HOST SELECTION, OVIPOSITION BEHAVIOUR, AND INTER- AND INTRA-SPECIFIC COMPETITION IN THE WHITE-SPOTTED PINE SAWYER BEETLE, *MONOCHAMUS SCUTELLA TATUS* (SAY) (COLEOPTERA: CERAMBYCIDAE)

by

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A thesis submitted in conformity with the requirements for the degree of Master of Science in Forestry
Graduate Faculty of Forestry
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Date: Sept. 27/2000
ABSTRACT

Host selection, oviposition behaviour, and inter- and intra-specific competition in the white-spotted pine sawyer beetle, *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae)

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This study examined host selection, competition, and oviposition behaviour in the white-spotted pine sawyer beetle, *Monochamus scutellatus* (Say). Adult beetles were attracted to mating and oviposition sites by host volatiles, turpentine and α-pinene. Ethanol, a by-product of plant decomposition, was determined to have no effect on host selection. Other members of the phloem-feeding guild had little or no effect on *M. scutellatus* oviposition and larval success. Niche partitioning, through spatial or temporal segregation, allowed co-existence by guild members *Pissodes nemorensis* Germ. and *Ips pini* (Say). The sequence of behaviour in *M. scutellatus* oviposition was generally stereotypic and uniform. The presence of eggs from another female deterred oviposition, while the presence of larvae or her own eggs had a less deterrent effect. Site selection, dominance in the guild, and avoidance of other progeny are all adaptive for *M. scutellatus* in securing resources for developing offspring, and reducing competition for these resources.
ACKNOWLEDGEMENTS

I would like to thank my supervisors. Dr. Peter de Groot, of the Canadian Forest Service Great Lakes Forestry Centre in Sault Ste. Marie, Ontario, and Dr. Sandy Smith, of the Faculty of Forestry, University of Toronto. Peter, thank you for the project and funding, as well as your never-wavering professional, academic and personal support. You have been a great mentor, and friend. You taught me how to be a scientist; I hope a hundred more students are as fortunate. Sandy, thank you for the academic and thesis support, for revisions of the final versions of the thesis, and for the open door. I would also like to thank the third member of my supervisory committee, Dr. Tim Myles of the Faculty of Forestry, University of Toronto, for his interest, for his contribution, and for teaching me the finer points of decomposition.

I would like to thank the Canadian Forest Service for full project funding, as well as the Faculty of Forestry, University of Toronto, for funding through the Louis Nozzilillo Graduate Fellowship in Forestry, and Faculty bursaries.

I would like to thank Reg Nott, of the CFS in Sault Ste. Marie, for his endless patience and personality in the field and lab, as well as for reviewing final versions of the thesis. I would also like to thank CFS summer students Shauna Dunn, Kevin McCracken, Melissa Montgomery, and Cheryl Morrison, for able bodies and constant humour in the field. I would like to thank Kelly Kirkland, Stephanie Erb, and Gary White, for their friendship, support and laughter. Finally, I would like to thank my parents. This is for you.
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Chapter One: Introduction

General Biology of Longhorned Beetles

Longhorned beetles are members of the family Cerambycidae, with 20,000 described species throughout the world (Yanega, 1996). In North America, the adults are generally short-lived, with the majority of feeding and development occurring in the larval stages (Craighead, 1923). Adult beetles feed on pollen, fungi, foliage and young twigs, whereas larvae feed on living, dead and decaying woody and herbaceous plant material (Craighead, 1923). Size in the majority of species is sexually dimorphic, with males being smaller and having longer antennae than females. Most cerambycids are capable of sound production in the adult and/or larval stages (Yanega, 1996). Many species of this family are of great economic and ecological importance, feeding in or on healthy and dead plant material.

Biology of Monochamus scutellatus (Say)

A number of authors have described the general biology of Monochamus scutellatus (Say). This chapter will provide an overview of the literature on the species, with some detail on topics that will be covered in subsequent chapters.

Identification

Taxonomy

Class Insecta
Family Cerambycidae
Subfamily Lamiinae
Tribe Monochamini
Genus Monochamus
Species scutellatus (Say)
Life Stages

*M. scutellatus* is one of the largest Coleoptera found in the boreal forest. The egg is ca. 3 mm in length, elongate, cylindrical and slightly flattened, smooth and shining white. Eggs are deposited singly in scars excavated under the bark of conifers. The larvae measure up to 2.5 cm in length, and up to 0.75 cm wide at the thorax. Four larval instars have been documented. Pupae average about 2.5 cm in length, and are found in pupal cells ca. 5 mm from the bark surface at the end of a feeding tunnel.

Adult beetles average 1.9-2.5 cm in length, and 0.5-0.75 cm in width. Adults of both sexes are black, with females generally being lighter in appearance due to pubescence on the elytra. Both sexes have a small white spot on the scutellum, between the elytra. The species exhibits sexual dimorphism – male antennae are twice body length, while female antennal length is approximately that of the body (Rose, 1957; Wilson, 1962a; Yanega, 1996).

Economic Significance

Some species of *Monochamus* are vectors of *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, the causative agent of pine wilt disease in Asia and North America (Dwinell, 1997). This nematode is not pathogenic to native pines, but kills exotic pines in North America, and is a major mortality factor for native pines in Japan (Dwinell, 1997). Nematodes enter the trees through adult feeding wounds made by *Monochamus*. The nematodes then mature and feed upon tree parenchyma cells, resulting in wilt symptoms and quick death of the tree (Dwinell, 1997). While a phoretic relationship has been demonstrated for *M. carolinensis* (Olivier), *M. alternatus* Hope, and *M. saltuarius* (Gebler) (Akbulut and Linit, 1999a; Shibata, 1984; and Jikmaru et al., 1994), there has been no evidence to support potential phoresis by *M. scutellatus*. 
In North America, primarily in boreal regions, *M. scutellatus* has a great economic impact through larval feeding on cut logs left in the field or at lumberyards. *Monochamus* beetles are considered to be one of the most destructive pests of coniferous logs in Canada (Morley, 1939). Adult feeding upon twigs and young foliage may result in girdling of the branch, but rarely damages living trees. Larval heartwood feeding damages logs, with a subsequent reduction in timber value. Larvae can tunnel an average of 7.5 cm into the wood, and it has been estimated that larval feeding can reduce wood volume by up to 5% (Cerezke, 1975; Wilson, 1962b). These tunnels may result in increased handling time at sawmill operations, and rejection of logs for particular uses, such as for power poles (Cerezke, 1975). Larval tunnels also facilitate entry into the wood by sap rot and stain fungi, which discolor and destroy the wood, reducing value by as much as 35% (Wilson, 1962a).

Larval tunneling, while resulting in an economic loss for cut logs, also plays an important ecological role. Larvae consume great amounts of woody material, structurally weakening the wood. Tunneling also allows for entrance of rot fungi, as well as other wood-boring insects, accelerating decomposition of woody material in the forest ecosystem. The economic implications of this feeding have generally overshadowed examination of the ecological role of these beetles.

**Life History of the Genus Monochamus**

All species of *Monochamus* have the same general attack sequence on dead and dying coniferous species. Females are attracted to host volatiles released by dead and dying trees. Pheromone attraction has only been documented in one species, *M. alternatus* (Kim et al., 1992). Beetles undergo a period of maturation feeding after emergence from pupal cells in logs. Females and males are found on logs during day or night, depending on species, with mating occurring on the log surface (Rose, 1957). After mating, females deposit eggs singly
in scars excavated in the bark surface. Larvae moult through four larval instars, emerging the following spring from a pupal chamber just under the bark surface. Adults feed on foliage until reproductively mature, and then mate.

**Life History of *M. scutellatus***

*M. scutellatus* is found throughout North America, with the exception of the central United States (Yaneza, 1996). Adult beetles emerge from logs in the spring, and undergo maturation feeding upon new conifer twigs and foliage (Wilson, 1962a). After 7-10 days of feeding, mating generally occurs in early afternoon, with oviposition immediately following (Rose, 1957; Hughes and Hughes, 1982). There has been no documentation of long-range pheromone attraction in *M. scutellatus*, suggesting that mate-finding on the surface of the log occurs by some other factor, such as short-range pheromones, visual cues, or acoustic cues. Male reproductive success in *M. scutellatus* is associated with body size, and ability to defend the log resource until arrival of the female (Hughes, 1981). Resource defense polygyny is seen, in which a male defends high quality areas of fallen logs until arrival of a female. He then defends the female from other males while she is on the surface of the log (Hughes and Hughes, 1985). This allows the male to ensure oviposition in a high-quality area, and the half-mount mate-guarding position assumed throughout the interspersed copulation/oviposition period ensures the female will deposit eggs that he has fertilized. Mate selection by the female may be based on mating ability of the male, and the quality of the resource he defends. Females are likely to choose larger males, a factor that can affect fitness of her offspring (Hughes and Hughes, 1985).
Oviposition and Larval Development

*M. scutellatus* females preferentially oviposit in dead and dying conifers (Wilson, 1962a). After mating, a female will excavate a scar in the bark surface with her mandibles to deposit her eggs. Scars excavated before mating are generally empty (Rose, 1957). Eggs are deposited singly in scars, and larvae hatch within 9-14 days (Rose, 1957). Larvae consume the egg casing, and begin to tunnel in the phloem layer, ingesting phloem and cambium. After approximately 2-3 weeks, larvae moult to the second instar, and continue feeding in the phloem layer, scoring this area under the bark (Rose, 1957).

Following a further 2-3 weeks of feeding, the larvae moult to the third instar and tunnel into the sapwood and heartwood of the log. Feeding in this and the fourth instar creates a characteristic “U” shaped tunnel (Wilson, 1962a). In southern regions, the life cycle is one year, with larvae over-wintering as a pre-pupa and pupating and emerging the following spring (Wilson, 1962a). In northern regions, larvae may have a one-year lifecycle as above, or a two-year cycle. These over-winter as third instar larvae in tunnels in the wood and spend the next summer feeding, then moult to fourth instar the following fall (Rose, 1957). These fourth instar larvae tunnel to ca. 5 mm from the outer bark surface, and construct a pupal cell, plugging the end of the tunnel with wood fibres (Wilson, 1962a). Larvae pupate and adults emerge from holes cut in the bark at the end of these pupal cells the following spring.

Previous work on *M. scutellatus*

Rose (1957) gave an overview of the general life history of *M. scutellatus* on balsam fir, defining the number of larval instars, and the life-cycle of the species in Ontario. Characteristics of damage in standing and downed trees was examined by Cerezke (1975, 1977), Wilson (1962a,b) and Raske (1975). Potential mitigation measures to remove logs
from cutting sites, or storage options to prevent or reduce the amount of damage to logs have been suggested (Cerezke, 1975; Wilson, 1962a.b; Post and Werner, 1988). The contribution of *M. scutellatus* to death and decomposition of fire-killed trees has also been examined (Gardiner, 1957).

Reproductive behaviour of *M. scutellatus* has been examined, particularly dealing with male mating success. Females chose larger males, resulting in an increase in the rate of oviposition, as females moved more slowly and were more likely to be receptive to copulation with a larger male (Hughes and Hughes, 1985). Larger males were able to attract and keep females by defending higher quality areas on the log, such as those with a larger circumference (Hughes and Hughes, 1982). Males that were able to guard females for longer periods of time also had increased reproductive success, as females were depositing eggs that the guarding male had fertilized (Hughes, 1981).

Members of this species often fight to severe injury or death in contests for resources, so a larger male would be better suited to defend the female and the resource from smaller males in combat (Hughes and Hughes, 1987). There is also competition between *M. scutellatus* and related species in the same habitat, such *M. notatus* (Hughes and Hughes, 1987). Combat over resources was generally avoided if the opposing beetle was the larger *M. notatus*. The longer antennae of male *M. scutellatus* beetles have also been examined, to determine their evolutionary significance and role in combat and communication (Hughes, 1979).

While there has been extensive work on the reproductive behaviour of *M. scutellatus*, there has been no examination of the oviposition behaviour of the species. The role of competition in oviposition site selection also has not been determined. Rose (1957) and others have provided the general life-cycle and ecological role of the species. However, the
role of *M. scutellatus* in the phloem-feeding guild, and interactions under bark has yet to be
determined. Dyer and Seabrook (1978) suggested that oviposition site selection by female *M.
scutellatus* beetles is mediated by chemical cues, such as host volatiles. However, they were
not able to conclusively determine the role of these chemicals in host selection. No author
has demonstrated the role of chemicals, as pheromones produced by insects, or allomones
released from host plants, in oviposition site selection by *M. scutellatus*.

**General Ecology of *M. scutellatus***

**Guild Structure**

Coleopteran community structure within dead wood changes from initial colonizers, such as the family Scolytidae, to secondary attack by borers of the families Cerambycidae and Buprestidae. These are followed by predaceous families such as Staphylinidae and Cicindelidae, and finally to fungivorous beetles such as those of the family Erotylidae (White, 1983). A variety of species arrive at the resource throughout the earliest stages of
decomposition, and community composition changes with time (Zhong and Schowalter, 1989).

In pine, the majority of these insects are found in and under the bark, and most are
found in the earlier stages of decomposition (Howden and Vogt, 1951). Thomas (1955)
found that a number of insects and other arthropods inhabit red pine (*Pinus resinosa* Ait.) and
white pine (*P. strobos* L.) logging slash in northern Ontario, and that the successional pattern
of this community changes over time with the degree of decay of wood.

