DISTRIBUTION OF FRASS PRODUCED BY LARVAL LEPIDOPTERA IN A HARDWOOD CANOPY

By

Jodi M. Haylett

Submitted in Partial Fulfillment of the requirements
for the Degree of
Master of Science
in the
Biological Sciences
Program

YOUNGSTOWN STATE UNIVERSITY
June, 2000

Distribution of Frass Produced by Larval Lepidoptera in a Hardwood Canopy

Jodi M. Haylett

I hereby release this thesis to the public. I understand this thesis will be housed at the Circulation Desk of the University Library and will be available for public access. I also authorize the University or other individuals to make copies of this thesis as needed for scholarly research.

Signature:

Jodi M. Haylett 4/27/00
Jodi M. Haylett Date

Approvals:

Courtenay N. Willis April 27, 2000
Courtenay N. Willis, Thesis Advisor Date

David B. MacLean 5/11/00
David B. MacLean, Committee Member Date

John D Usis Apr 27, 2000
John D. Usis, Committee Member Date

Lauren Schroeder 4/27/00
Lauren A. Schroeder, Committee Member Date

6/1/00
Peter J. Kasvinsky, Dean of Graduate Studies Date

ABSTRACT

I studied the distribution of frass produced by larval Lepidoptera in a late-successional, 10-ha forest plot at the Ravenna Army Ammunition Plant in Portage County, Ohio. From July through September, 1998, fallen frass pellets were collected from the dominant tree species, American beech (*Fagus grandifolia)* and sugar maple (*Acer saccharum)*, using 1m^2 frass nets. Two frass nets were placed beneath each selected tree in three areas of the plot: along a road edge, in the interior of a forest, and along the South Fork of Eagle Creek. Frass pellets were collected on a weekly basis from a total of 120 nets and were weighed to the nearest 0.01g. Frass weights for beech and maple did not differ between the three transects. However, frass weights were significantly greater from beech than from maple trees (Mann-Whitney test, $P= 0.01$). Frass pellets from the peak collection were also separated into size classes. Based on weights, the size of frass did not significantly differ between beech and maple. Live specimens were collected from June through July, 1999 and their frass pellets were used to develop a key for the identification of 14 late-season lepidopteran species found in a beech-maple canopy. Two species of geometrid larvae, *Plagodis fervidaria* and *Hypagyrtis unipunctata*, were distributed differently depending on their host. When feeding on beech, both species were more abundant on trees located along the creek edge but when feeding on maple, they were more abundant on trees growing along the road edge (Kruskall-Wallis, $P = 0.001$).

ACKNOWLEDGEMENTS

I sincerely thank Dr. Courtenay Willis and Dr. David MacLean for their scientific advisement and support of this research project. Additional advice came from Dr. Lauren Schroeder and Dr. John Usis. I also thank Dr. David Wagner for assisting in the identification of larval specimens. Special gratitude is given to Kim Ludt who helped set up nets and collect frass pellets. I also thank Trish Gundrum and Jeremy Hutchison for their excellent tree-beating abilities and Rob Adair for his statistical assistance. Further acknowledgement goes to Tim Morgan who approved our access to the arsenal and provided the opportunity to study such a biologically diverse ecosystem. This research was supported in part by the Biology Department at Youngstown State University and by a small institutional grant from the Ohio Biological Survey.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

CHAPTER PAGE

IV. DISCUSSION

APPENDICES

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

FIGURE PAGE

LIST OF FIGURES CONTINUED

CHAPTER I

INTRODUCTION

Lepidopteran larvae are the most abundant herbivores in a forest ecosystem and provide a major source of energy in forest food webs (Strong et al. 1984). Lepidopteran larvae consume plant biomass over the course of their development and provide food for insectivorous organisms, like the Worm-eating warbler (*Helmitheros vermivorous*), which hover gleans lepidopteran larvae from foliage in the lower canopy of a forest (Scriber and Slansky 1981). How larval Lepidoptera are distributed in a forest ecosystem may influence the breeding success of insectivorous species such as neotropical migrants that rely on seasonally abundant arthropods (Sherry 1984).

Little is known about the distribution and abundance of larval Lepidoptera in a temperate deciduous forest. This may be due to the difficulty involved with sampling larvae within a forest canopy. Fogging and branch removal have been used to study the distribution of larval Lepidoptera in a forest canopy (Zandt 1994). Fogging enables an extensive collection of arthropods from canopy foliage to be made (Moran and Southwood 1982). However, fogging with an insecticide is detrimental to the ecosystem since it decimates all arthropod species that come into contact with the spray and can alter the amount of prey available for insectivorous predators. Branch removal enables a sample to be taken directly from a particular host tree. This method requires access to the tree crown by means of a hydraulic lift or by climbing the trees (Holmes and

Schultz 1988). Branch removal can affect the canopy ecosystem by altering the host plant and by increasing the amount of solar radiation among the branches. This procedure also reduces the amount of habitat available for lepidopteran larvae.

A non-invasive method of determining the distribution of species involves collecting and identifying frass pellets. Frass collecting involves placing frass nets beneath trees to collect larval Lepidopteran feces. This method has been used by forest entomologists to study arboreal populations of larval Lepidoptera (Liebhold and Elkinton 1988, Coffelt and Shultz 1993, Kamata and Igarashi 1994). Frass collections can be used to estimate larval densities and the extent of herbivory of canopy foliage (Southwood 1978). Frass collection provides a non-invasive, unbiased method of assessing the distribution and abundance of lepidopteran larvae in a forest canopy. Collecting fallen frass pellets beneath individual trees allows one to estimate larval densities associated with specific host plants. Overall, frass production provides a reliable, passive approach to canopy research.

Objectives

The goal of this study was to examine the distribution of larval Lepidoptera in a hardwood canopy. Specifically, my objectives were (1) to determine if the abundance of larval Lepidoptera differs on the edge or in the interior of a forest, (2) to identify the most common lepidopteran larvae found on American beech and sugar maple, and (3) to construct a dichotomous key using frass pellets and head capsules in order to identify late-season lepidopteran larvae that feed on American beech and sugar maple.

Lepidoptera as Herbivores

The order Lepidoptera includes over 112,000 species of butterflies and moths worldwide (Arnett 1985). Within the eastern portion of the United States and Canada, there are more than 5,000 species of Lepidoptera (Wagner et al. 1997). Moths greatly outnumber butterflies by about 14 to 1 and their larvae are the dominant herbivores feeding on canopy foliage (Covell 1984).

Lepidoptera can be subdivided into two groups based upon the size of the adult. Microlepidoptera include all species that have a wingspan less than 20mm (Borror and White 1970). Macrolepidoptera typically have wingspans that exceed 20mm and include all remaining families. Both groups differ in feeding strategies on their host plants. The larvae of the microlepidoptera usually feed on their host plants by boring, mining, or forming galls. Most larval macrolepidoptera utilize the leaf surface area of their host as their major food source. I studied the distribution and abundance of macrolepidoptera because they are abundant on canopy foliage.

Caterpillars can be further separated depending on their nutritional requirements. Larvae that can only feed on one host family are referred to as specialists. Specialists are very limited by what food source is acceptable and will provide adequate nourishment for their development. There are more specialists that consume herbaceous vegetation when compared to woody plants (Futuyma 1976). Most tree-feeding caterpillars are classified as generalists. Generalist larvae are able to digest the nutrients of many host plants. Larvae that feed on tree foliage usually exhibit a slower growth rate than the forb-feeding specialists (Scriber and Feeny 1979). The lepidopteran larvae included in this study are late-season generalists.

The foraging behavior of lepidopteran larvae is influenced by predation. Palatable species are generally smooth and cryptically colored and they often feed from the underside of leaves, moving away from the damaged site after feeding. They may also clip off partially eaten leaves to remove evidence of their feeding activities or restrict feeding activities to the evening (Heinrich 1979). Unpalatable species typically have warning coloration or are covered with hairs or spines such as the gypsy moth larvae, *Lymantria dispar*. Since predation is less important for aposematic species, they often forage on the upper surface of a leaf or in gregarious clusters (Bowers 1993).

Herbivory by lepidopteran larvae typically is not detrimental to the forest ecosystem (Schowalter et al. 1986). With the exception of larval outbreaks, the amount of foliage consumed is usually minimal. Estimates of annual foliage consumption in temperate forests range from 3-8% (Mattson and Addy 1975) to 5-15% (Schowalter et al. 1986). Even at higher levels, herbivory has little effect on a mature forest stand. However, when caterpillar outbreaks occur, defoliation can result in the reduction of tree growth (Crawley 1983).

The nutritional ecology of caterpillars is an important aspect of forest herbivory. Once plant tissues have been consumed by a caterpillar, energy will either be used for maintenance and growth or will be expelled as frass (Crawley 1983). The most important nutrient required for growth and maintenance is nitrogen (Strong et al. 1984). If nitrogen is limited, the ability to assimilate proteins will be reduced. A herbivore must increase its nitrogen content 2.5-fold in order to convert food to body tissue (Crawley 1983). As a result, the nitrogen content in plant tissues can limit the growth of phytophagous insects (Scriber and Slanskey 1981).

Nitrogen levels within a leaf will change over the season. As a leaf matures, the amount of nitrogen and water decreases while non-nutrients such as lignins and tannins increase (Schroeder 1986). Many lepidopteran species present in a forest canopy consume leaves early in the season when nitrogen levels are highest (Berryman 1996). However, larvae that are present late in the season are better able to metabolize lower levels of nutrients (Scriber and Slanskey 1981). This ability to consume less nutritious foliage enables late-season larvae to exploit resources that are not available to the early feeders.

The efficiency of larval digestion is correlated with the characteristics of the host plants (Scriber and Feeny 1979). Many trees will produce secondary chemicals as a defense mechanism when exposed to herbivory. Leaf components such as lignins and tannins represent biochemical defenses that act as a selection pressure against larval Lepidoptera (Rhoades 1979). Once a secondary compound has been consumed, it may have a negative impact upon growth rate and reduce the fitness of the caterpillar (Harborne 1977). Species that feed on trees are exposed to a wider variety of secondary compounds than species that feed on herbaceous vegetation (Futuyma 1976). Late-season larvae typically have a higher midgut pH that enables them to digest leaves that possess high levels of tannins (Berenbaum 1980). The presence of chemical defenses has resulted in a well-documented coevolution between herbivores and their host plants.

Distribution and Abundance of Lepidoptera

The distribution of moths in a forest can be influenced by the species of host plant, the shape of the forest stand, forest composition, and the oviposition behavior of the adult moth. Trees support a wider variety of lepidopteran species than herbaceous vegetation and provide an abundant and stable food resource (Lawton and Strong 1981). Trees also provide oviposition sites, shelter from inclement weather, escape from predators, and overwintering sites for lepidopteran larvae (Lawton 1983).

The shape of a forest stand can influence the distribution of adult Lepidoptera that are inefficient at dispersal. The family Geometridae tend to have a much lower dispersal ability than stronger fliers such as the Noctuidae (Usher and Keiller 1998). Another family that has limited dispersal is the Lymantriidae. Many female tussock moths are wingless and therefore the population of these species is limited by resource availability (Wilson et al. 1999). Gypsy moth (*Lymantria dispar*) females are also unable to fly which can result in limited dispersal due to geographical barriers. Species with poor dispersal ability tend to benefit from compact woodland areas as opposed to elongated forest tracts (Usher and Keiller 1998). The amount of edge is greater along narrow woodlots than along a compact stand (Saunders et al. 1991). In a compact forest, species that are unable to disperse great distances can readily find a suitable host for their offspring without being exposed to predation along the edge.

Forest composition can influence the distribution of Lepidoptera in several ways. A mature, late successional stand has greater canopy closure and larger tree species than an early-successional forest. The canopy of a forest can be subdivided into different vertical zones which may affect the distribution of lepidopteran larvae (Nielson and Ejlersen 1977). The nutrients available to the herbivores will be variable according to the location within the vertical zones (Lawton 1983). Leaves at the top of the crowns will be exposed to greater variation in temperature and precipitation than those found deeper within the canopy structure. Due to such factors, water content within these leaves will be much lower. By establishing specific foraging behaviors, lepidopteran larvae can utilize their resources efficiently.

The distribution of larvae in a forest canopy may also be influenced by oviposition behavior. Presumably, an ovipositing female selects a host that will provide nourishment for her offspring. Both visual and chemical cues play a role in selection of the correct host species (Stadler 1986). Since the larvae do not disperse, oviposition preferences of the adult Lepidoptera automatically place the offspring on a food source. The ability to select the correct host that provides adequate nourishment for the larvae ensures the continued existence of the species (Dethier 1959).

Edge Effects

A forest stand can be divided into separate regions consisting of the edge and the core or interior. The edge can be defined as the portion of the habitat that begins with the perimeter of trees and includes all vegetation within the first 50 meters (Donovan et al. 1997). Edges can occur naturally, such as along rivers, creeks, valleys, or gorges or can be artificially induced, such as along logging roads, agricultural fields, and urban development.

Many of the trees and herbaceous plants growing along an edge are classified as shade-intolerant. Shade-intolerant plants colonize an area in the early stages of ecological succession (Smith 1990). Shade-tolerant species such as beech and sugar maple tend to be more prominent in the interior of the forest than on the edge (Whitney and Runkle 1981). The edge-to-interior vegetation gradient gradually blends the shade-intolerant and shade-tolerant species together. Beyond 10-15 meters from the forest edge, vegetation composition appears to consist of primarily mesic interior species (Ranney et al. 1981).

