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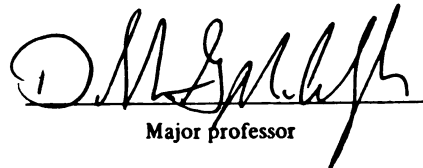
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Host Preference and Host Suitability of Ten Hardwoods
for the Asian Longhorned Beetle, Anoplophora
glabripennis and of Four Conifers for the White-
Spotted Pine Sawyer Monochamus scutellatus
presented by

Laura Lenore Lazarus

has been accepted towards fulfillment
of the requirements for

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HOST PREFERENCE AND HOST SUITABILITY OF TEN HARDWOODS FOR THE
ASIAN LONGHORNED BEETLE, *ANOPLOPHORA GLABRIPENNIS*
AND OF FOUR CONIFERS FOR THE WHITE-SPOTTED PINE SAWYER,
MONOCHAMUS SCUTELLATUS

By

Laura Lenore Lazarus

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Ecology, Evolutionary Biology and Behavior

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ABSTRACT

HOST PREFERENCE AND HOST SUITABILITY OF TEN HARDWOODS FOR THE ASIAN LONGHORNED BEETLE, *ANOPLOPHORA GLABRIPENNIS* AND OF FOUR CONIFERS FOR THE WHITE-SPOTTED PINE SAWYER, *MONOCHAMUS SCUTELLATUS*

By

Laura Lenore Lazarus

Host selection behavior, and suitability of ten North American tree species for *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae) oviposition, and early instar development were examined during laboratory tests in 1999 and 2000.

Female *A. glabripennis* oviposited and larvae developed to the first instar on Northern red oak, white oak, and hophornbeam, while Ironwood, hackberry, honeylocust and basswood were less suitable for oviposition and larval development. Tulip poplar, sycamore, eastern cottonwood were not suitable hosts.

Relationships between host preference and host suitability were assessed for *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) in 2001 and 2002 in Michigan. Female host preference and host suitability differed among jack pine, red pine, white pine, and white spruce. Intra-specific competition for phloem was minimal, but *M. scutellatus* deleteriously affected phloem-feeding scolytid bark beetles and curculionids by reducing the area of phloem consumed and intercepting egg galleries.

Two-choice tests were conducted in 2002 to assess *M. scutellatus* female host preference and larval performance on four conifers and larval conditioning. Adult *M. scutellatus* preferred white pine and white spruce during the choice tests, while red pine and white pine were most suitable for *M. scutellatus* larval development. Host preference and larval performance was not entirely consistent for *M. scutellatus*.

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PREFACE

When the Asian longhorned beetle, *Anoplophora glabripennis*, was first detected in New York and Chicago and eradication programs were initiated researchers began to realize the full extent of the gaps in knowledge of cerambycid host-selection behavior, the influence of the host on progeny survival, and about cerambycids in general. In this thesis, I addressed relationships between host preference and host suitability of two cerambycids, the nonindigenous *A. glabripennis* and the native *Monochamus scutellatus*. In the case of *A. glabripennis*, researchers didn't know how females select hosts, how far they are capable of dispersing, or the potential for adaptation to novel hosts in the United States. The white-spotted pine sawyer, *M. scutellatus*, is one of the most common cerambycids in the U.S., nonetheless, there has been little research on *M. scutellatus* host-selection behavior, host preferences and the suitability of different conifers for larval development. *Anoplophora glabripennis* and *M. scutellatus* are both polyphagous and are closely related species in the same tribe.

The host selection behavior and host range of *A. glabripennis* was studied in a quarantine lab in Ansonia during 1999 and 2000. In chapter 1, specific behaviors of *A. glabripennis* females associated with host selection and preferences among Northern red oak, white oak, honeylocust, eastern cottonwood, sycamore, tulip poplar, basswood, ironwood, hackberry and hophornbeam for oviposition were evaluated, as was the suitability of the ten hardwoods for early instar development. Researchers had a lot of problems with the availability of beetles for laboratory studies in 2000 since colony

beetles kept dying or emerging malformed and unhealthy, and there were other problems inherent when working with a non-indigenous species. We decided to leave the study of *A. glabripennis* to others and to focus on the native wood-boring beetle, *M. scutellatus*. There were no major constraints identified in obtaining adult *M. scutellatus* for laboratory studies and this beetle could be studied in a natural environment.

In Chapter 2, the adult female host preferences of *M. scutellatus*, a common cerambycid native to the lake states and much of North America were evaluated along with the suitability of jack pine, red pine, white pine and white spruce for larval development in a field experiment. In chapter 3, a more controlled experiment was conducted to assess the relationship between adult female host preference and larval performance of *M. scutellatus* and to enable comparisons of results from both field and controlled experiments. We hoped to gain valuable insight into the host-selection behavior of cerambycids in the subfamily Lamiinae in general, or to identify similarities in behaviors associated with host selection by studying this native beetle.

Each Chapter in this thesis is intended to be a prepared as a manuscript for publication. We have published a part of the *A. glabripennis* work presented in Chapter 1 in The Journal of Environmental Horticulture.

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CHAPTER 1

Oviposition And Early Instar Survival Of The Asian Longhorned Beetle (Coleoptera: Cerambycidae) In Ten North American Hardwood Species

INTRODUCTION

One of the most recent insects to become established in the United States is the Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky); (Coleoptera: Cerambycidae). This large, attractive beetle is an important forest pest in China and Korea. In China, *A. glabripennis* is considered a major pest throughout a wide range extending from 21°N to 43°N latitude and 100°E to 127°E longitude (Yan 1985), a band that spans the climatic zones found in North America from southern Mexico to the Great Lakes region (Haack et al. 1997). It reduces wood production in poplar (*Populus spp.*) plantations, kills trees in windbreaks and is a pest on species of elm (*Ulmus*) maple (*Acer*) and willow (*Salix*).

All life stages of *A. glabripennis* can be transported in logs, firewood and untreated lumber. It was probably introduced to the U.S. in crates, pallets, or dunnage on ships from China (Haack et al. 1997). Populations of *A. glabripennis* were first discovered in 1996 in Brooklyn and Amityville, New York (Haack et al. 1996, 1997). During the summer of 1998, three separate infestations were found in Chicago, Illinois (Poland et al. 1998). Additional pockets of infested trees continue to be found in New York and Chicago (Nowak et al. 2001). Quarantines and eradication programs have been

established in New York and Chicago to stop the spread of *A. glabripennis* (Nowak et al. 2001). The eradication program mandates that all trees with adult exit holes, egg niches, or larval frass be cut down and chipped. The USDA Forest Service, state governments and private groups have given millions of dollars to replace those trees cut down in Chicago and New York (Haack and Mastro 1997). However, the full host range of this beetle is still unknown and planting trees before host preference is understood could lead to reinfestation if eradication is not successful.

The life history of *A. glabripennis* has been studied extensively in China (Gao et al. 1993, He and Huang 1993, Li and Wu 1993, Zhao et al. 1997, Zhang et al. 2002) and several studies have been conducted in the United States (Cavey et al. 1998, Haack et al. 1997, Keena 2002, Smith et al. 2001, and Smith et al. 2002). *Anoplophora glabripennis* is bi- or univoltine throughout its range in China, but only one generation a year occurs in North America (Haack and Mastro 1997). *Anoplophora glabripennis* attacks healthy trees, as well stressed trees, and recently cut logs or branches. Adults are diurnal and volatiles (possibly sex pheromones) emitted from both males and females were shown to have long range attractant properties (He and Huang 1993, Li and Wu 1993). Females may also produce a short range contact pheromone (Zhang et al. 2002). Most beetles overwinter as larvae and new adults emerge the following summer through dime-sized holes chewed through the bark (Haack and Mastro 1997). Newly emerged adults may require up to 7 to 16 days of twig-feeding to reach sexual maturity. Adults live for 70 to 137 days and each female may oviposit from 50 to 193 eggs in the laboratory (Keena 2002, Smith et al. 2001). Females chew through the bark to the cambial region, and lay a single egg in a distinctive egg niche, often in branch junctures with the tree stem (Haack et al.

1997, Zhao et al. 1997). Eggs usually hatch in 1 to 2 weeks (Cavey et al. 1998). Larvae feed in the cambial region for up to three weeks. Later instars score the sapwood and tunnel into the sapwood where they overwinter. Adults emerge from June to September, most frequently during the hottest part of the day (Kucera 1996, Nowak et al. 2001). Adults can reinfest the larval host tree if it is still living, or, they may potentially disperse 1440 m or more (Smith et al. 2001).

Although adults can cause minor twig mortality during their maturation feeding, the larvae cause significant damage to trees as they tunnel through branches and boles (Gao et al. 1993, Haack and Mastro 1997). Individual branches or trees will die if larval densities are high or if the infestation continues for several years. In North America, *A. glabripennis* prefers maple (*Acer spp.*) trees and threaten the maple syrup and tourism industries. It can also attack over 20 genera found in the eastern deciduous forests of the U.S. (Haack et al. 1997, Nowak et al. 2001), larval feeding reduces the value of trees for lumber (Haack and Mastro 1997). Homeowner property values in Chicago and New York are also affected because all infested trees found on private property as well as on public property are cut, chipped and burned (Haack and Mastro 1997). The estimated maximum potential national urban forest impact of *A. glabripennis* is a loss of 34.9% of total canopy cover, 30.3% tree mortality (1.2 billion trees) and a value loss of \$669 billion (Nowak et al. 2001). Studies of several promising methods to control *A. glabripennis* are underway using nematodes, predators and parasitoids, fungal pathogens and systemic pesticides (Haack et al. 2001, Shimazu-Mitsuaki et al. 2002, Smith 2000, Solter et al. 2001).

In Asia, the primary host trees of *A. glabripennis* include *Acer* spp., *Salix* spp., *Populus*, and *Ulmus*, although they will also feed on several other genera (Wu and Jiang 1998). Boxelder (*Acer negundo* L.) is planted as a trap tree in parts of China to protect more valuable hardwood trees (He and Huang 1993, Sun et al. 1990). In North America, *A. glabripennis* has primarily attacked species of maple, including Norway maple (*Acer platanoides* L.), sugar maple (*Acer saccharum* Marsh), silver maple (*Acer saccharinum* L.), sycamore maple (*Acer pseudoplatanus* (Bergahorn)), and boxelder (Haack et al. 1997, Poland et al. 1998). It has also infested species of birch (*Betula* spp.), poplar (*Populus* spp.), willow (*Salix* spp.), horsechestnut (*Aesculus hippocastanum* L.), and elm (*Ulmus* spp.). At least three new host genera have so far been identified in the U.S.: *Aesculus*, *Fraxinus*, and *Hibiscus* (Nowak et al 2001).

Host selection of most Cerambycidae of the Lamiinae subfamily may be considered a three-step process where adults first find hosts using visual and olfactory cues, then accept a host for oviposition using mostly chemoreception and host quality characteristics, and finally offspring must be able to develop and survive (Bernays and Chapman 1994, Hanks 1999). Little is known about the host-selection behavior of *A. glabripennis* adults and how they respond to volatiles emanating from hardwood species. Some nonhost plants may elicit feeding and be nutritionally adequate, but are not suitable for development of egg to adult (Futuyma and Peterson 1985, Scriber 1984). Additional North American tree species need to be tested to document whether they are attractive to ovipositing females and suitable for larval development. Results will help to predict the potential susceptibility of newly planted trees and of central and northeastern forests in general. Evaluation of host suitability of North American tree species for *A. glabripennis*

could also help to develop guidelines for new plantings, monitoring protocols, and management strategies.

In this study, I assessed the host-selection behavior of *A. glabripennis* females during oviposition and evaluated the suitability of 10 North American tree species for *A. glabripennis* early instar development. My primary objectives were to: 1) evaluate preference of adult, virgin female *A. glabripennis* for six hardwood species native to the north central region of the U.S.; 2) evaluate specific behaviors of females during host selection; and 3) evaluate the suitability of 10 North American hardwood species for oviposition and larval development of the first instar.

METHODS AND MATERIALS

Olfactometer design. We developed a four-armed olfactometer to evaluate host preference and host-selection behaviors of adult, virgin females (Figure 1.1). The olfactometer was constructed out of acrylic and consisted of a central chamber 38 cm (15 in) tall with a diameter of 35.6 cm (14 in). Cylindrical chamber arms extended upward at 45° angles from the central chamber 42.7 cm (18 in) long and 7.6 cm (3 in) diameter. The floor consisted of a circular piece of acrylic that fit tightly inside the arena, and rested on brackets. A circular exhaust hole, 22.9 cm (9 in) diameter, was cut into the center of the floor and covered with 0.33 cm (1/8 in) gauge wire mesh screen to allow beetles to walk across the chamber floor. An acrylic lid, 38.1 cm (15 in) diameter was placed on top of the central chamber. A Gast DOA-P104-AA vacuum pump (Grainger Co., Lansing, MI) was attached to the exhaust hole on the chamber floor with 1.27 cm (0.54 in) diam. Tygon tubing to pull air down through the chamber arms, into the central chamber, and out the exhaust hole. Teflon tape was wrapped around all junctions to ensure a tight seal. Incoming air was filtered through 0.64 cm (0.25 in) thick charcoal filters attached to the distal opening of each arm. Smoke tests confirmed that the chamber was completely sealed except for the designed flows. The olfactometer was placed on a swiveling platform on the floor so that the position of the arms could be rotated between each replicate, and the olfactometer was thoroughly cleaned with 75% methanol before each bioassay.

All tests were conducted in an approved USDA Forest Service quarantine facility in Ansonia, CT. We conducted preliminary studies to evaluate beetle behavior in the olfactometer by placing individual female beetles into the olfactometer for 50 min. Two

arms of the olfactometer contained freshly cut sugar maple branch sections (5 x 20 cm) and twigs and the other two arms were left empty. Of the five females tested, all entered the arms containing sugar maple within 50 min. Therefore, we felt confident that beetles were able to detect and select particular host volatiles in the olfactometer.

Twenty-Four Hour Bioassays. We monitored mating, host selection, and oviposition behavior of a male-female pair of *A. glabripennis* adults in the olfactometer for a 24 h. The length of the test was designed to allow adequate time for the completion of behaviors associated with oviposition or host selection. Beetles used in the 24 hr bioassays emerged from maple logs collected from infested trees in New York that were reared at the Ansonia quarantine facility. Body weights were 0.62g, 1.05g, and 0.49g for female 1, 2 and 3, respectively and 1.00g, 0.68g, and 0.66g for males. Each 24 hour test began at 0600 Eastern Standard Time. We used a 16:8 (L:D) photoperiod at 23C where lights were turned off at 2200 hours.

Fresh sugar maple branch sections (5 x 20 cm / 2 x 8 in) and twigs were placed at the top of two opposing arms of the olfactometer and the other two arms were left blank. Seven to 10 fresh sugar maple twigs were placed with the wood sections to provide material for attraction by the beetles.

We tested mating pairs of beetles so that all behaviors associated with oviposition could be recorded in a more realistic sequence. Also, the presence of a male throughout the entire test increased the likelihood that females would actively seek out oviposition sites to deposit viable eggs. We placed a previously unmated male and female *A. glabripennis* pair in the olfactometer and allowed them to mate, move, excavate egg niches, oviposit and feed throughout the duration of the test. We repeated the bioassays

three times, using a new pair of beetles each time. Female 1 was nine days post emergence and was much smaller than the male or the other 2 females. Female 2 was 10 days post emergence and about the same size as the male. Female 3 was 10 days post emergence and was larger than the male and the other females.

All behavior during the 24 hr (1440 min) trial was videotaped using a Sony Digital camcorder, (model DCR-TRV103) (Park Ridge, NJ) mounted on a tripod. Video from each bioassay was viewed later and the frequency, sequence, and duration of behaviors were recorded. We determined the total time females were stationary and engaged in walking, twig feeding, excavating egg niches, ovipositing, and copulating. We also recorded the frequency and sequences of the behaviors throughout the 24 hr.

At the end of the test, branch sections from the bioassays were placed in a growth chamber at 21° C (71°F) for 21 d and then dissected. We counted the number of egg niches, eggs, and dead and alive larvae for each branch section.

Fifty minute bioassays. In this bioassay, we focused on host-selection behaviors rather than behaviors associated with mating, so only females were included. We monitored host selection of females in the olfactometer during 50 min bioassay using similar olfactometer conditions and protocols for filming as in the 24 min bioassays June 2000. A total of 15 virgin female beetles was used in the bioassays. Females typically initiate host selection and will excavate egg niches and oviposit even if they have not yet mated. Beetles used had intact antennae and no evidence of physical damage. Each female was tested with three to six host species because of the limited availability of healthy beetles.

Potential hosts tested included eastern cottonwood (*Populus deltoides* L.), honeylocust (*Gleditsia triacanthos* L.), northern red oak (*Quercus rubra* L.), sycamore (*Plantanus occidentalis* L.), tulip poplar (*Liriodendron tulipifera* L.), and white oak (*Quercus alba* L.). Sugar maple, known to be highly preferred by *A. glabripennis*, was included in each bioassay as a positive control. Sugar maple, sycamore, tulip poplar and white oak and twigs were collected from live trees in woodlots in Ansonia, CT. Northern red oak, honeylocust, and eastern cottonwood branch sections and twigs were cut from trees at W. K. Kellogg Forest, Augusta, MI and shipped in an insulated cooler by overnight mail to the quarantine facility in Ansonia. Cut ends of all branch sections were waxed with paraffin immediately after cutting to slow desiccation. Wood and branches were stored in a growth chamber at 21° C (70° F) in the Ansonia facility until used for bioassays (up to 1 wk). Paraffin was removed and wood sections and twigs were cut to appropriate size with a bandsaw just before the olfactometer bioassays.

To evaluate female host preference, we suspended branch section of a test species with bark attached (5 x 20 cm / 2 x 8 in) in two of the four arms of the olfactometer. Seven to 10 fresh twigs of the test species were placed with the wood sections to provide material to attract the beetles. Similarly-sized sections of sugar maple and twigs were placed in the other two arms. Tests were conducted in the dark to prevent beetles from simply responding to light. A glass Petri dish with a 1 g (0.002 lbs.) metal weight attached to the bottom was used to introduce beetles into the central chamber. The container was suspended with fishing wire through a pin-sized hole drilled through the chamber lid. Each female beetle was kept in the holding container in the center of the

chamber for 5 min to acclimate to chamber conditions before the 50 min observation period began.

To quantify behavior and attraction of female beetles to the alternative host species, we observed beetles and noted if they stayed in the central arena or moved into one of the arms, or onto the r branch sections. The central arena consisted of the lid, wall, and floor of the olfactometer. To simplify analysis of female host selection, we separated behaviors into first and second level choices. Beetles were said to have made a first level choice if they walked into an olfactometer arm. Beetles that moved onto the wood suspended in the arm were considered to have made a second level, or higher choice, than those that only walked into the arms. Behavior associated with second-level selection included: examining behaviors employing antennae or palps to sense the bark, twig feeding, egg niche excavation, or oviposition.

Host suitability. Suitability of hackberry (*Celtus occidentalis* L.), hophornbeam (*Ostrya virginiana* (Mil.) K. Koch), basswood (*Tilia americana* L.), ironwood (*Carpinus caroliniana* Walt.), and sugar maple for *A. glabripennis* oviposition and early larval survival was assessed using mating male-female pairs of beetles in 1999 and 2000. One pair of beetles was placed in a 3.8 liter (1 gal.) glass jar containing a fresh wood section (2 x 8 in) and 7-10 twigs of one alternate host species. Branch sections were waxed on the cut ends with paraffin to slow desiccation. The number of host species tested was determined by availability of healthy beetles; a total of 10 pairs was available to test basswood, hophornbeam, ironwood, and sugar maple; eight pairs were available to test hackberry. Age of females ranged from 9 to 48 days post emergence. The duration of each test was 6 to 8 d for all species.

In 1999, mating pairs were randomly assigned to basswood, hophornbeam, ironwood, hackberry, or sugar maple. Beetles were allowed to mate, feed, excavate egg niches, and oviposit on the branch section in each jar for 6-8 d. Each pair of beetles was exposed to only one test species and was used in only a single test.

At the end of each assay, wood sections were examined to determine the number of egg niches on the wood, where the female beetle had clearly used her mandibles to scrape the bark or create an egg niche. Wood sections were placed on end in a 21° C (68° F) growth chamber, 16:8 (L:D) photoperiod and dissected 21 days later. Number of eggs and first instars on each wood section were recorded.

In 2000, we followed similar protocols as in 1999 to assess suitability of eastern cottonwood, honeylocust, northern red oak, sycamore, tulip poplar, and white oak for *A. glabripennis* oviposition and early larval survival. Sugar maple twigs were provided during the assay instead of twigs of the test species to ensure that the beetles would survive. A total of three male-female pairs was available to test northern red oak, honeylocust, and eastern cottonwood (Test 1) and three pairs were used to test white oak, sycamore, and tulip poplar (Test 2). Beetles used in test 1 were 25 to 48 days old, and those used in test 2 were 54 to 55 days old. Beetles used in test 1 had all antennal segments intact, but one female was missing her left front tarsus and one female in test 2 had a malformed antenna. These beetles were used because of the limited number of healthy beetles available for concurrent *A. glabripennis* research projects in 2000.

In Test 1, the three mating pairs were randomly assigned to northern red oak, honeylocust, or eastern cottonwood, while one beetle pair remained on sugar maple for the duration of the test. Beetles were allowed to mate, feed, excavate egg niches, and

oviposit on the wood in each jar for 4 days. Thereafter, each mating pair was placed into a new jar containing sugar maple twigs and a sugar maple branch section for 2 days to allow beetles to recover. Each mating pair was then assigned to a new species for 4 days, followed by a 2 days recovery period on sugar maple. This process was repeated again, so that each pair was exposed to all three different host species.

