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Tree Diameter Effects on Mountain Pine Beetle Success

by

William Anthony Murphy

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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Abstract

Habitat-seeking dispersers are faced with the challenge of finding high quality habitats while minimizing the costs incurred during habitat selection; dispersers can facilitate habitat selection by using cues emitted by their habitat. Here I investigate the habitat selection of the mountain pine beetle (MPB, *Dendroctonus ponderosae*), a pest insect which kills large lodgepole pine (*Pinus contorta*) trees during outbreaks. I measured host quality traits (phloem thickness and defensive traits) with respect to tree size as well as MPB attack and brood production. I also tested MPB orientation to two host size treatments by using baited funnel traps.

Larger trees tended to be better MPB hosts. Larger trees had thick phloem and fewer to neutral defences compared to smaller trees. Larger trees were more likely to be attacked and sustained more attacks while smaller trees were nearly unattacked. After accounting for tree size, there was no evidence that MPB preferentially attacked trees with the thickest phloem or fewest defences which suggests that MPB attack the most detectable hosts rather than the highest quality hosts. Absolute brood production showed a hump-shaped relationship to tree size, suggesting that large trees may not necessarily benefit MPB offspring. More MPB were caught in large-diameter traps than small-diameter traps; however, this only occurred when the traps were paired. When traps were independent, the mean catch of both treatments was approximately equal. This work shows that larger trees tend to be better hosts for MPB but MPB do not appear to preferentially orient to large silhouettes, suggesting that visual host size information is a minor component of MPB host selection behaviour.

Keywords: Mountain pine beetle, lodgepole pine, forest ecology, habitat selection, tree physiology, insect behaviour

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Dedication

To my parents, who nurtured my curiosity.

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Chapter 1: General Introduction

Habitat selection is critical for dispersing organisms. Dispersal is defined as movement of individuals originating from some point on a landscape into a new habitat (Stamps 2001). Dispersal can occur for several reasons such as kin competition, inbreeding avoidance, and habitat variability (Bowler et al. 2005). Habitat variability (or 'quality') can encompass several metrics such as food availability, predation pressure, and a variety of environmental variables. Habitat quality can change as a function of time due to resource consumption, movement of other organisms, changes in weather or climate, etc. As individuals grow and become reproductively mature, the natal habitat may become unsuitable due to low resources and high potential for inbreeding which can force the individual to emigrate. Migratory birds and polygamous mammals exhibit high emigration behaviour (Pusey 1987), as do insects, though less frequently (Harrison 1980). Emigration is costly, and potentially fatal: time and energy spent searching for a habitat can incur deferred costs which take effect after an individual has become resident in a new habitat (Stamps et al. 2005). These deferred costs manifest after an individual has become resident in a habitat: a habitat may have degraded in quality during the search period or the disperser may have less energy to devote to some fitness increasing activity; the latter can be especially problematic for dispersers that do not replenish their energy stores while dispersing.

Habitat choice

Ecological theory suggests that organisms should select the best habitat available. The Ideal Free Distribution [IFD] (Fretwell and Lucas 1969) describes the mechanism and

consequences of such selection. Individuals are ‘ideal’ in that they are omniscient and capable of selecting the best habitat available to them. Individuals are also ‘free’ in that the movement of one individual does not inhibit the other. Under the IFD, a habitat is an area where organisms are able to colonize and live, and habitats are not necessarily contiguous or the same size. Habitat quality is defined by basic suitability, which is a fixed quantity representing predation pressure, moisture, cover etc. As habitats are settled their suitability (i.e. the ‘success’ of colonizers) declines from its basic suitability and eventually each habitat has equal suitability. The central prediction of the IFD is that adults have equal fitness across habitats. While the IFD has been frequently examined in the literature, organisms tend to ‘undermatch’ resource distribution: low quality patches (i.e. a collection of potential habitats) tend to have more organisms than would be predicted by the IFD while high quality patches tend to have fewer (Kennedy and Gray 1993). Simulation modeling suggests that organisms are constrained by their ability to perceive habitats and this lack of information likely leads to departure from the IFD (Abrahams 1986).

We can extend this idea to dispersers, as they may not be able to assess the quality of all possible habitats within a patch. If search/assessment costs are too great, dispersers may settle on lower quality habitat rather than not settle at all (Ward 1987). Dispersers can use cues produced by the habitat itself or other individuals resident within the habitat to acquire some information about its quality, alleviating search costs. For dispersing herbivores, such as insects, this is possible because plants produce a wide variety of visual and olfactory stimuli which can serve as attractants or deterrents (Painter 1958, Finch and Collier 2000, Mithöfer and Boland 2012). Integrating and interpreting multiple stimuli is neurologically complex and some cues may take

precedence at different stages or scales of dispersal behaviour (Balkenius and Balkenius 2016). The cost of assessing the cue or the individual's ability to tolerate that cost can affect the individual's search strategy and choosiness: high costs may drive a less choosy strategy (i.e. more variation in habitat selection) (Fawcett and Johnstone 2003). Cue assessment can have an indirect effect on fitness outcomes. For example, food-deprived black widow spiders (*Latrodectus hesperus*) were found to exhibit a less choosy search strategy than non-deprived spiders (Pruitt et al. 2011). Additionally, increased choosiness led to diminished investment in offspring as demonstrated in cabbage white butterflies (*Pieris rapae*) (Jaumann and Snell-Rood 2017).

Insects that feed on and live within live plant matter face additional challenges during dispersal because plants produce various physical and chemical defences to combat herbivores. However, plants cannot invest in growth and defence simultaneously and meta-analysis suggests that plants across taxa typically invest greatly in defence when they are small and young but less so as they accumulate resources and grow (Barton and Koricheva 2010). The Growth Differentiation Balance Hypothesis [GDBH] (Herms and Mattson 1992) provides a useful framework for understanding this trade off. The hypothesis is premised on the assumption that plants have a limited pool of dividing cells. These cells can be invested in growth or defence, but not both. Quantitatively this dichotomy is expressed via the relative growth rate which is the product of a plant's net assimilation rate (how much carbon is accumulated per unit time) and its leaf area ratio (the ratio of leaf area to other dry mass). Investment in defences via specialized anatomy (e.g. thorns or leaf hairs), or secondary metabolites (e.g. terpenoids, green leaf volatiles)

diverts cells that could be used to increase the leaf area ratio. The GDBH presents the idea that plants are not ‘growth specialists’ or ‘defence specialists’ and uses the illustration of a growth-defence continuum. Plants can lie closer to one end of the continuum than the other, and their position can change ontogenetically and with resource availability. For example, a young plant might invest more in defence if they are at risk of being damaged by herbivores because those plants have comparatively greater amounts of tissue to lose from a single herbivore attack than that same attack on a larger plant. Plants may also invest in defence when resources are scarce (i.e. due to poor site quality or competition from dominant plants) but a very shallow resource pool will likely kill the plant outright. Plants in resource rich sites will invest greatly in growth to become dominant and maximize future resource acquisition. The Plant Vigor Hypothesis [PVH] (Price 1991) can serve as a corollary to the GDBH by providing a mechanism by which herbivores select these high quality resources. The PVH proposes that insects will prefer large, vigorously growing plants or plant modules. This prediction can be updated by the GDBH: insects will prefer large, vigorously growing plants or plant modules because they have fewer defences compared to less vigorously growing structures. This prediction is perhaps most important for insects which live and produce offspring within plants such as bark beetles (Coleoptera: Curculionidae: Scolytinae).

Bark beetles

Most bark beetles (reviewed by Rudinsky 1962) breed and live within the twigs and stems of trees. Broadly, bark beetles fall into two ecological roles: most are ‘secondary’ bark beetles, which inhabit dead or dying trees. A smaller proportion are ‘primary’ bark beetles, which

inhabit live, healthy trees. The distinction between primary and secondary bark beetles is important because it informs several aspects of the beetle's ecology. Both primary and secondary beetles live within the tree's inner bark or phloem; (a thin, water-rich layer of tissue which translocates sugars produced during photosynthesis) and bark beetles tend to have higher quality (i.e. larger) offspring when reared in thick phloem than thin phloem (Amman 1972). Secondary beetle habitats are generally of low quality because the phloem is drier and subsequently thinner. Primary bark beetles live and breed within live trees which provides the beetle with higher quality phloem compared to secondary bark beetles (Lindgren and Raffa 2013). Primary bark beetles are challenged by host defences, such as resin, which is viscous liquid composed of compounds in the terpenoid family (Franceschi et al. 2005). Defences can be lethal and are capable of drowning or 'pitching out' beetles (Byers 1995) and potentially reduce egg size (Manning and Reid 2013). Given that the fitness outcomes of primary bark beetles are greatly influenced by host defence and phloem thickness, they should preferentially select hosts which have few defences and thick phloem. Energy lost during dispersal can influence the beetle's ability to tolerate defences (Manning and Reid 2013, Reid et al. 2017) and it is in the beetle's interest to quickly find suitable hosts, primary bark beetles may do this through olfactory and visual cues.

Bark beetles encounter a variety of olfactory stimuli from conspecifics and their host trees. Bark beetles produce aggregation pheromones, which chiefly serve to attract mates but also allow primary bark beetles to collectively attack trees ('mass attack') and overwhelm its defences, making the tree amenable to colonziation (Anderson 1948, Vité and Francke 1976,

Blomquist et al. 2010). Aggregation pheromones are highly effective, and they are applied to bark beetle traps as baits or components of baits (Lindgren et al. 1983, Lindgren 1983). Bark beetles also produce anti-aggregation pheromones and these are chiefly used by monogamous beetles post mating to maximize the area of inner bark usable for egg gallery construction (Vité and Francke 1976); for example, the compound verbenone reduced the catch of *Ips latidens*, *Ips pini*, and *Dendroctonus ponderosae* (Miller et al. 1995). Trees produce a range of volatile compounds and bark beetle antennae respond to these compounds; some, called kairomones, are known to be used in the host-finding process (Whitehead 1970, Seybold et al. 2006). These compounds are useful as host-finding cues because the composition of volatile plumes emanating from a tree tends to differ between species. For example, confers qualitatively share several compounds (e.g. α-pinene, β-phellandrene, limonene, etc.); however, the relative amount of these compounds is known to differ among species which may reduce host finding errors (Pureswaran et al. 2004). Qualitatively, bark beetles that feed on conifers are known to avoid green leaf volatiles emitted by non-host angiosperms, such as *Populus* spp. (Dickens et al. 1992, Wilson and Borden 1996). The detectability of these olfactory cues can suffer due to environmental factors, such as wind speed and direction, as well as competing stimuli overwhelming the insect's ability to detect and distinguish discrete sources of plumes (Andersson et al. 2013). Research suggests that at the small, within stand (i.e. 'patch') scale, bark beetle olfaction becomes less reliable, likely due to poor resolving power at small spatial scales and large, overlapping olfactory plumes (Saint-Germain et al. 2007). One way that bark beetles may compensate for this is by using visual information.

Insect vision (reviewed by Prokopy and Owens 1983), particularly that of bark beetles, has received comparatively less attention than olfaction. Most studies of bark beetle vision have concerned host colour, which is an important component in the host finding process. Beetles which feed on dark coloured stems are known to be attracted to dark coloured silhouettes and avoid lighter colours (Strom et al. 1999, Strom and Goyer 2001, but see Machial et al. 2012). In terms of discriminating host/non-host, vision may actually serve as a better cue than olfaction because the vision may cost less time and energy to assess than olfaction (sensu Fawcett and Johnstone 2003). Vision is primarily constrained by the observing organisms and the speed of light, while olfaction, can be constrained by many abiotic perturbations (Andersson et al. 2013). Evidence exists for the potential synergism of visual and olfactory information for some species such as *Trypodendron lineatum* and *Dendroctonus ponderosae.* Individuals of these species showed a greater preference for host coloured traps when the trap was baited with a host kairomone and the magnitude of this preference was greater than the simple addidition of both olfactory and visual stimuli. These results suggest that host finding is a complex, multifacted process (Campbell and Borden 2006a, 2009). One critically understudied aspect of bark beetle vision is their response to size stimuli. As discussed previously, the GDBH and PVH suggest that plants incur a trade-off between growth and defence, and that insects should select vigorously growing plants. As a result, size stimuli may contain host quality information and use of this information may benefit dispersers. To that end, I proposed the following research questions: (1) To what extent does host quality vary with host size? (2) Is host size information, in and of itself,

used in host selection? To answer these questions I used the mountain pine beetle (*Dendroctonus ponderosae* Hopkins*;* MPB) (reviewed by Safranyik and Carroll 2006)

Mountain pine beetle study system

MPB is an eruptive forest pest native to western North America which infests *Pinus* spp. trees. In western Canada, its range extends from Vancouver Island, British Columbia to the Alberta-Saskatchewan border, though the most destructive populations occur in the interior of British Columbia and in central/western Alberta (Lusebrink et al. 2013, Corbett et al. 2016). Adults are approximately 5 mm in length and 2 mm in width (Lachowsky and Reid 2014). The most common host of MPB is lodgepole pine (*Pinus contorta* ex Loudon). Lodgepole pine (reviewed by Lotan and Perry 1983) is a fire-propagated pine with a range extending east from coastal British Columbia to central Alberta. Lodgepole pine are valuable economically and ecologically by providing timber and serving as forage and refuge for various animals and plants. The interior variant (‘latifolia’), has a straight trunk with relatively few lower branches.

Host tree attack by individual MPB is a complex, multi-step process that is regulated primarily by conspecific pheromones (Pitman 1971, Borden et al. 1990, Blomquist et al. 2010). Females are the ‘pioneering’ sex which initiates attack on the host tree. Once a female has attacked a tree and begun tunneling into the inner bark she begins to produce the aggregation pheromone *trans*-verbenol which is the oxidized product of the monoterpene α-pinene (Pierce et al. 1987). This aggregation pheromone primarily attracts males, which produce their own aggregation pheromone *exo*-brevicomin. The ‘crescendo’ of this pheromone production is mass attack which allows beetles to completely overwhelm and kill live, healthy trees. Attack density

can vary widely, with some trees receiving well over 100 attacks/m^2. Raffa and Berryman (1983) suggest a minimal attack density of approximately 40 attacks/m^2 to successfully kill a mature tree with while 80 attacks/m^2 is necessary to prevent fully suppress the tree's defensive responses; beyond that threshold, intraspecific competition tends to reduce brood production. After penetrating the inner-bark, female MPB construct egg galleries in mid to late summer which run parallel to the stem. Eggs mature into larvae which construct their own galleries perpendicular to the maternal gallery, consuming phloem tissue in the process. Larvae progress through several instars before growth temporarily ceases in the winter. After winter, the larvae pupate in the spring and then mature into adults. Adults spend 1 to 2 weeks within their natal host before dispersing to find a new tree, emerging in mid to late summer (Safranyik and Carroll 2006). This process takes from one (univoltine) to two (semivoltine) years. Semivoltine populations tend to occur in colder areas and these populations are subject to greater winter mortality (Amman 1973, Dooley et al. 2015, Bentz et al. 2016).

Previous research shows that MPB caused tree death is not random: MPB often kill large trees during outbreaks (Hopkins 1905, Hopping and Beall 1948, Boone et al. 2011, Lindgren and Raffa 2013). At low population or endemic densities, MPB tend to persist in weakened trees which are more amenable to colonization. As population density increases to the incipient stage, MPB begin to access greater numbers and sizes of trees, progressing to the endemic or outbreak stage. During the outbreak stage MPB can kill millions of hectares of trees (Corbett et al. 2016). MPB population growth is positively related to large tree death because large trees tend to produce more beetles (Roe and Amman 1970, Amman and Cole 1983). Depletion of large trees

by MPB is considered to be a main driver of outbreak decline (Cole et al. 1976, Økland and Bjørnstad 2006, Kausrud et al. 2011).

The motive of my research is to better understand the role of host size in MPB host selection behaviour and if MPB predominantly select high quality hosts. It has long been observed that MPB tend to kill large trees during outbreaks (Hopkins 1905, Hopping and Mathers 1945, Hopping and Beall 1948, Björklund and Lindgren 2009). Mortality is generally low among small trees (less than 15 cm diameter) but greatly increases around 20 cm and trees ~ 30 cm or greater experience near 100% mortality. It is unclear if diameter or another related trait drives host selection or if MPB even need to explicitly select hosts at all (Byers 1996). Tree size encompasses a suite of related physiological traits, however it is commonly thought that MPB attack large trees because large trees tend to have thick phloem (Roe and Amman 1970, Cole 1973, Elkin and Reid 2004, Davis and Hofstetter 2014, Windmuller-Campione 2018) and this thick phloem leads to increased brood production (Amman 1972). There is much less understanding of the relationship between size and defence particularly in lodgepole pine; though work in ponderosa pine (*Pinus ponderosae*) suggests that large trees have relatively fewer defences (Davis and Hofstetter 2014, Hood and Sala 2015). Furthermore, it is unclear if MPB prefer large diameter silhouettes. Evidence suggests that walking MPB orient preferentially to large silhouettes (Shepherd 1966) but no study has examined this behaviour in the field. In Chapter 2 I investigate MPB host selection with respect to tree diameter and related traits in Jasper National Park. In Chapter 3 I discuss an experiment designed to test MPB orientation to

two silhouettes of different sizes. Finally, in Chapter 4 I synthesize the two chapters and revisit ideas presented here.