Primary insects arrive first, and often contribute to death of the tree in the process of
oviposition and larval development. The first wave of colonizers may be attracted to host
stimuli, with subsequent colonizers arriving in great numbers in response to pheromones
released by insects at the site (Brattli et al., 1998). Secondary arrivals at the tree are incapable
of killing the host, and are reliant upon some other agent to attack and kill the healthy tree (Gardiner, 1957). These species may not kill the tree directly, but may hasten death, or introduce pathogens that may result in decreased vigour and eventual death of the tree.

A guild is defined as a group of species sharing the same habitat, and having similar resource requirements and foraging strategies (Flamm et al., 1987). Insect families found in decaying wood are generally divided into four guilds, each using the resource in a distinct way: 1) phloem and sapwood borers; 2) fungus, frass, and detritus feeders; 3) parasites; and 4) predators (Thomas, 1955; Flamm et al., 1989). *M. scutellatus* is a phloem and sapwood borer, a member of a guild utilizing fresh phloem and sapwood for larval development. All are obligate feeders on phloem in the larval stages, with shallow feeders living entirely in the phloem layer, causing no appreciable damage to the wood. Deep-boring species like *M. scutellatus* feed in both the phloem and sapwood, causing great damage to the wood (Gardiner, 1957).

Competition between species in this two-dimensional feeding arena may be: 1) interference, or direct competition through cannibalism or predation; or 2) exploitative, in that one species excludes the other by utilizing the resource before arrival of the second species (Byers, 1989). Members of the phloem-feeding guild must contend with competition in order to maximize fitness and survival. Most members of the guild are able to successfully avoid competition through resource partitioning, or spatial or temporal segregation of feeding and oviposition sites (Byers, 1989).
Host-finding

Insect species use host plants as sites for feeding, mating, and oviposition. Host plant availability is often temporally or spatially limited within an ecosystem. This is particularly true for xylophagous insects, which require dead wood in a particular stage of decomposition for oviposition. These insects must be able to detect not only the appropriate host species, but also the right stage of decomposition for oviposition.

Two hypotheses are used to explain host tree selection by wood-feeding insects. The ‘primary attraction hypothesis’ postulates that beetles select a tree prior to alightment, based on a combination of visual and chemical cues. The ‘random attack hypothesis’ postulates that beetles randomly alight on a potential host tree, and accept or reject the host after arrival (Brattli et al., 1998). Primary attraction is mediated by a number of long-range chemicals released from the host plant, detected by insects at a distance. Random attack relies on cues that are detectable only after alightment, such as tactile or short-range chemical cues. Random attack could result in lost time, because insects could land on a number of trees before finally reaching a host suitable for feeding or oviposition. Long-range chemical cues would make host selection a much more efficient process, reducing the number of potential landings before a suitable host is found.

Visual cues, including the outline of a swarming mass of conspecifics, a vertical object, or the silhouette of a particular tree species, are vital for host-finding in many insect groups. These visual cues may result in location of a number of potential hosts, but cannot give an indication of the status of the tree. Most plant-breeding insects must rely on chemical stimuli to further narrow the search for an appropriate host plant. These stimuli are often used in combination with visual cues to make the site-selection process less time-consuming for female beetles.
Chemical cues for host finding include host tree volatile semiochemicals, or pheromones, both of which have an effect on the behaviour of insects that receive the signal. These can act as allomones, which benefit the emitter; kairomones, which benefit the receiver; or synomones, which benefit both emitter and receiver (Hagan et al., 1984). Upon reaching the host, chemotactic, tactile, gustatory or ovipositional cues may play a role. A suite of cues allows an insect to find a suitable host, possibly in an area that contains numerous similar or contradictory cues. Generalist species are attracted to a variety of hosts and cues, whereas specialist insects, those that require a specific host species or condition, are attracted to a narrow range of cues.

A number of scolytid beetle species rely on aggregation pheromones released by the first wave of colonizing insects to find a suitable host for mating and oviposition (Wood, 1982; Czokajlo and Teale, 1999; Billings, 1985; Brattli et al., 1998). These pheromones can serve as kairomones for inter-specific competitors, giving a xylophagous insect information on the host tree status if both species require similar stages of death or decay.

Many wood-feeding beetles use chemical cues produced by the host itself for selection. For those species that do not produce pheromones, or for initial insects arriving at a host, host volatiles are a cue for orientation. Allelochemicals such as terpenes released by the host plant can further narrow the host selection process, allowing a female to find a host for feeding or oviposition. Brattli et al. (1998) determined that a variety of conifer-living beetles, including bark beetles (Scolytidae), weevils (Curculionidae) and woodborers (Cerambycidae) used a combination of host volatiles and/or pheromones, and a number of species were able to detect a suitable host tree in flight. The use of host volatiles for attraction of conifer-feeding weevils is well known (Rieske and Raffa, 1991; Lindelöw et al., 1993; Hoffman et al., 1997; Tilles et al., 1986), with most species being attracted to a specific conifer volatile
that allows them to find a suitable host tree. Due to the patchy distribution of suitable hosts, most of these insect species are very specific in detection of chemical cues from the host, which enables them to efficiently find oviposition and feeding sites.

**Oviposition Behaviour**

Competition for resources occurs throughout the life of an insect. These resources may include shelter, mates, and sites for feeding and oviposition. High population numbers and limited resource availability result in competition, and may have a negative effect on insects in a particular habitat. Avoidance of competition can lead to increased survival and increased fitness amongst progeny (Prokopy et al., 1984). Successful foraging for exploitable resources must avoid competition, not only from members of the same species (intra-specific competition), but also from different species that share the same niche (inter-specific competition).

Parasitism and predation upon all life stages must also be avoided, while procuring the highest quality and quantity of the resource, whether for adult feeding or oviposition. The search for a host may be influenced by a number of factors, including chemical cues from the resource itself, or from other insects utilizing the resource, particularly chemically marked areas that have been previously exploited by conspecifics (Prokopy et al., 1984). Foraging by way of chemical cues from other insects may help reduce competition by preventing resource use by a number of different individuals. This is particularly important in oviposition, as progeny use the resource much later for larval development. Site selection by females can have a great effect on the survival of offspring, and avoidance of competition at this stage may increase size and robustness of offspring, thus increasing the fitness of the female.

One way to avoid competition is through resource partitioning to maximize resource use without encountering other insects in the area. There is a maximum density of individuals
that can successfully exploit a resource without detrimental effect upon any of the individuals involved. Partitioning of this resource, through chemical or physical means, may act to reduce contact between individuals, and maintain a density below competitive thresholds. Cues for avoidance of competition may include oviposition-deterring pheromones, which act intra-specifically to alert females to the presence of another egg in the immediate vicinity, pheromones, and visual and tactile cues.

Oviposition behaviour in insects involves all aspects of egg-laying, including site selection, site preparation, and eventual egg deposition. In species of Coleoptera that inhabit wood, such as *M. scutellatus*, site preparation often involves excavating a scar, and inserting the ovipositor for egg deposition beneath the bark. Female behaviour in site selection and egg deposition greatly affects survival of offspring, as a poor oviposition site may adversely affect feeding and development.

Oviposition behaviour has been studied in a number of insect species, particularly those that oviposit on fruit and foliage, such as *Rhagoletis pomonella* (Osten Sachen) (Prokopy, 1972), and *Hylema* sp. (Zimmerman, 1979). Female egg-parasitic *Trichogramma chilonis* Ishii wasps have been observed to discriminate between parasitized and non-parasitized host larvae (Miura et al., 1994), and numerous other species use a variety of cues to find their hosts, such as host odour in *Leptopilina clavipes* (Tumlinson et al., 1993). Host discrimination allows a female to provide the best possible environment for developing larvae.

Optimal oviposition behaviour in phytophagous insects assumes that the reproductive success or fitness of a female insect depends upon the success of a behavioural component in that female during the oviposition process. The quality and suitability of oviposition sites varies. A female, through behaviour modifications, must choose a suitable site in order to
maximize fitness of her progeny (Jaenike, 1978). As there is little or no parental care in most species of insects, a female would contribute most to survival of her progeny by choosing a site that is protected from competition, predators, and parasitoids, but also contains an adequate supply of nutritious food. This results in behaviour leading to extensive selectivity in host choice, maximizing success of progeny once oviposition is complete.

Factors affecting oviposition site selection prior to alightment on a host include host volatiles, host plant size and shape, and pheromones. Of these, only pheromones, and potentially the presence of other insects, continue to have an affect on female behaviour upon landing on the host. Numerous factors may influence female choice in site selection upon arrival at a host. These may include bark thickness (Nakamura et al., 1995b), presence of other insects on the log surface, presence of eggs and/or larvae (Anbutsu and Togashi, 1997a), or other signs of oviposition by conspecific females.

Larval survival may be influenced by predators, parasitoids, and competitors, and natural selection in development of host choice may be based on 'enemy-free space', in which survival is potentially increased by the absence of these factors (Thompson, 1988). A number of studies have determined that interspecific competition has an effect on the oviposition biology of insects (Shroeder, 1997; Prokopy et al., 1984). A female must be able to determine the presence and extent of threat from other insects before oviposition and incorporate this into the behavioural sequence upon arrival at a suitable host.

Objectives

Little is known about the process of oviposition site selection in *M. scutellatus*. There is no documentation of pheromone production in this species, and the role of host chemicals is unclear. Oviposition behaviour and the role of competition in site selection are also unknown in this species. This thesis was initiated to provide further insight into the chemical
ecology of host selection, niche dynamics of *M. scutellatus*, and the sequence of behaviours involved in oviposition. Chapter One provided a general overview of what is known about the species, as well as background information on the topics that were encountered in this study. Chapter Two provides an examination of the chemical ecology of host tree selection for *M. scutellatus*. Attraction to host volatiles, such as turpentine and α-pinene, and ethanol, a natural decomposition by-product, were examined for male and female beetles.

Chapter Three discusses inter-specific competition within the phloem-feeding guild, focussing on *M. scutellatus* and two species that share the niche, the northern pine/deodar weevil, *Pissodes nemorensis* Germ., and the pine engraver, *Ips pini* (Say). Aspects of temporal and spatial segregation that allow these species to exploit the same limited resources were examined, as well as the potential influence of insolation and host species on oviposition site selection and larval success. Chapter Four expands on aspects of competition in site selection, dealing with intra-specific competition in oviposition. The potential influence of the presence of oviposition deterring pheromones and progeny under the bark was examined, as was the sequence of events in oviposition. Chapter Five presents conclusions of these studies, and provides recommendations on how these results can be used in further studies and management of *M. scutellatus*. One overall bibliography for the thesis follows Chapter Five. Chapters Two through Four are presented in the format of journal articles, to facilitate later publication of this work. As a result, there exists some duplication and potential overlap in presentation of information and introductory and background material. However, the results, discussions and conclusions of all chapters are distinct and will be synthesized only in the final Chapter Five.
Chapter Two: Chemical ecology of host tree selection by *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae)

INTRODUCTION

*Monochamus scutellatus* (Say), the white-spotted pine sawyer beetle, is found throughout North America and is prevalent in the boreal forest of northern Ontario. Adults feed on twigs and foliage of living pine trees, and females deposit eggs in scars excavated in the bark of dead and dying conifer species. Larvae hatch to feed in the phloem layer under the bark and eventually tunnel into the heartwood, where they pupate and emerge in summer either one or two years later (Rose, 1957). Larval feeding tunnels degrade lumber (Wilson, 1962a) and contribute greatly to wood decomposition in the forest ecosystem.

Adult *M. scutellatus* beetles are known to be attracted to turpentine, a combination of various host volatile monoterpenes produced from distilled conifer oleoresin (Gardiner, 1957). Chenier and Philogene (1989a,b) determined that *M. scutellatus* beetles were attracted to turpentine and that this attraction was similar to that for a blend of monoterpenes including (±)-α-pinene, (−)-β-pinene, (±)-camphene, (±)-limonene, myrcene, and (+)-Δ-3-carene. *M. scutellatus* was most strongly attracted to commercial turpentine and (±)-α-pinene, the major attractive constituent of turpentine. Dyer and Seabrook (1978) also suggested that terpenes might be used for host selection by *M. scutellatus*.

Attraction to turpentine has also been demonstrated in the related species *M. titillator* (Fabricius) and *M. carolinensis* Olivier (Fatzinger, 1985; Phillips et al., 1988; Billings, 1985). Billings (1985) determined that the combination of turpentine and *Ips* bark beetle pheromones increased attraction to baited traps for *M. titillator*. Attraction to traps baited
*M. alternatus* Hope (Ikeda et al., 1980). The highest number of *M. alternatus* beetles were attracted to baited traps approximating the monoterpene vaporization ratio from bait logs in the field.

Ethanol is produced through microbial respiration during decomposition of plant material. Ethanol generally is not present in healthy trees but can be produced when a tree is under stress (Sjodin et al., 1989), or during anaerobic conditions (Kimmerer and Kozlowski, 1982). Ikeda et al. (1980) detected ethanol in conifers within 3-10 days of cutting, and these levels generally increase upon death, relative to the stage of decomposition (Phillips et al., 1988). The number of *M. scutellatus* beetles collected at traps baited with ethanol alone was similar to that for unbaited control traps (Chenier and Philogene, 1989a). Numbers of *M. carolinensis* and *M. titillator* collected at traps baited with ethanol alone were significantly less than that caught at turpentine-baited traps (Phillips et al., 1988; Fatzinger, 1985). These results demonstrate that ethanol alone is not highly effective in attraction for *Monochamus* species. As ethanol is produced during decomposition of all plant material, attraction to wood-feeding beetles must be mediated by some other factor, particularly the genus- or species-specific host volatile chemicals released by the tree (Brattli et al., 1998).

