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## Monochamus titillator Oviposition and Intraspecific Competition in Shortleaf Pine Bolts

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*Monochamus titillator* Oviposition and Intraspecific Competition  
in Shortleaf Pine Bolts

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Master of Science in Entomology

by

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July 2015  
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## Abstract

*Monochamus titillator* (Coleoptera: Cerambycidae) feed on trees in the family Pinaceae as adults and larvae. Adults feed on healthy twigs and branches and oviposit on stressed, dead, or dying trees. Prior to oviposition, females construct pits on the bark surface using their mandibles. The number of eggs laid beneath bark, where oviposition pits have been constructed, varies greatly. Developmental time and adult body size also vary greatly. I investigated oviposition and intraspecific competition with the goal of determining the degree to which various insect densities and oviposition times impact the following: 1) oviposition pit construction; 2) egg deposition; 3) emergence, 4) and adult body size. Females constructed 463 oviposition pits and laid 1002 eggs on 26 bolts. The average number of pits per bolt was 17.8 and the average number of eggs per bolt was 38.54. The average number of eggs per pit was 2.16 and differed significantly between our treatment combinations ( $P=0.0132$ ). Significant differences were detected between our treatment combinations for the number of pits constructed ( $P=0.0011^*$ ) and eggs deposited ( $P=0.0327^*$ ). There was a positive correlation between the number of pits per bolt and the number of eggs per bolt ( $P=-.0001^*$ ,  $R^2=0.691$ ). Emergence occurred in 49 out of 60 bolts and 222 *M. titillator* emerged in total. The average number to emerge was 3.9 *M. titillator* per bolt and the mean number for emergence differed significantly between our treatment combinations ( $P<0.0001$ ). A significant and positive correlation was detected between the mean number of pits per bolt and the mean number for emergence ( $P>0.0001$ ,  $R^2=0.448$ ). It took an average of 96 days for larvae to emerge. These data, when taken together suggest that density dependent responses were detected and can be attributed to intraspecific competition.

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## **Dedication**

I would like to dedicate this document to my grandparents for all the love and support they provided over the years.

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## Introduction

The southern pine sawyer (Coleoptera: Cerambycidae: *Monochamus titillator* (Fabricius)) is a wood-boring cerambycid beetle native to south and eastern North America (Webb, 1909). This beetle colonizes physiologically stressed, mechanically damaged, and freshly killed pines. Larval tunneling can degrade saw timber and cause economic losses (Webb, 1909). *Monochamus titillator* competes for phloem with economically important pine bark beetles. The competitive relationship between *M. titillator* and these bark beetle species is either strongly asymmetrical favoring *M. titillator* or commensal (Flamm et al., 1989). Because it is such an efficient competitor and facultative predator *M. titillator* can increase the rate of bark beetle mortality when both species are present and interacting (Coulson et al., 1980; Dodds et al., 2001). The genus *Monochamus* contains species that are the most important vectors of pinewood nematode (PWN), the pine wilt-causing organism (Nematoda: Aphelenchoididae: *Bursaphelenchus xylophilus* (Steiner and Buhner)) (Pimentel et al., 2014). Pine wood nematode is native to the United States and has a minimal impact on pines in its native range; however, it has been introduced into Europe and Asia where it kills pines and has caused substantial economic losses (Mamiya, 1988).

*Monochamus titillator* research and literature has focused primarily on its life history and biology (Alya, 1984; Alya & Hain, 1985; 1987; Flamm et al., 1989; Pershing & Linit, 1985; Pimentel et al., 2014; Webb, 1909), its relationship to economically important bark beetles (Coulson et al., 1976; Coulson et al., 1980; Dodds & Stephen, 2000; Miller, 1985; 1986; Schoeller et al., 2012), its vector relationships to PWN (Akbulut & Stamps, 2012; Alya & Hain, 1985; Esser et al., 1983; Luzzi et al., 1984; Pimentel et al., 2014), its chemical ecology (Allison et al., 2012; Billings & Cameron, 1984; Miller & Asaro, 2005), and its role as an intraguild

predator (Dodds et al., 2001; Schoeller et al., 2012). No studies have been conducted that examine the effects of intraspecific competition on *M. titillator* fecundity and fitness. The goal of this thesis is to investigate in the lab, and in the absence of other insect competitors and predators, how oviposition and intraspecific competition affects *Monochamus titillator* fecundity and fitness.

This thesis is composed of three chapters: the first chapter contains a literature review describing the biology and ecology of *M. titillator* and the prevailing theories comprising competition in endophytic insects communities. The second and third chapters describe two laboratory experiments conducted to examine the relationship between oviposition, intraspecific competition, and *M. titillator* fitness. In chapter two, the number of females ovipositing and the amount of time allocated to oviposition is examined in relation to (1) oviposition pit construction and (2) egg deposition in caged shortleaf pine bolts (short logs). In chapter three, I examine the relationship between number of ovipositing females and the amount of time allocated to oviposition on (1) developmental rate, (2) emergence density, (3) size, and (4) fecundity of offspring emerging from caged shortleaf pine bolts.



## I. Literature Review

### A. Life History of *Monochamus*

The southern pine sawyer, *Monochamus titillator* (F.), (Coleoptera: Cerambycidae) is a common coniferophagous wood-boring cerambycid native to south and eastern North America (Craighead, 1923; Linsley & Chemsak, 1984; Webb, 1909). The first and most comprehensive review of the life history, ecology, behavior, and economic status of *M. titillator*, cited in virtually all subsequent *M. titillator* publications, is Webb (1909). In Arkansas, adults emerge in late spring, ca. May, and flight occurs through October. Depending upon temperature there can be one to two generations completed per year (Alya & Hain, 1985; Dodds & Stephen, 2000; Webb, 1909). Adults are mottled brown in color and vary greatly in size, between 13 to 30 mm in length (Webb, 1909). *Monochamus* can reproduce in *Picea*, *Abies* and *Pinus*, but *M. titillator* prefers pines for adult feeding and oviposition (Craighead, 1923; Webb, 1909).

Adults of both sexes are attracted to hosts by a combination of pine volatiles ( $\alpha$ -pinene and ethanol), pheromones (male produced monochamol), and bark beetle kairomone attractants (e.g. frontalin, ipsenol and ipsdienol) (Allison et al., 2001; Billings & Cameron, 1984; de Groot & Nott, 2004; Miller et al., 2011). Host volatiles are emitted from trees exhibiting physiological stress. Lighting strikes, drought, wind or ice damage, logging damage, and bark beetle attacks are all factors, both biotic or abiotic, that cause trees to emit attractive volatiles (Baker, 1972; Hanks, 1999; Hanks et al., 1993). High populations of *Monochamus* may occur in areas where hosts are under physiological stress. Freshly logged pine stands with an abundance of slash and highly compacted soil may also provide suitable oviposition material for *M. titillator*.

Adults mate on the bole of host trees. Females use their mandibles to chew conspicuous pits on the bark surface into which eggs are laid. This behavior is not unique to the genus, but is

ubiquitous among the entire subfamily Lamiinae (Linsley, 1961). Pit construction can take a considerable amount of time; it can take over an hour to complete depending upon bark thickness (Hughes & Hughes, 1987). The shape of oviposition pits differs depending upon bark thickness. Thick bark yields deep ‘funnel-shaped’ oviposition pits while thin bark yields ‘slit-like’ oviposition pits. The distribution of oviposition pits across the bark surface for *M. titillator* has not been quantified, but *M. alternatus* (Hope) has a uniform pit distribution (Shibata, 1984). In a field study, Alya and Hain (1985) found that females prefer to oviposit in shaded areas of the tree. Males have been observed copulating with females as they construct oviposition pits (Webb, 1909). *Monochamus* males exhibit guarding behavior and will maintain contact with females for several hours after oviposition to keep other males at bay (Hughes, 1979). After the pit has been constructed the female places the apex of her abdomen into the oviposition pit, inserts her ovipositor and lays several eggs beneath the bark in a circular shape (Webb, 1909).

Oviposition may be regulated by tree physiology. *Monochamus titillator* is not known to successfully oviposit in healthy trees, but oviposition pits have been observed with resin flowing from them in trees freshly attacked by southern pine beetle (*Dendroctonus frontalis* Zimmermann) (Stephen, 2011). Although oviposition pits are constructed in such trees, it is likely that high mortality occurs in the egg and early larval stages as a result of resinosis. Oviposition will not be successful if the resin defenses of the trees are functioning efficiently; trees must be at the right stage—not too healthy or dead—in order for oviposition to be successful. For example, Akbulut et al. (2004) found a negative correlation between bolt holding time—the period of time between tree felling and oviposition—and the number of eggs laid per bolt by *M. carolinensis* (Oliver). Logs became attractive within seven days and after 42 days were no longer attractive to ovipositing females after (Akbulut et al., 2004). They attributed the

high generational mortality (88%) from egg to adult in freshly cut logs to resinosis and in older logs to substrate degradation, desiccation, competition, and cannibalism (Akbulut et al., 2004).

The number of eggs oviposited in a single pit varies greatly. In naturally colonized pines, Webb (1909) observed a maximum of nine and Alya and Hain (1985) observed 3-6 eggs in a single pit. I have observed a maximum of 20 eggs in a single pit. It may be possible for more than one female to lay eggs in a single pit. An average of 3.45 eggs per pit was observed by Dodds and Stephen (2000) in a southern pine beetle (SPB) infestation.

A sympatric species, *M. carolinensis*, lays fewer, between one and three eggs per pit (Alya & Hain, 1985) and when multiple eggs are laid per pit then they are laid side by side, not in a circle (Walsh & Linit, 1985). Two other North American species, *M. notatus* (Drury) and *M. scutellatus* (Say), only lay a single egg per pit (Hughes & Hughes, 1987). Following oviposition the phloem turns brown making it easy, once the bark has been removed, to detect oviposition sites. Eggs hatch between five (Webb, 1909) and nine days (Alya & Hain, 1985) depending upon latitude, temperature, and possibly host species. Resinosis, inviability, and/or predation are responsible for 37% of *M. titillator* egg mortality (Dodds & Stephen, 2000).

A phenomenon observed in many *Monochamus* species is that a high percentage of pits are left empty. In their experiment on oviposition biology, Walsh and Linit (1985) found that 26% of oviposition pits constructed by *M. carolinensis* were vacant. It is not clear exactly why this occurs because it takes a considerable amount of time to construct an oviposition pit during which the female is expending energy and is exposed to predators. Several hypotheses have been developed to explain this behavior in *Monochamus*. Competition among adults for oviposition sites may lead to oviposition site abandonment; one female may displace another and the oviposition pit may never be filled with eggs. After pit construction females may detect the

presence of conspecific eggs (Anbutsu & Togashi, 1996; Anbutsu & Togashi, 1997b; Anbutsu & Togashi, 2000), conspecific larvae (Anbutsu & Togashi, 1996; Anbutsu & Togashi, 2002), or oviposition deterring chemicals deposited by other conspecific adult females (Anbutsu & Togashi, 2001) and, as a result, choose to not to lay eggs in order to reduce intraspecific competition. Similar behaviors to reduce competition—both interspecific and intraspecific—have also been observed in other insect species (Corbet, 1973; Dixon et al., 1978; Hemptinne et al., 2001; Katsoyannos, 1975; Nufio & Papaj, 2001; Prokopy, 1981a; Prokopy, 1981b; Zimmerman, 1979). Bark beetles use anti-aggregation pheromones, which operate similarly to oviposition deterring chemicals by reducing intraspecific competition associated with overcrowding (Birch et al., 1980; Byers & Wood, 1981; Byers, 1989; Byers et al., 1984).

*Monochamus* larvae forage beneath the bark of dead and dying conifers and feed on phloem (Craighead, 1923; Webb, 1909) and bark beetle larvae (Dodds et al., 2001). A taxonomic description of the larvae is provided in Craighead (1923). The number of instars is highly variable and a discrete number has not been calculated for *M. titillator* (Dodds & Stephen, 2000), however *M. carolinensis* has three to six instars (Pershing & Linit, 1988) and *M. scutellatus* has four (Rose, 1957). Because of variability in number of instars and difficulty in detecting discrete instars, larval development is classified into three stages: 1) early stage larvae forage exclusively on the phloem; 2) middle stage larvae begin scoring the sapwood with their mandibles; and 3) after 18 to 32 days late stage larvae begin tunneling into sapwood for pupation (Dodds & Stephen, 2000; Webb, 1909). *Monochamus* larvae may consume between 40 and 100% of the tree's phloem (Craighead, 1923). When most of the phloem has been consumed by *Monochamus* larvae the bark becomes detached and begins to slough off (Craighead, 1923). Frass and excelsior are extruded from cracks in the bark onto the ground making it possible in

the field to detect trees in which *Monochamus* larvae have foraged (Craighead, 1923). Alya and Hain (1985) determined that ca. 85% of immatures overwintered as larvae, pupated in the spring, emerged as adults in summer then began laying eggs. Some of the adults produced by those eggs will emerge in the same year and the rest will overwinter as larvae and emerge the following year (Alya & Hain, 1985; Webb, 1909). Pupation occurs in the terminal end of u-shaped sapwood tunnels constructed by the larvae. Larvae bore into the sapwood for pupation and pack the tunnel with frass and excelsior. This provides a structural barrier that may protect the vulnerable pupae from predators and parasites (Crowson, 1981). Occasionally, larvae will not construct these tunnels but, as with *Rhagium* species, will pupate between the sapwood and the inner bark (Craighead, 1923). The highest *M. titillator* mortality (49%), occurs during mid-larval stages and results from competition, parasitoids, and predators (Dodds & Stephen, 2000). High larval mortality, mostly attributed to competition, has also been observed in other sawyer beetles (Rose, 1957).

