixth-instar larvae. All larvae tested were held overnight without food to increase their activity (Leonard 1967). For testing, larvae were gently coaxed from a Petrie plate with a camel-hair brush onto a piece of wooden doweling angled at ca. 30° against the vertical column being tested. As larvae began to climb on the column, the doweling was gradually removed from below.

After determining the frequency of laddering for the different instars, a second experiment, with a two X two factorial arrangement of treatments in a randomized complete block design was conducted with third-instar larvae (because this instar had the highest frequency of laddering) to test the hypothesis that silk was actually used as substrate while climbing a smooth surface. The two factors examined were a larva's spinneret (sealed with glue versus no glue) and the surface (smooth versus rough), providing four treatment combinations: larvae with the spinneret sealed with Crazy Glue®

(to make it inoperative) and larvae without the spinneret glued, climbing on the previously described smooth or rough columns. The number of larvae that were able to climb onto a column and then climb vertically for at least 10 cm was considered an indication that silk production was not necessary for climbing vertically; these data were analyzed with a contingency table. The mean times for larvae completing the 25-cm climb were compared by ANOVA. Each larva was allowed 30 min to complete the climb. For each of the 25 replications, four larvae were randomly selected from the appropriate instar and then anesthetized by placing them in a refrigerator at 4°C for 30 min before randomly selecting two of the four larvae for glueing. The remaining two larvae were handled by placing them under the microscope and touching the spinneret in the same manner used to apply glue to the other two larvae.

In 1988 I attempted to confirm the experiments conducted in 1987 with third-instar larvae, but I was unable to reproduce the observed laddering behavior. After examining larvae from egg masses collected at several different locations, I hypothesized that the likely explanations for the change in behavior between the two years were: (i) I had discovered an uncommon behavior in a particular population of gypsy moth that might be difficult to find again, or (ii) the artificial diet (Bell et al. 1981) substituted for the ICN diet in 1988 had influenced the behavior. (I had replaced the ICN diet with Bell's diet because larvae reared on the ICN diet exhibited developmental problems.) To investigate these possibilities, I compared the frequency of laddering for third-instar larvae randomly selected from several egg masses that were collected from areas near Kaladar with high and low population levels of gypsy moth. Larvae from each source were subdivided into two groups and reared on either Bell's or the ICN diet. The frequency of laddering and the time required to climb 25 cm on the smooth column were analyzed separately for a randomized complete block design with a two X two factorial arrangement of treatments, blocked by time and replicated 25 times with population level

(high versus low) and diet (Bell's versus ICN) as the two factors. After finding that the ICN diet was influencing laddering, I used ICN diet to rear gypsy moth larvae for a randomized complete block design experiment, blocked by time and diameter, with four replications of 10 larvae on each treatment to compare the frequency of laddering and the time required to climb 25 cm on 30-cm bolts of trembling aspen (Populus tremuloides Michx.), paper birch (Betula papyrifera Marsh.) and red oak (Quercus rubra L.). Because I could not see the strands of silk used for laddering on the wooden bolts, except with great difficulty under microscopic examination, I used the characteristic side-to-side head movement of the larvae that I had identified in the previous experiments as an indicator of laddering and silk production. The wood bolts, sealed at each end with paraffin to retard desiccation, were positioned 1 m off the floor by inserting a 2-cm-diameter piece of galvanized pipe into a slightly smaller hole drilled into the center of the base of each bolt. The galvanized pipe was then supported vertically by screwing the other end of the pipe into a floor flange that was fastened with screws to an 18- by 18-cm base of plywood. Bolts were randomly placed 1 m apart in a line between banks of overhead fluorescent lighting in the room. Each replication was repeated with bolts collected from different trees; bolts were randomly arranged within the line to remove the possibility that lighting and/or drafts from the ventilation system influenced the results. The bolts were always selected from what appeared to be the smoothest portion of the main stem below the foliage. Larvae for each replication were released individually from one of 10 L-shaped cardboard platforms previously fastened around the base of each bolt with Elmer's Glue-All® at 36° intervals; the order in which a platform and a treatment were selected for larval release was chosen at random. Between trials, each bolt was wiped with a cloth to remove any silk deposited during a previous test. A Student-Newman-Keuls test (α=0.05) was used for separation of the means.

Results and Discussion

In the initial experiment in 1987, first-, second-, third- and fourth-instar larvae (Table 13) laddered. However, the frequency of this behavior was only significantly different between the smooth and the rough surfaces for third- and fourth-instar larvae. Neonate larvae were never observed laddering; from my observations, it does not appear that they experienced difficulty climbing on either column. Although no laddering was observed for fifth- and sixth-instar larvae during the experiments described in this chapter, laddering was later observed (Figure 7) and recorded on VHS videotape for a single sixth-instar larva climbing on a smooth column of ABS plastic pipe. Copies of the event, which included a visible ladder, are available from the author through the Forestry Canada, Ontario Region, library.

The experiment with the glued spinneret clearly demonstrated that larval gypsy moth deposit silk as a substrate to assist climbing. The chi-square values for the main effects (spinneret and surface), 7.40 and 19.58, respectively, for the number of larvae climbing 10 cm or more were both statistically significant ($p<0.05$); the chi-square value for their interaction (1.90) was nonsignificant ($p>0.1$). All of the 25 larvae on the smooth column with the spinneret glued were unable to climb and repeatedly fell from the column when attempting to do so, whereas 64% of the larvae without the spinneret glued completed the 25-cm climb successfully. Most larvae climbing on the rough column did not experience difficulty climbing; 92% of the larvae with the spinneret glued and 100% of the larvae without the spinneret glued completed the 25-cm climb. Further, because both factors were independent, this indicates a difference in climbing ability between larvae with and without the spinneret sealed. This difference was noticeable on both the smooth and the rough columns; this suggests that larvae also use silk somehow to assist

Table 13. Mean number of larvae per replicate, by instar, that demonstrated laddering behavior on smooth and rough columns of ABS plastic pipe. All larvae were reared on ICN diet.

	Number of larvae*		
Instar	Smooth column (n=10)	Rough column (n=10)	MSE
Neonate	0.0a	0.0a	0.0
I	0.4a	0.0a	0.40
II	0.8a	0.0a	0.85
III	6.6a	0.4b	1.35
IV	4.2a	0.0b	1.35
V + VI	0.0a	0.0a	0.0

* values in a row followed by different letters are significantly different ($P<0.05$, Student-Newman-Keuls test).