Beetle attraction to monoterpenes such as *α*-pinene may be synergized by ethanol, with the additive attractive effect of the monoterpene and ethanol being greater than that of either of the two compounds alone (Tilles et al., 1986). A synergistic effect has been demonstrated for *M. scutellatus*, with higher numbers at traps baited with a blend of monoterpenes and ethanol than for monoterpenes alone (Chenier and Philogene, 1989a). However, the same effect was not seen for *α*-pinene alone and ethanol, as trap catches were lower when compared to *α*-pinene alone (Chenier and Philogene, 1989a). A synergistic effect has been demonstrated for turpentine and ethanol in *M. carolinensis* and *M. titillator*
(Fatzinger, 1985). Phillips et al. (1988) determined that while the effect was synergistic for
*M. titillator*, it was not for *M. carolinensis*. This is ecologically significant in that a specific
ratio of ethanol and α-pinene may have to be detected by a female before host selection.

While previous studies have demonstrated synergism between a monoterpenic blend
and ethanol, and commercial turpentine and ethanol for *M. scutellatus*, no study has
determined a synergistic effect for α-pinene and ethanol for the species. No direct
comparison has been made between attraction to turpentine and one of its major constituents,
α-pinene, for *M. scutellatus*. The study undertaken by Chenier and Philogene (1989a) used
one release rate for each compound studied, and stated that small sample sizes could not lead
to a conclusion on the variation in attraction between ethanol and turpentine, and ethanol and
a monoterpenic blend. No study on *M. scutellatus* has examined attraction to a variety of
ethanol and monoterpenic release rates, which change in a natural situation as monoterpenic
release slows and ethanol production increases upon death of a tree. The specific
combination that is most attractive to species of *Monochamus* has yet to be investigated.

This study was undertaken to expand upon the work of Chenier and Philogene
(1989a), to further examine the role of host volatiles in host tree selection for oviposition by
*M. scutellatus*. Trapping experiments were conducted in the field to compare the attractive
nature of turpentine and its major constituent, α-pinene. Studies were also undertaken to
examine the influence of ethanol upon attraction, and verify if a synergistic effect was
present between ethanol and turpentine. Finally, attraction to a range of α-pinene release
rates was examined to determine if an optimal release rate increased attraction by *M.
scutellatus*. 
MATERIALS AND METHODS

Study Sites

Four baited-trap experiments were conducted in 1998 and 1999 to determine the attractiveness of turpentine, α-pinene and ethanol to *M. scutellatus*. Experiments 1, 2 and 3 were conducted in a mixed conifer-hardwood forest located in Wells Township (46° 25' N, 83° 22' E), ca. 40 km north of Thessalon, Ontario. Predominant conifer species were mature white pine, *Pinus strobus* L., red pine, *P. resinosa* Ait., and white spruce, *Picea glauca* (Moench) Voss. Experiment 4 was conducted in a recent jack pine (*P. banksiana* Lamb.) clear-cut located in Lawlor Township (47° 05' N, 82° 50' E), ca. 140 km north of Thessalon, Ontario.

Experiments 1 & 2. Attractiveness of turpentine, ethanol and α-pinene

Experiment 1 compared the attractiveness of commercial grade turpentine and ethanol, either alone or in combination (released from separate bottles). Attractiveness of commercial grade turpentine was compared with that of (±)-α-pinene in Experiment 2. Both Experiments also contained an unbaited control.

Commercial grade turpentine (Mastercraft® Cat. No. 49-7179-0) (Canadian Tire Corporation Ltd., Toronto, Ontario) was determined by gas chromatography/mass spectrometry analyses to be composed of 73 % (±-)α-pinene, 2.6 % β-pinene, 15 % Δ-3-carene, 1.8 % limonene and 1.3 % terpinolene. Ethanol (95 % pure) was purchased from Commercial Alcohols Inc. (Toronto, Ontario) and (±)-α-pinene (98 % pure) was purchased from Aldrich Chemical Co. (Milwaukee, Wisconsin, USA).

In Experiments 1 and 2, 15 ml of turpentine, ethanol or α-pinene was released from a 20-ml high-density polyethylene bottle (HDPE) (Cat. No. 66021-679, VWR Canlab, Mississauga, Ontario) with a 4.8 mm hole drilled in the centre of the polypropylene screw
cap. Release rates were determined gravimetrically at 24°C in a fume hood by weighing five bottles of each compound daily for five days. The release rates of turpentine, ethanol and α-pinene were ca. 110, 732 and 22.5 mg/d, respectively.

**Experiments 3 & 4. Comparison of varying release rates of α-pinene**

Experiment 3 compared five release rates of α-pinene (30, 90, 150, 300 and 450 mg/d), and Experiment 4 examined α-pinene released at 150, 300, 450, 600 and 750 mg/d. Both experiments also contained an unbaited control. These release rates were chosen based on previous work by other authors demonstrating attraction of Monochamus to release rates from 26-590 mg/d. Experiments 3 and 4 used α-pinene lures purchased from Phero Tech Inc. (Delta, British Columbia). These lures consisted of 15-ml low-density polyethylene (LDPE) bottles containing 95% of the (-) isomer and 5% of the (+) isomer. Each bottle released 150 mg/day (24°C) (Phero Tech Inc.) and multiples were used for the higher release rates. Experiment 3 also used a 2-ml glass vial (Cat. No. 66020-936, VWR Canlab) with an open cap (Cat. No. 66010-654, VWR Canlab), filled with α-pinene, which released ca. 30 mg/day (release rates determined gravimetrically as above). Three vials were used to achieve a release rate of ca. 90 mg/d.

**Traps**

For Experiments 1, 2 and 3, traps consisted of an open 11.3-L Hunter Green (35 cm long X 25 cm wide X 17 cm deep) plastic pan (Cat. No. 2213, Rubbermaid Inc., Wooster, Ohio) placed on the ground. Each trap contained ca. 3.5 l of water to which 3 ml of unscented Sunlight® dish soap (Lever Pond’s, Toronto, Ontario) was added to reduce the surface tension of the water. Baits were suspended from a wire hung just below the top of the pan, along its length.
For Experiment 4, two 3 mm thick black polyvinyl chloride (PVC) plastic (Sintra®, Alucobond Technologies Inc., St. Louis, Missouri) cross vanes were placed above the pan to increase the trap catch of insects (Figure 2-1). The cross vanes (35 and 25 cm wide and 67 cm long) were slotted, placed at right angles to each other and trimmed to fit inside the pan, leaving 50 cm of vane exposed above the pan. Baits were hung in a 7.5 by 5 cm hole cut 21.5 cm from the top through the axis of the vanes. To prevent the traps from falling over, each pan was secured with spikes placed in the ground.

Figure 2-1. Cross-vane traps used for collection of beetles, 5 Aug through 3 Sept, 1999, Lawlor Township, Ontario.
Layout of Traps

All experiments were laid out in a complete randomized block design. Traps for Experiments 1 and 2 were spaced 50 m apart and those for Experiments 3 and 4 were placed 25 m apart. Each treatment was replicated five times for Experiments 1 and 2, and ten times for Experiments 3 and 4. All captured insects and debris were removed from the traps weekly and traps were then supplemented with fresh water and soap. Traps were rotated one position each week within each replicate block to reduce trap position effects. Captured Monochamus beetles were identified to species and sexed by antennal length (Yanega, 1996). An examination of the internal genitalia of 30 M. scutellatus and 10 M. mutator beetles indicated that antennal length correctly established gender.

Statistical Analysis

For Experiments 1 and 2, trap catches of each sex were transformed by \( \log_{10}(x + 0.5) \) to satisfy assumptions of normality and homogeneity of variance (Zar, 1999). Transformed data were analyzed by ANOVA by the General Linear Model for randomized block designs (SigmaStat\textsuperscript{®} version 2.03, SPSS Inc., Chicago IL) followed by the Tukey's test at \( P = 0.05 \). A two-sample t-test was used to compare differences between males and females within a single treatment. For Experiments 3 and 4, trap catches for each sex for both M. scutellatus and M. mutator Le Conte beetles were determined and the relationship between release rate and trap catch was analyzed by linear regression (SigmaStat\textsuperscript{®}). A two-sample t-test was used to compare differences between males and females within a single treatment.
RESULTS AND DISCUSSION

Attractiveness of turpentine, ethanol and α-pinene

In Experiment 1, traps baited with turpentine or turpentine plus ethanol caught significantly more beetles than ethanol alone or unbaited controls (Fig. 2-2a). There was no significant difference between attractiveness of turpentine alone and that of turpentine and ethanol in combination. Ethanol alone was no more effective in attracting beetles than control traps (Fig. 2-2a). In Experiment 2, turpentine and (±)-α-pinene were equally effective, capturing significantly more beetles than unbaited controls (Fig. 2-2b). Although more females were captured than males, the differences between sexes were not significant within treatments for either experiment.

Ethanol alone had no attractive effect for *M. scutellatus*. This supports findings of Ikeda et al. (1980) for *M. alternatus*. Chenier and Philogene (1989a) demonstrated a synergistic effect between ethanol and turpentine for *M. scutellatus*. Similarly, Phillips et al. (1988) and Fatzinger (1985) observed synergism in attraction to turpentine and ethanol for *M. carolinensis* and *M. titillator*. Ethanol release rates of 1.8-2.6 g/d (Chenier and Philogene, 1989a) and 23.6 g/d (Phillips et al., 1989) were considerably higher than 732 mg/d in the present study. Ikeda et al. (1980) also demonstrated that significantly more *M. alternatus* were captured at traps baited with α-pinene and ethanol than with α-pinene alone at α-pinene release rates of 400mg/d and unknown ethanol release rates. The release rates of ethanol in Exp. 1 may have been too low for detection by *M. scutellatus*. This suggests that there may be a threshold concentration of ethanol in the air below which there is no detection or subsequent response by *M. scutellatus*. Additional work is necessary to determine airborne concentrations of ethanol that are optimal for attraction of *M. scutellatus* and potential synergism of ethanol and monoterpenes.
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Figure 2-2. Response of male and female *M. scutellatus* beetles to traps baited with: A) ethanol plus turpentine, ethanol, turpentine, and blank control traps; and B) turpentine, α-pinene, and blank control traps, 22 Jun through 25 Aug, 1998, Wells Township, Ontario. Bars with the same letter are not significantly different at *P*=0.05 (ANOVA with Tukey's test). There were no significant differences (*P* >0.05) in number of males and females caught for any of the above treatments.
Turpentine, and its major constituent α-pinene, appear to be equally attractive to *M. scutellatus* at the release rates used in the present study. Chenier and Philogene (1989a) determined that (±)-α-pinene was more attractive than a monoterpene blend similar to turpentine for *M. scutellatus* at release rates of 0.59g/d and 1.36g/d, respectively. Turpentine was determined to have an attractive effect for *M. carolinensis* and *M. titillator* when released at a rate of 4.7g/d (Phillips et al., 1988); and Fatzinger (1985) determined that (±)-α-pinene was attractive for these species at 26-61 mg/d. Billings (1985) determined that turpentine alone was no more attractive than unbaited control traps for *M. titillator*.

Moeck (1970) determined maximum α-pinene concentrations in the field to be ca. 240 mg/d. Stromvall and Petersen (1991) determined that the air above freshly cut pine branches contained monoterpane concentrations of 1000μg/m³, which decreased to 500μg/m³ in pine cut a few days earlier. Four weeks after thinning in July, monoterpane levels in a related spruce stand were only 10% that of original levels (Ikeda et al., 1980). Ikeda et al. (1980) demonstrated that pine logs left in the field become unattractive to *M. alternatus* within three weeks. This could be because monoterpane release by the plant varies seasonally, but also decreases exponentially following death.
Attraction to varying release rates of α-pinene

Very few beetles were captured in Experiment 3, therefore the data were not analyzed further. In Experiment 4, the highest numbers of beetles were collected at baits releasing 450 mg/d of α-pinene. There was a significant positive relationship between release rates of α-pinene and trap catch for female but not for male M. scutellatus (Figs. 2-3, 2-4). Catches of female M. mutator did not increase with increased release rates of α-pinene (Fig. 2-45) but those of males did (Fig. 2-6). More females were caught than males in both species, but the differences between sexes were not significant for any of the treatments.

More beetles were collected at higher levels of α-pinene, those above 450mg/d for all groups. M. scutellatus was attracted to baited traps releasing α-pinene at 590mg/d (Chenier and Philogene, 1989a), and Ikeda et al. (1980) demonstrated M. alternatus attraction to release rates of 400mg/d. M. titillator was attracted to α-pinene release rates of 3600mg/d (Billings, 1985), while M. carolinensis and M. titillator were attracted to release rates of 26-61mg/d (Fatzinger, 1985). This suggests that the genus is able to detect and respond to a wide range of volatile release rates. There were large numbers of beetles collected at unbaited control traps in the present study, suggesting that some other factor, such as trap silhouette, may have been involved in attraction.
Figure 2-3. Relationship between release rates of α-pinene and trap catch of female *M. scutellatus* adults, 5 Aug through 3 Sept. 1999, Lawlor Township, Ontario. Slope of regression line is significantly different from zero (N=60 traps, $r^2=0.110$, $P=0.010$).