Test 2 included white oak, sycamore, and tulip tree along with sugar maple and the methods were those of Test 1. A 61-day-old female of one of the mating pairs died during the second resting period in Test 2. Another similarly aged mating pair of beetles was used to complete the test. At the end of each 4 day period, the number of egg niches were counted and branch sections were reared and dissected as before.

Statistical Analyses. Observations from the 24 hr bioassays were not analyzed because of low sample size. However, we summarized the behavioral sequences, frequency and duration of behaviors for each individual beetle. Data from fifty minute bioassays and 1999 and 2000 host suitability trials were not normally distributed, based on the Shapiro-Wilk test and residual plots (Shapiro and Wilk 1965). Data from 50 min bioassays were pooled to compare beetles duration spent in arms baited with sugar maple with duration spent in the arms baited with alternative host species using the nonparametric Kruskal-Wallis test. Additionally, data were pooled to compare differences in the percentage of time spent in arms of the olfactometer, and on wood in the olfactometer, among sugar maple and alternate hosts using the Mann-Whitney Test (Kruskal 1952). The Kruskal-Wallis test was also used to determine if the number of egg niches, eggs, and larvae differed among alternative host species (Kruskal and Wallis 1952). All analyses were conducted at the $P < 0.05$ level of significance, using SAS

statistical software (SAS Institute, Inc. 1989). The Kruskal-Wallis Multiple Comparison procedure was used to determine which treatment pairs differed significantly ($P < 0.05$) (Conover 1971).

RESULTS

Twenty-four hour bioassays. The three adult females we monitored in the olfactometer exhibited a range of behaviors during the 24 h period. Behaviors included copulation, twig feeding, egg niche excavation, oviposition, and walking. Figure 1.2 shows the percentage of time spent three female *A. glabripennis* in each behavioral state over 24 h. Females 1 and 3 spent more time twig feeding, about 20 % of the 24 h bioassay, than Female 2 (8 % of the time), although female 2 spent more time excavating egg niches (20 %) than females 1 (3 %) and 3 (12 %). Female 3 spent 20 % of the time ovipositing while females 1 and 2 spent only 7 % and 8 % of the time ovipositing, respectively. Female 1 spent the least time copulating, 3 %. All three females spent very little time grooming during the 24 h, less than 5 % of the total time. Female 1 flew three times during the test, while Females 1 and 2 never flew. Female 1 spent 5 h alone before the male found her. She twig fed and excavated a single egg niche before the male joined her and immediately attempted copulation and mate-guarding. We observed a similar scenario with female 2. Female 3 was in close contact with the male for the entire test.

A more detailed analysis of behaviors observed over the 24 h bioassay was achieved by dividing the 24 hours into 3 h increments and comparing percentage of time allocated to each behavior by each female (Figure 1.3). During the 24 h, Female 1 was not very active for the first three h, then she twig fed the majority of the time between 9 a.m. and 3 p.m. Copulation occurred four times in the morning for an average of 16.0 ± 5.7 min. Egg niche excavation and oviposition occurred for periods averaging 5.0 ± 1.9 and 20.0 ± 0.9 min, respectively, and occurred between 3 p.m. and 6 p.m. (Figure 1.3,

and Figure 1.4). The male bit Female 1 numerous times on the pronotum during copulation, and she “ran away” from the male three different times. She also spent more time apart from the male than the other females. From 6 p.m. to 3 a.m., Female 1 either walked or was stationary, except for a bout of twig feeding (Figure 1.3). This female excavated an egg niche, then oviposited five times. Female 1 fed on twigs after every oviposition event (Table 1.1). However, twig feeding preceded egg niche preparation in only 2 of 5 cases. In 2 of the 5 oviposition bouts, Female 1 chewed another egg niche immediately after laying an egg. Copulation was followed by twig feeding in 1 of the 2 copulations.

Female 2 was generally more active than Female 1 (Figure 1.3), although she was mostly stationary until 8 am when she began twig feeding (Figure 1.3). Female 2 copulated and excavated egg niches in mid-morning, and copulated, excavated egg niches and oviposited from noon until 3 pm. She spent 60 % of her time twig feeding from 3 to 6 p.m. and twig fed for 27 ± 9.90 min on average (Figure 1.3). Female 2 didn't become active again until 10 pm when bouts of copulation, egg niche excavation, and oviposition began. Female 2 oviposited directly after egg niche excavation in only 2 out of 5 egg niches and abandoned 7 egg niches without ovipositing in them (Table 1.1 and Figure 1.4). Mean duration of oviposition and egg niche excavation for this insect was 31.5 ± 2.7 and 27.2 ± 4.4 , respectively (Figure 1.4). Oviposition occurred after copulation in three of five oviposition events, egg niche excavation followed copulation five out of eight copulations and egg niche excavation followed oviposition three out of eight times. The beetle pair copulated seven times for 20 ± 3.45 min on average (Figure 1.4).

Female 3 was stationary for a few h after the test began and then became very active (Figure 1.3). Female 3 began twig feeding, copulating, and ovipositing in mid-morning and continued twig feeding, chewing egg niches, ovipositing and copulating for most of the day. At 6 p.m., activity slowed and she spent 70 % of the next 2 h twig-feeding. Female 3 copulated again around 8 p.m. and then excavated egg niches and oviposited until midnight. The female left the male and walked to the other olfactometer arm containing wood then continued excavating egg niches and ovipositing from midnight until 6 a.m. (Figure 1.3). This female also groomed more regularly than the other two females. Since Female 3 actively exhibiting host selection behaviors throughout most of the 24 hours, we saw more transitions between host selection behaviors than for the other females. Female 3 oviposited in ten of the 12 egg niches she excavated, but oviposited twice without excavating an egg niche in the bark. She copulated immediately following egg niche excavation twice (Table 1.1) and chewed new egg niches after 8 of the 14 oviposition events and after 5 of the 19 twig feeding events. Twig feeding, copulation, egg niche excavation, and oviposition, lasted 17.6 ± 4.52 , 17.5 ± 6.54 , 16.4 ± 2.41 , and 17.4 ± 1.74 min on average, respectively (Figure 1.4).

Fifty min bioassays. Overall, female time allocation to different parts of the olfactometer varied considerably. Beetles spent 25 to 45 min of the 50 min observation period in the central arena of the olfactometer and significantly less time in the chamber arms or on the branch section (Figure 1.5) ($P < 0.05$; d.f.=2). Forty-eight of 76 beetles attempted escaping when introduced into the olfactometer, which included walking up the central chamber walls and circling around the lid of the chamber. Beetles attempted escaping and stayed in the center arena for an average of 39.2 ± 5.1 min. Ten beetles

attempted escaping when honeylocust was the alternate host, nine beetles for eastern cottonwood, eight for northern red oak, nine for sycamore, seven for white oak, and five for tulip poplar. It was likely that the beetles had not yet acclimated to the olfactometer conditions after 50 min.

When any alternative host was present, beetles consistently spent less time on sugar maple wood than when the beetles were given only sugar maple and blank (empty) arms. When beetles left the central arena, there were significantly more visits to the sugar maple arm and wood than to the alternative species arm and wood ($P < 0.05$, d.f.=3). Of the 92 total trials in the olfactometer, 60 beetles entered arms with sugar maple sections and 31 beetles moved onto sugar maple wood (a second-level choice) (Table 1.3). In contrast, 15 beetles entered arms with an alternate host and six made a second level choice (Table 1). Similarly, when beetles entered a chamber arm, they spent significantly more time in sugar maple arms ($P = 0.004$, d.f.=1) and on sugar maple wood ($P < 0.001$, d.f.=1) than on all other alternative species arms combined.

We found no differences in time allocated to the arms and wood of the olfactometer when compared on a species by species basis, because relatively few beetles selected arms with alternative host species. However, when northern red oak was the alternative host, three beetles moved into the arms with red oak and two spent about 15 min on the wood (Table 1.2). In comparison, ten of the beetles moved into sugar maple arms and the five that made a second level choice spent about the same amount of time on the sugar maple wood as the beetles on the red oak wood (Table 1.2). Four beetles selected arms with either white oak or eastern cottonwood, but the two beetles that made a second level choice spent little time on the alternative host wood. Only two beetles

made a first level choice for sycamore and one beetle made a second level choice, but neither spent much time in these arms. No beetles made a second level choice for either tulip poplar or honeylocust (Table 1.2).

Twig feeding was rare; four beetles fed on sugar maple twigs ranging from 2 to 10 min. There was no twig feeding on any alternative species. Seven beetles excavated egg niches on sugar maple wood sections, when paired with an alternate host, a process that ranged from 1 to 21 min. A single beetle excavated five egg niches on northern red oak, with excavation activity persisting for 1 to 15 min per egg niche. This beetle appeared to be positioning her body for oviposition when the 50 min bioassay period ended. In addition, a single female excavated 4 niches on white oak lasting from 1 to 24 min. Only one beetle oviposited on sugar maple, for 13 min, and there was no oviposition on wood sections of alternate hosts.

Host suitability. In 1999, number of egg niches, eggs, and survival of first instar larvae varied widely among the host species tested (Table 1.3). Overall, egg hatch ranged from 44.6 to 96.0% for the species tested. Significantly more egg niches were created on hophornbeam than on any other species tested, including sugar maple ($P < 0.001$, d.f.=4). Similarly, significantly more eggs were laid ($P < 0.001$, d.f.=4) and larvae recovered ($P < 0.001$, d.f.=4) on hophornbeam than for any other species tested. Females caged on sugar maple laid 2 eggs per day, while females laid less than half as many eggs on alternate species. Significantly more egg niches were created on sugar maple than on ironwood ($P < 0.025$), hackberry ($P < 0.025$) but there were no differences between sugar maple and basswood.

During the 2000 bioassays, the excavation of egg niches, number of eggs laid, and survival of first instar larvae varied widely among the host species tested (Table 1.3). The number of eggs per wood section ranged from 0 to 23 per section. Overall, 68% of eggs hatched and those that did not hatch often appeared to be desiccated. Relatively little phloem feeding had occurred at the time of dissection; by the end of the 21-d rearing period, most first instar larvae had consumed an area slightly larger than their body size (4-7 mm).

In Test 1, more eggs and larvae were recovered from sugar maple than from any of the alternate species (Table 1.3) and the numbers were comparable to numbers of eggs and larvae reared in other *A. glabripennis* projects at the Ansonia facility (Keena 2002). In Test 2, however, relatively few eggs and larvae were recovered from the sugar maple sections, perhaps because beetles assigned to sugar maple in Test 2 were older than those used in Test 1. At the end of Test 2, the females were up to 73 days old, while at the end of Test 1, beetles were no more than 66 days old. Female *A. glabripennis*, however, are fairly long-lived beetles and average adult female survival may exceed 100 days on some hosts (Smith et al. 2002). Recent research has shown that egg production decreases as *A. glabripennis* age, especially after the first mating, although the proportion of viable eggs may increase (Keena 2000, Smith et al. 2002).

Northern red oak (Test 1) and white oak (Test 2) appeared to be more suitable hosts for ovipositing *A. glabripennis* beetles than we originally expected. Female beetles assigned to northern red oak sections usually excavated egg niches and oviposited around branch nodes where the bark was relatively rough and thick. The total number of eggs laid on northern red oak (23) was comparable to the number laid on sugar maple in Test 1

(22), although only 39% of the eggs on northern red oak hatched compared with 82% of the eggs on sugar maple. At least eight of the unhatched eggs on northern red oak appeared desiccated at the time of dissection and the northern red oak appeared to dry out more rapidly than sections of other species even though all cut ends of the branch sections were waxed. White oak sections had significantly more egg niches excavated than any other species in Test 2 ($P < 0.05$, d.f.=3) (Table 1.3), but the shape of the niches was unusual. We observed females repeatedly scraping the thick, corky bark on the white oak sections, presumably to find suitable sites for oviposition, but they actually laid eggs in less than half of the egg niches. Females laid significantly more eggs on white oak than on other species in Test 2 ($P < 0.05$, d.f.=3) and 87% of the eggs on white oak sections hatched.

Honeylocust, sycamore, eastern cottonwood and tulip poplar appeared less suitable for egg niche excavation and oviposition. The number of egg niches was significantly lower on honeylocust than on northern red oak and sugar maple ($P < 0.05$, d.f.=3), but the number of eggs and larvae did not differ significantly between honeylocust and northern red oak or sugar maple (Table 1.3). However, less than half as many eggs were laid on honeylocust as on the sugar maple in Test 1, and only 50% of the eggs on honeylocust hatched. Beetles did excavate a few egg niches on rough-barked areas of cottonwood and sycamore sections, but no eggs were laid on any of these sections. Tulip poplar appeared to be highly unsuitable as a host; there was no evidence of any attempts to excavate egg niches or oviposit on these sections.

DISCUSSION

The goals of the 24 h bioassays were: to observe the temporal pattern of host selection behaviors, to note when behaviors occurred, and the duration and sequence of behaviors. Behavior of the three females varied considerably, suggesting that behavior probably varies similarly in natural populations of *A. glabripennis* that will include an even wider range of beetle age and size.

The data suggest that, overall, *A. glabripennis* females display certain behavioral sequences associated with oviposition. The typical sequence of behaviors we observed was twig feeding and copulation succeeded by egg niche preparation then oviposition. Adult Lamiinae are the only cerambycids that excavate egg niches prior to oviposition (Hanks 1999). However, the sequences were not entirely consistent and at times this sequence was disrupted by copulation or excavation of another egg niche. Congeners *Anoplophora macularia* (Lee and Lo 1998), and *Anoplophora chinensis* (Wang et al. 1996) also chew an egg niche prior to oviposition and exhibit similar sequences associated with oviposition site selection (Lee and Lo 1996, Wang et al. 1996). Inconsistencies in the oviposition sequences described here could be explained by male interference. For example, the egg niche excavation to oviposition sequence in our bioassays were interrupted by copulation. Likewise, *A. chinensis* and *M. scutellatus* males are not always associated with females during oviposition (Hughes and Hughes 1982, Wang et al. 1996). Furthermore, all females were somewhat active in the dark period between 10 p.m. and 6 a.m.

Observations of the second stage of the host selection process indicate that females constantly tapped their palps and antennae along the surface of the wood while walking to assess the suitability of the host for oviposition. Contact chemoreception has been suggested to occur via drumming of the palps in *Monochamous scutellatus* (Say), and *Phoracantha semipunctata* (F.) (Hanks 1999, Hanks et al. 1993, Hughes et al. 1992).

Differences in relative size of females and males may also affect beetle behavior. For example, Female 3 was larger than her male mate and could effectively thwart his mating attempts. She allocated more time to oviposition than Female 1, who was smaller than her mate. Female 1 allocated more time to walking, being stationary, and twig feeding than to copulation, egg niche excavation, and oviposition combined, possibly because of male interference. Female 2 was intermediate in size and exhibited fewer behaviors than Female 3, but spent more time in each behavioral state. Here, the males seemed to interfere with egg niche excavation by trying to initiate further copulations as was found for *M. scutellatus* (Peddle 2000) but not for *A. chinensis* (Wang et al. 1996).

Anoplophora chinensis females consistently allocated separate periods of the day to copulation and to egg laying and females weren't receptive to males while laying eggs (Wang et al. 1996). However, *A. chinensis* females mate in the tree canopy and move down the stem for oviposition (Wang et al. 1996). In contrast, for *Monochamus scutellatus*, another Lamiinae species, activity peaks were not seen for mating and oviposition (Hughes 1979). Our females were confined in the olfactometer and could not easily escape mating attempts by males unless they were large enough to physically thwart them. In the U.S., males and females are typically seen feeding in tree canopies (Haack et al. 1997) but the extent of the role of males in oviposition is unknown. It would

be interesting to conduct further behavioral bioassays in a field setting or at least in larger areas with bigger logs to quantify separations of mating and oviposition activity peaks. Future studies of *A. glabripennis* oviposition and mating behavior should control for differences in body size. Wang et al. and Smith et al. are currently researching the above topics with populations in China.

During the 50 min bioassays, females spent a large percentage of their time in escape behavior while in the olfactometer and the 50 min may not have provided adequate time to assess the second level host selection process. These beetles showed a long acclimation period, sometimes remaining stationary for the duration of the test. Directed movement was observed in two cases but mostly females entered arms and seemed randomly locate the wood sections that were suspended in the olfactometer arms. This suggests that *A. glabripennis* females may use visual as well as olfactory cues to locate host plants during the first stage of the host selection process. Even though cells of freshly cut wood remain attractive to primary wood-boring pests for a few days (Hanks 1999), virgin *A. glabripennis* females may need the presence of live foliage and a full canopy to readily elicit a feeding response, as with *A. chinensis* (Wang et al. 1996). Additionally, twig feeding, egg niche excavation and oviposition occurred on sugar maple twigs but no twig feeding occurred for alternate species and egg niche excavation only occurred on the oak wood sections. In the presence of sugar maple, or other highly preferred hosts, females may not attack less preferred hosts such as tulip poplar and honeylocust in the field (Nowak et al. 2000).

Host preference studies for *A. glabripennis* would be more realistic in a large room or greenhouse where arrays of logs or young trees of test species would allow

females to fly and use both vision and olfactory cues to locate preferred hosts. Field studies of host preference using North American tree species in China would also be valuable. Host preference field studies have been conducted for other Lamiinae species such as *Monochamus scutellatus*, *Monochamus carolinensis* (Olivier), and the *Phoracantha semipunctata* (Hanks et al. 1993, Lazarus and McCullough in preparation, Peddle 2000, Walsh and Linit 1984).

Based on the results from the 1999 and 2000 host suitability tests, it appears that hophornbeam, basswood, northern red oak and white oak could be acceptable hosts for oviposition by *A. glabripennis* beetles, especially in situations where more preferred hosts are not available. Development to the first instar suggests that four of the alternate hosts tested may be at least somewhat suitable. In Lepidoptera, the major behavioral or toxicological barrier to favorable host suitability is determined by the first instar (Scriber 1984). Females also laid a few eggs on honeylocust, ironwood, and hackberry while females did not lay eggs on eastern cottonwood, sycamore and tulip poplar. The lack of oviposition on eastern cottonwood is interesting given that some types of hybrid poplars in China are readily attacked by *A. glabripennis* and are suspected of being the dissemination source for *A. glabripennis* throughout the world in the form of solid wood packing materials (Smith et al. 2001). Recently, egg niches were found on species in the same genera as sycamore (*Plantanus*) and eastern cottonwood (*Populus*) trees in New York (Nowak et al. 2001). The lack of eggs on sycamore is also notable because species of *Plantanus* are preferred hosts in China (He and Huang 1993, Li and Wu 1993, Li et al. 1999) and egg niches were found on trees in New York (Nowak et al 2001). Additionally, females excavated egg niches on oak trees in New York and females

excavated egg niches on basswood in Chicago (Nowak et al. 2001), but no exit holes were found even though species in the same genus as basswood are considered to be preferred hosts in China (He and Huang 1993, Li and Wu 1993, Li et al. 1999).

The suitability of sycamore as a larval host in the U.S. remains questionable because no larvae developed in our tests or on trees in New York. Since larvae developed to the first instar on small branch sections of white oak and Northern red oak, further testing on live trees is needed to quantify development rates of later instars. Moreover, larvae developed on Northern red oak and green ash for up to 90 days on potted trees in a greenhouse (Ludwig et al. 2002). Females were able to oviposit on seven tree species previously undocumented as susceptible hosts in the U.S. Likewise, females oviposited on three species with no current records of oviposition in New York and Chicago. This suggests that females may find many more hosts suitable for oviposition than for larval development. Perhaps *A. glabripennis* larvae have not yet had sufficient time to acquire mechanisms to adapt to novel host chemicals before discovery in 1996 and 1998. Host suitability classifications may change in subsequent generations as has occurred with other insects (Thompson 1988).

Our results should be considered preliminary, given that relatively few beetles were available for our bioassays. Additional research is needed to further assess how *A. glabripennis* responds to other species in genera where larvae developed to the first instar. Studies are also needed to evaluate whether the response and behavior of female beetles encountering live trees is similar to their response to cut sections of wood that we used in this study.

Table 1.1. Sequences of behaviors associated with oviposition for three female *A. glabripennis* during 24 h in 16:8 (L:D), 23°C.

Behavioral state		Frequency of Occurrences		
Preceding	Succeeding	Female 1	Female 2	Female 3
Egg niche excavation	Oviposition	5	2	10
Egg niche excavation	Copulation	0	5	2
Egg niche excavation	Twig feeding	0	0	0
Oviposition	Copulation	0	1	1
Oviposition	Egg niche excavation ¹	2	3	8
Oviposition	Twig feeding ²	5	0	2
Twig feeding	Egg niche excavation ³	2	1	5
Twig feeding	Oviposition	0	0	0
Twig feeding	Copulation	0	0	4
Copulation	Egg niche excavation ⁴	0	5	0
Copulation	Oviposition	0	0	2
Copulation	Twig feeding ⁵	1	1	7

¹Oviposition was followed by walking then egg niche excavation 1, 0, and 4 times for Females 1,2, and 3, respectively.

²Oviposition was followed by walking then twig feeding 0, 3, and 0 times for Females 1,2, and 3, respectively.

³Twig feeding was followed by walking then egg niche excavation 2, 1, and 5 times for Females 1,2, and 3, respectively.

⁴Copulation was followed by walking then egg niche excavation 0, 2, and 4 times for Females 1,2 and 3, respectively.