Chapter 2: Mountain Pine Beetle Attack and Reproductive Success in Relation to Host Diameter and Associated Traits

Introduction

Habitat seeking organisms, particularly dispersers which depart a natal habitat, must engage in a complex weighing of costs and benefits during habitat selection to maximize their fitness. Habitat selection can be divided into three phases — search, settlement, and residency (Stamps 2001). Problems can arise in each phase: for example, search may be unsuccessful if habitats are widely dispersed or cryptic, requiring more search time to successfully identify the habitat. Settlement can be disrupted due to time required to explore or otherwise make a habitat amenable to residency. Residency can be difficult if resources within the habitat are low or if predation pressure is high. Optimal habitat choice maximizes benefits while minimizing costs (MacArthur and Pianka 1966). Of interest to ecologists is whether organisms optimally select habitats and how they do so.

The Ideal Free Distribution [IFD] predicts how organisms should select habitats (Fretwell and Lucas 1969). The IFD predicts that all individuals within and among a habitat have the same per capita fitness, and that individuals distribute themselves to achieve equal per capita fitness such that colonizer density follows habitat quality. Additionally, the IFD assumes that organisms are ideal in that they are omniscient and able to reach the highest quality habitat, and they are free in that the ability of a settler to reside within a habitat is not influenced by previous settlers on that habitat. Further, the IFD predicts that a habitat's intrinsic quality should drive habitat selection; however, this may not always hold, particularly for ephemeral habitats in which

resource availability is temporally limited or competition is high. Here, organisms which can quickly disperse and find a suitable habitat, allowing them to spend more time in the settling and residency phases should be favoured. Organisms may use cues produced by the habitat itself (Stamps and Krishnan 2005) or conspecifics (Stamps 1988, 1991) to limit their time in the searching phase — a central question is whether these cues are indicative of habitat quality.

Bark beetles (Curculionidae: Scolytinae, reviewed by Rudinsky 1962) are suitable organisms to study habitat selection and the influence of cues. Adults disperse from a natal host tree and must find a new host tree to produce offspring, usually within the tree's inner bark or phloem (a thin layer of nutrient-conducting tissue). Bark beetles must limit their search time because host trees can reach saturation of beetles and other associated organisms (e.g. carnivorous beetles) (Raffa and Berryman 1983). Additionally, phloem can dry out reducing its quality and the condition of beetle offspring (Amman 1972, Steed and Wagner 2004). Some bark beetles attack live trees which employ lethal defences and kill beetles before they can reproduce (Phillips and Croteau 1999). These traits can vary considerably due to genetic and environmental factors (e.g. defence: Ott et al. 2011, phloem: Dooley et al. 2015) and bark beetles should select host trees which have few defences and thick phloem.

The mountain pine beetle (*Dendroctonus ponderosae*) is an eruptive forest pest endemic to western North America which attacks live *Pinus* spp. particularly lodgepole pine (*Pinus contorta*). MPB populations engage in outbreaks (i.e. reach high population density) and can kill millions of hectares of trees (Corbett et al. 2016). During these outbreaks, MPB typically attack trees via 'mass attack' which is facilitated by aggregation pheromones produced by attacking

MPB. Tree death occurs in part because MPB excavate the tree's phloem, disrupting its function (Safranyik and Carroll 2006). During MPB outbreaks, large trees (typically 25 cm diameter and greater) are killed more often than smaller trees (Hopkins 1905, Hopping and Mathers 1945, Hopping and Beall 1948, Björklund and Lindgren 2009). At the population level large trees are necessary to sustain an outbreak because they produce more beetles than do small trees (Roe and Amman 1970, Økland and Bjørnstad 2006, Kausrud et al. 2011). As such, a great deal of management effort has been expended to protect and manage these trees (Progar et al. 2013, Dymond et al. 2014, Vandygriff et al. 2015). By contrast, small trees tend to be attacked during endemic periods, when MPB populations are low (Roe and Amman 1970, Boone et al. 2011). Tree size encompasses a suite of traits related to the tree's ability to acquire resources and respond to pests. In particular, phloem thickness, xylem and phloem resin ducts, and resin exudation influence the ability of MPB to successfully colonize their habitats ('hosts') (Phloem: Amman and Pasek 1986, Resin: Kane and Kolb 2010, Ferrenberg et al. 2014).

Phloem thickness is commonly used as a metric of host quality because MPB feed and oviposit in phloem, activities which are critical for individual beetle fitness and propagation of outbreaks (Shepherd 1960). Trees with thicker phloem tend to produce more beetles (Berryman 1976), and those beetles are generally larger than beetles reared in thin phloem (Amman 1972, Amman and Pasek 1986). Thin phloem slows MPB development, which may place them in less cold tolerant life-stages during the onset of winter and increase mortality (Amman and Cole 1983). Previous research has indicated that MPB predominantly kill large trees because large trees tend to have thick phloem and that phloem thickness is a primary driver of MPB spread

(Amman and Baker 1972, Amman and Pasek 1986). However, the relationship between phloem thickness and diameter can vary greatly, particularly between stands. For example, Shrimpton and Thompson (1985) report positive, but generally non-significant relationships between phloem thickness and diameter in five plots and found that basal area increment from the previous 6 – 10 years was a better predictor of phloem thickness; more vigorously growing trees tended to have thick phloem. Working in jack pine (*Pinus banksiana*), Reid and Robb (1999) found that phloem thickness was significantly correlated with diameter in 126 and 77 year old stands but not in a 60-year-old stand. Dooley et al. (2015) found that phloem thickness was significantly related to diameter in one site but not another; they also found no significant relationship between phloem thickness and diameter in whitebark pine (*Pinus albicaulis*), another host of MPB. Taken together, these studies show that the relationship between phloem thickness and diameter should not be presumed for a given stand. MPB host selection may be driven in part by phloem thickness; however, its variability suggests that other factors such as tree defence also contribute to host selection.

As in other pine, lodgepole pine defend themselves with resin, a viscous liquid composed of compounds in the terpenoid family. Resin is transmitted via an extensive network of resin ducts in the xylem and phloem which serve as useful metrics of a tree's defensive capability (Franceschi et al. 2005). Defence is generally related to MPB colonization success, and trees that invest more carbon into xylem resin duct size and number generally survive MPB attack (Kane and Kolb 2010, Ferrenberg et al. 2014). However, the efficacy of tree defence decreases as MPB population size increases and trees are overwhelmed by mass attack (Boone et al. 2011). Tree

defence should not be discounted because it can serve as a useful indicator of resilience to MPB attack during the endemic stage. While pine defence is generally well characterized, it is unclear how defence varies with size. The Growth Differentiation Balance Hypothesis [GDBH] suggests that plants lie on a continuum of growth and defence and are unable to invest fully in both due to limited resources (i.e. dividing cells). As a result, some plants may lie closer on one end of the continuum than the other (Herms and Mattson 1992). As a corollary, the Plant Vigour Hypothesis [PVH] suggests that fast growing plants should be favoured by herbivores due to their relatively lower investment in defence (Price 1991). In the present system, it is possible that large trees have employed an aggressive growth strategy, and began growth with fewer competitors allowing them to quickly reach the canopy but at the cost of low investment in defence leaving them vulnerable to MPB attack. Conversely, small trees would be forced to adopt a slower growth strategy and consequently invest relatively more carbon in defence (Stephenson et al. 2014).

Evidence for size-based variation in resinous defences has been mixed and is dependent on how those defences are measured. A comprehensive study of defence metrics in ponderosa pine (*Pinus ponderosa*) found a negative relationship between standardized measures of defence (e.g. number of resin ducts per unit area) and growth rate, suggesting that faster growing trees invest relatively less resources into defence (Hood and Sala 2015). Conversely, absolute measures of defence tend to increase with growth rate; fast growing trees can quickly reach a large size and subsequently have more area to produce resin ducts (Ferrenberg et al. 2014, Hood and Sala 2015). Resin ducts serve as conduits for compounds attractive to MPB (Seybold et al.

2006) and as a consequence large trees with higher absolute numbers of resin ducts may produce a large attractive signal and suffer greater MPB attack compared to small trees. The above research concerns xylem resin ducts; a relatively understudied aspect of pine defence physiology are the radial resin ducts present in the phloem. While previous work suggests no strong relationship between phloem resin ducts and tree size it is worth further study because these ducts can influence MPB colonization (Berryman 1976). As well, the same processes that allow trees to invest in relatively greater numbers of xylem resin ducts may also hold for phloem resin ducts (Blanche et al. 1992). The relationship between resin flow and diameter is generally weak. For example, in ponderosa pine resin flow increases as trees grew from small- (5 cm) to medium-sized (20 cm) diameters but plateaus for trees greater than 20 cm (Davis and Hofstetter 2014) similar results have been found in lodgepole pine (Boone et al. 2011).

Tree age may modulate the above relationships. Large trees are generally older, however it is unclear if they necessarily undergo senescence. The concept of tree ‘decadence’ is understood to mean large, presumably old trees which are more susceptible to damage by fungi (Foster et al. 1951) though this usage also extends to bark beetles (Raffa 1988). Evidence suggests that as tree age they may become less resistant to herbivory. Young (less than 50 years) trees were better able to resist colonization by an MPB-vectored fungus which disrupts nutrient and water conduction in the phloem and sapwood (Shrimpton 1973). Additionally, resin duct formation appears to be greatest when trees are young, suggesting that MPB should avoid young trees (Reid and Watson 1966, DeAngelis et al. 1986). It is unclear if MPB necessarily attack the oldest trees in a stand or if old trees are attacked because age and size are correlated.

The mechanisms behind large tree mortality are not frequently considered in the literature, and studies which have attempted to investigate this phenomenon have suggested that MPB kill large trees due to the positive correlation between phloem thickness and diameter (Cole et al. 1976, Amman and Cole 1983, Björklund and Lindgren 2009). Although this pattern is generally well-supported, there are still gaps in our knowledge of how defensive traits relate to tree diameter in lodgepole pine and application of results obtained in ponderosa pine to lodgepole pine may be erroneous. Lodgepole pine is the principal MPB host in western Canada while ponderosa pine is more common in the coastal and southwestern United States and variation in climate (particularly water stress) between these locations can affect defence traits (Gaylord et al. 2007, 2013). Additionally, tree attack and death should be decoupled as different processes can give rise to these outcomes. Large trees may be excessively attacked even if MPB orient to their hosts randomly. A simulation model of the European spruce bark beetle (*Ips typographus*) (which serves a similar ecological role to MPB) suggested that beetles searching at random could still find suitable hosts and that post landing, aggregation pheromones could drive host selection (Byers 1996). When considering random landing with respect to tree size, MPB would be more likely to land on a large tree simply due large trees having greater surface area. Excessive mortality of large trees could occur if those trees are less well defended than small trees and/or if their phloem can support more attacking MPB leading to increased pheromone signal.

Study objectives and hypotheses

The objective of this study was to investigate the mechanism of large tree mortality by following several stands of lodgepole pine before, during, and after an MPB infestation. This was accomplished by the following sub-objectives: 1) Characterize the variation in several tree traits relevant to MPB with respect to tree diameter. 2) Understand how tree size and other traits relate to MPB attack probability and intensity. 3) Quantify brood production following the MPB flight season and relate this back to tree traits.

I hypothesized that host quality is positively related to host size and that host size information is used during host selection. From the first hypothesis I predicted that large trees would be more suitable hosts for MPB because they would have thicker phloem and weaker defences relative to small trees. Additionally, I predicted that large trees would produce more MPB brood. From the second hypothesis I predicted that within a stand, large trees would be more likely to be attacked by MPB and receive more attacks.

Methods

I conducted this study in Jasper National Park located in central Alberta, Canada (N 52º 52’ 22.9” W 118º4’ 55.65”). A 1 ha plot from each of five lodgepole pine dominated stands was selected for sampling. Plots were selected after consultation with Parks Canada in April 2016 and situated near roads for accessibility. Four sites were located along Highway 93A, approximately 12 km south from the town of Jasper while a fifth site (‘PLR’) was located along Pyramid Lake Road approximately 2 km north from the town (Table 2.1). Sites were selected based upon pine dominance (range: 85-100%), sufficient variation in tree size, low disturbance (e.g. beetle killed

trees, recently burned areas); density (minimum tree diameter: 10 cm) was estimated via the point quarter using Pollard's (1971) estimation method (Mitchell 2010). In mid July 2016, three *a priori* diameter at breast height [DBH] size classes were defined: small (10 – 18 cm diameter), medium (20 – 28 cm diameter) and large (30 cm diameter and greater) and 40 study trees were selected in each size class, providing a total of 120 trees. Prior to sampling, 10 points, at least 20 m apart, were randomly generated at each site using Google Earth ™. At each point, I selected the nearest apparently healthy (i.e. no evidence of beetle attack and full, green crowns) tree falling into each size class.

I sampled trees for several metrics from mid to late July 2016 (Fig. 2.1). Tree diameter was measured at breast height (approximately 1.3 m) using a diameter tape. A 4 by 4 cm sample of phloem was extracted from each tree from the north aspect at breast height using a knife and the outer bark was removed. Thickness was measured four times at the centre of each side of the square using a digital calipers (Mitutoyo Corporation Kawasaki, Japan). Phloem was stored in a 4ºC refrigerator in the field and then transferred to a -80ºC freezer in the laboratory in mid August 2016.

I measured several metrics of tree defence. I took a picture of the phloem sample using a 12 megapixel camera and counted phloem resin ducts using ImageJ (Schneider et al. 2012). I measured resin production at breast height by punching a hole with a 1 cm arc punch and attaching a resin collector (Karsky et al. 2004) which was removed after 48 hours. Resin was stored in a 4ºC refrigerator in the field and then transferred to a -20ºC freezer upon return to the laboratory in August 2016. Resin could not be quantified via volume due to the large size of the

tubes used to store the resin and the relatively little volume produced by each tree. Resin was weighed using an electronic balance (Sartorious MC2105 Ontario, Canada) in late September 2016 by taking the combined weight of the tube and resin and then subtracting the weight of the tube.

To further quantify defence and estimate tree age, a single 5.15 mm diameter tree core was extracted approximately 10 – 15 cm from the base of the tree. Increment cores were stored in plastic straws in the field and later I mounted them on cardboard in laboratory during October and November 2016. Cores were sanded using progressively finer grit sandpaper (60 to 200 to 400) to increase annual ring visibility (Phipps 1985). I counted and measured annual rings using WinDendro software (Regent Instruments Quebec, Canada). Cores were scanned at 1200 DPI in 24 bit colour using an Epson Perfection V800 scanner calibrated for the software (Seiko Epson Corporation Tokyo, Japan). To assess the tree's recent investment in growth the most recent five ring widths were averaged. To assess the tree's recent investment in defence I counted xylem resin ducts in the most recent five rings using a light microscope.

During the last week of July 2016 the MPB flight season began and 61 of 120 study trees were attacked. MPB attacks were counted along a 1 m column of the tree's main stem starting 10 cm from the base. I estimated brood production following attack by placing emergence traps on the tree's north and south aspects at breast height. Traps were fashioned from 11.4 L plastic buckets with a 20 cm diameter and secured using staples, duct tape, and caulk. Once the trap was attached, the bottom inner surface of the bucket was coated with diatomaceous earth (Bed Bug Killer Dust 90 percent silicon dioxide — Scotts Canada Ontario, Canada). Diatomaceous earth

was used instead of fumigant insecticide (e.g. dichlorvos) to avoid killing insects before they emerged from the tree (Prasantha et al. 2015). Traps were retrieved during late August 2017 and I counted MPB in the laboratory using a light microscope. The predominant colour of crown foliage was noted for each attacked tree to assess the tree's general health.

All data were analyzed in R version 3.4.3 (R Core Team 2017). To understand the relationship between tree size and host quality, tree diameter was modeled using MANCOVA from the package 'car' (Fox and Weisberg 2011). I considered MANCOVA appropriate because each study tree was sampled for several (presumably correlated) physiological variables. The dependent variables under consideration were: phloem thickness, age at coring height, resin production, xylem resin duct density within the previous 5 years, phloem resin duct density, and recent growth (the average of the 5 most recent ring width increments). MANCOVA requires multivariate normality which depends on the univariate normality of each dependent variable. To conform to this assumption phloem resin duct density was square root transformed, xylem resin duct density was square root transformed, recent growth was log transformed, and age at coring height was log transformed; phloem thickness did not need to undergo transformation. Normality of these variables was confirmed by inspecting histograms and the Shapiro-Wilk test for normality. Resin production was dropped because it was unable to be adequately transformed and 24 of 120 trees did not produce any resin during the sampling period. Residual plots of each dependent variable were inspected to assess heteroscedasticity. Various statistics are available for interpreting MANCOVA results but I used the Pillai-Bartlett Trace which is considered the most robust (Olson 1976).