Adults emerge after chewing round, pencil-sized, exit holes. The amount of time required for *Monochamus* to pass from egg to adult varies greatly, taking as few as 33 (Linit, 1985), but more often between 50 to 100, days and sometimes much longer (Akbulut et al., 2004; Alya & Hain, 1985). *Monochamus confusor* Kirby and *M. scutellatus* can take one to four years to develop from egg to adult (Graham & Knight, 1965). Newly emerged *Monochamus* adults must locate and feed upon fresh pine branches and twigs for an obligate period of maturation feeding lasting from one to four weeks (Linit, 1988). Feeding occurs during the day and is required for egg production and sexual maturation (Akbulut & Stamps, 2012; Alya & Hain, 1985; Beeson & Bhatia, 1939; Linsley, 1959; Linsley, 1961; Maehara et al., 2007; Walsh & Linit, 1985). After maturation feeding, adults fly to dead and dying pines for mating and oviposition and the life

cycle begins anew. Adults may live more than 70 days and will continue to feed throughout the duration of their lives.

## **B. Competition**

Interspecific competition between *M. titillator* and *Ips* and *Dendroctonus* bark beetles, has been studied (Coulson et al., 1976; Coulson et al., 1980; Hennier, 1983); however interspecific competition between *M. titillator* and *M. carolinensis* and intraspecific competition within *M. titillator* has not. To understand how interspecific competition operates at the community-level—the level that has received the most focus—we must first understand how each phytophagous species in the system functions in the absence of interspecies competitors or predators (Park, 1964). We must determine how fitness measurements like size, weight, and mortality relate to conspecific density dependent and density independent factors, and how these traits are altered in the presence of other species.

Competition is hypothesized to be one of the major ecological interactions, affecting the abundance and distribution of species in biological communities (Begon et al., 2006). As defined by Begon et al. (2006), “...competition is an interaction between individuals, brought about by a shared requirement for a resource and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned.” Competition occurs when two or more organisms overlap spatially and temporally while relying on the same resource. Food, water, territories, mates, and oviposition sites are all examples of resources for which competition occurs. In the biological system discussed in this thesis, competition can occur among *M. titillator* for food (pine phloem), mates (Hughes & Hughes, 1982), and oviposition sites (Hughes & Hughes, 1987).

### **C. Types of competition**

Competition is generally conceptualized as scramble competition and interference competition (Begon et al., 2006; Nicholson, 1954; Price et al., 2011). In reality these are two theoretical extremes and most competition likely occurs as some combination of both, which may change depending upon life stage (Griffith & Poulson, 1993). Scramble competition operates when individual organisms require, and draw from, the same limited resource. Scramble competition is also referred to as exploitative competition and is commonly characterized as a “free-for-all” among the competitors for the limited resource (Nicholson, 1954; Price et al., 2011). Scramble competition is most intense when the population density of the organisms drawing from the resource is large and the resource supply is limited.

Interference competition, also called contest competition, operates when interactions between organisms work in such a way that one organism acquires an excessive amount of a resource and obstructs access to others (Nicholson, 1954; Price et al., 2011). This occurs when an individual holds a monopoly on a resource by aggressively maintaining a territory, killing potential competitors, or producing chemicals that deter access to a resource (Denno et al., 1995; Kaplan & Denno, 2007; Price et al., 2011).

### **D. Interspecific Competition in *Monochamus* Communities**

In North America, two sympatric species of *Monochamus* generally co-occur in each region where the genus is present (Pimentel et al., 2014). Surveys of five different North American pine forests across the continent revealed different *Monochamus* species pairings in each region except for Arizona, where only a single species was detected (Pimentel et al., 2014). Taxonomic (Linsley & Chemsak, 1984) and ecological research (Akbulut & Stamps, 2012;

Hughes & Hughes, 1982; Pimentel et al., 2014) research state that each species in each pairing differs only slightly in size, behavior, and phenology.

Provided that the “competitive exclusion principle” (Gause et al., 1934) is a valid theory, why do we see two species of *Monochamus* with seemingly identical niche requirements coexisting in space and time? Competition is possible between these species because the populations exhibit some degree of niche overlap spatially and temporally, but not an entire overlap. The extent of overlap between *Monochamus* species pairings has not been explicitly determined for *M. titillator* and *M. carolinensis*. The slight differences observed between each species in size, behavior, and phenology are coevolutionary strategies that enable the stable coexistence of each species (Connell, 1980).

Coexistence occurs through resource partitioning (MacArthur & Levins, 1964; 1967) which occurs when two closely related species with the same ‘fundamental niche’ compete, dividing the resources and reducing the ‘realized niches’ of both species (Price et al., 2011). “Natural selection through competition” causes niche divergence, which reduces niche overlap of the two species, and eventually reduces interspecific competition and promotes coexistence (Lack, 1954; MacArthur, 1958; Price et al., 2011). Theoretically, these sympatric *Monochamus* species can only coexist if they differ slightly in their niche requirements, but these requirements have not been adequately outlined for each species. Differences in size, behavior, and phenology are likely adaptations each species has acquired in response to competition eventually resulting niche divergence.

A brief description of *M. titillator* and bark beetle interactions is important. These competitive interactions have been characterized as both interference and scramble competition and have been identified to occur between *M. titillator* and the sympatric *Ips* (Hennier, 1983;



Miller, 1984; Miller, 1985) and *Dendroctonus* (Coulson et al., 1976; Coulson et al., 1980) bark beetle species. Coulson et al. (1976) concluded that the form of competition between *M.*

*titillator* and the southern pine beetle, *Dendroctonus frontalis*:

“...contains elements of both interference and exploitation as defined by (Brian, 1956). The presence of *M. titillator* directly and measurably limits access by *D. frontalis* to the inner-bark region of the tree which constitutes a requisite resource for both species. In this sense, the process described herein is similar to that observed by Connell (1961) in competing species of barnacles, and can be considered interference or ‘contest’ Nicholson (1954) competition. *M. titillator*, being a much larger and more mobile insect than *D. frontalis*...has a greater ability to utilize the inner bark region of the tree, and in this regard, the form of competition can be considered of the exploitation or ‘scramble’ Nicholson (1954) type, i.e., *M. titillator* has a differential ability to obtain and utilize a greater portion of the common resource (Coulson et al., 1976).”

Timing is important when evaluating *Monochamus* bark beetle interactions. The bark beetles are at a competitive disadvantage after *Monochamus* arrives and larvae begin to develop.

*Monochamus* larvae are large and aggressive and feed upon both phloem and other members of their feeding guild—bark beetles included (Dodds et al., 2001). Although bark beetles tend to arrive before *Monochamus* there is a window of overlap in which *Monochamus* gains a competitive advantage that has been noted to correspond with increasing bark beetle mortality (Coulson et al., 1976; Coulson et al., 1980; Hennier, 1983). Coulson et al. (1980) estimated that southern pine beetle mortality was higher in areas where *M. titillator* had foraged, reaching nearly 70%, whereas southern pine beetle mortality was only ca. 14.6% across the entire tree bole. The section of the tree bole in which *Monochamus* larvae were foraging also impacted SPB mortality (Coulson 1980; Hennier 1983). Research also found similarly high mortality to *I. avulsus* (Hennier, 1983) and *I. calligraphus* (Hennier, 1983; Miller, 1986) in areas where *M. titillator* had foraged.

## **E. Intraspecific Competition**

Competition among members of the same species is called intraspecific competition and is the central theme of this research. Members of the same species compete more intensely for resources than members of two different species because members of the same species have the same resource requirements for survival, growth, and reproduction (Begon et al., 2006; Denno et al., 1995; Strong et al., 1984).

## **F. Intraspecific Scramble Competition**

Simply the way the system is structured leads to intense scramble competition among adult *Monochamus* for the limited and dying plant material on which their offspring depend for nourishment (Hanks et al., 1993). Only a finite amount of nutrition exists in a particular host and the larvae must derive all of their nutrition from the host in which they hatch (Crowson, 1981). Larvae will perish if the food runs out and they have not fully developed into adults because they are legless and cannot move to a new host. The hosts—dead and dying pine trees—colonized by *Monochamus* are sporadically available, patchily distributed, and ephemeral. It is generally believed that *M. titillator* cannot colonize healthy trees, therefore successful colonization depends upon sporadically occurring external factors such as damage from wind, ice, lightning, fire, bark beetles, logging or stress factors caused by drought and/or compacted soils to render the hosts suitable for oviposition. Hosts are patchily distributed across the landscape because of the random timing and spacing of these events. Hosts are ephemeral because they begin degrading as soon as they become suitable for oviposition. The narrow window of availability in which host trees are suitable for *Monochamus* colonization is ca. three to 45 days post felling (Akbulut et al., 2004). The period of availability may be substantially longer in tree species located in higher latitudes or for trees damaged in winter. For offspring to develop successfully,

the free-living adults must locate physiologically suitable host material. If the host is overcrowded with conspecific larvae, high rates of mortality and reduced fitness may result from intraspecific competition for phloem among these individuals (Hanks, 1999; Ikeda, 1979; Ochi & Katagiri, 1979).

## **G. Intraspecific Interference Competition**

*Monochamus* exhibit interference competition with conspecifics in the following separate, but not entirely independent ways: (1) Males compete with other males for females and females compete with other females for oviposition sites (Hughes & Hughes, 1987). Males aggressively guard and defend their mates from other males and females aggressively defend oviposition sites from other females (Hughes & Hughes, 1982; Webb, 1909). The forelegs of males are adapted for holding onto mates (Hughes, 1979) and larger males tend to have an advantage when guarding and holding onto mates (Hughes & Hughes, 1987). Larger females are more successful at acquiring and defending optimum oviposition sites. The possible outcomes of these aggressive interactions for the smaller insects are injury, death, and restricted access to mates and oviposition sites. Larger males and females can also be negatively impacted by expending an excessive amount of energy to maintain territories; losing mates outside the territory; and becoming injured. (2) After oviposition, females are known to deposit chemicals that deter conspecific oviposition (Anbutsu & Togashi, 1997b; Anbutsu & Togashi, 2001). This is hypothesized as an adaptation for reducing intraspecific competition among larvae. (3) If two larvae come into contact they will interact aggressively and the older and larger larva will often kill or consume the smaller and younger larva (Anbutsu & Togashi, 1997a; Anbutsu & Togashi, 2001; Dodds et al., 2001; Victorsson & Wikars, 1996). Victorsson and Wikars (1996) state that

the loud chewing sound generated by *Monochamus* larvae possibly prevents intraspecific competition by alerting conspecifics of their presence.

A laboratory experiment conducted by Anbutsu and Togashi (1997a) investigated the spatial and temporal role of *M. alternatus* larval competition in pine bolts. Larvae were artificially inoculated into bolts at two different times (simultaneously or two weeks apart) and two distances (either 2.5cm or 10 cm) from each other. When larvae were inoculated into bolts asynchronously (two weeks apart), those inoculated later and those spaced closer together (2.5cm apart) exhibited significantly higher mortality. Larvae inoculated simultaneously and closer together (2.5cm apart) exhibited significantly higher mortality than those inoculated simultaneously and further apart (10cm). This emphasizes the importance of larval age, size, and positioning within the bolt on the outcome of interference competition among *Monochamus* larvae.

## **H. Symptoms of Competition: Effects on Individuals**

Symptoms of competition do not only manifest as mortality, but also as changes in developmental rate, decreased body size, weight, and fecundity (Begon et al., 2006; Denno et al., 1995; Denno & Perfect, 1994; Price et al., 2011). All of these fitness traits are important and contribute to the eventual fate of individual organisms and their populations (Goldsmith et al., 1996; Hanks et al., 1996; Hughes & Hughes, 1982). This section reviews the potential impact of competition on adult body size.

Body size can influence the outcome of competitive interactions by influencing dispersal ability (Davis, 1984; Zera & Denno, 1997), resource partitioning (Flamm et al., 1989; Hughes & Hughes, 1982), resource acquisition (Hughes & Hughes, 1987; Vandermeer & Goldberg, 2013), and mating success (Hanks et al., 1996; Hughes & Hughes, 1982; Hughes, 1981; Hughes &

Hughes, 1987), but body size is also influenced by competition. Body size of adult *Monochamus* and other cerambycids is influenced by the quality and nutritional properties of the environment in which larvae develop (Andersen & Nilssen, 1983; Haack & Slansky Jr, 1987; Hanks, 1999). Since *Monochamus* larvae develop beneath the bark of dead and dying pines and must derive all of their nutrition from the phloem, which is limited in supply, the amount of nutrition available to any single larva decreases as the number of larvae increases. We, therefore, expect that the body size of an adult *Monochamus* would change in proportion to number and size of other conspecific foraging larvae present during their development. Competitive interactions that result in changes in body size have been characterized as density dependent in scale insects (*Fiorinia externa* and *Tsugaspidotus tsugae*) (McClure, 1980), plant hoppers (Denno & Roderick, 1992), aphids (Dixon, 1998), and many other phytophagous insect species.

The impact of population density on adult body size comes in several forms, which are all related to the concepts of scramble and interference competition (Nicholson, 1954). Individual organisms tend to acquire their share of resources proportional to their size, therefore, larger individuals tend to attain a disproportionately larger share of the available resources (Vandermeer & Goldberg, 2013). Larger individuals are more likely to displace smaller individuals in a way that resembles interference competition. Individuals arriving first at a food resource tend to grow larger. In insects (Denno et al., 2000) high population densities tend to produce a large number of smaller individuals and smaller populations tend to produce a few larger individuals (Vandermeer & Goldberg, 2013).