⁵Copulation was followed by walking then twig feeding 3, 0, and 2 times for Females 1,2, and 3, respectively.

Table 1.2. Mean ($\pm$ SEM) percentage of time spent by *A. glabripennis* females and the number of beetles out of the total tested for each tree species that entered olfactometer arms (first level choice) or moved onto wood sections (second level choice), n=12 to 14 beetles per tree species.

	Alternate Hosts					Positive Control	
	Northern red oak	White oak	Eastern cottonwood	Sycamore	Tulip poplar	Honeylocust	Sugar maple
Mean % Time							
No choice							
Central arena	70.2 $\pm$ 11.15	52.3 $\pm$ 13.99	73.5 $\pm$ 13.10	53.6 $\pm$ 11.79	35.8 $\pm$ 11.92	93.2 $\pm$ 6.83	42.7 $\pm$ 28.67
No. of beetles	14	12	12	13	13	12	4
1st Level Choice							
Sugar maple arm	24.2 $\pm$ 10.8	17.0 $\pm$ 10.42	4.9 $\pm$ 4.71	28.7 $\pm$ 10.86	49.1 $\pm$ 12.08	0	-----
No. of beetles	5	4	2	5	8	0	-----
Alternate host arm	1.9 $\pm$ 1.84	14.0 $\pm$ 9.51	17.4 $\pm$ 11.71	3.3 $\pm$ 3.28	7.4 $\pm$ 7.22	0	38.7 $\pm$ 28.15
No. of beetles	1	2	3	1	2	0	4
2nd Level Choice							
Sugar maple wood	3.5 $\pm$ 2.18	16.3 $\pm$ 10.49	4.2 $\pm$ 3.46	7.1 $\pm$ 4.42	8.0 $\pm$ 4.93	6.8 $\pm$ 6.83	-----
No. of beetles	5	5	3	5	8	1	-----
Alternate host wood	0.3 $\pm$ 0.31	0.3 $\pm$ 0.22	0	7.3 $\pm$ 6.83	0	0	18.7 $\pm$ 2.00
No. of beetles	2	2	1	1	0	0	4

Table 1.3. Mean number ($\pm$ SEM) of *A. glabripennis* eggs, egg niches and first instar larvae on 5 x 20 cm branch sections of ten North American tree species; n=8 to 10 logs per species were used in 1999 and n=3 logs per species were used in 2000. Within columns and year, means followed by the same letter are not significantly different ($P<0.05$).

1999 Mean $\pm$ (SEM)			
	Egg niches per branch section	Eggs per branch section	Larvae per branch section
Basswood	1.1 $\pm$ 0.22 a	0.4 $\pm$ 0.1 a	0.2 $\pm$ 0.1 a
Hackberry	0.6 $\pm$ 0.3 b	0.3 $\pm$ 0.1 ab	0.1 $\pm$ 0.1 ab
Hophornbeam	0.4 $\pm$ 0.30 c	1.4 $\pm$ 0.2 c	1.2 $\pm$ 0.2 c
Ironwood	0.2 $\pm$ 0.1 bd	0.01 $\pm$ 0.01 bd	0.01 $\pm$ 0.01 bd
Sugar maple	2.0 $\pm$ 0.4 ae	0.6 $\pm$ 0.2 abe	0.4 $\pm$ 0.20 abe
2000 Mean $\pm$ (SEM)			
	Egg niches per branch section	Eggs per branch section	Larvae per branch section
Test 1			
Northern red oak	2.3 $\pm$ 0.60 a	1.9 $\pm$ 0.36 a	0.8 $\pm$ 0.38 a
Honeylocust	1.3 $\pm$ 0.33 b	0.8 $\pm$ 0.30 a	0.4 $\pm$ 0.16 a
Eastern cottonwood	0.4 $\pm$ 0.30 c	0 a	0 a
Sugar maple	3.3 $\pm$ 0.22 d	1.8 $\pm$ 0.82 a	1.8 $\pm$ 0.87 a
Test 2			
White oak	10.2 $\pm$ 0.30 a	1.3 $\pm$ 0.22 a	1.2 $\pm$ 0.36 a
Sycamore	0.7 $\pm$ 0.36 b	0 b	0 b
Tulip poplar	0.9 $\pm$ 0.51 b	0 b	0 b
Sugar maple	4.5 $\pm$ 0.87 c	0.6 $\pm$ 0.36 c	0.3 $\pm$ 0.22 c

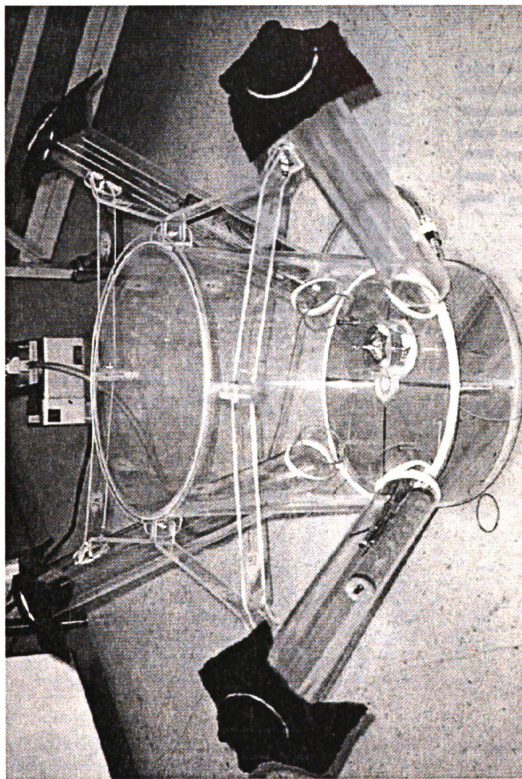


Figure 1.1. The olfactometer set-up used in 24 h and 50 min bioassays in Ansonia, CT during the summer of 2000. The olfactometer consisted of an acrylic central arena, four arms, and a glass lid.

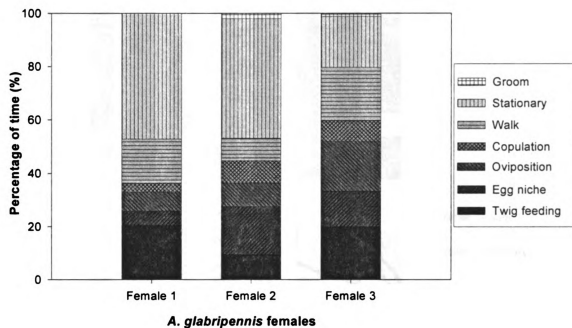


Figure 1.2. Total percentage of time spent in specific behavioral states by three *A. glabripennis* females over a 24 h period.

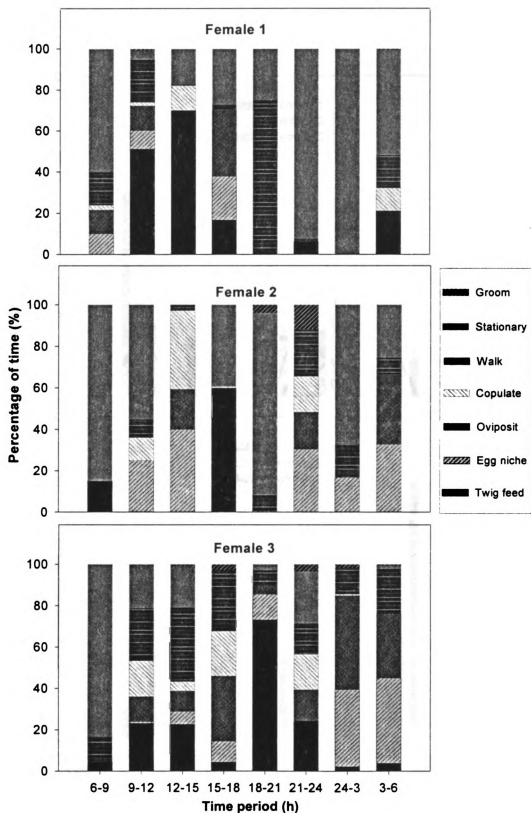


Figure 1.3. Percentage of time spent by three *A. glabripennis* females in specific behaviors during 3 hour increments of 24 h bioassays.

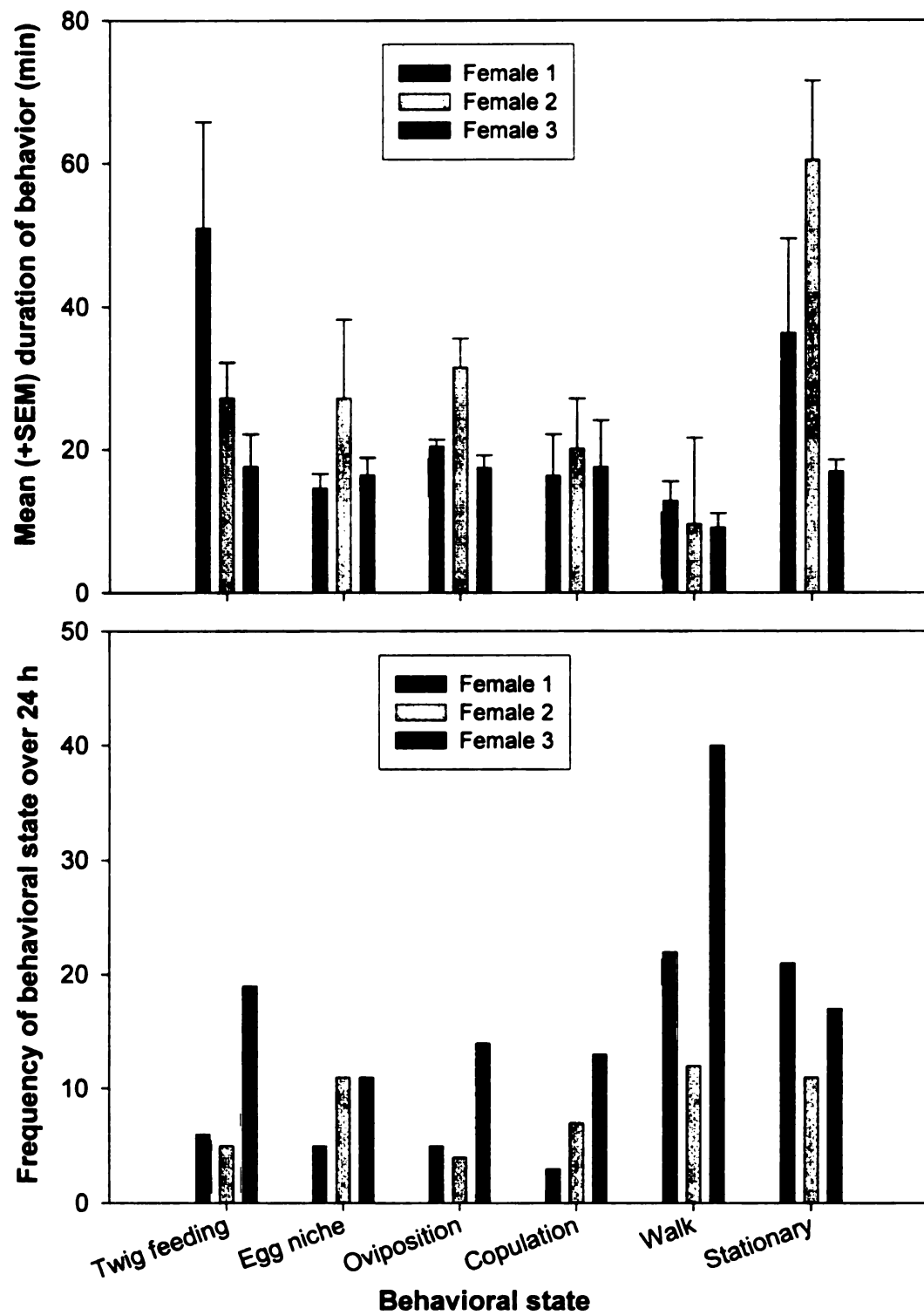


Figure1.4. Duration and frequency ($\pm$ SEM) of behavioral states for three *A. glabripennis* females in an olfactometer over a 24 hour period.

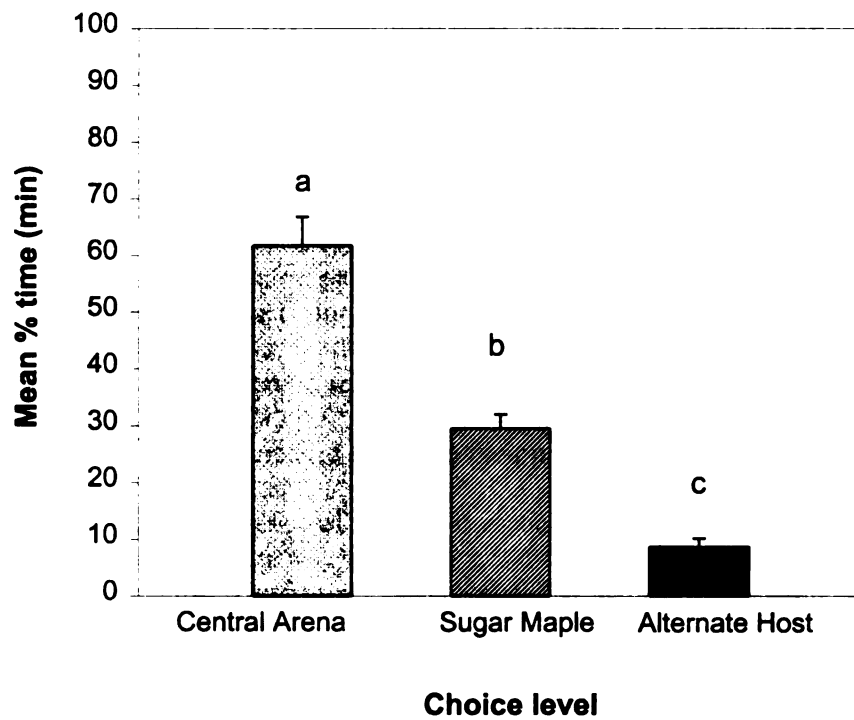


Figure 1.5. Mean percentage of time ($\pm$ SEM) that *A. glabripennis* females spent in the central arena, in an olfactometer baited with sugar maple or in the olfactometer arms that were baited with one of the alternate tree species. Significant differences are designated by different letters, $n = 92$.

CHAPTER 2

Host Preference and Larval Performance Of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) and Competition for Phloem on Four Conifer Species

INTRODUCTION

The relationship between host preference of adult insects and suitability of hosts for larval development is essential in understanding evolution of host plant associations in herbivorous insects (Futuyma and Peterson 1985, Thompson 1988). Presumably, adults females confronted with a variety of potential host plants should choose the one that would confer increased fitness to their progeny. In some populations of insects, however, host preference of females is associated with varying degrees of performance by their progeny. Thompson (1988) concluded that adult host preference does not always correlate with larval performance because some females oviposit on hosts unsuitable for larval development. Characteristics used to evaluate larval performance on potential hosts may include survival of immature stages, growth rate, pupal weight and the subsequent adult fecundity and longevity. These characteristics are not always positively correlated with each other, however, and evaluations of host suitability may be different depending on the criteria of performance (Thompson 1988, Via 1986).

Oviposition choices by female wood-boring insects are critical because larvae cannot disperse to alternate or more suitable hosts because most are legless (Hanks et al. 1993). Hosts of wood-boring beetles are often patchily distributed within forested areas, and wood-borers must rely on olfaction to locate potential hosts (Haack and Slansky 1987).

The white-spotted sawyer, *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) (subfamily: Lamiinae), is a common insect throughout Michigan (Parmalee 1941) and much of the northern U.S. and Canada (Rose 1957). *Monochamus scutellatus* is an important insect in Michigan conifer forests from both an ecological and economic perspective. Adults are thought to be polyphagous and larvae of *M. scutellatus* can develop in a wide range of conifer hosts throughout its range, including species of pine (*Pinus*), spruce (*Picea*), balsam fir (*Abies balsamea* (L.) Mill.), Douglas-fir (*Pseudotsuga menziesii* (Mirv.) Franco) and eastern larch (*Larix laricina* (Du Roi) K. Koch). *Monochamus scutellatus* is a cosmopolitan species found transcontinentally from Alaska throughout Canada (and the Northern United States) and southward to North Carolina in the east and New Mexico in the west. There are five species of *Monochamus* found in Michigan (Yanega 1996). Tunnels excavated by larvae of species of *Monochamus* contribute to decomposition and nutrient cycling, but can also damage logs that would otherwise be salvaged (Edmonds and Eglitis 1989, Rose 1957, Cerezcke 1975, and Post and Werner 1988).

The life history of *M. scutellatus* has been studied by various researchers (Belyea 1952, Chenier and Philogene 1989, Dyer and Seabrook 1978, Hanks 1999, Hughes and Hughes 1982, 1985 and Rose 1957). *Monochamus scutellatus* adults require a 3-7 day period of maturation feeding on conifer shoots before eggs mature (Rose 1957). Adults are not known to produce long range attractants or sex pheromones to locate hosts or mates, rather, they rely on olfactory detection of volatiles and individual tree characteristics to locate hosts (Dyer and Seabrook 1978). *Monochamus scutellatus* employs a resource-defense polygyny mating system whereby males compete for access

to the regions of the trees or logs most attractive to females (Hughes and Hughes 1982, 1985). In Michigan, adult beetles typically colonize stressed or dying trees and recently cut or fallen logs from late May through early August (Dyer and Seabrook 1978). Male and females arrive on the potential host and may be observed persistently palpitating the host surface as they walk (Hughes and Hughes 1985, Peddle 2000). Males are thought to use their long antennae to aide in mate location and will mate with receptive females after antennal contact (Hughes 1979, Hughes and Hughes 1982). After mating, females cut egg niches into the bark, often near old branch stubs or around branch whorls (Hughes and Hughes 1985, Peddle 2000, Rose 1957). Eggs hatch within two weeks and larvae begin tunneling in the cambium and phloem (Rose 1957). After three to four weeks, larval galleries are wide enough and deep enough to score the sapwood. By late summer, larval tunnels extend deeply into the sapwood, where larvae overwinter. Feeding resumes the following spring and in Michigan, most beetles complete development and emerge in late May to August. Adult *M. scutellatus* are most active in sunny locations in the forest (Post and Werner 1988, Rose 1957).

Potential host material for *M. scutellatus* is often highly localized, resulting from windstorms or logging events, or sporadic individual tree mortality. *Monochamus scutellatus* beetles must be able to locate potential hosts, often from a distance when walking or in flight, and secondarily decide if the material is a suitable host after landing (Bernays and Chapman 1998). *Monochamus scutellatus* responds strongly to host-specific volatiles from a distance (Peddle 2000), but whether females discriminate among potentially acceptable hosts or consistently respond differently to pine and spruce species is unknown. Female *M. scutellatus* arriving on potential hosts for oviposition use contact

chemoreception to detect host semiochemicals, terpenes, resin pressure, and moisture levels (Bernays and Chapman 1994, Brattli et al. 1998, Dyer and Seabrook 1977, Hanks 1999, Hughes and Hughes 1992). The presence of eggs or larvae of conspecifics can also influence oviposition choices of *M. scutellatus* by deterring female oviposition on host material already occupied by eggs of conspecifics (Hughes and Hughes 1992, Peddle 2002).

After oviposition, survival of offspring is driven by host suitability rather than by host preference, since larvae must feed and develop on the host chosen by the female (Hanks 1999). In the most basic sense, a host can be considered to be suitable if the larvae survive and develop into adults. However, for polyphagous species such as *M. scutellatus*, host quality may vary. Survival to the adult stage is one measure of suitability, but vigor and size of beetles has been shown to be correlated with fitness (Hanks 1999, Kato et al. 2000). Therefore, large and vigorous progeny may indicate a higher degree of suitability for *M. scutellatus* larval development. Adult preference was correlated to performance for a leaf-mining fly (Via 1986). Host preferences did not match up exactly with larval performance for many other insects (Cronin et al. 2001, Karban and Courtney 1987, Larsson et al. 1995).

Relationships between preference and performance have rarely been studied in wood-boring Cerambycidae (Hanks et al 1995). Host preference studies with wood-borers usually involve counting the number of egg niches (Walsh and Linit 1985), and eggs (Donley 1978) or twig feeding during choice tests (Walsh and Linit 1984, Kobaayashi et al. 1984). In the only evaluation of *M. scutellatus* host preference, Peddle (2000) found that females chewed more niches on red pine than on white pine logs.

Studies with other wood-boring species on multiple hosts reported differences among larval density (Hanks et al. 1993), development time (Hanks et al. 1995), abundance of galleries and mortality (Kobaayashi et al 1984), but suitability of potentially acceptable conifer species has not been evaluated for *M. scutellatus*.

Competition and cannibalism may be an important source of mortality for *M. scutellatus* and for other insects that utilize phloem. Early instar *M. scutellatus* are cannibalistic at high densities (Peddle 2002, Rose 1957). When two or more species occupy the same host species, some degree of resource partitioning often occurs. For example, bark beetles, weevils and *M. scutellatus* all occupy phloem but partition themselves phenologically or spatially on the host (Kennedy and McCullough 2002), and scolytid bark beetles partitioned themselves spatially on hosts in British Colombia (Poland and Borden 1994).

I postulated that female *M. scutellatus* adults would consistently exhibit preferences when four potentially acceptable hosts were available for oviposition. I further postulated that female host preference, or host selection behavior, would affect the development and survival of all progeny and that the four conifers would differ in suitability for *M. scutellatus* development. Additionally, I postulated that phloem feeders would partition themselves spatially on the logs to minimize mortality from interspecific competition. Jack pine, red pine, white pine and white spruce were selected as potential hosts in this study because they are native conifers within the host range of *M. scutellatus*, their attractiveness and suitability for *M. scutellatus* is unknown, with respect to each other, and they were available at the study site. The specific objectives of this study were to evaluate 1) host selection preference and behavior by *M. scutellatus*

females in the field; 2) the survival and development of *M. scutellatus* larvae on four conifers; and 3) the impacts of intra- and inter-specific competition on *M. scutellatus* larval development.