To understand how MPB attack related to tree traits of interest, I analyzed attack count using a negative binomial zero inflated model via the ‘zeroinfl’ function from the package ‘pscl’ (Jackman 2017). The model predictors were diameter, phloem thickness, phloem resin duct density, xylem resin duct density, recent growth, age at coring height, and site. This model was preferred to a negative binomial logistic regression because the zero inflated model estimated values closer to those observed in the field. Effects of each variable were assessed using Wald χ^2 tests from the package ‘car’. The same analysis was repeated for attack density (number of attacks/m^2) by adding an offset for sample area because the negative binomial distribution models integers. I considered modeling both count and density because they reflect the process of host attraction (assuming each attack is a beetle that survives to produce pheromones) and intraspecific competition respectively. Bootstrapped confidence intervals (1000 iterations) for both attack count and attack density as they relate to diameter were computed by fitting models with diameter alone and diameter and the area offset as this was computationally simpler than estimating diameter and the other parameters and diameter was the only significant predictor in both models.

To understand how tree traits related to brood production, beetle emergence was analyzed via negative binomial regression using the package ‘MASS’ (Venables and Ripley 2002). The model predictors were a second order polynomial of diameter (justified after inspecting the raw data), phloem thickness, phloem resin duct density, xylem resin duct density, attack density along the entire sampled area of the tree, and trap area. Assessment of brood production density (total number of brood divided by trap/sampled area) was attempted with both negative binomial and

zero inflated models, however these models did not converge so a linear model was fit with the same predictors as above except for trap area. Effects of each variable were assessed using Wald χ^2 tests from the package 'car'.

Results

Host quality metrics

Tree diameter, site, and their interaction affected the joint variation in tree traits of interest (Table 2.2). The interaction between diameter and site was significant for phloem thickness, recent growth, as well as age (Table 2.3). A significant positive relationship was observed between diameter and phloem thickness, tree age, and recent growth while a significant negative relationship was found between diameter and xylem resin duct density, broadly suggesting that host quality increased with diameter (Fig. 2.2). Phloem resin duct density was not significantly related to diameter. In general, phloem thickness increased with diameter and this relationship differed for each site: all sites had positive, significant relationships except by RB which was non-significant. Larger trees were older and tended to grow more vigorously: diameter and age at coring height were positively related, recent growth also increased with diameter except for site RB which was non-significant. These discrepancies are likely due to the low range of diameters sampled at RB.

MPB attack and brood production

Beetle attack count and attack density were both positively related to diameter (Fig. 2.4). In both zero inflated models, diameter was the only significant term. Larger trees were more likely to get attacked and received more attacks (Count: χ^2_1=14.5, n=120, p<0.005; Density:

χ^2_1=6.02, n=120, p<0.05, Table 2.4). There were significant positive correlations between attack density and recent growth, phloem thickness, and tree age at coring height though these variables were not significant in the zero inflated models (Fig. 2.3). When the models were refit without diameter recent growth was a significant predictor of attack count (χ^2_1=4.52, n=120, p<0.05) while no variables were significant predictors of attack density (Table 2.5).

MPB brood production count was greatest in medium-sized trees and declined in large trees (Fig. 2.5). The second order polynomial of diameter was the only significant predictor in the model (χ^2_2=17.6, n=61, p<0.005) and the linear model of brood production density did not find any significant variables (p>0.05, Table 2.6) although there were significant univariate correlations between estimated brood production density and tree age at coring height (Fig. 2.3). When the models were refit without diameter no variables were significant predictors of brood count or attack density (Table 2.7). Most attacked trees had red foliage in 2017 (n=50 of 61), including those which received few attacks (Fig. 2.6).

Discussion

During MPB outbreaks, large trees are often killed. The objective of this study was to better understand how traits relevant to MPB success related to tree diameter and how those traits influenced MPB attack and subsequent reproduction. I hypothesized that host quality would be positively related to host size and that larger trees would have thicker phloem, fewer defences, and produce greater numbers of MPB brood. I also hypothesized that this information is relevant to MPB during host selection, predicting that larger trees would be more likely to get attacked and receive more attacks.

Host quality metrics

Phloem thickness and diameter were positively and significantly correlated in agreement with my first hypothesis. Phloem is geometrically constrained to grow with tree size so this result was not particularly surprising (Hölttä et al. 2013) but it suggests that large trees should be more nutritious, on average, for MPB than small trees. The relationship between phloem thickness and diameter can vary substantially. Studies which have sampled large numbers of trees (e.g. Cole 1973, Elkin and Reid 2004) have found positive, significant relationships between phloem thickness and diameter though other studies have found different results. A study of phloem thickness in lodgepole pine found that diameter was a poor predictor of phloem thickness and this conclusion was based on combining data from five, differently aged plots with varying average diameters from 21.5 to 33.7 cm (Shrimpton and Thompson 1985). Combining plot/stand level data can result in no significant relationship (Reid and Robb 1999) to fairly robust correlations (Lahr and Sala 2014) and likely depends on the heterogeneity of the study plots. For MPB, the strength of the phloem thickness–diameter relationship could play a role in the disparity between size-based host quality within a plot/stand which could affect the host selection of MPB within that plot. Plots with weak relationships between phloem thickness and diameter may have more diffuse host selection, while plots with very strong relationships between phloem thickness and diameter may have many MPB concentrated in a few trees. Thin phloem is more prone to drying out, which may inhibit colonization by pioneer beetles and brood survival (Cole and Amman 1980). Thin phloem may also emit smaller amounts of monoterpenes compared to thick phloem which could potentially inhibit initial host finding and colonization by pioneer

beetles and lead to saturation of large trees with thick phloem (Cole et al. 1981). Both mechanisms may explain the ensuing results for attack and brood production.

The results for tree defence suggest that defence declines or is at least neutral with respect to diameter depending on the metric considered, in partial agreement with my first hypothesis. Xylem resin duct density significantly declined with increased diameter which tends to agree with previous work in lodgepole (Reid and Watson 1966) and ponderosa pine (Hood and Sala 2015). This decline is likely consequential to MPB because resin ducts are partially filled with resin and can remain biologically active for several years after formation (Blanche et al. 1992, Phillips and Croteau 1999). This result concerns a standardized metric of defence, but results of unstandardized measures show that resin duct count increases with diameter in lodgepole, ponderosa, and limber pine (*Pinus flexilis*) (Kane and Kolb 2010, Ferrenberg et al. 2014, Hood and Sala 2015). For MPB, this suggests that large trees produce a greater olfactory signal, which may make them easier to find and reduce dispersal costs. Studies of artificial baits have shown that those with greater release rates catch more beetles and this principle is likely transferable to trees with different amounts of resin ducts (Borden et al. 1983). Within larger study trees, resin ducts were less dense throughout the xylem, so a beetle is less likely encounter a resin duct during excavation. Other measures of defence did not vary significantly, contrary to my hypothesis. Phloem resin duct density did not significantly differ with respect to diameter, consistent with previous work in lodgepole pine (Berryman 1976). This is worth further study because phloem resin ducts have similar roles to xylem resin ducts and may be under similar constraints due to tree physiology (Blanche et al. 1992). A fifth of all trees did not produce any

resin during the sampling period with the rest generally exuding low volumes, consistent with previous research in lodgepole pine (Nebeker et al. 1995). Tree diameter did not significantly affect resin exudation, though opposite results have been found in both lodgepole (Boone et al. 2011) and ponderosa pine (Davis and Hofstetter 2014). This discrepancy may be due to site characteristics, as resin flow tends to increase during drought according to work in loblolly pine (*Pinus taeda*) (Lombardero et al. 2000). Large trees tended to be older and produce lower density of xylem resin ducts. This may be consequential for MPB as previous research has suggested that old trees are more susceptible to Ophiostomataceae fungus vectored by MPB (Shrimpton 1973).

MPB attack and brood production

Diameter alone best predicted tree attack count and attack density, large trees received numerically more MPB attacks and a greater number of attacks per unit area while small trees were virtually excluded from attack. This result agrees with previous work showing that large trees are frequently attacked during MPB outbreaks (Hopping and Beall 1948, Boone et al. 2011). The lack of attack on small trees is particularly striking because these trees are not incapable of supporting MPB, and MPB are known to enter such trees at least during endemic periods (Cole et al. 1976). A likely explanation is that they are not as easily perceived compared to large trees, either by vision or olfaction. In addition to producing a greater visual stimulus, large trees may also produce a greater olfactory stimulus due to the production of (numerically) more resin ducts which can contain attractive compounds and by having generally thicker phloem as explained above (Plomion et al. 2001). This greater standing attraction may have increased initial colonization by pioneer beetles and subsequent production of aggregation

pheromones. The high attack count for large trees suggests that these trees had high concentrations of beetle pheromones, further increasing their attraction. It is unclear if MPB are able to assess host quality during the attack process as MPB attack did not appear to be related to any other tree trait after accounting for diameter. Phloem monoterpene emissions may serve as an indicator of host quality, and behavioural assays of the red turpentine beetle (*Dendroctonus valens*) have shown that beetles prefer phloem from large trees (Liu et al. 2011) which could be due to quantitative variation in the phloem's chemical composition, most likely increased concentration of α-pinene (Burke and Carroll 2016). Perhaps at the low density, initial attack this signal may be useful in discriminating host quality, but as attack progresses and many more beetles arrive to a host, attack, and produce pheromones, the monoterpene signal may become less detectable compared to the pheromone signal. Alternatively small trees may sampled by MPB but eventually abandoned. Work by Amman (1975) found that many small trees had evidence of aborted egg galleries likely because these females were not fertilized, which may occur because these trees are less detectable. Additionally, gustatory stimuli may influence MPB host selection because excavation occurs via the mouthparts. Evidence suggests that encountering certain polar compounds (e.g. menthol-water extracts) can initiate or sustain feeding (Raffa and Berryman 1982b); consequently, the chemical composition of bark or phloem may lead to aborted attacks which may have occurred in the present study for those small trees which sustained very few MPB attacks.

Brood production count was non-linearly related to diameter and peaked at intermediate diameters. The initial increase with diameter likely occurred because small trees have thin

phloem which is a poor substrate for rearing bark beetles (Raffa and Berryman 1982b). At very large diameters, trees likely became oversaturated with MPB attacks, leading to high intraspecific competition and reduced brood production. Raffa and Berryman (1983) define oversaturation as attack densities greater than 80 attacks/m^2 and nine trees met this criterion. It is likely that per capita brood production in these highly attacked trees was low but this could not be explicitly tested because I was unable to fell each attack tree and acquire bolts for further sampling. Attacked trees generally had red crown foliage one year after attack even those which received few attacks. Crown colour serves as a rough estimate of tree status, and trees with predominantly red crowns are considered to have been successfully colonized by MPB (Graf et al. 2012). Many other disturbance agents such as needle blight (Welsh et al. 2009) and abiotic stressors such as drought (Arango-Velez et al. 2016) co-occur with MPB so it is difficult to clearly say what caused these low attacked trees to develop red crowns.

Conclusions

Previous work has provided a tree trait-based understanding of MPB attack and outbreaks. Work by Berryman (1976) found that diameter was a poor predictor of MPB brood productivity and that attack density was not significantly related to diameter. Rather, Berryman's results show that resin production, phloem thickness, and phloem resin duct density govern MPB attack and brood production. Curiously, MPB attack density appeared to increase with resin production. Berryman suggests that MPB could adjust their attack density given the tree's resin exudation (which serves as a proxy for physiological vigour) and that these vigorous trees are necessary in initiating and sustaining epidemic MPB populations. This latter point has been

discussed in later work which suggests that landing on vigorous trees increases a beetle's chance of encountering thick phloem, which is supported by the present study (Amman and Cole 1983). More recent work has found that as MPB population density increases the diameter of infested trees also increases (Boone et al. 2011). These studies are useful in understanding how MPB outbreaks are initiated and sustained; however, a limitation of these studies is that they do not necessarily explain how host selection occurs. It is reasonable to suggest that MPB would prefer trees in a given stand with the thickest phloem and greatest vigour because these trees should produce higher quality offspring (Amman and Pasek 1986).

Here, I show that MPB predominantly attack large trees during outbreaks and that those trees tend to have fewer defences and thicker phloem compared to smaller, less heavily attacked trees. Critically, MPB do not appear to select for any one host quality trait *per se*, and dispersion may be facilitated entirely by host detectability (i.e. kairomones, aggregation pheromones, host silhouettes), which appears to be coincident with quality. Perhaps some assessment occurs via gustation; but this could increase dispersal time and cost (due to the repeated landing/takeoffs required) which is detrimental to dispersers like MPB because they rely entirely on stored energy during dispersal. Such assessment probably does not occur very often because there appeared to be little evidence of MPB disturbance in small trees. These trees are largely ignored by MPB, leading to the attack patterns observed in Jasper as well as sites of other MPB outbreaks (Björklund and Lindgren 2009).

Table 2.1: Site characteristics. Density (stems per ha), upper and lower 95% confidence intervals estimated via the point quarter method (10 points, 40 trees per site).

Site	Latitude	Longitude	% Pine	Density	Lower CI	Upper CI
ECR	52°46'28.17"N	118° 1'35.04"W	92.5	1115.69	817.5	1525.19
93A	52°46'46.99"N	118° 2'2.90"W	100	1422.88	1042.59	1945.12
PLR	52°53'27.74"N	118° 5'12.24"W	85	587.77	430.68	803.5
MR	52°47'7.86"N	118° 2'18.07"W	100	2628.65	1926.1	3593.45
RB	52°47'7.82"N	118° 1'56.76"W	100	688.41	504.42	941.08

Table 2.2: MANCOVA for tree traits as predicted by DBH, Site and their interaction. Pillai: Pillai-Bartlett's Trace

Variable degrees of freedom	Pillai	P
DBH $_{1,110}$	0.63	<0.0005
Site $_{4,110}$	0.53	<0.005
DBH*Site $_{4,110}$	0.31	<0.05

Table 2.3: ANOVA tables for MANCOVA showing extent of variation in each tree trait of interest. Subscripts indicate degrees of freedom.

Term	$DBH_{1,110}$		$Site_{4,110}$		$DBH:Site_{4,110}$	
	F	P	F	P	F	P
Phloem thickness (mm)	89.7	<0.0005	19.8	<0.0005	3.12	<0.05
Phloem duct density (n/cm^2)	1.65	>0.2	1.69	>0.1	0.502	>0.7
Xylem duct density (n/mm^2)	7.11	<0.01	5.19	<0.005	1.31	>0.2
Recent growth (mm/yr)	326	<0.005	15.20	<0.005	5.51	<0.0005
Age at coring height (yr)	48.5	<0.0005	34.8	<0.0005	3.28	<0.05

Table 2.4: Model results for MPB attack count and attack density. All n = 120.

		Attack Count (n)		Attack Density (n/m^2)	
Term	**df**	**X^2**	**P**	**X^2**	**P**
Diameter (cm)	1	14.54	<0.005	6.0194	<0.05
Phloem thickness (mm)	1	0.8575	>0.3	0.8515	>0.3
Phloem duct density (n/cm^2)	1	0.0242	>0.8	0.0317	>0.8
Xylem duct density (n/mm^2)	1	0.3015	>0.5	0.3041	>0.5
Recent growth (mm/yr)	1	0.9151	>0.3	0.8975	>0.3
Age at coring height (yr)	1	2.892	>0.08	2.854	>0.09
Site	4	1.930	>0.7	1.960	>0.7

Table 2.5: Model results for MPB attack count and attack density fit without diameter. All n = 120.

		Attack Count (n)		Attack Density (n/m^2)	
Term	**df**	**X^2**	**P**	**X^2**	**P**
Phloem thickness (mm)	1	3.233	>0.07	2.398	>0.1
Phloem duct density (n/cm^2)	1	0.2919	>0.5	0.0585	>0.8
Xylem duct density (n/mm^2)	1	0.4273	>0.5	0.0570	>0.8
Recent growth (mm/yr)	1	4.521	<0.05	1.129	>0.2
Age at coring height (yr)	1	0.5479	>0.8	0.0456	>0.8
Site	4	1.582	>0.8	1.465	>0.8

Table 2.6: Model results for MPB brood production (negative binomial regression) and brood production density (linear regression). All n = 59.

		Brood Production (n)		Brood Production Density (n/cm^2)	
Term	**df**	**X^2**	**P**	**F**	**P**
Diameter^2 (cm)	2	17.63	<0.005	2.237	>0.1
Phloem thickness (mm)	1	1.260	>0.2	1.927	>0.1
Phloem duct density (n/cm^2)	1	2.090	>0.1	1.596	>0.2
Recent growth (mm/yr)	1	0.4954	>0.4	0.356	>0.8
Attack density (n/m^2)	1	1.882	>0.1	0.2198	>0.6
Xylem duct density (n/mm^2)	1	0.2803	>0.5	0.0004	>0.9
Trap area (cm^2)	1	1.091	>0.2	NA	NA
Age at coring height (yr)	1	0.6850	>0.4	0.5327	>0.4

Table 2.7: Model results for MPB brood production (negative binomial regression) and brood production density (linear regression) fit without diameter. All n = 59.