Figure 7. Silk ladder used by a sixth-instar gypsy moth larva to climb on a smooth column of ABS plastic pipe.

climbing on rough surfaces even though these surfaces provide structures for their crochets to grasp. Individual spinneret treatment responses, averaged across surface types, showed that 46% of larvae with the spinneret sealed completed the climb versus 84% of larvae without the spinneret sealed; 96% of larvae on the rough column versus 32% of larvae on the smooth column completed the climb when responses to the two surfaces were averaged across the spinneret treatments. The main effects and their interaction were each significant with respect to the time required for larvae to complete the 25-cm climb (Table 14). Larvae without the spinneret glued completed the climb substantially faster on the rough (2.4 min) than on the smooth column (4.86 min). Since larvae with the spinneret glued were unable to climb on the smooth column, no times were recorded. Interestingly, larvae with the spinneret glued required substantially longer to climb the rough column (12.61 min) than larvae without the spinneret glued on the smooth column (4.86 min), which supports previous observations that larvae also use silk to assist climbing on rough surfaces.

In the experiment comparing laddering by third-instar larvae from low- and high-density populations of gypsy moth reared on ICN or Bell's diet, laddering was affected only by diet. The chi-square value (25.99) for the main effect, diet, was significant ($p<0.001$); chi-square values for the population effect and the diet-population interaction, 0.76 and 0.01, respectively, were both nonsignificant ($p>0.1$). Averaged over the main effect of population density, significantly more of the larvae reared on the ICN diet used laddering to assist climbing on the smooth column compared with larvae reared on Bell's diet (66 and 10%, respectively). The time for the larvae to climb 25 cm was also affected only by the main effect of diet. Larvae reared on Bell's diet from both the high- and the low-density populations completed the climb significantly faster than larvae reared on the ICN diet (Table 15). The effect of diet on climbing behavior may be related to larval

Table 14. Mean time for gypsy moth larvae with and without the spinneret sealed with Crazy Glue® to climb 25 cm on a smooth or rough 50-cm column of 5-cm-diameter ABS plastic pipe. Standard error of the mean = 0.55.

	Mean time (min)	
Column surface	Spinneret glued	Spinneret without glue
Smooth	-	4.86
	(0)	(17)
Rough	12.61	2.40
	(23)	(25)

* numbers within brackets = number of larvae (total possible = 25) that completed the 25-cm climb within 30 min.

Table 15. Percent of larvae laddering and mean time for gypsy moth larvae reared on ICN and Bell's artificial diets (averaged over low and high population levels) climbing 25 cm in < 30 min on a smooth column of ABS pipe. Standard error of the mean time = 0.10.

Diet	% laddering	Time (min)*	No. of larvae**
Bell's	10	1.42	43
ICN	66	5.19	47

* differences were significant at $P<0.05$ (Student-Newman-Keuls test).
** number of larvae that completed the 25-cm climb, out of a total of 50.

Table 16. Measures of fitness for 15 larval gypsy moth reared on Bell's and ICN diets.

Population statistic	ICN diet*	Bell's diet*
Mean head-capsule size (mm ± SE)		
Neonate	0.56 ± 0.01a	0.55 ± 0.01a
III	1.52 ± 0.03a	1.62 ± 0.03b
VI	2.47 ± 0.06a	5.40 ± 0.10b
Mean pupal weight (g ± SE)		
Males	0.35 ± 0.03a	0.62 ± 0.02b
Females	0.94 ± 0.09a	1.94 ± 0.14b
Mean larval development time (days ± SE)		
Males	53.6 ± 0.59a	31.7 ± 0.42b
Females	69.6 ± 1.43a	35.4 ± 0.59b

* values in a row followed by different letters are significantly different ($P<0.05$, t-test).

fitness; larvae reared on Bell's diet are larger and develop faster than larvae reared on ICN diet (Table 16).

Frequency of laddering and the speed at which larvae climbed 25 cm on the three species of trees were inversely related. The results for red oak were also significantly different from those for the other two species (Table 17). On red oak larvae completed the 25-cm climb in the shortest time (2.35 min) and were not observed laddering. Larvae climbing on paper birch appeared to have the greatest difficulty climbing; they required the longest time (8.18 min) to complete the 25-cm climb and laddered most frequently (8.3). The climbing time (5.13 min) and frequency of laddering on trembling aspen (7.0) was intermediate between the other two treatments.

My discovery of the laddering behavior was accidental. I have not had an opportunity to search for it thoroughly in the field. Although laddering appears to be induced by an inadequate diet in the laboratory and occurs mostly when climbing on a smooth surface, I feel that because larvae reared on Bell's diet also exhibited the same behavior, there is reason to believe that laddering may occur in the field. Strong et al. (1984) indicated that many caterpillars spin silk thread to aid their attachment as they move about on smooth plant surfaces. Unfortunately, specific references were not cited by the authors; however, other references about the use of silk to aid attachment have usually considered this to be a mechanism that insects have evolved to enable them to skirt plant defences and exploit a defended resource. For example, larvae of the butterfly Mechanitis isthmai Bates (Ithomiidae) successfully avoid trichomes on their spiny host (Solanum spp.) by spinning a network of silk scaffolding across the underside of the leaf, hanging below the spines on silk threads, and feeding safely on the unprotected edges (Rathcke and Poole 1975). Laddering by gypsy moth larvae appears to be a specific larval adaptation that is "triggered" by surfaces that are difficult to climb. The behavior

Table 17. Mean number of gypsy moth larvae per replicate that exhibited laddering behavior on 30-cm bolts of red oak, paper birch and trembling aspen (MSE = 0.86) and the mean time per replicate for larvae to climb 25 cm (MSE = 0.38).

Treatment	Number laddering*	Mean time*	n**
Red oak	0.0a	2.35a	40
Trembling aspen	7.0b	5.13b	34
Paper birch	8.3b	8.18c	33

* values in a column followed by different letters are significantly different ($P<0.05$, Student-Newman-Keuls test).

** number of larvae that completed the 25-cm climb within 30 min. Total number possible = 40.

has not been documented before; however, it too would be advantageous for survival of a polyphagous herbivore such as gypsy moth because it would enable larvae to better exploit hosts that are difficult to climb. The experiment that examined laddering on red oak, trembling aspen and paper birch supports this possibility.

The bark surface of red oak is more irregular than the bark surfaces of trembling aspen and paper birch. It is possible that the smoother bark surface of trembling aspen and paper birch may have been too difficult for the less-fit larvae reared on the ICN diet to grasp firmly with their crochets; as a result, larvae used silk to construct a ladder to assist climbing. If this hypothesis is correct, then laddering in the field may be more common in wild populations with decreased fitness that result, for example, from reduced food quality of the host due to wound-induced plant defences (Schultz and Baldwin 1982; Mattson and Scriber 1987). A clear understanding of why laddering occurs, however, is confounded because of the similarities between the two diets and the developmental differences that occurred in larvae reared on the ICN diet.