The aspect of a forest edge can influence vegetation composition. Southern edges represent a xeric habitat that is favorable to species such as hawthorns (*Crataegus*) and hickories (*Carya*) (Ranney et al. 1981). Northern edges tend to receive less solar exposure and therefore support vegetation that is more tolerant of shade such as basswood (*Tilea*) and white ash (*Fraxinus*) (Palik and Murphy 1990).

The microclimate along a forest edge is influenced by exposure to solar radiation, evapotranspiration, temperature, and wind. One of the most prominent abiotic components affecting the microclimate is sunlight. The amount of solar radiation that reaches the ground layer is greater along an edge than in the interior (Saunders et al. 1991). Greater canopy foliage densities at edges may result from increased light availability (Palik and Murphy 1990). Although the density of canopy foliage may be higher, the overall size of leaves growing along an edge is significantly smaller than those growing in the interior (Niklas 1995).

Increased solar exposure along an edge can also result in elevated levels of both evapotranspiration and temperature (Forman and Godron 1986). Higher temperatures in combination with evapotranspiration will result in a decrease in water content in both soil and leaves (Smith 1990). Foliar water content is an important component in the development of lepidopteran larvae (Schroeder 1986). Growth rate can be reduced when larvae are exposed to leaves that have low amounts of water (Scriber and Feeny 1979).

Leaves located along a forest edge may have lower water content from evapotranspiration and therefore be less acceptable as a food source (Scriber and Slansky 1981).

Another factor that influences the edge microclimate is wind. Wind has a greater impact on vegetation growing along an edge than on vegetation located in a forest interior (Wales 1972). Trees located near an edge are exposed to wind shear forces which increases the chance of windthrow (Saunders et al. 1991). Wind also increases the rate of evapotranspiration and can cause dessication of soil along an edge (Smith 1990). Trees growing at the edge are exposed to more extreme weather conditions than those located within the interior. During storms, the increased amount of wind at a forest edge can cause more damage to canopy branches than branches present in an interior.

The penetration of edge effects into a forest fragment depends on variables such as the age of the stand and the fragment shape and size (Laurance and Yensen 1991). Edge penetration for an old growth forest stand has been recorded at 5–45 meters (Palik and Murphy 1990). An older edge usually supports a more gradual vegetation gradient than a newer edge (Laurance and Yensen 1991). There is a greater abundance of woody shrubs established along older forest edges (Gysel 1951). The greater amount of vegetation found along an older edge can reduce the penetration of edge effects into the forest stand (Wales 1972).

The edge index of a forest plot has been measured in order to assess how shape affects the amount of edge present. Circular forest stands have the greatest area and the least amount of edge when compared to other geometrical forms. Edge effects are more prominent on small forest fragments or irregular shaped forest plots (Forman and Godron 1986). Laurence and Yensen (1991) have used a Core-Area Model in order to calculate penetration distance of edge effects into a forest fragment. Their model has determined that when a fragment falls below a critical threshold (approximately 50-ha), the core area is drastically reduced. The interior of a woodlot or forest is the region at which mesophytic, low light conditions occur (Levenson 1981). The actual measurement of a core area depends on the entire size of the forest stand.

CHAPTER II

METHODS

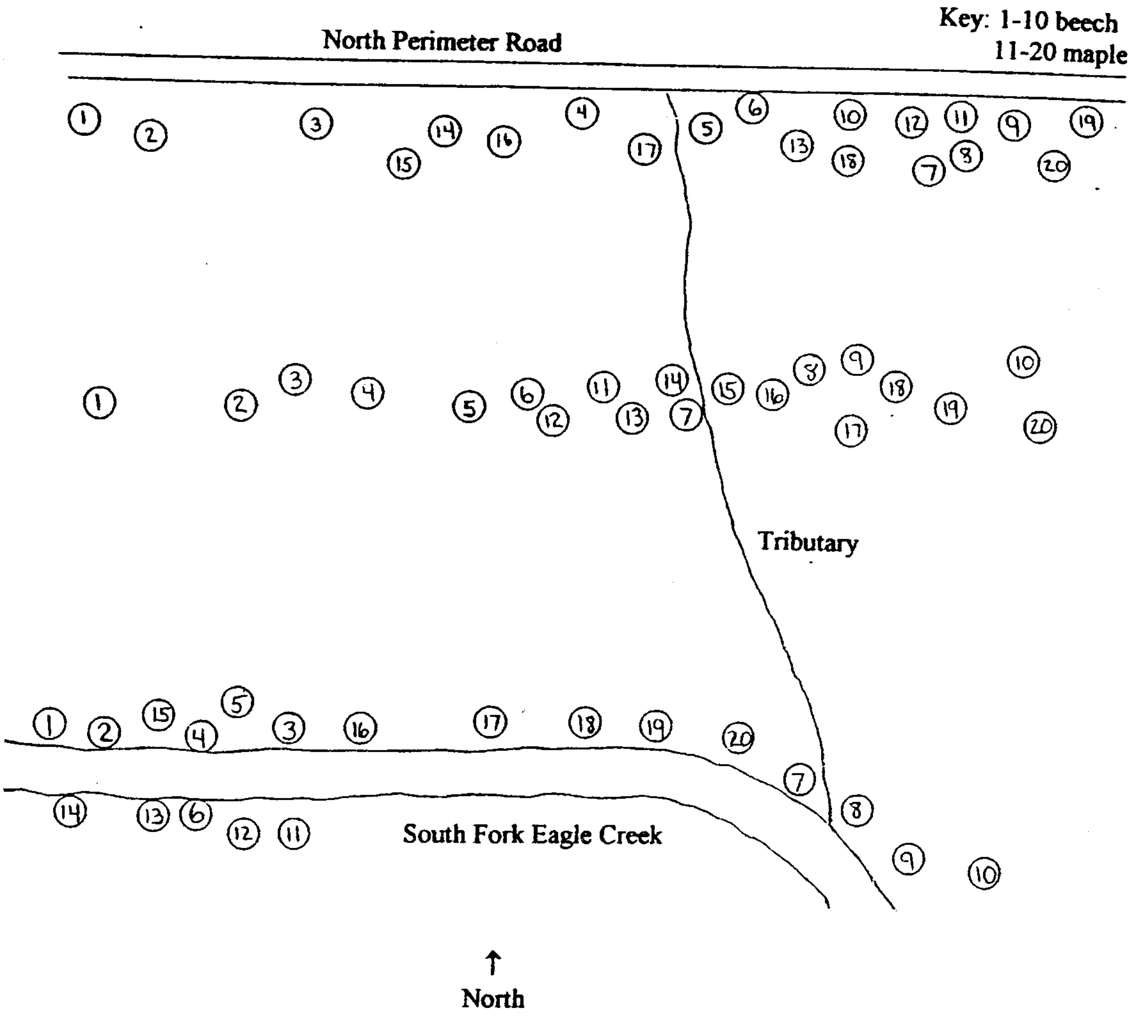
Study Design

This study was designed to test how the presence of a forest edge influences frass production of larval Lepidoptera. The forest plot used in this study was bordered by two edges: a road edge and a natural creek edge. Three 500m long transects extending east-west were established: one along the road edge, one in the interior of the forest, and one along the creek edge. Along each transect, 10 American beech and 10 sugar maple trees with a DBH greater than 25cm were selected (Figure 1). Trees chosen along the road edge were located less than 50m from the edge. Interior trees were located approximately 150m from the edge. Trees along the creek were located less than 25m from the waters edge. Two frass nets were placed 50cm from the base of each tree and were oriented randomly with respect to direction. Results from the two frass samples were averaged together to produce one average frass weight per tree for each week.

This study was designed to test the following null hypotheses:

1. Abundance of larval lepidopteran frass will not differ along the edge or in the interior of a forest.
2. Abundance of larval lepidopteran frass will not differ on American beech or sugar maple trees.
3. Abundance of larval lepidopteran frass in small, medium, and large size categories will not differ on American beech or sugar maple trees.

Figure 1. Location of the three transects across the beech-maple forest stand. All selected trees are depicted numerically: 1-10 are beech and 11-20 are maple.


Key: 1-10 beech
11-20 maple
North Perimeter Road
Tributary
South Fork Eagle Creek
North

Study Site

I conducted this study at the Ravenna Army Ammunition Plant (RAAP) in Portage County, Ohio (Figure 2). The area of study was a 10-ha plot of forest located within a 100-ha late-successional hardwood stand. A road was cut into the northern perimeter of the forest stand resulting in an abrupt change in vegetation and microclimate. The South Fork of Eagle Creek runs along the southern edge of the study plot. The beech-maple forest stand continues approximately 30m from the northern edge of North Perimeter Road and also extends to the south of Eagle Creek (Figure 3).

The dominant tree species within the plot are American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*). Both species are often found growing in close association with one another in mixed mesophytic hardwood stands. Many forest caterpillars are able to feed on either tree over the course of their development (Wagner et al. 1997). Many trees with a DBH greater than 30.5cm were harvested from the plot in 1940. Most canopy species within the study site are currently over 80 years old. Soil within the study site is classified as silt loam with 0-2% slopes (ODNR 1977).

Forest density was determined by using the point-quarter technique (Cox 1990). A total of 50 points were randomly selected throughout the forest plot. The area around each point was then divided into four quadrants. The tree closest to the center point in each quadrant was selected and identified. Diameter-at-breast-height (DBH) and point-to-individual distances (m) were measured. Only trees with a DBH greater than 9.0cm were chosen for density data. Data was used to calculate density, dominance, frequency, and importance values.

Figure 2. Location of the Ravenna Army Ammunition Plant, Portage County, Ohio. The enlargement shows the position of the RAAP in relation to surrounding transportation routes. The darkened region within the RAAP indicates the location of the study site.

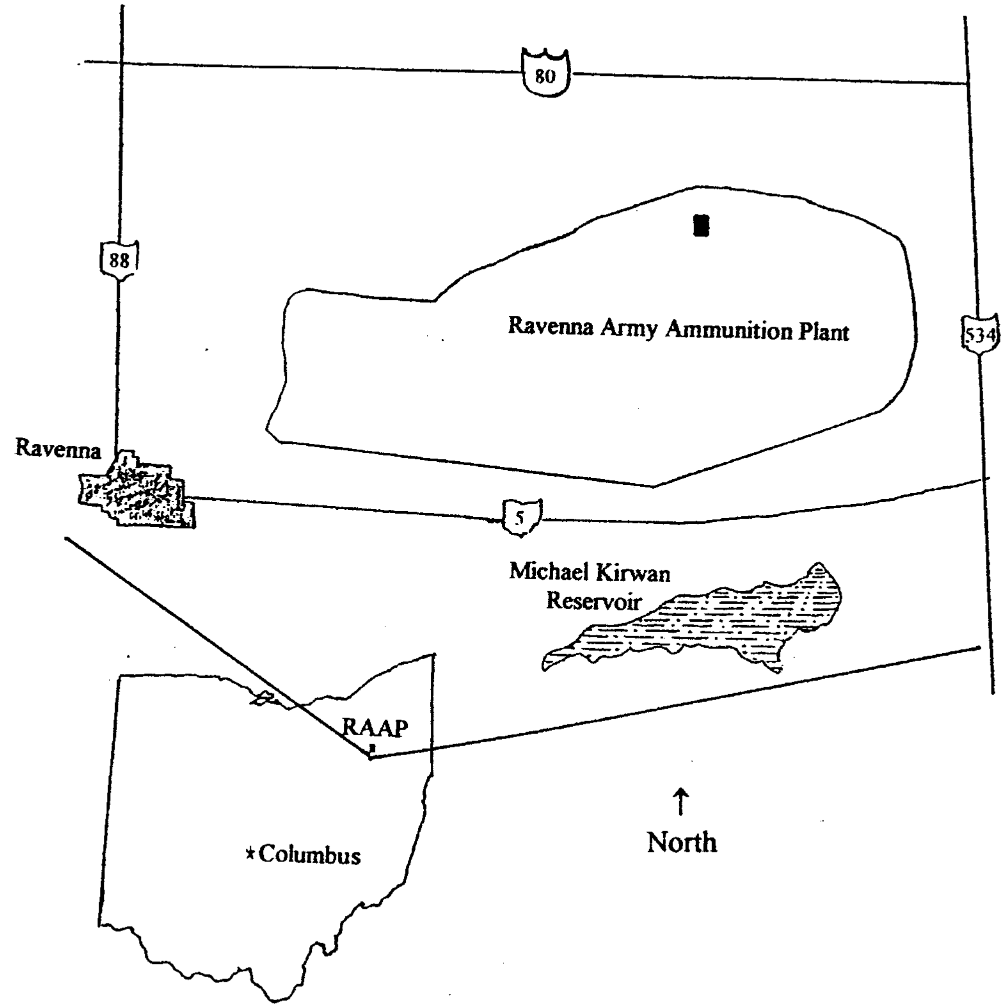

80
88
534
Ravenna Army Ammunition Plant
Ravenna
5
Michael Kirwan
Reservoir
RAAP
Columbus
North

Figure 3. Aerial photograph of the beech-maple forest stand at the RAAP. The highlighted area indicates the study site within the forest.

I selected this study site for three reasons: (1) the RAAP has a representation of lepidopteran diversity that currently consists of 748 recorded species (Rings and Downer 1996), (2) the identification of larval Lepidoptera within this plot will contribute to ongoing avian diet studies, and (3) the study site is in close proximity to YSU.