METHODS AND MATERIALS

Study sites: In May 2001, one compartment each of red pine (*Pinus resinosa* Ait.), jack pine (*Pinus banksiana* Lamb.), Norway spruce (*Picea abies* (L.) Karst) and white spruce (*Picea glauca* (Moench) Voss) were selected in Michigan State University's W. K. Kellogg Experimental Forest in Kalamazoo County. Compartments were 0.3 ha (0.8 acres), 2.8 ha (7 acres), 0.4 ha (1 acre) and 0.4 ha (1 acre) in size for jack pine, red pine, Norway spruce and white spruce, respectively (Greg Kowalewski, pers. comm.). Each stand had coarse woody debris from logging and windthrow with recent *M. scutellatus* frass piles and/or entrance holes into the sapwood. Each compartment had gaps in the canopy where overstory trees had been felled in previous years. Compartments were even-aged and shrub and forb layers varied but mainly included European buckthorn (*Rhamnus cathartica* L.), glossy buckthorn (*Rhamnus frangula* L.), black cherry (*Prunus serotina* L.), sugar maple (*Acer saccharum* Marsh), and sassafrass (*Sassafrass albidum* (Nutt.) Ness).

Site characteristics varied among compartments. All stands had a medium site index of 51-56, based on site index charts for Michigan pine and spruce stands, and so were of similar quality for tree growth (Avery and Burkhart 1983) (Table 1). Basal area of the compartments, measured with a 10 BAF prism, ranged from 36 m²/ha (155 ft²/acre) for jack pine to 40 m²/ha (175 ft²/acre) for Norway spruce (Table 1) (Greg Kowalewski pers. comm.). Tree height ranged from 17.8 m (53.5 ft) (jack pine compartment) to 21.5 m (64.6 ft) (Norway spruce compartment).

Eight trees of each species, jack pine, red pine, white pine and white spruce, at W.K. Kellogg Forest were felled 1-3 May 2001 and the stems were cut into logs, 46 cm

(18 in) in length and 10 to 18 cm in diameter. Two log arrays were centered under two canopy gaps in each compartment. Each log array consisted of logs from two trees each of jack pine, red pine, white pine, and white spruce, placed end to end by increasing size in the north and south sides of each compartment under gaps in the canopy. Each essentially reassembled tree was placed parallel to logs of the next species, 3.3 m (10 ft) apart. I placed from 44 to 62, 59 to 90, 49 to 63, and 45 to 65 jack pine, red pine, white pine and white spruce logs in compartments, respectively (Table 2.1). The order that species were placed in each of the two arrays in each stand was randomized. The canopy cover directly over the log array was measured once at mid-day with a convex spherical crown densiometer, and showed that sun exposure on all log arrays was consistent because the surrounding dominant trees provided similar amounts of shade in all compartments.

Host preference of adult females

Field observations: Compartments were visited at least three times each week from 22 May to 14 August 2001. Each log array was observed for 25 min, four times a day between 10 a.m. to 6 p.m. Compartments were visited sequentially, with the initial stand determined by random draw. Our observations involved carefully walking along the sides of the logs and inspecting all areas, including shaded areas adjacent to the ground, without disturbing the logs. Observations were made for log species sequentially. We used focal sampling within the observational period for each compartment location, so that the first *M. scutellatus* seen was observed for the full 25 (Martin and Bateson 1993). If the first *M. scutellatus* observed flew away or fell into the leaf litter before the 25 min observational period was finished, observations for *M.*

scutellatus activity on the other logs were continued. The number of male and female *M. scutellatus* seen on logs was quantified. The frequency and duration of behaviors of interest including walking, stationary, egg niche excavation, oviposition, feeding and copulation was also quantified.

Log Retrieval and dissections. I assessed host preference of adult *M. scutellatus* females by quantifying the attack rates on each conifer species. The top of each log was marked with paint before it was collected from the field sites. From 25 to 31 August 2001, every third log in each log array was collected and transported to the laboratory at Michigan State University. The remaining logs were transported to a screened enclosure on campus that exposed logs to ambient conditions but not precipitation. Logs were stored over the winter to allow adults to develop and emerge the following spring. The first third of the logs were brought directly to the laboratory were designated as Batch-1. The other two-third of the logs that were stored overwinter were designated as Batch-2. Batch-1 logs were dissected in September 2001 to January 2002. Batch-2 logs were dissected from April to June 2002. Female *M. scutellatus* host preference was again assessed by counting attacks on Batch-1 and Batch-2 logs combined. Suitability for larvae, however, was measured separately for Batch-1 and Batch-2. Because logs remained in the forest for four months, egg niches could not be accurately counted due to natural weathering of the bark. Instead, host preference using the number of galleries per log was estimated. While some eggs initially laid on hosts may not have hatched, we assumed that this rate would be similar among species. The number of *M. scutellatus* galleries found on each region of the log (top, left side, right side, and bottom) was

quantified. Galleries that covered more than one position were assigned to the one where the majority of the gallery occurred.

Physical characteristics that could affect *M. scutellatus* host preference were assessed for each log. On each log two length measurements, three diameter measurements and four bark thickness measurements were made (measurements were made on only the outer bark at the end of the study) and the mean of each variable for each log was calculated. The number of curculionid and scolytid bark beetle exit holes (distinguishable by size) was recorded on each log. Each log was debarked and a grid system was used to quantify the number of *M. scutellatus* galleries and the area of larval feeding on each log. A gridwriter apparatus was used to accurately draw seven equidistant lines, 4.5 cm (1.75 in) apart, around the diameter of each log. Each log was marked four times lengthwise corresponding to the top, sides and bottom of the log as it lay during the field study, to assess the effect of microhabitat on *M. scutellatus* oviposition site selection.

Host suitability

Log retrieval and dissections: I measured 72, 97, 72, 71 jack pine, red pine, white pine and white spruce logs were measured, respectively in Batch-1. For Batch-2 logs 118, 147, 131, and 115 jack pine, red pine, white pine and white spruce logs were measured, respectively. Host suitability was estimated by counting larval gallery area, number of entrance holes and percentage early instar survival for both Batch-1 and Batch-2 logs. Suitability was also measured by counting the number of exit holes and total percentage survival for only Batch-2 logs. The total area phloem consumed by *M. scutellatus* larvae for each log was recorded by summing the percentage of area

consumed within each grid-square and then multiplying that by the surface area of each log. Early instar survival was assessed by counting the number of galleries with no larva or entrance hole into the sapwood (survival=# larvae that died prior to the third instar)/total number of galleries. The number of entrance holes refers to the oval-shaped tunnel larvae make as they chew into the sapwood at an angle and can be used to estimate whether larvae survival to the fourth instar (Cerezke 1977). The exit hole refers to the circular-shaped hole that is created as adults chew out of the sapwood during emergence. Suitability was also measured by overall percentage survival of *M. scutellatus*, calculated as the number of emerging progeny/the total galleries per log.

Rearing F1 generation from Batch-2 logs. Batch-2 logs were placed in individual cardboard rearing containers consisting of a cardboard tube (4, 6, 8, and 10 in diameter, 0.32 –0.64 cm wall, 71 cm overall length (Michigan Can and Tube, Inc., Saginaw, MI)) with screened endcaps on both ends and left undisturbed until spring 2002. I removed 200 logs from the screened enclosure and transported them to a 4.4C (40F) cold storage room on MSU campus in March 2002.

Groups of logs (120-200 logs) representing all log species from each compartment were brought into the laboratory to rear out *M. scutellatus* on four separate occasions; 11 April, 2 May, 21 May, and 10 June 2002. Logs were soaked in water for 1-3 minutes until bark was thoroughly moistened to hasten F1 emergence. Logs were then placed into 121.1 L (32 Gallon) Rubbermaid® trash cans in which the plastic covering the tops of the trash can lids was cut out and replaced with fiberglass mesh screen so that newly emerged beetles would crawl up to the light. In this way, emerging *M. scutellatus* could be easily collected from the lid.

Adult *M. scutellatus* were collected from the rearing containers twice daily beginning 23 April, 2002. Newly emerged beetles were weighed, assigned an identification number and placed individually into a 1.9 L (2 qt) plastic container with a screened lid. Every time a new *M. scutellatus* was discovered in a trash can, its corresponding exit hole was found and the number of the log it emerged from was recorded. Adult *M. scutellatus* were provided with fresh Scotch pine (*Pinus sylvestris* L.) shoots in 2 dram glass vials filled with water weekly. Scotch pine was fed to the progeny because it was available and was not one of the conifers focused on in the experiments.

Intra- and Interspecific Competition

I recorded the number of times *M. scutellatus* larval galleries intersected each other on each log as an estimate of potential intraspecific competition. Galleries were traced with a red wax pen to assist in accurate visualization of the interceptions. To assess inter-specific competition for phloem between *M. scutellatus* and scolytid bark beetles or curculionids, I traced scolytid bark beetle egg galleries and curculionid cocoons and feeding galleries. The number of times a *M. scutellatus* gallery intercepted a scolytid bark beetle gallery or curculionid gallery or cocoon was recorded. The area of phloem consumed by scolytids and curculionids for the top, sides and bottom of each log was quantified using the grid method as previously described.

Statistical Analyses

All variables were tested for normality with the Shapiro-Wilk test (Shapiro and Wilk 1965). Variables were non-normal even after transformations, except for the area of phloem consumed by scolytid bark beetles per log and *M. scutellatus* progeny weight. Differences in initial number of logs colonized, and the number of logs where at least one

M. scutellatus emerged per species were tested using the Mantel-Haenszel Chi-square statistic in a 2 X 4 contingency table (Rayner and Best 2001, Stokes et al. 2000). The Nonparametric Rank *F* test was used to determine if number of galleries differed among the 4 conifers (Neter et al. 1996). The Nonparametric Rank *F* test was used to determine if the number of entrance holes per log, area of phloem consumed per log, and percent early instar mortality differed for Batch-1 and 2 logs. Additionally, the Nonparametric Rank *F* test was used to test for differences in number of exit holes and total percentage *M. scutellatus* mortality among conifers for Batch-2 logs. I could not test for an interaction between conifer species and log position because area of *M. scutellatus* phloem consumption was not normally distributed and violated assumptions of a split-plot design. Analyses of differences in the area of phloem consumption on the four conifers and of area of phloem consumed on the tops, sides and bottom of logs were conducted at the $P < 0.025$ level of significance (after Bonferroni adjustment) using the Nonparametric F-test (Kuehl 2000). One-way analysis of variance (ANOVA), was used to determine if progeny weight differed among conifer species (SAS Institute, Inc. 1989). When results of the Nonparametric F-test or ANOVA were significant, a Nonparametric Rank *F* test Multiple Pairwise Testing Procedure and Fischer's protected least significant difference (LSD) test was used to determine which conifer species differed, respectively (Neter et al. 1996). The nonparametric Mann-Whitney test was used to determine differences in area of phloem consumed by scolytid bark beetles and curculionids between logs with and logs without *M. scutellatus* galleries (Mann and Witney 1947). Spearman's rank correlation (R_s) was used to test for associations among log diameter, bark thickness and the number of *M. scutellatus* galleries for the 4 conifers species.

Spearman's Rank Correlation was also used to test for associations between *M. scutellatus* and scolytid bark beetle phloem consumption and *M. scutellatus* and Curculionids phloem consumption. Unless specified differently, analyses were conducted at the $P < 0.05$ level of significance, using SAS statistical software (SAS Institute, Inc. 1989).

RESULTS

Host Preference

Observations of *M. scutellatus* at Kellogg Forest: A total of 16 female *M. scutellatus* and 17 male *M. scutellatus* was observed from 22 May to 14 August 2001 to identify behaviors associated with selection of oviposition sites. Figure 2.1 shows the frequency of the observed behaviors. Females oviposited on red pine, white pine, and white spruce logs, for an average of 12 n out of the 25 min observation period. Females oviposited on the sides of the logs in three of the four ovipositional events and once on the top of the log. Females excavated six egg niches and three were on white pine. Females were observed in a stationary state six times; on the top and the sides of red pine, white pine and white spruce logs. A female walked only once on a white pine log and pair of *M. scutellatus* copulated one time on a white pine log.

An interesting behavioral event observed was an escape behavior designated as dropping. Because beetles had to be approached very closely to monitor behavior, a shadow or noise was often unavoidable. On two occasions, females dropped from a red pine log to the leaf litter where they were hidden from sight. *Monochamus scutellatus* “squeaked” as they dropped. Three different females flew from logs of red pine, white pine and white spruce when approached too closely.

Male *M. scutellatus* were stationary during most of our observations. Two stationary males were observed on red pine, ten males on white pine logs, one male on a jack pine log, and one on a white spruce log. On average, males were stationary 20.2 ± 3.5 min of the 25 min observation period. Males walked on red pine logs twice and once on a white spruce log. A male was also observed feeding on the side of a red pine log

and one male fed on the top of a white pine log. Males were not observed in flight but two males dropped from red pine logs and one male from a white pine log and they squeaked as they dropped.

Two related species, *M. notatus* (Drury) and *M. titillator* (Fabricius), were observed on log arrays on a few occasions. One female *M. titillator* walked on red pine, one female chewed an egg niche on white pine and two stationary females were observed on white pine logs. One stationary male *M. notatus* was seen on a white pine log.

Overall, 69.1% of experimental logs were colonized by *M. scutellatus*. Female *M. scutellatus* colonized 64%, 67%, 68% and 76% of jack pine, red pine, white pine, and white spruce logs, respectively. A significantly different percentage of logs were colonized by *M. scutellatus* females ($X^2=24.26$, $P<0.001$, d.f.=3). Only logs with *M. scutellatus* attacks were included in further analyses of variables related to galleries and survival. Host preference is represented in Table 2.2 by the number of galleries per log. For Batch-1 logs, the number of *M. scutellatus* galleries per log ranged from 1 to 11 for jack pine, 1 to 23 for red pine, 1 to 17 for white pine and 1 to 21 for white spruce logs. There were significantly more galleries on white pine and white spruce logs than on jack pine and red pine logs ($P=0.001$, $F=5.72$, d.f.=3) (Table 2.2).

Results of correlation tests comparing associations between variables related to log characteristics and the number of *M. scutellatus* galleries differed. Log diameter was not significantly correlated to number of galleries when all logs across species were pooled together ($P=0.09$, $R_s=-0.07$). Log diameter was significantly correlated to the number of *M. scutellatus* galleries when jack pine logs ($P=0.04$, $R_s=0.19$) and white pine logs ($P=0.007$, $R_s=-0.23$) were analyzed separately, but not for red pine and white spruce

logs. However, bark thickness was negatively correlated with the number of galleries but explained little of the variation ($P=0.003$, $R_s=-0.15$) when species were pooled.

Additionally, bark thickness was weakly and negatively correlated to the number of *M. scutellatus* galleries for red pine logs ($P=0.006$, $R_s=-0.22$), and white pine logs ($P=0.004$, $R_s=-0.27$) when conifer species were analyzed separately.

Host suitability

Batch-1 logs: Suitability of the 4 conifer species for larval development was assessed by the area of phloem consumed per gallery and per log, percentage early instar survival, and progeny weight. On average, *M. scutellatus* larvae consumed 8.4 ± 0.9 , 9.9 ± 0.9 , 12.7 ± 1.3 and 10.8 ± 1.6 percent of the phloem on the Batch-1 jack pine, red pine, white pine, and white spruce logs, respectively (Tables 2.2, 2.3 and Figure 2.2). For Batch-1 logs, dissected in fall 2001, the total area of phloem consumed per log ranged from a low value of 2.1 cm^2 on a jack pine log, to a high of 603.2 cm^2 on a white pine log. The area of phloem consumed per gallery ranged from minimum values of 2.1 (jack pine) to 5.4 cm^2 (red pine) while maximum values ranged from 71.9 cm^2 (white spruce) to 80.4 cm^2 (red pine). However, for Batch-1 logs, the log species did not significantly influence *M. scutellatus* phloem consumption ($P<0.254$, $F=15.74$, $d.f.=3$) (Table 2.2). but significantly more phloem was consumed on the sides of logs than on the tops and bottoms ($P=0.003$, $F=6.88$, $d.f.=3$) (Figure 2.3). *Monochamus scutellatus* consumed 15, 13, 14 percent of phloem on the tops, sides and bottoms of logs. Again, the number of measurements for log sides was double that of the top and bottom position. The number of larvae that entered the sapwood ranged from 0 to 9 per log for jack pine, 0 to 21 for red pine, 0 to 14 for white pine and 0 to 20 for white spruce and did not significantly

differ among species (Table 2.2). The percentage of larvae that entered into the sapwood was 65%, 88%, 89%, 89% for jack pine, red pine, white pine and white spruce, respectively. Early instar survival was generally high, averaging nearly 80 % for all conifer species (Table 2.2).

Batch-2 logs: For the logs dissected after *M. scutellatus* beetles emerged, total phloem consumption ranged from 3.1 to 342 cm² for jack pine, 23.9 to 753.2 cm² for red pine, 24.5 to 571.9 cm² for white pine, and 12.8 to 637.2 cm² for jack pine logs. On average, larvae on jack pine, red pine, white pine and white spruce consumed 9.1, 14.5, 18.7, and 14.0 percent of the phloem, respectively. However, *M. scutellatus* larval galleries were significantly larger on red pine and white pine than on white spruce logs ($P<0.001$, $F=4.85$, $d.f.=3$). Gallery size was statistically similar among the pines and between jack pine and white spruce. The number of entrance holes per log where late instar larvae entered the sapwood ranged from 0 to 7, 0 to 12, 0 to 17, and 0 to 19 for jack pine, red pine, white pine, and white spruce per log, respectively and the number of entrance holes were statistically similar among the four conifers. The percentage of larvae that entered the sapwood was 95%, 96%, 98%, and 97% for jack pine, red pine, white pine, and white spruce, respectively. Early instar survival and total survival both ranged from 0 to 100 percent for all conifer species. Total percentage of survival was significantly lower for the white spruce logs than for any of the pine species ($P=0.04$, $F=8.29$, $d.f.=3$), but early instar survival did not differ. The maximum number of exit holes per log where F_1 adults emerged was 2, 6, 6, and 7 for jack pine, red pine, white pine and white spruce logs, respectively, and differences among the conifer species were not significant (Table 2.3). *Monochamus scutellatus* consumed 15, 16, and 13 percent of

phloem on the tops, sides and bottoms of logs, respectively. There was no significant difference in the area of phloem consumed for the log position ($P < 0.296$, $F = 1.24$, d.f.=3) (Figure 2.3).

Progeny: F_1 *Monochamus* spp. adults emerged from 57.4% of the jack pine logs, 73.9 % of the red pine logs, 66.3 % of the white pine logs, and 64.8 % of the white spruce logs. The number of logs with at least one emerging beetle did not vary among the conifers ($\chi^2 = 0.24$, $P > 0.05$) (Table 2.3). Beetles emerging from white spruce were significantly smaller than beetles emerging from all three pine species ($P < 0.001$, $F = 47.89$, d.f.=3) (Table 2.2). Female and male weights were very similar for beetles reared on the same host (Table 2.3). The largest beetles reared from each conifer species were typically the first of the group to emerge for both males and females. However, the first beetles emerged from white spruce 5-7 days later than beetles from the pines. The ratio of males to females differed among conifer species (Table 2.3), with 42%, 53%, 58%, and 55% females for jack pine, red pine, white pine and white spruce, respectively.

Compartment effects: We could not statistically analyze differences among compartments because compartments were not replicated. Characteristics of compartments, however, may have influenced the rate of their colonization by *M. scutellatus*. The mean number of galleries per log was consistently lower for logs placed in the white spruce study areas and much higher for logs placed in the red pine study areas. The percentage of colonization of logs in compartments was 70.4%, 84.2%, 70.2%, and 53.1% for jack pine, red pine, Norway spruce and white spruce compartments, respectively. The number of galleries and area of phloem consumed for conifers of Batch-2 were compared. The range of galleries per log was 1-8, 2-5, 2-3, and

0.5-3 placed in jack pine, red pine, Norway spruce, and white spruce compartments, respectively. Also, when we reared progeny, the mean number of exit holes per log was lower for logs that were placed in the white spruce study areas.

Intra- and Interspecific Competition

Intraspecific competition: Potential competition among early instar *M. scutellatus* larvae was assessed by counting the number of times galleries intercepted other *M. scutellatus* galleries in Batch-1 logs. For Batch-1 logs, the number of logs with *M. scutellatus* gallery interceptions ranged from 18 % of jack pine logs to 43 % of white pine logs. There were no statistically significant differences among the conifer species (Table 2.3). The number of interceptions between *M. scutellatus* galleries per logs ranged from 1 to 3 (jack pine) and 1 and 20 (white spruce), but did not differ significantly among conifers. For Batch-2 logs, the mean number of logs where *M. scutellatus* gallery interceptions occurred ranged from 6 % of jack pine logs to 37 % of red pine logs, but differences among conifers were not significant (Table 2.3). For Batch-2 logs, the number of interceptions between *M. scutellatus* and *M. scutellatus* galleries per log ranged from 1 interception (jack pine) to 17 (white spruce), but the number of *M. scutellatus* gallery interceptions was not significantly different among conifers.

