Effects of Host Quality Parameters on Fitness of the Mountain Pine Beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae)

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ABSTRACT

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is a destructive forest pest endemic to western North America. It breeds in the phloem of *Pinus* species, and during epidemic population levels, healthy trees are killed. The objective of this study was to determine how the quality of brood trees affects the fitness of mountain pine beetle offspring. The lipid content of offspring was measured relative to brood tree quality. Maternal effects were tested by rearing beetles of different sizes in hosts of constant quality and measuring brood characteristics. The population characteristics of beetles responding to aggregation pheromones were compared to that of beetles emerging from infested trees. The largest offspring were found to emerge first, but did not have the highest lipid contents. Large and small beetles were found to have similar absolute fat contents. Females were not affected by their mother's condition, but males were marginally affected.
# TABLE OF CONTENTS

Abstract ii

Table of Contents iii

List of Tables iv

List of Figures v

Acknowledgements vi

1.0 Chapter One: Introduction 1
   References 8

2.0 Chapter Two: Size and lipid content of mountain pine beetles emerging from trees of varying sizes. 11
   Abstract 11
   Introduction 11
   Materials and Methods 14
   Results 17
   Discussion 20
   References 27

3.0 Chapter Three: Size of mountain pine beetles with mothers of different sizes and emerging from trees of varying diameters. 32
   Abstract 32
   Introduction 33
   Materials and Methods 35
   Results 38
   Discussion 43
   References 51

4.0 Chapter Four: Are mountain pine beetles responding to synthetic pheromone representative of the entire population? 56
   Abstract 56
   Introduction 57
   Materials and Methods 59
   Results 62
   Discussion 65
   References 72

5.0 Chapter Five: Synthesis 75
   References 81
LIST OF TABLES

Table 2-1. Summary of mixed effects model. Lipid content (both % dry body weight and absolute fat content) and beetle size with regard to tree size, emergence date, and attack density for male and female mountain pine beetles. 18

Table 3-1. Summary of mixed effects model. Beetle size (pronotum width) with regard to tree size and emergence date for male and female mountain pine beetles is shown. 40

Table 3-2. Number of offspring emerging from trees of different sizes and from small and large mothers. 42

Table 3-3. Mean percentage of females that emerged from galleries with large and small mothers, and from trees in the three diameter classes. 42
<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Relative (%) and absolute (mg) lipid content, and beetle size (± 1 SE) for five tree diameter classes and three emergence dates.</td>
<td>19</td>
</tr>
<tr>
<td>3-1</td>
<td>Phloem thickness and diameter of live trees from each of the three stands.</td>
<td>39</td>
</tr>
<tr>
<td>3-2</td>
<td>Mean beetle size (+/- SE) for six emergence dates and three diameter classes.</td>
<td>41</td>
</tr>
<tr>
<td>4-1</td>
<td>Mean (± SE) pronotum width of mountain pine beetles captured in pheromone-baited Lindgren traps (observed) compared to expected population means for males and females based on beetles emerged from naturally infested trees in the same stand.</td>
<td>63</td>
</tr>
<tr>
<td>4-2</td>
<td>Percentages of male and female mountain pine beetles captured in pheromone baited Lindgren traps (observed) compared to expected percentages based on emerged beetles from naturally infested trees in the same stand.</td>
<td>64</td>
</tr>
<tr>
<td>4-3</td>
<td>Mean (± SE) pronotum width of the expected female distribution based on emerged beetles from naturally infested trees (left point and horizontal line) and the mean (± SE) pronotum widths of females sampled weekly from pheromone-baited funnel traps.</td>
<td>65</td>
</tr>
</tbody>
</table>
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1.0 Chapter 1 - Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is a destructive forest pest that is endemic to western North America. It breeds in the phloem of most species of *Pinus*, and its primary host is lodgepole pine, *P. contorta* Dougl. var. *latifolia* Engl.. During epidemic population levels, healthy lodgepole pine trees are mass attacked and killed over large areas (Safranyik & Carroll 2005), making this bark beetle one of the most important forest health agents of coniferous forests in western North America.

The survival and reproductive success of mountain pine beetles depend on their ability to find a suitable host tree (Pureswaran & Borden 2003). To successfully attack a live tree, and in order to ensure the survival of their offspring, attacking beetles must attract enough conspecifics to overwhelm the defence mechanisms of the tree. Large diameter trees are preferentially attacked, since these are best suited for reproduction (Amman 1969; Pureswaran & Borden 2003). However, as an outbreak escalates and the beetle population density grows, there is an increased frequency of attacks on small-diameter, low-quality trees. Also, the attraction of too many conspecifics to any one tree leads to overcrowding and decreased resources for each beetle (Pureswaran & Borden 2003). Both of these scenarios should lead to reduced fitness of emerging brood beetles because of inadequate conditions and/or intraspecific competition in the brood tree. This should have important implications for the population dynamics of the mountain pine beetle. The research presented in this thesis will be important in determining how attacks on sub-optimal hosts, which often occur during mountain pine beetle outbreaks, contribute to the population dynamics of this insect.
Mountain pine beetles are typically univoltine, though in some regions this varies depending on temperature conditions (Safranyik & Carroll 2006). Between late July and mid-August emergence and dispersal occurs, followed by host selection and colonization, then mating and oviposition. Depending on temperature conditions, eggs usually hatch within a week of oviposition and the resulting larvae immediately begin feeding. Development stops when fall and winter temperatures become too cool, but larvae often reach the third or early fourth instars by this time. When spring temperatures increase, larvae again begin feeding and develop into pupae by June. Pupae transform to new adults between late June and mid-July and these new adults need about one to two weeks before they have matured enough to undergo emergence and dispersal (Safranyik & Carroll 2006).

Broods that develop under suboptimal conditions should exhibit lower fitness-related characteristics, e.g., they may be smaller and have lower fat reserves than broods from high quality hosts. This would affect dispersal, host selection, and breeding success. Insect size relates directly to fecundity (Honek 1993) e.g., larger D. frontalis Zimmerman females produce longer brood galleries and more eggs than smaller females (Coppedge et al. 1995). Smaller breeding females, and females breeding under poor host conditions, may produce offspring that are small in size and that require an extended development time. Thus, both the quality and quantity of host resources are important in the reproductive biology of the mountain pine beetle.

Tree vigour is an important factor contributing to the susceptibility or resistance of a lodgepole pine tree to mountain pine beetle attack. Host susceptibility or resistance to attack determines whether colonization will be successful (Coulson 1979). Younger trees have thinner phloem, as well as more, and larger cortical resin ducts than older trees. As the size
and number of resin ducts present in the phloem increases, there is less phloem available for
the larvae (Amman & Cole 1983). Young trees also tend to be more vigourous than older
trees. As trees reach maturity and begin to compete for limited resources, their vigour
declines (Safranyik & Carroll 2006). Lodgepole pine stands with the majority of trees
between the ages of 40 and 60 years old have been observed to be the most resistant to
mountain pine beetle attack (Safranyik et al. 1974). Stands tend to become more susceptible
as their mean age increases beyond 60 years old, and at age 80 to 100 years they have
become highly susceptible (Shrimpton 1973; Safranyik & Carroll 2006), as their vigour and
defensive capabilities have declined, and they provide a huge amount of high-quality habitat
for bark beetle reproduction.

Lodgepole pine trees have two lines of defence to protect themselves against
mountain pine beetle attack. First, when bark beetles penetrate the bark and phloem, resin
ducts are severed and constitutive resin is released to create a physical barrier against the
beetles (Berryman 1972). The secondary or induced tree defence causes resinosis in tissues
around the wound or beetle gallery (Berryman 1972; Raffa & Berryman 1982, 1983). This
induced resinosis is caused by the breakdown of parenchyma cells in the local areas around
the beetle-caused wounds. Traumatic resin ducts are formed, and secondary resin is
produced that contains a high concentration of terpene and phenolic compounds that are toxic
to the insects (Raffa & Berryman 1982, 1983). More vigorous trees have stronger defensive
responses to attack than weaker trees (Reid & Robb 1999). In order to quickly exhaust host
tree defenses, mountain pine beetles mass attack trees in response to aggregation pheromones
(Safranyik et al. 1974, Berryman 1976, Raffa & Berryman 1983). Successful colonization
occurs when the rate of beetle attack sufficiently exceeds the defensive capacity of the tree.
Historically, small, young trees with thin bark and small, slow-growing older trees are rarely attacked, and they only infrequently sustain enough damage to be killed (Safranyik & Carroll 2006). As the beetle population increases, these insects may no longer have the opportunity to be selective about their host. Mountain pine beetles frequently attack small diameter, sub-optimal hosts during outbreaks, and they may produce low-quality broods in such trees (Safranyik & Carroll 2006).

In order to overcome the defences of their host, mountain pine beetles make use of a group attack strategy, which is an adaptive behaviour associated with predators that attack and kill prey items larger than themselves (Berryman et al. 1985). This strategy allows small individual predators to conserve energy while still gaining the benefit of subduing the large prey. The group attack strategy generally benefits individual beetles, but disadvantages become apparent when the population becomes very large as the host tree under attack must be shared by all attacking group members (Berryman et al. 1985). When the number of attacking beetles is large, decreased resources are available for each beetle.

At high attack densities, both male and female bark beetles emerge earlier and show an earlier response to pheromone cues than in lower competition situations (Botterweg 1983; Anderbrant & Schlyter 1989). Time of emergence also influences bark beetle size and lipid content. Beetles emerging early tend to be smaller, and to have lower lipid contents than beetles emerging later in the emergence period (Botterweg 1983). This information indicates that in high density situations, all beetles are forced out early in the emergence period, and an unusually high number of small beetles may be produced. Thus, individuals that develop under crowded conditions may have a limited ability to search for an optimal host (Wallin & Raffa 2004).
Once the host has been colonized, mountain pine beetle reproductive success depends on the suitability of the host. Suitability characteristics include qualitative characteristics such as the nutritional quality of the phloem, as well as quantitative characteristics, such as surface area and phloem thickness (Coulson 1979). Reproductive potential has been shown to be positively correlated with phloem thickness (Amman 1969; Amman & Cole 1983), as larvae use the phloem as a food source (Amman 1969). Phloem thickness has been shown to be a very important factor in mountain pine beetle population dynamics (Amman & Pasek 1986). Phloem thickness is related to tree vigour, stand and site factors, habitat type, elevation, total tree height, tree size, and tree age (Amman 1969; Cole & Amman 1980). The thickness of a tree’s phloem determines whether or not the mountain pine beetle can successfully reproduce and generally maintain or increase its population numbers (Cole & Amman 1980). A minimum phloem thickness of 1.5 mm is necessary for successful mountain pine beetle gallery construction and brood production (Safranyik & Carroll 2006). Thick inner and outer bark also provides an effective physical barrier for protection against enemies, extreme temperatures, and desiccation (Reid 1963; Safranyik et al. 1974; Safranyik & Carroll 2006).

Trees with thicker phloem generally are understood to provide better resources to reproducing and developing mountain pine beetles, and they may preferentially select these trees (Cole & Amman 1980). In trees with thicker phloem, beetles are able to lay more eggs per centimetre of gallery, and to undergo faster development (Amman & Cole 1983). Under these high-quality conditions, mountain pine beetle larvae are also subjected to less intraspecific competition (Cole 1973), and generally develop to be larger, more numerous
and higher-quality (Amman & Pace 1976) than those offspring emerging from trees with thinner phloem.

Open stands often have trees with thicker phloem, so these stands tend to have greater beetle production and consequently, greater tree mortality (Cole & Amman 1980). The potential rate of increase of beetles breeding in smaller trees is limited (Safranyik et al. 1974; Safranyik & Carroll 2006). Phloem and bark thickness decrease with bole height, as does mountain pine beetle attack density (Safranyik & Carroll 2006). Larger trees can also be infested to greater heights, as they have a greater circumference and a greater surface area of bark available to insect attack, so more beetles can be produced in larger trees (Cole & Amman 1980). Safranyik et al. (1974) reported that on average, trees above 25 cm diameter at breast height (dbh) produced more emerging than attacking beetles, i.e., they may effectively be beetle sources (Safranyik et al. 1974; Safranyik & Carroll 2006). This implies that the mountain pine beetle performs better in larger, more vigorous trees, with thicker phloem. Conversely, this information also implies that trees smaller than 25 cm dbh may produce fewer emerging beetles than attacking beetles, meaning that these trees are potentially mountain pine beetle population sinks.