Collection of Samples

Frass nets were constructed from 1m X 1m cotton muslin with a brass grommet placed in each corner. A 2.5cm hex nut that weighed 32g was sewn to the bottom of each net in order to create a funneling effect and prevent the net from fluttering in the wind (Southwood 1978). The nets were suspended above the ground by 48cm galvanized steel stakes. All nets were placed in the three transects on June 30th and allowed to accumulate fallen frass pellets for 1 week before the collections began. From July 6th through September 1st ,1998, fallen frass pellets were collected once per week from 120 nets. A total of 7 collections were made over the course of this study. Twice during this research, on July 26th and August 10th, all net contents were destroyed due to heavy rain. On both occasions, all 120 nets were cleaned off and allowed to accumulate frass pellets for another week prior to collection.

During each collection, debris greater than 1cm in length was cleared from the net before placing the remaining contents into 6cm glass vials with rubber stoppers. Back in the laboratory, the remaining debris was removed from each sample using entomological forceps. Debris primarily consisted of leaf particles, tree bark, dirt, and insect body parts. After clearing the debris, each sample was transferred to a 5cm tin drying cup lined with absorbent paper towel to aid in removing moisture. Samples were air dried (Bean 1959, Volney et al. 1983) for one week before weighing. Saturniid frass pellets were considered to be outliers and were removed from all samples prior to weighing.

Fallen frass pellets from the peak collection were also separated using standard soil sieves and placed into 5 size categories: extra small (<1mm), small (1<2mm), medium (2<3mm), large (3<4mm), and extra large (>4mm). Pellets from the 5 most common species were counted from peak samples in order to compare larval frass abundance from each transect. Head capsules were also present among the frass and were retained for future identification.

In order to obtain live specimens from the study site, understory trees from each transect were beaten. This technique is used to dislodge larvae from foliage (Wagner et al. 1997). From each transect, 10 American beech and 10 sugar maples (DBH 2.0-5.0 cm) were randomly selected. Four white sheets measuring 200cm X 240cm were placed around the base of each tree. Each tree was beaten 10 times with a wooden baseball bat and also shaken by hand. Individual specimens and a leaf from their host tree were placed into 5cm plastic cups with lids. Three collections were made from June through July 1999. Larvae were placed on a table between two windows at a distance of 36cm from each window edge in order to provide a natural light source. No artificial light was used near the larvae in order to limit their exposure to a normal daily photoperiod. Every morning, all frass pellets were removed from the cups and their food supply was replenished. Data was recorded on all specimens regarding daily frass production, molts, behavioral observations, and parasitism. Representatives of the 14 most common specimens were shipped to Dr. David Wagner, University of Connecticut to confirm identification.

Species Identification

Frass pellet morphology is species specific. The characteristics of each pellet are created from the internal anatomy of the rectum. There are two types of rectal organs present in the form of pads and papillae (Weiss and Boyd 1950). As the digested food passes through the rectum, it is exposed to these organs which engrave unique patterns and markings upon each pellet. Many species have six rectal pads present which results in six very significant, longitudinal grooves etched into the outer surface (Weiss and Boyd 1950). Keys have been written in order to identify frass pellets to species based on the presence of such characteristics(Morris 1942, Hodson and Brooks 1956). Key descriptions are based upon fifth instar larvae. This can represent a potential problem unless positive identification of fifth instar frass has been established. For accuracy, live specimens should be collected and hand-reared. This will establish a reliable correlation between fifth instar larvae and their frass.

In addition to fallen frass pellets, head capsules may also provide a means of species identification. The sclerotized head capsules have many unique characteristics ranging from colored patterns to specific setal arrangements. Across the front of the head is an inverted Y-shaped ecdysial suture. This suture represents a line of weakness which may split during the last molt (Hinton 1947). Most species possess six stemmata that are arranged in a semicircle along each side of the cranium (Stehr 1987). Other notable features of the head capsule include the labrum, antennae, and maxillary palps (Figure 8, Appendix A). Located behind the labrum is a pair of opposable mandibles that are heavily sclerotized with toothlike projections along the inner margin (Eaton 1988). All of the mentioned features can easily be seen using a standard dissecting microscope.

Paramonov (1959) collected head capsules as a means of estimating larval numbers in tree crowns. Head capsules are not soluble and therefore are not affected by rainfall. However, they are extremely light weight and can easily be blown from collection nets by wind. For accuracy in calculating densities, a modified collection apparatus must be incorporated if head capsules are to be efficiently retained (Higashiura 1987). Larval head capsules for my study were used to aid in the identification of the species present in the RAAP and were incorporated into a written key. No density values were calculated from collected head capsules.

Based on their characteristics, fallen frass pellets were identified using a key written by Hodson and Brooks (1956). Since this key was written for frass pellets from fifth instar larvae, it is difficult to apply to field samples unless the age of the larvae is known. Also, many species that are present at the RAAP are not represented in the key. Therefore, the most accurate method of identifying frass from my collection was to hand-rear larvae and record specific frass characteristics from each species as viewed under a standard dissecting microscope. Pellets were measured using an ocular micrometer in order to provide a size range for frass from fifth instar larvae. This data was used to write a key for 14 common species found in a beech-maple canopy. Rapidograph drawings of all 14 frass pellets were included. Drawings were also incorporated from fifth instar head capsules from most of the hand-reared specimens.

Statistical Analysis

Both frass samples from each tree were averaged to produce one mean frass weight per tree, yielding a sample size of ten for each host species from each transect per week. Data from beech trees from the peak collection date was normally distributed and variances were proportional to means, so transformation of the data was not required. A one-way ANOVA ($\alpha = 0.05$) was used to compare mean frass weights from beech trees from the peak collection date across the three transects (SPSS, version 8.0). Data from maple trees was not normally distributed even after a log transformation (Kolmogorov-Smirnov). Therefore, Kruskal-Wallis was used to compare mean frass weights from maple trees from the peak collection date across the three transects (Zar 1984). Mean frass weights from all beech trees from the peak collection were compared to mean frass weights from all sugar maples using a Mann-Whitney test (Zar 1984).

The species pellet count data was analyzed for each of the five most abundant species on both tree hosts during the peak collection. Kruskal-Wallis was used to compare the mean number of pellets collected from American beech and sugar maple across the three transects (Zar 1984). Size classes of frass pellets from the peak collection were also compared across the three transects. Mean frass weights from the three most abundant size classes from American beech were analyzed using a one-way ANOVA (SPSS, version 8.0). Mean frass weights from the size classes from sugar maple were analyzed using a Kruskal-Wallis test (Zar 1984).

CHAPTER III

RESULTS

Seasonality of Frass Production

Frass weights were combined from all three transects for all 7 collection dates in order to observe the seasonality of larval frass production (Figure 4). The amount of frass pellets collected from the transects showed a steady increase over the first 3 weeks of the study. Frass production from American beech was greatest during the week prior to August 3, 1998. The amount of frass production from larvae feeding on sugar maple was greatest from the collection on July 20, 1998. Frass production declined sharply during the final 3 collections.

Many late-season lepidopteran larvae found on beech and maple foliage in this plot were in their fifth instar of development during the first week of August. The reduction in the number of fallen frass pellets found later in August may correspond with the migration of larvae to the forest floor to pupate. During the peak collection when larval biomass appears to be highest, forest insectivorous birds such as the Acadian flycatcher (*Empidonax virescens*), Hooded warbler (*Wilsonia citrina*), Scarlet tanager (*Piranga olivacea*), Eastern wood pewee (*Contopus virens*), and Red-eyed vireo (*Vireo olivaceus*) are feeding nestlings and fledglings.

Effect of Location and Host Plant on Frass Production

For each host plant, there was no significant difference in the mean frass weight recorded per tree along the road edge, in the interior, and along the creek edge when frass from all lepidopteran larvae were combined (Figure 5).

Figure 4. Seasonality of larval lepidopteran frass production from American beech and sugar maple canopy foliage. Values are mean frass weights (g) from beech (black bars) and maple (white bars) for each collection date.

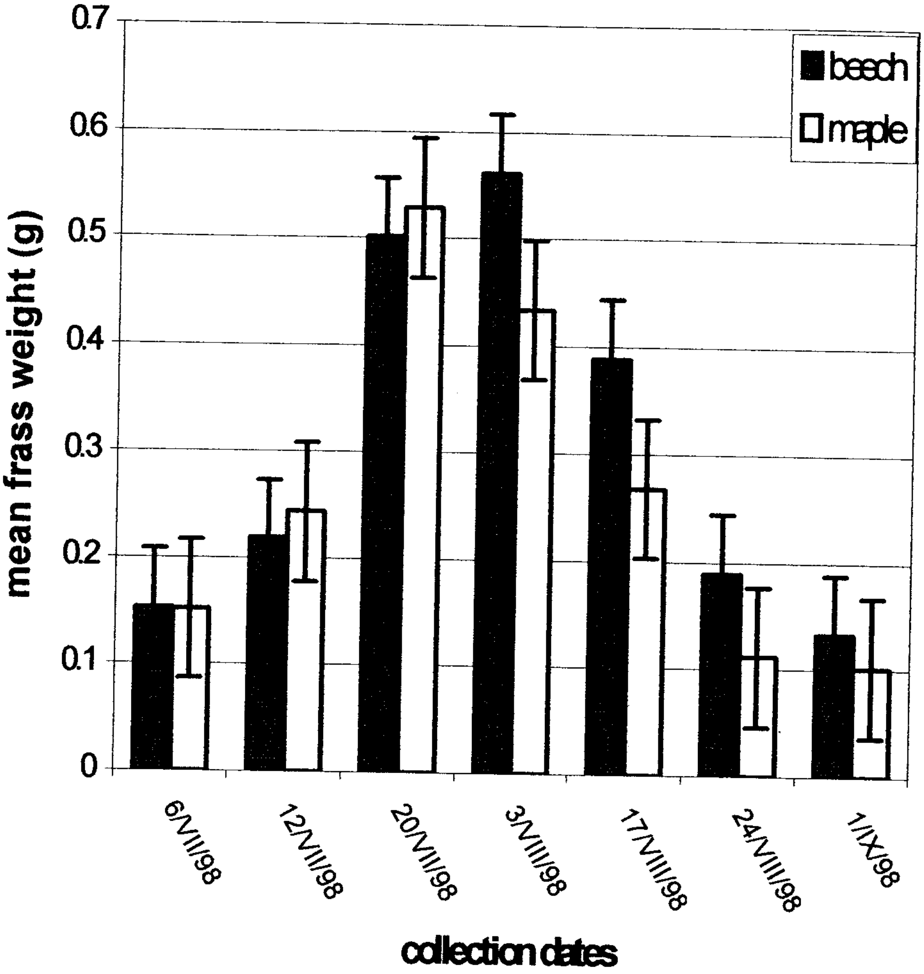
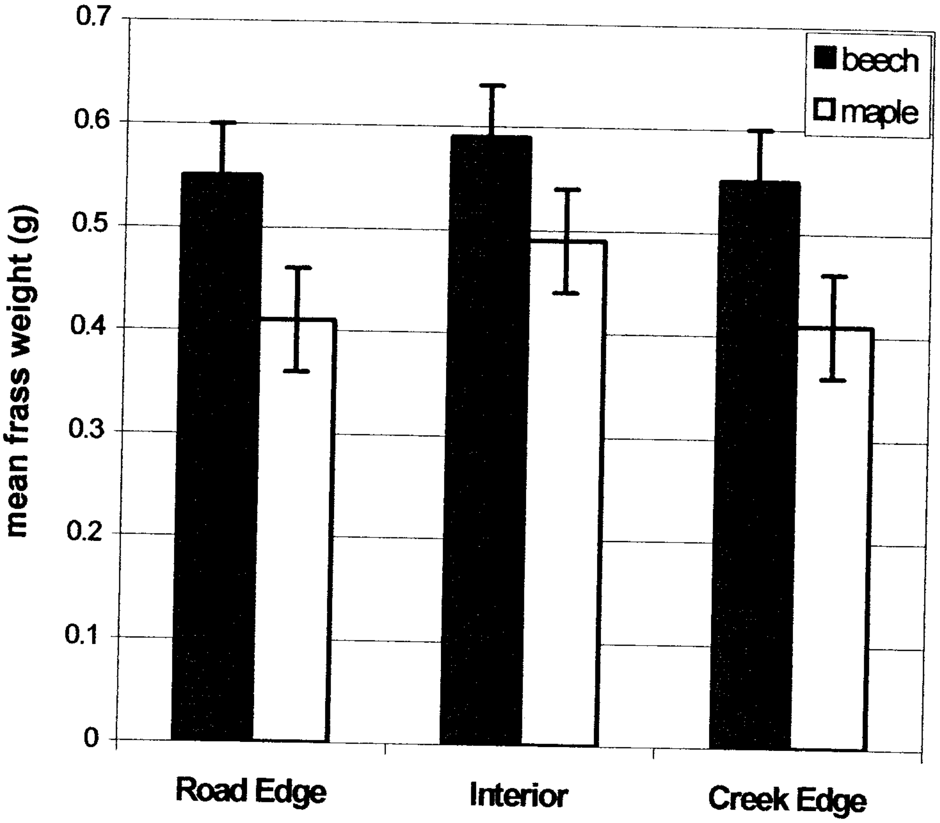

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
mean frass weight (g)
beech
maple
6/VII/98
12/VII/98
20/VII/98
3/VIII/98
17/VIII/98
24/VIII/98
1/IX/98
collection dates

Table 1. Mean frass weights (g) ± 1 SD from American beech (n = 10) and sugar maple (n = 10) from each transect. Values are taken from the peak collection date (August 3, 1998)

	American beech	Sugar maple
Interior	0.59 ± 0.15	0.49 ± 0.08
Creek	0.55 ± 0.19	0.40 ± 0.14
Road	0.55 ± 0.20	0.41 ± 0.20

Figure 5. Comparison of mean frass weights ± 1 SD from American beech and sugar maple from each transect. Values represent mean frass weights (g) for the peak collection date (August 3, 1998).