Figure 2-4. Relationship between release rates of α-pinene and trap catch of male *M. scutellatus* adults, 5 Aug through 3 Sept. 1999, Lawlor Township, Ontario. Slope of regression line is not significantly different from zero (N= 60 traps, $r^2=0.0409$, $P=0.121$).
Figure 2-5. Relationship between release rates of α-pinene and trap catch of female *M. mutator* adults, 5 Aug through 3 Sept, 1999, Lawlor Township, Ontario. Slope of regression line is not significantly different from zero (N=60 traps, r²=0.0301. P=0.185).

Figure 2-6. Relationship between release rates of α-pinene and trap catch of male *M. mutator* adults, 5 Aug through 3 Sept, 1999, Lawlor Township, Ontario. Slope of regression line is significantly different from zero (N=60 traps, r²=0.0752. P=0.034).
There was a positive relationship between $\alpha$-pinene release rate and trap catch for female *M. scutellatus* and male *M. mutator*. The reason why there was no such relationship for male *M. scutellatus* and female *M. mutator* is unclear. If attraction to $\alpha$-pinene were a function of beetle gender, it would be expected that there would be significant positive relationships between release rate and trap catch for females or males of one or both species. Although positive results were seen in the present study, they were relatively weak for both female *M. scutellatus* and male *M. mutator*. This may have been a function of marginal response to low release rates. as a 400mg/d $\alpha$-pinene release rate approximates that from only 30kg of bait logs in the field (Ikeda et al., 1980). Further examination of a wider range of $\alpha$-pinene release rates is necessary to better understand host volatile attraction in both species.
CONCLUSION

Results from this study indicate that Monochamus beetles are able to detect a range of &-pinene release rates. This study was unable to demonstrate attraction to ethanol, or synergism between ethanol and either turpentine or &-pinene, at the release rates examined. There was little or no difference in attraction to release rates under 300mg/d, and the majority of beetles were attracted to traps releasing greater than 300mg/d. This supports previous research into Monochamus species, which demonstrated increasing attraction to higher levels of &-pinene. No upper level of attraction has been demonstrated in Monochamus. Examination of a broad range of release rates would give a clear picture of attraction to dead and dying trees in the boreal forest.

Previous authors used one release rate of &-pinene and all studies have demonstrated attraction to Monochamus. Further work could increase the release rates of &-pinene, and use a broad range to determine upper limits for attraction. Examination of increasingly higher release rates would give an indication of the upper limit for attraction to M. scutellatus and M. mutator. It may also determine if sex-based differences in attraction are demonstrated by these species. Further work could also attempt to measure &-pinene release rates above log piles after cutting, to determine levels in a field situation. A number of trap designs could also be examined, to determine if trap silhouette combines with &-pinene release to enhance attraction in species of Monochamus.
Chapter Three: Influence of inter-specific competition and niche partitioning on oviposition by *Monochamus scutellatus* Say (Coleoptera: Cerambycidae)

INTRODUCTION

*Monochamus scutellatus* (Say), the white-spotted pine sawyer beetle, is found throughout North America, with the exception of the central United States (Yanega, 1996). After emerging from dead pine logs, adults undergo a period of maturation feeding on young pine twigs and foliage (Wilson, 1962a). After mating, females oviposit in scars excavated in the bark of dead and dying pine species. Larvae emerge and feed in the phloem layer until the third larval instar, in which they tunnel into the sapwood and later heartwood, where they can feed for up to two years (Rose, 1957). Larval feeding reduces structural qualities of the wood and facilitates entrance of other insects and fungal pathogens, contributing to wood decomposition in the forest ecosystem (Parmelee, 1941; Gardiner, 1957; Wilson, 1962a).

A number of insect families utilize wood for feeding, and sites for mating and oviposition. Many are capable of attacking living trees, but the majority of these insects are dendrophagous, using dead and dying wood. The community structure within dead wood changes from the initial colonizers, such as bark beetles of the family Scolytidae, feeding on fresh dead phloem, to secondary attack by borers such as the family Cerambycidae. A variety of species arrive at the resource throughout the earlier stages of decomposition, and community composition changes with time (Thomas, 1955; Zhong and Schowalter, 1989). Primary insects arrive first, and most complete oviposition and larval development before the arrival of secondary species. *M. scutellatus* is a secondary insect, generally incapable of killing the host, and reliant upon some other agent to attack and kill the healthy tree, such as
the scolytid bark beetle *Ips pini* (Say) (Gardiner, 1957). These species may not kill the tree directly, but may hasten death, or introduce pathogens that decrease vigour and eventually kill the tree.

A guild is defined as a group of species sharing the same habitat, and having similar resource requirements and foraging strategies (Flamm et al., 1987). *M. scutellatus* is a phloem and sapwood borer, part of a guild with obligate phloem-feeding larvae. An average phloem surface area of 31.75 cm² was required for foraging by *M. titillator* (Fabricius) (Coulson et al., 1976), a beetle of similar size to *M. scutellatus* (Yanega, 1996), and assumed similar nutritional requirements. These larvae reach up to 2.5 cm in length in the fourth instar (Wilson, 1962a), and therefore have greater nutritional requirements than smaller species sharing the resource. After the second instar, as the amount of phloem is greatly reduced, *M. scutellatus* larvae can tunnel up to 7.5 cm into the heartwood (Gardiner, 1957). returning periodically to the phloem to feed. The smaller bark beetle species require less surface area for larval feeding; however, these are prolific breeders, with much higher population numbers exploiting the phloem resource (Coulson et al., 1976). Resource use may result in intra-specific competition between members of the same species, or inter-specific competition with other insect species sharing the resource. Competition could be intense if both groups were to feed in the same area at the same time. The sequence of sub-cortical insects arriving at a host and the influence of competition on insect species feeding within fallen logs has been examined by previous authors (Yoshikawa, 1987a, b; Stephen and Dahlsten, 1976; Flamm et al., 1989; Post and Werner, 1988: Rankin and Borden, 1991: Poland and Borden, 1994: and Miller, 1985, 1986).

Competition between species in this two-dimensional feeding arena may be: 1) interference or direct competition through cannibalism or predation; or 2) exploitative
through exclusion by utilizing the resource before arrival of the second species (Byers. 1989). Most members of the phloem-feeding guild are able to successfully avoid this competition through resource partitioning by spatial or temporal segregation of feeding and oviposition sites. Spatial segregation has been demonstrated in *Ips calligraphus* Germ., with highest numbers found in areas where insect associates had been mechanically removed or excluded (Miller, 1984a,b, in Miller. 1986). Yoshikawa (1987a) determined that *Monochamus alternatus* Hope larvae were not affected by other species under the bark, because larvae were successful in either inter-specific competition or niche segregation.

The influence of competitive interactions between *M. titillator*, *Dendroctonus frontalis* Zimmermann and *Ips calligraphus* (Germ.) has been documented by various authors (Coulson et al., 1976; Flamm et al., 1989; Miller. 1985, 1986). However, there has been no examination of competition between *M. scutellatus* and other species within the phloem-feeding guild. The purpose of this study was to examine the factors influencing success of *M. scutellatus* larvae under the bark of dead pine. The objective of the study was to determine if different members of the phloem-feeding guild were present in the same area at the same time in the season, and if so, to examine the extent of temporal and/or spatial segregation between *M. scutellatus* and other insect species. Competition may also be influenced by host species characteristics. Red and white pine logs of similar diameter were used in this study to examine the influence of host tree species upon guild structure and competitive interactions of *M. scutellatus*. Other factors, such the predator and parasitoid complex, and sun exposure of logs, were also examined, to determine any potential effect on population dynamics of *M. scutellatus*. 
MATERIALS AND METHODS

Experiment 1

Twelve red pine (Pinus resinosa Ait.) and ten white pine (Pinus strobus L.) logs, each 2 m in length and averaging 18.5 ± 1.9 cm in diameter, were cut in late May 1998, and placed at a site in Wells Township, ca. 30 km N of Thessalon, Ontario (46° 25' N, 83° 22' E). Logs were placed in a semi-shaded thinned pine stand, in a grid formation with 5 m spacing between each log. Red and white pine logs were used to determine if oviposition and survival varied between host species. Logs were alternated. red pine and white pine. throughout the grid.

One half of each log (1 m) was covered with 0.625 cm galvanized hardware cloth, and the other half was left open. This was done to exclude the larger *M. scutellatus* beetles from the log surface, in order to examine potential differences in guild dynamics between two adjacent areas, one with *M. scutellatus* and one without. Two logs of each species were removed randomly at two-week intervals throughout the study period, June through August, and were taken to the laboratory. The hardware cloth was removed and each log was cut in half, at the screen/no screen interface, with each half kept separately in screened cages in the laboratory. All Scolytidae emerging from logs were collected until the end of the study period, in late August. The number of *M. scutellatus* oviposition scars on the surface of the logs was counted, and the bark was removed from each log later in the fall of 1998. All *Monochamus* beetles reared through in the process of this and subsequent experiments were identified as *M. scutellatus* (Yanega, 1996).

The number of oviposition plugs was also determined. In Chapter 4, it was observed that 96% of scars containing a brown sticky substance (the 'plug') contained an egg upon dissection. This approximately 1:1 ratio allowed the assumption that each plug would
represent a scar containing an egg. These plugs were clearly visible under 4X magnification, and were used as an indication of the presence of eggs in excavated scars.

The number of *M. scutellatus* feeding galleries and entrance holes into the sapwood were counted for comparison of larval success between red and white pine logs. The surface area required by *M. scutellatus* for larval feeding has not been established in the literature. The total surface area of each gallery was measured using a dot grid method. This involved using a 20 X 20 cm grid, with the dimensions of each centimeter marked in a block with a dot in the centre. This grid was randomly placed on a log, and the number of dots within the dimensions of each gallery was noted, to give an indication of the number of square centimeters within the gallery. The accuracy of the grid method was tested on a sub-sample of ten feeding galleries using a planimeter to measure actual dimensions after measurement with the grid. It was determined that the method was accurate within an average of 1.7 ± 0.3 cm².

*M. scutellatus* females were able to get under the mesh and oviposit in the bark of both red and white pine logs, making it impossible to examine differences between areas with and without *M. scutellatus*. Therefore, only uncaged data were used for analysis in this study, because this area most closely resembled a natural situation. Two-sample *t*-tests were used to examine differences between uncaged red and white pine logs in number of scars excavated, oviposition plugs, entrance holes into the sapwood, and surface area of feeding galleries for *M. scutellatus*. Two-sample *t*-tests were also used to examine the number of *Ips pini* adults emerging from red and white pine logs caged in the lab (SigmaStat®, version 2.03. SPSS Inc., Chicago, IL).
Experiment 2

Nine red pine (P. resinosa) and ten white pine (P. strobus) logs (each 1 m in length and averaging 17.4 ± 2.6 cm in diameter) were cut in late May 1998 at the Wells Township site. These logs were placed in a grassy area near a logging road in a red pine plantation in Kirkwood Township, ca. 20 km north of Thessalon, Ontario (46° 20' N, 83° 33' E). The purpose of this study was to examine spatial distribution of M. scutellatus and other members of the phloem-feeding guild around the circumference of the log. Logs were placed in a grid, with 5 m spacing between each log. Logs were restricted by species to one side of the grid, with all red pine on one side, and all white pine on the other.

The circumference of each log was divided into zones, based on the face of a clock (Fig. 3-1), with the middle of zone 11-1 representing the top of the log, and the middle of zone 5-7 representing the bottom of the log.

Figure 3-1: Diagrammatic representation of the cross-sectional division of the circumference of study logs into 6 equal zones.
Two logs of each species were removed randomly at 2-week intervals between June and August 1998, and were taken to the laboratory. The number of *M. scutellatus* oviposition scars in the bark of each log was counted, and all bark was removed from the logs. During bark removal, a significant number of pupal cells of the northern pine weevil, *Pissodes nemorensis (=approximatius)* Germ., were observed, so these were included, as well as any other insects observed under the bark.

All data were transformed using \( \log_{10} (x + 0.5) \) to satisfy assumptions of normality and homogeneity of variance (Zar, 1999), and all subsequent analyses were performed on transformed data. Two sample *t*-tests were used to examine differences between pine species for the mean number of *M. scutellatus* scars and *P. nemorensis* pupal cells. One-way ANOVAs, followed by the Tukey’s test, were used to compare the number of scars and pupal cells per log zone for red and white pine (SigmaStat®).

**Experiment 3**

Based on 1998 results indicating that some spatial segregation had occurred (refer to Experiment 2), it was hypothesized that sun and shade and log placement on the ground could influence site selection. Experiment 3 was conducted in 1999 to examine these factors. Twelve white pine (*P. strobus*) logs were cut at the Kirkwood Township site and placed at the Wells Township site in early June. These logs were 1 m in length, averaged 19.1 ± 1.3 cm in diameter, and were placed in a grid with 5 m spacing between each log. Six of the logs were placed in full sun, and six were placed in a semi-shaded, thinned pine stand, in order to examine the influence of sun and shade conditions on oviposition site selection. All logs were raised ca. 10 cm above the ground by nailing two 5 X 10 X 10 cm blocks on each end of the log. This was done in order to expose the entire circumference of the log. The 12 logs were left at the site throughout the field season. Each log was examined weekly, and all new
*M. scutellatus* oviposition scars and *P. nemorensis* oviposition holes were counted in order to examine the oviposition periods for both species.