A proportion of emerging mountain pine beetles disperse, i.e., they leave their current patch or resource in search of a new patch or resource. Bark beetles exhibit both within- and between-stand dispersal flights (Atkins 1966). Knowledge about migration by flight, i.e., flight potential and dispersal patterns, is important in understanding bark beetle population dynamics as beetles must move to a new host every generation (Forsse & Solbreck 1985). The variation in bark beetle flight ability is in part a function of beetle size and how much lipid is available as fuel. Many factors have been shown to influence size and lipid content of
bark beetles. Phloem thickness, intraspecific competition, and time of emergence affect emerging bark beetle size and lipid content (Amman & Pace 1976; Botterweg 1983; Slansky & Haack 1986).

Mountain pine beetle search-efficiency is modified by several constraints including dispersal flight potential. Flight potential is a function of insect health, and lipid content limits the amount of time and the distance that many scolytids can travel (Atkins 1969; Slansky & Haack 1986; Williams & Robertson 2008). Resource availability or the proximity to available resources dictates the distance that a mountain pine beetle must cover in order to find a suitable host.

The objective of my research is to determine how the quality of brood trees affects fitness of emerging mountain pine beetles by a) measuring fat content of emerging beetles, relative to host quality; b) testing for maternal effects on brood by rearing beetles of different sizes in hosts of constant quality and measuring brood success and brood characteristics; and c) determining if the beetles responding to aggregation pheromones have the same characteristics as those emerging from infested trees. “Quality” is a function of any quantitative or qualitative characteristics that affect insect reproduction and development, e.g., chemistry, size, etc. In this thesis, quality will be viewed primarily as a function of quantitative characteristics, e.g., host tree size and phloem thickness.

To achieve these objectives, I tested the following hypotheses:

\( H_01: \) the fat content and size of mountain pine beetles emerging from host trees of different sizes do not differ (Chapter 2);

\( H_02: \) there is no difference in the size of offspring produced by small and large females when breeding in host trees of the same size (Chapter 3); and
H03: the size distribution of beetles responding to synthetic aggregation pheromones is not different from that of the population of emerging beetles (Chapter 4).

The implications of my findings in the context of mountain pine beetle ecology and management are discussed in Chapter 5.

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Reid RW. 1963. Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the East Kootenay region of British Columbia. III. Interaction between the beetle
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2.0 Chapter 2 – Size and lipid content of mountain pine beetles emerging from trees of varying sizes

Abstract

Mountain pine beetles emerging from hosts of varying qualities can display physiological and anatomical differences, as well as developmental differences. The objective of this study was to determine the effects of host quality and intraspecific competition on the fitness of emerging beetles, using lipid content and beetle size as measures of beetle fitness. Beetles were emerged in the laboratory from freshly attacked bolts from trees of five diameter classes collected from six stands in two locations near Prince George, BC. Fat was extracted from a subset of ten beetles collected at the beginning, middle, and end of the emergence period for each bolt, and the data analyzed for differences in lipid content and beetle size with regard to tree size and emergence date (quality), and attack density (competition). Tree size negatively affected relative (%), but not absolute (mg), lipid content for both males and females, and positively affected beetle size. Larger male and female beetles emerged earlier in the emergence period. Thus, beetles may optimize the absolute amount of lipids stored, while using any excess energy for growth, as size is positively correlated with fecundity. There was no effect of attack density on either fat content or beetle size in this study.

Introduction

Variation in host quality may lead to physiological and anatomical plasticity in insects (Bell 1991). Insects from poor quality hosts may be better equipped for adverse
conditions than insects from high quality hosts. Developmental differences may also result from differences in host quality; for example, broods in poor quality hosts may develop more slowly than broods in high quality hosts (Bell 1991). Host-preferences and requirements for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), depend on factors such as tree species, tree size (phloem thickness) (Amman 1969, 1972b; Amman & Cole 1983), current attack density (Raffa & Berryman 1983), and tree health and vigour (Shrimpton & Thompson 1983).

Insect fecundity and offspring health are directly influenced by host plant quality (Awmack & Leather 2002). Many bark beetles, including the mountain pine beetle, establish mating galleries, and undergo larval development and pre-emergence feeding in the phloem of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engl.) trees, as this is where nutrients are concentrated (Steed & Wagner 2004). Larger diameter trees generally have thicker phloem and thicker bark, which provide favourable conditions for many bark beetles (Cole & Amman 1969; Steed & Wagner 2004). Tree characteristics, such as phloem thickness can vary between trees of different ages, growth conditions, and physiological states. These characteristics influence the success of mountain pine beetle attack, gallery establishment, reproduction, and larval development (Amman & Pace 1976; Hynum & Berryman 1980; Slansky & Haack 1986).

Beetle production per tree depends on the size and quality of the tree (as related to phloem thickness) as well as the attack density (Amman 1972a, 1972b; Amman & Pace 1976). Attack density is the number of gallery starts per unit area under the bark, and this measure of intraspecific competition has been shown to affect the reproductive rate of bark beetles (Coulson 1979). Atkins (1967) and Botterweg (1983) found that size and relative fat
content of bark beetles have are negatively correlated with attack density, though Williams and Robertson (2008) found a positive correlation in the Douglas-fir beetle when breeding densities were low. Intermediate attack densities usually lead to maximum brood production because attack density influences egg production, as well as egg survival and development (Berryman 1976; Safranyik & Linton 1985). When phloem is not limited, emergence of brood adults increases exponentially with an increase in length of egg gallery (Amman 1972a). The average number of eggs laid per unit length of gallery increases with increasing distance between egg galleries, parent female size, phloem thickness, and temperature (Amman 1972a). High attack densities have an inhibitory effect on egg gallery length and number of eggs laid per unit of gallery length in mountain pine beetles, thus affecting overall egg production (Safranyik & Linton 1985). High attack density may also have a negative effect on the size and fitness of brood adults (Amman 1972a), and the fecundity of the females from these broods (Reid 1963; Cole 1973; Safranyik & Linton 1985).

Coppedge et al. (1994) found that larger, heavier beetles have greater lipid contents than smaller beetles, but this is contrary to what was found by Williams and Robertson (2008) in the Douglas-fir beetle. Insects with larger bodies are understood to contain greater amounts of flight muscle and water (Williams & Robertson 2008). Lipids are directly metabolized in flight, changing insect weight over time (Atkins 1969; Coppedge et al. 1994) when searching for a new host tree. Larger bark beetles, with larger fat stores have been shown to have increased flight activity, and to have the ability to fly for longer periods of time than smaller beetles (Kinn 1986; Slansky & Haack 1986). For example, Ips calligraphus larvae that develop in high quality host trees tend to become larger and heavier adults with larger lipid contents, providing these beetles with a greater ability for extended
flight, than those larvae developing in low quality host trees (Slansky & Haack 1986). Bark beetles also respond to internal stimuli such as hunger and their physiological state when searching for hosts (Wallin & Raffa 2004). This indicates that larger, healthier mountain pine beetles should be better equipped for extended flights when searching for suitable hosts.

The energetic condition of a female mountain pine beetle also influences the reproductive potential of that beetle. A female in better physiological condition should have more energy available to contribute to reproduction leading to a greater number and larger size of eggs (Elkin & Reid 2005). However, it is possible that smaller beetles may be able to fly further as an adaptive mechanism to escape unsuitable habitats (Slansky & Haack 1986).

The objective of this study was to determine the effect of host size, and emergence patterns as direct and indirect measures of host quality, respectively, and attack density as a measure of intraspecific competition, on the size and lipid content of emerging mountain pine beetles. It has been suggested that the emergence patterns of mountain pine beetles from lodgepole pine trees is related to host characteristics such as tree diameter and stem height (Safranyik & Jahren 1970). It was expected that larger beetles with higher lipid contents would emerge from higher quality hosts, and that intraspecific competition would negatively affect beetle size and lipid content.

**Materials and Methods**

Infested bolts from trees of five diameter classes (10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, and 30-35 cm) were collected in the spring. One 50 cm bolt was cut from each tree at approximately 1.0 m to 1.5 m from the ground. Three stands from each of two areas were chosen, separated by a minimum of 500 m, and three trees were selected per diameter class in
each stand. Trees were selected from two areas as stands with currently attacked lodgepole pine trees in each of the five diameter classes could not be found in either region. Bolts from the middle diameter class (20–25 cm) were collected from both areas. A total of 54 bolts were collected, 27 from each of the two areas. Bolts from the three smallest diameter classes were collected from the Norman Forest Service Road, west of Prince George (site 1: 10U 469622E 5959075N, site 2: 10U 471113E 5956303N, site 3: 10U 469009E 5954424N). The bolts from the three largest diameter classes were collected from the Salmon Forest Service Road, north of Prince George (site 1: 10U 505724E 6017198N, site 2: 10U 506492E 6016280N, site 3: 10U 508306E 6013376N). The two areas were 70 - 73 km apart.

Selected trees were felled, bolts cut, and immediately transported to the lab, where the cut ends were waxed to prevent desiccation. The bolts were then placed in emergence cages constructed from high density polyethylene screening with a 32x32/square inch black polyethylene mesh (Synthetic Industries, Gainesville, GA). A collection funnel consisting of the bottom funnel from Lindgren funnel traps (Contech (formerly Pherotech) International, Inc., Delta, BC) was fitted to a wooden frame on which the bolts were placed. The bolts were enclosed in the mesh with staples. Emerging beetles were collected daily for the entire period of emergence. Beetles were immediately frozen at -40 °C and stored until subsequent fat extraction. After all the beetles had emerged, the attack density (number of gallery starts) within a 15 cm by 30 cm rectangle was measured for each bolt. The average attack density (± 1 SEM) was 68.8 (± 3.87) galleries / m². The attack density was not significantly different between tree diameters ($F_{5,46} = 0.641, P = 0.809$) or between stands ($F_{5,46} = 2.083, P = 0.085$).
Three emergence dates were chosen for fat extraction, at the beginning, middle, and end of the emergence period for each bolt. Each of these dates was approximately seven days apart. Ten beetles that emerged on each selected date from each bolt were randomly selected for fat extraction. These beetles were measured (pronotum length, pronotum width, and body length), their sex determined (Hopkins 1909; Lyon 1958), and then dried for 16 hours at 75°C. Beetles were weighed individually on a microbalance (Sartorius, Model MC 5, Germany), then extracted with petroleum ether (99.999% purity, Fisher Chemicals, New Jersey) in a soxhlet apparatus for 8h (Atkins 1969; Slansky & Haack 1986). The beetles were then dried again for 16 hours at 75°C and re-weighed. Percent fat was calculated based on the difference between the dry weights for each beetle.

The data were analyzed for differences in lipid content and beetle size with regard to tree size, emergence date, and attack density using a Mixed-Effects Model ANOVA in R v.2.4.1 (R Development Core Team, 2008). Stand nested within area was treated as a random effect in this model. The differences in beetle characteristics between emergence dates were tested using Tukey’s HSD tests. No data transformation was needed on the percent lipid content as the percentages were mainly between 30% and 70% (Zar 1999).

Pronotum width was used in the analysis as it was a more accurate measurement than pronotum length or body length, was more easily attained, and had been used extensively in the literature (McGheehey 1971; Safranyik 1976; Coppedge et al., 1994, 1995). The coefficient of variation was also calculated for each beetle size measurement (pronotum width, pronotum length, body length) and pronotum width was found to have the lowest value (8.84% for females and 8.40% for males), indicating that it was the most reliable size measurement.
Results

A total of 637 females and 405 males were used in this analysis. Females and males were analyzed separately as males are generally smaller in size and have lower lipid contents than females. The summary of the mixed effects model is shown in Table 2-1. In this model, bolt DBH was analyzed as a continuous variable.

There was a negative effect of tree size on female and male percent lipid content. Beetles with higher percent lipid content emerged from smaller trees, and the percent lipid content decreased as tree size increased (Table 2-1). There was no effect of tree size on the absolute fat content of either females or males (Table 2-1). On the other hand, there was a positive effect of tree size on beetle size for both female and male beetles, i.e., beetles increased in size, measured by pronotum width, as the host tree size increased (Table 2-1, Figure 2-1).

Females that emerged in the middle of the emergence period, or on emergence date 2, had significantly higher percent fat contents than those females that emerged on emergence date 1 (Tukey’s HSD, $P < 0.001$). There was no significant difference between the percent lipid content of males emerging on the three emergence dates (Tukey’s HSD, $P > 0.7$). There was no significant difference in absolute (mg) fat contents in either males or females between the three emergence dates (Tukey’s HSD, $P > 0.1$). Both female (Tukey’s HSD, $P < 0.001$) and male (Tukey’s HSD, $p < 0.001$) beetles that emerged on the first emergence date were significantly larger in size than beetles that emerged later in the emergence period (Table 2-1, Figure 2-1).