Although population density influences body size, it is not necessarily the sole causal factor contributing to intrapopulation body size variation. Other factors influencing adult body size are host species, host nutritional quality, host defenses, moisture availability, and a genetic

predisposition to grow within a specific size range (Andersen & Nilssen, 1983). It is clear that the conditions within the larval host environment are essential to the development and success of *M. titillator* and that the number of foraging larvae may explain why we observe body size variation in adults. One objective of this research is to examine competition as a potential factor leading to adult size variation.

## **I. Research Objectives**

I address the following questions in this thesis. In cages containing uniformly treated shortleaf pine bolts, how does number of ovipositing females and the amount of time allocated to oviposition impact: (1) number of oviposition pits constructed by adult females, (2) egg deposition by adult females, (3) offspring developmental rate, (4) offspring emergence density, (5) offspring survivorship, (6) offspring size, and (7) offspring fecundity.

I chose to measure these traits because they are known to respond to competition (Begon et al., 2006; Denno et al., 1995; Denno & Perfect, 1994; Price et al., 2011). I hypothesize that competition among larvae for the limited phloem resource leads to a density dependent response causing a reduction in size, weight, developmental rate, survivorship, fecundity and overall fitness.

## **II. Effects of Oviposition Time and *Monochamus titillator* Density on Oviposition Pit Density and Egg Deposition in Caged Shortleaf Pine (*Pinus echinata*) Bolts**

### **A. Introduction**

Life history tradeoffs occur when individual organisms allocate resources in different ways in order to maximize reproductive success (Partridge & Farquhar, 1981; Price, 1974; Smith & Fretwell, 1974; Tanaka, 1993; Zera, 1984; Zera & Denno, 1997). Individual *Monochamus titillator* (Fabricius) (Coleoptera: Cerambycidae) females may distribute eggs in different ways, presumably to maximize individual reproductive success. For example, individual *M. titillator* females (Fig. 1) in a population will vary the number of eggs laid in a single oviposition pit. They may choose to leave a pit vacant or oviposit any number between 1 and 20 eggs per pit. Multiple eggs are laid in a circular fashion (Fig. 2). More eggs, however, does not necessarily equate to the survival and reproductive success of more offspring (Price, 1974). More eggs per pit may mean more larvae foraging and competing for the limited phloem resource. Conversely, fewer larvae will be foraging beneath the bark if fewer eggs are laid and competition among conspecifics would be reduced. If this is true, then we might expect to see the number of eggs being laid in a single reproductive event—per pit—decrease as the number of conspecifics (either eggs or larvae) increase within a particular host environment. Oviposition pits are conspicuous ‘funnel-shaped’ depressions on the bark surface (Fig. 3a), easy to count, and may provide an external indicator of *M. titillator* population density in naturally colonized trees in the field. Oviposition pits are visible, but less conspicuous on thinner bark where they resemble slits on the bark surface (Fig. 3b).

Using field collected adult *M. titillator*, I examined oviposition on individually caged pine bolts and formulated the following hypothesis: I hypothesize that the number of ovipositing females and the time allotted for oviposition affect: (1) the number of pits constructed, (2) the number of eggs deposited, and (3) the number of eggs laid per pit.

## **B. Materials and Methods**

### **Monochamus Trapping and Handling**

Trapping of live *Monochamus titillator* adults was initiated April 1, 2013 and continued through mid-September (Fig. 4). Traps (Fig. 5) of the same design used by Lynn-Miller (2013) were erected approximately 15 miles west of Fayetteville, AR, in shortleaf pine (*Pinus echinata* Mill.) stands of the Wedington Tract of the Ozark National Forest. All traps were baited with lures consisting of a host volatiles ( $\alpha$ -pinene,  $\beta$ -pinene, and ethanol) and *Ips* bark beetle pheromones (ipsenol, ipsdienol, and lanierone) obtained from Synergy Semiochemicals, Burnaby, BC, Canada. Two traps erected on June 27, 2013 were baited with monochamol in addition to pine volatiles and *Ips* bark beetle pheromones. Lures were replaced monthly. Pine twigs, branches, and foliage were placed in the collection receptacle (Fig. 5b) of each trap and replaced with fresh pine branches every other day to provide food and refuge for adult *Monochamus*. Fluon<sup>®</sup> (Fisher Scientific, Pittsburgh, Pennsylvania)—a substance that increases trap catches by providing a slippery surface—was sprayed on to the panels and inner surfaces of each trap (Miller et al., 2013; Morewood, 2002). The first *M. titillator* adults were captured on May 28 and insects continued to be collected until trapping ceased in mid September (Fig. 4).

Trap contents were collected every other day throughout the summer of 2013. Adult *Monochamus* were removed by hand and placed singly in 162 ml cups (Fig. 6) to eliminate aggressive interactions among insects. If not separated, adult *Monochamus* chew off legs and



antennae of other *Monochamus* in close proximity (Hughes, 1981; Hughes & Hughes, 1987). Holes were cut in the lid of each cup to provide ventilation. Cups from each trap were stored in bags labeled with the date and trap location information. Trap catches were then transported to the University of Arkansas Forest Entomology Lab for further processing.

Field-collected insects were weighed, sexed, and identified to species based on the shape of the elytral apex (Fig. 7) (Dillon & Dillon, 1941). This external diagnostic is used to differentiate *M. titillator* from *M. carolinensis*. Both species occur in Arkansas and were collected in our traps (ca. ¼: *M. carolinensis*/*M. titillator*). Only positively identified *M. titillator* were used in our study. *Monochamus carolinensis* and *Monochamus* exhibiting traits from both species were not used in this experiment.

### **Bolt Preparation and Oviposition Cages**

Thirty bolts, ca. 75 cm in length, were cut from eight shortleaf pines (*Pinus echinata*) of ca. 16 cm dbh (diameter at breast height) that were felled at the Wedington Tract throughout the summer of 2013. The bottom 1.5 m of each tree was discarded in order to maintain bolt uniformity in diameter, phloem thickness, and bark thickness. The top of each bolt was marked and labeled with the date and a unique bolt identification number. Each bolt received standard treatment throughout the study; the top of each bolt was always up. Both ends of each bolt were dipped in hot paraffin to slow the rate of desiccation (Akbulut et al., 2004). All bolts were held in a greenhouse, to exclude insect associates, until used for experimentation. Holding time, the interval between tree felling and oviposition, can influence the number of *M. carolinensis* eggs laid per bolt (Akbulut et al., 2004). Optimal holding time for bolts in our study was based on Akbulut et al. (2004) and personal observations which we determined to be between three and 17 days.

Bolt surface area with bark attached averaged 3062 cm<sup>2</sup> and bolt length averaged 74.5 cm. Bolt diameter averaged 12.1 cm., and phloem thickness averaged 0.85 mm. None of the above measurements differed significantly among treatments for any of the experiments.

Healthy field-collected *M. titillator* adult females were assigned randomly to oviposition cages and paired with males (3♀:2♂). Cages (Fig. 8) were constructed out of wood and fine wire mesh (30w x 34w x 77h cm), with each cage containing a single shortleaf pine bolt. All bolts in the study were oriented vertically in each cage with the label on top. Fresh shortleaf pine branches, twigs, and foliage were placed in each cage to provide food. Twigs and branches were placed in jars filled with water and perlite™ to prevent branches from desiccating and insects from dehydrating. Temperature averaged 28°C and photoperiod was 14:10 (light: dark).

### C. Experimental Design

The experimental design was a 2x3 factorial consisting of two time periods (24 and 48 hours) during which oviposition could occur on individually caged shortleaf pine bolts, at three *Monochamus* densities ((1 ♀: 1 ♂), (6 ♀♀: 4 ♂♂), and (12 ♀♀: 8 ♂♂)) (Table 1). After the designated oviposition time period of either 24 or 48 hours had elapsed, the insects were removed from the cages and stored in a freezer in containers filled with 95% ethanol.

Following treatment, the bolt from each cage was removed and all oviposition pits were marked and recorded. Within five days following oviposition, the bark over each pit was removed using a hammer and (3.81 cm dia.) arc punch (Fig. 2). The number of eggs in each pit was counted and then summed to provide total number of eggs per bolt. A total of 30 bolts representing five replications was designated for the experiment, however complications occurred, reducing the number of bolts to four in four replications (total 26 bolts). This led to unequal sample sizes, but the numbers were still sufficiently high to perform appropriate

analyses.

### **Data Analysis**

All statistical analyses were performed using JMP<sup>®</sup>, Version 11.0. SAS Institute Inc., Cary, NC, 1989-2007. Normality was tested using Shapiro-Wilk goodness of fit test. Homogeneity of variance was tested using Levene's test. The data were square root transformed ( $\sqrt{Y + 1/2}$ ) because the Shapiro-Wilk goodness of fit test indicated lack of normality and Levene's test indicated unequal variances. Analysis of variance (ANOVA) was used to analyze the transformed data to determine if the mean number of oviposition pits per bolt, the mean number of eggs per bolt, and the mean number of eggs per pit per varied significantly among treatments. Mean comparison tests were conducted when necessary using either Tukey's HSD or the Least Significant Difference (LSD) tests. Regression analyses were used to investigate the following: (1) The relationship between the number of oviposition pits per bolt and the number of eggs per bolt and (2) the number of oviposition pits per bolt and the number of eggs per pit. Data from all bolts exposed to each treatment combination were combined and the regressions were calculated on the mean values obtained from each bolt.

## **D. Results**

### **Oviposition Pits**

The total number of oviposition pits on the 26 bolts examined was 463 and averaged 17.8 pits per bolt (Table 2). The range of eggs laid per pit was 20 (min=0 and max=20). The mean number of oviposition pits was significantly different between the treatments for the oviposition experiment ( $P = 0.0011^*$ , d.f.=5,25, n=26). The mean number of oviposition pits in the highest treatment combination (High 48: 12 females for 48 hours) was significantly higher than the two

lowest treatment combinations. The two lowest treatment combinations (Low 24: 1 female 24 hours and Low 48: 1 female 48 hours) were not significantly different from each other, nor were they different from any of the other combinations, except High 48 (Table 2; Fig. 9). No significant difference ( $P = 0.1024$ , d.f.=1,25,  $n=26$ ) was detected between the 24 hour and 48 hour time periods when the data were analyzed based on time (24 and 48 hours) without regard to the three female densities (1, 6, and 12 females). Significant differences were detected ( $P = 0.0078^*$ , d.f.=2,25,  $n=26$ ) when examining the mean number of pits constructed in relation to the number of females present without regard to time period. Mean comparison revealed that the high treatment (12 females) constructed significantly more oviposition pits ( $P = 0.0021^*$ ) on average (30 pits) than the low treatment (one female) (5 pits).

### **Eggs Per Bolt**

Bolts were dissected within five days following oviposition and none of the eggs detected had hatched by this time. On the 26 of 30 bolts analyzed, 463 oviposition pits were constructed and 1002 eggs laid. The mean number of eggs per bolt increased with increasing number of females and time allocated to oviposition, but the only significant difference was between the Low 24 and High 48 treatment combinations, with High 48 being significantly higher than Low 24 (Fig. 10). The mean number of eggs differed significantly among the treatments ( $P=0.0327^*$ , d.f.=5,25,  $n=26$ ). Tukey's mean comparison (Table 3) indicated that the highest treatment combination (High 48: 12 females 48 hours) had a significantly higher mean number of eggs per bolt than the lowest treatment combination (Low 24: 1 female 24 hours). Regression analysis indicated a significant and positive relationship (Fig. 11) between the number of pits per bolt and the number of eggs per bolt ( $P=0.0001^*$ ,  $R^2=0.691$ ,  $n=26$ ).

### **Eggs Per Pit**

The grand mean number of eggs per pit for the 25 bolts analyzed was 2.16 eggs per pit. The mean number of eggs per pit (Fig. 12) was significantly different among treatments ( $P=0.0132^*$ , d.f.=5,462,  $n=463$ ). Further analysis comparing means using the Least Significant Difference (LSD) test indicates that the treatment combinations Med 24, Med 48, and High 24, were all significantly higher than the High 48 (Table 4). There were no significant differences observed between the other combinations. It should be noted that oviposition pits with zero eggs were included in the analysis in order to represent the mean number of eggs for all pits constructed. The number of pits with zero eggs was 40.82%, or 189 of 463 of the oviposition pits. One pit contained 20 eggs, which was the maximum number of eggs laid in a single pit. If we choose to remove all of the pits with zero eggs from the analysis then no significant differences are detected at  $\alpha=0.05$  ( $P=0.0711$ , d.f.=5,273,  $n=274$ ). Mean number of eggs per pit per bolt do not differ significantly among treatments ( $P=0.1337$ , d.f.=5,24,  $n=25$ ). Regression analysis did not reveal a significant relationship between the number of pits per bolt and the mean number of eggs per pit per bolt ( $P=0.8573$ ,  $R^2=0.001435$ ,  $n=25$ ). The number of eggs per pit were significantly lower for the 48 hour time period (1.88 eggs per pit) than the 24 hour time period (2.54 eggs per pit) when the data were analyzed without regard to insect density ( $P=0.0401^*$ , d.f.=1,462,  $n=463$ ) (Fig. 13). When analyzed by insect density without regard to time period, the medium density of six females was significantly higher (1.34 eggs per pit) than the low density of one female (0.94 eggs per pit) and the high female density of 12 females (1.06 eggs per pit) ( $P=0.0077^*$ , d.f.=2,462,  $n=463$ ) (Fig. 14). One bolt was eliminated from this analysis because it contained zero oviposition pits and the number of eggs per pit could not be calculated.