The data sheet provided with the ICN diet lists ingredients and proportions identical to those that are used in Bell's diet. The reduced growth and longer development times that were observed with the ICN diet suggest an inadequate source of essential fatty acids and sterols (Chapman 1982a; McFarlane 1985). It is possible that the ICN diet may have been damaged during storage or shipping, although I observed similar symptoms of reduced larval fitness with it when it was purchased on two separate occasions more than a year apart; alternatively, for some other unrecognized reason, it is possible that the dietary requirements of the specific Ontario population of larvae used in the study were not met by the ICN diet. Further studies would be useful in clarifying how laddering is influenced by diet and the possible role that silk production may play in host-plant interactions of the gypsy moth.

Chapter Four

A Laboratory Technique to Study a Change in Feeding Behavior Between Small and Large Larvae of the Gypsy Moth, Lymantria dispar (L.)

Introduction

The gypsy moth, Lymantria dispar (L.), is an important defoliator of deciduous forests that was introduced into eastern North America from Europe (Forbush and Fernald 1896). After eclosion and air-borne dispersal in the spring (McManus 1973; Mason and McManus 1981), first-instar larvae become established in the crown of a tree, where they remain until the fourth instar (Leonard 1981). Feeding during this period of larval development occurs primarily in the early morning, after temperatures have increased, and secondarily in the late afternoon (Leonard 1981). However, fourth-instar larvae exhibit a profound change in their feeding behavior, marked by the migration of larvae towards the base of a tree each day at dawn to seek shelter and then ascent into the crown after dusk to resume feeding. (In this chapter, "feeding behavior" implies a change in microhabitat selection and should not be confused with "feeding rhythm", which refers to the time of day when larvae feed.) At high larval densities such a change in the feeding behavior may not occur (Leonard 1970, 1974; Campbell et al. 1975a). The change in behavior of late-instar larvae also involves movement from one host tree to another (Barbosa 1978; Liebhold et al. 1986). To investigate these matters further, I

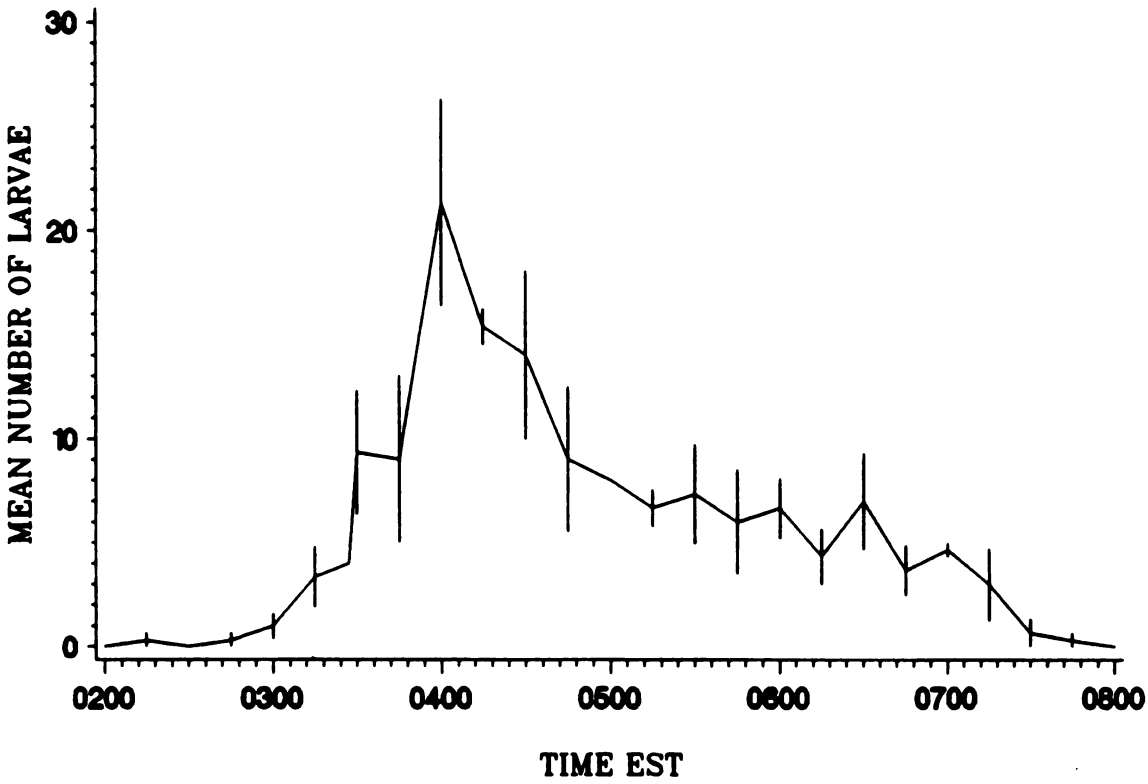
developed a lighting system for the laboratory that would elicit field-like changes in larval behavior. Construction of the lighting system and artificial tree stems is described in this chapter.

Materials and Methods

Lighting System. A change in the intensity of light at dawn and dusk is thought to be the cue that large gypsy moth larvae use to begin their diurnal movement on a tree (Leonard 1981; Weseloh 1989). In Ontario, the movement of larvae down a tree begins at approximately 0300 h EST, about 15 min before dawn; larval migration peaks ca. 1 h later, and is complete, except for stragglers, by 0700 hours (Figure 8).

To model the spectral properties and the change in intensity of light that occur in the field, I used a combination of incandescent and fluorescent light in a 4- by 5-m rearing room with a 17L:7D photoperiod. Incandescent lights were used to approximate the changes in intensity and spectral properties that occur at dawn and dusk because peaks in the spectroradiometric curve at this time shift from the blue wavelengths at midday to the red wavelengths predominant in incandescent light (Moon 1961). Incandescent lights also provide an inexpensive way to regulate the intensity of light. The color temperature of the bulb was also selected to approximate the color temperature of the sun 1 h after sunrise because the color of light produced affects the way in which the color of an object is perceived (Brill 1980). The color temperature of the sun at sunrise is ca. 1800°K; this increases to 3500°K within the first h and approaches 5000°K by noon (Brill 1980). Changes in spectral properties that occur as the sun rises were simulated with fluorescent lamps with spectral-distribution curves similar to those of measurements of midmorning and midday solar radiation (Riordan et al. 1989). This was accomplished with four banks of two in-line and two adjoining 122-cm two-lamp

Figure 8. Mean number of larvae (± SE) descending below 1.5 m on three white oak, Quercus alba L., trees (mean dbh = 38.1 ± 4.59 cm; mean height = 17.2 ± 0.61 m) during subsequent 15-min intervals between 0200 and 0800 hours EST on 30 June 1989 (Kaladar, Ont).