Interspecific competition. Potential competition between *M. scutellatus* and other phloem feeders varied among conifers. All Batch-1 logs were colonized by scolytid bark beetles, while curculionids colonized 90%, 93%, 97%, 37% of the jack pine, red pine, white pine and white spruce log, respectively. Scolytid bark beetles and/or curculionids colonized 31, 20, 23, and 22 percent of jack pine, red pine, white pine and white spruce logs, respectively, in the absence of *M. scutellatus*. Scolytid bark beetles

consumed significantly more phloem on logs where *M. scutellatus* were absent ($P < 0.05$, 27.51, d.f.=3). The area of phloem consumed by scolytid bark beetles was greater on jack pine and white spruce than on red and white pine logs ($P < 0.05$, $F = 15.64$, d.f.=3) (Figure 2.2). Scolytid bark beetles consumed 8, 11, and 9 percent of the phloem on the tops, sides and bottoms of logs, respectively, and they consumed more area of phloem on the top and bottoms than on the sides of logs ($p < 0.003$, $F = 6.88$, d.f.=3) (Figure 2.3). The number of interceptions between *M. scutellatus* and scolytid bark beetle galleries ranged from 1 to 10 (red pine) and 1 to 21 (white pine and white spruce) and significantly more interceptions were found on white pine and white spruce logs than on jack pine or red pine logs ($P < 0.001$, $F = 7.67$, d.f.=3). Curculionids consumed more phloem on logs with no *M. scutellatus* galleries than on logs with at least one *M. scutellatus* gallery ($P < 0.05$). Curculionids consumed a greater area of phloem on pines than on white spruce ($P < 0.001$, d.f. = 3) (Table 2.4) (Figure 2.2). Curculionids consumed 5, 7, and 11 percent of phloem on the tops, sides and bottoms of logs, respectively, and they consumed more phloem on the bottoms of logs than on the tops or sides ($P < 0.001$, d.f.=3) (Figure 2.3). The number of *M. scutellatus* and curculionid interceptions ranged from 1 to 9 (jack pine) and 1 to 22 (white pine), but differences were not significant among conifers.

All of the Batch-2 jack pine and white pine logs were colonized by scolytid bark beetles, and they colonized 94% red pine logs and 97% white spruce logs. Curculionids colonized 92% of the jack pine logs, 100% of the red pine, 94% of the white pine, but only 25% of white spruce logs. Like the Batch-1 logs, significantly more phloem was consumed by scolytid bark beetles on logs with no *M. scutellatus* galleries than on logs with one or more cerambycid galleries ($P < 0.05$). Significantly more phloem was

consumed by scolytid bark beetles on the white spruce logs than on pines ($P=0.002$, $F=41.58$, $d.f.=3$) (Figures 2.2, 2.3). Scolytid bark beetles consumed 4, 3, and 3 percent of phloem on the top, sides, and bottoms of logs. Scolytid bark beetles consumed more phloem on the top than on the sides of logs, but area of phloem consumed on the bottom did not differ from the tops and the sides ($P=0.021$, $d.f.=3$). The number of interceptions of *M. scutellatus* and scolytid bark beetle galleries ranged from 1 to 4 (red pine) to 1 to 17 (white spruce) and significantly more interceptions were found on white spruce logs than on jack pine or red pine logs ($P<0.005$, $F=12.67$, $d.f.=3$). Significantly more phloem was consumed by curculionids on logs with no *M. scutellatus* galleries than on logs with at least one gallery ($P<0.05$). Again, curculionids consumed significantly more phloem on the pines than on white spruce ($P<0.001$, $F=67.99$, $d.f.=3$) and more phloem was consumed on the bottom of logs than for other positions on the logs ($P<0.001$, $F=13.81$, $d.f.=3$). Curculionids consumed 3, 5, and 8 percent of the phloem on the tops, sides and bottoms of logs. The number of *M. scutellatus* and curculionid gallery interceptions ranged from 1 (white spruce) and 1 to 24 (red pine), and significantly more interceptions were found on red pine, white pine and jack pine than on white spruce ($P<0.003$, $F=5.57$, $d.f.=3$).

Galleries of *M. scutellatus* intercepted galleries of scolytid bark beetles on 62 % of jack pine logs and 86 % of white spruce logs. The mean number of *M. scutellatus* bark beetle gallery interceptions was significantly greater on white pine and white spruce than on red pine and jack pine (Table 2.4). Galleries of *M. scutellatus* intercepted weevil galleries on 12 % of white spruce to 63 % of white pine logs. Differences among conifer species were not significant (Table 2.3).

For Batch-2 logs, galleries of *M. scutellatus* intercepted galleries of scolytid bark beetles on 18 % of jack pine to 76 % of white spruce logs. The mean number of *M. scutellatus* bark beetle gallery interceptions was significantly greater on white pine and white spruce than on red pine and jack pine (Table 2.4). Galleries of *M. scutellatus* intercepted weevil galleries on 20 % of white spruce to 82 % of white pine logs. The number of *M. scutellatus*-curculionid galleries was significantly greater on the pines than on white spruce logs (Table 2.4).

For Batch-1 logs, pooled across all species, the area of phloem consumed by *M. scutellatus* was negatively correlated to the area of scolytid bark beetle feeding ($P<.001$, $R_s=-0.22$), but not to the area of curculionid feeding. Phloem consumed by *M. scutellatus* was positively correlated to weevil feeding ($P<0.004$, $R_s=0.37$) when jack pine was analyzed separately. The area of *M. scutellatus* feeding was negatively correlated to scolytid bark beetle feeding ($P<0.003$, $R_s=-0.39$) and weevil feeding ($P<0.03$, $R_s=-0.29$).

For Batch-2, pooled across species, the area of phloem consumed by *M. scutellatus* was not correlated to the area of scolytid bark beetle feeding, or to the area of curculionid feeding. The area of *M. scutellatus* feeding wasn't correlated to bark beetle and weevil feeding on jack pine, red pine, white pine or white spruce when conifer species were analyzed separately.

DISCUSSION

Host Preference and Suitability

I attempted to assess whether *M. scutellatus* females in southwestern Michigan demonstrate a preference hierarchy for four conifer species within their host range. Female *M. scutellatus* prefer white pine and white spruce for oviposition over jack pine and red pine. This conclusion was based on different numbers of galleries, the index of preference in this study, and on the percentage of logs *M. scutellatus* oviposited on for each species. In general, fewer beetles were observed visiting log arrays than originally expected, but most of the beetles observed during the summer were on white pine and red pine logs. Adult *M. scutellatus* are active throughout much of the day and beetles were seen at varying times during observation periods Hughes (1979) and Peddle (2000). One reason few beetles were observed was probably because harvesting occurred in compartments adjacent to red pine, white spruce and Norway spruce compartments during most of June. Adult *M. scutellatus* were frequently seen in other logged compartments. Some *M. scutellatus* may have been attracted to the logged compartments and passed over the log arrays because of the amount of terpenes and other volatiles emitted from the logged area.

All of the conifer species presented to females were accepted for oviposition by at least some *M. scutellatus* females, but females colonized jack pine logs less frequently than the other pine species and white spruce logs. Many logs were not colonized by *M. scutellatus* perhaps because of the abundance of cut pine in adjacent and nearby compartments of Kellogg Forest. However, more jack pine logs were left uncolonized

than for other conifer species. A greater number of galleries was found on white pine and white spruce logs than jack pine and white spruce and so were initially more preferred than red pine and jack pine. In a related study, during 2-choice trials, females preferred either white pine or white spruce over jack pine and red pine consistently, while similar numbers of eggs and galleries were on white pine and white spruce (Lazarus and McCullough in preparation). Preference for white pine by *M. scutellatus* has been also shown by Peddle (2000). In addition, females were attracted to white spruce decks in Alberta causing much loss in merchantable timber (Cerezke 1977), and attacked downed white spruce more often than jack pine in northern Ontario (Gardiner 1975).

In general, log diameter did not influence female preference. There was a slight correlation between diameter and number of *M. scutellatus* galleries for jack pine and white pine logs. The logs in this study were all probably large enough to support a year-long life cycle, but I would expect greater mortality on smaller branch-size wood. The diameter or height of trees did influence host preference of *Monochamus sutor* L. when diameters ranged from 6 cm to 27 cm (Zhang et al. 1993). In this study, the number of galleries was slightly negatively correlated to bark thickness of red pine and white pine. Females may have specifically chosen a certain bark thickness for oviposition (Hughes and Hughes 1982).

Once females selected a log for oviposition, relative suitability of the four conifers influenced the fate of the F1 generation. Overall, white pine and red pine were most suitable for *M. scutellatus* development and white spruce was least suitable for a number of reasons. Early instar larvae utilized more total phloem on the Batch-1 white pine and white spruce logs but differences among species were not apparent for the

Batch-2 logs that were dissected after the F1 adults emerged. A study in Canada found that *M. scutellatus* galleries were larger on white pine than on red pine logs, but jack pine and white spruce were not evaluated (Peddle 2002). Galleries on our jack pine, red pine and white pine logs were consistently larger than those in the Peddle (2002) study, although the galleries were significantly smaller on our white spruce logs. Log diameters were similar in the two studies, but phloem thickness was not measured.

Additionally, *M. scutellatus* preferred the sides of logs for oviposition. Females allocate much time and energy to egg niche excavation and oviposition and egg placement influences progeny survival in this species (Hughes and Hughes 1982). The sides of the logs may be optimal for oviposition because phloem on the tops of the logs may dry out faster than other areas, and the bottom of logs on the ground may be too moist and cool. Larvae consumed more phloem on the sides of the Batch-2 logs, regardless of conifer species, although differences were not significant for Batch-1 logs. In Canada, *M. scutellatus* preferentially oviposited on the sides of logs in white spruce log decks (Post and Werner 1988, Cerezke 1977), but there were no differences in number of egg niches or phloem consumption between the top and bottom halves of logs that were on the ground (Peddle 2000). Female beetles, however, may have been more restricted in regions of the log available for oviposition in log decks than when logs were layed singly on the ground. Raske (1975) found the density of *M. scutellatus* galleries was twice as high on scattered logs than on decked logs.

Total survival is one of the key indicators of suitability in this study. Nevertheless, the survival of *M. scutellatus* on white pine and white spruce was quite different when we compare all life stages on these two hosts. There were no differences

among conifer species in early larval instar survival for either Batch-1 or Batch-2 logs. Once larvae hatched and began feeding, they generally survived long enough to begin tunneling into the sapwood. In white spruce logs in Alberta there was 29% *M. scutellatus* total survival (Cerezke 1977), while 31% survived on white spruce (Table 2.2). Total percentage survival was almost double on pines than on spruce in our study. Differences in survival between the period of late instar/pupation and emergence may have been due to differences in chemical composition between pine and spruce logs, or simply that some dietary needs of *M. scutellatus* were not met by white spruce prior to the period between overwintering and pupation of the beetles. Pine and spruce contain varying concentrations of monoterpenes such as alpha-pinene, camphene, beta-pinene, myrcene and limonene (Drew and Pylant 1966).

The final measure of suitability among the four conifer species was obtained when progeny emerged from the host logs. Adult female size directly affects fecundity of cerambycid females and also affects fitness of the beetles (Hanks 1999, Larsson and Kustvall 1990). Pines were more suitable hosts for *M. scutellatus* offspring because the F₁ adults were larger than those that developed in spruce. Spruce-reared beetles were small, but a similar number of beetles emerged as for pines. Competition may also influence progeny size, but size varied for progeny that developed on equally preferred white pine and white spruce. However, F₁ beetles began emerging from spruce 5-7 days after those from the pines began emerging which is suggestive of delayed development in spruce logs, especially since all logs were treated similarly in the field.

It is more difficult to discern if the three pine species differed in suitability for *M. scutellatus* development because the percentage of progeny survival was similar among

the three pines. Jack pine may be the least suitable pine species because females colonized fewer jack pine logs than other pines, and progeny were significantly smaller than those reared on red pine and white pine. Interestingly, more female beetles emerged from red pine, white pine, and white spruce, while more males emerged from jack pine. A sex ratio favoring males may have implications for the abundance of *M. scutellatus* in future generations. Jack pine-reared females often died within a week after emergence compared with a life span of up to 70 days on other species. This suggests that individuals that developed on jack pine had lower vigor or were sick.

Thompson (1988) stated that an ovipositional choice that confers greatest fitness to offspring would seem to be favored evolutionarily, but preference and performance often are not correlated. This is probably especially true for insects that cannot change hosts while developing. Host preferences did not match up exactly with larval performance in this study, as was found for other insects (Cronin et al. 2001, Karban and Courtney 1987, Larsson et al. 1995, Via 1986). Female *M. scutellatus* did not demonstrate a neat hierarchical ranking of preferences, or one host that was preferred over all others consistently. If preference is correlated to performance, than progeny developing on white pine and white spruce should have performed better than those on red pine and white spruce. I expected a tighter linkage between preference and performance for wood-borers because oviposition site-selection influences offspring survival. Explanations for inconsistencies between female preference for white spruce and poor offspring performance on white spruce are unknown. Inconsistencies between preference and performance may be explained by ecological conditions affecting populations such as abundance of hosts from year to year or enemy-free space (Cronin et

al. 2001, Hanks et al. 1993, Thompson 1988). Kellogg Forest is composed of compartments of a number of different conifer species with varying amounts of host material from conifers available every year. Perhaps the inconsistencies between preference and performance found among conifers are due to the variability of available hosts for colonization each generation. However, the survival on all hosts of differential chemical composition is suggestive of adaptation to a more generalized diet, as was found in gall-making flies (Cronin et al. 2001). Future studies on correlation of preference and performance of wood-borers should address the importance of host abundance to host suitability and implications of small body size and delayed development on the fitness of wood-borers.

Intra- and Interspecific Competition

I postulated that intraspecific competition would vary among the four conifers if females preferred one species over others. High densities of larvae may provide more opportunities for contact interference or cannibalism if phloem is limited. Intraspecific competition did not vary among the host species, even though the number of galleries was greater on white pine and white spruce than on jack pine and red pine logs. Many logs had more than one interception per log, indicating that galleries may be concentrated on certain positions of the log, or that some logs were more attractive than others for oviposition leading to a higher probability of competition among larvae for phloem on specific logs. Larval galleries often came within a few millimeters of each other but didn't intersect on white pine and red pine logs in Ontario (Peddle 2000). Intraspecific competition resulted in 60 to 80% mortality in other studies (Belyea 1952, Kobayashi et al. 1984, Rose 1957), much higher values than the 4 to 18% larval mortality we recorded,

but there were more larvae in those studies than this one. Mortality estimates in this study are relatively low, however, because first and second instar competition was not directly measured. Rose (1957) noted that small, early instar galleries often coalesced around branch whorls. Additionally, *M. scutellatus* females preferentially oviposited on logs with no eggs rather than on logs with her own eggs or eggs of other females (Peddle 2002). Females may have perceived occupied phloem and avoided ovipositing in those regions of the log.

Additionally, I attempted to assess the effects of other phloem feeders on *M. scutellatus* oviposition and larval gallery distribution among the top, bottom and sides of the conifer logs. Since some scolytid bark beetles, such as *Tomicus piniperda* and *Ips pini*, and curculionids colonize logs earlier than *M. scutellatus*, they may affect the ovipositional site selection by female *M. scutellatus*, perhaps causing females to partition egg laying differently or to choose less occupied areas of phloem.

Monochamus scutellatus probably reduced the density of scolytid bark beetles or may have inhibited scolytid bark beetle oviposition on red pine and white pine logs through interference competition when individuals were abundant on the logs. Host preference of scolytid bark beetles for certain pines or spruce increased the probability of interference competition with *M. scutellatus* larvae. Gallery interceptions among *M. scutellatus* and Scolytidae occurred more often on the sides of logs. When interferences were found for species that consume phloem concurrently with *M. scutellatus* larvae, bark beetle feeding would be altered as was the case for *Dendroctonus frontalis* by foraging *M. titillator* (Coulson et al. 1976, 1980, Miller 1985). Scolytid bark beetles were most prevalent on white spruce and white pine and we saw more of these

interceptions on white pine, the favored host of *M. scutellatus*. Additionally, negative correlations between *M. scutellatus* and bark beetle feeding suggest bark beetle feeding is influenced by the presence of *M. scutellatus*. In the absence of *M. scutellatus* larvae, scolytid phloem consumption per log was greater. In the presence of *M. scutellatus*, we found that scolytid bark beetle phloem consumption was generally greater on the tops and the bottom of logs. Since *M. scutellatus* galleries were found most often on the sides of the logs, and scolytid bark beetles preferentially colonize sides of the logs (Haack and Lawrence 1995a), scolytid larval feeding was likely deleteriously affected if larvae actively fed at the same time as *M. scutellatus* larvae.

Monochamus scutellatus probably reduced the density of curculionids. Gallery interceptions did not occur as often as with scolytid bark beetles. However, Curculionids feeding was greater on the bottom of logs, with or without *M. scutellatus*. More *M. scutellatus* feeding occurred on the side regions of logs, thereby indicating that these phloem feeders partitioned themselves on the log. Weevils were found more often on pine logs than on spruce in our study and there were more interceptions on white pine. *Pissodes approximatus* pupal cells were found most often on the cool, moist bottom region of white and red pine logs in Canada (Peddle 2000, Phillips et al. 1987).

It is unlikely that *M. scutellatus* females avoid other phloem feeders when locating host material, but locating unoccupied phloem for oviposition is probably more important to females. It is likely that *M. scutellatus* will intercept galleries of other phloem feeders if they are abundant on the log. *Monochamus scutellatus* used bark beetle pheromones as kairomones to locate hosts in British Columbia (Allison et al. 2001), suggesting that *M. scutellatus* employs a competitive strategy for utilizing phloem.

However, the tendency of greater *M. scutellatus* larval feeding on sides of logs, compared to weevil feeding on log bottoms indicates some partitioning. Progeny of *I. pini* may suffer increased mortality because they have three generations a year and *M. scutellatus* larvae are feeding in phloem for much of the second and third generations of *I. pini*. Scolytid bark beetles may employ a strategy of occupying as many regions of the log as possible thereby combating *M. scutellatus* induced mortality. *Pissodes approximatus* were pupating at the time of Batch-1 log dissections and so populations were likely reduced by *M. scutellatus* foraging. Future field studies addressing intra and inter-specific competition should involve the removal of logs in smaller batches every week or two after the first *M. scutellatus* females have been observed in study areas to count the number of egg niches, eggs and egg placement on logs just after hatch.

Table 2.1. Characteristics of jack pine, red pine, Norway spruce and white spruce compartments, and the number and size of logs of jack pine, red pine, white pine, and white spruce set out in each compartment May 2001 at W.K. Kellogg Experimental Forest, Kalamazoo, MI used to assess host preference of *M. scutellatus*. Comparisons among conifers are made across columns.

	Jack Pine	Red Pine	Norway Spruce	White Spruce
Compartment				
Size (ha)	0.3	2.8	0.4	0.4
Site Index	52	51	56	52
Age	50	65	61	61
Basal Area	110	175	155	160
Number of logs per species				
Jack pine	54	56	44	62
Red pine	73	59	73	90
White pine	63	62	49	53
White spruce	52	45	65	46
Mean log diam. (cm)				
Jack pine	16.5 ± 1.08	15.9 ± 0.55	13.5 ± 0.52	14.6 ± 0.41
Red pine	15.2 ± 0.45	16.0 ± 0.57	15.0 ± 0.36	16.1 ± 0.34
White pine	14.0 ± 0.32	14.4 ± 0.43	16.0 ± 0.64	13.9 ± 0.42
White spruce	11.7 ± 0.50	14.1 ± 0.50	14.0 ± 0.45	13.1 ± 0.40
Mean log length (cm)				
Jack pine	40.6 ± 0.32	40.3 ± 0.14	40.6 ± 0.26	40.0 ± 0.27
Red pine	40.9 ± 0.28	40.5 ± 0.20	41.2 ± 0.25	40.6 ± 0.15
White pine	40.1 ± 0.18	40.4 ± 0.17	40.4 ± 0.18	40.2 ± 0.14
White spruce	40.2 ± 0.13	40.2 ± 0.18	39.2 ± 0.26	39.6 ± 0.45
Mean outer bark thickness (cm) of logs				
Jack pine	0.3 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.01
Red pine	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.01	0.2 ± 0.01
White pine	0.2 ± 0.01	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02
White spruce	0.2 ± 0.01	0.3 ± 0.02	0.2 ± 0.01	0.2 ± 0.01

Table 2.2. Mean ($\pm$ SEM) number of *M. scutellatus* galleries per log for colonized logs only, area of phloem consumed per log (cm^2), number of entrance holes into the sapwood, and the percentage of larvae that died before entering the sapwood for Batch 1 September to December 2001. These variables along with mean ($\pm$ SEM) number of exit holes and total survival are also shown for Batch 2 logs dissected in June to July 2002. Significant differences among log species (rows) are indicated by different letters after the value.