## E. Discussion

The duration of oviposition was chosen as 24 hours and 48 hours for convenience and to maintain all foraging offspring at the similar age structure and competitive ability. It was convenient to use the two time periods of 24 hours and 48 hours because the insects would be removed at the same time of day they were added to the cages. These time periods also enabled us to utilize the entire day as an interval instead of a partial day. By using the entire day as the time interval for this experiment, we eliminated the possibility of time of day impacting the study. For example, adults may be more or less active at different times throughout the day or night than other times. Utilizing an entire day as an interval, such as 24 hours and 48 hours, instead of partial day intervals, such as six or 15 hours, eliminates the possibility that the time of day in which the insects were added to, or removed from, the cages would impact the study. Competitive ability is related to the relative size of the competing individuals, which is related to larval age. Larvae continue to grow as they feed and age. The maximum possible age difference between foraging offspring was 48 hours. If ages were too staggered, then the earliest to emerge would likely gain a competitive advantage by being larger in size. Older and larger larvae will out compete and feed upon smaller larvae (Anbutsu & Togashi, 1997a). If ovipositing females were left in the cage too long, then they could expend all of their eggs before the end of the experiment.

The ratio of males to females in each treatment was chosen based on the proportion of males and females collected in traps (2♂:3♀). Assuring that females mated seemed important to ensure fertilization of eggs. Although *Monochamus* mate multiple times and the spermatheca is

known to store sperm from multiple males (Hughes & Hughes, 1987), we were not positive that all field collected females had mated prior to collection.

The only significant increases in the number of pits (Fig. 9: Table 2) were from Low 24 to High 48 and from Low 48 to High 48, otherwise the apparent increase from treatment to treatment has no statistical meaning. No significant increase in the number of pits was detected from the 24 to the 48 hour time periods as would be expected when the data were examined in relation to time without regard to the number of females. It is likely that the number of females present has more of an impact on oviposition pit construction than our two time periods. The high number of females (12 females) constructed significantly more oviposition pits than the low number of females (one female), but the middle female density (6 females) did not differ from either the high (12) or low (one female) female densities. The differences detected between the high and low female densities were likely a result of the stark range exhibited in female numbers between the low and high treatments and reveals information that would be expected. I think it would not be appropriate to assume that increasing the female density beyond our highest female density of 12 to some indefinite maximum would yield a linear increase in the number of pits constructed per bolt because there can only be a specific maximum number of pits constructed, defined simply as a restriction of the bolts surface area. In bolts treated identically to those in our study, the realistic maximum number of pits that can be constructed per bolt is likely well below this theoretical extreme, but well above the numbers detected in our experiments, and likely plateaus after some undefined female density beyond 12. Further research would have to be conducted to verify or refute these broad claims.

The only significant increase in the number of eggs per bolt (Fig. 10: Table 3) was from Low 24 to High 48, otherwise the apparent increase from treatment to treatment has no statistical

meaning. The 48 hour time period yielded significantly greater number of eggs per bolt than the 24 hour time period when the data were analyzed without regard to female density. The middle and high female densities did not differ, but both laid significantly more eggs per bolt than the lowest female density. A positive correlation is exhibited when the mean number of pits per bolt and the mean number of eggs per bolt are analyzed using regression analysis (Fig. 11) suggesting a link between eggs and pits. These data suggest that some degree of competition may be operating when we examine the number of eggs per bolt and that the female density has more of an impact on oviposition than time.

The mean number of eggs per pit (Fig. 12) increased in relation to treatment with the exception of the highest treatment combination (High 48), which was significantly lower than treatment combinations High 24, Med 48, and Med 24, but was not significantly different from Low 24 or Low 48. The number of pits with zero eggs was 40.82%, or 189 of 463 of the oviposition pits. Probably the most interesting outcome detected in our experiment was that females in the highest treatment combination (High 48) constructed significantly more pits and laid significantly more eggs per bolt, but laid significantly fewer eggs per individual pit than High 24, Med 48, and Med 24. This suggests that there is a link between the number of females ovipositing and the time allocated to oviposition, and that the highest treatment combination (High 48) reached some density dependent threshold causing them to lay fewer eggs per pit. Pit construction, egg deposition, and the number of eggs per pit are clearly not random and are linked to adult female density.

Interestingly, while great variation occurs in the number of eggs laid in a single reproductive event, *M. titillator* does not exhibit a tradeoff between number of eggs and egg size; all eggs measured in our experiment were uniform in length (4mm) and width (1mm) and only



the number of eggs laid varies. This means that the number of eggs in each clutch at a particular location within the tree can vary greatly and the size of the foraging offspring—which also varies greatly—cannot be linked to the size of the egg, therefore body size variation (competitive ability) more likely results from timing of oviposition and post emergence nutrient quality within the host (i.e. nutrients supplied by the host to the larvae and not from the egg).

Why then do we see this variation in the number of eggs laid per oviposition pit by *M. titillator*? We may speculate that that increasing the number of eggs will inundate a resource with one's progeny, thus ensuring colonization over other species, but greater intraspecific competition will result from this strategy because the resource will be divided up among many more individuals. Females may detect the presence of conspecifics (Anbutsu & Togashi, 1996; 2001; Anbutsu & Togashi, 2002) and alter their oviposition behavior in response by laying fewer eggs per pit, and spreading the total number of eggs laid across greater area, instead of concentrating more eggs in a localized area. This was suggested in our results when we examined the number of eggs per pit in relation to our treatment combinations. More pits were constructed and more eggs laid overall in relation to our treatment combinations, but the number of eggs per pit actually decreased in our highest treatment combination. Females may detect host quality and lay eggs accordingly; the oviposition pits in the most suitable hosts may receive more eggs than less suitable hosts, but this does not explain egg variation per pit within the same host when oviposition occurs at the same time. Host suitability would include the quality of the host, amount of available phloem (size of the host), and the presence of competitors. The impact of host quality on egg deposition could not be calculated from these data because the experimental bolts were uniform in size, shape, and age and any variation was too subtle to detect.

Timing of oviposition may explain egg variation per pit within the same host; females arriving first at a suitable host will have access to more resources than those arriving much later so that those arriving later may lay fewer eggs per pit to compensate for reduced access to resources. All females in an oviposition cage were exposed to the study bolts simultaneously and for the same amount of time, therefore further experiments will have to be conducted to address the impact of synchronous and asynchronous arrival of females on egg deposition. Some of the eggs laid in each clutch may be unfertilized and serve as a food source for emerging larvae so that maybe we see females arriving later actually laying more eggs. The rate of egg fertilization will have to be examined in future experiments. It is likely that the unique egg laying behavior exhibited by *M. titillator*—many eggs laid in a circular pattern—is an adaptation that has evolved in response to competition. Eggs may hatch asynchronously from the same clutch and the first to emerge may acquire more nutrients and a competitive advantage by feeding upon the unhatched eggs and later emerging (smaller) larvae. None of these hypotheses have been adequately tested and are beyond the scope of this research, but they imply interesting possibilities and complexities involved in oviposition.

We cannot directly observe the competitive interactions among *Monochamus* beneath the bark without substantially altering the host environment. However, experimental evidence indicating that *Monochamus* larvae in close proximity to one another interact aggressively, in conjunction with experimental evidence demonstrating the ubiquity of cannibalism among *Monochamus* species (Anbutsu & Togashi, 1997a; Dodds et al., 2001; Rose, 1957; Victorsson & Wikars, 1996), makes it highly probable that intense intraspecific competition among *M. titillator* larvae does occur. Personal observations suggest that intense competition also occurs among not only conspecifics but also *M. titillator* siblings—larvae from the same brood—and is

a major factor leading to high overall conspecific mortality. These conclusions are derived from the fact that the diameter of the *M. titillator* egg circle is less than 2.54 cm—approximately the same distance as the larvae spaced closest together and exhibiting the highest mortality in the experiment conducted by Anbutsu and Togashi (1997a)—and larvae from the same *M. titillator* brood have been observed feeding upon each other (personal observation). Larvae exhibiting cannibalistic behavior have been observed in many *Monochamus* species (Dodds et al., 2001; Victorsson & Wikars, 1996), but no evidence has been presented on the possibility of sibling cannibalism in *M. titillator*. Other insects have been observed feeding upon their own egg chorion, conspecific eggs, and possibly sibling eggs (Barros - Bellanda & Zucoloto, 2001).

#### **F. Figures and Tables**

Figure 1. Adult *M. titillator* male (left) and female (right).

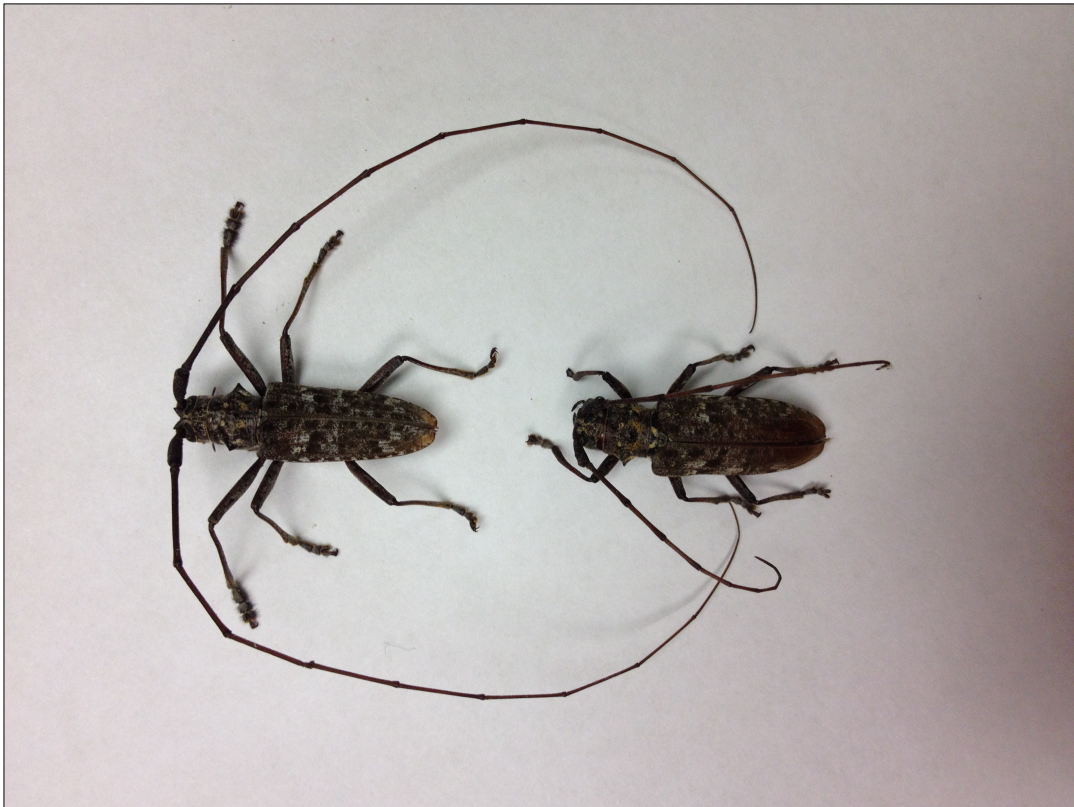


Figure 2. Circular arrangement of *Monochamus titillator* eggs beneath the bark of a shortleaf pine bolt and browning of the phloem, which is a defensive tree response induced by oviposition.



Figure 3. *M. titillator* oviposition pits in shortleaf pine. (A) Deep cone-shaped oviposition pit typically found on thicker bark. (B) Slit-like oviposition pit typically found on thinner bark.

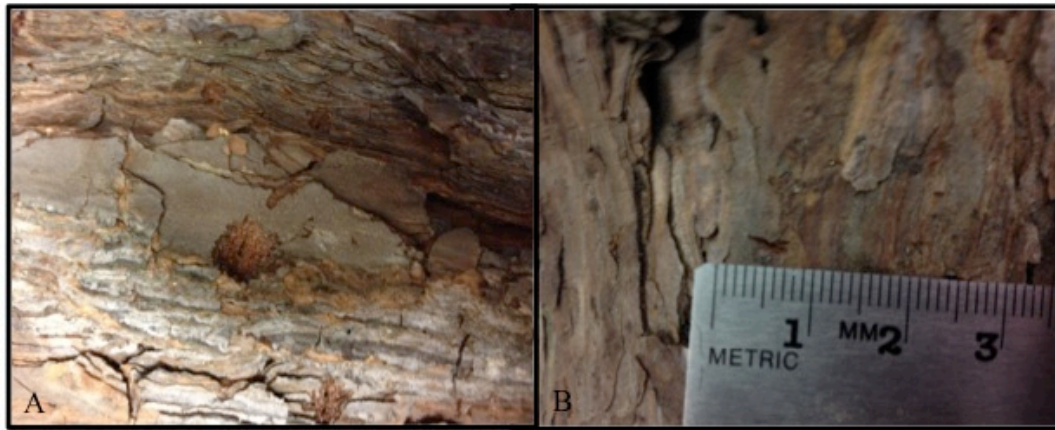


Figure 4. *Monochamus titillator* numbers collected from baited live traps, late May to mid-September, 2013.