Two-sample *t*-tests were used to examine differences between logs in sun and shade conditions for number of oviposition scars and oviposition holes (SigmaStat®). The number of oviposition scars and holes was also collected to determine the temporal oviposition pattern for *M. scutellatus* and *P. nemorensis* in the field.
RESULTS

Experiment 1

*M. scutellatus* females were able to get under the screening to oviposit on both red and white pine logs, so only uncaged logs were used for analysis. There were significantly more *M. scutellatus* oviposition scars excavated on white pine than red pine (Table 3-1). The number of oviposition plugs deposited was determined to be indicative of the number of scars containing eggs. There were significantly more plugs deposited on white pine, compared to red pine (Table 3-1). On red pine, 73.5 % of scars contained an egg, while on white pine, 81.3 % of scars contained an egg, but the difference was not significant.

The mean number of larval entrance holes into the sapwood was also significantly greater for white pine than for red pine (Table 3-1), as it is a function of the number of eggs deposited. Examination of the ratio of entrance holes to eggs can indicate larval survival to third instar, where they begin to tunnel into the sapwood. In white pine, 42.1 % of eggs reached the third instar, whereas in red pine, only 27.9 % of eggs reached this stage. The average surface area consumed by larvae was also significantly greater on white pine logs, 37.2 cm², compared to 24.9 cm² on red pine (Table 3-1).

The majority of emerging scolytid beetles were *Ips pini*, so this was the only species examined for competition studies in 1998. Peak emergence for this species occurred from mid- to late-June on red pine, and in early July for white pine (Fig. 3-2). The number of *I. pini* adults emerging from logs in the lab was significantly greater for red pine than white pine (Fig. 3-3). Logs were taken to the lab and insects were removed from caged logs immediately following emergence, preventing reentry and oviposition by offspring. All offspring were thus the first generation of beetles seen in the field (Thomas, 1961).
Table 3-1. Mean number of *M. scutellatus* oviposition scars, scars containing oviposition plugs, entrance holes into the sapwood, and gallery surface area for uncaged red and white pine logs in exclusion cage studies, 1998, Wells Township, Ontario.

<table>
<thead>
<tr>
<th>Pine species</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red</td>
</tr>
<tr>
<td>Oviposition scars</td>
<td>36.9 ± 7.9a</td>
</tr>
<tr>
<td>Oviposition plugs</td>
<td>27.2 ± 5.4a</td>
</tr>
<tr>
<td>Entrance holes into the sapwood</td>
<td>7.6 ± 6.0a</td>
</tr>
<tr>
<td>Gallery surface area (cm²)</td>
<td>24.9 ± 2.7a</td>
</tr>
</tbody>
</table>

Row means followed by the same letter are not significantly different at $P = 0.05$ (two-sample $t$-test).

Figure 3-2. Number of *Ips pini* adults collected in cages in the lab from uncaged red and white pine logs collected 9 June through 18 Aug, 1998 from field sites in Wells Township, Ontario.
Figure 3-3. Cumulative emergence in cages in the lab, 25 June through 14 Aug, 1998, of adult *Ips pini* from uncaged red and white pine logs from field sites in Wells Township, Ontario. There was a significant difference between totals of *Ips* emerging from red and white pine logs at $P = 0.05$ (two-sample *t*-test).

**Experiment 2**

The majority of oviposition scars were excavated by *M. scutellatus* on the sides of red pine logs, in zones 1-3, 3-5, and 9-11; however, the differences were not significant (Table 3-2). The number of scars was lowest on the top of red pine logs, in zone 11-1, and the bottom, in zone 5-7 (Table 3-2). In white pine, oviposition was similar in all zones, regardless of location on the log surface (Table 3-2), and none of the differences were significant. Between red and white pine, the differences between mean number of scars excavated in each zone were not significant at $P = 0.05$ (Table 3-2). There were significantly more *P. nemorensis* pupal cells in zones 5-7 and 7-9 than the top of the log, zones 9-11 and 11-1, for white pine. The number of *P. nemorensis* pupal cells on red pine was not examined, because all cells observed were found on only one sample log.
Table 3-2. Number of *M. scutellatus* oviposition scars and *P. nemorensis* pupal cells found in zones around the circumference of red and white pine logs placed on the ground 16 Jun through 11 Aug 1998, Kirkwood Township, Ontario. The circumference of the logs was divided into equal zones based on a clock face (Fig. 3-1a).

<table>
<thead>
<tr>
<th>Log zone</th>
<th>No. <em>M. scutellatus</em> scars (mean ± SE)</th>
<th>No. <em>P. nemorensis</em> pupal cells (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red pine</td>
<td>White pine</td>
</tr>
<tr>
<td>1-3</td>
<td>15.1 ± 5.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12.6 ± 4.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>3-5</td>
<td>16.2 ± 6.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.9 ± 5.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>5-7</td>
<td>5.2 ± 3.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.6 ± 4.5&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>7-9</td>
<td>9.6 ± 3.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12.6 ± 3.5&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>9-11</td>
<td>12.2 ± 4.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.1 ± 3.7&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>11-1</td>
<td>6.7 ± 4.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.7 ± 4.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>1</sup> Means within a column followed by the same letter are not significantly different at *P* = 0.05 (ANOVA with Tukey’s test).
<sup>2</sup> Data from white pine is presented because only one red pine log was infested, and data were not used in the analysis.

To further examine differences in oviposition and larval success between the top and bottom regions of the logs, data from zones 9-11, 11-1, and 1-3 were combined into the ‘top’ region, and data from zones 3-5, 5-7, and 7-9 were combined into the ‘bottom’ region. There were no significant differences in number of *M. scutellatus* scars excavated on top and bottom of red pine logs (*P* = 0.481), or of white pine logs (*P* = 0.470). There were significantly more *P. nemorensis* pupal cells on the bottom of white pine logs (*P* = 0.020).
Experiment 3

There were significantly more scars excavated by *M. scutellatus* on logs when placed in full sun, compared to logs placed in a shaded area (Fig. 3-4). There was no significant difference in number of *P. nemorensis* oviposition holes on logs for shaded or sunny conditions (Fig. 3-5).

For *M. scutellatus*, oviposition began in late June and continued until the end of August, with peak oviposition extending from mid- to late-July (Fig. 3-6). For *P. nemorensis*, oviposition also began in late June, and continued until early August, with a peak in mid- to late-July (Fig. 3-7).

Figure 3-4. Cumulative number (±SE) of *M. scutellatus* oviposition scars on white pine logs in sun and shade conditions, examined 29 Jun through 31 Aug, 1999, Wells Township, Ontario. There was a significant difference between cumulative totals under sun and shade at \( P = 0.05 \) (two-sample t-test).
Figure 3-5. Cumulative number (±SE) of *P. nemorensis* oviposition holes on white pine logs in sun and shade conditions, examined 29 Jun through 31 Aug, 1999. Wells Township, Ontario. There was no significant difference between cumulative totals under sun and shade at *P* = 0.05 (two-sample *t*-test).

Figure 3-6. Number of new *M. scutellatus* oviposition scars excavated on white pine logs. 29 Jun through 31 Aug, 1999, at field sites in Wells Township, Ontario.
Figure 3-7. Number of new *P. nemorensis* oviposition holes on white pine logs, 29 Jun through 31 Aug, 1999, at field sites in Wells Township, Ontario.
DISCUSSION

Temporal Segregation of Oviposition

The oviposition period for *M. scutellatus* extends from June through August, with a peak seen in mid- to late-July. This supports Rose (1957), who documented that 90% of *M. scutellatus* eggs were laid in a four to six week period in June and July. Adult *M. scutellatus* emergence begins in June in the boreal forest, and adults undergo a period of maturation feeding for 7-10 days before searching for mating and oviposition sites (Rose, 1957). There is a sharp decline in oviposition in early August. This is consistent with the life history of *M. scutellatus* in this region, as eggs laid in August would still be in the second instar in the phloem layer when temperatures dropped in October, and would not be able to enter the sapwood to over-winter, resulting in mortality.

For *P. nemorensis*, the oviposition period extends from June through August, with a peak from mid- to late-July in the boreal forest. These results support the conclusions of Phillips et al. (1987) for an oviposition peak occurring in early summer. Adults that have over-wintered in the duff or under the bark emerge in May and feed for approximately three weeks before the start of the oviposition period (Finnegan, 1958). *P. nemorensis* has four larval instars, before pupating under the bark. Oviposition by females later than early August would also result in offspring in fourth instar or in pupal cells under the bark when temperatures dropped in October, resulting in mortality.

The first *Ips pini* adults emerged in late June, suggesting that oviposition occurred in May, as this species has a 4-week development period (Thomas, 1961). This supports Thomas (1961), who determined that the first emergence of *I. pini* adults in the boreal forest occurred in early May, with attack and oviposition in late May. *I. pini* has two generations per year, the first with 2-3 broods, and the second with one brood (Thomas, 1961). This also
supports findings that scolytid numbers were usually on the decline when cerambycid larvae were noted at logs (Howden and Vogt, 1951). Peak emergence for the first brood of *I. pini* occurs just before peak oviposition for *M. scutellatus* and *P. nemorensis*. There was no second-generation emergence observed in this study, because logs were removed from the field and caged in the lab to observe emergence, and all adult beetles were removed before oviposition could take place.

Temporal segregation (e.g., ovipositing early in the season and having a short development period) allowed *I. pini* to effectively avoid competition, as *Monochamus* larvae can ingest any eggs or larvae they encounter under bark (Flamm et al., 1989). The earlier development of *Ips* allowed them to get a head start on the larger larvae, and leave the area before foraging began. Miller (1985, 1986) and Coulson et al. (1976) suggested that *Monochamus* was an important mortality factor, resulting in reduced *Ips* emergence. Schroeder (1997) suggested that the timing of cerambycid oviposition, in relation to the developmental stage of bark beetles sharing the same habitat, might have an effect on competition and subsequent survival of larvae of both species. By temporally segregating oviposition and emergence, *I. pini* females were able to survive in a habitat where the larger cerambycid larvae would otherwise have a competitive advantage and greatly reduce population numbers.

**Spatial Segregation of Oviposition Sites**

The number of *M. scutellatus* oviposition scars was lowest, and the number of *P. nemorensis* oviposition holes was greatest, on the bottom of logs resting on the ground. This result for *M. scutellatus* supports those of Rose (1957) and Raske (1975), that beetles do not use the bottom region of logs flat on the ground. Some factor related to proximity to the ground prevented oviposition on the bottom of logs, because when logs were raised, females
preferentially oviposited in the bottom region. When raised, the females had free access to the bottom of the log, and the influence of vegetation may not have been as great. This supports conclusions of Raske (1975) that beetles were most likely to oviposit on the lower regions of decked spruce logs.

The smaller *P. nemorensis* may have been able to exploit areas of the log where *M. scutellatus* were not found, because the larger cerambycids were not able to fully access this area, due to proximity to the ground, shade, and surrounding vegetation. Shroeder (1997) suggested that bark beetle species that share the same log generally breed in different areas, and can thus avoid niche overlap; however, in the absence of competitors these beetles are able to fully exploit the new area. When *M. scutellatus* was excluded from an area by constriction, *P. nemorensis* numbers increased because larvae were more likely to survive to the pupal stage without encountering the larger cerambycid larvae.

Female *M. scutellatus* perhaps were not able to oviposit on the bottom of the logs, or the number of larvae foraging in the phloem may have been reduced due to other factors. Upon peeling the bark from study logs, *M. scutellatus* feeding galleries were evident in most regions of the log, and no other insects were detected in these areas. Competitive release was seen, as *P. nemorensis* numbers were greatest in areas where *M. scutellatus* numbers were most limited. *P. nemorensis* survival to the pupal stage was greatest here, suggesting that *M. scutellatus* larvae had a detrimental effect on survival of *P. nemorensis* under the bark.
Effect of Sun Exposure on Site Selection

For *M. scutellatus*, there were significantly more scars excavated when logs were placed in sunny conditions. *M. scutellatus* beetles have been observed to mate in full sunlight, but oviposit in the shade (Rose, 1957; Raske, 1975; Chapter 4). It may be that females mated in full sun, then remained at the same site for oviposition. The degree of sun exposure may have varied over the surface of the log, and females may have chosen shadier places for oviposition. The reduction in sun exposure in shaded areas may have prevented mating, and subsequent oviposition. There was no significant difference in numbers of *P. nemorensis* holes excavated on logs in sun or shade, suggesting that *P. nemorensis* females are unaffected by sun exposure. Phillips and Lanier (1983), concluded that shaded field conditions are preferential for oviposition by *P. nemorensis*. Potentially higher temperatures in sunny areas did not deter oviposition, as females utilized both sites in the same manner.