	Jack Pine	Red Pine	White Pine	White spruce	P value
Host Preference					
No. logs	181	243	202	184	
No. logs colonized by <i>M. scutellatus</i>	116	163	140	139	
No. galleries	3.0 $\pm$ 0.19 b	3.7 $\pm$ 0.23 b	4.6 $\pm$ 0.29 a	4.9 $\pm$ 0.39 a	0.001
Host Suitability					
Batch 1 logs					
No. logs	55	76	54	51	
Area phloem per log (cm^2)	131.2 $\pm$ 15.80 a	150.2 $\pm$ 14.04 a	174.0 $\pm$ 19.41 a	143.5 $\pm$ 21.06 a	0.254
Area phloem consumed per gallery (cm^2) ³	36.7 $\pm$ 3.80 a	46.8 $\pm$ 7.1 a	34.5 $\pm$ 2.42 a	28.8 $\pm$ 1.9 a	0.300
No. entrance holes	2.2 $\pm$ 0.28 a	3.5 $\pm$ 0.35 a	4.4 $\pm$ 0.46 a	4.6 $\pm$ 0.69 a	0.205
Early instar survival (%) ¹	86.7 $\pm$ 3.40 a	83.9 $\pm$ 3.23 a	83.8 $\pm$ 3.84 a	81.5 $\pm$ 4.23 a	0.795
Batch 2 logs					
No. logs	61	88	86	88	
Area phloem per log (cm^2) ³	120.3 $\pm$ 28.01 a	199.5 $\pm$ 37.26 a	245.1 $\pm$ 35.54 a	194.1 $\pm$ 40.41 a	0.173
Area phloem consumed per gallery (cm^2) ³	51.4 $\pm$ 11.79 ab	64.4 $\pm$ 8.25 a	54.2 $\pm$ 5.80 a	35.5 $\pm$ 5.71 b	0.006
No. entrance holes	2.3 $\pm$ 0.35 a	3.1 $\pm$ 0.56 a	4.4 $\pm$ 0.79 a	5.4 $\pm$ 0.97 a	0.082
No. exit holes	1.0 $\pm$ 0.15 a	1.4 $\pm$ 0.18 a	1.5 $\pm$ 0.19 a	1.3 $\pm$ 0.19 a	0.177
No. gallery interceptions	0.2 $\pm$ 0.07 a	0.6 $\pm$ 0.17 a	0.7 $\pm$ 0.18 a	0.6 $\pm$ 0.15 a	0.155
Early instar survival (%) ¹	93.0 $\pm$ 2.94 a	96.8 $\pm$ 1.42 a	94.3 $\pm$ 2.15 a	96.0 $\pm$ 1.6 a	0.752
Total survival (%) ²	41.2 $\pm$ 5.47 a	44.1 $\pm$ 4.34 a	37.7 $\pm$ 3.18 a	26.4 $\pm$ 3.40 b	0.040

¹ Percentage early instar survival reflects the proportion of galleries with no entrance hole into the sapwood and no live larva.

² Percentage total survival reflects the number of exit holes per log divided by the total number of galleries per log.

³ A total of 36 logs per species were used to quantify the area of phloem per gallery.

Table 2.3. Number of adult *M. scutellatus* progeny and mean weight (g) ($\pm$ SEM) of beetles that emerged summer 2002 from all jack pine, red pine, white pine, and white spruce Batch-2 logs. Logs were colonized summer 2001 at W.K. Kellogg Experimental Forest. Significant differences among log species (within rows) are indicated by different letters after the value.

	Jack pine	Red pine	White pine	White spruce	P value
No. logs colonized	116	162	138	139	
No. logs with F ₁ adults	34	65	57	57	
Total no. logs beetles	61	123	123	100	
Weight (g)	0.27 $\pm$ 0.01 b	0.33 $\pm$ 0.01 a	0.31 $\pm$ 0.01 a	0.20 $\pm$ 0.01 c	0.0001
No. females	25	65	72	55	
No. males	35	58	51	45	
Weight of females (g)	0.27 $\pm$ 0.02 b	0.31 $\pm$ 0.01 a	0.31 $\pm$ 0.01 a	0.19 $\pm$ 0.01 c	0.0001
Weight of males (g)	0.27 $\pm$ 0.02 b	0.35 $\pm$ 0.01 a	0.31 $\pm$ 0.02 a	0.19 $\pm$ 0.01 c	0.0001

Table 2.4. Mean number of *M. scutellatus* gallery interceptions, *M. scutellatus* and scolytid bark beetle gallery interceptions and *M. scutellatus* and curculionid gallery interceptions on Batch 1 logs. Only logs with at least one interception were used in analyses. Significant differences among log species (within rows) are indicated by different letters after the value.

	Jack pine	Red pine	White pine	White spruce	P value
Batch 1 logs					
No. <i>M. scutellatus</i> / <i>M. scutellatus</i>	1.6 ± 0.27a 10	3.7 ± 1.27 a 19	2.7 ± 0.33 a 26	5.2 ± 1.49 a 16	0.368
No. <i>M. scutellatus</i> / Scolytidae	4.1 ± .63 b 34	3.2 ± 0.36 b 51	5.1 ± 0.6 b 43	6.4 ± 0.71 a 44	0.008
No. <i>M. scutellatus</i> / Curculionidae	3.5 ± 0.55 b 23	2.8 ± 0.38 b 44	5.4 ± 0.84 a 34	3.3 ± 1.94 b 6	0.019
Batch 2 logs					
No. <i>M. scutellatus</i> / <i>M. scutellatus</i>	0.1 ± 0.06 a 1	1.1 ± 0.43 a 9	1.1 ± 0.48 a 7	1.7 ± 0.75 a 8	0.352
No. <i>M. scutellatus</i> / Scolytidae	2.3 ± 0.33 b 3	2.7 ± 0.56 b 6	2.3 ± 0.42 b 16	5.6 ± 0.91 a 19	0.008
No. <i>M. scutellatus</i> / Curculionidae	3.8 ± 0.72 a 9	6.9 ± 1.44 a 18	4.9 ± 0.81a 18	1.0 ± 0 b 5	0.004

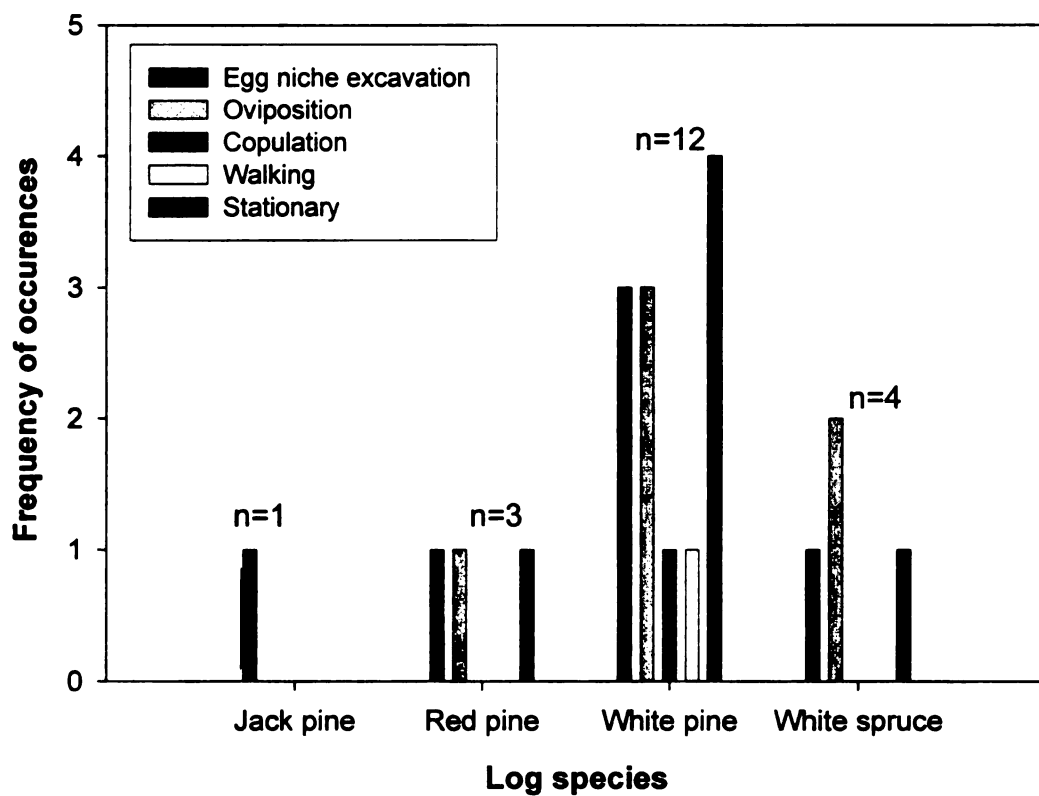


Figure 2.1. Frequency of behaviors associated with female *M. scutellatus* host selection observed at Kellogg Forest from May 22 to August 14, 2001 between 10 a.m. to 6 p.m.

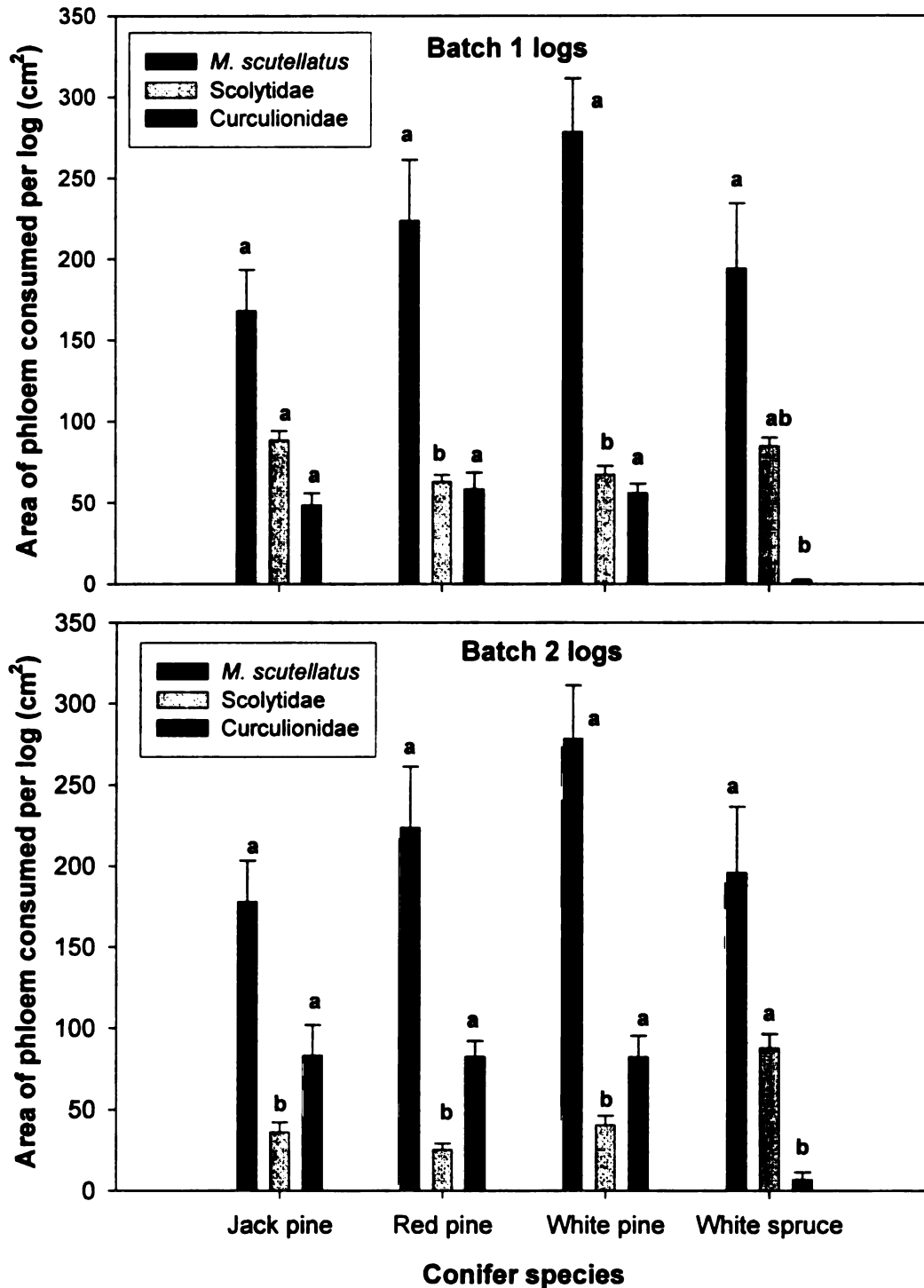


Figure 2.2. Mean area of phloem ($\pm$ SEM) consumed by *M. scutellatus*, scolytid bark beetles, and curculid weevils on Batch 1 logs that were dissected in October to December, 2001 and Batch 2 logs that were dissected in June and July, 2002. Only logs with *M. scutellatus* galleries were used in analyses. Batch 1 included 55, 76, 54, and 51 for jack pine, red pine, white pine and white spruce logs. Batch 2 included 17, 24, 22, and 25 Jack pine, red pine, white pine, and white spruce logs, respectively, in analyses. Significant differences among log species are indicated by different letters above columns for each type of phloem feeder.

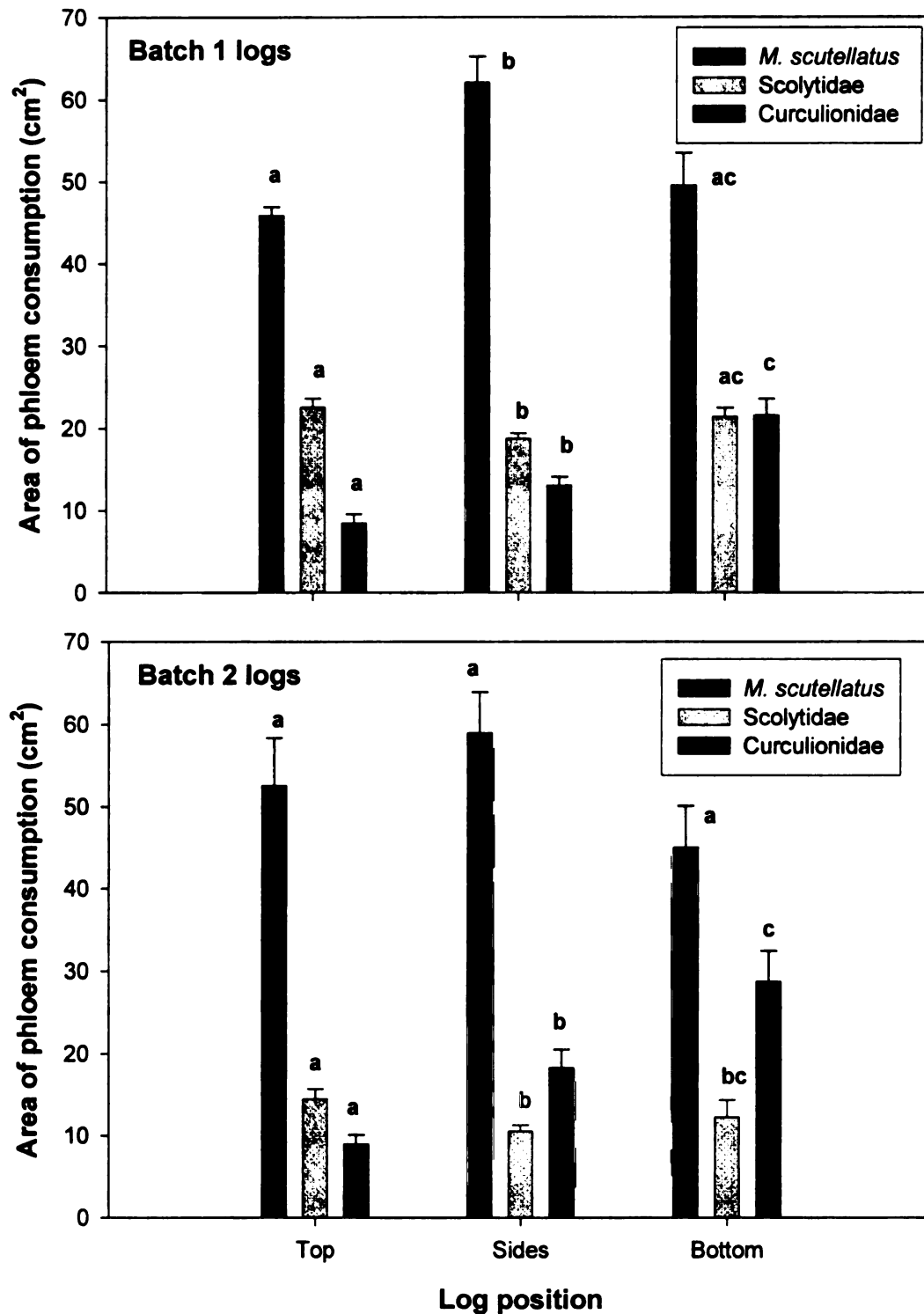


Figure 2.3. Mean area of phloem consumed by *M. scutellatus* larvae, scolytid bark beetles, and weevils on the top, sides, and bottom of logs. Batch-1 logs were dissected September to December 2001 and Batch-2 logs were dissected summer 2002. Significant differences among log species are indicated by different letters above the column for each type of phloem feeder.

CHAPTER 3

Effects Of Host Preference On Larval Performance Of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae)

INTRODUCTION

Understanding the relationship between adult host preference and relative performance of offspring is essential to assess the evolution of host plant associations in herbivorous insects (Futuyma and Peterson 1985, Thompson 1988). Presumably, adult females confronted with a variety of potential host plants should choose the host that will maximize larval fitness. However, in some populations of insects, host preference of ovipositing females does not always correlate with larval survival or successful development (Thompson 1988). Poor correspondence between ovipositional preference and offspring performance may indicate that factors such as host abundance (Williams 1983), predation rates on larvae (Denno and Larsson 1990), and intraspecific competition (Anbutsu and Togashi 1997, Hanks et al 1993) influence larval fitness.

Oviposition choices by adult female wood-borers are critical for offspring survival because larvae cannot disperse to alternate or more adequate hosts (Hanks et al. 1993). Additionally, hosts of wood-boring beetles are often patchily distributed within the forest resource (Haack and Slansky 1987) and beetles must largely rely on chemical communication to detect by potential hosts.

The white-spotted sawyer, *Monochamously scutellatus* (Say) (Coleoptera: Cerambycidae), is a common insect in conifer forests throughout Michigan (Parmalee 1941), and much of the northern U.S. and Canada (Rose 1957). Adults are thought to be polyphagous and larvae of *M. scutellatus* can develop in a wide range of conifer hosts, including pine (*Pinus spp.*), spruce (*Picea spp.*), balsam fir (*Abies balsamea*), Douglas-fir (*Pseudotsuga mensiesii*) and eastern larch (*Larix laricina*). Tunnels excavated by *M. scutellatus* larvae contribute to decomposition and nutrient cycling, but can also damage logs that would otherwise be salvaged (Cerezcke 1975, Edmonds and Eglitis 1989, Post and Werner 1988, Rose 1957).

The life history of *M. scutellatus* has been studied by numerous researchers (Belyea 1952, Chenier and Philogene 1989, Dyer and Seabrook 1978, Hanks 1999, Hughes and Hughes 1982, Hughes and Hughes 1985, Rose 1957). After emergence, adult *M. scutellatus* females require a 3-7 day period of maturation feeding on conifer hosts before eggs mature (Rose 1957). Adults of *M. alternatus* Hope are the only species of *Monochamus* known to produce pheromones to locate hosts (Kim et al. 1992), and *M. scutellatus* adults are thought to rely on olfactory detection of host volatiles and individual tree characteristics to locate hosts (Dyer and Seabrook 1978). *Monochamus scutellatus* employs a resource-defense polygyny mating system whereby males compete for access to the regions of the trees or logs that are most attractive to females (Hughes and Hughes 1982, Hughes and Hughes 1985). Adult beetles typically colonize stressed or dying trees and recently cut or fallen logs from late May through early August in Michigan (Dyer and Seabrook 1978). Male and female adults arrive on the potential host and may be observed persistently palpitating the host surface as they walk (Hughes and

Hughes 1985, Peddle 2000). After mating, females cut egg niches into the bark often near old branch stubs or around branch whorls (Hughes and Hughes 1985, Peddle 2000, Rose 1957). Eggs hatch within two weeks and larvae begin tunneling in the cambium and phloem (Rose 1957). After two to three weeks, larval galleries are wide enough and deep enough to score the sapwood. By late summer, larval tunnels extend deeply into the sapwood, where larvae overwinter. Feeding resumes the following spring and in Michigan, most beetles complete development and emerge in the summer. Interspecific competition and cannibalism may be an important source of mortality for *M. scutellatus* and for other insects that utilize phloem (Peddle 2000, Rose 1957).

Studies of preference versus performance for polyphagous cerambycid species and species that utilize dead or dying woody hosts are rare and mainly focus on either adult preference or larval performance, but not both. Host preference studies for wood-borers are usually limited to counting the number of egg niches (Walsh and Linit 1985) or eggs (Donley 1978) found on logs in adult choice tests. *Monochamus carolinensis* was shown to prefer feeding on Scotch pine (*Pinus sylvestris* L.) and jack pine (*Pinus banksiana* Lamb.) in the lab (Walsh and Linit 1984) and *M. alternatus* consistently chose *Pinus elliottii* Engelm. over *Pinus densiflora* Sieb. and Zucc. during choice tests (Kobayashi et al 1984). A recent study of host preference of *M. scutellatus* found more egg niches on white pine than on red pine logs (Peddle 2000). Studies comparing larval performance of woodborers among multiple hosts have typically assessed only differences in larval density (Hanks et al. 1993), abundance of galleries and late-instar mortality (Kobayashi et al 1984). Other studies of *M. scutellatus* focused on oviposition

behavior, host quality, fecundity, and survival rates but were restricted to only a single conifer species (Cerezke 1977, Dyer and Seabrook 1978, Peddle 2000 and Rose 1957).

Hopkin's host-selection principle refers to the adaptation of insects to their host plants or the idea that variation in host plant selection can be found (Craighead 1921).