		Brood Production (n)		Brood Production Density (n/cm^2)	
Term	**df**	**X^2**	**P**	**F**	**P**
Phloem thickness (mm)	1	1.058	>0.3	2.132	>0.9
Phloem duct density (n/cm^2)	1	0.6512	>0.4	0.7509	>0.1
Recent growth (mm/yr)	1	1.520	>0.2	1.052	>0.3
Attack density (n/m^2)	1	2.407	>0.1	0.2851	>0.3
Xylem duct density (n/mm^2)	1	2.593	>0.1	0.4555	>0.5
Trap area (cm^2)	1	0.2211	>0.6	NA	NA
Age at coring height (yr)	1	3.541	>0.05	1.646	>0.2

Fig. 2.1: Methods used to sample each tree. Row 1: A phloem sample and calipers; an increment core; annual increment rings (dark bands) and xylem resin ducts (white spots) – credit: K. Wilkinson. Row 2: A resin collector; pitch tubes produced after MPB attack; emergence traps attached to a study tree.

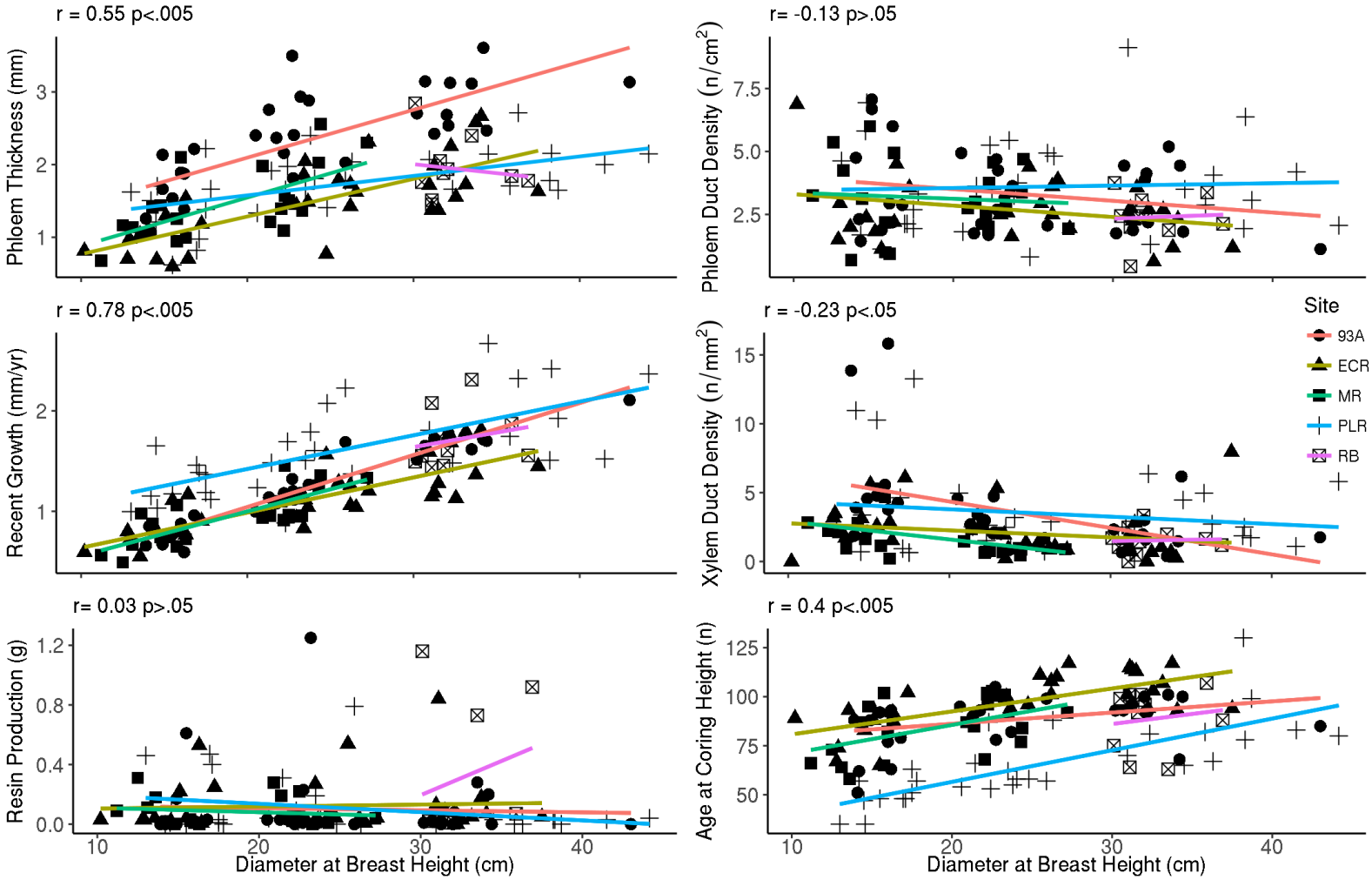

Fig. 2.2: Diameter at breast height regressed against tree variables of interest, coloured lines represent regression line for each site. All n = 120.

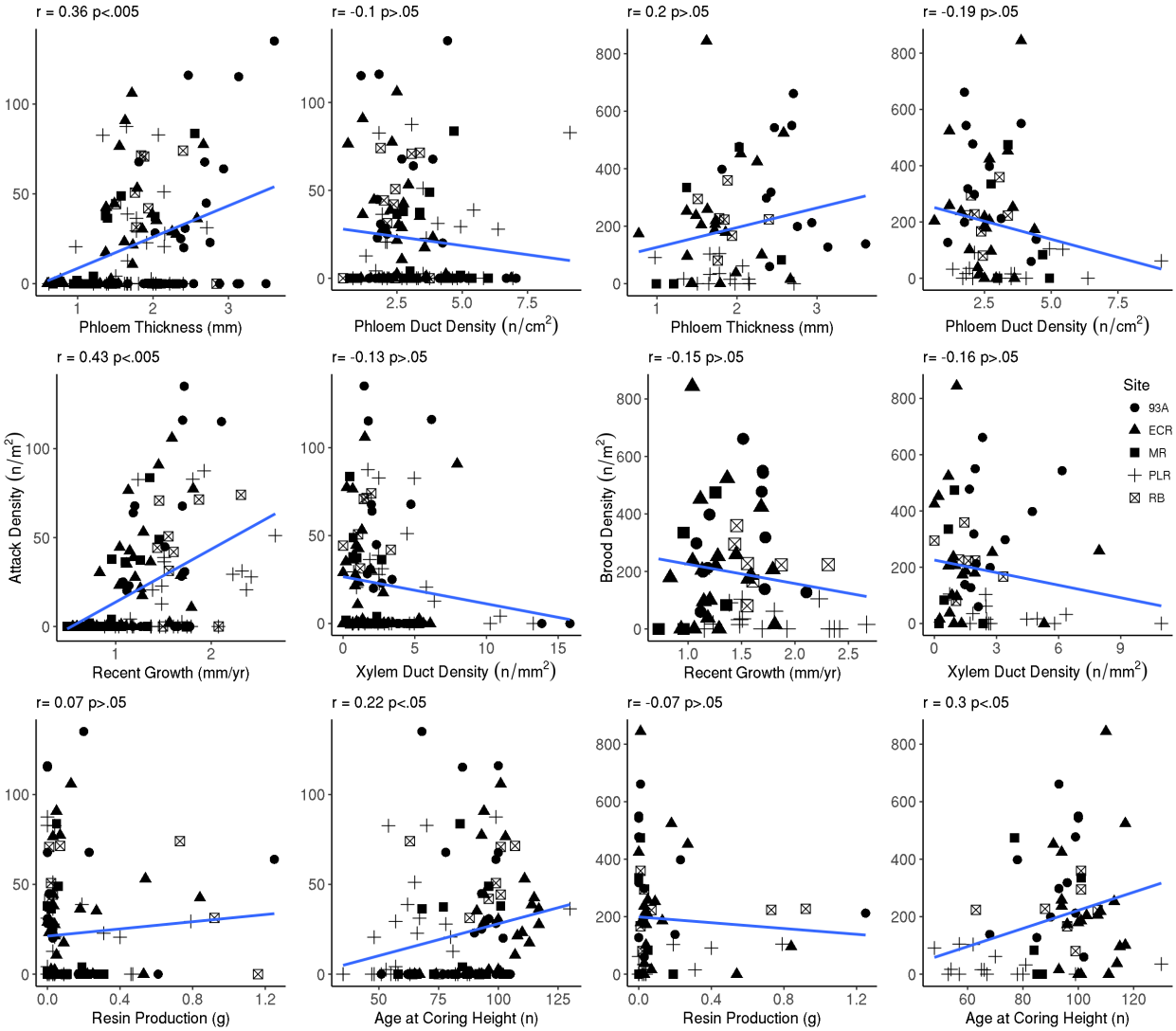

Fig. 2.3: Univariate regressions for tree traits of interest by attack density (left two columns, n = 120) and brood production density (right two columns, n = 59).

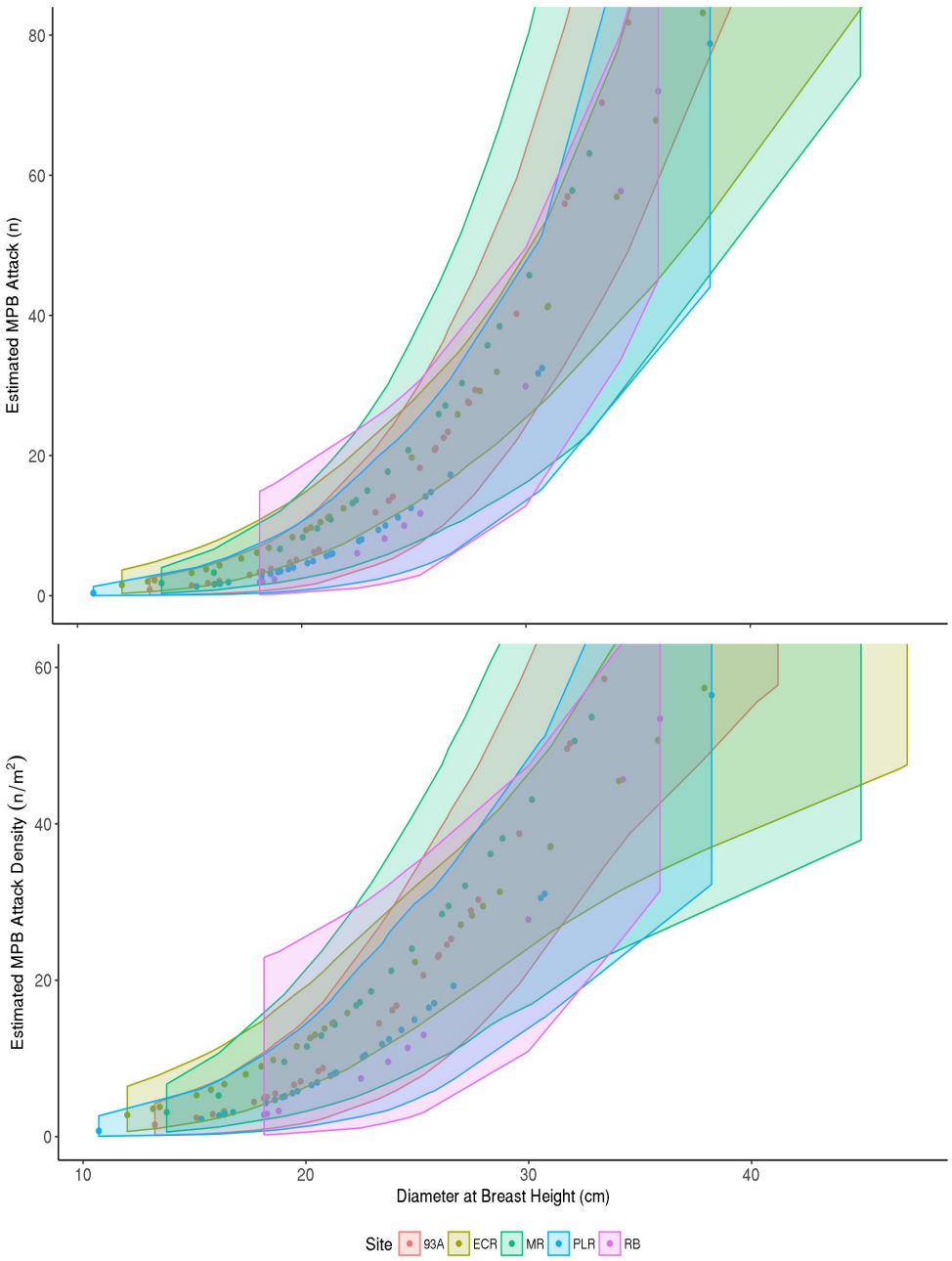

Fig. 2.4: Bootstrapped 95% confidence intervals for MPB attack count (left) and attack density (right) predicted by diameter.

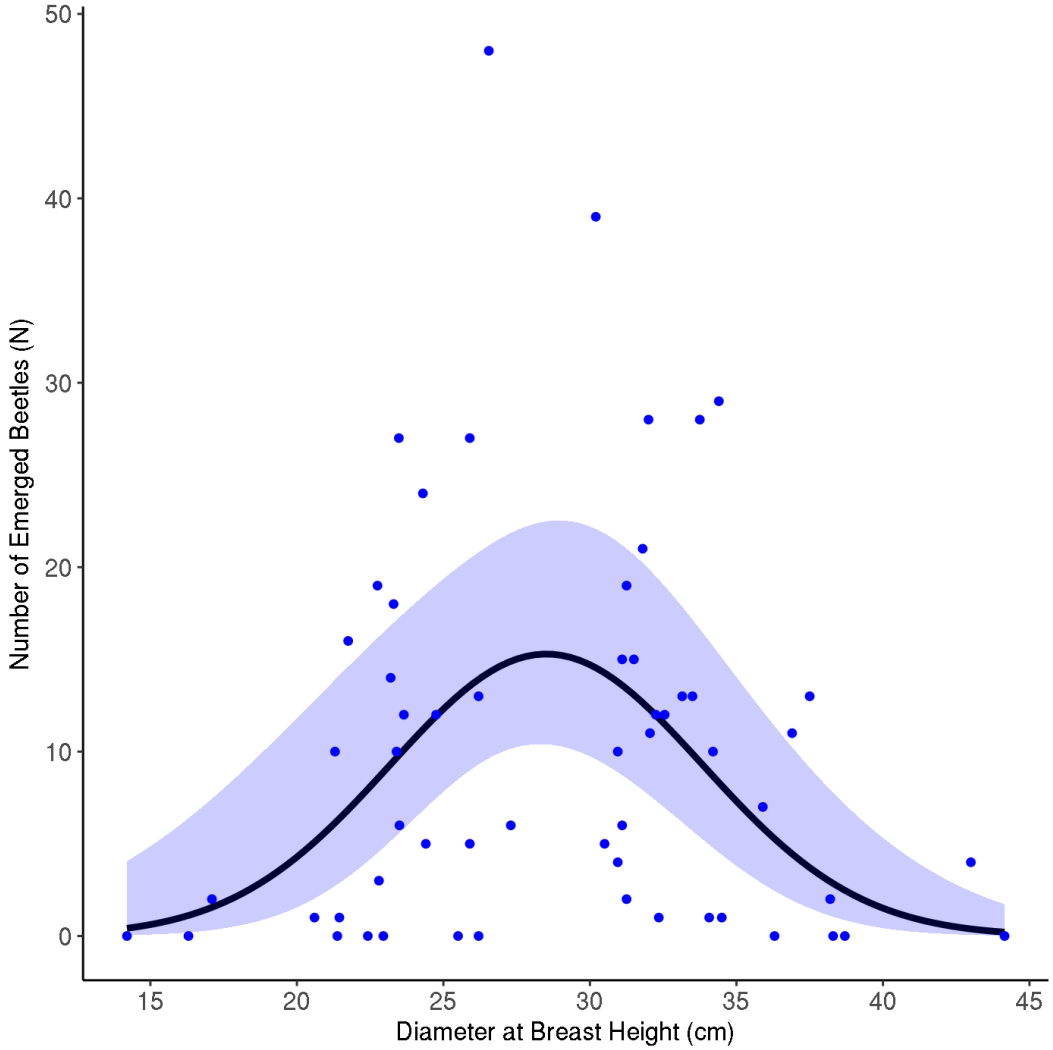

Fig. 2.5: Effect of second order polynomial of diameter on number of emerged beetles, bands represent 95% confidence intervals, points represent raw values counted from emergence traps.