Host Tree Species

Significantly more *I. pini* emerged from red pine than white pine, suggesting that oviposition and larval success were greater on red pine. The greatest numbers of *Ips* were collected at logs removed from the field early in the season, before oviposition by *M. scutellatus*, and thus before larval foraging by the larger cerambycid. It is unknown if oviposition was higher on red or white pine, but increased numbers would suggest it was higher on red pine. This may be indicative of spatial segregation, as *Ips* choice of a species not oviposited upon as heavily by other guild members may have reduced the potential for interactions under the bark.

The greatest numbers of *P. nemorensis* pupal cells were found on white pine in 1998, suggesting that larvae were more successful on white pine logs, and many more individuals reached the pupal stage than on red pine. Phillips and Lanier (1983) stated that red pine is the
preferred species for oviposition for *P. nemorensis*. It is unknown if oviposition was higher on red or white pine, and therefore impossible to support or refute this conclusion. Interactions with *M. scutellatus* or other larger insects in the phloem-feeding guild also were not examined in that study, so it is not possible to determine if competition had any role in this discrepancy.

*M. scutellatus* oviposition scars were found in significantly greater numbers on white pine compared to red pine. It was observed in the present study that white pine logs generally had a thinner bark than red pine logs. Bark thickness does play an important role in oviposition site selection in *M. sutor* (Zhang et al., 1993) and *M. alternatus* (Nakamura et al., 1995b), with an increase in oviposition on logs with a thinner bark. Results here support those of Nakamura et al. (1995b) for *M. alternatus* - even in logs where she had excavated scars, females were more likely to oviposit on logs with a thinner bark. A female may reduce the amount of time invested in excavation by choosing a thinner bark. In behavioural studies conducted in Chapter 4, it was observed that a female invested a shorter amount of time excavating on white pine, perhaps because she did not have to dig as deeply into the outer bark to reach the phloem layer to deposit an egg. A female ovipositing on thinner bark reduces the investment in a single oviposition event, and increases her fitness by improving her efficiency over time, which may explain the increase in oviposition and larval success on white pine.

The mean number of third instar entrance holes into the sapwood was significantly greater for white pine than red pine. Larval survival to third instar was also greater on white pine, although still less than 45 %. These results would suggest that there is a high level of mortality prior to the third larval instar in this species, supporting previous conclusions that *M. scutellatus* mortality under the bark is quite high. 70 % on balsam fir (Rose. 1957), and
71% on white spruce (Cerezke, 1977). It is unknown why larval survival was greater on white pine than on red pine. This may be due to a number of factors outside the scope of the present study, such as temperature, phloem characteristics, and moisture levels.

The surface area consumed by *M. scutellatus* larvae was also significantly greater on white pine logs. The diameter of white pine (17.0 ± 0.8 cm) was similar to that for red pine (17.8 ± 0.8 cm), indicating that the amount of surface area available for larval foraging was similar as well. Results here are similar to those reported by Coulson et al. (1976), of 31.75 cm² for *M. titillator* feeding galleries on loblolly pine (*Pinus taeda* L.). Anbutsu and Togashi (1997b) found that *M. alternatus* larvae consumed an average of 107 cm² from hatching to formation of the pupal chamber in *P. densiflora* Sieb. et Zucc.. Larvae were able to utilize a greater surface area on white pine, but the depth of these galleries is not known. Larvae will periodically return to feed on phloem, as they generally do not feed on the less nutritious sapwood or heartwood, unless phloem resources are depleted (Hanks, 1999). It may be that larvae have to tunnel deeper into red pine phloem, and the surface area would be reduced, while the same mass of phloem would be consumed.

All of these factors suggest that *M. scutellatus* and *P. nemorensis* are more successful on white pine than red pine, and *I. pini* is more successful on red pine, although it is unknown if oviposition was actually greater on one host tree species compared to the other, or if success was influenced by other factors.
Mortality Factors

There were no predators or parasitoids observed emerging from logs caged in the lab, therefore it was determined that these have little influence on population dynamics of *M. scutellatus*, as found by Parmelee (1941) and Rose (1957). Reduced *M. scutellatus* survival observed during this study must have been due to other factors, such as a reduction in quality and quantity of phloem, or an increase in crowding, competition or cannibalism. Poor conditions resulting from crowding, such as decreased food availability, result in adults that are smaller, with reduced fecundity (Leather, 1995). In less crowded conditions, larvae have greater access to food resources, and thus improve their own chances for survival and future reproductive success.

Larval cannibalism may have been a factor in reduced survival of early instars, as *Monochamus* larvae will consume larvae, eggs and pupae of its own and different species (Rose, 1957). Rose (1957) documented that when *M. scutellatus* larval density was high, particularly in earlier instars, cannibalism resulted in considerable mortality. Anbutsu and Togashi (1997b) also determined that conspecific bites resulted in considerable mortality in *M. alternatus*. Victorsson and Wikars (1996) suggested that *M. sutor* L. larvae used sound production in territorial defense, signaling their presence to other larvae to avoid competition and cannibalism under the bark. Saliba (1972, in Victorsson and Wikars, 1996) showed that *M. sutor* larvae were able to turn sharply in feeding galleries to avoid other larvae in close proximity. A similar pattern was observed in the present study: galleries often missed intersecting with other galleries by millimeters, and larvae produced a loud chirping sound when under the bark.
CONCLUSION

Subcortical tissues of dead and dying trees represent a high quality food source, but one which is in short supply and degrades very quickly after death (Hanks, 1999). The ephemeral nature of the resource results in extreme competition during larval feeding, often resulting in mortality due to cannibalism and reduced resource quality and availability. Larger species are able to out-compete smaller and weaker species under the bark, and exploit available resources (Miller, 1985), and those species that share the resource must have adaptations to avoid larger larvae. It is unknown if avoidance is determined by acoustic or olfactory means, as Monochamus larvae are capable of sound production (Victorsson and Wickars, 1996), and bark beetles can use pheromones from other species to determine the extent of competition (Byers, 1989).

Niche partitioning, through spatial and/or temporal segregation, allows insect species in the phloem-feeding guild to avoid competition, improve fitness, and maintain their place in the guild. Evasion behaviours such as timing of brood development, and segregation to portions of the log inaccessible to M. scutellatus, allowed the smaller I. pini and P. nemorensis to remain in the guild and share resources with the larger cerambycid. This system exists in a similar fashion to that of M. titillator, I. calligraphus, and D. frontaldis described by Flamm et al. (1989). Direct contact with the larger indiscriminate forager is avoided through these strategies, encouraging co-existence amongst guild members.

Some degree of spatial segregation was seen in I. pini, which oviposited more frequently in red pine over white pine. However, this segregation was not complete, as some females chose white pine as well. Ips was also temporally segregated, with two generations per year. Earlier oviposition by over-wintering females allowed for adult emergence from logs before the arrival of larger guild members. There was no evidence of spatial or temporal
segregation between *M. scutellatus* and *P. nemorensis*. There was no demonstrated effect of the smaller *Pissodes*, as *Monochamus* larvae are cannibalistic, and probably feed upon *Pissodes* eggs, larvae and pupae encountered under the bark. This supports results of Yoshikawa (1987a) for the related *M. alternatus*, which is also unaffected by other insect species under the bark.

Further study is required to better understand niche dynamics and avoidance competition under the bark of coniferous species. This study has determined that other insect species have no effect on *Monochamus*, but further study is needed into the impact of *Monochamus* upon other guild members. In the populations studied, predators and parasitoids did not have a measurable effect. Further work is needed to examine influences on population dynamics outside the guild. This could eventually be used in biocontrol programs for reduction of *Monochamus* populations where required.

This work has provided a better understanding of the timing of oviposition by *M. scutellatus*. To reduce economic loss at field sites and mill yards, logs should be removed from the field in spring or early summer, before the start of the *M. scutellatus* oviposition period. Cerezke (1975) suggested storing logs in high piles, and this was supported by the present study, to reduce the amount of surface area available for oviposition. Also, logs should be stored in shade, as suggested by Post and Werner (1988).
Chapter Four: Oviposition behaviour and intra-specific competition of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae)

INTRODUCTION

*Monochamus scutellatus* (Say), the white-spotted pine sawyer beetle, is found throughout North America with the exception of the central United States (Yanega 1996). Males arrive first at logs, and guard positions on the log surface until arrival of the female. Upon her arrival, the male copulates repeatedly with her, often disrupting oviposition (Hughes and Hughes. 1985). Eggs are deposited singly in scars excavated in the bark of dead and dying conifers. After emergence, larvae feed in the phloem layer and eventually tunnel into the heartwood of the log, where they continue to feed until pupation (Gardiner, 1957).

After one to two years, adults emerge and begin a period of maturation feeding on young twigs and foliage (Rose. 1957). Oviposition site selection is important in this species, as females leave the area shortly after oviposition, suggesting that progeny have no parental care.

Intra-specific competition has been determined to have an effect on the oviposition biology of insects (e.g., Schroeder, 1997; Prokopy et al.. 1984). Interference competition generally involves direct access to a resource. Indirect interference may involve chemical cues that prevent access to a resource by other insects, whereas direct interference involves contact between individuals, through territoriality, cannibalism, combat, or suppression (Prokopy et al.. 1984). For several insect species, females are able to differentiate between areas that are available for oviposition, and those that have been exploited or are otherwise unsuitable. One way to avoid competition is through partitioning of a resource through
physical or chemical means, which may act to reduce contact between individuals, and maintain a low population density (Rausher, 1979). Chemical cues for avoidance of direct competition may include oviposition deterring pheromones (ODP), which act intra-specifically to alert females to the presence of another egg in the immediate vicinity (Prokopy et al., 1984).

Sites selected by females for oviposition can have a significant effect on the survival of her offspring, as high quality food resources and avoidance of competition at this stage may increase size and robustness of offspring, thus increasing fitness of the female. To optimize fitness, a female must be able to assess the presence and extent of threat from other insects before oviposition, and this must be incorporated into the behavioural sequence upon arrival at a suitable host. Because larval survival may be influenced by predators, parasitoids, and competitors, the evolution of host choice may be based on ‘enemy-free space’, in which survival is increased by the absence of these factors (Thompson, 1988).

In species of *Monochamus*, an appropriate host is found through visual (aggregation of conspecifics, tree silhouette) or chemical (pheromones or host volatile semiochemicals) cues (Chenier and Philogene, 1989b). After arrival at a suitable host, several factors may influence female choice in site selection, including bark thickness (Nakamura et al., 1995b), presence of other insects, eggs or larvae (Anbutsu and Togashi, 1997a), or other signs of oviposition by conspecific females. Female site choice may reduce larval competition and cannibalism, as larvae will consume other eggs, or larvae, or will engage in combat resulting in death of larvae if they encounter each other in the phloem region (Anbutsu and Togashi, 1997b; Victorsson and Wikars, 1996).

Oviposition behaviour has been examined in several species of *Monochamus* in North America and Japan (Walsh and Linit, 1985; Edwards and Linit, 1991; Jikumaru et al., 1994:...
Anbutsu and Togashi, 1996, 1997a&b; Shibata, 1984; Akbulut and Linit, 1999a&b; Zhang and Linit, 1998). However, there has been no previous examination of oviposition behaviour in *M. scutellatus*. The objective of this study was to document the oviposition behavioural sequence in *M. scutellatus*, and to examine factors influencing this sequence and oviposition site selection after the female has arrived at the log, such as the presence of eggs and/or larvae under the bark.
MATERIALS AND METHODS

Insects

All female and male *M. scutellatus* adults used in 1998 experiments were hand-collected in June and July from red pine (*Pinus resinosa* Ait.) logs cut in the winter, ca. 25 km NE of Thessalon, Ontario (46° 20' N 83° 33' E). In 1999, beetles were hand-collected in July and August from recently felled jack pine (*P. banksiana* Lamb.) logs at a clear-cut site in Lawlor Township, ca. 140 km NE of Thessalon, Ontario (47° 05' N 82° 50' E). Insects were stored individually in screened plastic cages (12 cm long x 7 cm wide x 4 cm high) in environmental chambers set at 20° C, 16:8 L:D, 70 % RH. Beetles were sexed in the lab or the field based on antennal length described by Yanega (1996). The genitalia of 30 adult *M. scutellatus* beetles were dissected to confirm that antennal length could be used to identify gender. Each beetle was provided with a jack pine twig and a 15 % aqueous sugar solution on cotton batting, and was caged for ca. 2-3 days prior to the start of the experiments.

Oviposition behaviour

To develop a description of the sequence of events involved in oviposition, preliminary behavioural observations were made at field sites in early- to mid-afternoon, when insects were most actively mating and females were laying eggs. In the laboratory, behaviour was usually observed in early- to mid-afternoon, under fluorescent lighting at ca. 25°C. Male and female insects were placed in plastic cages (30 cm long x 20 cm high x 11 cm wide) containing a red pine bolt (10 x 10 cm) for oviposition, and a jack pine twig for feeding. The various components of oviposition behaviour were timed with a stopwatch. Between one and four oviposition events were observed for each female.
Choice tests

Five experiments were conducted to determine how the presence of eggs or larvae affected the abundance and distribution of eggs by an ovipositing female. In all Experiments in 1998 and 1999, a female beetle was given a choice between two bolts. In the first Experiment, a female was given a choice between a control bolt (no eggs), and one which contained her own eggs. The second Experiment was a choice test between a control bolt and one which contained eggs from a different conspecific female. Experiment 3 was a choice test between a control bolt and a bolt containing larvae from the study female. In the fourth Experiment, a study female was given a choice between a control bolt, and one which contained larvae from a different female. In Experiment 5, a female was given a choice between a bolt containing her own eggs, and one containing eggs from a different conspecific female.