30
20
10
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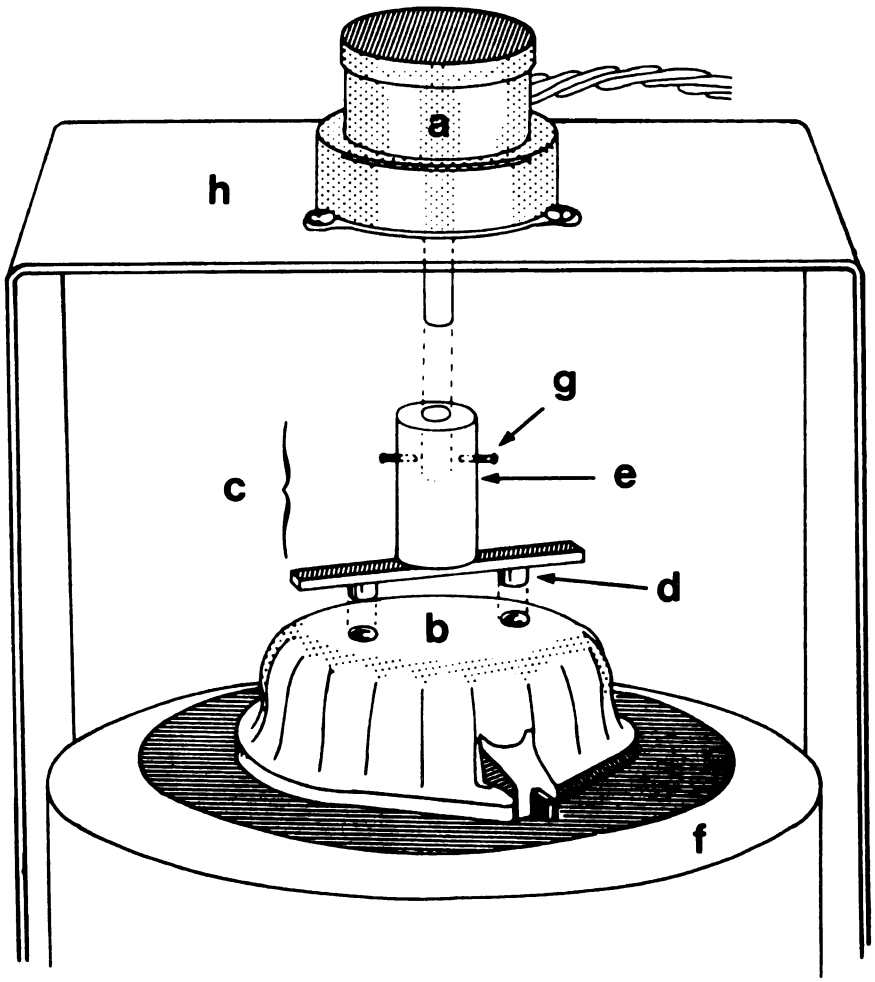
fluorescent fixtures. These were arranged symmetrically on either side of a central line of three 100-watt incandescent bulbs. The set of fluorescent lamps on either side of the incandescent lights (General Electric F40CWX) simulated the spectral properties and color temperature (4175°K) of light during the early morning and late afternoon; the second set (General Electric F40/C75) simulated the spectral properties and color temperature (7500°K) at midday, when sunlight is more intense. Photoperiods of 13L:9D and 4L:20D, respectively, for each set of fluorescent lamps were regulated with mechanical timers (Paragon Electric Company, Two Rivers, WI 54241; Model Number 4001-00).

The increase and the decrease in the intensity of light that occur at dawn and dusk, respectively, were simulated with three Phillips 130-volt incandescent 100-watt bulbs, which were lined up in a row fastened to the ceiling in plastic incandescent light fixtures. The rated color temperature of each bulb at an applied voltage of 110 to 115 volts was 2800°K. The intensity of light and the rate at which the intensity changed were regulated by a variable rheostat (Superior Electric Company, Bristol, CN) driven by a reversible geared motor (Hurst Instrument Motors, Hurst Manufacturing Division, Emerson Electric Company, Princeton, IN 47670; Model Number A-SP 2881) that completed 0.5 revolutions per hour (Figure 9). The chosen gear ratio of the motor was based on a compromise between the period during which I considered larvae to be active in the field at dawn (0300-0700 EST) and a desire to match the color temperature and period of elapsed time after first visible light to the color temperature of the bulb (2800°K), a period of approximately 50 min.

Incandescent lights were not turned off completely at night (< 30% = off). I found, through trial and error, that a change in larval behavior did not occur when the room was completely dark. However, a level of light in the room at night such that the

Figure 9. Schematic of the brass union that coupled the drive motor to the handle of the rheostat: **a**, drive motor; **b**, rheostat handle; **c**, brass union; **d**, 5-mm pin; **e**, brass rod; **f**, rheostat; **g**, set screws; **h**, drive-motor mounting bracket.


a
h
g
e
c
d
b
f

silhouette of an object could just be differentiated corrected the problem; this was accomplished with a rheostat setting of 36% power. In my judgment, this approximates the level of light in a forest on an overcast night.

Power to the red and black wires on the motor that reversed the rheostat was controlled by two PET 71-120 digital timers (Paragon Electric Company). The precision of a digital timer was employed to insure that the distance traveled by the motor was exactly the same when power was increased or decreased; otherwise, an error of more than 1 or 2 min in the power applied to the drive motor would have forced the handle of the rheostat past the stop at full power (100%). As an additional margin for error, I further reduced the maximum rheostat setting to 99%. This also allowed for the error that occurred when the two timers were being synchronized; I was never able to reduce this to below 10 sec. Components for the incandescent light circuit (rheostat, drive motor, mounting-bracket for the drive motor, two digital timers and a terminal strip with 10 terminals for connecting wire) were all mounted inside a transformer box (Bell Products Inc., Montreal, Que. Model Number MC-302010) that was fastened to the wall.

The cycle used to light the room with incandescent and fluorescent lamps overlapped so that the intensity of light in the room either increased or decreased, respectively, as each set of lights turned on or off. The first digital timer (henceforth referred to as the "sunrise" timer) regulated the clockwise rotation of the motor and began to increase the level of incandescent light in the room at 0600 h. When the level of light reached full power (99%) at 0715 h, the motor stopped; however, the incandescent lights remained on throughout the day until 2145 h, when the second digital timer (henceforth referred to as the "sunset" timer) began the counterclockwise rotation

of the motor. This decreased power over the same period (1.25 h) to the level of light used at night (36%). Midmorning fluorescent lights came on at 0800 and went off at 2100; midday fluorescent lights came on at 1230 h and went off at 1630 h.