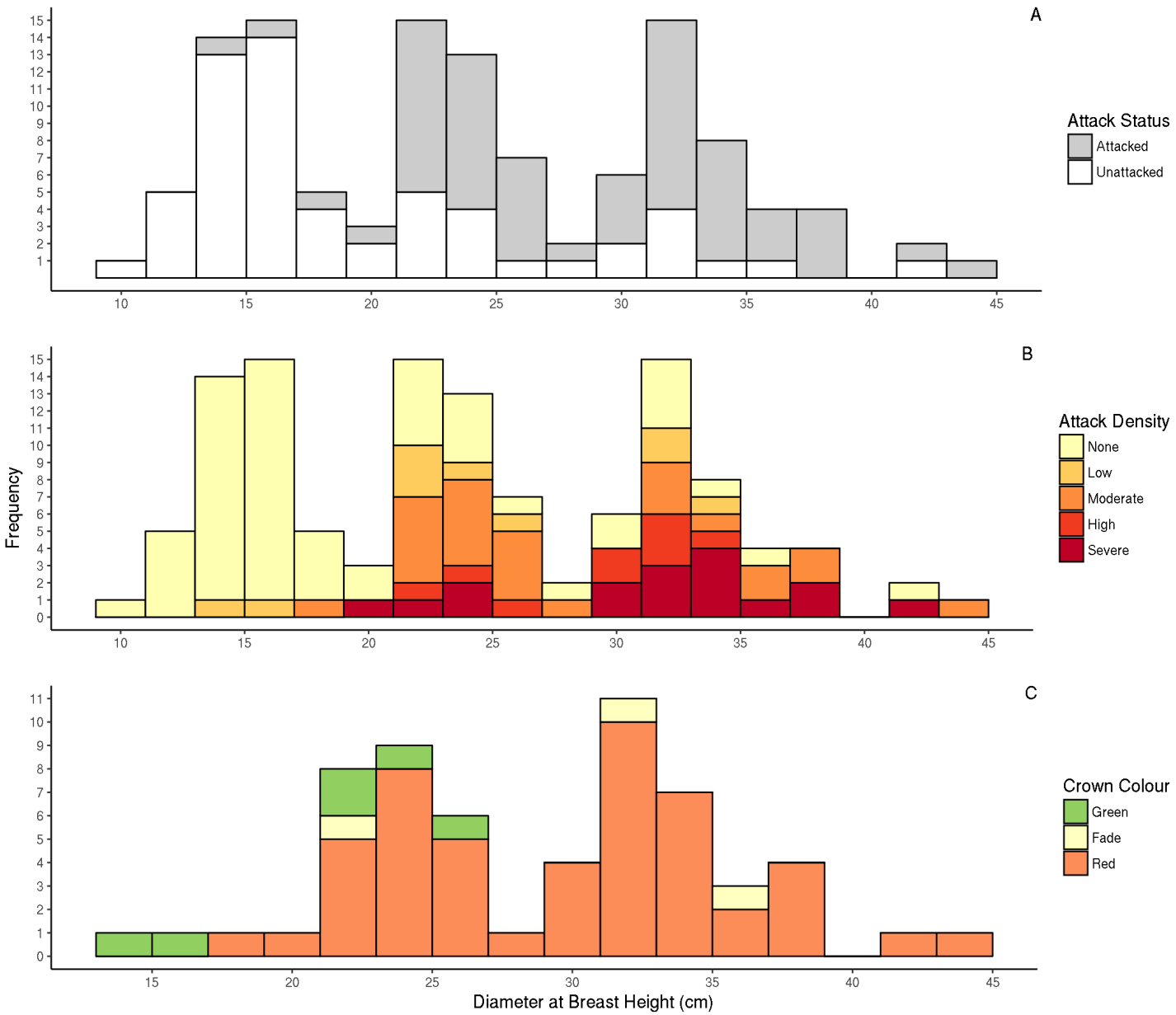

Fig. 2.6: Histograms of tree diameter and A) Attack status, B) Attack density, C) Crown colour. Attack densities (n/m^2):
None = 0
Low = 0-19.9
Moderate = 20-39.9
High = 40-59.9
Severe = 60 or greater

Chapter 3: Extending the Primary Attraction Hypothesis: Testing Visual Host Finding in Mountain Pine Beetle

Introduction

Host finding organisms, particularly herbivorous insects which live and feed within a plant, face challenges in identifying suitable hosts. Such insects have an available 'food range' (Thorsteinson 1960) and selection outside this range or a host 'mismatch' can lead to reduced reproductive output or even death (Awmack and Leather 2002). However, within a food range, potential host plants vary in quality and it is in the herbivore's interest to select the plant which provides the greatest payoff (Charnov 1976). Failure to distinguish a good host from a poor host may incur the same kinds of costs to the herbivore as failure to distinguish host from non-host, but the recognition process may involve different cues.

Many insects find their hosts using olfaction and vision and these modalities each have benefits and costs. Plants produce a variety of volatile chemicals and while many of these chemicals overlap between plant species (e.g. Pureswaran et al. 2004), host specific information can be encoded in the ratios of overlapping compounds, particularly in sympatric species in the same family (e.g. Gray et al. 2015). Non-overlapping compounds can also assist in distinguishing host from non-host: for example, conifer-feeding bark beetles (Curculionidae: Scolytinae) are repelled by green leaf volatiles produced by angiosperms (Dickens et al. 1992, Wilson and Borden 1996). Olfactory information can also allow insects to avoid low quality hosts within their food range: *Ips* spp. which specialize on stressed or damaged trees, seek out ethanol and other fermentation products released during decay, avoiding non ethanol emitting trees (Miller et al. 1986, Byers 1995). Plant volatiles are released in plumes, complex

aggregations of molecules (reviewed by Murlis 1992, Beyaert and Hilker 2014). These plumes are spatially heterogenous and insects within a plume may experience brief bursts of attractive olfactory stimuli followed by 'clean' air or repellent stimuli. Plumes are also subject to physical perturbations at small scales due to the kinematics of individual molecules, and at large scales due to other conditions such as spatial clutter, wind speed and direction, as well as temperature (Thistle et al. 2004). If a plume is difficult to localize, an insect may expend a great deal of energy searching for their host or simply not find the host at all.

Compared to chemical cues, visual stimuli do not incur a cost in assessment and depend on the insect's visual acuity (i.e. the ability to discriminate granular details of an object) and the speed of light (Prokopy and Owens 1983). Vision may be useful in discriminating host and non-host; conifer-feeding bark beetles prefer dark, host coloured silhouettes compared to light, non-host (i.e. angiosperm) coloured traps (Strom and Goyer 2001). Additionally, cabbage root flies (*Delia radicum*) have been shown to prefer green to red leaves within and between host species, likely due to the increased concentrations of anthocyanin in red leaf tissues. While colour vision may be useful, a potential problem could arise in distinguishing high and low quality food items within a herbivore's food range. Here, size based information may be useful in distinguishing finer scale differences in host quality. The Plant Vigor Hypothesis predicts that larger plants provide greater amounts of nutritive tissue for herbivores such that herbivores should predominantly feed on large plants (Price 1991); meta-analysis has supported this hypothesis (Cornelissen et al. 2008). The redbay ambrosia beetle (*Xyleborus glabratus*) displays enhanced attraction to large diameter silhouettes (Mayfield and Brownie 2013). Similarly, bumble bee

(Hymenoptera: Apidae) visits to *Polemonium viscosum* increased with flower diameter (Galen and Newport 1987). Syrphid fly (Diptera: Syrphidae) visitation to wild radish (*Raphanus raphistrum*) also increased with flower size (Connor and Rush 1996). Understanding the relative influence of these cues is challenging because vision and olfaction can produce additive or synergistic effects (e.g. Rojas and Wyatt 1999, Campbell and Borden 2009). Trap catches of the pine weevil, *Hylobius abietis*, were greater when olfactory or visual stimuli were present than trap catches without stimuli. When stimuli were presented together, the resultant trap catches were greater than trap catches with only a single stimulus; however, the effect of either stimulus was not enhanced in the presence of the other (Björklund et al. 2005). Similarly, the bark beetles *Hylastes ater* and *Hylurgus ligniperda* exhibit greater attraction to dark coloured stimuli than light coloured stimuli but this attraction is contingent on the presence of olfactory attractants and suggeststhat the relative influence of olfaction as a host finding cue is high (Kerr et al. 2016). We can inform both ecological theory and management decisions by further study on the relative influence of individual cues on host selection.

The mountain pine beetle (*Dendroctonus ponderosae*; MPB) is a forest pest native to western North America which specializes on *Pinus* spp. particularly lodgepole pine (*Pinus contorta*) (Safranyik and Carroll 2006). MPB feed and oviposit within the host's inner bark/phloem and are repelled by the host's resinous defences (Safranyik and Carroll 2006) and variation in host phloem quality and defensive response can influence the fitness outcomes of the beetle. Trees with thick phloem tend to produce more beetles (but see Chapter 2) and those beetles are generally larger while those with thin phloem produce fewer, smaller beetles (Roe

and Amman 1970, Amman 1972, Esch et al. 2016). Trees which have more robust defences (e.g. greater resin production, higher density of xylem resin ducts) can successfully resist invading MPB (Kane and Kolb 2010, Ferrenberg et al. 2014, Erbilgin et al. 2017). Given that the success of individual MPB is contingent on selecting a high quality host, it is worth understanding what cues MPB use to select their host and the relative importance of those cues.

Attempts to understand and test MPB host orientation have typically been framed in an olfactory context with comparatively less research conducted on vision. The primary attraction hypothesis proposes that MPB utilize host-produced volatile organic compounds (i.e. monoterpenes) to locate their host, avoiding non-host compounds (e.g. green leaf volatiles) (Person 1931, Byers 1995). Green-leaf volatiles, such as those produced by *Populus* spp.have been shown to reduce MPB attack on live trees (Wilson and Borden 1996) and trap catches (Borden et al. 1998, Campbell and Borden 2006a). However, primary attraction alone may not suffice because MPB cannot reliably discriminate between extracts of sympatric conifers (Pureswaran and Borden 2005). The secondary attraction hypothesis proposes that host selection is driven by changing fluxes of conspecific aggregation and anti-aggregation pheromones (Anderson 1948). Once a female MPB penetrates the phloem layer of a host tree, she emits the aggregative pheromone *trans*-verbenol, attracting additional MPB which emit their own aggregation pheromones creating a positive feedback loop. MPB also produce antiaggregation pheromones after mating, and eventually the concentration of these pheromones become sufficient to prevent further attack (Pitman 1971, Vité and Francke 1976, Blomquist et al. 2010). While these two hypotheses may be useful in explaining how MPB discriminate between host

and non-host, they are insufficient in explaining how MPB may select within their food range for high quality hosts, i.e. trees with thick phloem and few defences. Evidence from *D. valens* suggests that beetles in y-tube assays prefer thick phloem tissue compared to thin phloem tissue which may suggest some qualitative difference in monoterpene content but there does not appear to any additional evidence to support this result (Liu et al. 2011). Studies of resistant and susceptible host trees show that the most important predictor of the tree's ability to defend itself is the tree's induced defensive response during MPB attack, rather than its constitutive defences (Shrimpton 1973, Raffa and Berryman 1982a). This suggests that MPB may not be able to discriminate between resistant and susceptible trees based on host-volatiles alone. Conspecifc pheromones are highly attractive to MPB and may override host stimuli, hence their use in commercial baits (Lindgren et al. 1983). For example, MPB do not normally attack small, presumably lower quality trees (i.e. < 20 cm diameter) but baiting small trees with *trans*-verbenol can override this behaviour suggesting that pheromones take precedence over host volatiles (Rasmussen 1972). With respect to vision, *Dendroctonus* spp. including MPB are most sensitive to blue-green wavelengths (500-525 nm) and ultraviolet (<425 nm) (Schönherr 1971, Groberman and Borden 1981). During the host finding process, MPB and related species (e.g. *D. frontalis* and *D. brevicomis*) avoid white stems or traps because they indicate non-host (Strom et al. 1999, 2001, Campbell and Borden 2006b). Both olfaction and color discrimination can provide MPB with a means of distinguishing host and non-host; however, host size information may allow MPB to distinguish quality within a patch of potential hosts.

Host size appears to be relevant to MPB host selection. Of particular interest to ecologists and managers is MPB's propensity to attack and kill large, commercially viable trees. MPB pest activity has been noted since at least the early 1900s in its native range in western North America (Hopkins 1905, Keen 1927). Investigators later found that MPB attack incidence was positively related to tree diameter, but landing rates were proportionate to tree area which suggests that beetles did not necessarily prefer large trees (Hopping and Beall 1948). However, later work showed that trees around 30 cm diameter and greater were much more likely to be killed by MPB than smaller trees (e.g. 20 cm diameter) (Roe and Amman 1970, Cole and Amman 1980), leading to disproportionate mortality of large trees in stands attacked by MPB (Amman and Baker 1972, Björklund and Lindgren 2009, Chapter 2). Tree size may encode host quality information because large trees tend to have thick phloem (Cole 1973, Amman and Pasek 1986, Lahr and Sala 2014, Chapter 2). The Growth Differentiation Balance Hypothesis (Herms and Mattson 1992) predicts that plants should face a trade-off between growth and defence. Evidence in ponderosa pine (*Pinus ponderosae*), an MPB host species, suggests that large trees have relatively fewer defences compared to small trees (Kane and Kolb 2010, Hood and Sala 2015). Preferential orientation based on size has not been well studied in MPB though some evidence suggests that walking MPB prefer large, flat silhouettes (Shepherd 1966).

Field data from attacked stands may give the impression that MPB prefer large trees. However, as trees grow they produce a greater visual stimulus and may produce greater olfactory stimuli assuming that monoterpene production scales with tree size. Both of these factors may contribute to increased attraction to MPB and subsequent tree mortality; observational data alone

cannot determine the relative importance of these cues. Host orientation may also depend on context: a small tree may be preferential if there are no other suitable trees nearby but less suitable if it is close to a large tree. MPB are known to abandon trees and sample others via gustation before entering (Amman 1975, Raffa and Berryman 1979) and similar assessment may occur with vision.

While the above presumes that MPB exhibit selectivity, the random landing hypothesis predicts that bark beetles orient toward any upright silhouette (Hynum and Berryman 1980). MPB may benefit from landing on hosts randomly if host stimuli are difficult to resolve, which may occur at close range in high density stands (Saint-Germain et al. 2007). Random landing may also occur if a patch of host trees are relatively equal in quality and it would not 'pay' to sample many hosts if the increase in quality is negligible (Fawcett and Johnstone 2003). Increased choosiness can cause the beetle to expend energy that could otherwise be spent on excavating the host tree and reproduction. Simulation modeling of the European spruce bark beetle (*Ips typographus*) suggests that outbreaks and aggregation can still occur if beetles land randomly because those beetles eventually die or find a suitable host and produce aggregation pheromones which then direct additional beetles (Byers 1996).

Study objectives and hypotheses

The objective of this study was to understand if host size information is used during MPB host selection by testing MPB orientation to disparately sized host-mimics. I hypothesized that MPB would use host size information during the host finding process and predicted that large multiple funnel traps, a cylindrical host mimic (Lindgren 1983), would capture

disproportionately more MPB compared to small traps. The random landing hypothesis predicts that MPB would land on large traps proportionate to their surface area, assuming that MPB utilize all the surface area and approach the trap randomly. Safranyik et al (2004) found that MPB land on unequally sized cylindrical traps in ratios approximately equal to their surface area though they note that trap catches were subject to substantial variability due to environmental conditions such as weather and the location of unknown MPB sources. As a consequence, MPB may land in lower proportion on large traps than their surface area would predict and vice-versa for small traps. Stimulus attraction may be dependent on its two-dimensional area, while stimulus effectiveness may be dependent on its three-dimensional surface area. A beetle flying toward a host tree would see a flat, two-dimensional projection and any host landing decision is likely informed (in part) by that information. The three-dimensional surface area of a stimulus is not completely perceptible to an individual beetle but could still be struck by other beetles depending on their angle of incidence (Prokopy and Owens 1983, Safranyik et al. 2004). If one stimulus captures more MPB than another in proportion to its two-dimensional area, the stimulus with the greater number of MPB is likely more attractive. Additionally, if the stimulus captures more MPB than would be predicted by its three-dimensional surface area then host orientation with respect to vision is likely non-random.

Stimuli may be more or less attractive when presented independently or paired. If stimuli are independent then attraction may be approximately equal if no similar comparator is present. However, if stimuli are presented as a pair, attraction to the large stimulus may be more apparent. It is worth considering if MPB host attraction is context dependent because previous research has

shown that MPB can integrate colour and olfactory information, suggesting their response to cues is complex (Campbell and Borden 2006a).

Methods

Two experiments were conducted in Jasper National Park [JNP] located in Alberta, Canada in the summer of 2016 and 2017. JNP has been the site of a growing MPB outbreak since 2014 due to migration of MPB from British Columbia (Parks Canada 2016). Treatments were employed to test MPB orientation to small and large silhouettes using multiple funnel traps. The small treatment consisted of a single, black, 12-unit funnel trap (20 cm diameter, 1 m height) while the large treatment consisted of three traps bound together with rope and cable ties to form a complete silhouette (31 cm diameter) with 2.4 times the (three-dimensional) surface area of the small treatment but approximately 2 times the (two-dimensional) area because MPB can only perceive two traps of the large treatment at one time. Both treatments were hung approximately 1 m from the ground. A small 1 cm^2 block of solid dichlorvos based insecticide (Ortho Home Defense Max Scotts Canada – Mississauga, ON) was placed in the collection cup of each trap to prevent insects from escaping. To control for olfactory stimuli, treatments were baited with a single MPB lure consisting of the aggregative pheromones exo-brevicomin, trans-verbenol, and the monoterpene terpinolene (Synergy Semiochemicals — Burnaby, BC).