Preparation of bolts for choice tests

Red pine logs (10 cm diameter) used in choice tests were cut prior to the M. scutellatus flight season, in June 1998 or 1999. These were stored in the laboratory at 25°C until needed for study, ca. 4 weeks after cutting. Log sections (bolts) measuring 10 cm in length were cut from these as needed, and were labeled with permanent marker prior to study. The bolts used in each choice test, one test and one control for 1998, and two tests in 1999, were contiguous from the same red pine log to ensure similarity in factors which may influence oviposition site selection, such as bark thickness, phloem quality, moisture, and log diameter.

For all five Experiments, female beetles were randomly assigned to 'same' or 'different' female groups. To obtain bolts containing eggs or larvae for Experiments 1-4, red pine bolts were introduced to female beetles in both groups for oviposition, and were used in
choice tests after 3-5 days (to allow for egg development), or 2-3 weeks (to allow for larval development). Those females in the 'different' group were allowed to oviposit on bolts for 2-3 days to provide eggs or larvae for use in future Experiments. These bolts were then labeled 'different female egg' or 'different female larvae'. These 'different' females were not used for the purposes of examining experimental treatments, but some were used for observation of oviposition behaviour. Those females that were to be used to examine differences in egg abundance and distribution between treatments were also allowed to oviposit for 2-3 days on bolts. These were labeled 'same female egg' (to be used after 3-5 days) or 'same female larvae' (to be used after 2-3 weeks). These bolts were later used in choice tests involving a bolt containing the female's own eggs, or her own larvae, and a control bolt that had not been previously exposed to beetles. For Experiment 5, each bolt was placed in a cage with a test female or a different female for oviposition, and was removed from the cage after a 24h period.

To conduct choice tests for Experiments 1-4, a female was placed in a cage with two bolts, a control, and one containing oviposition scars. A male beetle, a jack pine twig, and sugar water solution, were also placed in the cage. The female was allowed to oviposit on the bolts for 48h, then both bolts were removed. For Experiment 5, two bolts, one containing eggs from the test female, and one with eggs from a different female, were placed in a cage with the test female and a male beetle for 48 hours for a choice test. A rest period of 24 hours was given between each choice test, to reduce learning, experience and subsequent bias in consecutive choice tests. In both study years, all females were used at least once, and a maximum of four times for choice tests, again to reduce the influence of experience. Copulation and oviposition behaviour were observed and documented sporadically over the study period. Bolts were then removed from the cage, and all oviposition scars on the surface
were counted. Bolts were also examined for the presence of an 'oviposition plug', a brown, sticky substance deposited in excavated scars and visible under a stereomicroscope.

**Determination of the presence of eggs for choice tests**

On bolts used in choice tests, oviposition scars were marked with permanent marker, and examined under a stereomicroscope for presence of a 'plug' prior to reintroduction of bolts to the female. The presence or absence of an oviposition plug, a sticky brown substance in the oviposition scar, could be an indication of oviposition. Fifty-three oviposition scars were dissected by pulling the outer bark back from a scar until a 1 cm² area of phloem was exposed. If an egg was present, it was clearly visible within this area surrounding the scar, and no further dissections were necessary. Ninety-six percent (51 of 53) of scars containing an egg also contained the brown sticky substance that was easily visible using a stereomicroscope (4X magnification), and it was therefore assumed that if this plug was visible, the scar contained an egg. Any scar without this plug was assumed to be empty. This allowed determination of the presence of an egg in these scars without destroying the oviposition site. The oviposition success (%) was calculated as the number of eggs deposited divided by the number of scars excavated.

**Statistical analysis**

Two-sample *t*-tests were used to examine differences in total amount of time spent in the oviposition behavioural sequence by female beetles under field and laboratory conditions (SigmaStat®, version 2.03. SPSS Inc., Chicago, IL). Numbers of scars cut and eggs laid, and subsequent oviposition success, were compared between test and control bolts for each of Experiments 1-4 with two-sample *t*-tests. For Experiment 5, two-sample *t*-tests were used to examine the differences in number of scars cut, eggs laid and oviposition success in bolts containing eggs from the same or a different female. Prior to the *t*-tests, data were
transformed by $\log_{10} (X + 0.5)$ to satisfy assumptions of normality and homogeneity of variance (Zar, 1999), and all subsequent analyses were performed on this transformed data.
RESULTS AND DISCUSSION

Oviposition behaviour

Observations were made of 35 oviposition events involving 14 females over a total of 13 hours in 1998, and of 23 oviposition events involving 13 females over a total of 22 hours in 1999. The *M. scutellatus* oviposition behaviour sequence was observed and divided into components (Fig. 4-1, Table 4-1). Of the 58 observations, ten were of females in the field, and the remaining 48 were of females under laboratory conditions. The components of the sequence were similar, and followed the same order, in both the field and the laboratory, and there was no significant difference between total amount of time spent on oviposition for females under field or laboratory conditions (*P* = 0.269). Therefore, laboratory observations were used for the remainder of the study.

The general oviposition sequence began when the female arrived at the log and began to palpate on the bark surface with her labial and maxillary palpi (sequence (S) 1&2: Fig. 4-1 and Table 4-1). The female excavated a scar in the bark with her mandibles once a suitable oviposition site was found (S3). After excavation was complete, she turned 180° (S4), trailed her abdomen along the surface until the scar was found (S5), and then inserted her ovipositor into the newly excavated scar (S6). She then pumped her abdomen to deposit the egg under the bark surface (S7), removed the ovipositor (S8), turned 180° (S9), inserted her mandibles again into the scar (S10), and then walked away (S11). When alone, this sequence showed little variation for all 27 females observed, and in most cases, eggs were deposited singly.
Figure 4-1. Sequence of components of oviposition behaviour by female *M. scutellatus* beetles, based on 27 females observed over a total of 35 hours in 1998 and 1999.
Figure 4-2. Components of the oviposition behavioural sequence of *M. scutellatus*, and percentage of total time devoted to each portion of the sequence. The sequence began with walking, and concluded with the insertion of mandibles into the scar.
Upon arrival, a female walked over the surface of the log, palpating with her maxillary and labial palpi, until a suitable oviposition site was found. A number of females were observed inserting mandibles into scars encountered during random walking over the surface of the log. Dyer and Seabrook (1978) observed prolonged periods of palpation at oviposition scars cut in the bark, and suggested that contact chemoreception may play a role in site selection. One explanation for this is detection of an 'oviposition plug' containing an oviposition deterring pheromone, or ODP. Anbutsu and Togashi (1997a) observed that subsequent females that encountered scars left the area after palpation, suggesting that this plug had a potentially deterrent effect on site selection. Thus, palpation by females in the present study may have been to assess the status of the site, and also the presence of a plug in any scars the female encountered. The plug potentially deterred females from oviposition, and was detected by palpation on the log surface.

Oviposition behaviour was similar in all female *M. scutellatus* beetles observed in the laboratory and field (Table 4-1). The behavioural sequence was not always uniform, but was stereotypic, occurring in all observed behavioural sequences (Brockerhoff et al., 1999) between walking and excavating a scar, and remained so until removal of the ovipositor. From this point, the sequence was probabilistic, and under the influence of numerous factors, including the presence of other beetles. Insertion of mandibles into the scar occurred in the majority of observed cases, but was not as highly stereotyped as other behaviours. Mandibular insertion after pumping of the abdomen was perhaps related to detection of an oviposition deterring pheromone (ODP) in those scars that contained an egg. Anbutsu and Togashi (1996, 1997a) observed the deposition of a jelly-like substance in oviposition scars cut by female *M. saltuarius* beetles, followed by rubbing the scar with the tip of the ovipositor. As every scar does not necessarily contain an egg, it would be expected that some
scars would not be plugged with pheromone. In such cases, the female would leave the area without turning and inserting her mandibles into the newly excavated scar.

Table 4-1. Behavioural sequence associated with 58 oviposition events by female *M. scutellatus* under field (n=10) and laboratory conditions (n=48) in 1998 and 1999.

<table>
<thead>
<tr>
<th>Behaviour segment</th>
<th>Frequency of segment</th>
<th>Mean duration (sec) ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Arrival on log</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2) Walking/palpating</td>
<td>58/58</td>
<td>232.9 ± 24.2</td>
</tr>
<tr>
<td>3) Excavation of scar</td>
<td>58/58</td>
<td>524.9 ± 60.8</td>
</tr>
<tr>
<td>4) 180° turn</td>
<td>58/58</td>
<td>6.5 ± 0.8</td>
</tr>
<tr>
<td>5) Trailing abdomen</td>
<td>58/58</td>
<td>36.9 ± 6.9</td>
</tr>
<tr>
<td>6) Insertion of ovipositor</td>
<td>58/58</td>
<td>10.7 ± 1.2</td>
</tr>
<tr>
<td>7) Pumping of abdomen</td>
<td>58/58</td>
<td>328.9 ± 37.8</td>
</tr>
<tr>
<td>8) Removal of ovipositor</td>
<td>58/58</td>
<td>7.1 ± 0.8</td>
</tr>
<tr>
<td>9) 180° turn</td>
<td>45/58</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>10) Insertion of mandibles into scar</td>
<td>43/58</td>
<td>9.7 ± 1.8</td>
</tr>
<tr>
<td>11) Leave area</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The majority of time was spent in excavating the scar (45.2%), and pumping the abdomen in egg deposition (28.4%) (Table 4-1, Fig. 4-2). A female also invested a large amount of time walking over the surface of the log to find a suitable site for oviposition (20.1%). This suggests that a female invests the majority of her time in preparation of the site, with her fitness depending on the adequacy of the site she has chosen.

All aspects of this oviposition sequence may be altered or interrupted if a male beetle is present in the cage with the female. The majority of females completed the sequence without interruption by the male (49 of 58 oviposition events). In one event, the female did not complete oviposition, and in the other 8 events, the male slowed the progress of oviposition. Male and female beetles often encountered each other on the log surface, leading to antennal thrashing, followed by the male initiating a 'half-mount' with the female prior to
copulation. The male remained in this position until dislodged by the female, regardless of whether copulation had occurred. This allowed the male to guard the female while she located and excavated oviposition sites (Hughes and Hughes, 1982). In this position, the male stood behind the female, with his forelegs on her elytra, following behind her on his mid- and hind-legs. This slowed progress of the female in locating suitable sites for oviposition, and prevented her from moving to a more attractive portion of the log. At indeterminate intervals, the male copulated with the female, a process that lasted ca. 30-45 sec. In one instance, the male directly interfered with oviposition by mounting a female in the process of ovipositing and immediately forcing her abdomen up out of the scar in order to copulate with her.

**Effect of eggs on site selection**

*Control bolt with no eggs vs. bolt with eggs from same female (Exp. 1)*

When females were offered a choice between control bolts with no eggs and bolts containing her own eggs, the number of scars excavated and number of eggs deposited on both bolts was similar (Table 4-2). The differences between number of scars or number of eggs were not significant between treatments (Table 4-2). Oviposition success (the percentage of excavated scars that contained an egg) was greater on control bolts, but the difference was not significant (Table 4-2). More than half of the total oviposition (54%) occurred on control bolts (Fig. 4-3).
Table 4-2. Response of female *M. scutellatus* to bolts with or without eggs or larvae from herself or a different female during laboratory choice tests, 1998.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Treatment</th>
<th>No. of scars or eggs on test bolts prior to experiment (mean ± SE)</th>
<th>No. of new scars (mean ± SE)</th>
<th>No. of new eggs (mean ± SE)</th>
<th>Oviposition success (%) (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Same female egg</td>
<td>Test (N=11)</td>
<td>8.4 ± 1.8</td>
<td>6.3 ± 1.6</td>
<td>5.1 ± 1.1</td>
<td>3.2 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>Control (N=11)</td>
<td>0</td>
<td>0</td>
<td>4.7 ± 1.0</td>
<td>3.8 ± 0.6</td>
</tr>
<tr>
<td>2 Different female egg</td>
<td>Test (N=27)</td>
<td>18.8 ± 2.2</td>
<td>12.2 ± 1.5</td>
<td>1.7 ± 0.4</td>
<td>0.8 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>Control (N=27)</td>
<td>0</td>
<td>0</td>
<td>8.1 ± 1.1</td>
<td>5.7 ± 1.0</td>
</tr>
<tr>
<td>3 Same female larvae</td>
<td>Test (N=10)</td>
<td>11.9 ± 1.6</td>
<td>8.8 ± 1.3</td>
<td>3.1 ± 1.3</td>
<td>2.3 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>Control (N=10)</td>
<td>0</td>
<td>0</td>
<td>9.5 ± 2.2</td>
<td>3.3 ± 0.7</td>
</tr>
<tr>
<td>4 Different female larvae</td>
<td>Test (N=28)</td>
<td>19.8 ± 1.5</td>
<td>14.0 ± 1.4</td>
<td>3.5 ± 0.6</td>
<td>1.8 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>Control (N=28)</td>
<td>0</td>
<td>0</td>
<td>8.9 ± 1.4</td>
<td>5.4 ± 1.0</td>
</tr>
</tbody>
</table>

1 Means followed by the same letter within a column and Experiment are not significantly different at $P = 0.05$ (log transformation of raw data, followed by a two-sample *t*-test).
2 Test bolts are those containing eggs or larvae from the same or a different female (see materials and methods). Control bolts are those that had not been previously exposed to beetles.