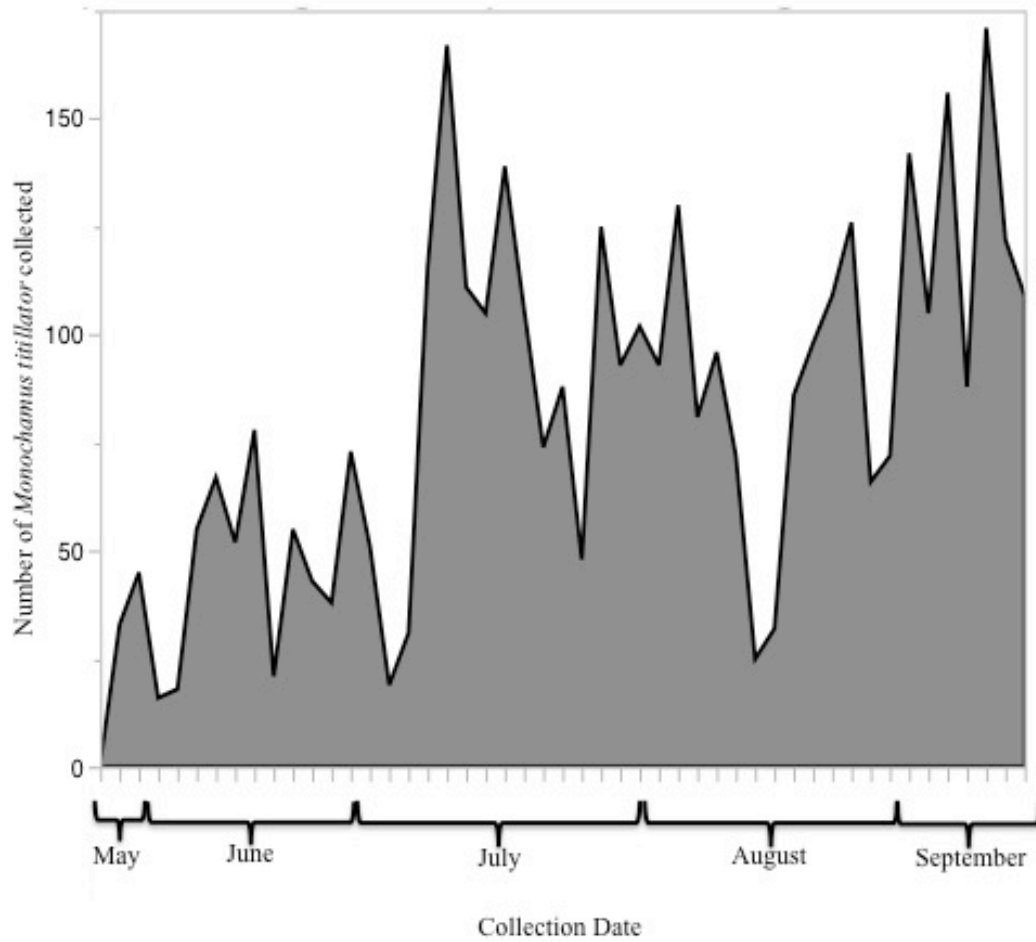


Figure 5. Modified panel trap used to collect adult *M. titillator* for our experiments. (A) depicts the panels where lures are attached and (B) depicts that modified trashcan used as the receptacle. The entire trap is approximately 175 cm tall. Trap design adapted from Lynn-Miller (2013)

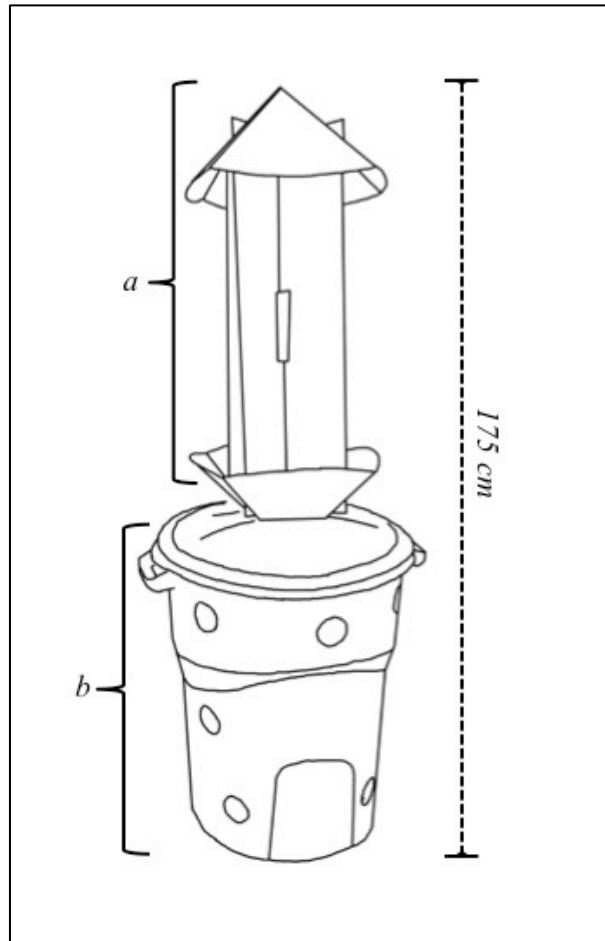




Figure 6. Cups used to transport *M. titillator* adults collected from live traps to the University of Arkansas Forest Entomology Laboratory in Fayetteville, AR.





Figure 7. The apex of the elytra exhibits a key morphological difference between (A) *Monochamus titillator* and (B) *Monochamus carolinensis*. Photo by Jessica Hartshorn.

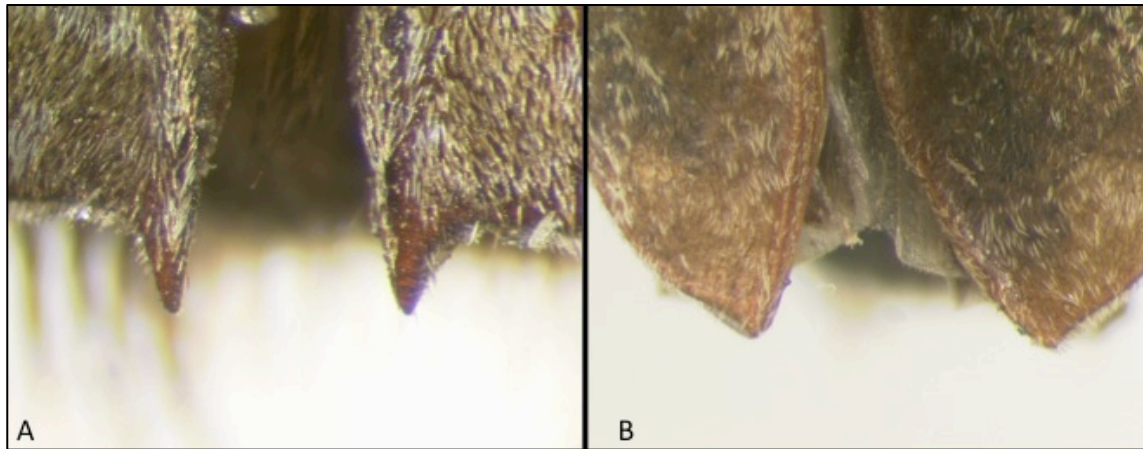


Figure 8. An oviposition cage containing an experimental bolt. Feeding material is displayed in the bottom left corner of the cage as a pine twig in a jar containing water and perlite™.



Figure 9 Number of oviposition pits constructed by female *Monochamus titillator* adults per bolt per treatment. A total of 26 bolts and six different treatment combinations are represented. The top and bottom horizontal bars indicate the maximum and minimum values respectively. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles respectively. The horizontal line between each box displays the median values. Statistics were calculated using ANOVA from transformed data. ( $p=0.0011^*$ ;  $df=5,25$ ;  $n=26$ ). Figure depicts untransformed data.

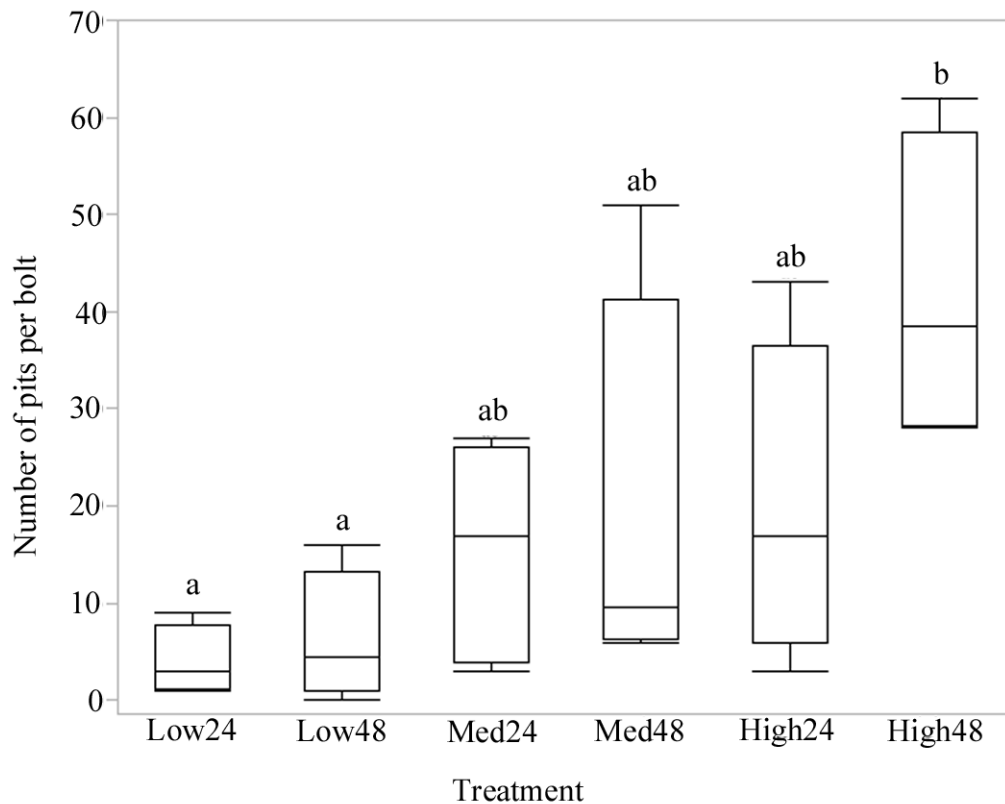


Figure 10: Number of eggs oviposited by female *Monochamus titillator* adults per bolt per treatment. A total of 25 bolts and six different treatment combinations are represented. The top and bottom horizontal bars indicate the maximum and minimum values respectively. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles respectively. The horizontal line within each box displays the median values. Statistics were calculated from transformed data  $p=0.0327^*$ .  $df=5,25$ .  $n=25$ . Grand mean is 40.08. Figure depicts untransformed data.

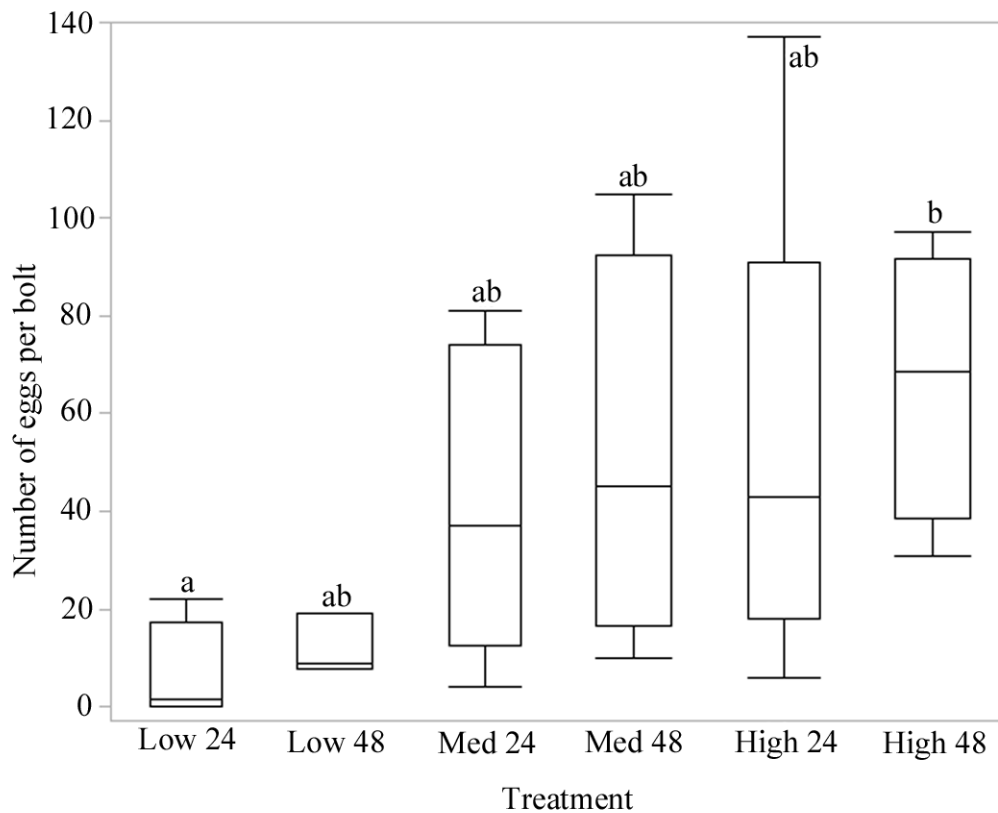


Figure 11. Regression analysis depicting a significant and positive relationship between the number of pits per bolt and the number of eggs per bolt ( $P=0.0001^*$ ,  $R^2=0.691$ ,  $n=25$ ). One bolt was eliminated from the analysis because it had zero pits.