Attack density had no effect on lipid content or beetle size for females or males (Table 2-1).
Table 2-1. Summary of mixed effects model. Lipid content (both % dry body weight and absolute fat content) and beetle size with regard to tree size, emergence date, and attack density for male and female mountain pine beetles. Region and stand were random factors in this model. For treatment factors, bold type denotes significance.

<table>
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<th>Factor</th>
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<td></td>
<td></td>
<td>Value  SE  t  p</td>
<td>Value  SE  t  p</td>
<td>Value  SE  t  p</td>
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<td></td>
<td>20.586  2.603  7.908  &lt;0.001</td>
<td>0.745  0.141  5.301  &lt;0.001</td>
<td>1.825  0.037  48.986  &lt;0.001</td>
</tr>
<tr>
<td>Bolt dbh</td>
<td>626</td>
<td></td>
<td>-0.289  0.098 -2.941  <strong>0.003</strong></td>
<td>-0.002  0.005 -0.445  0.657</td>
<td>0.010  0.001  6.779  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Emergence date 2</td>
<td>626</td>
<td></td>
<td>3.607  0.818  4.408  <strong>&lt;0.001</strong></td>
<td>0.040  0.044  0.925  0.355</td>
<td>-0.111  0.014 -7.752  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Emergence date 3</td>
<td>626</td>
<td></td>
<td>1.307  0.898  1.456  0.146</td>
<td>-0.082  0.048 -1.707  0.088</td>
<td>-0.127  0.016 -8.057  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Attack density</td>
<td>626</td>
<td></td>
<td>0.427  0.317  1.346  0.179</td>
<td>0.009  0.017  0.505  0.614</td>
<td>-0.007  0.005 -1.318  0.188</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>394</td>
<td></td>
<td>18.178  2.528  7.190  &lt;0.001</td>
<td>0.596  0.103  5.800  &lt;0.001</td>
<td>1.686  0.045  37.712  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Bolt dbh</td>
<td>394</td>
<td></td>
<td>-0.284  0.090 -3.147  <strong>0.002</strong></td>
<td>-0.006  0.004 -1.659  0.098</td>
<td>0.007  0.002  4.478  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Emergence date 2</td>
<td>394</td>
<td></td>
<td>0.739  1.030  0.717  0.474</td>
<td>-0.048  0.042 -1.135  0.257</td>
<td>-0.088  0.017 -5.161  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Emergence date 3</td>
<td>394</td>
<td></td>
<td>-0.060  0.954 -0.063  0.950</td>
<td>-0.079  0.039 -2.011  <strong>0.045</strong></td>
<td>-0.129  0.016 -8.165  <strong>&lt;0.001</strong></td>
</tr>
<tr>
<td>Attack density</td>
<td>394</td>
<td></td>
<td>0.299  0.337  0.888  0.375</td>
<td>-0.001  0.014 -0.025  0.979</td>
<td>-0.005  0.006 -0.858  0.391</td>
</tr>
</tbody>
</table>
Figure 2-1. Relative (%) and absolute (mg) lipid content, and beetle size (± 1 SE) for five tree diameter classes and three emergence dates. Tree diameter classes 1 - 5 represent trees 10 – 15 cm (N = 29 F, 31 M), 15 – 20 cm (N = 135 F, 88 M), 20 – 25 cm (N = 240 F, 160 M), 25 – 30 cm (N = 119 F, 79 M), and 30 – 35 cm DBH (N = 63 F, 46 M), respectively. Emergence dates 1 – 3, represent beetles that emerged on days 1 (N = 615 F, 154 M), 7 (N = 205 F, 111 M), and 14 (N = 157 F, 139 M) of the emergence period, respectively. White bars represent females and grey bars represent males. Where ANOVA indicated significant differences (α=0.05), bars within sex with the same letter are not significantly different as determined by Tukey’s HSD.
Discussion

My finding that mountain pine beetles that emerged from trees with larger diameters were larger than those from smaller trees (Table 2-1, Figure 2-1) is consistent with the literature in regards to beetle size in relation to tree diameter. Mountain pine beetle success has been linked to phloem thickness (Amman 1972b; Berryman 1976; Haack et al. 1987), and several studies have indicated that larger-diameter trees with thicker phloem and bark produce brood beetles that are larger in size (Amman & Pace 1976; Amman & Cole 1983; Safranyik & Carroll 2006). Cole (1973) showed that phloem thickness tends to increase with tree size and growth rate. A minimum phloem thickness of 1mm – 1.5mm has been suggested to be required by the mountain pine beetle for successful reproduction (Safranyik 1971; Shrimpton & Thompson 1983; Safranyik & Carroll 2006). Below this thickness beetles are forced to abandon galleries due to their physical inability to “fit” within the phloem. When beetles are too large, or when the phloem is thinner than this minimum, large beetles break through the bark when constructing their galleries. This results in both the beetles and the inner bark being exposed to the outside air, which leads to rapid drying of the phloem, rendering it unsuitable for reproduction. Mountain pine beetles have been observed to abandon these types of galleries (Safranyik & Carroll 2006). It has also been suggested that thicker phloem may have a greater nutritional value for developing larvae (Amman 1969; Amman 1975; Amman & Cole 1983). Lodgepole pine trees are usually made up of a single age cohort, so larger trees also indicate faster growth rates and *Ips pini* have been shown to be more successful in these faster growing trees (Reid & Robb 1999).

It is known that mountain pine beetles strongly favour larger diameter trees; these trees tend to be attacked early in an infestation (Cole & Amman 1969). Host selection must
then change as an outbreak progresses due to the constantly changing distribution and abundance of large, high-quality host trees. Wallin and Raffa (2004) suggest that as beetle pressure increases, *Dendroctonus rufipennis* shifts its range of acceptable hosts to include hosts that may have been unsuitable in lower density situations. These previously unsuitable trees may be densely attacked, or have high defensive capacities (Wallin & Raffa 2004). It makes sense that lower fat beetles would behave as energy-maximizers and would be forced to immediately search and settle on hosts that may be of marginal suitability if they have lower energy reserves for dispersal (Bell 1991), while beetles with larger energy reserves would carry out longer migrations and display a higher degree of selectivity when searching for hosts.

Host plant quality has a strong influence on offspring fitness, search potential, and fecundity in the mountain pine beetle and other herbivorous insects. The quality of the host from which an individual emerges partially determines that individual’s fitness, and therefore, the searching and reproductive strategies used by that individual (Bell 1991). In herbivorous insects that must find a new host each generation, e.g., the mountain pine beetle, energy allocation is an important factor in fecundity. The size and quality of eggs depends on the amount of energy available after dispersal (Elkin & Reid 2005). Low quality individuals, with low energy reserves, may either select an available poor quality host and produce several eggs, or may allocate more energy to searching for a high quality host, and produce fewer or lower quality eggs (Awmack & Leather 2002). This question of resource allocation to eggs or to host selection is especially important in populations where high quality hosts are not readily available. Low quality mountain pine beetles may also invest
energy in improving their somatic condition at their breeding site at the expense of their reproductive investment (Elkin & Reid 2005).

Herbivorous insects, including the mountain pine beetle, can also be fairly plastic in response to differences in host plant quality (Bell 1991). Insects that develop under poor host conditions are smaller (Amman & Pace 1976; Amman & Pasek 1986; Safranyik & Carroll 2006), and may be better suited to lower quality hosts than larger beetles as they would be physically able to breed in trees with thinner phloem. Plastic responses give these insects a competitive advantage when low quality hosts are abundant, as they are not forced to compete with healthier individuals for higher quality resources. These smaller individuals have the potential to be quite successful in lower quality hosts.

Mountain pine beetles and other herbivorous insects also change the condition of their host over time, which has a large impact on intraspecific competition interactions (Awmack & Leather 2002). When a greater number of individuals are present and competing for the same resource, the quality of that resource is decreased for all the individuals. It seems reasonable, then, that mountain pine beetles emerging from host trees with different quality characteristics may behave differently and have different searching and foraging strategies. Specifically, bark beetles emerging from high quality host trees should be larger (Amman & Pace 1976), have higher fat reserves (Amman & Pace 1976; Botterweg 1983; Slansky & Haack 1986), and be able to produce large broods (Amman & Cole 1983) of high quality individuals. These higher quality beetles should have greater flight and search potential (Kinn 1986; Slansky & Haack 1986). Mountain pine beetles emerging from low quality host trees should be smaller, have lower fat reserves, and only be able to produce small broods of
weaker individuals. These smaller individuals may be better equipped to utilize smaller trees, thus decreasing or avoiding competition with larger beetles.

Mountain pine beetles may exhibit phenotypic plasticity that causes beetle size to be determined by overall host quality. When the host quality is low, such as under high density situations (Atkins 1967; Botterweg 1983; Anderbrant & Schlyter 1989), or in trees with thin phloem (Amman & Pace 1976; Amman & Cole 1983), developing beetles may not be able to grow to their maximum potential size, but may be forced to initiate pupation earlier, or they may display an earlier response to pheromones in order to have a chance at survival (Anderbrant & Schlyter 1989). This may mean that mountain pine beetle body size is a constraint limited by the quality of the host, and that beetles with smaller body sizes may employ a different strategy than larger beetles when searching for brood trees.

Mountain pine beetle quality or fitness is an important factor when considering population dynamics and the course of an outbreak (Atkins 1969; Forsse & Solbreck 1985). Many other factors in the relationship between host quality and beetle size must be considered before using size as an index of beetle quality. In addition to beetle size, other physiological factors must be considered in order to assess beetle fitness. I found that beetles emerging from smaller trees had higher percent lipid content, but similar absolute fat contents than those from larger trees (Table 2-1, Figure 2-1). As larger diameter trees are commonly thought to be higher-quality hosts for mountain pine beetles, and higher lipid contents indicate higher beetle fitness levels, this finding was contrary to the expected outcome. The energy needs for flight of a larger beetle may not be higher in direct proportion to its body size, so that a large beetle containing a lower percent fat content, may have the same flight or dispersal potential as a smaller beetle with a higher proportion of fat.
Thus, beetles may optimize the absolute amount of lipids stored, while using any excess energy for growth, since size is positively correlated with fecundity. Coppedge et al. (1994) stated that because *Dendroctonus frontalis* Zimmermann eggs are approximately 78% lipid, and because females change in lipid composition during egg-laying, it is reasonable to suggest that females with higher absolute lipid contents, regardless of their percent lipid contents, may have the ability to produce more eggs than those with lower absolute fat contents. In our study, this may indicate that all beetles, regardless of their size, have a similar reproductive potential. It has not yet been determined which measure of fat content (absolute or percent) may be a better indicator of beetle dispersal and reproductive potential (Coppedge et al. 1994).

Amman and Pasek (1986) reported a negative relationship between beetle density and offspring size. It has also been observed that beetles emerging from densely attacked trees tended to have lower fat contents (Cole et al. 1976). Maximum brood production usually occurs in trees with intermediate attack densities (Berryman 1974; Safranyik & Linton 1985) because these beetles benefit from the group attack strategy, but are still left with sufficient resources for each brood. Larger trees tend to be attacked at a higher density, as these are the most desirable hosts. The results of this study correspond with a scramble competition model of intraspecific competition (Reeve et al. 1998). Scramble competition means that resources are divided equally between all individuals, so each individual is affected equally when resources become depleted. When the larger trees are densely attacked, this leads to a severe intraspecific competition situation. In my study, attack density had no significant effect on either lipid content or beetle size. Only moderately attacked bolts were used, however, so resource limitation due to high intraspecific competition would not have been
expected. The average attack density was close to the optimum attack density of about 70 galleries / m$^2$, where brood production and beetle survival are maximized, as determined by Raffa and Berryman (1983). If trees are attacked more densely than this optimal level, brood production begins to decline (Raffa & Berryman 1983). The attack densities found in our study indicate that in most of the bolts, the threshold level at which high attack density begins to negatively affect larval productivity was not reached. A regression was also performed and there was no significant effect of attack density on brood size (number of emerged offspring/attack) ($F_{1,50} = 0.809, P = 0.372$).

Parental investment may also help to explain the results of this study. Females are faced with a trade-off between dispersal and reproduction. An investment in dispersal has the potential to increase the quality of the breeding habitat, but may limit the amount of energy available for reproduction. A female beetle must face this trade-off with an assessment of her energetic fitness and an assessment of the surrounding breeding habitat (Elkin & Reid 2005). In later stages of an infestation, when large host trees are not readily available, mountain pine beetles may be forced to migrate longer distances to find available host trees, or to breed in trees that are of lower quality. Both of these outcomes may lead to lower quality offspring, though it is possible that smaller beetles would have more success in smaller trees as they are physically well-suited to breeding in trees with thinner phloem.