The procedure used to wire the time clock for each bank of fluorescent lights should not present a problem for the do-it-yourself entomologist. However, the wiring for the incandescent light circuit and for the motor that operated the rheostat (Figure 10) was more intricate. Instructions for wiring the incandescent light circuit can be found in Appendix A.

Artificial Trees. I fabricated 12 artificial trees from 5-cm ABS plastic pipe to serve as hosts in my tests to determine whether or not the lighting system induced a change in larval behavior. Each tree (Figure 11), an inverted Y-shaped column 1.5 m in height, was supported by two 0.75-m vertical arms inserted at the base of a toilet flange that was fastened with wood screws to a 50-cm square of 18.5-mm plywood. The upper portion of the tree, the inverted Y, was constructed by gluing two 15-cm pieces of pipe at a 45° angle with ABS cement and then welding these to a single 0.6-m upper vertical stem with a hot-air welder (Leister-Kombi, Type: Triac, purchased from Johnson's Industrial Plastics, Toronto, Ont.). The 15-cm arms were then inserted into two 45° elbows at the top of each lower vertical supporting stem. A 6-cm circular plate, cut from 5-mm Plexiglass and glued in place with ABS cement, sealed the top of the tree. For a feeding station I used a 20-mL coffee creamer filled with artificial diet that was suspended by the rim of the creamer at the top of each tree in an opening cut in the center of the circular plate. The creamer was replaced daily. Strips of 2.5- by 15-cm black felt were used to fabricate artificial bark flaps to provide a refuge for late larval instars. Several strips of felt, attached with Elmer's Glue-All, were fastened around each of the 45° elbows. The thicker plastic on the elbow positioned the strips of felt away from the surface of the

Figure 10. Wiring diagram for the incandescent light circuit: **DM**, drive-motor; **VR**, variable rheostat; **CP**, 0.25 MFD capacitor.

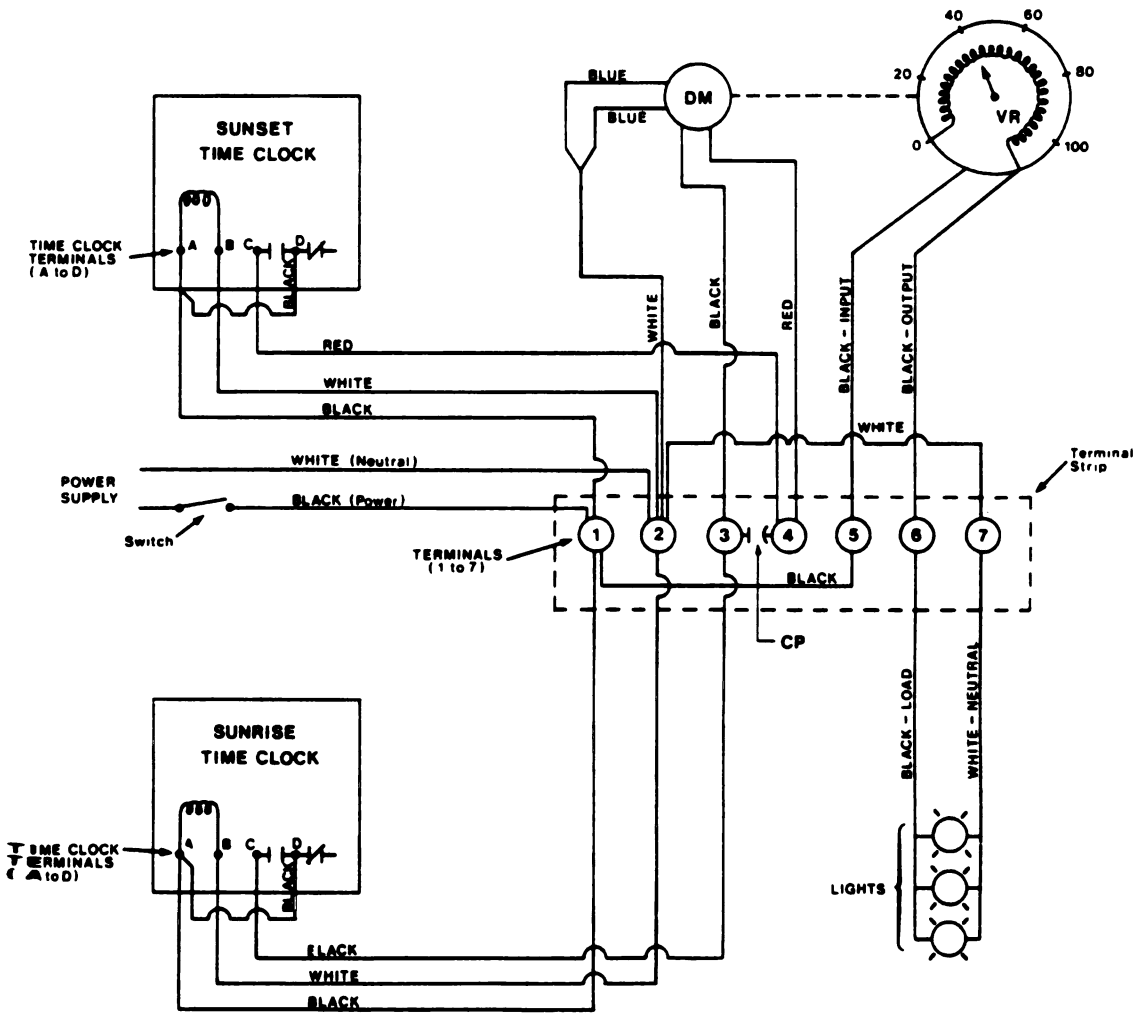
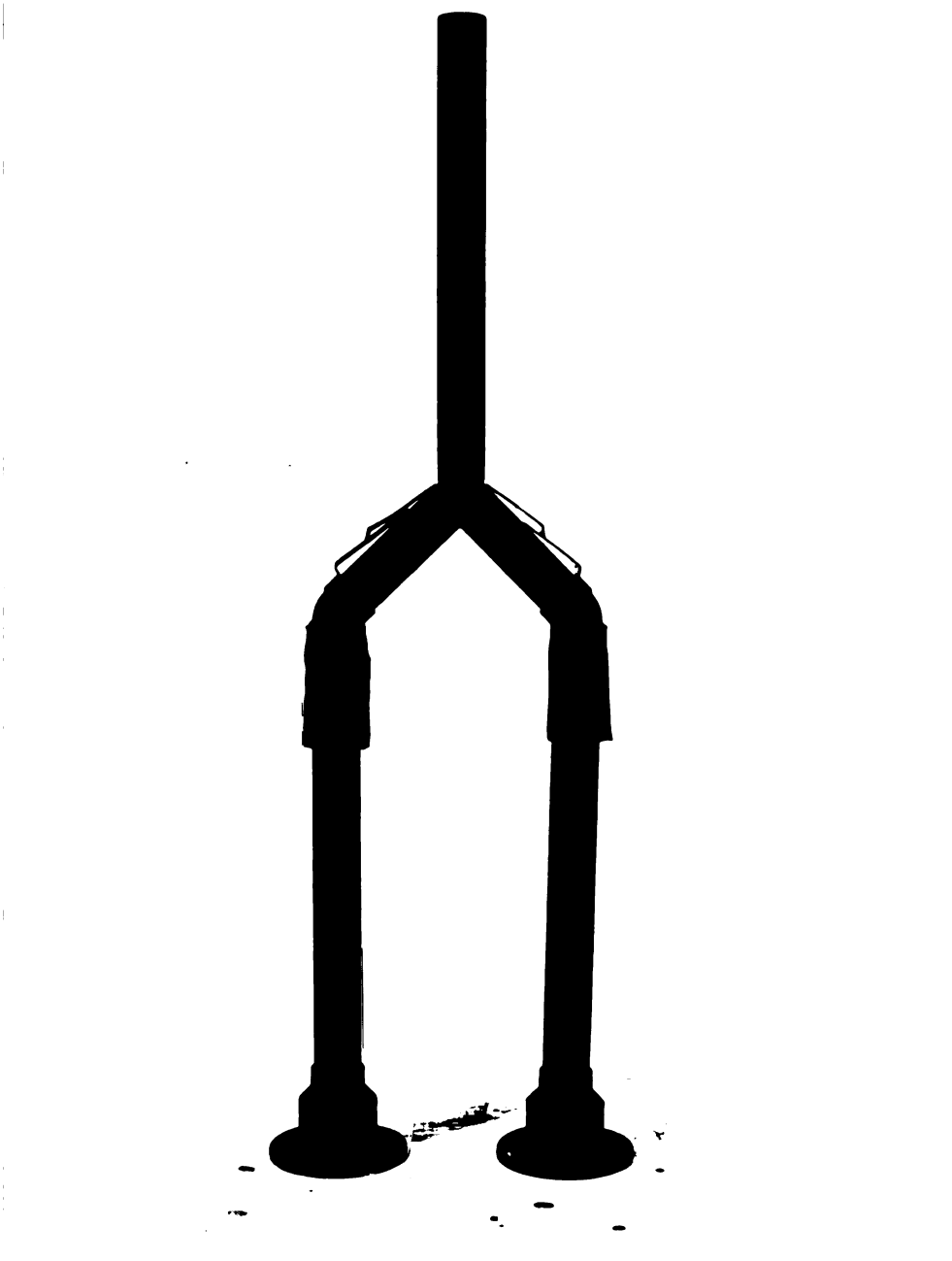