Larval conditioning is an idea based upon Hopkin's host-selection principle and refers to the idea that many adult insects prefer host species on which they themselves developed as larvae (Barron 2001, Craighead 1921). Craighead (1921) concluded that a conditioning response of larvae to hosts over several generations was common for most species of cerambycidae. Larval conditioning did not occur after one generation when *M. carolinensis* was reared on Scotch pine (Walsh and Linit 1984). Futuyma and Peterson (1985) concluded that there is little or no evidence for larval conditioning in phytophagous insects. However, it is not known for certain whether conditioning affects host selection by adult *M. scutellatus*.

In this study I evaluated whether ovipositing adult females consistently preferred one conifer over another in two-choice tests. I evaluated potential differences in suitability for *M. scutellatus* larval development. I assessed whether larval conditioning affects host selection by adult females. I also evaluated whether the host preference of ovipositing adult females is consistent with suitability for larval development. Jack pine, red pine, white pine and white spruce were selected as potential hosts in this study because they are native conifers within the host range of *M. scutellatus* and their attractiveness and suitability for *M. scutellatus* is unknown, with respect to each other.

METHODS AND MATERIALS

In 2001, preliminary host choice tests were conducted to develop methodologies for 2002 tests at the Tree Research Center, MSU campus. We collected newly emerged *M. scutellatus* beetles from a one-year old Norway spruce (*Picea abies*) log deck at Michigan State University's W.K. Kellogg Forest (Kalamazoo Co., MI) and gave them in a choice of two conifer species in 1.8 m high x 3.7 m long x 1.8 m wide, tents made of 1 mm Lumite amber screen (Synthetic Industries, Inc., Gainesville, GA). In each tent we placed two logs, 45.7 cm (18 in) long, of each test species (four logs total) and 1 to 6 pairs of sawyers. The number of *M. scutellatus* added to each tent depended on the number of beetles collected from the log deck at Kellogg Forest the previous day. Black cherry (*Prunus serotina*), red pine (*Pinus rubra*), white pine (*Pinus alba*), jack pine (*Pinus banksiana*) and white spruce logs (*Picea glauca*) were cut to 46 cm (18 in) lengths from trees felled at Kellogg Forest biweekly, beginning 15 May, 2001. Two logs were placed 1 m from the other two logs, and 1 m from each other in the middle of the tent.

Two-choice tests were conducted during 2002 to assess host preference of four conifer species. Prior to the choice tests in 2002, jack pine, red pine, white pine, and white spruce logs from 2001 field study were brought into the lab to rear out adult sawyers in batches of 100 to 150 at a time. Adult sawyers were provided with fresh Scotch pine shoots in water-filled 2 dram glass vials for maturation feeding and were placed in 21°C environmental, Michigan State University campus.

Adult *M. scutellatus* began to emerge on 1 April, 2002 and progeny were collected twice daily until emergence ceased. Newly emerged beetles were weighed, assigned an identification number and placed in a 1.9 L (2 qt) plastic container with

screening covering the lid. Every time a new adult *M. scutellatus* emerged its corresponding exit hole was located and the identity of the log it emerged from was recorded. Scotch pine was cut from trees on the Michigan State University campus. Logs of jack pine, red pine, white pine, and white spruce were cut in March 2002 to 38 cm (15 in) lengths at Kellogg Forest, and transported to the Michigan State University campus, East Lansing, and logs were stored outdoors in three 2.43 x 4.87 m (8 x 16 ft) screen tents placed in the shade to exclude other phloem feeding insects.

Three-day, two-choice host tests were conducted to assess oviposition preferences of females. We placed sixteen 1 m³ Lumite screen tents 20 meters apart from each other in a zigzag pattern in a field at the Tree Research Center, Michigan State University campus. Jack pine, red pine, white pine and white spruce shoots were collected from nearby trees. A total of two logs, each a different conifer species, was placed in each tent along with a previously unmated pair of beetles reared from logs used in 2001 field study. Beetle ages ranged from 7 to 24 days post emergence. To assess whether the larval host affects host preference of adult *M. scutellatus* we placed one log of the larval host species in one corner of the tent and a log of a different conifer species in the opposite corner. One shoot, with the current and last years growth, of the conifers being tested was placed in a water pic and placed each on top of the corresponding log species. Beetles were left undisturbed for 3 days, then we collected the logs and the beetles from each tent and returned them to the laboratory.

The number of egg niches on each log was counted immediately after each 3-day choice test was completed. We measured the diameter, length and bark thickness of each log and stored them in the lab. Mean log diameter ranged from 14.6 cm (jack pine) to

16.8 cm (red pine) (Table 3.1). Thirty days after the logs were removed from the tents we removed the bark of each log to quantify the number of eggs and larvae on each log. Each larva was weighed and body length was measured with calipers.

Female oviposition preferences was assessed by determining the mean number of egg niches and eggs laid by each female during the 3-day trial, and the number of larvae and galleries per log. Eggs, larvae and galleries were counted during bark dissections. Host suitability for larval development was assessed based on the weight and length of larvae, the length and width of larval galleries, the number of entrance hole per log and percentage survival. Differences in larval growth rate were estimated by comparing the larval weight and the number of entrance holes into the sapwood after 30 days of development, since it is typically the third instar that begins to tunnel in sapwood. Percentage survival was assessed by counting the number of live larvae/number of dead eggs and larvae.

Statistical analyses.

All variables were tested for normality with the Shapiro-Wilk test (Shapiro and Wilk 1965). When we pooled the data by log species for the 3-day host preference and host suitability trials, the number of egg niches, eggs, galleries, larvae, entrance holes, gallery width, gallery length, and percent survival for 3-day tests were not normal even after transformations. These variables were analyzed using the Nonparametric Rank F test, and the Nonparametric Rank F test mean comparison procedure was used to determine which treatment pairs were significantly different (Neter et al. 1996). Larval weight and length were normalized by square-root transformations and were analyzed using ANOVA to see if it differed among conifers. Variables associated with host

preference (the number of egg niches, eggs, larvae, and galleries) were analyzed for all conifer species combinations using 2-sided T-tests or the Mann-Whitney test when data was not normally distributed (Zar 1984). Variables associated with host suitability (larval weight, larval length, gallery length, gallery width, and percentage survival) were analyzed for all conifer species combinations using 2-sided T-tests or the Mann-Whitney test when data were not normally distributed.

For the larval conditioning trials, the number of egg niches and eggs in each conifer species combination were analyzed using a 2-sided T-test when normally distributed and the nonparametric Mann-Whitney test when variables were not normal even after transformation (Zar 1984). Results of the Mann-Whitney test were consistent with the T-test results in all cases.

Spearman's Rank correlation test was used to test for associations between number of egg niches, number of eggs, number of larvae, and number of galleries (host preference variables) and larval weight, larval length, and percentage survival (larval performance variables) for each conifer species. Spearman's Rank correlation test was also used to test for associations between log diameter, bark thickness and the number of egg niches, number of eggs, number of larvae, and number of galleries (host preference variables) and larval weight, larval length, and percentage survival (larval performance variables). All analyses were conducted at $P < 0.05$ level of significance, using SAS statistical software (SAS Institute, Inc. 1989).

RESULTS

Host Preference

Adult *M. scutellatus* preferred white pine and white spruce during the choice tests. All the logs of each species were pooled across all conifer paired-combinations to test for differences in the number of egg niches, eggs, larvae, and galleries (Table 3.2). Female adults excavated significantly more egg niches and laid more eggs on white pine than on the other conifers (Table 3.2). Females preferred to excavate niches on red pine and white spruce over jack pine. Jack pine logs were the least preferred species. More than twice as many egg niches were found on white pine than on jack pine and significantly fewer eggs were laid on jack pine than on the other log species. Significantly more larvae were recovered from white pine and red pine than from jack pine and white spruce. The number of galleries were similar on red pine and white pine logs, but the number of galleries on red pine was not significantly different from jack pine and white spruce. Galleries were longer but not wider on red pine than on the other four conifers. Galleries on white spruce were about half the size of galleries on the other species.

Female rank order of host preference was white pine, white spruce and red pine, and jack pine for oviposition conifer paired-comparisons of four conifers to test for host preferences. Table 3.3 shows results of 2-choice tests conducted to rank female preferences between two conifers. White pine logs always had the most egg niches, eggs, larvae and larval galleries, even though the number of eggs and egg niches wasn't significantly different from white spruce. Female *M. scutellatus* excavated almost twice as many egg niches on white pine when paired with either red pine or jack pine than with

white spruce and twice as many larvae were recovered on white pine than on the other pines. Females excavated significantly more niches, laid more eggs and more larvae were recovered on red pine than on jack pine and about the same number of egg niches, eggs, larvae and galleries were on white spruce. Jack pine always had the lowest number of egg niches, eggs, larvae and galleries for all species combinations.

Host Suitability

Pooled variables measuring suitability for larval development yielded varying results (Table 3.2). Overall, red pine and white pine were most suitable for *M. scutellatus* larval development. Larvae found in red pine logs weighed at least twice as much and were significantly longer than those found in the other conifers. Larvae developing on red pine consistently weighed significantly more and were longer, however, than larvae that developed on white pine logs. Larval galleries were longer on red pine than on white pine logs, but gallery widths were not significantly different. Growth rate, assessed by larval weight and number of entrance holes after 30 days of development, was different for larvae on red and white pine logs because larvae on red pine were twice the size of larvae on white pine. Larvae developing in white spruce logs weighed significantly less and were smaller than those found in all the other conifers. Larvae found in white spruce were actually only first or second instars possibly experiencing a delay in hatch. When red pine and white pine logs were dissected most of the larvae were third instars, and larvae of earlier instars were rarely encountered. When found, first and second instar larvae were always on logs with multiple galleries and with other third instar larvae still feeding on phloem. Significantly more entrance holes into the sapwood were found on red pine and white pine logs than on jack pine and white pine, suggesting that larvae

grew faster on red and white pine. Early instar survival was not significantly different among the four conifers, but survival was poorest on jack pine logs.

Results from the six different conifer paired-combinations revealed similar patterns in larval performance on the pines and spruce (Table 3.3). There was no significant difference in gallery length and width and early instar survival between jack pine and red pine logs (Table 3.3). However, *M. scutellatus* larvae grew larger, weighed more and were longer when they developed on red pine logs compared with jack pine logs. They also developed faster; they were larger and more larvae excavated tunnels into the sapwood after 30 days on red pine logs than on jack pine logs.

Again, suitability of white pine and jack pine logs for *M. scutellatus* development varied depending on the variable considered (Table 3.3). Significantly more entrance holes into the sapwood were on white pine logs than jack pine logs. No significant differences in larval weight, length, or gallery length and width were found between white pine and jack pine logs.

No significant differences in number of entrance holes into the sapwood, or percentage of survival were found between jack pine and white spruce logs (Table 3.3). However, larvae from jack pine logs weighed more and were longer than larvae reared from white spruce logs. Larvae consistently consumed more phloem on jack pine than on white spruce logs in 30 days.

Larvae weighed significantly more and their body was longer when they developed on red pine than on white pine (Table 3.3). Significantly more larvae survived on white pine than on red pine, even though they were smaller in body size. There were about the same number of entrance holes into the sapwood after 30 days on red pine and

white pine. The smaller size of larvae developing on white pine didn't likely affect their ability to tunnel into the sapwood at the same rate as larvae on red pine.

Red pine was considered more suitable than white spruce logs because larvae that developed on white spruce were only a small fraction of the size of those that developed on red pine (Table 3.3). Larvae consumed less than half as much phloem on white spruce logs than on red pine logs and they excavated significantly more entrance holes on red pine, which makes sense because larvae were much larger on red pine. Larvae on white spruce logs experienced significantly greater survival on logs in the red pine and white spruce combinations than for other combinations for some reason.

When white pine and white spruce log combination was tested, no differences in the numbers of recovered larvae, larval weight or mortality were found (Table 3.3). However, larvae grew longer when they developed on white pine than on white spruce and they consumed significantly more phloem on white pine logs. Additionally, larvae developed faster on white pine logs because significantly more entrance holes were found after 30 days.

Results of correlation tests comparing associations between variables related to host preference and larval performance differed depending on the indices that were tested. For jack pine, egg niches ($P < 0.01$, $R = 0.47$), eggs ($P < 0.001$, $R = 0.60$), larvae ($P < 0.001$, $R = 0.60$) and galleries ($P < 0.012$, $R = 0.59$) were correlated to the number of entrance holes. There were no significant correlations between variables that measure host preference and host suitability on white spruce. For red pine, the number of egg niches ($P < 0.001$, $R = 0.59$) eggs ($P < 0.001$, $R = 0.73$), larvae ($P < 0.001$, $R = 0.80$) and galleries ($P < 0.001$, $R = 0.81$) were correlated to the number of entrance holes. For white

pine, egg niches were correlated to larval weight ($P<0.04$, $R=0.43$) and length ($P<0.03$, $R=0.45$) and number of entrance holes ($P<0.01$, $R=0.36$). Additionally, the number of eggs ($P<0.001$, $R=0.58$), larvae ($P<0.001$, $R=0.54$), and galleries ($P<0.002$, $R=0.54$) were correlated to the number of entrance holes. Correlations between the four estimates of host preference (number of egg niches, eggs, larvae, and galleries) and the two important indicators of larval performance, larval weight and percentage larval survival, were not significant for any of the conifer species.

Figure 3.1 provides a summary of the relationship between adult female *M. scutellatus* host preference and larval performance on the four conifers. The preference and performance of *M. scutellatus* was rated as strong, medium and poor for each of the conifers. White pine was highly preferred for oviposition and for larval development. Red pine was not preferred as much as white pine, but was a highly suitable host for larval development. Jack pine was not preferred for oviposition and was rated as a medium host for larval development. Females showed a strong oviposition preference for white spruce, but it was a poor host for larval development.

Results of correlation tests comparing associations between variables related to log characteristics and variables related to host preference and larval performance were similar. Log diameter, bark thickness were not correlated to the number of egg niches, eggs, larvae, or galleries. Log diameter and bark thickness were also not correlated to the variables used to estimate larval performance: larval weight, larval length, number of entrance holes, percentage survival or area of phloem consumed.

Larval conditioning

Females that were given only their larval host for oviposition over the 3-day test layed a similar number of eggs over the 3-day test as for females given two logs to choose between. Table 3.4 shows results of no choice tests to assess the effects of larval conditioning on host preferences. As expected, the number of egg niches, eggs, and the number of galleries did not differ significantly among red pine, white pine and white spruce (Table 3.4). Jack pine could not be included in the statistical analysis because of issues with healthy female availability. The control tests demonstrated that females reared in red pine, white pine, and white spruce found their larval host acceptable for oviposition.

Larval conditioning does not appear to influence female *M. scutellatus* host preference (Table 3.5). On average, females excavated 25.3 egg niches and laid 7 eggs during the 3 day trials. The number of egg niches excavated by females, eggs laid and number of galleries was lower for the jack pine versus white spruce combinations than for any other jack pine combination. A higher percentage of egg niches, out of the total excavated during the 3-day test, was consistently on the alternate host paired with jack pine when we tested for conditioning effects of females that developed in jack pine. Females that developed on jack pine also laid a significantly higher percentage of eggs on the alternate host, white spruce. However, there were no differences in the percentage of eggs laid, or in number of galleries between jack pine and red pine combinations and jack pine and white pine combinations (Table 3.5).

Female *M. scutellatus* reared from red pine logs did not show a consistent oviposition preference for red pine logs (Table 3.5). Females reared in red pine

excavated 31 egg niches and laid 10 eggs on average during 3 days. Females excavated 60% of the egg niches on red pine and 40% on jack pine, but females preferred to excavate niches on white pine and white spruce over red pine, excavating about 60% of the niches on these conifers. However, females laid twice as many eggs and twice as many galleries were found on white pine than on red pine logs ($P < 0.05$).

Females that were reared on white pine logs excavated 32.5 niches and laid 12 eggs on average over the 3-day test period (Table 3.5). Females from white pine logs excavated two-thirds of the total egg niches and laid about two-thirds of her eggs on white pine during white pine versus jack pine combinations (Table 3.5). Similarly, females excavated about 66% of the egg niches and laid two-thirds of her eggs on white pine during white pine versus red pine combinations, and the percentage of niches excavated on logs in other species combinations was similar (Table 3.5).

Females that emerged from white spruce logs excavated 18.9 egg niches and laid 8 eggs on average on the two logs in the tents over a 3-day period. Females did not consistently prefer white spruce over the other conifer species (Table 3.5). There was no significant difference in the percentage of egg niches excavated, eggs laid, or number of galleries found on white spruce and other conifers (Table 3.5).

DISCUSSION

One of the principal questions posed in this thesis is whether *M. scutellatus* females prefer certain hosts when presented with several potentially suitable hosts for oviposition. Thompson (1988) and Via (1986) show that preference is best expressed as the proportion of eggs laid on each of the plant species offered in choice trials, or a hierarchical ordering of species. The results suggest that, in general, *M. scutellatus* females preferred to oviposit on white pine over other conifers. Females equally preferred to oviposit on white spruce and red pine, while jack pine was the least preferred conifer species. More than 50% of the female's total egg niches and eggs over 3 days were consistently on white pine over other species in paired conifer comparisons. More larvae developed on white pine and red pine than on white spruce and jack pine logs. In a related study, females preferred white pine and white spruce for oviposition in the field (Lazarus and McCullough, in preparation). In another study in Ontario *M. scutellatus* excavated more niches and laid more eggs on white pine over red pine (Peddle 2000), again suggesting that females have the ability to rank potentially acceptable host species according to preference.

Another question addressed herein is whether the conifer species tested differed in suitability for larval development. Overall, red pine and white pine were more suitable hosts for *M. scutellatus* larval development than jack pine and white spruce. Characteristics used to estimate larval performance could include survival of immature stages, larval growth rate, pupal mass and the resulting adult fecundity and longevity (Thompson 1988). The number of entrance holes, larval weight, larval length and percentage survival did not consistently indicate larval performance in this study.

White pine was preferred for oviposition, but larvae performed well on red pine also. Larvae that developed on red pine were consistently larger than those from the other conifer species. Similar numbers of larvae developed on red pine and white pine logs, thus differences in larval size could be attributable to either higher nutritional quality of red pine or increased feeding rates by larvae on red pine. Larvae on red pine and white pine appeared to develop faster than larvae on jack pine and white spruce because more entrance holes into the sapwood were found on red pine and on white pine logs. This was another indication that larval growth rate was greater for larvae developing on red pine and white pine than on the other two conifers. Larvae consumed the most phloem on red pine logs, followed by white pine, then jack pine and finally white spruce. Percentage survival was very similar among the conifer species in our study. Other studies have shown that mortality rate is high for first instar larvae (Dyer and Seabrook 1978, Rose 1957). Since logs were debarked after 30 days, most larvae on the pines were second or third instar and we may not have been able to accurately record some of the first instar mortality noted in other studies.

Phloem nutritional quality or different chemical composition between pines and spruce was probably responsible for reduced performance of larvae in white spruce. Larvae were smaller on white spruce than on other conifers. An explanation for the discrepancy in development time and body size is unclear, but is most likely related to a reduced ability to utilize spruce terpenoids or delaying egg hatch, since bark thickness and diameter were not correlated to any of the variables that estimate host preference and larval performance. Monoterpenes and resin acids found in pine and spruce differ, and pine and spruce contain different percentages of monoterpenes such as alpha-pinene,

camphene, beta-pinene, myrcene, carene and limonene in oleoresin (Drew and Pylant 1966, Westfall, 1972). For example, 14 percent of white pine and white spruce oleoresin is made of beta-pinene, but only 4 percent of Scotch pine oleoresin is made of beta-pinene (Westfall 1972). In addition, white pine contains camphene, but white spruce does not (Westfall 1972). Fungal associations (ectosymbiotic fungi) and micro-organisms (endosymbionts) are known to have relationships with xylem-feeding insects, but specific symbiotic associations with *M. scutellatus* that influence phloem quality and suitability of jack pine, red pine, white pine and white spruce are not certain (Chapman 1998).

Indices or characteristics of host preference and host suitability are not always positively correlated and evaluations of host preference may depend on the criteria of interest (Thompson 1988). I tried to determine whether larval performance estimated by survival of the immature stages, and growth rate (larval weight and number of entrance holes) was correlated to adult host preference. Ovipositing females preferred white pine and white spruce over jack pine and red pine, while the suitability of hosts for larval development was not as easy to discern. Larval survival didn't vary among conifers and larvae were largest on red pine and then on white pine. There is a lack of correspondence between *M. scutellatus* female host preference and larval performance since we found no correlations between the indices of host preference and host suitability for any of the conifers in this experiment. Our lack of correspondence between a white pine preference and best performance on red pine larvae, using larval weight and percentage survival as indicators of performance, is puzzling. Ultimately, there was high survival for larvae on all conifer species even if larval growth rate on white spruce was slower. An explanation

for the inconsistencies found here may confer greater fitness to this polyphagous species. The progeny reared on these logs may have been more adapted to Kellogg Forest where females would have access to several conifer species every year, in varying abundance. The lack of correspondence between preference and all of the indicators of performance suggest that *M. scutellatus* females oviposit on some hosts that are moderately adequate for survival, as was found in other studies (Singer 1983, Thompson 1988). Adult females of polyphagous species may benefit by finding numerous hosts attractive for oviposition in situations where host abundance is highly variable from year to year.