The largest male and female mountain pine beetles emerged earliest in the emergence period. These early-emerging females had the lowest percent lipid contents, while females emerging in the middle of the emergence period had the greatest percent lipid contents (Table 2-1, Figure 2-1). Botterweg (1983) found that the lipid content of *Ips typographus* first increases, then declines throughout the emergence period, just as was found for female
mountain pine beetles in this study. Safranyik (1976) and Safranyik and Jahren (1970) also found that adults emerging early in the emergence period were the largest individuals. This observation means that the beetles migrating and colonizing early in the emergence period are larger than average in size (Safranyik 1976). These large, early emerging female beetles also tend to have the lowest percent fat contents. It is possible that since beetles with lower percent fat contents have a limited flight potential, and may not be capable of long migrations, they may benefit the most from having the widest choice of local host trees. This supports Jactel’s (1993) finding with Ips sexdentatus, that long range flyers do not emerge first.

Lipid content is an important measure of the energy content of bark beetles, and it may provide information about flight potential (Botterweg 1982). The percent lipid content of males did not change significantly throughout the emergence period (Table 2-1, Figure 2-1). As females are the pioneer sex and initiate colonization, their increased flight potential determines the migration strategy (Jactel 1993). Females are faced with the task of locating and colonizing a suitable host tree, thus benefitting the most from an increased flight potential, whereas male beetles must migrate only far enough to find an unmated female.

It is possible that the females with the lowest lipid contents emerge first because earlier in the flight period the likelihood of finding unoccupied suitable host trees is greater so this may be a strategy employed by a portion of the brood, i.e., emerging before fat levels have been built up in order to beat others to new resources. This finding corresponds with the contest competition model for the gallery construction and oviposition stages as suggested for D. frontalis by Reeve et al. (1998). When the mountain pine beetle carrying capacity of a stand is smaller than the number of beetles looking for host trees, only the first
beetles to a site will be successful. The remainder of the beetles will have to either search over a longer distance, or die. Females with higher lipid contents may emerge in the middle of the emergence period because they have sufficient resources in their brood tree to spend additional time maturation feeding. These beetles have higher lipid contents, so they have larger dispersal potentials and have the option of migrating in order to locate a suitable host. The females that emerge late in the emergence period have low percent lipid contents due to resource depletion. These beetles have the fewest options for new host trees as they are the last to emerge and they have low energy resources for their search. It is possible that maternal condition is an additional factor that influences offspring size, emergence time, and breeding success, and will be discussed in the following chapter.

References


Amman GD, Pace VE. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. United States Department of


R Development Core Team. 2008. Version 2.4.1.


Chapter 3 – Size of mountain pine beetles with mothers of different sizes and emerging from trees of varying diameters.

Abstract

Parent female condition and physiological state factors can be transmitted to the offspring and may influence offspring development and success. I evaluated the effects of mother size and host quality on offspring fitness in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, a destructive pest of lodgepole pine, *P. contorta* Dougl. var. *latifolia* Engelm. Large and small female mountain pine beetles were confined on fresh lodgepole pine bolts of varying diameter, and a single male was added to each female after one day. The bolts were kept at room temperature (~23 °C) for one month, placed into cold storage at 5 °C for two months, and then returned to room temperature for emergence. Emerging offspring were collected and their size measured and analyzed as a function of mother size, tree size, and emergence date. Both males and females emerging earlier in the emergence period were larger than later emerging brood, but there was no significant effect of either tree size or mother size on the size of either male or female offspring. Both large and small mothers were successful in all tree sizes tested, indicating no maternal effect on offspring size in this insect.

I used host tree diameter as a measure of host quality, but other factors may be more important to mountain pine beetle brood fitness. The effects of maternal investments may only be apparent under adverse environmental conditions, such as in high competition situations, or when developing in low quality hosts. Attack density and depletion of energy reserves during host finding were not factors in our study.
and tree sizes used in our study did not appear to affect female reproductive potential. This suggests that offspring size is largely a function of the environment, and maternal vigour may be more important for dispersal, host location, and attack.

Introduction

The foraging efficiency of adult insects influences the number of eggs laid and the quality of the sites available for use. If females lay their eggs within close proximity to resources or specifically provision their brood with resources, larval survival will most likely increase (Bell 1991). The efficiency of a searching free-living larva will influence the time period that it spends in each instar, and the ultimate size of the resulting adult (Bell 1991; Prokopy & Roitberg 2001). The number of eggs laid and the quality of the site chosen by or available to those adults can be correlated to the foraging efficiency of adults (Bell 1991).

Parental experience may be passed on to offspring through genotypic or phenotypic expression. For example, parent female condition and physiological state factors can be transmitted to the offspring, and may influence offspring development (Mousseau & Fox 1998). Parental experience may also be passed on to offspring to prepare them for their search environment (Mousseau & Fox 1998). Young bark beetles that mature in high quality hosts may be more likely to search for hosts of the same quality. These insects may be capable of longer-range travel due to good health, but may not need to disperse far because at outbreak population levels, most trees are susceptible (Raffa & Berryman 1983).

The mountain pine beetle, Dendroctonus ponderosae Hopkins (Coleoptera: Curculionidae: Scolytinae), is an eruptive bark beetle native to western North America. Its primary host is mature lodgepole pine, Pinus contorta Dougl. var. latifolia Engelm.
(Safranyik & Carroll 2006). During outbreaks suboptimal host trees are often attacked. Brood from such trees are of lower quality than those developing in large diameter trees with thick phloem (Amman & Cole 1983).

The energetic condition of a female mountain pine beetle also influences the reproductive potential of that beetle. A female in better physiological condition should have more energy available to contribute to reproduction leading to a larger size and number of eggs (Pureswaran & Borden 2003; Elkin & Reid 2005). Reproducing females are faced with a trade-off between dispersal and reproduction. Beetles that invest in dispersal may be able to find a high quality breeding site, but this may come at the cost of low quality eggs (Elkin & Reid 2005).

Phloem thickness has been shown to positively influence brood production in several bark beetle species. Thicker phloem provides mountain pine beetles with access to a larger quantity of the resource, and a higher quality food source (Amman 1969; Amman 1972b; Berryman 1976; Amman & Cole 1983; Safranyik & Carroll 2006). Reproductive fitness, measured by short larval development time, early emergence, and large quantity of offspring per parent female, was greater in Ips calligraphus (Germar) beetles developing in trees with thick phloem (Haack et al. 1987). Mountain pine beetles from small trees have been shown to produce broods with a slightly different genotype, a sex ratio strongly skewed towards females, and slower development, than broods from larger trees (Amman & Cole 1983). The different genotype could conceivably give these insects an advantage under adverse environmental conditions, e.g., at the end of an outbreak when only small trees with thin phloem remain (Wallin & Raffa 2004), although this has not been shown. A sex ratio skewed towards females means that there might be more chances for successful new attacks.
Slow development may just be a consequence of developing in a less hospitable environment.

Time of emergence also influences bark beetle size and lipid content. Botterweg (1983) reported that *Ips typographus* L. offspring emerging early tend to be smaller, and have lower lipid contents, than beetles emerging later in the emergence period, though this finding is not supported by the results of my research. Botterweg’s (1983) findings indicate that in high density situations, all beetles are forced out early in the emergence period, and an unusually high number of small beetles may be produced. Individuals that develop under crowded conditions may have a limited ability to search for an optimal host (Wallin & Raffa 2004).

The objective of this study was to determine how the quality of brood trees affects fitness of emerging mountain pine beetles by testing for maternal effects on brood by rearing beetles from mothers of different sizes in hosts of constant quality and measuring brood success and brood characteristics. To achieve this objective, I tested the following hypothesis: $H_0$: there is no difference in the size or number of offspring produced by small and large females when breeding in host trees of the same size.

**Materials and Methods**

Green, unattacked lodgepole pine bolts were collected from three stands along the Salmon Forest Service Road, north of Prince George (site 1: 10U 505724E 6017198N, site 2: 10U 506492E 6016280N, site 3: 10U 508306E 6013376N). In each stand, three trees from each of three diameter classes (10 - 17 cm, 17 - 24 cm, and 24 - 31 cm) were selected and felled, and bolts were collected for a total of 27 bolts. The three diameter classes were
distributed as follows: Diameter class 1: mean DBH = 16.23 cm, SD = 0.77, Min DBH = 14.4 cm, Max DBH = 16.9 cm; Diameter class 2: mean DBH = 20.81 cm, SD = 2.00, Min DBH = 17.9 cm, Max DBH = 23 cm; Diameter class 3: mean DBH = 26.72 cm, SD = 1.64, Min DBH = 24.8 cm, Max DBH = 29.8 cm. The 50cm-long bolts were removed from approximately 1.0 m to 1.5 m from the base of the tree. The bolts were then immediately put into garbage bags to prevent attack from secondary beetles, and transported to the lab. In the lab, growth rings were counted, and the ends of the bolts were waxed to prevent desiccation. The bolts were put in 5°C cold storage for approximately one month. Phloem thickness samples were measured from trees in the same diameter classes and in the same stands using a 25 mm diameter bark punch (Arch Punch®, C.S. Osborne and Co., Harrison, NJ, USA) and a digital calliper. Two bark samples were taken from each tree, one on the north side and one on the south side, and the average of the two measurements was used.

Emerging males and females were collected from naturally infested bolts (See Chapter 2). No females or males older than three days were used, and care was taken to avoid the mating of siblings. Beetles were separated by sex by examining the posterior margin of the seventh abdominal tergite (Hopkins 1909; Lyon 1958), and their total body length was measured using a dissecting microscope fitted with an ocular micrometer and was used to categorize the beetles as large (>4.9 mm in overall length) or small (<4.4 mm). Males of a consistent size were used (4.0 – 4.3 mm in length) to ensure that any effects were due to maternal influences only. The size distribution of the parent beetles is as follows: Small mothers: Mean body length = 4.29 mm, SD = 0.10, minimum body length = 4 mm, maximum body length = 4.4 mm; Large mothers: Mean body length = 5.04 mm, SD = 0.19, minimum body length = 4.9 mm, maximum body length = 5.5 mm; Fathers: Mean body
length = 4.20 mm, SD = 0.11, minimum body length = 4 mm, maximum body length = 4.3 mm.

Each bolt was separated into four vertical quadrants. Using a 5 mm bark punch (Arch Punch®, C.S. Osborne and Co., Harrison, NJ, USA), a small hole was made in the bark and phloem in each quadrant about 10 cm above the bottom of each bolt. Two large females and two small females were inserted into each bolt, one in each hole, so that females in the same size category were placed on opposite sides of the bolts from each other. The placement of the mating pairs was such that no interaction would take place between different sets of mating pairs within an individual bolt, and non-sibling competition would not occur. The females were left to begin excavating their gallery for one day before one randomly selected, healthy male was inserted into each hole. The holes were then sealed with high density polyethylene screening with a 32x32/square inch mesh (Synthetic Industries, Gainesville, GA) and tape to discourage the beetles from abandoning their galleries. Success was monitored daily, and beetles were replaced up to three times if necessary.

The pairs were left to mate, excavate brood galleries and oviposit at room temperature (ca. 23 °C) for one month, and then placed in 5°C cold storage for two months. Bolts were then removed from cold storage, and emergence traps were placed on each quadrant to capture the emerging offspring. The traps were constructed from high density polyethylene screening with a 32x32/square inch mesh (Synthetic Industries, Gainesville, GA), fitted with a funnel made from the inverted tops of 2L clear plastic pop bottles. Fifteen ml plastic specimen cups for collection of emerging beetles were attached to the funnel by drilling a hole in the lid to fit the neck. This allowed for easy removal of the specimen cup. Emergence traps were attached to the bolts with staples placed close enough together to prevent beetles
from escaping. Emerging offspring were collected every second day for the entire period of emergence. All beetles that emerged during this emergence period were measured (pronotum length, pronotum width, and body length), sexed, and counted.

In this study, an assumption was made that tree diameter would correlate with phloem thickness, and hence would be a good proxy for host quality. To demonstrate the actual relationship between phloem thickness and tree diameter, simple linear correlations were performed in SYSTAT 9 (Systat Software, Inc., Richmond, CA, USA) using the phloem thicknesses and tree diameters of the trees measured from each of the three stands.

The beetle data were analyzed for differences in offspring size with regard to mother size, tree size, and emergence date, using a mixed-effects model in R v.2.4.1 (R Development Core Team, 2008). Tree nested within stand was treated as a random factor in this analysis. An analysis of variance was also performed in SYSTAT 9 (Systat Software, Inc., Richmond, CA, USA) to compare the total number of offspring emerging from galleries with small and large mothers, as well as from trees from the three size classes.