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
mean frass weight (g)
beech
maple
Road Edge
Interior
Creek Edge

However, mean frass weight per tree differed by host plant when all transects were combined for the peak collection date (Figure 6). Significantly more frass was collected beneath American beech than beneath sugar maple trees (Mann-Whitney; P= 0.01).

A total of 20 species were identified based on characteristics of their frass pellets or head capsules (Table 2). Each species was recorded along with their MONA identification number (Hodges et al. 1983). MONA is the abbreviation for moths and butterflies of North America (Rings and Downer 1996). The five most common species were: *Hypenodes fractilinea, Heterocampa guttivitta, Morrisonia latex, Hypagyrtis unipunctata*, and *Plagodis fervidaria.* All five of these species were present on every tree included in this study.

Frass pellets and head capsules collected from 80 hand-reared specimens from 14 species were measured using an ocular micrometer and drawn using a rapidograph #.25 pen (Figures 9 and 10). A dichotomous key was constructed using both frass pellets and head capsules for the 14 most common species of late-season larval lepidoptera found in this study (Appendix A).

The most abundant species from the 1998 frass collection was *Hypenodes fractilinea* (Family: Noctuidae), a pale green caterpillar about 15mm in length. The most unique feature of this larvae is the absence of the first set of prolegs from the third abdominal segment. When disturbed, *H. fractilinea* often dangles from a silken thread attached to the leaf where it was last feeding. There was no difference in the number of pellets collected from this species across all three transects during the peak collection (Kruskal-Wallis). However, significantly more *H. fractilinea* pellets were collected from American beech than from sugar maple (Mann-Whitney, P = 0.001).

Figure 6. Comparison of larval lepidopteran frass production from American beech and sugar maple. Values are combined mean frass weights (g) ± 1 SD from the peak collection date (August 3, 1998).

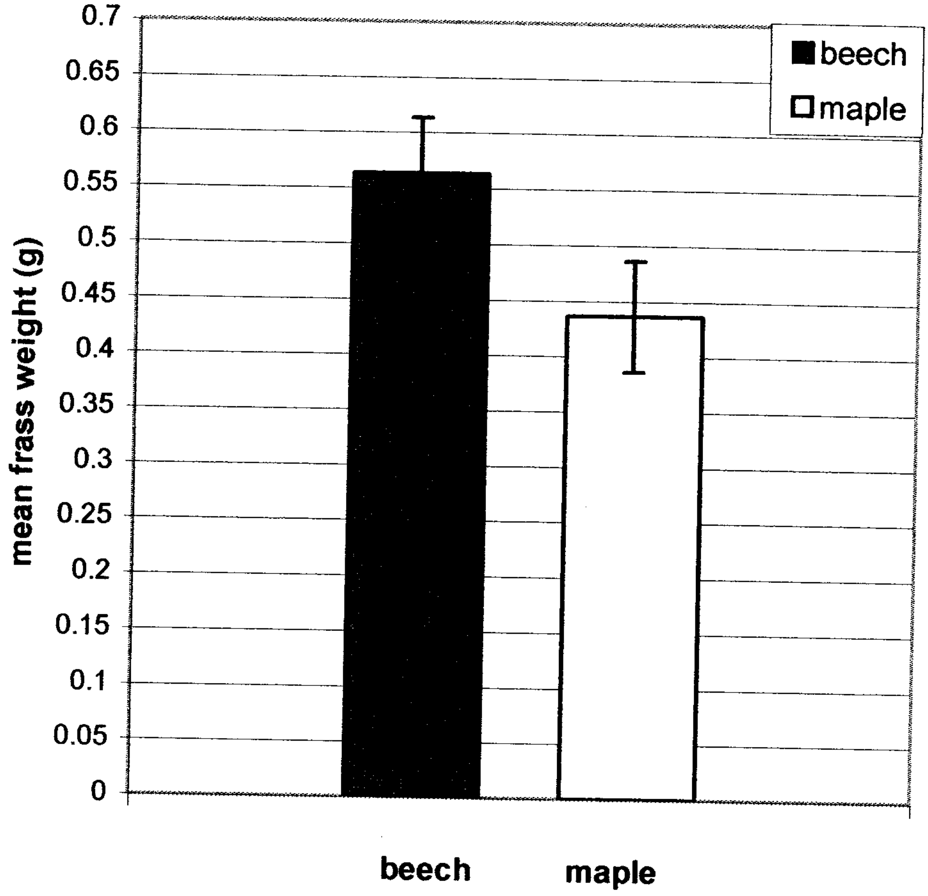

0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
mean frass weight (g)
■ beech
□ maple
beech
maple

Table 2. Species list of larval Lepidoptera identified by frass and/or head capsules from beech-maple canopy foliage at the RAAP in 1998. The MONA identification number (Hodges et al. 1983) is recorded in the first column.

MONA #	Scientific name	Common name
4665	*Lithacodes fasciola* (H.S.)	Yellow-shoulder slug
6640	*Biston betularia cognataria* (Gn.)	Cleft-headed looper
6654	*Hypagyrtis unipunctata* (Haw.)	One-spotted variant
6843	*Plagodis fervidaria* (H.S.)	Fervid plagodis
6894a	*Lambdina fervidaria athasaria* (Wlk.)	Curve-lined looper
7670	*Tolype velleda* (Stoll)	Velleda lappet moth
7715	*Dryocampa rubicunda* (F.)	Green-striped mapleworm
7757	*Antheraea polyphemus* (Cram.)	Polyphemus moth
7758	*Actias luna* (L.)	Luna moth
7827	*Cressonia juglandis* (J.E. Smith)	Walnut sphinx
7915	*Nadata gibbosa* (J. E. Smith)	Green oak caterpillar
7994	*Heterocampa guttivitta* (Wlk.)	Saddled prominent
8140	*Hyphantria cunea* (Drury)	Fall webworm
8203	*Halysidota tessellaris* (J. E. Smith)	Pale tussock moth
8211	*Lophocampa caryae* (Harr.)	Hickory tussock moth
8314	*Orgyia definata* (Pack.)	Definite-marked tussock
8318	*Lymantria dispar* (L.)	Gypsy moth
8421	*Hypenodes fractilinea* (Smith)	Broken-line hypenodes
9200	*Acronicta americana* (Harr.)	American dagger moth
10521.1	*Morrisonia latex* (Gn.)	Fluid arches

The second most abundant species was *Heterocampa guttivitta* (Family: Notodontidae). This species is 34mm long and is bright green with two pale yellow stripes along the dorsal surface. One of the distinguishing characteristics of this caterpillar is the multi-colored band on the head capsule. These bands are still conspicuous on the head capsule after it is shed. The saddled prominent can cause severe defoliation to both beech and sugar maple in the northeastern United States. This species often feeds along the leaf margin and will readily consume one to two entire leaves a day. *H. guttivitta* showed no difference in the number of frass pellets collected from all three transects during the peak collection or from American beech and sugar maple.

Morrisonia latex (Family: Noctuidae) was the third most abundant species at the study site. This caterpillar is 30mm long and has two distinct darkened spots on the head capsule. The dorsal surface is a rich brown color, and the ventral surface is light tan. This species formerly belonged to the genus *Polia* but was reclassified in 1989 (Rings et al. 1992). Although it is a common species, field specimens were heavily parasitized by a tachinid fly and all specimens perished in captivity. The number of pellets produced by *M. latex* was greater on American beech than on sugar maple (Mann-Whitney, P = 0.001) but did not differ by transect.

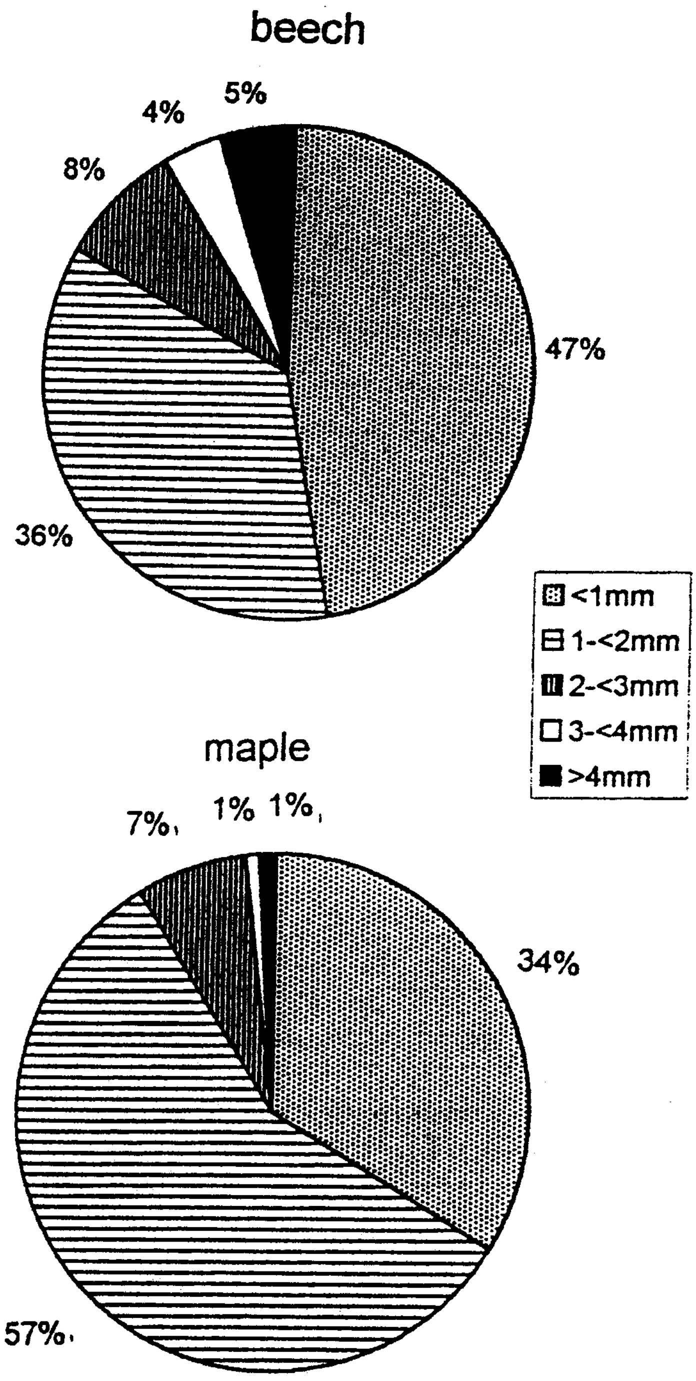
A fourth well-represented species was *Hypagyrtis unipunctata* (Family: Geometridae). This small geometrid is approximately 20mm in length. It is highly variable in color depending on the instar. During the early stages of development, this species appears brown but will change to a greenish color after the fourth instar. There was a significant difference in the number of pellets collected from *H. unipunctata* across all three transects (Table 7). More pellets were collected from beech along the creek than in the interior or along the road. However, the opposite was found for maple trees. More pellets were collected from maple along the road than in the interior or along the creek.

Another common caterpillar at the study site was *Plagodis fervidaria* (Family: Geometridae). This is a larger geometrid approximately 35mm in length. It is an excellent twig mimic that usually rests in an upright position supported by a fine thread of silk attached to the surface of a leaf or branch from the labrum. Similar results were found for *P. fervidaria* as for *H. unipunctata*, with higher pellet counts recorded for beech along the creek than in the interior or along the road, and higher pellet counts recorded for maple along the road than in the interior or along the creek (Table 8).

Size Classes of Frass

No significant differences were observed when comparing the three most common size categories across all three transects from beech or maple. Total frass weights from all transects from the peak collection were broken down by percentages to further classify larval biomass from the two hosts (Figure 7). The greatest abundance of frass pellets from beech trees (47%) was classified as being extra small (<1mm) whereas the greatest abundance of pellets from maple (58%) was classified as small (1-<2mm). On both hosts, the extra small and small size classes combined represent the majority of the collected frass pellets.

Figure 7. Comparison of the percentage of frass from American beech (a) and sugar maple (b) that belong to various size classes based on sieving frass pellets from the peak collection. Frass pellets were placed into one of five categories: extra small (<1mm), small (1-<2mm), medium (2-<3mm), large (3-<4mm), and extra large (>4mm).


beech
5%
4%
8%
47%
36%
▨ <1mm
▤ 1-<2mm
▥ 2-<3mm
☐ 3-<4mm
■ >4mm
maple
7%
1%
1%
34%
57%

CHAPTER IV

DISCUSSION

Seasonality

Forest ecosystems support a wide variety of lepidopteran larvae. From the beginning of leaf emergence in the spring, caterpillars are either hatching from eggs or waking from their winter slumber. As the summer months advance, lepidopteran larvae are actively passing through their developmental instars. As larvae grow, their feeding rate and frass production will increase. The amount of frass pellets collected from a forest canopy can be expected to show this trend in population dynamics.

An increase in frass production over the season may also reflect an increase in larval abundance. Large amounts of frass may be correlated with high larval densities. On sugar maple, the greatest amount of frass was collected one week earlier than when the peak frass production occurred on beech. This may be due to an earlier leaf emergence in the sugar maple (Carl Chuey, personal communication). In order to extrapolate larval densities in the canopy, crown measurements from each host would be needed.