Independent traps experiment

On 21 July 2016 I deployed traps near Decoigne Warden Station (N 52° 53' 9.963” W -118° 23' 49.6464"), located near the Trans-Canada Highway. Bordering the site was a gravel road which ran parallel to a mixed pine-aspen forest with prominent moss, fireweed

(*Chamanerion angustifolium*), juniper (*Juniperus communis*), and wild rose (*Rosa acicularis*) ground cover. I deployed traps along a 10 wide by 2 long grid covering an area of approximately 0.85 ha. The two points on the “y” axis were 25 and 50 m north of the road while the points (‘plots’) along the “x” axis were at least 25 m apart. Each point was randomly assigned a small or large trap treatment such that there were 10 points with a small treatment and 10 with a large treatment. Due to the spacing, each plot was considered independent (McMahon et al. 2010). Traps were secured using rope tied between two trees, either a non-host tree or a dead host tree (Fig. 3.1). This was done to mitigate living host trees as potential sinks for MPB, or sources of attractive compounds. A 5 m fixed radius plot, centred on the treatment, was used to calculate the basal area of any nearby tree stems (i.e. clutter). Catches were collected every four days from 25 July to 14 August, providing 6 collections. Catches were stored in a -3°C refrigerator in the field and later transferred to a -20°C freezer upon return to Calgary on 20 August. Catches were processed by counting the number of MPB caught; non-MPB were recorded as ‘other’.

Paired traps experiment

On 29 June 2017 I deployed traps along both sides of Moab Lake Road (N 52°42'36.1" W 117° 55'48.0") in JNP. The site consisted of a pine-dominant forest. Ground cover consisted of mosses, juniper, buffalo berry (*Shepherdia canadensis*), wild strawberry (*Fragaria vesca*) and wild rose. Ten trees (‘blocks’) were selected to host both the small and large treatments so that each treatment was paired. Blocks were designated at least 15 m apart to ensure independence (McMahon et al. 2010) and trees were not designated as blocks if they were near recently attacked trees (i.e. trees with dry pitch tubes or red-green foliage). Traps were secured to the tree

using angle irons and shelf brackets to ensure the trap was 1 m out from the tree, in addition to being 1 m off the ground (Fig. 3.2). Collections occurred once a week from 14 July to 20 August, providing 7 collections. A fixed 5 m radius plot was conducted as before.

Data analysis

Data were analyzed in R version 3.4.3. For the independent traps, MPB catch was analyzed using a negative binomial generalized linear mixed model with the glmer.nb function from the package 'MASS' (Venables and Ripley 2002). MPB catch was the dependent variable and treatment, collection date, plot, and distance from the road were specified as fixed effects. Trap identity was specified as a random effect with varying intercept. Basal area of stems at each trapping point was included as a covariate. For the paired traps, MPB catch was analyzed using a negative binomial generalized linear mixed model. Here, MPB catch was again the dependent variable with treatment and replicate as fixed effects. Block was specified as a random effect with varying intercept and basal area of stems at each block was included as a covariate.

Effects of each variable were assessed using Wald χ^2 tests from the package 'car' (Fox and Weisberg 2011) and least squares means from the package 'lsmeans' (Lenth 2016). To test hypotheses related to stimulus attraction and stimulus effectiveness, χ^2 goodness of fit tests with Yates continuity correction were used to compare the observed mean catch of each treatment to the expected catch from ratio of area (2 : 1; L:S) and surface area (2.4 : 1).

Results

Independent traps.

MPB catch differed among plots (χ^2=39.87, df=9, p<0.0001) and one large trap at plot '3' produced two catches with greater than 10 times the MPB catch in other traps (Fig. 3.3). Catch was also affected by distance from the road (χ^2=11.68, df=1, p<0.001) traps 25 m from the road caught more beetles than traps 50 m from the road. MPB catch varied during the study: the number of MPB decreased until the third collection date and increased afterwards (χ^2=133.73, df=5, p<0.001, Fig. 3.4). Basal area of neighbouring stems did not affect the number of MPB caught (χ^2=0.514, df=1, p>0.5) and was subsequently removed as a covariate.

Controlling for other factors, large traps caught more MPB than small traps on average (χ^2=7.25, df=1, p<0.01, Fig. 3.5). The mean catch of large and small traps did not differ significantly from the expected ratio of 2:1 or 2.4:1 (Table 3.1). The effect of treatment appeared to be driven by the two catches with >100 MPB. Removal of the associated plot (3) rendered both treatment and distance from the road non-significant (Treatment: χ^2=0.217,df=1,p>0.05; Road: χ^2=2.20, df=1, p>0.05).

Paired traps

MPB catch differed among collection dates and by block (Fig. 3.6), MPB catch was the greatest on the first collection date and decreased markedly with a minimum on the fifth date (χ^2=739, df=6, p<0.0001, Fig. 3.7) Basal area of neighbouring stems did not affect the number of MPB caught (χ^2 =0.488, df=1, p > 0.05).

The large traps caught more MPB than did the small traps on average(χ^2=19.4, df=1, p<0.005, Fig. 3.8). The mean catch of large and small traps differed from both the expected ratio of 2:1 and 2.4:1 (Table 3.2). In both cases, the small traps caught more MPB than expected, while the large traps caught fewer MPB than expected (Fig. 3.9).

Discussion

This study was conducted to assess size-based host selection biases in mountain pine beetle. During MPB outbreaks, large trees are frequently killed and small trees escape attack (Roe and Amman 1970, Björklund and Lindgren 2009). I hypothesized that MPB use host size as a cue in host selection, and predicted that they would disproportionately land on large traps compared to small traps. Broadly, this hypothesis was rejected although there was some evidence that MPB catch increased in large traps when paired with small traps. In both experiments, MPB were not caught in proportion to trap surface area. Trap catches are subject to high variation and this was true in the present study (Safranyik et al. 2004). In the independent traps experiment, MPB may have simply alighted to the first attractive olfactory plume encountered and followed it to its source irrespective of the trap's treatment. In the paired traps experiment, the traps may have been placed too close together to ensure accurate landing by MPB (Klutsch et al. 2017).

When traps were presented independently, the large traps caught more MPB than the small traps, but the effect was weak and dependent on two large observations. Upon removing these observations, it became clear that MPB were caught in similar numbers in both the small and large traps, suggesting that both silhouettes were equally attractive to MPB in partial support of the random landing hypothesis. Trap catches are highly variable and MPB may not have

landed in proportion to trap surface area due to the unknown location of MPB sources in the study site (Safranyik et al. 2004). Some sources may have been present close to traps, which likely explains the two outlier observations. Beetle flight behaviour may also explain this result: newly emerged beetles fly with the wind, likely to minimize energy spent in flight; however, when beetles encounter attractive plumes of aggregation pheromones they will fly against the wind and follow the plume (Gray et al. 1972). Chemical cues rather than visual cues are likely most responsible for the present result. It is possible that MPB in this experiment simply flew until they contacted the nearest attractive plume, leading to similar mean catch between the two treatments. Plumes may have overlapped, perhaps leading to 'plume switching' but because each bait was equally attractive this likely did not occur (Beyaert and Hilker 2014).

When traps were paired, the large trap generally caught more MPB than the small trap though less than the trap's surface area, or two-dimensional area would predict. The result in this experiment seems to suggest that host selection may be context dependent and that host size could be a relevant cue if there is a similar comparator nearby. To elaborate, if MPB orient to baited traps by initially following a chemical plume before visualizing the traps each trap should be perceived as equally attractive (i.e. the stimuli are equally powerful). After following the plume, the beetle receives visual stimuli which contradicts the olfactory stimuli and the beetle should make a landing decision based upon this new information. MPB have been shown to use visual information when olfactory information is inaccurate: when myrcene (a host compound attractive to MPB) was placed on black and white traps presented together MPB predominantly

landed on black traps despite the attractive olfactory stimulus present on the white traps (Campbell and Borden 2006a).

Accurate discrimination of size may not be as important as accurate discrimination of colour, which could explain the weak effect of trap size. The small trap had a diameter of 20 cm while the large trap had a diameter of 32 cm and these correspond to trees encountered and colonized by MPB in nature, though trees greater than 30 cm are killed more often than 20 cm trees (Björklund and Lindgren 2009, Chapter 2). To an individual MPB, the difference between the two sizes may be relatively unimportant because a tree of either size offers virtually unlimited resources. By contrast, selecting a non-host plant could make mate finding difficult due to non-host volatiles, or the beetle could be killed depending on the tree's defensive response (Dickens et al. 1992, Pureswaran and Borden 2003). A similar concept was demonstrated in flower choice tests of honey bees (*Apis mellifera*). Bees can distinguish between one relatively more profitable flower than another but did not always choose the more profitable flower when both flowers were highly profitable (Waddington and Gottlieb 1990). The authors suggest that discrimination between these two high quality flowers may have occurred, but the difference was not great enough to influence the bee's choice. Here, a wider range of trap sizes may have produced a stronger effect. For example, redbay ambrosia beetles prefer large, 18 cm, silhouettes compared 2 or 9 cm silhouettes (Mayfield and Brownie 2013). It is possible that MPB would avoid traps which approximate non-mature trees (<10 cm) as they do not normally attack trees of that size (Chapter 2).

The above discussion is premised on the idea that MPB can discriminate differences between host size at all and from the present experiment it is not clear if this actually occurs. The maximum range for MPB to visually perceive a host stem is likely low: a test of MPB response to visual stimuli found that beetles placed 23 cm away from a visual stimulus elicited a response (Shepherd 1966) though it is unclear if this is the maximum distance at which a response would occur. At this distance the size differences between each trap may become negligible with both appearing as large, black objects occupying the visual field (Kirschfeld 1976). This lack of discrimination may lead to promiscuous landing on dark vertical objects which occurs in the southern pine beetle (*Dendroctonus frontalis*), a related species of bark beetle with similar ecology to MPB (Strom et al. 1999). Similarly, Warren's root collar weevil (*Hylobius warreni)* a pest of lodgepole pine saplings, uses vision to orient to any standing vertical stem with no apparent discrimination of colour or size (Machial et al. 2012). As well, *Ambrostoma quadriimpressum*, a pest of elm trees, will walk to any dark, columnar object in its field of view (Sun et al. 2016).

The present result, and results from insects with similar ecology, suggest that MPB has low visual acuity. Insect visual acuity is typically quantified by counting ommatidia, the optical units of the insect's compound eye. Other Scolytinae, including the Douglas-fir beetle (*Dendroctonus pseudotsugae*) have 300 – 370 ommatidia per eye (Chapman 1966). Similarly, several species of aphids (Hemiptera: Aphidae) have few ommatidia (< 300) (Döring and Spaethe 2009). These counts are much lower than diurnal foraging Hymenoptera, which can have >1000 ommatidia per eye (Muscedere et al. 2014, Fig. 2c). This apparent lack of high

visual acuity is likely due to life-history. Insects with “complex” vision (e.g. colour detection, movement tracking) such as wasps (Hymenoptera: Vespidae) (Shafir 1996) and dragonflies (Odonata) (Paloma et al. 2013) are tasked with hunting and tracking prey items. By contrast, MPB spend a large portion of their lives in tree stems, feed on stationary plants, and primarily communicate via pheromones which precludes the need for such vision (Safranyik and Carroll 2006). Ommatidia aside, there is a lack of knowledge regarding other aspects of eye morphology in Scolytinae which could provide greater context for these behaviours as the size and shape of eyes influences the visual field (Prokopy and Owens 1983). For example, three species of *Asaphidion* (Coleoptera: Carabidae), a predatory ground beetle, demonstrated between species variation in head size, eye surface area, and ommatidia density, which affects the number of regions with binocular overlap and the visual acuity of the insect (Bauer et al. 1998). A similar assessment of MPB and other *Dendroctonus* species would be useful in connecting visual anatomy to ecology.

Disproportionate mortality of large trees may still occur even if MPB are poor image formers. Production of attractive volatiles likely increases as trees grow and produce more wood, which can stretch existing resin ducts or create new ducts that accumulate and transport volatile compounds (Plomion et al. 2001). Resin ducts are at least partially filled with resin and the production of resin itself is known to attract MPB (Raffa and Berryman 1983, Christiansen et al. 1987). As a consequence, large trees likely produce greater plumes of attractive volatiles, which are more likely to attract randomly flying MPB than plumes produced by small trees. Upon landing and producing aggregative pheromones, subsequent MPB can follow the pheromone

plume (Gray et al. 1972). At close range, MPB may use a combination of colour information and gustatory information to accept or reject potential hosts (Raffa and Berryman 1982b).

An important consideration is that host size may not necessarily indicate host quality. Within a stand, phloem thickness has been found to be well correlated with tree diameter (Cole 1973, Cole and Amman 1980, Lahr and Sala 2014, Chapter 2); however some studies have found weaker relationships (Shrimpton and Thompson 1985, Reid and Robb 1999, Dooley et al. 2015). The relationship between host size and defence is also uncertain depending on the metric considered. Xylem resin duct density (i.e. the number of xylem resin ducts produced per unit area) tends to decrease with increasing diameter (Kane and Kolb 2010, Hood and Sala 2015, Chapter 2) and trees with a higher density of xylem resin ducts are more difficult (though not impossible) for MPB to colonize (Kane and Kolb 2010, Ferrenberg et al. 2014). Resin ducts also occur in phloem tissue and the (limited) evidence suggests that they are not strongly related to tree diameter (Berryman 1976, Chapter 2). Such lines of evidence suggest that the information encoded by silhouette size may not be as immediately useful to MPB compared to colour or olfactory stimuli. This is further compounded when considering MPB visual acuity which may not be accurate enough for MPB to discriminate the size of two hosts at close range.

Although MPB did not land in proportion to trap surface area, they tended to land more often on large traps when they were presented with small traps and this has implications for the positive feedback loop of MPB infestation. If MPB accumulate at slightly higher rates on large trees than small trees due to surface area, then the concentration of aggregative pheromones in

each tree should also initially increase at a similar rate, eventually outpacing the smaller trees leading to disproportionate attack and mortality of large trees.

Conclusions

To conclude, size discrimination may play a role in MPB host orientation but its contribution is likely low relative to olfaction and colour discrimination. Host size information may not be important to MPB because the consequences of selecting a small host are less severe than selecting a non-host. Size information does not aid in host recognition so its utility is likely restricted to situations when olfactory information is unreliable or redundant. The results open the possibility that MPB may not be able to visually discriminate between host size at all and simply accumulate in greater numbers on large trees in part due to their greater surface area but also due to greater quantities of attractive host volatiles. This may be particularly consequential for MPB at the endemic, low density stage which do not have the benefit of abundant aggregation pheromones but serve to foster MPB outbreaks.

Table 3.1: χ2 Goodness of Fit test results for expected mean MPB catch of independent traps.

	Large (n=60)	**Small (n=59)**	$\mathbf{X^2_1}$	**P**
Observed Mean Catch (SE)	12.32 (3.145)	7.83 (1.427)	NA	NA
Expected 2:1	13.43	6.72	0.0013	>0.9
Expected 2.4:1	14.23	6.92	0.0075	>0.9

Table 3.2: χ2 Goodness of Fit test results for expected mean MPB catch of paired traps.

	Large (n=67)	**Small (n=70)**	$\mathbf{X^2_1}$	**P**
Observed Mean Catch (SE)	80.29 (12.80)	68.97 (13.79)	NA	NA
Expected 2:1	99.5	49.75	4.640	<0.05
Expected 2.4:1	105.41	43.84	8.294	<0.01

Fig. 3.1: Trap treatments as deployed in the 2016 independent traps experiment.

Fig. 3.2: Trap treatments as deployed in the 2017 paired traps experiment.