**Control bolt with no eggs vs. bolt with eggs from different female (Exp. 2)**

More scars were excavated and eggs deposited on control bolts, and the differences between treatments were significant (Table 4-2). Oviposition success was significantly higher on control bolts without eggs (62.3 %) than on bolts containing eggs from a different female (35.3 %) (Table 4-2). Eighty-seven percent of eggs were deposited on control bolts, a significantly greater number than that deposited on bolts containing eggs from a different female (Fig. 4-3).

The presence of eggs from a different female deterred oviposition in choice tests, as females preferentially oviposited on a bolt that had not been previously exposed to another female. This supports results from Anbutsu and Togashi (1996) who showed that *M.*
*alternatus* Hope females were less likely to oviposit on bolts with oviposition scars, especially those with scars from a different female. This suggests that female *M. scutellatus* beetles used cues in the immediate area of an oviposition scar to detect the presence of eggs and also to determine if the progeny are her own, or from a different female.

In contrast, in Experiment 1, no significant difference was seen in oviposition between control logs and those with eggs from the study female. The number of excavated scars left empty was greater on test logs, indicated by a lower oviposition success on test logs. This suggests that females did excavate scars on test bolts containing eggs, but they oviposited in these scars with lower frequency than in scars on control logs. This may be because they detected the presence of other eggs near newly excavated scars.

**Effect of larvae on site selection**

*Control bolt with no larvae vs. bolt with larvae from same female (Exp. 3)*

There was a significantly higher number of scars cut in control bolts than in bolts containing larvae from the same female (Table 4-2): however, there was no significant difference between these two treatments in the number of eggs laid or oviposition success (Table 4-2). The majority of eggs were laid on control bolts (60.8 %), but the difference was not significant.
Figure 4-3. Percentage of total oviposition by *M. scutellatus* females on each of test and control bolts during laboratory choice tests. Those columns denoted by an asterix (*) have significantly different means at *P* = 0.05 (Two sample *t*-test).

**Control bolt with no larvae vs. bolt with larvae from a different female (Exp. 4)**

When females were offered a choice between a control bolt and a bolt containing larvae from another female, significantly more oviposition scars were cut and eggs laid on the control bolts (Table 4-2). The number of excavated scars containing an egg was higher on control logs (53.9 % vs. 38.3 % on test logs), but the difference was not significant (Table 4-2). Seventy-five percent of oviposition occurred on control bolts, somewhat higher than that for bolts containing larvae from the same female (Fig. 4-3).

In comparing Experiments 3 and 4, only the presence of larvae from a different female acted to deter oviposition in choice tests, with females preferentially ovipositing on a bolt that did not contain larvae. This supports Anbutsu and Togashi (1996), who stated that,
in *M. alternatus*, fewer oviposition scars were found on bolts containing larvae, particularly when the larvae were from another female, however, the difference was not significant. This would suggest that the deterrent effect was similar if the larvae were from the same or a conspecific female. This may have been due to the presence of an oviposition deterring pheromone, or to frass from feeding larvae, or the detection of reduced phloem availability due to larval feeding under the bark. These results suggest that the effectiveness of the plug as an oviposition deterrent decreased with time after deposition, such that the difference between plugs was negligible. The plug may have degraded with time, as at least 2-3 weeks had passed between deposition and reintroduction to the female. The chemical composition or physical barrier of the plug may have changed, or the plug may have been consumed by emerging larvae.

**Effect of eggs from the same or a different female on site selection**

*Bolt with eggs from same female vs. bolt with eggs from different female (Exp. 5)*

There were no significant differences between numbers of scars cut or eggs laid in bolts prior to the choice tests (Table 4-3), ensuring that the baseline conditions for both experiments were similar. When females were given a choice between a bolt containing her own eggs or one containing eggs from another female, the difference in number of scars excavated was not significant. There was, however, a significant difference in number of eggs deposited (Table 4-3). There was no significant difference in oviposition success between bolts containing eggs from the same or a different female prior to choice tests (Fig. 4-4). However, there was a significant difference in oviposition success between same and different female bolts after the choice tests (Fig. 4-4).
Table 4-3. Number of oviposition scars and eggs deposited in bolts presented to female *M. scutellarus* beetles during choice tests in 1999.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>No. oviposition scars (mean ± SE)¹</th>
<th>No. eggs deposited (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Same female</td>
<td>Different female</td>
</tr>
<tr>
<td>Pre-test</td>
<td>11.2 ± 0.7a</td>
<td>12.6 ± 0.7a</td>
</tr>
<tr>
<td>Choice test</td>
<td>7.7 ± 0.7a</td>
<td>6.3 ± 0.6a</td>
</tr>
</tbody>
</table>

¹Means followed by the same letter within a row for a measured variable (scars, eggs) are not significantly different at *P* = 0.05 (two-sample *t*-test).

When given a choice between a bolt containing her own eggs and one with eggs from a different female, a female preferentially oviposited on bolts containing her own eggs. This suggests that females recognize and avoid oviposition sites excavated by other females. This supports results from Experiments 1-4, which suggested that a female was able to avoid oviposition on bolts containing progeny from a different female with greater frequency than she would avoid a bolt containing her own. It may be adaptive for females to crowd oviposition, which may lead to competition amongst her offspring, because even if combat ensues, at least some offspring would be guaranteed to survive. However, it may be advantageous for the female to avoid competition with progeny from another female. If the competing progeny were not siblings, survival of at least some of her larvae could not be guaranteed, particularly if the competing progeny were better adapted, and cannibalism occurred.
Figure 4-1. Oviposition success on red pine bolts by female *M. scutellatus* beetles during laboratory choice tests. Pre-test refers to oviposition on bolts by females prior to choice tests. Same female refers to oviposition on a bolt containing eggs from the test female, and different female refers to eggs laid on a bolt containing eggs from a different female. There is a significant difference between oviposition success on bolts during the choice test at $P=0.05$, denoted by an asterix (*) (two-sample $t$-test).
CONCLUSION

After arrival on the log, female *M. scutellatus* beetles walked over the surface, palpating and assessing the suitability of the area. During this process, the presence of an oviposition deterring pheromone (ODP) may have acted to prevent oviposition in the immediate area of eggs or larvae. Once a female had found a suitable site, the sequence of behaviours involved in oviposition was generally stereotypic amongst all females examined in this study, until the ovipositor was removed. At that point, the female either turned to insert her mandibles and perhaps deposit a pheromone into the scar, or left the area. This was likely tied to the presence of an egg in the scar.

Insects will preferentially oviposit on host plants on which potential larval survival is greatest (Rausher, 1979), so the ability to detect the presence of competitors would act to reduce competition and improve larval survival. It has been observed that larvae of *Monochamus* are cannibalistic, and that cannibalism can act as a great source of mortality (Rose, 1957; Victorsson and Wikars, 1996). These larvae require a substantial amount of available phloem and sapwood for larval feeding. Survivorship would therefore be greatly decreased if population numbers were high in any given area. Ability to detect eggs and/or larvae at a potential site could improve survival, and oviposition could be deterred by the presence of other progeny.

Oviposition deterrence is adaptively significant in that it allows females to avoid areas that are already being exploited, and thus prevent competition for available resources amongst offspring. Resource partitioning is particularly important in an insect species such as *M. scutellatus*, in which development of offspring and use of resources generally does not begin until some time after the female has oviposited and left the area. If a female is able to
determine that the area is unsuitable for further oviposition, she may increase the likelihood of survival for her offspring, and thus improve her own fitness by ovipositing elsewhere.

Oviposition deterrence has been demonstrated in a number of species, including species of *Rhagoletis* (Prokopy, 1975), and *Battus philenor* (Rausher, 1979). This has been the initial observation in a number of studies investigating the presence and effect of oviposition-dettering pheromones (Anbutsu and Togashi, 1996, 1997a; Kohno et al., 1986; Prokopy et al., 1977; Quiring and McNeil, 1984; Renwick and Radke, 1980; and Zimmerman, 1979). Results from this study would suggest the presence of an oviposition deterring pheromone for *M. scutellatus*. As this compound has been detected in the related Asian species *M. alternatus*, the presence of a brown sticky plug in scars excavated by *M. scutellatus* and an avoidance of oviposition on logs containing progeny from the same or a different female would suggest a chemical deterrence. Further examination of the chemical composition of this plug may determine if the plug acts as a physical or chemical barrier, or if it is involved at all. Behavioural choice tests examining the plug may also determine the role of the plug, and the potential for chemical oviposition deterrence in this species. This will also give a better understanding of avoidance competition and its role in oviposition site selection by female *M. scutellatus* beetles.
Chapter Five: Summary

The white-spotted pine sawyer beetle, Monochamus scutellatus (Say), is a major contributor to wood decomposition in the boreal forest of Ontario. Larval feeding also results in economic losses for logs left at cutting sites. Previous studies have examined the life history, economic importance, and reproductive behaviour of the species in Ontario and elsewhere. This thesis presents information on the influence of chemical cues from the host tree and competition on oviposition by female M. scutellatus beetles.

Attraction to suitable host plants by M. scutellatus was determined by this study to be chemically mediated. Beetles were attracted to turpentine and α-pinene. There was no demonstrated effect of ethanol, a natural by-product of plant decomposition. Further study is required to elucidate the relationship between ethanol and turpentine in attraction by male and female beetles, as it was determined that ethanol has no synergistic effect at the release rates studied. An attraction or synergy with α-pinene has been demonstrated by other authors in species of Monochamus and further study would determine if the release rates used here perhaps were too low to be detected by M. scutellatus. There was a positive relationship between increasing release rates of α-pinene and trap catch for female M. scutellatus and male M. mutator beetles. It is unclear why this relationship was not seen for male M. scutellatus and female M. mutator. Further study with higher α-pinene release rates would also clarify attraction to this host volatile.

This study determined that both spatial and temporal segregation of resources occurs between M. scutellatus and other members of the phloem-feeding guild. The smaller species had no appreciable effect upon survival and oviposition site selection by M. scutellatus. However, I. pini oviposited earlier in the season, so that progeny of the first generation could
emerge before foraging by *M. scutellatus* began. *P. nemorensis* was seen to have highest larval survival in that portion of the log where *M. scutellatus* was not prevalent. Larger species, such as *M. scutellatus*, appear to be unaffected by the smaller and weaker species under the bark, and were able to exploit available resources. Niche partitioning, through spatial and/or temporal segregation allows most insect species in the phloem-feeding guild to avoid detrimental effects of competition, and improve fitness. Competitive exclusion and competitive release can only be accurately demonstrated in a system from which one competitor has been mechanically excluded. Further studies into segregation should focus on caging logs to successfully remove *M. scutellatus* from the system, to obtain an accurate picture of the behaviour and survival of *I. pini* and *P. nemorensis* in this system.

The oviposition behaviour sequence in *M. scutellatus* is stereotypic until after egg deposition, and is probabilistic thereafter. Deposition of an egg in the scar appeared to influence the remainder of the sequence. After pumping of the abdomen to deposit an egg, females may not necessarily turn around and insert the mandibles into the hole. Further research is required to determine if this action is connected to deposition of an oviposition deterring pheromone (ODP) into the scar following oviposition. This study determined that a female will avoid ovipositing near scars containing her own eggs or those from a different female. She will avoid eggs from a different female with the greatest frequency. However, a female will avoid her own larvae or those from a different female with equal frequency. This suggests that the deterrent effect is not as strong 2-3 weeks after deposition of the chemical plug. Further study into the chemical nature of the plug deposited into scars is required, as well as an examination of female deterrence based solely on this plug, as with a Y-tube olfactometer.
Resource partitioning is particularly important in an insect species such as *M. scutellatus*, in which development of offspring and utilization of the resource provided by the female generally does not begin until some time after the female has oviposited and left the area. If a female is able to determine that the area is unsuitable for further oviposition, she may increase the likelihood of survival for her offspring, and thus improve her own fitness by ovipositing elsewhere. This process begins with detection of chemical cues in-flight, which give an indication not only of host tree species, but also of condition. Upon landing at the site, a female must find an area that is free from competition with similar-sized insects, or those that would have similar resource requirements and may reduce the chances of survival of her offspring. The carnivorous nature of larval *M. scutellatus* reduces the requirement for avoidance of smaller species. Further studies on the chemical ecology, natural attack dynamics and influence of intra-specific competition will give insight into the role of this beetle in the phloem-feeding guild.

A knowledge of the chemical ecology of host selection in *M. scutellatus* can be used to determine which compounds act in attraction of beetles to suitable hosts. This can then be applied to developing trapping programs to reduce the impact of *M. scutellatus* at logging sites and mill yards. As there is no demonstrated pheromone in the species, host volatiles are the most promising compounds for use in trapping. As these insects are attracted to hosts in a particular stage of decomposition, understanding attraction to host volatiles and ethanol can clarify the role of *M. scutellatus* in wood decomposition in the boreal forest. This study documented the oviposition season and peak for this species. This is valuable for development of protocols for removal of logs from field sites before oviposition begins. This may be useful in developing protocols for storing logs at field sites, in high piles, to reduce the amount of surface area available for oviposition.
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