Results

Although there was a great deal of variance, the correlation analyses showed that phloem thickness and tree diameter were positively and significantly correlated in each of the three stands. (Stand A: $r = 0.635, t_{(1),7} = 2.17, P = 0.039$; Stand B: $r = 0.504, t_{(1),10} = 1.85, P = 0.047$; Stand C: $r = 0.647, t_{(1),11} = 2.82, P = 0.008$) as shown in Figure 3-1. There were significant differences in phloem thickness between diameter classes one and two, and one and three ($t_{(2),23} = 5.039, P <0.0001$ and $t_{(2),17} = 3.250, P = 0.0047$, respectively), but not between diameter classes two and three ($t_{(2),32} = 0.863, P = 0.400$). When the phloem
thickness data from diameter classes two and three were pooled, there was a significant
difference between the phloem thickness in diameter class one and the phloem thickness in
the larger two diameter classes ($t_{232} = 4.257, P = 0.0002$). When the beetle size data were
pooled across the two larger diameter classes, and the size of beetles emerging from the
smallest diameter class were compared to the size of beetle emerging from the two larger
diameter classes, there was no significant difference in either females or males ($t_{2405} =
0.748, P = 0.455$ and $t_{262} = 1.264, P = 0.208$, respectively).

Figure 3-1. Phloem thickness and diameter of live trees from each of the three stands.

A total of 407 females and 264 males were used in the analysis of beetle size. Of the
108 pairs that were started in all 27 bolts, 28 were successful in bolts of the smallest diameter
class, 25 were successful in the middle diameter class, and 31 pairs were successful in the
largest diameter class, for an overall brood gallery establishment success rate of 77.8%.
Mean number of brood produced for all diameter classes was 6.20 ($\pm 6.74$ SD) offspring,
ranging from 1 to 29. Males and females were analyzed separately as males are generally smaller in size than females. The summary of the mixed effects model is shown in Table 3-1. In this model, DBH was analyzed as a continuous variable.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>Value</td>
</tr>
<tr>
<td>Intercept</td>
<td>395</td>
<td>2.131</td>
</tr>
<tr>
<td>emergence day</td>
<td>395</td>
<td>-0.002</td>
</tr>
<tr>
<td>bolt dbh</td>
<td>395</td>
<td>-0.003</td>
</tr>
<tr>
<td>mother class (small)</td>
<td>395</td>
<td>0.006</td>
</tr>
</tbody>
</table>

There was a significant negative effect of emergence date on pronotum width for both males and females (Table 3-1, Figure 3-2). Both female and male beetles emerging earlier in the emergence period were larger in size than those beetles emerging later. There were no significant effects of either tree diameter or mother size on pronotum width of either males or females. Phloem thickness was considered in similar models, but had a non-significant effect on offspring size, and the overall model fit was better when phloem thickness was excluded.
Figure 3-2. Mean beetle size (+/- SE) for six emergence dates and three diameter classes. Emerging beetles were grouped based on the week in which they emerged, from week 1 to week 6. Diameter classes 1–3 represent trees 10–16.9 cm, 17–23.9 cm, and 24–30.9 cm DBH, respectively. White bars represent females and grey bars represent males. Upper graphs show offspring of large mothers, and lower graphs from small mothers. Where ANOVA indicated significant differences (α=0.05), bars within the same sex with the same letter are not significantly different as determined by Tukey’s HSD.
The number of offspring emerging from trees of different sizes and with mothers of different sizes is shown in Table 3-2. The analysis of the number of offspring emerging from the bolts showed that there was no difference between the number of offspring emerging from galleries with small and large mothers ($F_{1,77} = 0.925$, $P = 0.925$), or from galleries in trees of different sizes ($F_{2,77} = 0.680$, $P = 0.510$). There was no significant interaction between tree size and mother size ($F_{2,77} = 0.301$, $P = 0.741$).

Table 3-2. Mean number of offspring per female ($\pm 1$SD) emerging from trees of different diameters, and from small and large mothers.

<table>
<thead>
<tr>
<th>Diameter Class</th>
<th>Large Mother Female ($\pm 1$SD)</th>
<th>Large Mother Male ($\pm 1$SD)</th>
<th>Small Mother Female ($\pm 1$SD)</th>
<th>Small Mother Male ($\pm 1$SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.73 (4.75)</td>
<td>2.47 (2.48)</td>
<td>4.15 (3.52)</td>
<td>3.44 (2.91)</td>
</tr>
<tr>
<td>2</td>
<td>5.25 (3.67)</td>
<td>2.94 (2.05)</td>
<td>5.04 (4.51)</td>
<td>4.46 (3.99)</td>
</tr>
<tr>
<td>3</td>
<td>4.15 (3.13)</td>
<td>2.69 (2.03)</td>
<td>5.96 (5.45)</td>
<td>2.67 (2.45)</td>
</tr>
</tbody>
</table>

The percentage of females that emerged from galleries with large and small mothers, and from trees in the three diameter classes is shown in Table 3-3. There was no significant difference between the percentage of females that emerged from galleries initiated by small or large mothers, or from trees in any of the three diameter classes ($F_{2,44} = 1.329$, $P = 0.27$).

Table 3-3. Mean percentage of females that emerged from galleries with large and small mothers, and from trees in the three diameter classes. No significant difference was found between any of the classes.

<table>
<thead>
<tr>
<th>Diameter Class</th>
<th>Mother Size</th>
<th>Mean % Female</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>large</td>
<td>68.5</td>
<td>7.09</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>62.2</td>
<td>8.05</td>
</tr>
<tr>
<td>2</td>
<td>large</td>
<td>67.1</td>
<td>13.74</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>41.9</td>
<td>9.14</td>
</tr>
<tr>
<td>3</td>
<td>large</td>
<td>64.0</td>
<td>6.32</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>69.0</td>
<td>6.14</td>
</tr>
</tbody>
</table>
Discussion

Our assumption that tree size could be used as a proxy for host quality was supported by the correlation analysis. It is possible, however, that some trees included in the correlation reduced the amount of variation explained, e.g., the larger trees which may have begun to stagnate in growth. Older or larger lodgepole pine trees become limited by increasing carbohydrate demands and restricted photosynthetic capacity, at which point stem and diameter growth are constrained or stopped (Kimmins 1997; Waring & Pitman 2004).

The significant difference between the phloem thickness from the smallest diameter class and the phloem thickness from the pooled larger two diameter classes, and the non-significant difference between the size of beetles from the smallest diameter class and the size of beetles from the pooled larger two diameter classes also indicates that under the conditions of this experiment, and in the diameter classes that were tested, phloem thickness did not appear to be a limiting factor to these insects.

Safranyik (1976) and Safranyik and Jahren (1970) found that adults emerging early in the emergence period were the largest individuals, just as we found (Table 3-1, Chapter 2). This observation means that beetles migrating and colonizing early in the emergence period are larger than average in size (Safranyik 1976), and may benefit from having the greatest number of host tree options available. Smaller beetles emerge later, and have a wider range of acceptable hosts because they can successfully breed in trees that are physically too small for large beetles.

Mountain pine beetle success has been linked to phloem thickness (Amman 1972b; Berryman 1976; Haack et al. 1987). Several studies have indicated that larger-diameter trees
with thicker phloem and bark produce brood beetles that are larger in size (Amman & Pace 1976; Amman & Cole 1983; Safranyik & Carroll 2006). Cole (1973) showed that phloem thickness tends to increase with tree size and growth rate. It has also been suggested that thicker phloem may have a greater nutritional value for developing larvae (Amman 1969; Amman 1975; Amman & Cole 1983). Based on this research, we used tree size to characterize host quality in our study, though in this case, we believe that phloem thickness was not a limiting factor.

It is widely believed that host size dramatically affects the growth, survival, and the ultimate size of offspring (Safranyik & Jahren 1970; Amman 1972a; Amman & Pasek 1986; Mousseau & Fox 1998), and that the provisions made available for the offspring by the mother through her host selection are a key determinant in the success of the offspring (Mousseau & Fox 1998). In our study, there was no significant effect of host tree diameter on the size of the emerging offspring. This is contrary to what was expected as our smallest diameter trees should not have been acceptable hosts. Overall host quality has been suggested as the most important factor in the population dynamics of bark beetles (Raffa & Berryman 1982; Steed & Wagner 2004), as well as an important factor in determining fecundity of herbivorous insects (Awmack & Leather 2002).

Host quality is difficult to characterize as it encompasses a whole suite of characteristics and varies considerably with changing external environmental factors. It also varies a great deal between and within individual trees (Awmack & Leather 2002). Safranyik and Jahren (1970) suggest that certain physical characteristics of host trees have a large impact on the size of emerging mountain pine beetle offspring. The complicated nature of attempting to characterize host quality makes it difficult to find measurable host tree
attributes useful for making general predictions about host quality effects on mountain pine beetle populations. Though phloem thickness and tree size were found to be correlated, the results of our study indicate that in the range of tree diameters that we used, host tree size is not a good measure of host quality, and other variables may be more important to mountain pine beetle fitness. This lack of significance of tree size should mean that the effects of the maternal quality should have been more easily identified.

Food quality is the nutrition provided by the host tree, and is one aspect of overall host quality that may have a significant impact on mountain pine beetle offspring fitness (Safranyik & Carroll 2006). Amman (1972a) suggested that in smaller trees with thinner phloem, beetles constructing galleries are forced to excavate deeper into the sapwood, and may be afforded less energy than those beetles excavating galleries in thicker phloem. Varying nutrient quality in plant tissue has been shown to directly affect insect performance (Awmack & Leather 2002). Wainhouse et al. (2001) found a positive relationship between the number of eggs, larval size, and survival of the weevil *Hylobius abietis* L. on logs of four different conifer species representing a range of host qualities. Thorpe and Day (2002) concluded that larval feeding history, or host species during development, has a large impact on survival, development time, and size of *H. abietis*. For example, *H. abietis* larvae feeding on pine mature earlier and emerging adults are larger than those developing in spruce (Thorpe & Day 2002, 2008). Larger *H. abietis* eggs develop to become larger larvae, and larger larvae have increased survival rates, so larger *H. abietis* have a clear advantage (Wainhouse et al. 2001). The differences shown between larvae developing on different species of conifer logs indicate that variations exist between the nutritional quality or the levels of defensive compounds between these conifer species (Wainhouse et al. 2001;
In addition, these developmental differences indicate how well these weevils have adapted to feed on the different conifer species (Thorpe & Day 2008). Bark beetles, which are pre-social (Wilson 1971; Costa 2006), and hence are subject to intraspecific competition, may employ different strategies than the solitary *Hylobius* weevils, however. In our study, larger mountain pine beetle offspring emerged first, but this was not significantly related to tree size or mother size.

Female mountain pine beetles must overcome the defences of lodgepole pine trees in order to successfully attract a mate and breed. Mountain pine beetles prefer to colonize the largest trees within a stand, and these are most often the trees that are most vigorous and best equipped to defend themselves against attack (Safranyik & Carroll 2006). Wainhouse et al. (2001) found that large *H. abietis* had an advantage over smaller weevils when attacking stumps protected by residual preformed defences (immediately after clearcutting), and also in competitive interactions when exploiting a limited host resource. Larger mountain pine beetles may also have a better chance at withstanding lodgepole pine defences than smaller beetles, though this advantage may not be apparent during epidemic conditions. When many beetles are present, the cooperative mass attack behaviour would be initiated rapidly, and host defences would be quickly exhausted leading to many successful attacks on vigorous trees. In this study, both large and small females were successful in a range of tree sizes, and there was no difference in the size of their offspring. The bolts that were used were stored in cold storage for approximately one month before the mating pairs were added, and during this time it is possible that host defences were greatly diminished. In species that attack dead hosts, there is no need to overcome host defences, so in this respect, there is no advantage to being larger in size. In these situations, it is possible that maternal investment in offspring
quality as reflected in variation in egg and larval size may vary a great deal between insects that exploit different host types.