Location and Host

Sugar maple is thought to be a more suitable host than American beech for forest lepidopteran larvae (Covell 1984). However, in this study, larval Lepidoptera appeared to prefer beech compared to maple. This is consistent with a food availability study by

Holmes and Schultz (1988), where beech had higher larval abundance compared to sugar maple.

Frass weights within each transect were highly variable which may reflect the patchy distribution patterns of the larvae. A trend in spatial preference was not detected until a species approach was taken. The spatial preferences observed in the Geometridae included in this study are not clearly understood. Predation pressure from birds nesting along the forest edges may have influenced the abundance of the caterpillars. Species such as the Hooded warbler (*Wilsonia citrina*) nested along the road edge in 1998 whereas the Acadian flycatcher (*Empidonax virescens*) nested primarily along the creek edge. Since different species of birds exhibit different foraging behaviors, avian prey selection will be the focus of future studies

Another possible reason for the shift in host preference may pertain to differences in leaf chemistry. The higher amount of solar radiation found along the forest edges may influence the chemical processes within the leaves. In the future, beech and maple leaves from all three transects will be analyzed for levels of water, nitrogen, lignin, and tannins.

Frass Size

The size class comparison of fallen frass pellets can be used to assess the sizes of available larvae as an avian food source from each host. American beech had high amounts of extra small frass pellets (<1mm) which may be due to high densities of *H.fractilinea*. Forest insectivorous birds may cue in on the locally abundant populations of this caterpillar when foraging. The high level of small frass pellets on sugar maple may also be due to high densities of geometrids feeding on this host. Both size classes of frass correspond to cryptic species that were abundant on beech and maple foliage at the study site. The five most abundant species of larval Lepidoptera present during the peak collection were in a size range considered to be acceptable to most birds nesting at the study site.

Energy Budget

As leaf biomass is consumed by lepidopteran larvae, energy is transferred from the host plant to the developing caterpillars. The assemblage of phytophagous larvae on canopy foliage then creates an important linkage to vertebrate food webs. The seasonal abundance of lepidopteran larvae coincides with the breeding of many forest insectivorous birds. Birds are able to take advantage of this flush of nutrients in the ecosystem when their energy needs are at a high demand (Barba et al. 1994).

Birds may selectively feed upon certain species when food is plentiful but will typically increase the variety of acceptable food items when seasonal arthropod abundance is very low (Emlen 1966). The weather over the course of this study did not deviate greatly from the previous two years (NOAA 1996, 1997, 1998). When weather conditions are extreme, such as a drought or above average rainfall, arthropod abundance will be low (Berryman 1996). The lack of extreme weather patterns during the frass collection indicates that the forest birds would have been selectively feeding on larvae during the 1998 breeding season since larvae were abundant.

Lepidopteran larvae that escape predation may still become part of the food web once they emerge as adults. Adult Lepidoptera that were selected in bird feeding trials indicate that medium-sized moths (those with a wingspan of 38-52mm) are a highly acceptable food source to insectivorous birds (MacLean et al. 1989). *H. guttivitta, M. latex*, and *H. unipunctata* all emerge as medium-sized moths based on their wingspan (Covell 1984). *H. fractilinea* is a very small adult with a wingspan of only 11-14mm. It may possibly be overlooked as a food item in the adult stage which can release predation pressure on this species and allow for high reproduction rates. *P. fervidaria* may also be less acceptable prey as an adult based on wingspan (23-31mm).

Conclusion

Results of this study support the following conclusions:

1. Spatial preferences exist among the geometrid species included in this study, *H. unipunctata* and *P. fervidaria*. Other species such as *Lymantria dispar* and *Hyphantria cunea* are known to prefer hosts oriented along an edge (Bellinger et al. 1989). Since different species appear to have different spatial preferences, the result was an even distribution of frass production across the beech-maple canopy.
2. American beech trees support higher frass production than sugar maples. If high frass production is correlated with high larval densities, then beech represents an optimal foraging site for avian predators compared to maple.
3. The three most abundant size classes of frass pellets from beech and maple do not significantly differ throughout the transects. Most frass pellets from both hosts are being produced by small or medium sized larvae. Therefore, large species such as the saturniids do not constitute a major portion of the phytophagous assemblage found on our beech-maple canopy. This implies that the majority of caterpillars at

the study site are within a size range that would be acceptable to forest insectivorous birds.

REFERENCES

Arnett, R.H. 1985. *American Insects : A Handbook of the Insects of America North of Mexico.* Van Nostrand Reinhold Co. New York.

Barba, E., Garcia, D.M., Gil-Delgado, J.A., and Lopez, G.M. 1994. Moth abundance and breeding success in a great tit population where moths are the main nestling food. Ardea 82: 329-334.

Bean, J.L. 1959. Frass size as an indicator of spruce budworm larval instars. Canadian Entomologist 52:605-608.

Bellinger, R.G., Ravlin, F.W., and McManus, M.L. 1989. Forest edge effects and their influence on gypsy moth (Lepidoptera: Lymantriidae) egg mass distribution. Environmental Entomology 18: 840-843.

Berenbaum, M. 1980. Adaptive significance of midgut pH in larval Lepidoptera. The American Naturalist 115:138-146.

Berryman, A.A. 1996 What causes population cycles of forest Lepidoptera? Trends in Ecology & Evolution 11: 28-32.

Borror, D.J. and White, R.E. 1970. *A Field Guide to Insects: America North of Mexico.* Houghton Mifflin Co. New York.

Bowers, M.D. 1993. Aposematic caterpillars: life-styles of the warningly colored and unpalatable. *In* Stamp,N.E. and Casey, T.M. (eds.). *Caterpillars: Ecological and Evolutionary Constraints on Foraging.* Chapman & Hill, New York.

Coffelt, M.A. and Schultz, P.B. 1993. Relationship among orange-striped oakworm (Lepidoptera: Saturniidae) frass length, frass production, host plant, and defoliation. Journal of Entomological Science 28: 291-298.

Covell, C.V. 1984. *A Field Guide to Moths of Eastern North America.* Houghton Mifflin Co., Boston.

Cox, G. 1990. *Laboratory Manual of General Ecology, Sixth edition.* Wm.C. Brown Publishers, Dubuque, Iowa.

Crawley, M.J. 1983. *Herbivory:The Dynamics of Animal-Plant Iinteractions.* Blackwell Scientific Publications, University of California Press Volume 10.

Dethier, V.G. 1959. Egg-laying habits of Lepidoptera in relation to available food. The Canadian Entomologist 91: 554-561.

Donovan, T.M., Jones, P.W., Annand, E.M., and Thompson, F.R. 1997. Varation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064-2075.

Eaton, J.L. 1988. *Lepidopteran Anatomy.* John Wiley & Sons, Inc. New York.

Emlen, J.M. 1966. The role of time and energy in food preference. The American Naturalist 100: 611-617.

Forman, R.T.T. and Godron, M. 1986. *Landscape Ecology.* John Wiley & Sons, Inc. New York.

Futuyma, D.J. 1976. Food plant specialization and environmental Predictability in Lepidoptera. The American Naturalist 110:285-292.

Harborne, J.B. 1977. *Introduction to Ecological Biochemistry.* Academic Press, Inc. New York.

Heinrich, B. 1979. Foraging strategies of caterpillars. Oecologia 42:325-337.

Higashiura, Y. 1987. Larval densities and a life-table for the gypsy moth, *Lymantria dispar*, estimated using the head-capsule collection method. Ecological Entomology 12:25-30.

Hinton, H.E. 1947. The dorsal cranial areas of caterpillars. Annual Magazine of Natural History 14:843-852.

Hodges, R.W. et al., 1983. *Checklist of the Lepidoptera of America North of Mexico.* London: E.C. Classey Ltd. & The Wedge Entomological Research Foundation.

Hodson, A.C. and Brooks, M.A. 1956. The frass of certain defoliators of forest trees in the north central United States and Canada. Canadian Entomologist 88:62-68.

Holmes, R.T. and Schultz, J.C. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology 66: 720-728.

Kamata, N. and Igarashi Y. 1994. Problems in estimating the density of larval beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep.,Notodontidae), using frass drops by the modification of the Southwood-Jepson method. Journal of Applied Entomology 118:92-99.

Laurance, W.F. and Yensen, E. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55:77-92.

Lawton, J.H. and Strong, D.R. 1981. Community patterns and competition in folivorous insects. The American Naturalist 118:317-338.

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28:23-39.

Levenson, J.B. 1981. Woodlots as biogeographic islands in southeastern Wisconsin. *In* Burgess, R.L. and Sharpe, D.M. (eds.). *Forest Island Dynamics in Man-dominated Landscapes.* Springer-Verlag, New York.

Liebhold, A.M. and Elkinton, J.S. 1988. Techniques for estimating the Density of late-instar gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations using frass drop and frass production measurements. Environmental Entomology 17:381-384.

MacLean, D.A., Sargent, T.D., MacLean, B.K. 1989. Discriminant analysis of lepidopteran prey characteristics and their effects on the outcome of bird-feeding trials. Biological Journal of the Linnean Society 36: 295-311.

Mattson, W.J. and Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. Science 190:515-521.

Moran, V.C. and Southwood T.R.E. 1982. The guild composition of Arthropod communities in trees. Journal of Animal Ecology 51:289-306.

Morris, R.F. 1942. The use of frass in the identification of forest insect damage. Canadian Entomologist 74:164-167.

Neilson, B.O. and Ejlerson, A. 1977. The distribution pattern of herbivory in a beech canopy. Ecological Entomology 2:293-299.

Niklas, K.J. 1995. Differences between *Acer saccharum* leaves from open and wind-protected sites. Annals of Botany 78:61-66.

NOAA, National Climatic Data Center 1996, 1997, 1998. Youngstown Municipal Airport

ODNR, 1977. Soil survey of Portage County, Ohio. U.S. Department of Agriculture: Soil Conservation Service

Palik, B.J. and Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management 32:187-202.

Paramonov, A. 1959. A possible method of estimating larval numbers in tree crowns. Entomologist's Monthly Magazine 95:82-83.

Ranney, J.W., Bruner, M.C., and Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. *In* Burgess, R.L. and Sharpe, D.M. (eds.). *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York.

Rhoades, D.F. 1979. Evolution of plant chemical defense against herbivores. *In* Rosenthal, G.A. and Janzen, D.H. (eds.). *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York.

Rings, R.W., Metzler,E.H., Arnold, F.J., and Harris, D.H. 1992. *The Owlet moths of Ohio Order: Lepidoptera (Family: Noctuidae)*. College of Biological Sciences, The Ohio State University Research Report No. 4

Rings, R.W. and Downer, R.A. 1996. Lepidoptera of Ravenna Arsenal. Ohio Agricultural Research and Development Center, Department of Entomology 25p.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation. Conservation Biology 5:18-32.

Schowalter, T.D., Hargrove, W.W., and Crossley, D.H. 1986. Herbivory in forested ecosystems. Annual Review of Entomology 31:177-196.

Schroeder, L.A. 1986. Changes in tree leaf quality and growth performance of lepidopteran larvae. Ecology 67:1628-1636.

Scriber, J.M. and Feeny, P. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. Ecology 60:829-850.

Scriber, J.M. and Slanskey, F. 1981. The nutritional ecology of immature insects. Annual Review of Entomology 26:183-211.

Sherry, T.W. 1984. Comparitive dietary ecology of sympatric, insectivorous neotropical flycatchers (Tyrannidae). Ecological Monographs 54: 313-338.

Smith, R.L. 1990. *Ecology and Field Biology, Fourth edition.* HarperCollins Publishers, Inc.

Southwood, T.R.E. 1978. *Ecological Methods, Second edition.* Halsted Press, New York.

SPSS, 1998. Version 8.0. SPSS Inc. Chicago, Illinois.

Stadler, E. 1986. Oviposition and feeding stimuli in leaf surface waxes. *In* Juniper, B. and Southwood, S.R. (eds.). *Insects and the Plant Surface.* Edward Arnold Publishers, Ltd. London.

Stehr, F.W. 1987. *Immature Insects, First edition.* Kendall/Hunt Publishing Co., Dubuque, Iowa.

Strong, D.R., Lawton, J.H., and Southwood S.R. 1984. *Insects on Plants: Community Patterns and Mechanisms.* Harvard University Press Cambridge, Mass.

Usher, M.B. and Keiller, S.W. 1998. The macrolepidoptera of farm woodlands: determinants of diversity and community structure. Biodiversity and Conservation 7:725-748.

Volney, W.J., Koehler, C.S., Browne, L.E., Barclay, L.W., Milstead, J.E., and Lewis, V.R. 1983. Sampling for California oakworm on landscape oaks. California Agriculture 37:8-9.

Wagner, D.L., Giles, V., Reardon, R.C., and McManus, M.L. 1997. *Caterpillars of Eastern Forests.* United States Dept. of Agriculture FHTET-96-34:

Wales, B.A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs 42:451-471.

Weiss, H.B. and Boyd, W.M. 1950. Insect feculae. Journal of the New York Ent. Soc. 58:154-168.

Whitney, G.G. and Runkle, J.R. 1981. Edge versus age effects in the development of a beech-maple forest. Oikos 37:377-381.

Wilson, W.G., Harrison, S.P., Hastings, A., and McCann, K. 1999. Exploring stable pattern formation in models of tussock moth populations. Journal of Animal Ecology 68: 94-107.

Zandt, H.S. 1994. A comparison of three sampling techniques to estimate the population size of caterpillars in trees. Oecologia 97: 399-406.

Zar, J.H. 1984. *Biostatistical Analysis, Second edition.* Prentice-Hall, Inc. New Jersey.