SUNSET
TIME CLOCK
TIME CLOCK
TERMINALS
(A to D)
A
B
C
D
BLACK
RED
WHITE
BLACK
POWER
SUPPLY
WHITE (Neutral)
BLACK (Power)
Switch
TERMINALS
(1 to 7)
BLUE
BLUE
DM
40
60
20
80
0
100
VR
WHITE
BLACK
RED
BLACK - INPUT
BLACK - OUTPUT
WHITE
Terminal
Strip
1
2
3
4
5
6
7
BLACK
CP
SUNRISE
TIME CLOCK
TIME CLOCK
TERMINALS
(A to D)
BLACK
WHITE
BLACK
BLACK - LOAD
WHITE - NEUTRAL
LIGHTS

Figure 11. Artificial tree used to observe a change in feeding behavior.



artificial tree and provided a space between the tree and the felt beneath which larvae could rest beneath during the day. In addition, inverted U-shaped pieces of cardboard (bark flaps) were also fastened to the 15-cm arms to provide a larval retreat. The surface of each artificial tree was also textured with a mixture of 150 mL of sand sifted through a 20-mesh screen and 250 mL of black latex paint. Previous experiments showed that larvae preferred a dark color with a rough surface (Roden, unpublished data).

Larval gypsy moth used in the study were obtained from egg masses collected on 20 October 1987, from Kaladar, Ont. (44°39'N, 77°07'W). These were held at 5°C until 4 January 1987, then were surface-sterilized (Shapiro 1977) and incubated in the rearing room described above at 22°C and 70% RH. Electric lights increased the temperature during the photophase by ca. 6°C; I did not attempt to rectify this increase because the diurnal variation in temperature further simulated conditions in the field. Larvae that emerged from eggs were reared individually on artificial diet (Bell et al. 1981) in screened 150- by 25-mm plastic Lab-Tek Petri plates until the second instar. When sufficient second-instar larvae were obtained, 36 were randomly selected and three were placed on each of the 12 artificial trees. The trees were centered approximately 1 m apart with six on either side of the central incandescent bank of lights to balance the effect of room lighting. Larval positions on each tree were recorded daily during the photophase at three times: 0900, 1500 and 2100 h. Periodically, positions were also recorded during scotophase to confirm feeding and observe activity. Whenever a molt occurred, the instar of that particular larva was recorded. Instances when gypsy moths in late larval instars descended the artificial trees for a day (0900 until 2100 h) to seek refuge, and remained motionless under the black strips of felt, the cardboard flaps, or the crevice of the Y, were considered indicative of a change in feeding behavior.

Results and Discussion

The lighting system assembled to change the intensity and the spectrum of light automatically in the laboratory clearly influenced the feeding behavior of late larval gypsy moth on artificial tree stems. When larvae were placed on the trees, they moved about on their new hosts; however, excessive larval movement ceased within 24 h. For the following 8 days, second- and third-instar larvae were observed feeding only during daylight hours (0600 to 2300) and remained within 25 cm of the top of each tree; larval resting locations were on the rim of or inside the creamer of diet, or on the side of the tree. The first change in larval behavior was recorded on day 10. By day 22, the day before pupation began, 85% of the population (N = 30) migrated down the artificial tree stems each day to seek shelter, and remained nearly motionless under the black strips of felt, the cardboard flaps, or the crevice of the Y; only fourth-, fifth- and sixth-instar larvae exhibited this behavior. Eventually, however, all larvae changed their feeding behavior. During sunrise (the period between 36% and 99% power), most larvae had begun moving for shelter by the time the rheostat had reached 70% power. All migrating larvae attained shelter before the midmorning fluorescent lights came on. In previous experiments I was unable to change the feeding behavior of larvae with only the on/off effect of fluorescent lights; however, all larvae in the current experiment selected resting locations below the felt for pupation. Obviously, midmorning and midday fluorescent lights were not responsible for initiating a change in feeding behavior, although an increase in the intensity and a change in the spectrum of fluorescent light may have ensured that larvae remained inactive throughout the photophase. Furthermore, I cannot be certain that the diurnal temperature change in the room did not also contribute to the success of my lighting system.