Steed and Wagner (2004) did not observe an increase in reproduction in preferred larger log sizes with the pine engraver, *Ips pini* (Say). To explain this observation, two ideas were presented. First, it was suggested that factors other than tree diameter and phloem thickness, such as pre-mortem tree vigour, could be more important to beetles during host selection (Steed & Wagner 2004). Thus, tree vigour, the strength of defensive responses, phloem moisture content, and many tree characteristics other than tree size and phloem thickness, may be important in mountain pine beetle host selection, and ultimately offspring quality (Reid & Robb 1999; Reid & Glubish 2001). The second explanation presented by Steed and Wagner (2004) was smaller logs potentially provide a more vulnerable habitat for bark beetles, and that the beetles in these trees are more susceptible to negative effects under extreme environmental conditions. In our study, no effect of tree size on offspring size was observed. Logs of different sizes were artificially infested in the lab, and the entire offspring development took place under laboratory conditions. Thus, no adverse environmental conditions would have been experienced by developing offspring at any time during development. Under natural field conditions, environmental extremes or weather events would have differentially affected beetles in trees of different sizes. Larger trees with thicker phloem would afford a greater degree of protection, due to the thicker layer of material within which the beetle was positioned. Beetles developing in smaller trees, or any tree with thinner phloem would be more exposed to these environmental extremes and may be more susceptible to showing negative physical effects (Steed & Wagner 2004). Even assuming random landing, larger trees would be disproportionately attacked, and under natural
environmental conditions, more beetles would be afforded the greater degree of protection offered by these larger trees. This may be the reason that more beetles breed in larger host trees (Steed & Wagner 2004). However, no size differences were observed in beetles developing under laboratory conditions.

It has also been suggested in maternal effects studies on other insect species, that the effects of egg size on survival are only apparent under negative environmental conditions, such as high competition situations, or when developing in very low quality hosts (Solbreck et al. 1989; Fox & Mousseau 1996). Such negative environmental conditions were not experienced by the developing mountain pine beetles in this study, as the experiment took place under controlled laboratory conditions. However, Wainhouse et al. (2001) found that *H. abietis* survival was affected by egg size on both high and low quality host trees.

No significant effect of mother size was observed on either male or female offspring in this study. It is believed that the environmental experience of the mother influences her growth, condition, and physiological status, and leads to variation in offspring fitness (Mousseau & Fox 1998). This variation in initial offspring condition can be propagated through life and has a large impact on growth and survival of the individual, creating a pathway for phenotypic plasticity through the generations (Mousseau & Fox 1998). Individual females have been shown to have the ability to adjust egg size based on their somatic condition, and the quality of the host (Awmack & Leather 2002). In addition to the genetic component of egg size, it has been suggested that females may lay larger eggs on poor hosts, in order to give the offspring the best chance at survival (Wainhouse et al. 2001; Awmack & Leather 2002; Thorpe & Day 2008) as in many insect species larger egg size has been correlated with greater larval survival rates (Wainhouse et al. 2001; Awmack & Leather
2002; Thorpe & Day 2008). It has also been shown that in many insect species, including the mountain pine beetle, larger females lay more eggs than smaller females as larger females have greater fat stores, and this resource aids the maturation of eggs (Reid 1962; Safranyik & Jahren 1970; McGhehey 1971; Amman 1972a; Thorpe & Day 2008), though no such difference in egg laying capacity was found in this study. However, Amman (1972a) found a great deal of variation in egg-laying capacity in mountain pine beetles of similar sizes, even under similar food, temperature, and substrate conditions. Elkin & Reid (2005) found that starvation decreased the size, but not the number of eggs laid.

Female mountain pine beetles with low energy reserves may produce lower quality offspring due to energy allocation tradeoffs. These females may be physiologically constrained in the number or size of eggs they are able to produce, as well as constrained in the amount of energy they are able to expend when searching for a suitable host tree (Elkin & Reid 2005). The choice of host tree or breeding site is especially important for bark beetles, because the quality of the host tree is directly related to the provisions available for the developing offspring. Elkin and Reid (2005) found that beetles arriving at breeding sites with low energy reserves were less likely to successfully enter the host tree, and had a limited ability for a large reproductive investment. Feeding at the breeding site was observed and this action disconnected reproductive potential from the energetic condition of beetles arriving at the breeding site (Elkin & Reid 2005). This suggests that beetles must have large enough energy reserves to successfully locate, and enter a host tree. Upon entering the host tree, a beetle may feed to increase the energy available for reproduction. In our study, beetles were inserted under the bark of the tree, and did not have to carry out any host searching. Beetles with low energy reserves could then have fed at the breeding site in order
to increase the amount of energy available to be allocated to reproduction. This could potentially have reduced the variation observed in the sizes of offspring from mothers of different sizes and energetic conditions. It would then be expected that the difference in mother quality should be reflected in offspring quantity, however, no difference in offspring quantity was observed between broods from large and small mothers. It was also found that small and large offspring had the same absolute amounts of fat (Chapter 2). This suggests that in the mountain pine beetle offspring size is largely a function of environment, and maternal vigour is correlated more to dispersal, host location and attack success. Because mountain pine beetles usually have to overcome and kill their host, the condition of the offspring may not have been selected for in the sense that large genotypes are more successful.

In many insects, maternal investment, linked to female size or host quality have been shown to influence the ability of offspring to withstand competition, starvation, or negative environmental conditions (Fox & Czesak 2000). It is also likely that many factors, in addition to mother size and tree size, influence the size of offspring. Host quality encompasses a large number of physiological, chemical, and physical characteristics, which may be only weakly related to tree size. It is possible that in every beetle – host tree interaction, the offspring perform to their full potential until they reach a limiting factor, which could be any one of the factors affecting host quality characteristics, and could be different in every circumstance. Natal nutrition (Elkin & Reid 2005), phloem thickness (Amman 1969; Berryman 1976; Amman & Cole 1983; Shrimpton & Thompson 1985), defensive capabilities (Shrimpton 1973), environmental conditions (Steed & Wagner 2004),
intraspecific competition (Raffa & Berryman 1983), along with many other factors could potentially limit offspring quality in different situations.

Interestingly, a marginal effect of mother size on male offspring size was observed ($P=0.077$). This indication that males may be affected by their mother's condition or genotype may have some biological importance. Larger males may be more successful at gaining entrance to the gallery of a potential mate (Ryker & Rudinsky 1976), and hence may have a greater chance of successfully mating and carrying on their mother's genotype. Larger males have also been shown to produce more anti-aggregation pheromones, so would be better able to discourage competition than smaller males (Pureswaran & Borden 2003). Males have also been shown to be less able to tolerate adverse conditions such as high competition or cold temperatures. Safranyik (1976) stated that following stress-induced mortality in mountain pine beetle larval or adult stages, male to female ratios decrease as males die at a higher rate. Safranyik and Jahren (1970) also found that male to female ratios in field populations were significantly lower after a winter with temperatures below their minimum supercooling point (Safranyik & Jahren 1970; Safranyik 1976).

This study has indicated that offspring size is mainly a factor of environment, and maternal condition has a larger effect on dispersal, host location, and attack success. Larger emerging female mountain pine beetles may be better equipped for longer searches, and better able to withstand host tree defences, as will be discussed in the following chapter.

References


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4.0 Chapter 4 – Are mountain pine beetles responding to synthetic pheromone representative of the entire population?

Abstract

When using pheromone-based management of bark beetles, it is important to determine if pheromone responders are representative of the population, in order to know if management efforts affect the entire population, or just a subset. To address this issue, the size and sex ratio of mountain pine beetles, *Dendroctonus ponderosae* Hopkins, emerging from naturally infested lodgepole pine (*Pinus contorta* Dougl. var *latifolia* Engelm.) bolts collected from three stands north of Prince George were compared to that of mountain pine beetles from the same generation responding to pheromone-baited Lindgren funnel traps in the same stands. The population size and sex distributions of a randomly selected subset of the trapped beetles were compared to expected distributions calculated from beetles that emerged from the collected bolts. Both males and females collected from traps were significantly larger than the expected distribution. There was also a significant difference between the observed and the expected population sex ratios. Beetles caught earlier in the flight period were significantly larger than expected. Larger mountain pine beetles may have a physical advantage and greater survivorship than smaller beetles. The skewed sex ratio of trapped beetles may be a function of the synthetic pheromone bait, as well as differences between the pheromone-responding strategies of males and females. Beetles attracted by synthetic pheromone may represent a stronger subset of the population. I conclude that trap catches are not representative of the population in terms of size and sex ratio.
Introduction

Bark beetles respond to a large number of internal and external stimuli during their search for a suitable host (Borden et al. 1986). External cues, such as plant-produced volatile chemical compounds that act as attractants may give the insect clues as to the susceptibility as well as nutritional and overall suitability of that plant as a host (Wallin & Raffa 2004). These chemical cues may be used by insects to select hosts even when there is little difference in tree size (Amman & Cole 1983). Internal cues include each individual’s genetically determined response to these compounds (Wallin & Raffa 2004).

Eruptive bark beetles like the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) must attack and kill relatively healthy host trees in order to breed (Safranyik & Carroll 2006). Hence, host selection involves both the location of susceptible trees, and cooperative behaviours to overcome host resistance (Berryman et al. 1985). The population phase of eruptive bark beetles has been shown to influence the host acceptance behaviour of these insects. In the spruce beetle, *D. rufipennis* Kirby, non-aggressive genotypes dominated during the endemic population phase, but during population eruptions aggressive genotypes dominated, and the bark beetles attacked relatively large, healthy trees (Wallin & Raffa 2004). Their study also suggested that host acceptance may have a genetic or maternal component, i.e., host selection behaviour of a bark beetle’s mother may influence the response to host chemicals by the offspring.

The response of bark beetles to conspecifics also depends on the population phase of the insect. Within epidemic bark beetle populations, individual beetles are less repelled by the presence of many other beetles (Wallin & Raffa 2004). This makes sense, as with an increase in bark beetle population levels, the selective pressures shift from host tree defences...
to intraspecific competition (Wallin & Raffa 2004). This shift in host acceptance follows the optimal foraging theory (MacArthur & Pianka 1966) such that when higher population densities exist and when food resources are scarce, insects may accept a wider range of host trees or food sources. When intraspecific competition increases, individual generalization, or acceptance of a wider range of hosts, can be observed, as well as decreased variability in generalization across the entire population (Bigger & Fox 1997; Hopper 1999; Fontaine et al. 2008). This high population density-induced shift in host or food plant acceptance has been observed in bark beetles (Wallin & Raffa 2004), as well as in other insects, e.g., the diamondback moth (Plutella xylostella (L.)) (Bigger & Fox 1997), and a bumblebee (Bombus terrestris (L.)) (Fontaine et al. 2008).

In bark beetles, high density brood situations may lead to smaller beetles that respond poorly to plant host cues (Wallin & Raffa 2004). Smaller mountain pine beetles have been shown to construct shorter galleries, lay fewer eggs, and lay their eggs at a slower rate than larger beetles (Amman & Cole 1983). Large Ips pini (Say) beetles have been shown to be more successful at breeding in nature than smaller beetles (Robertson & Roitberg 1998). They showed that the mean length of all male Ips pini emerging as offspring was significantly smaller than that of males breeding in nature. The combination of high brood densities and the reduced ability of smaller beetles to find suitable hosts and to reproduce may ultimately lead to a population decline.

Research on bark beetles, including the mountain pine beetle, has benefited from the identification and synthesis of compounds that are specific to attack and colonization processes (Bentz 2006). These semiochemicals can be used in traps (Lindgren 1983) to allow researchers and managers to monitor and study beetle flight. Pheromone-baited
Lindgren traps are commonly used in a wide variety of resource management and research applications for bark beetles. It is important to determine if pheromone responders are representative of the population, in order to know if management or research efforts affect the entire population, or just a subset.

The objective of this research was to compare the size of mountain pine beetles emerging from naturally infested trees, representing the available pool of insects, to the size of mountain pine beetles from the same generation responding to pheromone baited traps within the same stand. I hypothesized that synthetic pheromones should attract smaller beetles, as these beetles are in theory less fit, and are more likely to be attracted to a host that has already been identified as an acceptable host. Larger beetles may be more able to initiate new attacks and overcome tree defences.

**Materials and Methods**

Five pheromone-baited Lindgren funnel traps were set up in each of three stands along the Salmon Forest Service Road, north of Prince George (site 1: 10U 505724E 6017198N, site 2: 10U 506492E 6016280N, site 3: 10U 508306E 6013376N), for a total of 15 traps. Each stand was a minimum of 500 m apart. Captured insects were collected once per week from June 30 to July 25, 2006. Each trap was baited with a mountain pine beetle trap lure containing trans-verbenol, myrcene, and exo-brevicomin (Contech (formerly Pherotech) International, Inc., Delta, BC). A minimum of twenty beetles from each trap and collection date, for a total of >80 beetles per trap, were separated by sex by examining the posterior margin of the seventh abdominal tergite (Hopkins 1909; Lyon 1958), and measured (pronotum width, pronotum length, and body length).
An expected population size-distribution was calculated from beetles that emerged from infested bolts collected from the same stands (See Chapter 2). Five variable radius plots (BAF 4) were established in each of the three stands in order to determine general stand characteristics. The basal area factor (BAF) is used to determine the number of units of basal area per hectare represented by each tree.