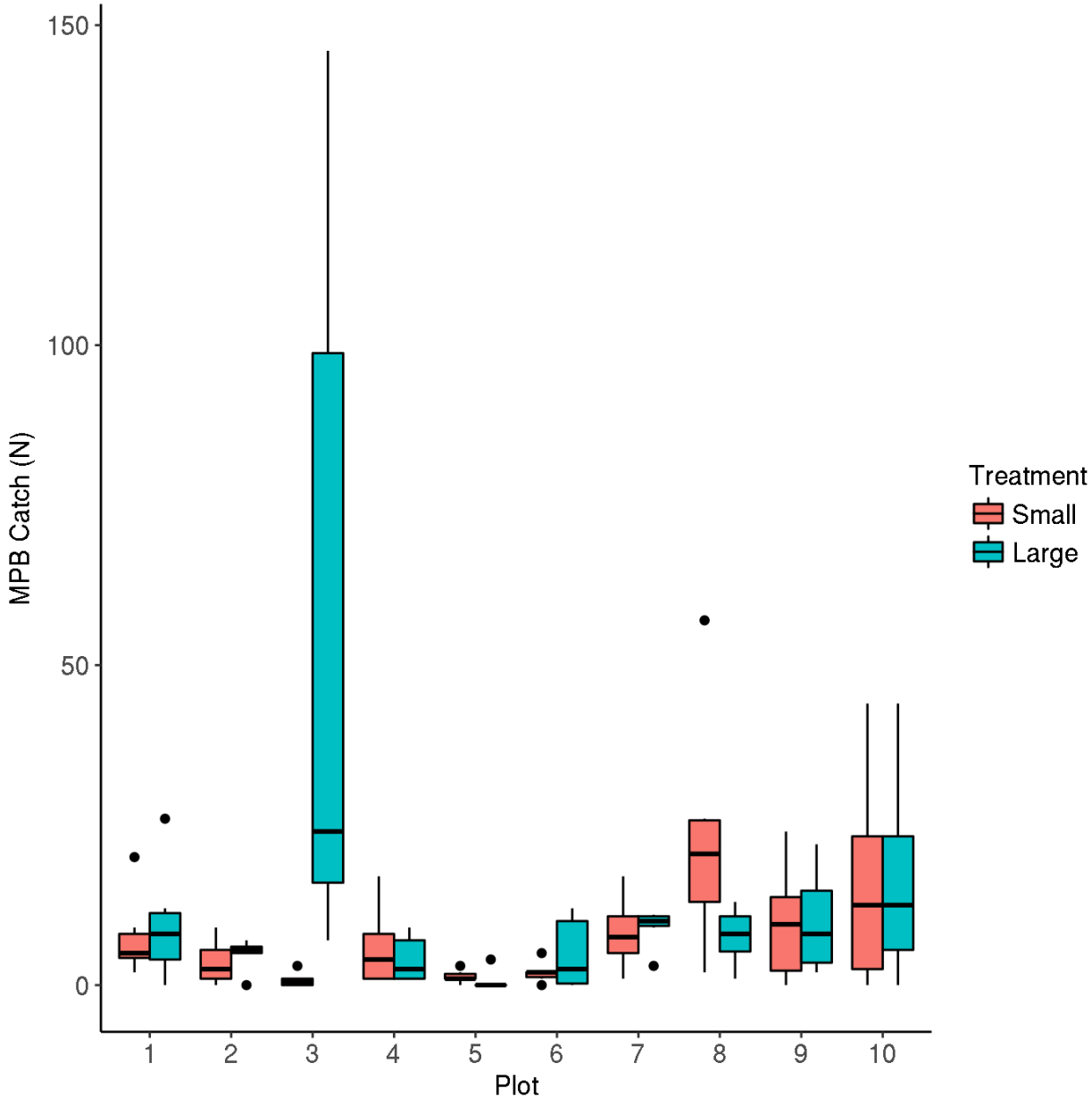

Fig. 3.3: Boxplot of MPB catch by plot in the independent traps experiment. Bars represent median, ends of the box represent the upper and lower quartiles, whiskers represent 1.5 * interquartile range.

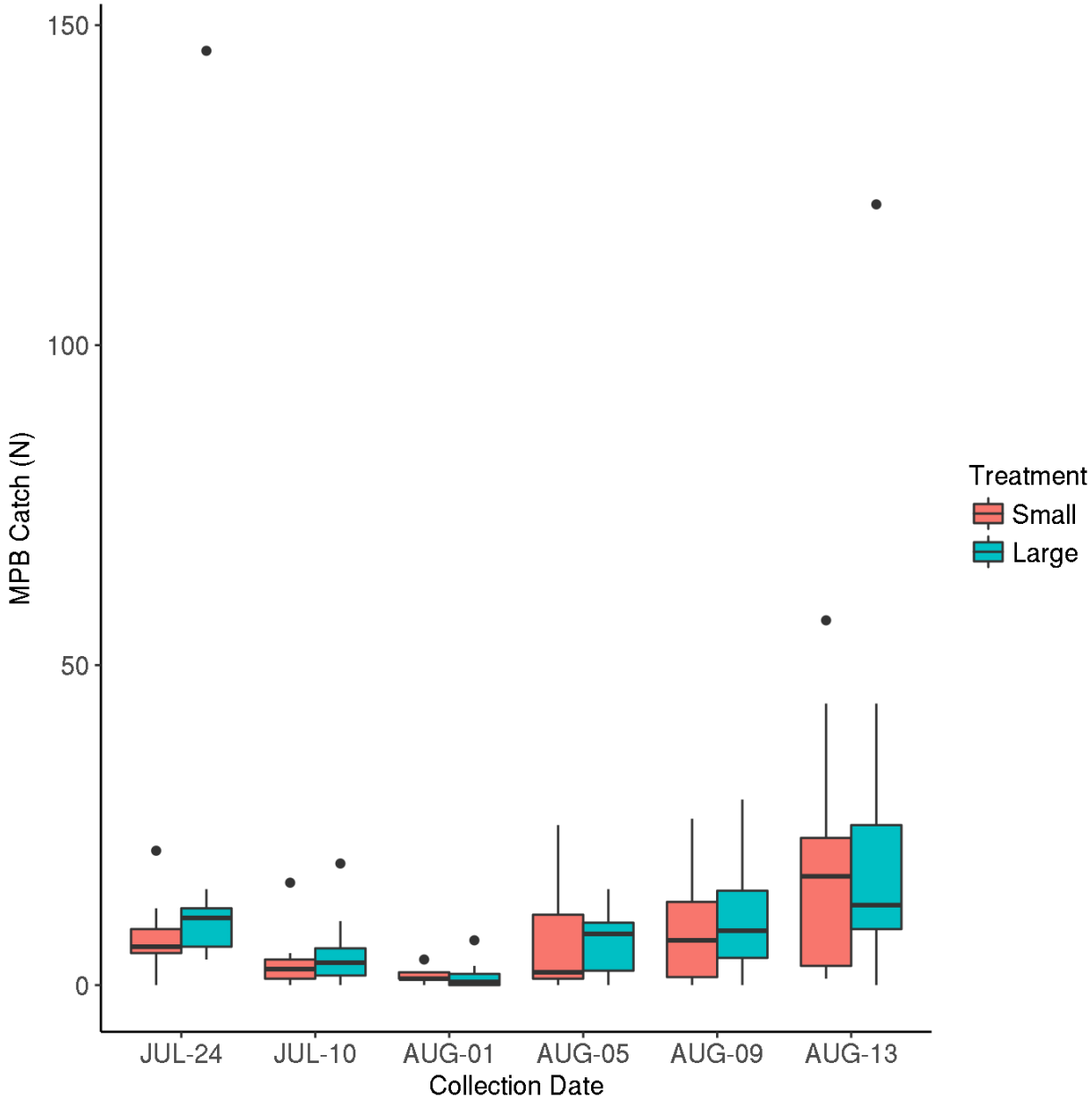

Fig. 3.4: Boxplot of MPB catch by collection date in the 2016 independent traps experiment. Bars represent median, ends of the box represent the upper and lower quartiles, whiskers represent 1.5 * interquartile range.

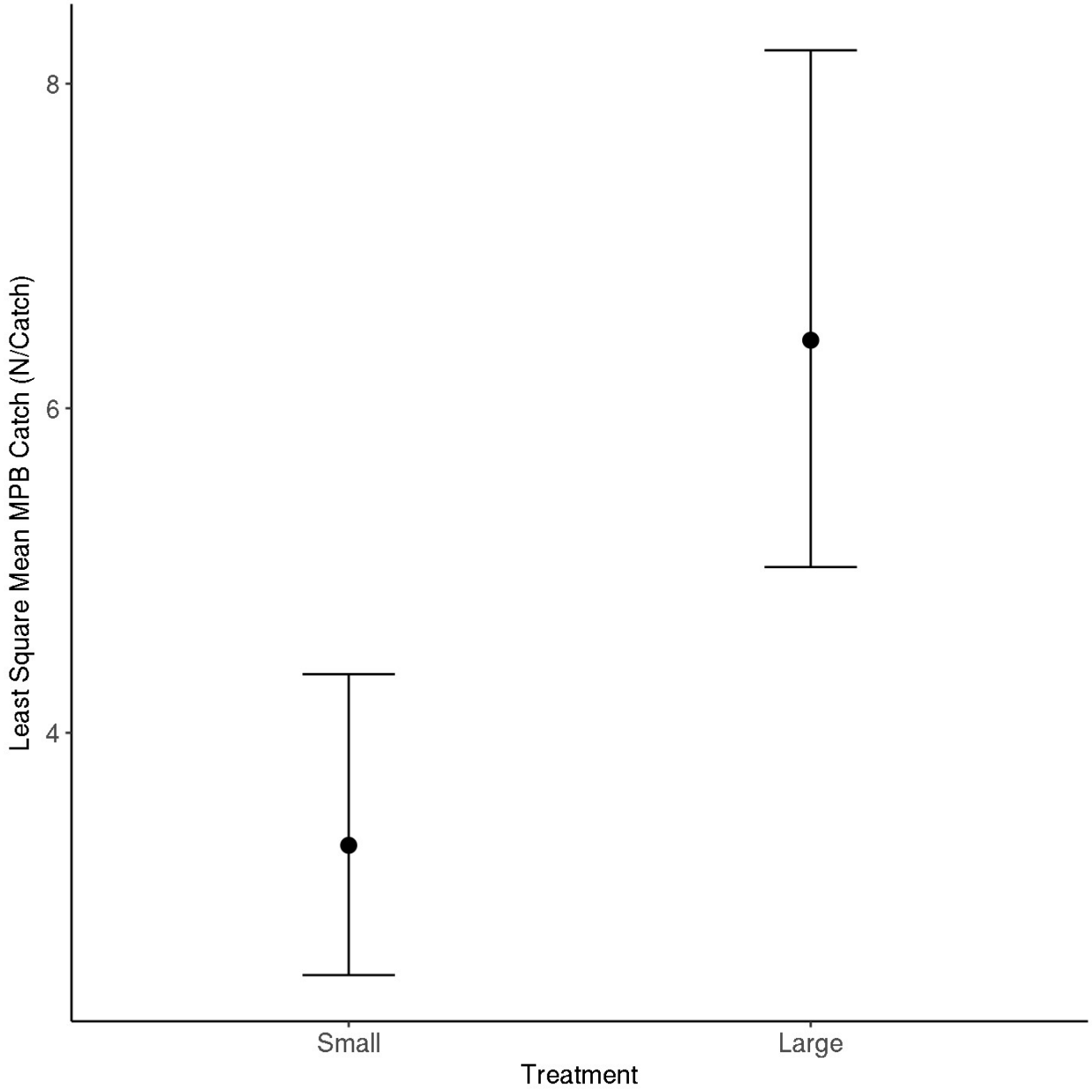

Fig. 3.5: Least squares mean MPB catch by treatment for the 2016 independent traps experiment. Bars represent 95% confidence intervals computed with the 'effects' package.

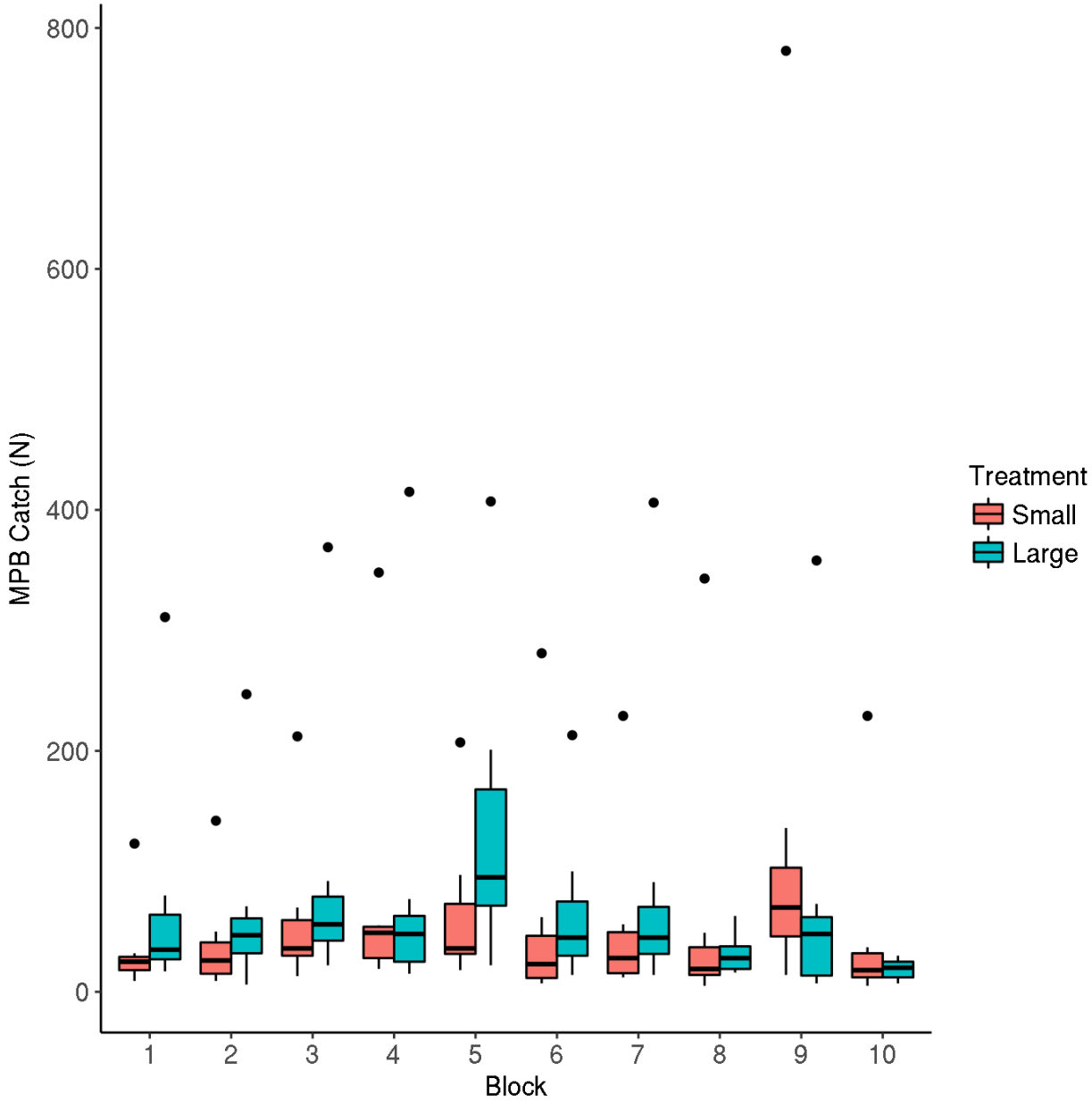

Fig. 3.6: Boxplot of MPB catch by block for the 2017 paired traps experiment. Bars represent median, ends of the box represent the upper and lower quartiles, whiskers represent 1.5 * interquartile range.

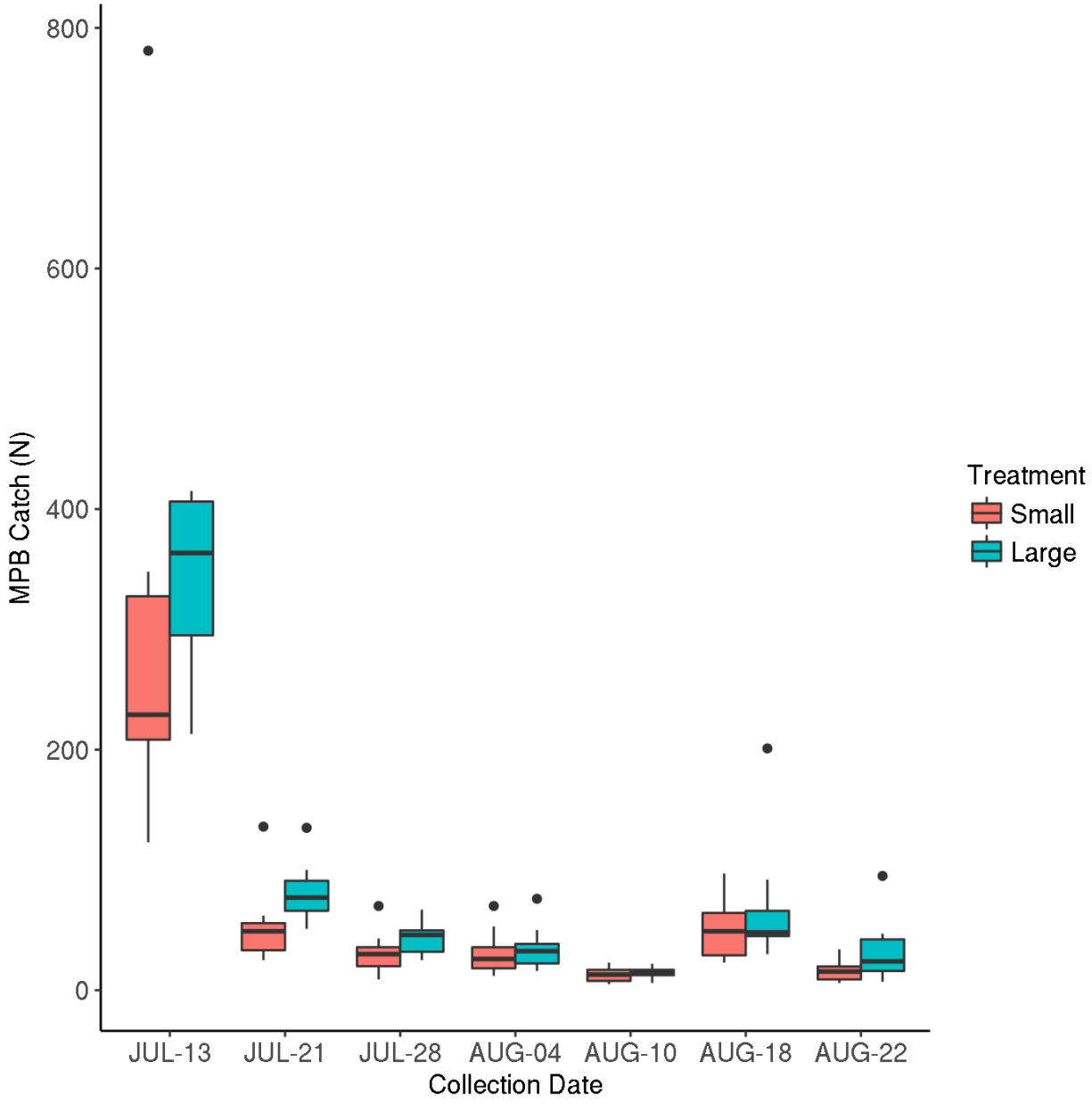

Fig. 3.7: Boxplot of MPB catch by collection date for the 2017 paired traps experiment. Bars represent median, ends of the box represent the upper and lower quartiles, whiskers represent 1.5 * interquartile range.