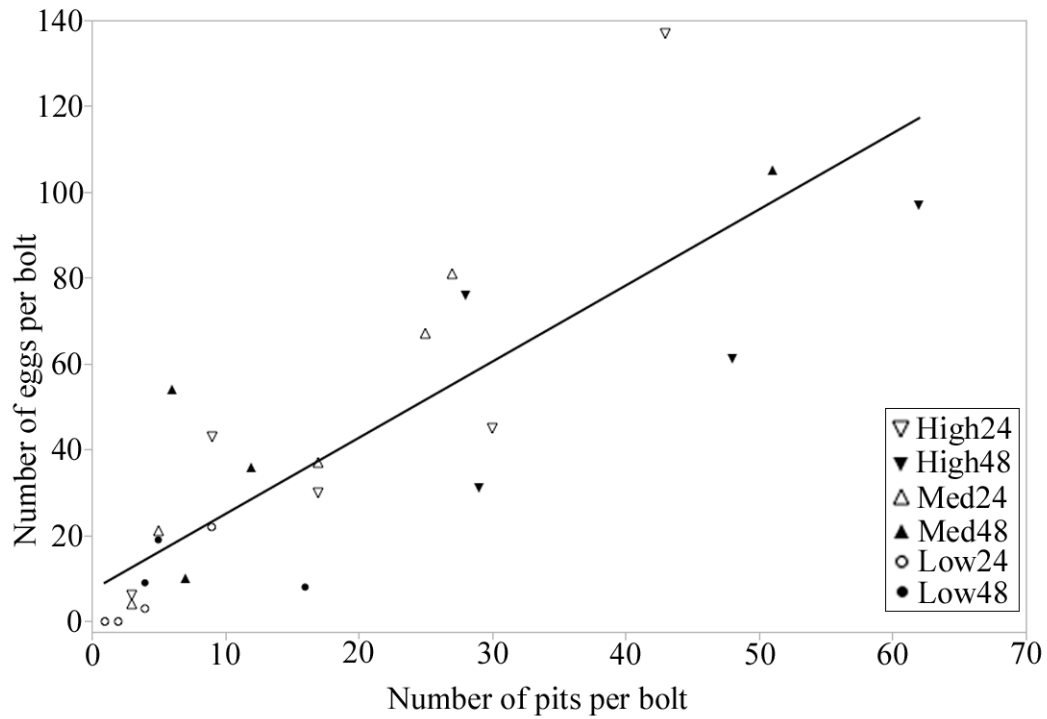


Figure 12. Mean number of eggs per pit analyzed by treatment combination. A total of 25 bolts and six different treatment combinations are represented. A total of 1002 eggs were laid in the 463 pits constructed by females on the 25 bolts. One bolt with zero oviposition pits was excluded from the analysis. Dots represent outliers. The top and bottom horizontal bars indicate the maximum and minimum values respectively. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles respectively. The horizontal line between each box displays the median values. Statistics were calculated from ANOVA on transformed data. Significant differences among treatments were detected in the mean number of eggs per pit ( $p=0.0132^*$ ,  $df=5,462$ ,  $n=463$ ). LSD was conducted for mean comparisons and treatments with same letter are not significantly different. Figure depicts untransformed data.

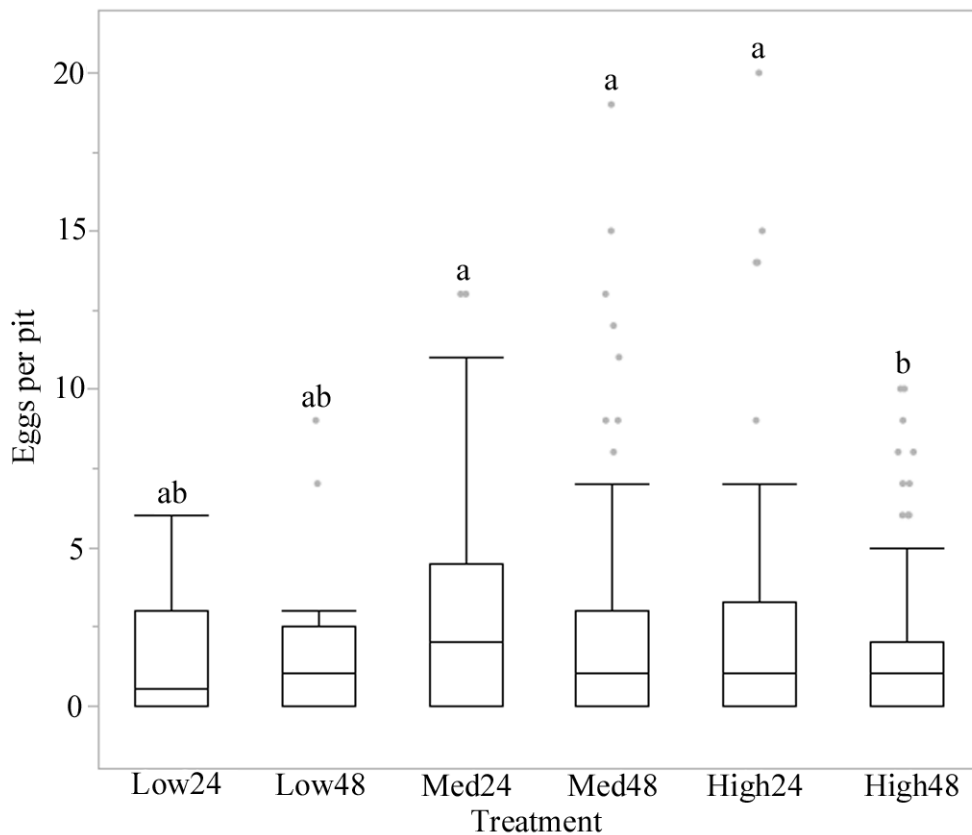


Figure 13. Mean number of eggs per pit analyzed by time. A total of 25 bolts and two different time periods (24 and 48 hours) are represented. One bolt with zero oviposition pits was excluded from the analysis. Dots represent outliers. The top and bottom horizontal bars indicate the maximum and minimum values respectively. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles respectively. The horizontal line between each box displays the median values. Statistics were calculated from ANOVA on transformed data. Significant differences among treatments were detected in the mean number of eggs per pit ( $p=0.0401^*$ ,  $df=1,462$ ,  $n=463$ ). LSD was conducted for mean comparisons and treatments with same letter are not significantly different. Figure depicts untransformed data.

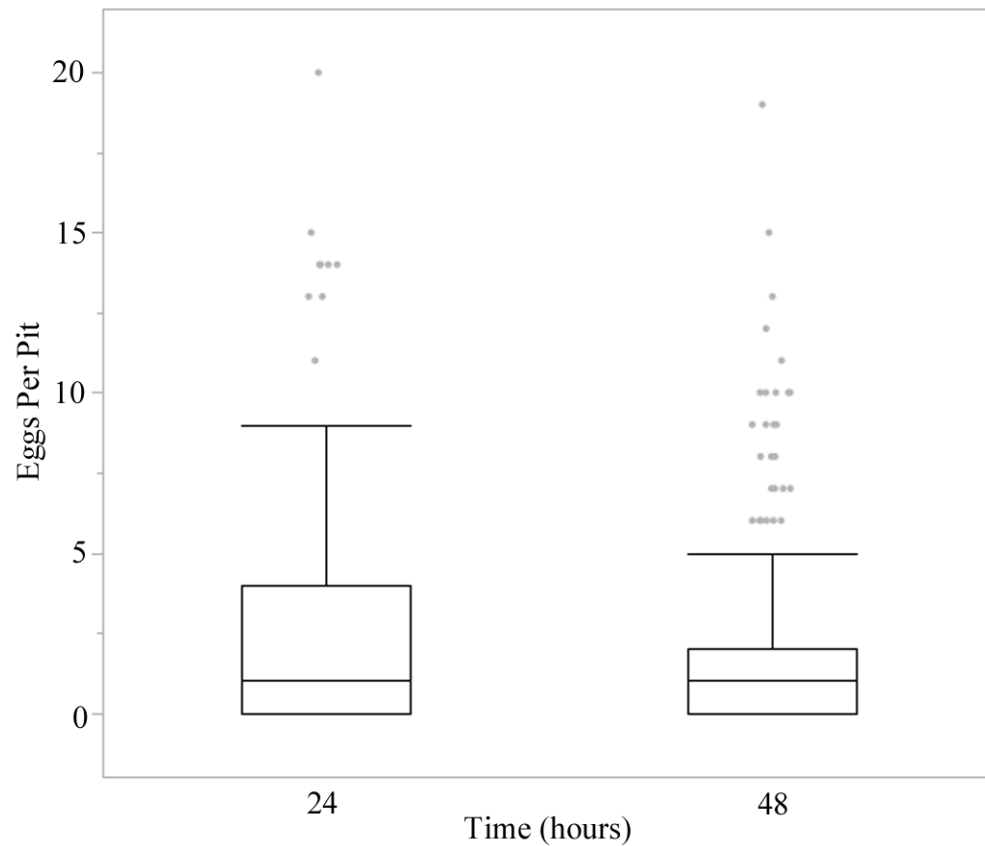


Figure 14. Mean number of eggs per pit analyzed by density. A total of 25 bolts and three different densities (1, 6, and 12 females) are represented. One bolt with zero oviposition pits was excluded from the analysis. Dots represent outliers. The top and bottom horizontal bars indicate the maximum and minimum values respectively. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles respectively. The horizontal line between each box displays the median values. Statistics were calculated from ANOVA on transformed data. Significant differences among treatments were detected in the mean number of eggs per pit ( $p=0.0077$ ,  $df=2,462$ ,  $n=463$ ). LSD was conducted for mean comparisons and treatments with same letter are not significantly different. Figure depicts untransformed data.

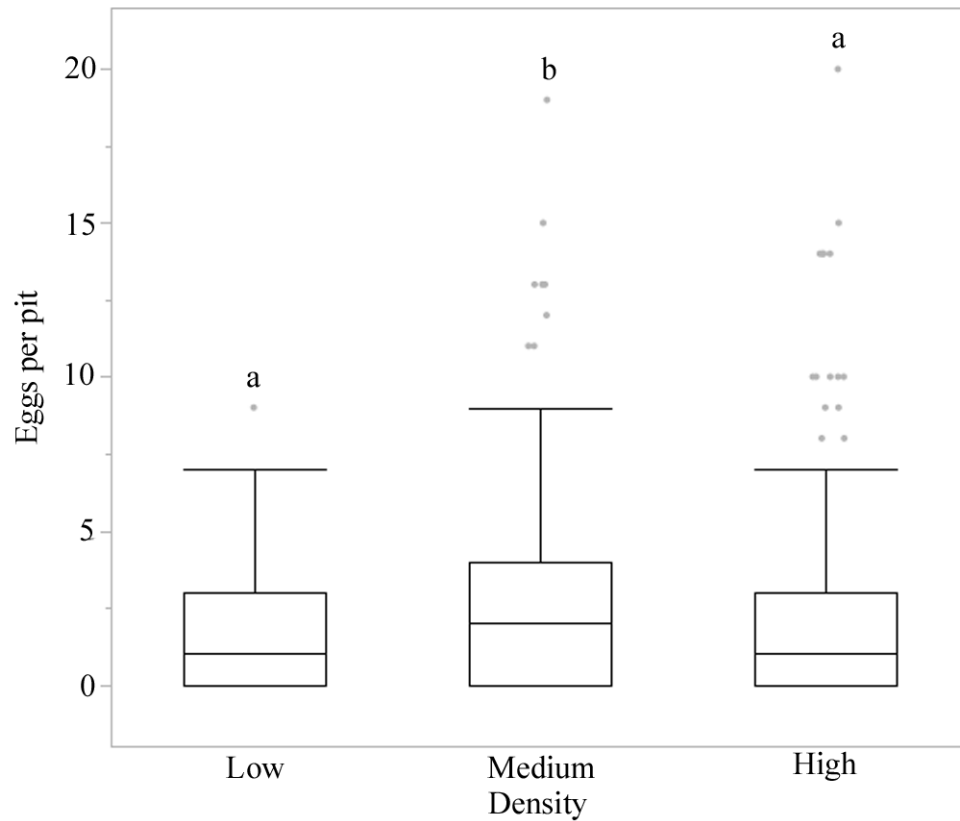




Table 1. Experimental design treatment combinations

	<i>Monochamus</i> density combinations		
24 hr oviposition	Low – 24 1 ♀: 1 ♂	Med – 24 6 ♀♀: 4 ♂♂	High – 24 12 ♀♀: 8 ♂♂
48 hr oviposition	Low – 48 1 ♀: 1 ♂	Med – 48 6 ♀♀: 4 ♂♂	High – 48 12 ♀♀: 8 ♂♂

Table 2: Summary statistics for the oviposition pits. N is the number of bolts. Mean is the mean number of pits per treatment. Sum is the sum of oviposition pits per treatment. Mean comparisons were calculated using Tukey-Kramer HSD and treatments with different letters are significantly different. The P-value and degrees of freedom were calculated from ANOVA ( $\alpha=0.05$ ).

Treatment	N	Mean	Sum	Significance P-value	df
low24	4	4	16	b	--
low48	4	6.35	25	b	--
med24	5	15.4	77	ab	--
med48	4	19	76	ab	--
high24	5	20.4	102	ab	--
high48	4	41.75	167	a	--
Total	26	17.81	463	0.0011*	5,25

Table 3. Summary statistics for the mean number of eggs per bolt per treatment. ANOVA was used to analyze means and Tukey's HSD was used for mean comparisons. Treatments with the same letter are not significantly different. N is the number of bolts and sum is the number of eggs. Mean is the mean number of eggs per bolt.

Treatment	N	Mean # of eggs	Sum	SE	p-value
low24	4	6.25	25	5.3	b
low48	3	12	36	3.51	ab
med24	5	42	210	14.24	ab
med48	4	51.25	205	20.06	ab
high24	5	52.2	261	22.31	ab
high48	4	66.25	265	13.88	a
Totals	26	38.54	1002	7.36	0.0327*

Table 4. Summary statistics for the mean number of eggs per pit compared among treatment combinations. ANOVA was used to analyze means and Least Significant Differences (LSD) was used for mean comparisons. Treatments with the same letter are not significantly different. N is the number of oviposition pits. Sum is the total number of eggs.