Larvae usually began moving up a tree when the rheostat decreased to approximately 40 to 45% power. These larvae were active through scotophase and frequently changed trees during the night and then clustered on another tree for the next resting period. Similar inter-tree larval movement was reported by Liebhold et al. (1986) and may indicate a larval searching behavior for suitable hosts with resting locations that increase survival (Campbell 1981). Large larvae were not observed on the walls of the chamber and did not select resting locations that were off the trees during photophase; larvae were also not observed feeding during photophase. Lance et al. (1986b) reported similar feeding observations and suggested that the agreement between field and laboratory data imply that it would be possible to study the influence of environmental factors that affect feeding rhythm. My results support their observations. The increase in variance (Table 18) after a change in feeding behavior shows that there is a tendency for the distribution of larvae to become more random over time; however, the maximum variance (1.91 on day 18; mean = 2.50) did not depart from that of a normal distribution. It is possibly that a larger sample size would have shown a negative binomial distribution of larvae among trees. I did not mark larvae individually; therefore, I was unable to discern any particular differences or patterns of behavior related to sex or individual uniqueness. Movement of fourth-, fifth- and sixth-instar larvae between tree stems occurred only at night. However, movement between hosts in the field often occurs during the day among high population levels (Leonard 1970). I speculate that larval movement between trees that occurred only at night in the laboratory is typical of larval behavior at low population densities.

As a result of the compromise between the period during which larvae were active at dawn (4.0 h) and the gear ratio of the motor designed to match the color temperature to natural light, natural color temperature was not accurately simulated at the time of day when the bulb reached full power. Incandescent lights operated at lower than

Table 18. Variance and maximum/minimum number of larval gypsy moth per tree (n=12) on 5 subsequent days before (days 5-9) and after (days 16-20) a change in feeding behavior was observed. During photophase on days 16-20, 80-85% of the population (n=30) changed feeding behavior.

Day	Variance	Maximum/minimum no. larvae/tree
5	0.27	3/2
6	0.27	3/2
7	0.27	3/2
8	0.27	3/2
9	0.27	3/2
16	0.46	4/2
17	1.18	4/1
18	1.91	5/1
19	1.36	5/1
20	1.61	5/0

the rated voltage will reduce the color temperature of a bulb (Brill 1980). Changes that occurred took place over 75 min instead of 50 min. The sensitivity of gypsy moth larvae to flickering light is also unknown. Insect flicker-fusion frequencies (FFF) between 20 cps (Chapman 1982b) and 300 cps (Wigglesworth 1974) have been reported. An insect with a FFF > 120 cps would be able to detect the on-off effect of my AC-powered fluorescent lamps and incandescent light and this could possibly disrupt normal behavior. Nevertheless, differences between my lighting system and natural daylight were not sufficient to prevent the change in feeding behavior that occurs in the field between small and large larval instars of gypsy moth.

In conclusion, the lighting system and the artificial tree stems developed for use in the laboratory will make it possible to study various aspects of the biology and feeding behavior of the gypsy moth that could not have been investigated before. For example, by manipulating the physical features of an artificial tree in the laboratory, it may be possible to learn about the key factors that influence the insect's choice of a host. Barbosa (1978) speculated that the physical features of a host play an important role in host selection by penultimate and ultimate larval instars. At this point, very little is known about how physical traits of the host affect the host preference and feeding behavior of larval gypsy moth. Clearly, chemical cues are important stimuli (Barbosa and Capinera 1977; Hough and Pimentel 1978; Barbosa et al. 1979); however, visual or structural cues, or both, may be equally important. Studies with adult Diptera (Harris and Miller 1983; Moericke et al. 1975; Prokopy 1977) have demonstrated that host selection is a very complex process that involves host information from many different sensory modalities. The ecological significance of the responsiveness of larval gypsy moth to different stimuli remains to be elucidated.

SUMMARY AND CONCLUSIONS

The objectives of this research were: (1) to evaluate the host potential that trembling aspen and paper birch offer for gypsy moth, (2) to compare these hosts to red oak in the Great Lakes basin, and (3) to investigate the possible influence of a host's physical features on larval behavior. Over a 6-year period, it was shown that the physical features of a host strongly influence the larval behavior of all gypsy moth instars. In laboratory and field experiments, with artificial and authentic tree trunks, larval attraction to an object was positively correlated with the angle at which the diameter and height were presented. Research studies also demonstrated that larval attraction to a host was strongly influenced by tree species. The attraction of larvae to red oak was frequently fifteen-fold greater than to paper birch or trembling aspen. Since larvae are influenced by diameter, height and species of the host, these variables should be important considerations in standardizing burlap banding in operational monitoring systems; they may also help explain the gypsy moth "wolf tree" phenomenon.

Research in this thesis also demonstrated that gypsy moth development on both defoliated and undefoliated trembling aspen and paper birch is superior to larval development on a traditional host such as red oak. Female gypsy moth larvae fed on defoliated red oak produced significantly smaller pupae (0.84 g) than females feeding on paper birch (1.13 g) or trembling aspen (1.43 g). Tree species was the only factor that affected male pupal weight. Male larvae reared on red oak yielded pupae that weighed less (0.37 g) than male larvae reared on paper birch (0.40 g), and both weighed significantly less than pupae from male larvae reared on trembling aspen (0.49 g).

The number of days required by both male and female larvae for development was only affected by host species. Female larvae that fed on trembling aspen required significantly fewer days (46) to complete development than females reared on red oak (50); the number of days for female larval development on paper birch (48) was intermediate, but not significantly different from the times for either trembling aspen or red oak. Male larvae fed on trembling aspen also required significantly fewer days (41) for development than larvae that fed on paper birch (44) and red oak (44).

Gypsy moth mortality in the experiment was not affected by either host species or the level of defoliation. However, these results should be viewed cautiously. Predatorial attacks by Podisus placidus Uhl. (Pentatomidae) from outside the cage through the screening on the ventral surface of larvae seriously reduced the number of larvae in all treatments by ≅ 60% and may have masked possible mortality effects that could have been attributed to the different tree species. The number of larvae that escaped from cages in the experiment, or that died from injestion of NPV was less than 4%.