Finally, I hypothesized that the larval host species would influence adult host preferences. If a conditioning effect existed there should have been a preference for the larval host no matter what alternate log species was paired with it during the 3-day tests. We did not find this to be the case for any females regardless of whether they were reared in jack pine, red pine, white pine or white spruce. Females reared in jack pine always excavated more niches and laid more eggs on the alternate species. Females reared in red pine logs consistently laid more eggs on the alternate species, while females reared in white spruce logs demonstrated no preference for either white spruce or alternative species. The only exception was for females reared in white pine logs. Here, females did consistently excavate more egg niches and oviposit most frequently on white pine no matter what alternative host was available. This pattern likely reflects a preference of ovipositing females for white pine rather than conditioning effects of the larval host predisposing females to oviposit on white pine. *Monochamus carolinensis*, a congener of *M. scutellatus*, was also not influenced by larval conditioning (Walsh and Linit 1985). Futuyma and Peterson (1985) conclude that the Hopkins host selection principle, or the

idea that larval host influences the adult host preference, does not hold for most phytophagous insects.

In this study, I attempted to understand patterns of host use within a population of *M. scutellatus* studied by investigating the variability of behavior among ovipositing adults and subsequent effects of their host selection on larval performance. Research with butterflies has shown that individuals often oviposit on more than one host species (Singer 1983), thereby showing that variations of preference exist even within the individual. For this population of *M. scutellatus* there was much variability in the preferences of females for the conifers studied. There is also phenotypic variability in growth rates of individuals within a population of *M. scutellatus* depending on the host, and an absence of a host preference-larval performance correlation. It would be interesting to test for phenotypic and genetic variation in other populations of *M. scutellatus* perhaps in other geographic locations to differences in the abundance and diversity of conifer species.

Table 3.1. Mean ($\pm$ SEM) bark thickness (inner+outer bark), diameter, and length of logs used in 2-choice tests of *M. scutellatus* host preference conducted summer 2002.

Variables	Jack pine	Red pine	White pine	White spruce
No. logs	32	49	57	52
Mean bark thickness (cm)	0.3 $\pm$ 0.03	0.5 $\pm$ 0.12	0.2 $\pm$ 0.02	0.3 $\pm$ 0.01
Mean diameter (cm)	14.6 $\pm$ 0.56	15.7 $\pm$ 0.44	15.3 $\pm$ 0.44	16.8 $\pm$ 0.33
Mean length (cm)	41.5 $\pm$ 0.76	41.7 $\pm$ 0.92	40.8 $\pm$ 0.55	40.9 $\pm$ 0.62

Table 3.2. Mean ($\pm$ SEM) of variables associated with *M. scutellatus* host preference and host suitability pooled for Jack pine (n=42), red pine (n=49), white pine (n=57), and white spruce (n=52) logs during 3-day trials in 2002. Significant differences within rows are indicated by different letters after the value. (P<0.05)

	Jack pine	Red pine	White pine	White spruce	P-value
Host preference					
No. egg niches	8.6 $\pm$ 1.29 b	12.8 $\pm$ 1.39 b	20.6 $\pm$ 1.93 a	12.3 $\pm$ 1.37 b	0.0001
No. eggs	2.2 $\pm$ 0.50 c	4.6 $\pm$ 0.67 b	7.5 $\pm$ 0.89 a	4.2 $\pm$ 0.69 b	0.0001
No. galleries	2.3 $\pm$ 0.5 bc	4.6 $\pm$ 0.68 ab	6.8 $\pm$ 0.85 a	4.3 $\pm$ 0.73 b	0.0024
No. larvae	2.1 $\pm$ 0.47 b	4.41 $\pm$ 0.67 a	6.4 $\pm$ 0.82 a	3.9 $\pm$ 0.68 b	0.0008
Host suitability					
Larval length (mm)	21.7 $\pm$ 1.84 b	35.4 $\pm$ 2.34 a	25.1 $\pm$ 1.52 b	10.1 $\pm$ 1.16 c	0.0001
Larval weight (mg)	73.1 $\pm$ 11.7 c	205.3 $\pm$ 15.1 a	104.4 $\pm$ 8.4 b	27.3 $\pm$ 3.25 d	0.0001
Gallery length (cm)	10.8 $\pm$ 1.08 b	15.9 $\pm$ 1.43 a	9.7 $\pm$ 0.82 b	5.4 $\pm$ 0.66 c	0.0011
Gallery width (cm)	6.7 $\pm$ 0.68 a	8.4 $\pm$ 0.90 a	6.5 $\pm$ 0.59 a	3.9 $\pm$ 0.48 b	0.0001
No. entrance holes	0.24 $\pm$ 0.12 b	1.9 $\pm$ 0.44 a	1.9 $\pm$ 0.36 a	0.02 $\pm$ 0.02 b	0.0001
Survival (%)	85.6 $\pm$ 5.82 a	94.0 $\pm$ 2.96 a	90.2 $\pm$ 3.32 a	91.2 $\pm$ 3.40 a	0.4514

Table 3.3. Mean ($\pm$ SEM) of variables associated with host preference and host suitability during 3-day choice tests in 2002. Each female was presented logs of two conifer species. Significant differences between the paired conifer species (in a row) are indicated by different letters after the value. ($P < 0.05$)

	Jack pine vs. Red Pine		Jack pine vs. White pine		Jack Pine vs. White spruce	
Host Preference						
No. egg niches	9.6 $\pm$ 3.03 b	15.9 $\pm$ 2.62 a	6.7 $\pm$ 1.62 b	26.8 $\pm$ 4.63 a	10.0 $\pm$ 2.00 a	12.0 $\pm$ 2.43 a
No. eggs	1.9 $\pm$ 0.62 b	5.1 $\pm$ 1.34 b	2.2 $\pm$ 0.94 b	7.8 $\pm$ 1.72 a	1.7 $\pm$ 0.64 b	3.7 $\pm$ 0.98 a
No. galleries	2.1 $\pm$ 0.70 a	5.1 $\pm$ 1.36 a	2.4 $\pm$ 1.01 b	8.5 $\pm$ 1.63 a	1.8 $\pm$ 0.69 a	4.0 $\pm$ 0.97 a
No. Larvae	1.8 $\pm$ 0.62 a	5.0 $\pm$ 1.33 a	2.2 $\pm$ 0.94 b	7.1 $\pm$ 1.59 a	1.7 $\pm$ 0.64 a	3.7 $\pm$ 0.98 a
Host Suitability						
Larval weight (mg)	75.7 $\pm$ 12.99 b	177.8 $\pm$ 9.02 a	62.7 $\pm$ 15.45 a	100.6 $\pm$ 11.88 a	61.2 $\pm$ 20.27 a	24.4 $\pm$ 2.88 b
Larval length (cm)	23.9 $\pm$ 1.43 b	34.6 $\pm$ 1.20 a	24.6 $\pm$ 1.69 a	26.7 $\pm$ 1.24 a	19.5 $\pm$ 4.12 a	10.9 $\pm$ 1.57 b
Gallery width (cm)	6.2 $\pm$ 1.17 a	9.9 $\pm$ 1.93 a	7.5 $\pm$ 1.43 a	8.3 $\pm$ 1.51 a	6.7 $\pm$ 1.28 a	3.5 $\pm$ 0.73 b
Gallery length (mm)	10.6 $\pm$ 2.44 a	16.5 $\pm$ 2.26 a	11.3 $\pm$ 2.17 a	11.5 $\pm$ 1.66 a	11.3 $\pm$ 1.57 a	5.8 $\pm$ 1.05 b
No. entrance holes	0.0 $\pm$ 0.0 b	2.1 $\pm$ 0.85 a	0.4 $\pm$ 0.29 b	2.5 $\pm$ 0.78 a	0.2 $\pm$ 0.16 a	0.0 $\pm$ 0.0 a
Survival (%)	78.0 $\pm$ 2.72 a	97.1 $\pm$ 1.90 a	93.7 $\pm$ 4.27 a	81.8 $\pm$ 7.58 a	85.6 $\pm$ 9.94 a	89.4 $\pm$ 5.03 a
	Red pine vs. White pine		Red pine vs. White spruce		White pine vs. White spruce	
Host Preference						
No. egg niches	10.7 $\pm$ 2.31 b	23.4 $\pm$ 3.11 a	12.5 $\pm$ 2.30 a	13.7 $\pm$ 2.88 a	14.3 $\pm$ 2.18 a	11.4 $\pm$ 1.98 a
No. eggs	4.2 $\pm$ 1.18 b	9.8 $\pm$ 1.70 a	4.7 $\pm$ 0.99 a	6.1 $\pm$ 1.66 a	5.5 $\pm$ 8.14 a	3.3 $\pm$ 0.88 a
No. galleries	4.1 $\pm$ 1.23 b	7.9 $\pm$ 1.63 a	4.6 $\pm$ 0.98 a	5.4 $\pm$ 1.79 a	4.5 $\pm$ 0.91 a	3.3 $\pm$ 0.78 a
No. larvae	3.9 $\pm$ 1.20 b	7.9 $\pm$ 1.63 a	4.4 $\pm$ 0.97 a	5.3 $\pm$ 1.68 a	3.7 $\pm$.85 a	2.4 $\pm$ 0.66 a
Host Suitability						
Larval weight (mg)	195.4 $\pm$ 34.15 a	123.7 $\pm$ 11.65 b	252.2 $\pm$ 24.60 a	19.8 $\pm$ 6.23 b	64.4 $\pm$ 15.02 a	27.5 $\pm$ 2.78 a
Larval length (mm)	35.9 $\pm$ 3.92 a	28.5 $\pm$ 2.12 b	35.5 $\pm$ 5.40 a	9.3 $\pm$ 1.83 b	15.9 $\pm$ 3.04 a	7.9 $\pm$ 2.00 b
Gallery width (cm)	8.0 $\pm$ 1.49 a	5.7 $\pm$ 0.84 a	7.8 $\pm$ 1.38 a	3.3 $\pm$ 0.87 b	5.9 $\pm$ 0.76 a	4.7 $\pm$ 0.85 a
Gallery length (cm)	17.5 $\pm$ 2.89 a	8.6 $\pm$ 1.44 b	14.4 $\pm$ 2.36 a	4.0 $\pm$ 0.75 b	9.5 $\pm$ 1.24 a	6.0 $\pm$ 1.32 b
No. entrance holes	1.9 $\pm$ 0.73 a	2.6 $\pm$ 0.76 a	1.9 $\pm$ 0.75 a	0.1 $\pm$ 0.06 b	0.9 $\pm$ 0.29 a	0.0 $\pm$ 0.0 b
Survival (%)	88.9 $\pm$ 9.01 b	97.8 $\pm$ 1.21 a	95.8 $\pm$ 2.52 a	98.6 $\pm$ 0.97 a	89.4 $\pm$ 6.54 a	87.4 $\pm$ 7.45 a

Table. 3.4. Mean ($\pm$ SEM) of variables associated with host selection and host suitability during no choice trials to test larval conditioning effects among conifers for adult female *M. scutellatus* host selection. Jack pine (n=1 trial), red pine (n=9 trials), white pine (n=7 trials), and white spruce (n=6 trials) in 2002. Significant differences within rows are indicated by different letters after the value. (P<0.05)

	Jack pine ¹	Red pine	White pine	White spruce	P-value
Host Preference					
No. egg niches	27.0	12.4 $\pm$ 4.13 a	9.9 $\pm$ 3.73 a	8.2 $\pm$ 3.34 a	0.3667
No. eggs	3.0	9.7 $\pm$ 2.96 a	11.1 $\pm$ 2.24 a	7.2 $\pm$ 2.95 a	0.2790
No. galleries	3	8.7 $\pm$ 1.54 a	10.3 $\pm$ 2.36 a	7.0 $\pm$ 3.02 a	0.6107
No. larvae	3.0	9.6 $\pm$ 0.98 a	9.7 $\pm$ 5.93 a	7.0 $\pm$ 3.02 a	0.5498
Host Suitability					
Gallery length (cm)	1.68	1.5 $\pm$ 0.03 a	1.2 $\pm$ 0.07 b	1.0 $\pm$ 0.09 b	0.0150
Gallery width (cm)	0.11	0.5 $\pm$ 0.09 b	0.5 $\pm$ 0.089 b	0.9 $\pm$ 0.46 a	0.0291
Larval length (cm)	13.3	38.0 $\pm$ 1.29 a	26.7 $\pm$ 2.9 b	14.2 $\pm$ 5.99 b	0.0005
Larval weight (mg)	27.5	214.4 $\pm$ 17.46 a	115.4 $\pm$ 23.61 b	76.7 $\pm$ 19.95 b	0.0006
No. entrance holes	1.68	1.5 $\pm$ 0.03 a	1.2 $\pm$ 0.07 a	1.0 $\pm$ 0.09 b	0.0467
Survival (%)	99.8	99.5 $\pm$ 0.09 a	99.5 $\pm$ 0.09 a	99.1 $\pm$ 0.46 a	0.1705

¹Tests for host preference and host suitability of jack pine were not included in statistical analyses because females oviposited on logs during only one replicate.

²The percentage of mortality refers to galleries found without larvae or with dead larvae.

Table 3.5. Mean percentage of egg niches, eggs and number of galleries ($\pm$ SEM) during larval conditioning trials in 2002. Female *M. scutellatus* emerged from jack pine, red pine, white pine, and white spruce logs. Each female was presented logs of 2 conifer species. Significant differences within rows and between each pair of conifer species are indicated by different letters after the value. ($P < 0.05$)

Host Preference	Jack pine ¹ vs. Red pine		Jack pine ¹ vs. White pine		Jack pine ¹ vs. White spruce	
	4		5		3	
No. replicates						
No. egg niches	3.2 $\pm$ 1.44 a	17.0 $\pm$ 5.12 b	9.0 $\pm$ 2.34 a	18.6 $\pm$ 5.78 a	10.0 $\pm$ 5.03 a	18.0 $\pm$ 3.06 a
No. eggs	1.3 $\pm$ 1.25 a	7.0 $\pm$ 2.54 a	2.4 $\pm$ 3.36 a	5.2 $\pm$ 2.42 a	0.3 $\pm$ 0.33 a	5.0 $\pm$ 2.08 b
No. galleries	1.3 $\pm$ 1.25 a	7.0 $\pm$ 2.55 a	1.25 $\pm$ 1.25 a	7.0 $\pm$ 2.55 a	0.3 $\pm$ 0.33 a	2.1 $\pm$ 2.25 a
	Red pine ¹ vs. Jack pine		Red pine ¹ vs. White pine		Red pine ¹ vs. White spruce	
No. replicates	10		9		8	
No. egg niches	15.4 $\pm$ 3.23 a	12.2 $\pm$ 3.98 a	13.3 $\pm$ 3.96 a	24.0 $\pm$ 4.02 a	10.3 $\pm$ 2.71 a	17.9 $\pm$ 4.63 a
No. eggs	0.3 $\pm$ 0.33 a	5.0 $\pm$ 2.08 a	3.6 $\pm$ 10.60 a	9.4 $\pm$ 1.56 b	4.4 $\pm$ 1.41 a	7.1 $\pm$ 2.37 a
No. galleries	4.3 $\pm$ 1.63 a	2.5 $\pm$ 0.86 a	3.3 $\pm$ 1.26 a	6.6 $\pm$ 1.63 b	4.5 $\pm$ 1.48 a	6.1 $\pm$ 2.69 a
	White pine ¹ vs. Jack pine		White pine ¹ vs. Red pine		White pine ¹ vs. White spruce	
No. replicates	10		10		12	
No. egg niches	30.9 $\pm$ 6.09 a	5.5 $\pm$ 2.11 b	22.8 $\pm$ 4.89 a	8.3 $\pm$ 2.53 b	16.7 $\pm$ 3.61 a	13.3 $\pm$ 3.43 a
No. eggs	9.1 $\pm$ 2.24 a	2.1 $\pm$ 1.25 b	10.1 $\pm$ 3.01 a	4.7 $\pm$ 2.02 a	7.0 $\pm$ 1.95 a	3.0 $\pm$ 1.09 a
No. galleries	11.5 $\pm$ 2.16 a	12.3 $\pm$ 2.69 b	9.1 $\pm$ 3.01 a	4.8 $\pm$ 2.08 a	5.8 $\pm$ 1.67 a	3.1 $\pm$ 1.07 a
	White spruce ¹ vs. Jack pine		White spruce ¹ vs. Red pine		White spruce ¹ vs. White pine	
No. replicates	10		8		12	
No. egg niches	10.2 $\pm$ 2.85 a	10.0 $\pm$ 2.28 a	9.5 $\pm$ 3.02 a	14.5 $\pm$ 3.77 a	16.7 $\pm$ 3.61 a	13.3 $\pm$ 3.43 a
No. eggs	3.3 $\pm$ 1.15 a	2.1 $\pm$ 0.81 a	5.1 $\pm$ 2.45 a	5.0 $\pm$ 1.49 a	7.0 $\pm$ 1.95 a	1.1 $\pm$ 2.75 a
No. galleries	3.7 $\pm$ 1.15 a	2.2 $\pm$ 0.88 a	4.8 $\pm$ 2.52 a	4.8 $\pm$ 1.39 a	3.6 $\pm$ 1.17 a	3.4 $\pm$ 1.17 a

¹The larval host of the female *M. scutellatus* used in trials.

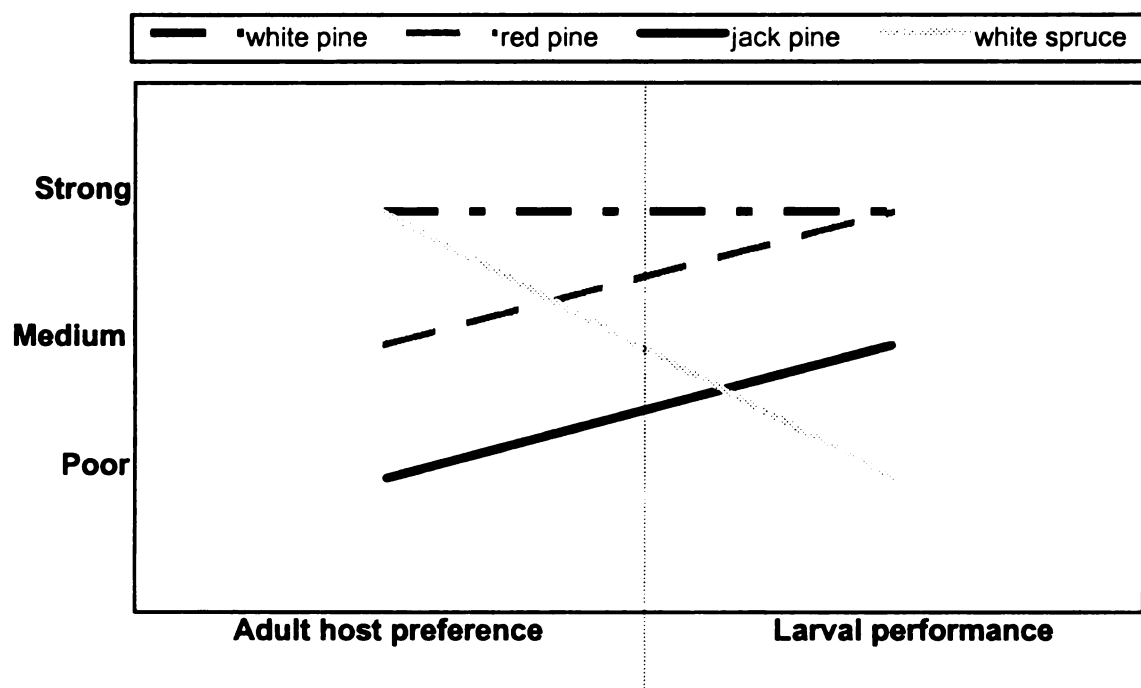


Figure 3.1. A graphic representation of the relationship between adult female *M. scutellatus* host preference and larval performance on white pine, red pine, jack pine, and white spruce logs from a 2-choice test experiment conducted summer 2002.

APPENDIX

Appendix 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2003-01

Title of thesis or dissertation (or other research projects):

HOST PREFERENCE AND HOST SUITABILITY OF TEN HARDWOODS FOR THE ASIAN LONGHORNED BEETLE, *Anoplophora glabripennis* (Motshulsky) AND OF FOUR CONIFERS FOR THE WHITE-SPOTTED PINE SAWYER, *Monochamus scutellatus* (Say)

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Appendix 1.1

Voucher Specimen Data

Page 1 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Eggs	Larvae	Nymphs	Pupae	Adults ?	Adults ?	Other	Museum where deposited
<i>Monochamus scutellatus scutellatus</i> (Say)	Mich. Kalamazoo Co. May-June 2002					2	2		MSU
	Emerged from jack pine logs Laura Lazarus								
<i>Monochamus scutellatus scutellatus</i> (Say)	Mich. Kalamazoo Co. May-June 2002					3	2		
	Emerged from red pine logs Laura Lazarus								
<i>Monochamus scutellatus scutellatus</i> (Say)	Mich. Kalamazoo Co. May-June 2002					1	3		
	Emerged from white pine logs Laura Lazarus								
<i>Monochamus scutellatus scutellatus</i> (Say)	Mich. Kalamazoo Co. May-June 2002					3	2		
	Emerged from white spruce logs Laura Lazarus								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Laura L. Lazarus

Date 14 February, 2003

Voucher No. 2003-01

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

[Signature] Date 14 MAR 2003

Curator

Appendix 1.1

Voucher Specimen Data

Page 2 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:						
		Eggs	Larvae	Nymphs	Pupae	Adults ?	Other	Museum where deposited
<i>Anoplophora glabripennis</i> (Motschulsky)	Illinois, Cook Co., near O'hare airport infestation Emerged from logs June 2000 Melody Keena	3				4		MSU
<i>Anoplophora glabripennis</i> (Motschulsky)	New York, New York Co., Manhattan - near Central Park Emerged from Norway maple logs June 2000 Melody Keena					2		

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Laura L. Lazarus

Voucher No. 2003-01

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Date 14 February 2003

Curator

Date

LITERATURE CITED

LITERATURE CITED

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