APPENDIX A

FRASS KEY

Key to late-season larval lepidopteran frass from a beech-maple canopy in Northeastern Ohio

1. Frass pellets found either in webbing on the host tree or beneath a tree containing webbing....................................2

   Frass found on the ground among leaf litter or on understory vegetation...3

2. Frass pellets 2.0-2.5mm, rough surface with embedded plant fragments present, shallow cup-like depression found on one end, rectangular shape with no grooves present...... ....*Hyphantria cunea*
   Head capsule 1.5mm wide, amber with darker brown along lower portion of the frontoclypeus and around stemmata, labrum very dark, many long setae present along top of head capsule attached to a thoracic shield, most head setae appear long (1mm) and are only located near stemmata, frons, and clypeus.

   Frass pellets variable in size, may be rough or smooth, found beneath beech or sugar maple trees..................................3

3. Frass with longitudinal grooves present, surface may be smooth or textured..4

   No grooves present, may have an irregular shape...............7

4. Surface smooth or slightly textured, six longitudinal grooves present...5

   Surface very coarsely textured, six longitudinal grooves present but all may not be distinct...6

5. Frass pellets 2.0-2.5mm, smooth texture, larger end is blunt or truncate, the other end is tapered ....*Heterocampa guttivitta*
   Head capsule elongated, 2.0mm wide at the base tapering to 1.0mm at the top, appears white with two very distinct parallel tan bands that run along the entire length of the head capsule, mandibles dark amber.

Frass pellets 2.5-3.0mm, slightly textured surface, truncate on one end, tapered end has a shallow, cup-like depression..*Nadata gibbosa*
Head capsule 3mm wide, white with occasional short setae, labrum is deeply cleft, long antennae (1.25mm), mandibles white with a dark amber margin, third stemmata is ringed in black.

6. Frass 2.0-2.5mm, longitudinal grooves are deep, each section is further subdivided by incomplete transverse grooves, both ends truncate with one end being slightly larger, texture is coarse...*Lymantria dispar*

Frass 2.0-2.5mm, longitudinal grooves may be hard to distinguish, very coarse texture, truncate at both ends, neither end is tapered.....................................*Orgyia definata*
Head capsule 2.0mm, clear with a heavily dimpled surface, long setae present on lower portion of head capsule, two pencil tufts attached to small protuberances on either side of capsule consisting of both yellow and black hairs, top of head capsule with large amount of long yellow hairs that project forward.

7. Frass with a smooth texture or with plant fragments firmly embedded in embedded in the surface giving a uniform appearance...8

Frass with a coarse texture, pellet is composed of large plant fragments, very irregular appearance..............................13

8. Transverse constriction present, shape variable....................9

No transverse constriction; elongated or rectangular shape.....12

9. Pellets with one or two constrictions, usually large..............10

Pellets with only one constriction 11

10. Frass 3.5-4.0mm, one or two transverse constrictions present, plant particles are evenly embedded in surface giving a granular appearance, pellet is slightly tapered with smaller end having a

shallow cup-like depression ....*Halysidota tessellaris*
Head capsule 3.0mm,shiny black surface, clypeus is clear, labrum and antennae are amber, stemmata white, few short setae present on lower portion of capsule.

Frass not as above, only one constriction present, most pellets < 3.0mm...11

11. Frass pellets1.0-1.5mm, transverse constriction is shallow, ends are slightly rounded....................................*Lithacodes fasciola*

Frass pellets 2.0-2.5mm, transverse constriction deep, pellet is nearly divided in half, cup-like depression present on one end...*Morrisonia latex*
Head capsule 3.0mm, light amber with two large dark brown markings that resemble eye spots, stemmata are dark brown, clypeus and labrum are pale tan.

12. Pellets 1.0-1.5mm, rectangular shape, green color, very smooth surface with no grooves or markings.........*Hypenodes fractilinea*
Head capsule 1.5mm, white with very few short setae present, labrum deeply cleft, mandibles white with a dark brown edge.

Pellets 4.5-6.0mm, dark olive color, plant particles can be seen but are compressed to the surface, blunt end has a shallow cup-like depression, other end is slightly tapered...........*Biston betularia*

13. Frass pellets very irregular, plant fragments may give pellet a jagged appearance, one end tapers to a point................14

Frass not tapered, both ends are blunt, surface is composed of large overlapping plant fragments....................................15

14. Frass pellets 2.0-2.5mm, one end may appear flat, other end is tapered,plant fragments cause a highly irregular shape..*Plagodis fervidaria*
Head capsule 2.0mm, tan with two distinct dark brown bands that gradually branch, faint brown mottling across entire surface; labrum, mandibles, and antennae dark brown.

Frass pellets 1.0-1.5mm, surface variable, plant fragments loosely compressed, one end is slightly tapered, edges are not uniform... *Lambdina fervidaria*

15. Pellets 1.5-2.0mm, consists of compressed plant fragments, rectangular shape, both ends blunt .... *Hypagyrtis unipunctata* Head capsule 2.0mm, two parallel dark brown stripes on dorsal surface, brown mottling across entire capsule, anteclypeus is convoluted, mandibles dark amber.

Pellets 2.5-3.0mm, very coarse texture, many large overlapping plant fragments embedded in surface; if longitudinal lines are present they are difficult to distinguish................ *Tolype vellada*

Definitions: longitudinal grooves = six grooves that are etched into the outer surface of each pellet, run from one end to the other

transverse constriction = a constriction that usually occurs around the middle

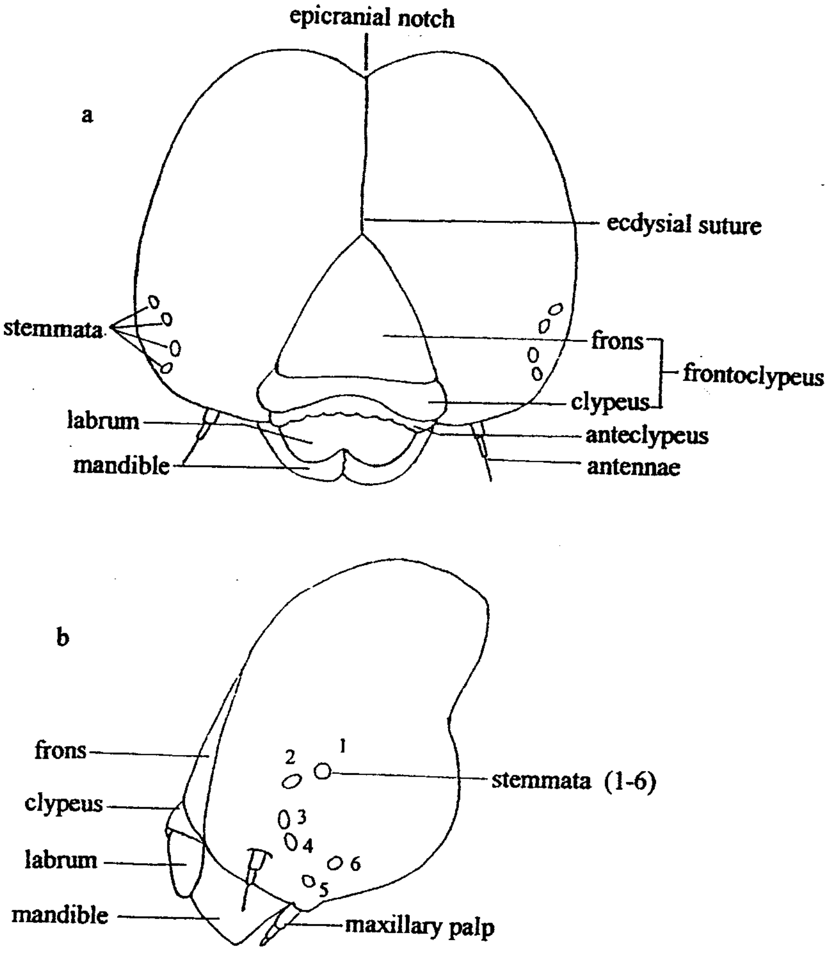


Figure 8. Diagrammatic representation of a larval lepidopteran head capsule illustrating the diagnostic characteristics from the frontal view (a) and the side view (b).

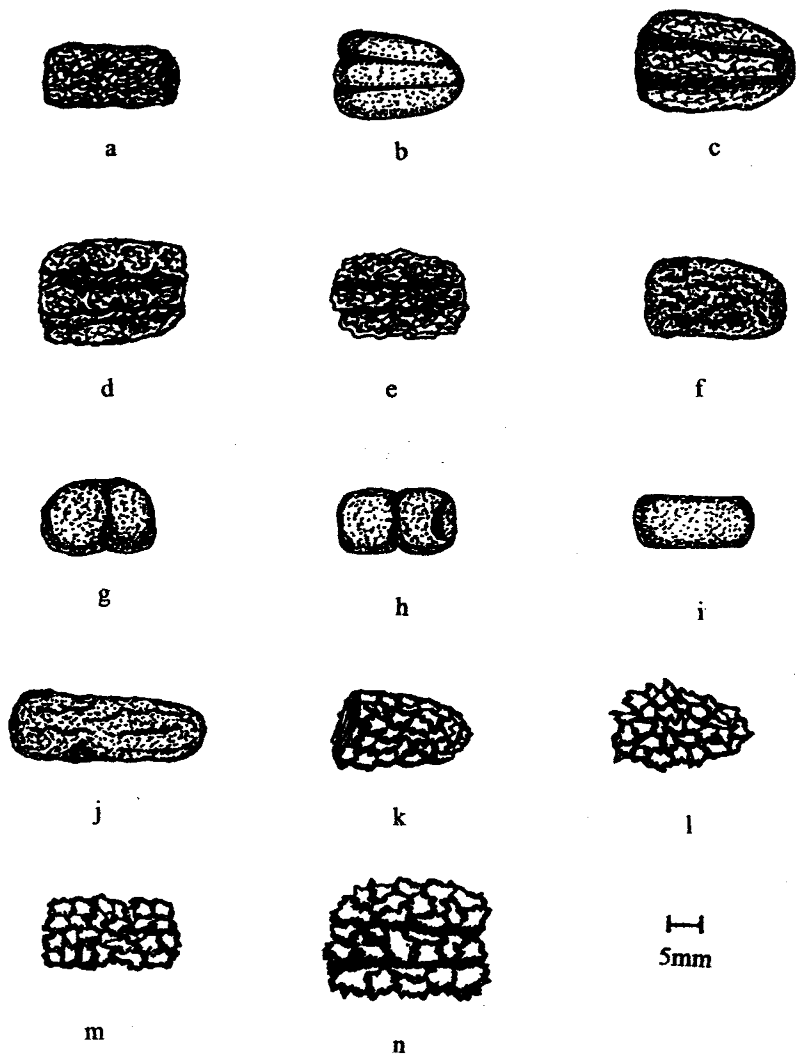


Figure 9. Rapidograph drawings of fifth instar frass pellets from 14 common late-season lepidoperan larvae from a beech-maple canopy. (a) *Hyphantria cunea*, (b) *Heterocampa guttivitta*, (c) *Nadata gibbosa*, (d) *Lymantria dispar*, (e) *Orgyia definata*, (f) *Halysidota tessellaris*, (g) *Lithacodes fasciola*, (h) *Morrisonia latex*, (i) *Hypenodes fractilinea*, (j) *Biston betularia*, (k) *Plagodis fervidaria*, (l) *Lambdina fervidaria*, (m) *Hypagyrtis unipunctata*, (n) *Tolype vellada*.

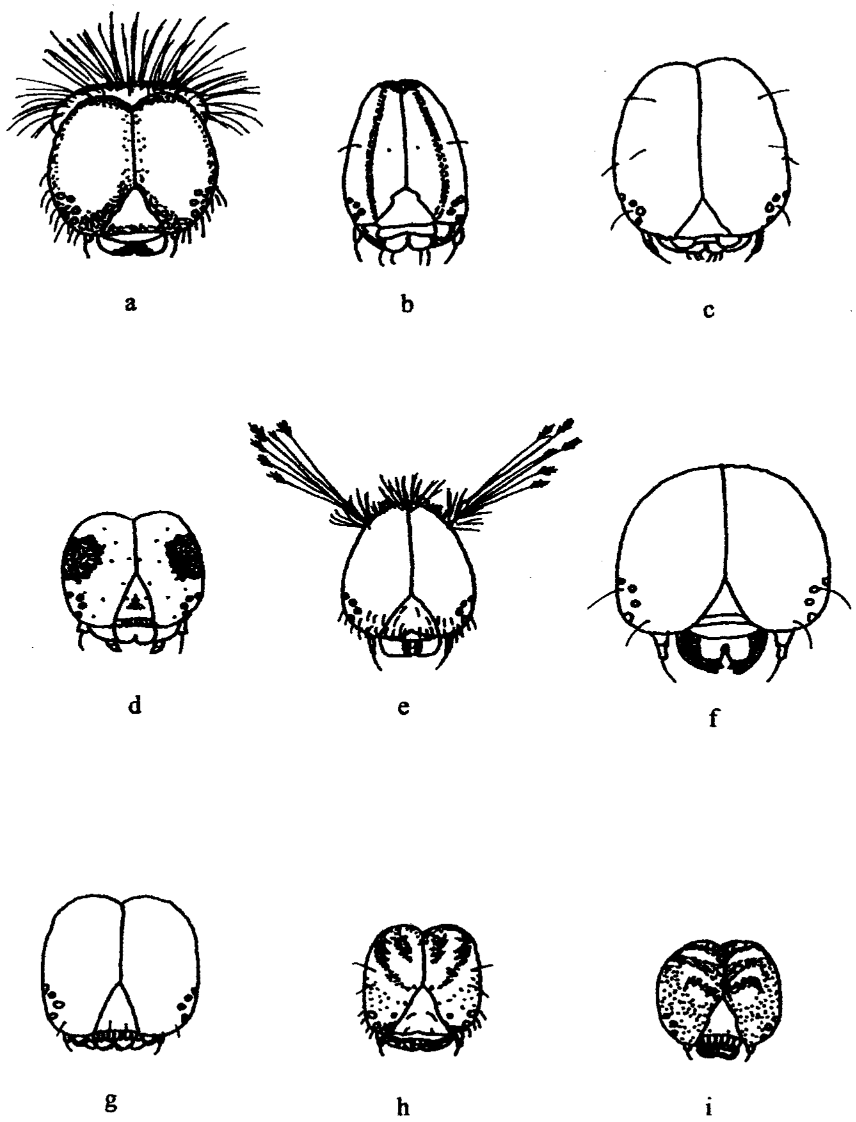


Figure 10. Rapidograph drawings of fifth instar head capsules from hand-reared larval Lepidoptera from a beech-maple canopy. (a) *Hyphantria cunea*, (b) *Heterocampa guttivitta*, (c) *Nadata gibbosa*, (d) *Morrisonia latex*, (e) *Orgyia definata*, (f) *Halysidota tessellaris*, (g) *Hypenodes fractilinea*, (h) *Plagodis fervidaria*, (i) *Hypagyrtis unipunctata*.