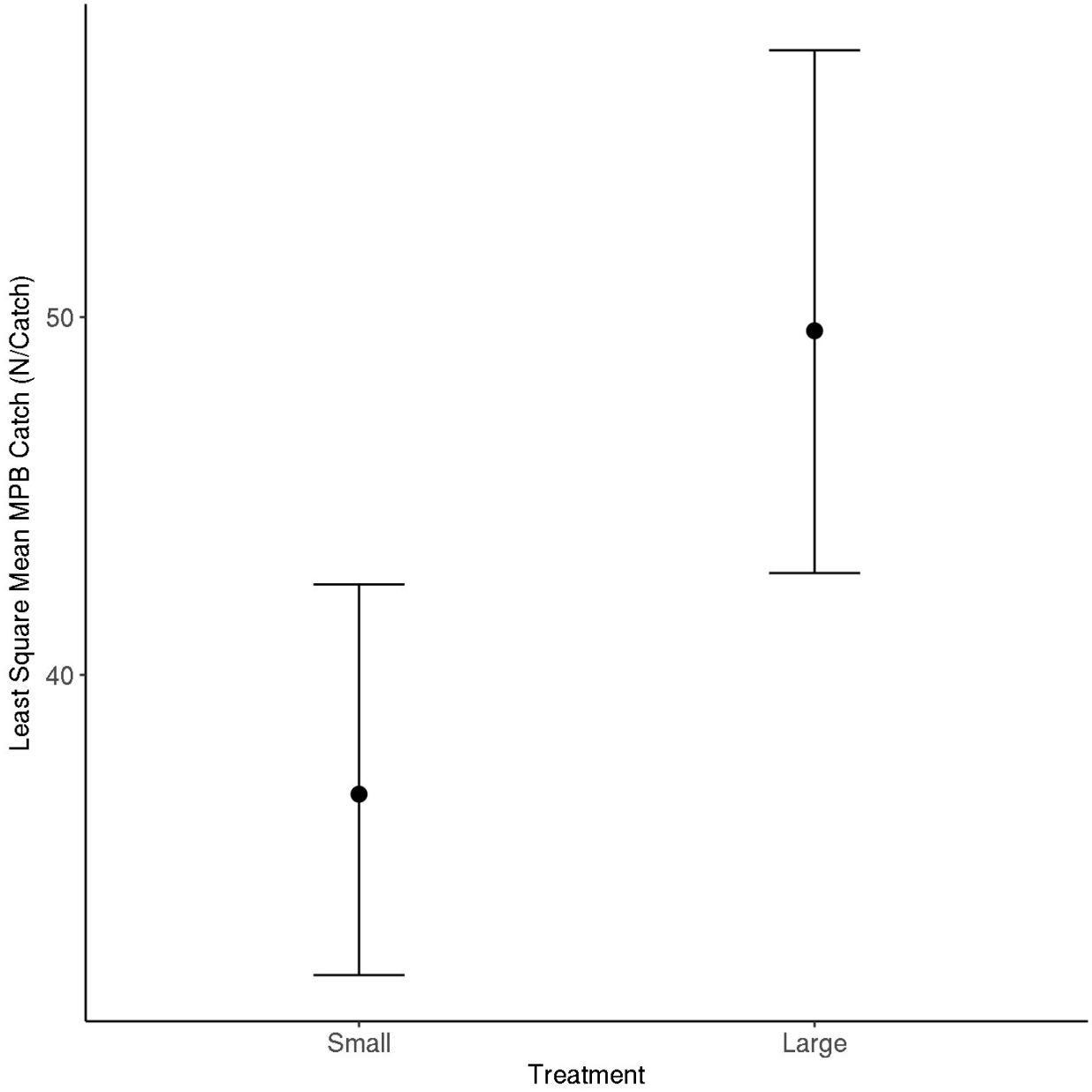

Fig. 3.8: Least squares mean MPB catch by treatment for the 2017 paired traps experiment. Bars represent 95% confidence intervals computed with the 'effects' package.

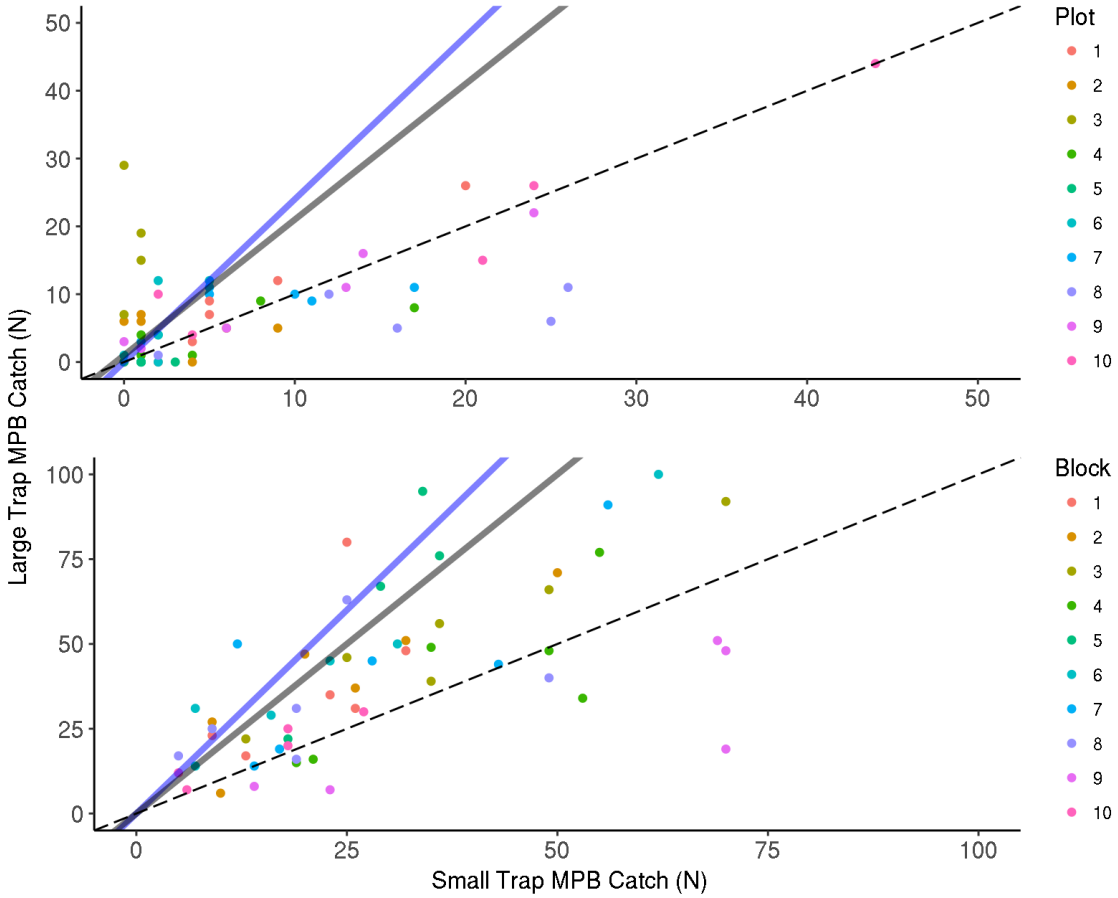

Fig. 3.9: Small trap catch plotted against large trap catch for independent traps (upper) and paired traps (lower) experiments, traps grouped by plot or block respectively. The slope of the blue line is 2.4 while the slope of the black line is 2. Points falling above either line indicate that the large trap caught greater than 2.4 or 2 times as many beetles as the associated small trap. The dashed line is a 1:1 reference. Plot area truncated by 'coord_cartesian'.

Chapter 4: General Discussion and Future Direction

Dispersers face challenges in finding suitable habitats and using appropriate cues to facilitate habitat finding. Habitats are unequal in their quality (i.e. properties which increase the habitat seeker's fitness) and theory suggests that dispersers should select the highest quality habitats (Stamps 2001). The process of finding these habitats incurs costs, which can be especially great for dispersers that do not feed during dispersal (Stamps et al. 2005). Habitat seekers should use cues which minimize search time and provide reliable information about the habitat (Fawcett and Johnstone 2003). The Ideal Free Distribution (Fretwell and Lucas 1969) predicts that dispersers will have equal fitness across all habitats and that the abundance of colonizers will follow that habitat's quality.

For herbivorous insects which live and feed within a plant, costs can be incurred as a consequence of the plant's investment in growth and defence. The Growth Differentiation Balance Hypothesis (Herms and Mattson 1992) suggests that plants cannot invest equally in both growth and defence due to limited resources (i.e. dividing cells). The Plant Vigor Hypothesis (Price 1991) serves as useful corollary which predicts that plants which are vigorous (ie large and possessing greater resources) should be preferred by herbivores over stressed or sub-optimal plants (ie smaller).

These ideas provided the following general research questions: 1) To what extent does host (i.e. habitat) quality vary with host size? 2) Is host size information in and of itself used in host selection? To answer these questions I collected observational and experimental data using the mountain pine beetle (*Dendroctonus ponderosae*) and its principle host lodgepole pine (*Pinus contorta*) (reviewed by Safranyik and Carroll 2006). MPB are an eruptive forest pest

capable of killing many millions of trees during periods of high population density (‘outbreaks’). During outbreaks, MPB tend to predominantly kill large trees (Björklund and Lindgren 2009). This could indicate that large lodgepole pine trees are more suitable hosts than small trees and/or MPB are attracted to large silhouettes.

In Chapter 2 I hypothesized that large trees would be more suitable hosts. I predicted that large trees would be older, have thicker phloem, would have fewer defences, and that brood production would be greatest in these trees. I also hypothesized that host size information would be used in host selection and predicted that large trees would be more likely to get attacked, and receive more attacks compared to small trees. The results show that host quality tended to increase with host size: large trees had thicker phloem and were generally older. The results for defence were mixed: xylem resin duct density decreased with diameter; however, resin production and phloem resin duct density did not vary significantly with diameter. Large trees were more likely to be attacked and received more attacks while small trees were nearly excluded from attack. MPB brood production in the following year appeared to have a non-linear relationship with diameter and brood production peaked at intermediate diameters.

In Chapter 3, I hypothesized that host size provides relevant information regarding host quality, and that MPB would disproportionately prefer the large trap treatment compared to the small trap treatment when olfactory stimuli were controlled. The results from the 2016 experiment, when traps were presented independently suggested that large traps caught the same number of MPB, on average, as the small traps (after accounting for two influential observations). The results for the 2017 experiment, when traps were presented together, shows

that the large traps caught significantly more MPB than the small traps. However, small traps appeared to catch more MPB than would be expected for their effective trapping area, while large traps caught fewer MPB than would be expected for their effective trapping area.

Taken together, the results show that large trees are heavily attacked in the field; however, silhouette size likely plays a small role in the tree attack process. As discussed in Chapter 3, MPB spend most of their lives inside trees and communicate via pheromones both of which preclude the need for sophisticated vision. Discrimination of colour (i.e. host/non-host) is likely more important than discriminating size within hosts in terms of the consequences of making of wrong choice. A hypothetical beetle in a poplar is much less likely to successfully mate than a beetle that happens to be in a small pine. It is likely that MPB orient to their hosts using an array of cues but olfactiory cues are the most important component of the host finding process, particularly conspecific pheromones as MPB will fly against the wind upon detecting a pheromone plume (Gray et al. 1972). Female pioneer MPB do not have the benefit of conspecific pheromones and must use host stimuli to locate their hosts. Based on the disproportionate attack of large trees in the field, it is likely that these large trees are more detectable, though increased detectability likely comes from olfactory, rather than visual stimuli. These large trees are, on average, better hosts for MPB which allows these pioneers to persist and create pheromones which then attract joiner beetles via positive feedback. It is possible that pioneer beetles have greater visual and olfactory acuity, for example female MPB seem to more consistently choose black baited traps over white baited traps compared to male MPB (Campbell and Borden 2006b).

There may be other differences between the sexes such as ommatidia count or sensitivity to host attractants.

MPB do not appear to follow the ideal free distribution as brood production peaked at intermediate diameters, likely due to oversaturation of large diameter trees and subsequent intraspecific competition. The IFD may not apply to MPB due to the nature of their dispersal. MPB rely entirely on their stored reserves to reach a host and it is in the beetle's interest to spend much of that energy excavating the host and mating/laying eggs. Pioneers may be ideal, (i.e. able to select the best host in a given stand) particularly those which have high energy reserves allowing them to be choosier and sample a greater number of potential hosts (Latty and Reid 2010). Joiners may not be ideal because their habitat selection choices are at least partially influenced by conspecifc pheromones causing them to spillover into other trees that may not normally be attacked by pioneers (Klutsch et al. 2017).

The results for lodgepole pine host quality seemed to at least partially support the Growth Differentiation Balance Hypothesis and the Plant Vigour Hypothesis. Large trees tended have fewer defences but had larger radial increment grown, on average, compared to small trees. It is worth considering the potential caveats in assuming a growth defence trade off. First, carbon, while an important resource for plants, may not necessarily be the limiting resource in synthesizing defensive compounds, which could potentially obscure a trade off (Mole 1994). Plants in resource rich environment could invest greatly in both growth and defence (van Noordwijk and de Jong 1986). Furthermore, long-lived trees may not necessarily follow this pattern because they can store carbon over long periods of time for future use, exhibiting low

growth for several years or more. Storage is likely an important strategy for plants in resource poor environments than rich environments (Chapin et al. 1990). Plants in resource rich environments can afford to utilize carbon quickly so as grow and increase their rate of assimilation. By contrast, plants in resource poor environments will likely need to store carbon and utilize this reserve at key times when it would be most beneficial, such as when a pulse of new resources becomes available. Carbon storage may be important due to the formation of ad-hoc 'induced' defences which are activated upon sensing some stressor such as a fungus or herbivore (Hudgins and Franceschi 2004).

Future work should further consider the relationship between host tree size and tree defence particularly as MPB expand further from their historic range in southern British Columbia. Trees outside of the MPB historic range are more vulnerable to attack and successful infestation. In northern British Columbia for example: Lodgepole pine trees tend to produce greater quantities of constitutive monoterpenes, presumably making them more attractive (Clark et al. 2010); similar results have been found in the novel host jack pine (*Pinus banksiana*) which produce greater quantities of α-pinene (Burke and Carroll 2016). If the relationships found in this study are robust this could make large trees outside of MPB's historic range particularly vulnerable to infestation and priorities for management actions such as preemptive felling (Vandygriff et al. 2015) or chemical control (Progar et al. 2013). Future work could attempt to identify and plant resistant trees which have strong induced defence responses, or trees with less pronounced constitutive defences which may disrupt MPB attraction. Given that lodgepole pine chemical defences are at least under some genetic control this could be a worthwhile area to

devote management resources (Ott et al. 2011). Other management actions should encompass stand diversification by planting non-host trees such as *Populus* spp. to 'screen' host trees (Dymond et al. 2014). Additionally, preemptive removal of dominant trees could reduce a stand's potential MPB load, leading to less severe MPB-caused damage (Schmitz et al. 1988). Decades of fire suppression in the 20th century created even-aged, overgrown stands which proved highly susceptible to MPB infestation (Axelson et al. 2009). Rectifying this issue is not trivial but Keyes et al. (2014) suggest that practitioners should create uneven aged stands by employing variable-retention harvesting. This practice could coincide with removing dominant trees and subsequent planting of non-host trees to create a complex stand at the species and age level and reduce the amount of contiguous MPB habitat. Such practices have been successfully employed in managing the southern pine beetle (*Dendroctonus frontalis*) (Asaro et al. 2017).

This research has attempted to bridge plant ecology and behavioural ecology. Here I have demonstrated that large trees are higher quality hosts for MPB primarily due to their thicker phloem and fewer defences compared to small trees; however, large trees tended to produce fewer MPB offspring, suggesting that they become oversaturated with invading MPB. MPB trapping experiments showed that visual host size information likely plays a small role in orienting the beetle during the host finding process. Future work should consider how other host traits relate to host size, such as quantitative variation of individual monoterpenes, and host resistance to inoculation with MPB vectored fungi. As well, further assessment of the relative influence of host cues in MPB host selection may prove fruitful for behavioural ecology and forest management.

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