Treatment	N pits	Mean # eggs per pit	Sum eggs	SE	p-value
low24	16	1.56	25	0.78	ab
low48	25	1.44	36	0.63	ab
med24	77	2.73	210	0.36	a
med48	76	2.70	205	0.36	a
high24	102	2.56	261	0.31	a
high48	167	1.59	265	0.24	b
Totals	463	2.16	1002	3.13	0.0132*

### **III. Effects of Varying *Monochamus titillator* Oviposition Density on Survival of Offspring in Shortleaf Pine Bolts**

#### **A. Introduction**

When more individuals of the same species inhabit and use a resource in short supply, then intense intraspecific competition occurs and increased mortality, changes in developmental times (Denno et al., 2000), and changes in adult body size (Andersen & Nilssen, 1983) result from the decreased availability of nutrients, which must be split among many individuals, instead of few individuals (Denno et al., 1995; Kaplan & Denno, 2007; Price et al., 2011)

Increased mortality in response to intraspecific competition occurs for two main reasons in *M. titillator* populations. First, larger larvae have a competitive advantage (chapter 1) and feed on a disproportionately greater share of the phloem resource. This limits phloem access to other larvae, which may starve to death as a result. Second, larvae that interact with one another may harm, kill, or consume one another. The outcome of these larval interactions is related to body size and the larger individuals will tend to win such contests (Anbutsu & Togashi, 1997a). This is also true for adult body size (Hughes & Hughes, 1982; Hughes & Hughes, 1987).

Developmental time may be related to nutrient availability and by extension competition. The link between competition and developmental rate is complicated and manifests in several ways. Competition can result in longer or shorter developmental times depending upon the situation and the species involved. Low nutrient environments can result from intense competition and may lead to slower developmental times, but the opposite has also been observed (Denno et al., 2000; Roff, 1992).

*Monochamus titillator* populations exhibit a high degree of body size variability (Webb, 1909), which is typical of many wood-boring insects (Andersen & Nilssen, 1983). Body size

both influences the outcome of a competitive interaction and can result from competition.

Larvae that have been feeding for a longer period of time tend to be larger than larvae feeding for a shorter period of time, given that the food resource is of equal quality and equally available to all larvae. A contest between a smaller larva and a larger larva tends to favor the one with the largest body size (Anbutsu & Togashi, 1997a). Larger adults will tend to hold territories more efficiently and acquire mates more readily than smaller adults (Hughes & Hughes, 1982; Hughes & Hughes, 1987).

All three of these traits are highly interrelated and important to the ultimate fate of the individual. These traits are highly variable in *M. titillator* populations and it is the hope of this research to reveal the underlying mechanisms driving this variation in order to determine how and why we see it in natural populations.

## **B. Objectives**

I address the following objectives in this thesis. How does number of ovipositing females and the amount of time allocated to female oviposition in cages containing uniformly treated shortleaf pine bolts impact: (1) offspring development time, (2) offspring emergence, and (3) offspring size?

This research examines whether number of ovipositing *Monochamus titillator* females and time allocated to oviposition affect offspring emergence, developmental rate, and size. I hypothesize that competition among larvae for the limited phloem resource leads to a density dependent response causing a reduction in size, weight, development time, survivorship, fecundity and overall fitness. These are all highly variable in wild *M. titillator* populations and may result from competition.

## C. Materials and Methods

Methods used for collection, handling, and experimentation were the same as those explained and described in Chapter 2. Where techniques differ, or are needed for clarity of explanation, they are summarized below.

### Monochamus Collection, Bolt and Cage Preparation

*Monochamus titillator* adults were collected in live traps baited with host volatiles and *Ips* bark beetle pheromones. Adults were collected from the end of May to mid-September, 2013. Only *M. titillator* adults were used for the experiments described below.

### Bolts and Oviposition Cages

Sixty shortleaf pine bolts (*Pinus echinata*) were used in this study. Three bolts of the original 60 were subsequently eliminated because they contained no oviposition pits. Mean bolt length for the six treatments varied from 73.3 to 74.9 cm and averaged 74.4 cm. Average bolt surface area for the six treatments was 2973 cm<sup>2</sup>, and ranged from 2899 to 3272 cm<sup>2</sup>. Mean bolt diameter was not significantly different among treatments and averaged 11.8 cm. Likewise, mean phloem thickness was not significantly different among treatments and averaged 0.9 mm. The temperature at which bolts were held averaged 28°C and photoperiod was 14:10 (light: dark).

Insects were removed from the oviposition cages after either 24 hours or 48 hours then placed in 95% ethanol and stored in a freezer. After insects were removed, the bolts from each cage were also removed and all oviposition pits were counted, marked, and the number of pits recorded. The bolts were then placed individually into cages and emergence was monitored. Larvae feed in the phloem for about one month before entering the sapwood for pupation. Therefore, bolts were examined a minimum of once per week for the first 45 days following

oviposition because no emergence was likely to occur during this time. The bolts were examined for emergence a minimum of once per day 45 days after oviposition. Daily bolt monitoring took place at various times throughout the day, typically in late afternoon. All emergence holes were marked with the date of emergence and the sex of the emerging individual. When a female emerged from a bolt she was removed from the cage, weighed, marked and placed in a feeding chamber for two weeks with other females. Feeding chambers were constructed out of wood and fine wire mesh (30w x 34w x 77h cm) and contained freshly cut shortleaf pine (*P. echinata*) twigs, branches, foliage, and water. Twigs and branches were placed in jars filled with water and perlite™ to prevent branches from desiccating and insects from dehydrating. Feeding material was replaced every other day or as needed depending upon how many females were feeding. It was difficult to provide adequate nutrition when the number of females reached 15-20 per cage. After two weeks of feeding, females were weighed, measured, and placed in 95% ethanol in a freezer. Females were later dissected and number of mature eggs counted. When males emerged from the study bolts they were immediately marked, placed in 95% ethanol in the freezer, and later measured. The experiment was terminated when no insects had emerged from any bolts for four weeks. Bolts were then dissected and the number of remaining larvae and pupae were tallied. A total of 60 bolts were used in these competition experiments.

### **Monochamus Dissections**

It is important to consider both the number of eggs deposited on a host and the number remaining within the female following oviposition to determine the degree to which each individual female is or is not laying eggs. All of the undamaged females were dissected and the number of mature eggs was counted. A subset of 433 females was dissected following oviposition in the lab. This number was then compared to dissections conducted from 145 field-



collected females that had not oviposited in the lab. There was no way to verify if field-collected females had oviposited in the field prior to collection. Females that emerged from our study bolts were also dissected and eggs counted after they had been placed in the feeding cages for two weeks. Feeding is necessary for *M. titillator* egg development.

#### **D. Data Analysis**

All statistical analyses were performed using JMP®, Version 11.0. SAS Institute Inc., Cary, NC, 1989-2007. Normality was tested using Shapiro-Wilk goodness of fit test. Homogeneity of variance was tested using Levene's test. Data were not normal, and the square root transformation,  $\sqrt{Y + 1/2}$ , was used to generate normal distributions and equal variances. Analysis of variance (ANOVA) and Tukey's HSD was used for mean comparisons. Transformed data were analyzed to determine if the mean number of emergence holes, the mean development time (days from oviposition to emergence), and mean elytral length of offspring varied significantly among treatments. ANOVA was also used to analyze the mean elytral length of the ovipositing and emerging generations. Regression analyses were used to investigate the following: (1) The relationship between the number of oviposition pits per bolt and the number of adults emerged from each bolt and (2) the number of oviposition pits per bolt and the development time for each bolt. Data from all bolts exposed to each treatment combination were combined and the regressions were calculated on the mean values obtained from each bolt.

#### **E. Results**

##### **Monochamus Emergence**

Two hundred twenty two *M. titillator* adults (mean of 3.9 per bolt) emerged from 49 of the 60 study bolts. Emergence only occurred from the 57 bolts with oviposition pits. The mean

number of *M. titillator* that emerged among treatments was significantly different ( $P < 0.0001$ ,  $df = 5, 56$ ,  $n = 57$ ) (Figure 1). Tukey's HSD mean comparison test indicated that the four treatment combinations (Med 24, Med48, High24, and High48) with higher densities of ovipositing females and longer exposure times were not significantly different from one another, but were different from the lowest density treatment combinations (Low24 and Low48). Med24 was not significantly different from any of the other five treatment combinations. The mean number of pits per bolt and mean number of emergence holes per bolt was positively correlated ( $P > 0.0001$ ;  $n = 57$ ;  $R^2 = 0.448$ ) (Figure 2).

### **Sex Ratio and Elytral Length**

Male and female *M. titillator* are sexually dimorphic with relation to size and thus were analyzed by sex. A total of 222 *M. titillator* (103 males, 104 females, and 15 unknown) emerged from the study bolts (Fig. 3). No significant differences were observed for elytral length among the treatments for either females ( $P = 0.4647$ ;  $df = 6, 90$ ;  $n = 91$ ), or males ( $P = 0.1873$ ;  $df = 5, 87$ ;  $n = 88$ ). Males' elytra were significantly smaller ( $15.42 \pm 0.193$  mm) than females ( $16.94 \pm 0.189$  mm) ( $P < 0.0001$ ;  $df = 1, 178$ ;  $n = 179$ ). Ovipositing females ( $16.56 \pm 0.07$  mm) had significantly ( $P = 0.0071$ ,  $df = 1, 919$ ,  $n = 920$ ) longer elytra than emerging females ( $16.12 \pm 0.15$  mm).

### **Development Time**

The development time from oviposition to emergence was recorded for 208 of the 222 *M. titillator* that emerged from our study bolts. Those missing had escaped from the emergence cages and the exact date of emergence could not be determined. Analysis of variance indicated no significant differences exist ( $P = 0.1474$ ,  $df = 5, 207$ ,  $n = 208$ ) between the treatments. The grand mean and SE of emergence time was  $96 \pm 12.5$  days. Mean and SE development time (days) for treatments were Low24 ( $N = 7$ )  $107 \pm 4.7$  days, Low 48 ( $N = 5$ )  $94 \pm 5.6$  days, Med24 ( $N = 34$ )  $93$

$\pm 2.1$  days, Med48 (N=52)  $98 \pm 1.7$  days, High24 (N=58)  $96 \pm 1.6$  days, and High48 (N=52)  $95 \pm 1.7$  days. A significant relationship did not exist between development time and elytral length of emerged adults ( $P=0.3988$ ,  $R^2=0.004$ ).

### **Insect Dissections**

Following completion of oviposition, 433 females were dissected to determine the degree to which individual females were laying eggs. This mean was then compared to data from dissections of 145 field-collected females. The mean number of eggs within the body cavity of the ovipositing females (9.8 eggs) was significantly lower than from field-collected females (25.7 eggs) ( $P<0.0001$ ;  $df=1,576$ ;  $n=577$ ). In addition, 100% of the field-collected females contained eggs (min=7 eggs) whereas several of the females from the ovipositing females contained zero eggs.

### **F. Discussion**

Quantifying the impact of intraspecific competition among *Monochamus titillator* on their size, developmental rate, and mortality is complicated for several reasons. First, larvae could not be observed directly in a way that does not drastically alter the host environment, without the aid of specialized, expensive, and novel tools or technology, because their entire development occurs beneath the bark. This makes quantifying generation mortality from egg to adult difficult because the number of eggs cannot be counted directly without adversely impacting larval development and thus the degree to which competition contributes to generation mortality cannot be calculated with any certainty. Second, the outcome of competition in nature depends upon many different factors that our experiment did account for, including host quality, timing of oviposition, and seasonality. Host quality likely has a major impact on adult size and development time. We standardized host quality and timing of oviposition in our experimental

bolts so variation in insect size, development time, or mortality cannot be attributed to those variables. The time at which a female arrives at an oviposition site relative to other females should affect the competitive ability of her offspring. The season in which oviposition occurs likely has an impact on size, developmental rate, mortality and overall success of offspring because trees may allocate resources to different processes like growth, defensive compounds, or reproduction at different times of year (Herms & Mattson, 1992). These changes in host physiology will cause changes in the composition of the host when it eventually becomes damaged and suitable for oviposition. Seasonality may also impact the quality of the ovipositing females. Females may be older and less fecund as the season progresses or they may exhibit changes in insect behavior such as diapause or mass emigration.

While variation occurred in the development times of the study insects it was not significantly different among treatment combinations. From individual bolts with two or more insects emerging, the fewest days between first and last emergence (range) was 11 days. The greatest number of days between first and last emergence (range) for a single bolt was 59 days. It is impossible to tell from this experiment if these asynchronous emergence patterns result from competition or some other phenomena.

The number of males and females emerging from the experimental bolts did not differ ( $\chi^2 = 0.08$ ; 2, N=202;  $p=0.7784$ ), which was also true for those collected in our traps ( $\chi^2 = 0.05$ ; 2, N=1320;  $p=0.8257$ ). This suggests that males and females respond similarly to the lures on our traps and similar mortality rates occur for both males and females in the field. This is contrary to differences observed in other insect species where males also actively search for and defend females. This behavior expends energy and exposes them to hazardous interactions with other males. These tradeoffs have been observed in male fruit-flies (Partridge & Farquhar,

1981). Male fruit flies with the highest level of reproductive activity live shorter lives (Partridge & Farquhar, 1981). Our simple comparison suggests this does not occur in *M. titillator* populations when we compare sex ratios for field-collected and lab-reared insects because they do not differ in either case.

Male elytra were significantly shorter than female elytra which is consistent with results of other researchers for *M. titillator* and *Monochamus* species generally (Pimentel et al., 2014). Our results gave no indication that the treatment combinations had any effect on elytral size of the offspring. This is peculiar because we manufactured artificially high larval competition in the highest treatment combinations, but no alterations in size or development time occurred.

The mean elytral length for females emerging from the study bolts was significantly shorter than for females of the ovipositing generation collected in the field. This is likely due to an artificial and highly competitive larval laboratory environment.