Based on the information collected, for each stand, the number of trees in each diameter class per hectare was calculated as follows:

*Equation 1*

\[
\text{Trees/ha} = \frac{(\text{BAF} / (0.00007854 \times (\text{DBH}^2))) \times (\text{total # trees})}{\text{# sample points}}
\]

Where: 
- DBH = the average DBH in each diameter class in each stand
- Total # trees = sum of total # trees in each plot per stand
- #sample points = # of variable radius plots performed in each stand

With this stand information, the total number of trees per hectare (the sum of all diameter classes) was calculated for each stand. The proportion of the total trees in each diameter class in each stand was then determined, and is hereafter referred to as the “stand characteristics.”

Data on emergence timing, size and sex were collected from beetles emerging in the lab (see Chapter 2). These emergence data were used to calculate the proportion of beetles of each sex that emerged in the lab from each diameter class and from each stand (“lab data”). The expected proportion of beetles emerging from each diameter class in each stand was then calculated based on stand characteristics and lab data using the following equation:

*Equation 2* (applied to each stand, diameter class, and sex combination):
X proportion of expected beetles = (proportion of beetles in lab / proportion of trees in lab) * 
(proportion of trees in stand)

Where (for example):
-X proportion of expected beetles = the proportion of females emerging from 15–20 cm trees in stand 1
-Proportion of beetles in lab = the proportion of females emerging from 15-20 cm trees in lab
-Proportion of trees in lab = the proportion of 15-20 cm trees in the lab (0.2 for all size classes)
-Proportion of trees in stand = the proportion of 15-20 cm trees in stand 1 as calculated above

These proportions were then used to calculate the expected sex ratios for each stand and diameter class.

Using the lab-emerged beetle data, the average sizes (pronotum width, pronotum length, and body length) of beetles from each sex, in each diameter class and stand were calculated. These average sizes were then used as the expected sizes of beetles from each sex, in each diameter class, caught in the traps in each stand ("expected population"), e.g., the expected pronotum width of females from diameter class 1 in stand 1.

The observed population distribution for each stand (from the Lindgren traps) was then compared to the expected population distribution for each stand using a two-sample Kolmogorov-Smirnov test using SYSTAT 9 (Systat Software, Inc., Richmond, CA, USA). Pronotum width was used in the analysis as it was a more accurate measurement than pronotum length or total body length, was more easily attained, and had been used extensively in the literature (McGhehey 1971; Safranyik 1976; Coppedge et al. 1994, 1995).
A correlation analysis carried out using SYSTAT 9 (Systat Software, Inc., Richmond, CA, USA) to determine the relationship between pronotum width and length indicated that these two measures were relatively poorly correlated ($r = 0.332$, $f_{(2),1513} = 13.69$, $P<0.001$).

**Results**

There was no significant difference in the mean size of beetles from trap-catches among stands ($F_{2,1512} = 1.18$, $P = 0.31$), but this was not the case for the mean size of the beetles used to calculate the expected population distribution ($F_{2,561} = 5.025$, $P = 0.0069$), so the data were analyzed by stand. Mean size (pronotum width) of mountain pine beetles collected from pheromone-baited funnel traps was significantly larger than the mean size of mountain pine beetles in the expected (calculated) distributions for both males and females in each of the three stands (Stand 1 Males: $D = 0.4503$, $P < 0.001$; Stand 1 Females: $D = 0.5612$, $P < 0.001$; Stand 2 Males: $D = 0.5147$, $P < 0.001$; Stand 2 Females: $D = 0.4831$, $P < 0.001$; Stand 3 Males: $D = 0.5518$, $P < 0.001$; Stand 3 Females: $D = 0.5101$, $P < 0.001$) (Figure 4-1).
Figure 4-1. Mean (± SE) pronotum width of mountain pine beetles captured in pheromone-baited Lindgren traps (O = observed) compared to expected population means (E = expected) for males and females based on beetles emerged from naturally infested trees in the same stand. A significant difference (<0.001) between expected and observed pronotum width (two-sample Kolmogorov-Smirnov test) was found for each stand and sex combination. N = 95-105 / trap.

Figure 4-2 shows that there was also a significant difference between the observed and expected population sex ratios in each of the three stands (Stand 1: $D = 0.4418$, $P < 0.001$; Stand 2: $D = 0.3728$, $P < 0.001$; Stand 3: $D = 0.3209$, $P < 0.001$). The expected sex ratios were skewed towards females (Stand 1: 1.54:1 female:male; Stand 2: 1.48:1 female:male; Stand 3: 1.82:1 female:male), whereas the sex ratios of the observed distributions were strongly skewed towards males (Stand 1: 0.3:1 female:male; Stand 2: 0.29:1 female:male; Stand 3: 0.4:1 female:male). The sex ratios also changed significantly over time, decreasing in the proportion of females as the emergence period progressed ($F_{3,8} = 8.814$, $P = 0.006$). There was no difference in the sex ratios between stands ($F_{2,9} = 0.605$, $P = 0.567$).
When analyzed by week of catch, the mean pronotum width of female mountain pine beetles collected during the third week of the emergence was significantly smaller ($t_{(1),682} = 7.593, P < 0.005$) than the expected female size calculated from the lab-emerged beetles (Figure 4-3), while females caught during the second and the fourth week of the emergence were significantly larger ($t_{(1),713} = 9.56, P < 0.005$ and $t_{(1),692} = 6.227, P < 0.005$, respectively) than the expected female size calculated from the lab-emerged beetles. There was a marginally non-significant difference between the mean pronotum width of females collected during the first week of emergence and the expected female size ($t_{(1),817} = 2.958, P = 0.056$).
Figure 4-3. Mean (± SE) pronotum width of the expected female distribution based on emerged beetles from naturally infested trees (left point and horizontal line) and the mean (± SE) pronotum widths of females sampled weekly from pheromone-baited funnel traps. The asterisks indicate a significant difference in pronotum width between females collected from emergence cages in the lab, and females collected from pheromone-baited funnel traps (**=<0.01).

Discussion

For this study, it was assumed that the majority of trap-captured beetles were from the local stand and generally had not carried out long-distance flights. The difference between pheromone-responding and emerging females was greater than the difference observed in males, but pheromone-responding beetles were consistently larger than the emerging beetles (Figure 4-1). Although larger beetles do not always have larger percent lipid contents than smaller beetles (Chapter 2), the flight capacity of large and small beetles was not determined. Lipids are directly metabolized in flight changing insect weight over time (Atkins 1969; Coppedge et al. 1994) when searching for a new host tree. As discussed in Chapter 2, larger beetles may not have energy needs that are directly in proportion with their larger size, and
may still have a physical advantage over smaller beetles. Larger bark beetles have been shown to have increased flight activity, and to have the ability to fly for longer periods of time than smaller beetles (Kinn 1986; Slansky & Haack 1986). Bark beetles also respond to internal stimuli such as hunger and their physiological state when searching for hosts (Wallin & Raffa 2004). This indicates that larger, healthier beetles should be better equipped for extended flights when searching for suitable hosts. *Ips calligraphus* larvae that develop in high quality host trees tend to become larger and heavier adults with higher lipid contents, providing these beetles with a greater ability for extended flight, than those larvae developing in low quality host trees (Slansky & Haack 1986). The energetic condition of a female mountain pine beetle also influences the reproductive potential of that beetle. A female in better physiological condition should have more energy available to contribute to reproduction leading to a larger size and number of eggs (Elkin & Reid 2005). However, it is possible that smaller beetles may be able to fly further as an adaptive mechanism to escape unsuitable habitats (Slansky & Haack 1986).

As female mountain pine beetles are the pioneer sex, being of high quality may improve a female's chances of finding a suitable host and initiating a breeding gallery. Larger male pine engravers, *Ips pini*, which is the pioneering sex in *Ips* spp., were more likely to locate host trees and initiate breeding galleries, possibly because they have the ability to fly farther and at higher velocities than smaller males (Robertson & Roitberg 1998). They also suggest that because suitable host trees for *I. pini* are unpredictably distributed throughout the environment, as this species breeds in dying or recently dead trees, larger males with a greater flight capacity have a competitive advantage over smaller males, and have a greater chance of finding a breeding site. In both epidemic and endemic situations,
high quality female mountain pine beetles may be better equipped for extended flights while searching for brood trees, so these females may have a higher probability of finding suitable breeding sites and initiating breeding galleries. As was discussed in Chapter 3, larger females may also have a better chance at withstanding lodgepole pine defences. In this study, larger beetle were caught in traps, possibly indicating that larger beetles have more success with migrating and host searching than smaller beetles.

Larger mountain pine beetles may also have a greater survivorship than smaller beetles (Safranyik 1976), possibly due to larger insects' ability to withstand poor weather or the threat of predation. A difference in survivorship between small and large mountain pine beetles may explain the observed difference between the size of the pheromone-responding and the emerging beetles. In a laboratory setting, where the emerging population was reared, no adverse environmental conditions were experienced by the developing offspring at any time during development. Under natural field conditions, environmental extremes or weather events would have differentially affected beetles of different sizes and qualities, and in trees of different sizes. Smaller and weaker beetles that may have been killed under these types of field conditions, would have survived in the lab, resulting in a smaller mean size of the overall population.

The larger insects captured in pheromone-baited traps may represent the strongest, and most long-lived members of the whole emerging mountain pine beetle population. These females responding to synthetic pheromones would be the beetles that would attack trees and successfully establish breeding galleries. Small beetles may be too weak to initiate a host search, and would never become a member of the pool of “responders”. Alternatively, Lindgren funnel traps may be more efficient at capturing large beetles that respond to the
pheromone than small ones, since capture depends on the insect falling into the collecting cup at the bottom of the trap (Lindgren 1983). In this study, no significant difference was observed between the mean size of beetles from trap-catches between stands, but a significant difference was observed in the calculated expected population distribution between stands. This may indicate that traps favour a certain size of beetle, regardless of the size of the emerging population.

Safranyik (1976) suggested that larger mountain pine beetles emerge before smaller beetles as was found in my own research (this chapter and Chapter 2). This would mean that the beetles emerging first essentially have a head-start on their search, and will have the first chance to select a host tree. Thus, large beetles may be able to attack the highest quality trees before the smaller beetles emerge, and will have a better chance of positioning their offspring near a high-quality food source. In the study stands, most of the large trees had been attacked in the previous year, so there were few high-quality host trees available. A minimum phloem thickness of 1mm – 1.5mm has been suggested for mountain pine beetles (Safranyik 1971; Shrimpton & Thompson 1983; Safranyik & Carroll 2006), below which beetles are forced to abandon galleries due to their physical inability to fit under the phloem. Smaller beetles would be better able to physically fit in small trees, and would have a better chance of reproducing in thin phloem, though in Chapter 3 no effect of tree size was found on brood quality.

The sex ratio of mountain pine beetles that emerged from bolts was skewed with 60% females (Figure 4-2). It is commonly accepted that natural mountain pine beetle sex ratios vary depending on brood conditions, but they are almost always in favour of females (Amman & Cole 1983). It is also understood that any factor that stresses the population,
decreases male survivorship (Amman & Cole 1983). Counter to what was expected, the sex ratio of the mountain pine beetle population captured in pheromone-baited traps was strongly skewed in favour of males (Figure 4-2). This skewed sex ratio is similar to that found by Hunt and Borden (1988) in their trapping experiment. They found sex ratios in the range of 50 – 73% male in baited traps, and determined these ratios to be significantly different than those ratios found in unbaited traps. A similar phenomenon was observed by Botterweg (1982) with Ips typographus. Clear differences were observed between beetles captured in pheromone traps and emerging beetles. These differences were attributed to different mortality rates due to selective parasitism and/or predation between males and females, and between different locations (Botterweg 1982). However, in the case of the mountain pine beetle, the skewed sex ratio in the trapped beetles is most likely a function of the synthetic pheromone blend used as bait. Pheromones are the principal means of communication for mountain pine beetles (Lindgren & Borden 1989). Aggregation pheromones facilitate mass attack while anti-aggregation pheromones decrease the chance of excessively high attack densities. trans-Verbenol, a terpene alcohol derived from the monoterpene α-pinene (Hunt et al. 1989), is the primary aggregation pheromone. It is produced by females and is the primary attractant for male mountain pine beetles (Rasmussen 1972). exo-Brevicomin is a pheromone that is released by males and at low concentrations it mainly attracts females (Lindgren & Borden 1989). Myrcene and terpinolene are host-produced kairomones that synergize the activity of the beetle produced pheromones (Raffa & Berryman 1983; Borden et al. 2008). Male mountain pine beetles may be more responsive to the combination of pheromones used in these traps, which would explain the sex ratio in the responding beetle population (Hunt & Borden 1988). The potency of trans-verbenol is dependent upon the
abundance of the host tree-produced terpene, alpha-pinene (Pitman 1971). Less vigorous, poor quality trees, or trees that have been attacked beyond their critical defensive capacity threshold (approximately 40 galleries / m$^2$ (Raffa & Berryman 1983)), may produce less alpha-pinene, so less of the beetle-produced trans-verbenol is produced leading to slower colonization rates (Raffa & Berryman 1983).