APPENDIX B

FOREST DATA

Table 3. Summary of forest density analysis by the point-quarter technique at RAAP study site. Values included are number of each species (N), average dominance (Avg. Dom.), density, relative density (Rel. Density), dominance (Dom.), relative dominance (Rel. Dom.), frequency (Freq.), relative frequency (Rel. Freq.), and importance value (I. Value).

Species	N	Avg. Dom.	Density	Rel. Density	Dom. (basal area)	Rel. Dom.	Freq	Rel. Freq	I. Value
American beech (*Fagus grandifolia*)	65	.2080	71.1	32.5	14.8	38.1	.68	25.4	96.0
Sugar maple (*Acer saccharum*)	37	.1591	40.5	18.5	6.4	16.6	.46	17.2	52.3
Red maple (*Acer rubrum*)	27	.1509	21.9	10.0	3.3	8.5	.34	12.7	31.2
Black cherry (*Prunus serotina*)	20	.2031	29.5	13.5	6.0	15.4	.30	11.2	40.1
Tulip (*Liriodendron tulipifera*)	15	.1398	16.4	7.5	2.3	5.9	.28	10.4	23.8
White ash (*Fraxinus americana*)	14	.1532	15.3	7.0	2.3	6.0	.22	8.2	21.2
Red oak (*Quercus rubra*)	8	.1510	8.8	4.0	1.3	3.4	.12	4.5	11.9
Bitternut hickory (*Carya cordiformis*)	7	.1813	7.7	3.5	1.4	3.6	.14	5.2	12.3
Pin oak (*Quercus ellipsoidalis*)	2	.1948	2.2	1.0	.43	1.1	.04	1.5	3.6
Butternut (*Juglans cinerea*)	1	.2027	1.1	0.5	.22	0.57	.02	.75	1.82
Eastern cottonwood (*Populus deltoides*)	1	.0794	1.1	0.5	.09	0.22	.02	.75	1.47
Shagbark hickory (*Carya ovata*)	1	.0693	1.1	0.5	.08	0.20	.02	.75	1.45
Cucumber magnolia (*Magnolia acuminata*)	1	.0683	1.1	0.5	.08	0.19	.02	.75	1.44
American elm (*Ulmus americana*)	1	.0603	1.1	0.5	.07	0.17	.02	.75	1.42
(TOTAL)	200				38.7		2.6		

Table 4. DBH (cm) of selected beech and sugar maple trees from each transect. Mean DBH (**X**) and ± 1 standard deviation (SD) are listed.

	Road edge		Interior		Creek edge
Beech	DBH (cm)		DBH (cm)		DBH (cm)
1	34.54		34.04		45.21
2	68.07		47.75		54.61
3	73.91		51.31		46.74
4	96.77		40.64		34.54
5	87.12		45.97		73.66
6	70.87		69.09		53.34
7	73.15		59.69		49.02
8	76.71		51.82		75.95
9	53.09		46.99		48.26
10	32.76		67.82		48.64
	X = 66.19 SD= 21.78		**X = 51.51** SD= 11.21		**X = 52.99** SD= 12.71
	Road edge		Interior		Creek edge
Maple	DBH (cm)		DBH (cm)		DBH (cm)
11	28.96		67.82		33.53
12	58.42		43.69		30.23
13	68.07		27.43		53.59
14	38.86		40.89		57.15
15	46.23		49.53		31.50
16	31.75		48.51		34.80
17	54.36		56.64		35.56
18	35.81		82.04		55.37
19	52.07		49.28		76.17
20	43.18		34.04		42.16
	X= 45.77 SD= 12.49		**X=49.99** SD= 15.91		**X = 44.81** SD= 15.03

APPENDIX C

ANOVA TABLES

Table 5. Analysis of variance table of frass weights (g) from American beech from each transect. Results are based on mean frass weights from each tree for the peak collection date (August 3, 1998).

American beech

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Interior	10	5.92	0.592	0.0235289
Creek	10	5.49	0.549	0.0364989
Road	10	5.53	0.553	0.0408011

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.0112867	2	0.0056433	0.1679082	0.8463074	3.3541312
Within Groups	0.90746	27	0.0336096			
Total	0.9187467	29				

Table 6. Analysis of variance table of frass pellets from three size classes: extra small (<1mm), small (1-<2mm), and medium (2-<3mm). Frass was collected from American beech from each transect. Values are based on log transformed data of frass pellet weights (g) from the peak collection date (August 3, 1998).

Beech (<1mm)
Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	10	1.0014	0.10014	0.001183
Column 2	10	1.1289	0.11289	0.003192
Column 3	10	1.0148	0.10148	0.000862

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.000982	2	0.000491	0.281225	0.757042	3.354131
Within Groups	0.047132	27	0.001746			
Total	0.048113	29				

Beech (1-<2mm)
Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	10	0.858	0.0858	0.000509
Column 2	10	0.7447	0.07447	0.000288
Column 3	10	0.9364	0.09364	0.001112

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.001858	2	0.000929	1.459308	0.25015	3.354131
Within Groups	0.017186	27	0.000637			
Total	0.019044	29				

Table 6. Continued

Beech (2-<3mm)
Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	10	0.1982	0.01982	6.48E-05
Column 2	10	0.2274	0.02274	4.99E-05
Column 3	10	0.2309	0.02309	0.000121

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	6.45E-05	2	3.22E-05	0.409913	0.667769	3.354131
Within Groups	0.002123	27	7.86E-05			
Total	0.002188	29				

APPENDIX D

STATISTICAL TESTS

Table 7. Nonparametric Tukey-type multiple comparisons for determining significance of pairwise contrasts in the amount of *Hypagyrtis unipunctata* frass pellets from each transect on American beech and sugar maple.

American beech

	Road	Interior	Creek
Rank:	3	2	1
Mean	78	167.5	219.5

Comparison	Differences	SE	q	$q_{0.05,\infty,3}$
3 vs.1	141.5	27.84	5.08*	3.486
3 vs. 2	52.0	27.84	1.87	3.486
2 vs. 1	89.5	27.84	3.21	3.486

Sugar maple

	Creek	Interior	Road
Rank:	3	2	1
Mean	79.0	181.0	205.0

Comparison	Differences	SE	q	$q_{0.05,\infty,3}$
3 vs.1	126.0	27.84	4.53*	3.486
3 vs. 2	24.0	27.84	0.86	3.486
2 vs. 1	102.0	27.84	3.66*	3.486

Table 8. Nonparametric Tukey-type multiple comparison for determining significance of pairwise contrasts in the amount of *Plagodis fervidaria* frass pellets from each transect on American beech and sugar maple.

American beech

	Road	Interior	Creek
Rank:	3	2	1
Mean	77.0	165.0	223.0

Comparison	Differences	SE	q	$q_{0.05,\infty,3}$
3 vs.1	146.0	27.84	5.24*	3.486
3 vs. 2	58.0	27.84	2.08	3.486
2 vs. 1	88.0	27.84	3.16	3.486

Sugar maple

	Creek	Interior	Road
Rank:	3	2	1
Mean	82.0	180.5	202.5

Comparison	Differences	SE	q	$q_{0.05,\infty,3}$
3 vs.1	120.5	27.84	4.32*	3.486
3 vs. 2	22.0	27.84	0.79	3.486
2 vs. 1	98.5	27.84	3.54*	3.486

APPENDIX E

FIELD DATA

Table 9. Frass weights (g) from each net located along the forest interior for seven collections. Beech trees are numbered 1-10 and maples are numbered 11-20. Nets were oriented in a north (N), south (S), west (W), or east (E) position.

Tree/Net	7/6/98	7/12/98	7/20/98	8/3/98	8/17/98	8/24/98	9/1/98
1S	0.09	0.2	0.42	0.33	0.15	0.17	0.07
1E	0.16	0.23	0.49	0.27	0.33	0.11	0.04
2N	0.13	0.18	0.46	0.45	0.35	0.2	0.17
2E	0.14	0.27	0.69	0.55	0.29	0.23	0.13
3E	0.09	0.17	0.58	0.71	0.29	0.17	0.09
3W	0.21	0.21	0.75	0.55	0.33	0.18	0.08
4W	0.13	0.26	0.43	0.81	0.45	0.3	0.21
4S	0.19	0.16	0.33	0.58	0.56	0.24	0.14
5N	0.17	0.34	0.43	0.7	0.48	0.28	0.06
5S	0.14	0.2	0.41	0.58	0.4	0.22	0.08
6S	0.15	0.14	0.47	0.44	0.32	0.35	0.27
6E	0.03	0.04	0.46	0.7	0.38	0.26	0.34
7N	0.16	0.21	0.28	0.43	0.39	0.05	0.11
7W	0.1	0.16	0.33	0.42	0.23	0.12	0.09
8N	0.14	0.17	0.45	0.58	0.28	0.12	0.06
8S	0.21	0.27	0.56	0.57	0.22	0.2	0.07
9N	0.15	0.24	0.7	0.79	0.47	0.38	0.26
9E	0.05	0.24	0.42	0.73	0.45	0.44	0.16
10W	0.06	0.18	0.32	1.06	0.39	0.2	0.1
10E	0.06	0.11	0.41	0.55	0.13	0.16	0.09
11N	0.12	0.21	0.36	0.48	0.03	0.15	0.05
11S	0.12	0.17	0.54	0.47	0.16	0.09	0.08
12N	0.1	0.15	0.55	0.85	0.26	0.12	0.02
12E	0.19	0.21	0.7	0.51	0.31	0.21	0.04
13N	0.12	0.24	0.48	0.45	0.32	0.34	0.36
13S	0.27	0.34	0.62	0.57	0.67	0.49	0.41
14S	0.11	0.18	0.42	0.39	0.2	0.09	0.08
14E	0.11	0.16	0.33	0.51	0.26	0.14	0.22
15N	0.13	0.16	0.58	0.44	0.17	0.13	0.11
15E	0.15	0.12	0.57	0.61	0.23	0.11	0.12
16S	0.11	0.24	0.69	0.42	0.2	0.05	0.07
16W	0.18	0.22	0.64	0.4	0.16	0.09	0.03
17N	0.12	0.29	0.58	0.42	0.27	0.07	0.15
17W	0.13	0.23	0.53	0.47	0.41	0.06	0.08
18S	0.11	0.21	0.3	0.39	0.13		0.07
18W	0.15	0.18	0.32	0.41	0.23	0.01	0.14
19N	0.12	0.16	0.5	0.49	0.26	0.01	0.14
19E	0.13	0.23	0.43	0.51	0.27	0.03	0.2
20N	0.11	0.18	0.34	0.44	0.42		0.06
20W	0.11	0.2	0.35	0.45	0.32		0.17

Table 10. Frass weights (g) from each net located along the creek edge for seven collections. Beech trees are numbered 1-10 and maples are numbered 11-20. Nets were oriented in a north (N), south (S), west (W), or east (E) position.