The answers to many of our questions concerning competition and life history tradeoffs in *M. titillator* populations still remain a mystery worth exploring in greater detail. Competition likely plays a critical role in shaping the abundance and distribution *M. titillator* populations as well as individual fitness.

## G. Figures and Tables

Figure 1. Mean number of emergence holes analyzed by treatment combination. The top and bottom horizontal bars are maximum and minimum values. The upper and lower boxes represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles. The horizontal line within each box is the median value. Dots represent outliers. Statistics were calculated by ANOVA on transformed data (square root transformation), untransformed data are shown. Significant differences exist among treatments ( $P > 0.0001$ ;  $df = 5, 56$ ;  $n = 57$ ). Tukey's HSD was conducted for mean comparisons. Treatments with same letter are not significantly different.

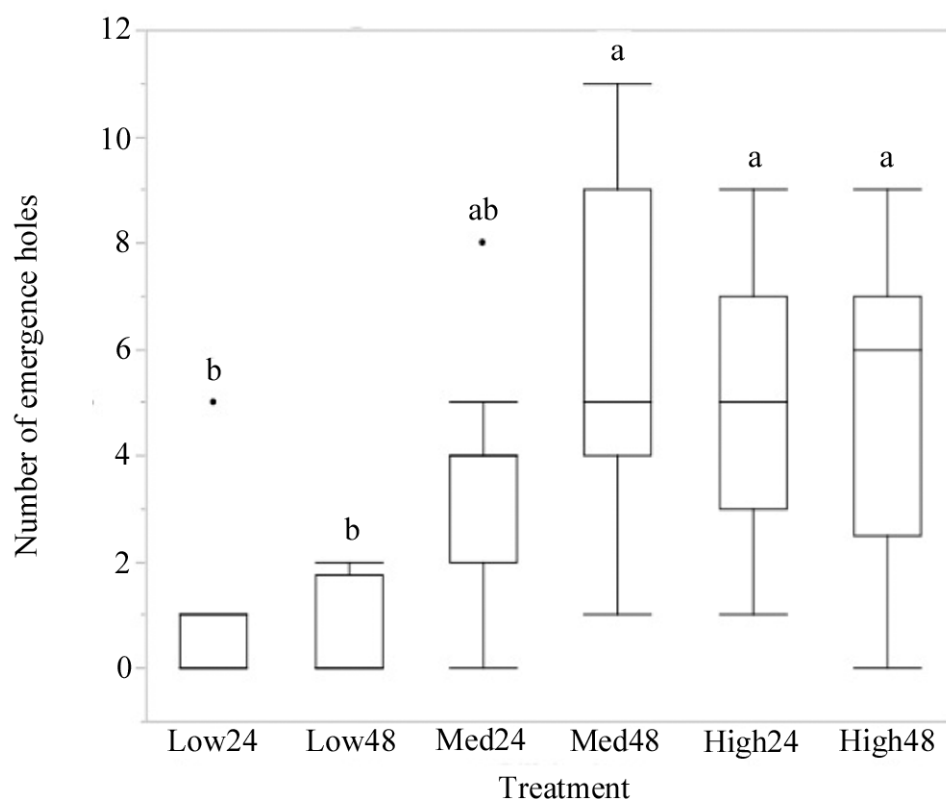


Figure 2. Regression analysis depicting a significant and positive relationship between the number of pits per bolt and the number of emergence holes per bolt ( $P>0.0001$ ;  $R^2=0.448$ ;  $n=57$ ).

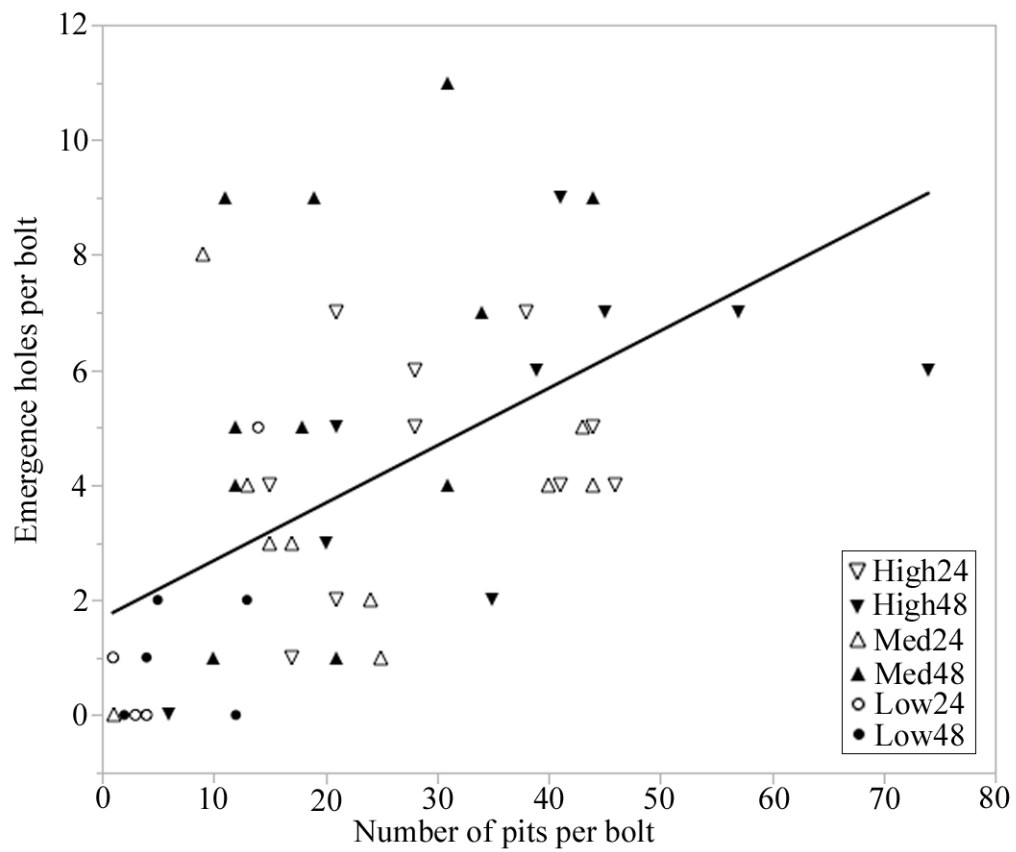
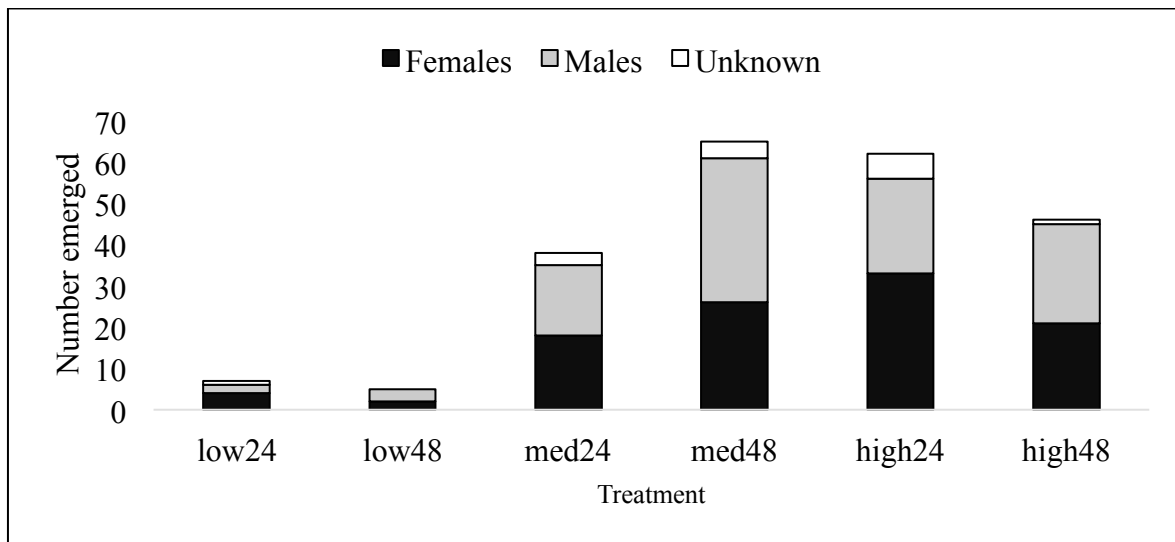


Figure 3. Each bar indicates the total number of insects emerging from each treatment type. The black gray, and white boxes within each bar indicate the proportion of females, males, and unknown emerging from the total for each treatment type.





## Summary and Conclusion

Previous studies suggested that high egg-to-adult *Monochamus titillator* mortality occurred as a result of interspecific competition, intraspecific competition, predation, parasitism, and resinosis (Dodds & Stephen, 2000). The purpose of this study was to examine one of these mortality factors, intraspecific competition. I did this by eliminating all associates, except fungi, which were impossible to exclude. All predators, interspecific competitors, and parasites were successfully excluded. I standardized study bolts to eliminate the impact of host quality on our study organisms by only using trees of a single size class (16 cm dbh), from the same location, that were then cut into standard lengths (ca. 75 cm), and held for a reasonable amount of time (ca. 3-20 days). Bolts were not used immediately after felling to prevent the impact of resinosis on eggs and early larval instars. Bolts were not used that were held over 20 days to prevent the impact of nutrient degradation associated with bolt age and degradation. I also standardized the duration of oviposition to reduce the impact of asynchronous oviposition periods on the larvae in our study. Presumably, eggs laid sooner would gain a competitive advantage by being the first to hatch, feed, and grow; the increased size would give larvae hatching sooner a competitive advantage over larvae hatching later. The larger larvae tend to confer an advantage over smaller larvae when the large and small larvae interact. Future research will have to be conducted to investigate asynchronous oviposition and its role in competition.

I am confident that within bolt mortality resulted from intraspecific competition and cannibalism. This is because all other mortality factors were excluded, except possibly pathogenic fungi, but I have no reason to believe that pathogenic fungi were present in our bolts. Interspecific competition and predation were not mortality factors because all other associates

were excluded. I observed larvae feeding upon eggs of the same ‘brood’ in two instances in a subset of four bolts dissected between seven and nine days following oviposition. All undeveloped embryos and freshly emerged larvae were facing the center of the egg circle. More research will have to be conducted to determine the prevalence of this observation, but I suspect that this may be an adaptation to facilitate nutrient acquisition extracted by consuming animal proteins. Nearly 100% bolts out of the 26 bolts where all of the oviposition pits were counted and all eggs removed had larvae foraging and sapwood entry tunnels. This suggests that eggs are being laid in the cracks and the crevices of the bark where we could not detect oviposition. This had been observed by other researchers, but not with nearly the degree of prevalence.

I am not sure if females had oviposited in the field prior to collection nor am I sure whether the time of year in which the insects were collected and trees were felled impacted the results. Seasonality is likely an important consideration that was not accounted for in this research. Tree physiology will differ depending upon the time of year because plants allocate more or fewer resources to either growth or defenses at different times throughout the year (Herms & Mattson, 1992). Therefore, the time of year in which a tree is damaged and suitable for oviposition will likely impact oviposition and larval development. More research will have to be conducted to demonstrate how seasonality impacts *M. titillator*.

## **Challenges and Future Directions**

The greatest challenge in forest entomology is to provide a complete and accurate description of the complex interactions between species and their environment. We attempt to do this by simplifying or breaking each system down into its many constituent parts and exploring all of these parts separately and later we attempt to reassemble them as mathematical models or explanatory theories. The main challenge and only way to successfully understand

insect species interactions in Arkansas pine forests is to ensure that our models and theories are accurate and predictive, otherwise our potential observations may fall short or be misleading. I will describe how such experiments can be conducted using *Monochamus*.

Since both species are collected in our traps we could also have tested intraspecific competition among *M. carolinensis* and interspecific competition between *M. titillator* and *M. carolinensis* using similar methodology, but we did not have the time or resources to do this. I would simplify the methodology by eliminating the two lowest insect densities and the 24-hour time period. To replace the two densities eliminated, and to determine carrying capacity and measure a density dependent response, I would add a new density of 24 females. The design would be a two-factor design with two female densities, 12 and 24 females, held in a cage for one time period, 48 hours. The treatment combinations would be used on each species separately to examine intraspecific competition and the species would be combined to examine interspecific competition. For example, 2 factor design, 12 or 24 females for 48 hours, for one species, *M. titillator* or *M. carolinensis*. We can test interspecific competition by combining the two species into one treatment combination; for example, add 6 of one species and six of the other to one cage, and 12 of one species and 12 of the other to another cage for our 12 and 24 female densities, respectively. We can then determine which species is the better competitor by comparing these data to those of the single species treatment combinations. Of course, this will only determine which species is the better competitor in one tree species of a particular size category (bolts 75 cm long and 16 cm dbh). Future studies will have to determine how resources are actually partitioned in nature. This information would lend valuable insight into our field observations and trap collections.

Trees can be felled and naturally colonized in the field to determine how pine resources are partitioned between *M. titillator* and *M. carolinensis* in nature. After colonization begins the researcher can mechanically partition the tree into several size or resource zones from the base to the canopy. Emergence cages can then be added to each ‘resource zone’ at several time intervals post felling to account for temporal succession of different species. All cages must be placed prior to emergence, but not before oviposition. The proportions of the species emerging from each zone can be determined. This will tell you which species emerges from what zones of the tree and at what time oviposition must have occurred for this to happen. This experiment may provide a quantifiable measure of which species is most successful at a particular ‘zone’ of a felled tree. It is apparent from our trap collections that these two species interact, but we do not know to what degree. All of these experiments and the data collected from them will reveal information on the competitive interactions involved for maintaining *M. titillator* and *M. carolinensis* populations in nature.

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