As females are the pioneer sex, they are faced with locating an acceptable host tree, attracting conspecifics to overcome the tree defences, and attracting a mate. Once a female is in proximity of host trees, they use visual or other host cues to locate a specific tree (Borden et al. 1986; Campbell & Borden 2006), whereas males are primarily interested in finding females. Once a male has joined a female, compounds to discourage competition are produced (Lindgren & Borden 1989). This means that males are primarily responders and do not respond to host volatiles in the same way as females do. This in turn would suggest that a male bias would be expected in pheromone-baited traps, as was found in this and other studies (Hunt & Borden 1988). A higher proportion of females were also caught in traps earlier in the emergence period indicating that larger females prefer traps.

The mean size of the females caught in the pheromone-baited funnel traps was largest during the first week of emergence, and then decreased until the third week. In Chapter 2, the largest mountain pine beetles emerged first, and the average size of beetles emerging in subsequent weeks decreased. The mean size of the females caught during the third week was significantly smaller than the mean size of the females emerging in the lab (Figure 4-3). This observation is consistent with Safranyik (1976), who found that larger mountain pine beetle individuals emerge at the beginning of the emergence period. This means that the individuals found searching for hosts, or attempting to initiate breeding galleries in the initial
stages of the emergence period are more likely to be larger in size than those beetles found later in the emergence period. Botterweg (1982) and Robertson and Roitberg (1998) also determined that larger *Ips pini* were the first to successfully colonize host trees and that there is a decline in the length of male *Ips pini* initiating nuptial galleries later in the season. Female mountain pine beetles emerging first, with a larger size have a better chance of colonizing high-quality breeding sites and securing mates.

In the fourth week of the emergence period, the average female size increased. This increase in female size at the end of the emergence period may have been due to parents re-emerging from poor hosts, or re-emerging to make a second egg gallery (Bentz 2006). She found that beetles emerging late in the emergence period had lower lipid contents than those beetles collected during the peak emergence period, suggesting that at least a portion of those late emerging beetles may be re-emerging adults. This finding is also supported by data from Chapter 2. For the beetles captured immediately after emergence, after the initial emergence date, beetle size decreased in subsequent weeks of emergence. The size of emerging beetles did not increase towards the end of the emergence period, indicating that the captured beetles during the last week of trapping were from a different source than those emerging in the stand. Bentz (2006) found that pheromone-baited traps captured beetles both before and after the local emergence period, indicating that many captured beetles are either immigrants or reemerging adults.

Larger female mountain pine beetles may be better equipped for extended flights when searching for suitable host trees. These larger beetles may have a number of competitive advantages when compared to those of lower quality, such as higher survivorship (Safranyik 1976), or earlier emergence leading to greater opportunities to
colonize breeding sites (Safranyik 1976; Botterweg 1982). When using pheromone-baited funnel traps, it may be important to consider that mass trapping may target only a portion of the entire population.

References


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5.0 Chapter 5 – Synthesis

Abstract

Mountain pine beetle survival and reproductive success depends on their ability to find a suitable host tree and differences in host quality may lead to developmental differences in offspring. The main objective of this research was to determine how the quality of brood trees affects fitness of emerging mountain pine beetles. The lipid content of emerging beetles was measured and related to host quality, maternal effects on broods were tested by rearing beetles of different sizes in hosts of constant quality and measuring brood success and brood characteristics, and beetles responding to aggregation pheromones were compared to beetles emerging from infested trees. The largest offspring were found to emerge first, but they did not have the highest lipid content, indicating that these beetles have the most to gain from having a head start on their host search, and benefit from a wide selection of potential host trees. There appear to be advantages associated with both large and small sizes of mountain pine beetles. Beetles may change their search behaviour based on their size and overall phenotype to best exploit the resources available. Lower quality beetles also have the ability to feed at the breeding site in order to improve their somatic condition before breeding, which could potentially make their energetic condition upon arrival of little importance. Large and small beetles were found to have similar absolute fat contents which could indicate that energy requirements are not proportional to body size. Females may benefit more from being of high quality than males, as females are the pioneer sex and high quality females may be better equipped for extended flights. Males were found to be marginally affected by their
mother’s condition. Male offspring are more susceptible to cold temperatures and adverse conditions, and stronger males have been shown to be more successful at gaining entry to the breeding gallery of a potential mate. Males are more sensitive to external factors than females, so it is possible that they are better able to utilize the provisions from their mothers.

Synthesis

Mountain pine beetles are one of the most important forest health agents in coniferous forests in western North America. These beetles are endemic to western North America and breed in the phloem of most species of Pinus, but primarily in lodgepole pine, P. contorta Dougl. var. latifolia Engl. Healthy lodgepole pine trees are mass attacked and killed over vast areas during epidemic mountain pine beetle population levels (Safranyik & Carroll 2006). Mountain pine beetle survival and reproductive success depends on their ability to successfully locate suitable host trees (Pureswaran & Borden 2003). Large diameter trees are preferentially attacked, as they are better suited for reproduction (Amman 1969; Pureswaran & Borden 2003). As an outbreak escalates, attacks on smaller, lower quality host trees become more common, as does overcrowding in each brood tree, both leading to decreased resources for each beetle (Pureswaran & Borden 2003). Beetles developing under these suboptimal conditions should be lower in quality, and this trend should have important implications with respect to the population dynamics of the mountain pine beetle.

The objective of this research was to define how the quality of brood trees affects mountain pine beetle fitness. I determined the effects of host quality and intraspecific competition on the fitness of emerging beetles by measuring their fat content, relative to host
quality (Chapter 2), evaluating the effects of mother size and host quality (size) on offspring fitness by rearing beetles of different sizes in hosts of constant quality and measuring brood success and brood characteristics (Chapter 3), and comparing an emerging to a pheromone-responding beetle population to determine if pheromone-responders are representative of the entire mountain pine beetle population (Chapter 4).

In all three studies, larger beetles were found to emerge earliest in the emergence period, but females emerging during the middle of the emergence period were found to have the highest percent lipid content (Chapter 2). Tree size was found to negatively affect percent lipid content of males and females, but there was no effect of tree size on the absolute lipid content of either males or females. In Chapter 3, no effect of tree size or mother size was found on either male or female offspring, and both large and small mothers successfully bred in all tree sizes tested. There was a marginal positive effect of mother condition on male offspring size. In Chapter 4, both males and females collected from the pheromone-baited traps were significantly larger than the expected population distribution. There was also a significant difference between the observed and expected population sex ratios.

Beetles emerging, migrating, and colonizing early in the emergence period were found to be larger than average in size, but did not have the highest lipid contents. These beetles may benefit from getting a head start on the search, as they will have the greatest number of host tree options available. Smaller beetles emerging later in the emergence period may benefit from having a wider range of acceptable hosts as they can successfully breed in trees that may be physically too small for larger beetles. Beetles emerging later in the emergence period may also benefit from being able to focus on already attacked trees, which are guaranteed to be suitable and already have weakened defenses from early attackers.
There appears to be advantages both to being small and large for mountain pine beetles. As mentioned above, smaller beetles may be able to exploit a larger range of host trees due to their physical ability to fit within the thinner phloem of smaller trees. This extended acceptable host tree size range may give these smaller beetles a greater number of host options when searching for a new brood tree. Larger beetles may have a better chance at withstanding lodgepole pine defenses as well as adverse weather conditions and the threat of predation. Under natural field conditions, environmental extremes would differentially affect beetles of different qualities in hosts of different qualities. Smaller and weaker beetles would be killed first, which would result in a higher mean size of responding beetles in nature as was shown in Chapter 4. It is likely that these larger insects represent the strongest and most long-lived members of the entire emerging population, whereas the smaller members of the population may be lost in extreme weather events, or may be too weak to initiate a search.

Beetles may adapt their searching or foraging behaviour and their acceptable range of host trees to reflect their phenotype, the availability of suitable hosts, as well as the amount of intraspecific competition. Large, early emerging beetles appear to be using a contest competition model where they benefit from having the greatest number of host trees available and either must travel further or select less suitable hosts. During high competition situations, host selection and attack appears to follow a scramble competition model in which beetles accept heavily colonized hosts, and when the resource is depleted, all the developing offspring suffer. In the later stages of an infestation, when few suitable hosts are available, beetles carry out a longer search or settle on a suboptimal host; both of these scenarios should lead to lower offspring quality. Low quality beetles may also feed at the breeding site in order to increase the amount of energy they can allocate to reproduction, which could make
their energetic state upon arrival irrelevant. This would potentially reduce the amount of variation observed in the offspring from mothers of different qualities as was observed in Chapter 3, suggesting that offspring size is primarily a function of the environment, and maternal fitness is more important in dispersal, host selection, and attack success. Energy allocation to eggs or to host selection may be more important when high quality hosts are not available as mountain pine beetles would be forced to expend greater amounts of energy during longer migrations.

In Chapter 2, it was found that small and large beetles had similar absolute lipid contents. It is possible that small and large beetles may not have energy needs that are directly proportional to their body sizes. This may indicate that beetles optimize their absolute lipid contents while using any excess energy for growth, which is positively correlated to fecundity. It is possible that smaller and larger beetles have similar reproductive potentials, just different ranges of acceptable hosts, however. Smaller beetles may also be able to fly further as an adaptation to escape unsuitable habitats (Slansky & Haack 1986).

As the pioneer sex, female beetles may benefit more from higher lipid contents than males. Mountain pine beetle egg size has been shown to be dependant on the energy levels of females after dispersal (Elkin & Reid 2005). The lipid content of females was found to be the greatest during the middle of the emergence period, whereas the lipid content of males remained constant throughout the emergence period (Chapter 2). High quality females may be better able to undertake extended flights while searching for suitable host trees, so these females should have a greater chance of locating suitable brood trees and successfully initiating breeding galleries, while also retaining high lipid contents to contribute to the production of high quality eggs. Males, on the other hand, do not have to search for suitable
hosts or maintain high lipid stores for egg production; they must only follow chemical signals and locate unmated females.

In Chapter 3, a marginal effect of mother quality on male offspring size was observed. Male offspring may be more affected by their mother’s condition or genotype than female offspring. Larger males are more successful at gaining access to the breeding gallery of a potential mate (Ryker & Rudinsky 1976). Also, males have been shown to be more susceptible to adverse environmental conditions such as cold temperatures and extreme weather (Safranyik 1976). During particularly harsh years, male to female ratios decrease as males tend to die first and at a higher rate than females (Safranyik & Jahren 1970; Safranyik 1976). For these reasons, it may be more important to ensure that male offspring are of high quality.

Overall host quality is complicated in nature, and it is difficult to characterize and find measurable host tree attributes useful for making general predictions about host quality effects on mountain pine beetle populations. Steed and Wagner (2004) suggested that factors other than tree diameter and phloem thickness, such as post mortem tree vigour, could be more important to *Ips pini* during host selection. Tree vigour, the strength of defensive responses, phloem moisture content, among other attributes may be important in mountain pine beetle host selection, breeding success, and offspring fitness. It is likely that limiting factors of the host tree play an important role in determining offspring size. It is possible that smaller logs provide a more vulnerable habitat for bark beetles, and that beetles in these trees may be more susceptible to extreme environmental conditions (Steed & Wagner 2004). It has been suggested that only under negative environmental conditions, such as high competition or in very low quality hosts, are the effects of egg size on survival apparent.
The studies in chapters 2, 3, and 4 all involved lab reared beetles, which were not subjected to any extreme environmental conditions. By gaining a greater understanding of mountain pine beetle population dynamics, population distributions, and their range of suitable hosts, forest managers will be able to more accurately predict stand susceptibility to mountain pine beetle attack. This will enable managers to focus their energy to proactively harvest the stands at highest risk. Also, through the implementation of advanced silviculture techniques, it may be possible to encourage the growth of more vigorous trees. These trees would have higher defensive capabilities, and would only be minimally susceptible to attack under endemic beetle population levels, or susceptible only to the strongest beetles under epidemic population levels.

References