Tree/Net	7/6/98	7/12/98	7/20/98	8/3/98	8/17/98	8/24/98	9/1/98
1W	0.24	0.31	0.6	0.23	0.22	0.11	0.05
1E	0.18	0.25	0.47	0.27	0.27	0.17	0.07
2N	0.17	0.21	0.31	1.07	0.42	0.25	0.12
2E	0.14	0.32	0.81	0.3	0.96	0.2	0.14
3N	0.16	0.23	0.39	0.58	0.45	0.28	0.35
3S	0.15	0.17	0.52	0.65	0.59	0.37	0.24
4N	0.11	0.14	0.34	0.43	0.22	0.13	0.1
4E	0.16	0.27	0.83	0.24	0.45	0.24	0.08
5E	0.21	0.23	0.46	0.39	0.39	0.2	0.08
5W	0.15	0.2	0.42	0.42	0.33	0.17	0.17
6W	0.19	0.22	0.49	0.41	0.3	0.03	0.09
6E	0.14	0.26	0.44	0.34	0.24	0.08	0.08
7N	0.19	0.16	0.46	0.58	0.55	0.24	0.16
7S	0.16	0.19	0.39	0.63	0.32	0.15	0.14
8E	0.11	0.16	0.53	1.04	0.36	0.35	0.17
8W	0.15	0.12	0.51	0.59	0.31	0.17	0.09
9N	0.16	0.16	0.14	0.58	0.35	0.28	0.16
9W	0.22	0.19	0.48	0.66	0.38	0.28	0.16
10N	0.29	0.23	0.52	0.66	0.3	0.26	0.15
10W	0.19	0.19	0.47	0.84	0.53	0.33	0.34
11S	0.12	0.12	0.2	0.4	0.19	0.1	0.05
11W	0.14	0.12	0.32	0.6	0.2	0.02	0.03
12S	0.19	0.19	0.82	0.13	0.21	0.18	0.17
12E	0.16	0.24	1.09	0.11	0.16	0.06	0.03
13N	0.28	0.12	0.63	0.43	0.27	0.2	0.05
13S	0.09	0.14	0.32	0.26	0.02	0.03	0.05
14S	0.13	0.23	0.44	0.48	0.41	0.07	0.06
14W	0.14	0.23	0.47	0.3	0.2	0.03	0.14
15S	0.24	0.55	0.64	0.48	0.56	0.32	0.26
15E	0.31	0.46	0.93	0.45	0.54	0.32	0.33
16E	0.31	0.44	0.9	0.61	0.2	0.2	0.07
16W	0.24	0.62	0.88	0.7	0.17	0.2	0.04
17E	0.24	0.46	0.64	0.44	0.22	0.26	0.05
17W	0.09	0.3	0.47	0.39	0.28	0.27	0.04
18N	0.22	0.21	0.48	0.41	0.12	0.24	0.07
18E	0.26	0.35	0.45	0.37	0.1	0.11	0.07
19N	0.17	0.14	0.29	0.27	0.12	0.17	0.1
19E	0.09	0.17	0.34	0.35	0.34	0.18	0.09
20E	0.18	0.24	0.07	0.38	0.29	0.15	0.07
20W	0.21	0.25	0.67	0.51	0.22	0.12	0.06

Table 11. Frass weights (g) from each net located along the road edge for seven collections. Beech trees are numbered 1-10 and maples are numbered 11-20. Nets were oriented in a north (N), south (S), west (W), or east (E) position.

Tree/Net	7/6/98	7/12/98	7/20/98	8/3/98	8/17/98	8/24/98	9/1/98
1E	0.08	0.17	0.56	0.22	0.24	0.07	0.08
1W	0.11	0.16	0.49	0.32	0.21	0.09	0.08
2W	0.13	0.1	0.27	0.41	0.16	0.11	0.02
2E	0.08	0.23	0.42	0.25	0.4	0.06	0.02
3N	0.13	0.21	0.62	0.54	0.61	0.23	0.02
3S	0.53	0.62	1.22	0.45	0.15	0.11	0.25
4E	0.08	0.25	0.49	1.03	0.45	0.14	0.04
4W	0.03	0.31	0.44	0.58	0.33	0.08	0.08
5N	0.07	0.25	0.71	1.09	0.48	0.16	0.34
5W	0.17	0.17	0.82	0.67	0.62	0.11	0.33
6N	0.15	0.28	0.6	0.5	0.31	0.06	0.03
6W	0.1	0.2	0.3	0.41	0.66	0.08	0.04
7N	0.32	0.31	0.59	0.63	0.71	0.22	0.32
7W	0.19	0.22	0.52	0.51	0.49	0.28	0.14
8W	0.1	0.25	0.66	0.85	0.53	0.18	0.09
8S	0.16	0.28	0.52	0.63	0.46	0.09	0.16
9N	0.07	0.17	0.48	0.59	0.45	0.08	0.06
9E	0.11	0.29	0.46	0.51	0.41	0.08	0.03
10N	0.11	0.19	0.45	0.45	0.36	0.14	0.06
10W	0.07	0.15	0.29	0.39	0.36	0.17	0.06
11N	0.09	0.19	0.47	0.25	0.32	0.05	0.1
11S	0.11	0.13	0.42	0.36	0.17	0.05	0.03
12W	0.2	0.46	0.92	0.8	0.38	0.11	0.1
12S	0.17	0.32	0.61	0.58	0.39	0.17	0.06
13N	0.21	0.22	1.05	0.54	0.28	0.07	0.03
13W	0.13	0.32	0.66	0.51	0.48	0.06	0.02
14N	0.11	0.24	0.54	0.36	0.24	0.05	0.07
14E	0.12	0.19	0.63	0.33	0.21	0.09	0.06
15N	0.01	0.14	0.27	0.21	0.19	0.02	0.08
15E	0.07	0.15	0.18	0.15	0.19	0.1	0.07
16N	0.1	0.27	0.46	0.36	0.21	0.1	0.04
16W	0.07	0.3	0.45	0.21	0.18	0.04	0.02
17S	0.08	0.47	0.82	0.27	0.28	0.07	0.07
17W	0.09	0.12	0.21	0.26	0.51	0.01	0.09
18N	0.21	0.32	0.77	0.78	0.41	0.06	0.09
18W	0.16	0.27	0.76	0.79	0.43	0.07	0.14
19S	0.07	0.13	0.14	0.21	0.15	0.06	0.01
19W	0.11	0.15	0.35	0.27	0.17	0.09	0.12
20S	0.18	0.22	0.45	0.53	0.32	0.2	0.13
20E	0.11	0.21	0.43	0.33	0.3	0.08	0.1

Table 12. Mean frass weights (g) ± 1 standard deviation (SD) for each collection date from each transect. Values are from averaged nets for each host tree.

American beech

		7/6/98	7/12/98	7/20/98	8/3/98	8/17/98	8/24/98	9/1/98
Interior	x	0.13	0.20	0.48	0.59	0.35	0.22	0.13
	1 SD	0.04	0.05	0.11	0.15	0.09	0.09	0.08
Creek	x	0.18	0.21	0.48	0.55	0.40	0.22	0.15
	1 SD	0.03	0.04	0.08	0.19	0.13	0.08	0.07
Road	x	0.14	0.24	0.55	0.55	0.42	0.13	0.10
	1 SD	0.08	0.08	0.18	0.20	0.12	0.06	0.04

Sugar maple

		7/6/98	7/12/98	7/20/98	8/3/98	8/17/98	8/24/98	9/1/98
Interior	x	0.14	0.21	0.50	0.49	0.27	0.12	0.13
	1 SD	0.03	0.04	0.12	0.08	0.12	0.09	0.10
Creek	x	0.19	0.28	0.56	0.41	0.24	0.16	0.09
	1 SD	0.06	0.15	0.24	0.14	0.12	0.09	0.08
Road	x	0.12	0.24	0.53	0.41	0.29	0.08	0.07
	1 SD	0.05	0.08	0.21	0.20	0.10	0.03	0.03

Table 13. Pellet count of *Hypenodes fractilinea* from American beech and sugar maple from each transect. Data was recorded from the peak collection date (August 3, 1998). Mean pellet count (**x**) and ± 1 standard deviation (SD) are included

		beech	maple
interior		1757	528
		2224	3360
		4260	960
		5648	600
		4480	1344
		4560	876
		2328	1908
		4196	780
		4352	1008
		3824	780
	x	3763	1214
	SD	1245	853
creek		2544	4080
		7140	680
		4948	200
		3328	219
		3680	1092
		2544	1464
		6032	1080
		6632	228
		3776	252
	x	4514	1033
	SD	1742	1236
road		4454	2376
		1224	936
		2644	408
		1552	1632
		2208	328
		7072	592
		3072	376
		1952	368
		2720	288
		2512	1056
		4396	472
	x	3073	803
	SD	1677	665

Table 14. Pellet count of *Heterocampa guttivitta* from American beech and sugar maple from each transect. Data was recorded from the peak collection date (August 3, 1998). Mean pellet count (**x**) and ± 1 standard deviation (SD) are included.

		beech	maple
interior		328	324
		360	736
		508	396
		496	504
		608	396
		300	348
		228	500
		375	363
		528	480
		736	380
	x	447	443
	SD	156	121
creek		160	184
		275	37
		112	385
		384	274
		336	468
		720	276
		640	295
		383	288
		242	192
		583	372
	x	384	277
	SD	205	121
road		283	291
		89	784
		389	368
		500	341
		467	136
		297	272
		575	320
		662	896
		630	240
		224	280
	x	412	393
	SD	188	245

Table 15. Pellet count of *Morrisonia latex* from American beech and sugar maple from each transect. Data was recorded from the peak collection date (August 3, 1998). Mean pellet count (**x**) and ± 1 standard deviation (SD) are included.

		beech	maple
interior		96	108
		136	93
		168	132
		144	84
		85	111
		114	120
		79	140
		100	132
		115	86
		117	105
	x	115	111
	SD	28	20
creek		112	81
		95	10
		256	32
		110	73
		116	156
		118	125
		121	180
		128	84
		143	106
		80	107
	x	128	95
	SD	48	52
road		22	72
		43	88
		53	64
		139	109
		97	104
		148	82
		155	56
		181	99
		145	48
		192	173
	x	118	90
	SD	60	36

Table 16. Pellet count of *Plagodis fervidaria* from American beech and sugar maple from each transect. Data was recorded from the peak collection date (August 3, 1998). Mean pellet count (**x**) and ± 1 standard deviation (SD) are included.

		beech	maple
interior		48	105
		72	172
		126	106
		140	127
		84	131
		115	80
		93	137
		71	114
		100	87
		132	113
	x	98	117
	SD	30	26
creek		92	119
		128	46
		116	42
		97	38
		133	81
		118	120
		134	87
		148	57
		124	45
		104	91
	x	119	73
	SD	18	31
road		46	130
		68	120
		54	115
		60	144
		56	83
		66	136
		54	134
		61	150
		90	94
		117	102
	x	67	121
	SD	21	22

Table 17. Pellet count of *Hypagyrtis unipunctata* from American beech and sugar maple from each transect. Data was recorded from the peak collection date (August 3, 1998). Mean pellet count (**x**) and ± 1 standard deviation (SD) are included.

		beech	maple
interior		144	315
		216	516
		385	313
		408	381
		252	393
		345	245
		279	411
		213	342
		300	263
		396	344
	x	294	352
	SD	89	78
creek		276	346
		384	139
		348	126
		274	114
		396	243
		350	358
		398	261
		444	171
		372	135
		312	270
	x	355	216
	SD	55	92
road		138	392
		204	360
		162	351
		180	432
		168	247
		198	404
		162	390
		181	450
		270	282
		352	306
	x	202	361
	SD	64	66

Table 18. Frass weights (g) from three size classes of frass pellets: extra small (<1mm), small (1-<2mm), and medium (2-<3mm). Frass was collected from American beech from each transect. Data was obtained from the peak collection date (August 3, 1998). Mean frass weights (**x**) and ± 1 standard deviation (SD) are included

		<1mm	1-<2mm	2-<3mm
interior		0.12	0.16	0.02
		0.19	0.26	0.05
		0.34	0.25	0.05
		0.38	0.25	0.04
		0.36	0.25	0.02
		0.32	0.2	0.05
		0.2	0.14	0.07
		0.22	0.25	0.07
		0.36	0.32	0.07
		0.14	0.12	0.03
	x	0.26	0.22	0.05
	SD	0.09	0.06	0.02
creek		0.58	0.11	0.03
		0.33	0.25	0.05
		0.17	0.13	0.07
		0.16	0.19	0.04
		0.12	0.21	0.06
		0.3	0.24	0.07
		0.56	0.18	0.08
		0.37	0.18	0.06
		0.38	0.23	0.05
		0.1	0.16	0.03
	x	0.31	0.19	0.05
	SD	0.17	0.05	0.02
road		0.2	0.07	0.01
		0.2	0.23	0.06
		0.36	0.35	0.06
		0.47	0.32	0.1
		0.28	0.15	0.04
		0.19	0.27	0.08
		0.28	0.36	0.08
		0.23	0.27	0.04
		0.25	0.16	0.03
		0.2	0.26	0.05
	x	0.27	0.24	0.06
	SD	0.09	0.09	0.03

Table 19. Frass weights (g) from three size classes of frass pellets: extra small (<1mm), small (1-<2mm), and medium (2-<3mm). Frass was collected from sugar maple from each transect. Data was obtained from the peak collection date (August 3, 1998). Mean frass weights (**x**) and ± 1 standard deviation (SD) are included.

		<1mm	1-<2mm	2-<3mm
interior		0.14	0.3	0.02
		0.24	0.34	0.06
		0.17	0.28	0.04
		0.1	0.3	0.05
		0.17	0.31	0.02
		0.12	0.25	0.02
		0.16	0.25	0.02
		0.1	0.23	0.04
		0.17	0.28	0.03
		0.18	0.22	0.02
	x	0.16	0.28	0.03
	SD	0.04	0.04	0.01
creek		0.28	0.18	0.05
		0.08	0.05	0.01
		0.06	0.26	0.02
		0.1	0.26	0.02
		0.15	0.3	0.04
		0.28	0.32	0.01
		0.15	0.24	0.05
		0.21	0.17	0.03
		0.11	0.15	0.05
		0.21	0.22	0.02
	x	0.16	0.22	0.03
	SD	0.08	0.08	0.02
road		0.11	0.25	0.02
		0.14	0.52	0.02
		0.17	0.32	0.04
		0.18	0.17	0.02
		0.07	0.08	0.08
		0.06	0.18	0.05
		0.07	0.17	0.01
		0.13	0.59	0.02
		0.12	0.1	0.02
		0.14	0.23	0.03
	x	0.12	0.26	0.03
	SD	0.04	0.17	0.02