A previously undescribed behavior of gypsy moth larvae used for climbing on a smooth vertical surface was serendipitously discovered. By spinning a "ladder of silk" on surfaces that do not provide structures that can be grasped by the crochets, larvae are able to climb vertically. The use of silk for climbing occurred more frequently in populations that were less fit (as measured by head-capsule size, reduced pupal weight and increased development time). For example, the mean female pupal weight for fit and unfit populations were, respectively, 0.94 versus 1.94 g. I suggest that the use of silk for climbing in the field may be associated with decreased larval fitness that results from wound-induced plant defences.

A lighting system with incandescent and fluorescent light in the laboratory was also developed that induced a change in feeding behavior similar to the change that occurs in the field. The change in feeding behavior was observed on artificial "tree stems" constructed from 5-cm ABS plastic pipe and fitted with felt and cardboard "bark flaps". On the day before pupation, 85% of the population migrated down the artificial stems to seek shelter under the bark flaps; only fourth-, fifth-, and sixth-instar larvae were observed exhibiting this behavior. The development of the lighting system and the artificial tree stems should make it possible to identify other key factors that influence gypsy moth's choice of a host under controlled conditions.

RECOMMENDATIONS

The identification of visual stimuli that influence the behavior of larval gypsy moth and the knowledge that the nutritional benefits of trembling aspen exceed those of red oak, a traditional gypsy moth host, pose as many questions as they answer. Questions that should be addressed by future research are:

1) All measurements of stimuli that affected the visual foraging behavior of larval gypsy moth in this research were conducted at distances of 0.5 m. What is the maximum distance at which these stimuli (such as diameter, height and species) affect larval behavior?

2) Is there a synergistic affect between diameter and height that makes specific combinations or ratios of a diameter and height more attractive? Such effects have been noted for adult Diptera (Moericke et al. 1975; Miller and Harris 1985).

3) What are the other stimuli that affect gypsy moth larval behavior? For example, from preliminary studies that were initiated, but not completed, it is apparent that gypsy moth larval behavior is also influenced by the wavelength of light.

4) What affect do diameter, height and species of a tree have on operational monitoring system that use burlap bands to quantify population levels?

5) What effect does the color of the material used for tree bands have on population measurements? Based on research in this thesis, it is evident that larvae do not respond equally to all colors.

6.) My data suggest that both defoliated and undefoliated trembling aspen and white birch are more nutritious, and would yield potentially more fecund gypsy moth females than a traditional host such as red oak. However, I propose that outbreaks of gypsy moth will not occur in stands that contain primarily these species. Better gypsy moth performance on trembling aspen and paper birch is attributed to an imprecise correspondence between host and herbivore that inhibits naturally occurring outbreaks of gypsy moth on these tree species. I suggest that the gypsy moth NPV, which influences populations levels, and physical features of the host that effect gypsy moth larval behavior are responsible for this imprecise correspondence. Since Schultz et al. (1990) suggest one of the keys to understanding the susceptibility within a tree species may be the relationship between condensed and hydrolyzable tannins, this aspect should be investigated for trembling aspen and paper birch.

7) What is the predatorial potential of the pentatomid, P. placidus? The frequency of attacks on caged gypsy moth larvae in this study suggest that the impact of this predator should be investigated.

8) What is the relationship between first-instar weight and pupal weight? The significant covariate for male and female larvae observed in this thesis suggests that the largest first-instar larvae also produce the largest and potentially the most fecund pupae.

9) What effect do plant-induced defences have on the physical ability of larvae to exploit a host? The influence of diet on the construction of a silk ladder to assist climbing suggests that the ability of larvae to exploit a host may be physically impaired by wound-induced plant defenses.

10) What is the potential of laboratory studies for measuring and quantifying gypsy moth larval behavior? The development of a laboratory lighting system and a suitable artificial tree stem suggest that it may be possible to rigorously quantify various aspects of the biology and feeding behavior of the gypsy moth.

APPENDIX

APPENDIX A

Instructions for Wiring The Incandescent Light Circuit

When following the incandescent wiring instructions outlined below, the reader should refer to Figure 10. A black or red wire indicates a wire carrying a load (power) and white or blue, a wire that is neutral. I used only the first seven of the ten terminals on the terminal strip for connecting wires to the transformer box. To clarify the numerical designation between the 7 terminals on the terminal strip that I used and the 8 terminals on the time clock, terminals on the time clock were assigned a designation A through H from left to right. Note, however, that the last three (8, 9 and 10) on the terminal strip and the last four on each time clock (E to H) were not used.

To bring power to the terminal strip fastened to the transformer box, I used Type SW 14-gauge 2-wire with a male plug that inserted in a female wall receptacle; I elected to use the male plug instead of the switch shown in Figure 10 simply because it was more appropriate for my installation. The black and white wires that entered the transformer box fastened, respectively, to 1 (load) and 2 (neutral). The third wire, green, (note: Canadian electrical numerical wiring designations do not include the ground wire) fastened to ground on the mounting plate. This plate attached to the back of the transformer box with machine screws and anchored the rheostat, the drive-motor mounting plate and the time clocks. Grounding for each of these and for the motor that fastened to the drive-motor mounting plate was accomplished by scraping away paint between points of contact. Power to each time clock was provided by black wires that ran

from 1 to A, the power input terminal on each time clock. A common point (D) on each time clock between an internal set of contacts received power through a black wire from A. The neutral terminal on each time clock, B, was connected by separate white wires to 2. Terminal 2 was also connected by a white wire to the two blue neutral leads from the motor. A black wire from 1 provided power to 5; the terminal that supplied power to the input on the rheostat. Power from the output on the rheostat supplied power to 6. This terminal was connected to the load (i.e., the black wire that delivered power to the incandescent lights); the neutral wire (white) to the lights was connected to 7. Terminal 7 was also wired to 2. Terminals 3 and 4 connected with black and red wires, respectively, to C on each time clock. These terminals also connected, respectively, to the black and red wires from the motor. When the program for the sunrise time clock completed the circuit, power was supplied from C through 3 to the black wire from the motor; this initiated clockwise rotation of the rheostat and increased the voltage, subsequently increasing the intensity of light. Similarly, power regulated by the sunset time clock supplied power from C through 4 to the red wire from the motor; this initiated counterclockwise rotation of the motor and reduced the intensity of light. A capacitor of 0.25 MFD (supplied with the motor) was inserted between terminals 3 and 4. This reversed the phase sequence of voltage applied to the stator on the motor, thereby reversing the direction of the magnetomotive force.

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