INDIVIDUAL HOST SELECTION DECISIONS AND POPULATION-LEVEL RESPONSES IN A TIME- AND ENERGY-LIMITED FORAGER, *DENDROCTONUS PONDEROSAE* HOPKINS

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Abstract

My thesis explores the link between habitat selection decisions made at the individual level and the resulting population-level distributions, using a combination of field, laboratory, and theoretical studies in mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae). Settlement decisions in MPB depend on complex interactions among the size and nutritional quality of the host tree, its defensive capabilities, beetle attack densities, and beetles' energy reserves. Limited somatic energy reserves and time available for dispersal and habitat search impose restrictions on individuals' settlement decisions, and can have substantial effects on the resulting population distributions. I characterized the variation in individual somatic condition and timing of emergence in a field population of beetles and tested the effect of somatic condition on beetles' habitat settlement decisions. I derived, from first principles, a dynamic state variable model of inter-stand dispersal and tree selection by individual beetles. The model and experimental results showed that considerable individual variation exists and that settlement decisions are modulated both by the beetle's lipid reserves and tree nutritional quality. This model provided the foundation for a spatial dynamic game model of beetle attack on multiple host tree species. I examined how the predicted evolutionarily stable strategies differ for beetles utilizing different pine species, and examined the resulting population distributions on these different tree species. Finally, using beetle dispersal estimates obtained from the dynamic game model, I explored the spread of an engineered genetic control element through MPB populations and describe how such control may be effective to suppress beetle outbreaks. I discuss the utility of considering individual variation together with state- and condition-dependent behaviours in assessing population-level phenomena.

Keywords: Habitat settlement; dispersal; state-dependent behaviour; condition-dependent behaviour; population dynamics; bark beetles

To my dear friends Roma, Jalyn, and Henry;
parents Daria and Jerry;
and imzadi *Jessica.*

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Chapter 1

Introduction

1.1 Introduction

Habitat selection theory attempts to describe the distribution of individuals across two (or more) habitats of varying resource quality. Related to habitat selection is dispersal, which is the movement of animals from their points of origin to another area. These two concepts are intimately related: habitat settlement is the end point of dispersal, and the processes underlying habitat selection influence where individuals disperse to (Stamps, 2001). Settlement decisions are commonly examined using optimal foraging theory and are thus assumed to be made by individual organisms in a manner that maximizes their perceived payoff (e.g., energy gains, fitness) in the chosen habitat relative to the costs of searching or travel (e.g., time, energy losses, missed opportunities) (e.g., Charnov, 1976). This evaluation of profitability requires the ability to assess and appropriately respond to environmental heterogeneity, including assessment of resource availability and the level of competition for these resources (i.e., density-dependent payoffs) (e.g., Fretwell and Lucas, 1970; Rosenzweig, 1981; Brown, 2000).

Individuals' habitat selection and dispersal decisions ultimately lead to the distributions of population across habitats. Depending on the scale used, variation in individual selection behaviour have profound implications for a wide variety of biological fields, from metapopulation and community dynamics (especially relevant for conservation and pest management) to evolutionary biology including local adaptation and sympatric speciation (Rosenzweig, 1981, 1985; Lima and Zollner, 1996; Brown, 2000; Davis and Stamps, 2004).

Thus, understanding habitat selection provides critical insights into the general ecology of dispersing organisms and the resulting population distributions. Historically, models of habitat selection have assumed equal habitat preferences and have not considered the contribution of individual variation toward these population-level phenomena, until recently. Furthermore, they rarely consider energetic costs and other constraints. Two major goals of my thesis are (1) examine the effects of individual variation in energy reserves and time available for search limits dispersal and habitat settlement, and (2) to examine the effects of individual search behaviour on the resulting population-level distributions. To these ends, I consider habitat selection and dispersal decisions in a bark beetle species whose populations are subject to strong Allee effects.

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae)(MPB), is responsible for one of the most devastating insect outbreaks in North America. The ongoing outbreak, already having destroyed hundreds of millions of trees in British Columbia, Canada and throughout the western United States, continues to spread eastward threatening the boreal pine forests of Canada (Nealis and Peter, 2008; Safranyik et al., 2010). This outbreak has been driven by increased susceptibility of forest stands through a combination of fire suppression and global climate change, leading to more favourable as for the beetle (Safranyik et al., 2010).

Successful reproduction in bark beetles requires search for and colonization (attack) of a suitable host tree, followed by mating, oviposition, and subsequent larval overwinter survival (Rudinsky, 1962; Reid, 1963; Safranyik and Carroll, 2006). Unlike in other bark beetle species, MPB typically attacks live trees and kills them through a combination of pheromone-coordinated ‘mass attack’ and introduction of mutualistic blue-stain fungi that are pathogenic to the tree and accelerate its death. At low beetle population densities, beetles frequently fail to achieve the sufficiently high attack densities needed to overcome the defences of large-diameter, well-defended hosts. In these environments, MPB attack smaller-diameter, low-quality, or stressed trees. However, at high beetle densities like those achieved during the ongoing outbreak, MPB attacks larger diameter, higher quality trees (Rudinsky, 1962; Safranyik and Carroll, 2006). Despite the host tree’s secretion of defensive resins and toxic secondary compounds, the host’s defensive capabilities are overwhelmed and host death is inevitable given a sufficient number of attacking beetles (Atkins, 1966a; Wood, 1982; Raffa and Berryman, 1983; Berryman et al., 1985).

Habitat settlement (i.e., host choice) decisions in MPB are complex and depend not only on the size and quality of the host tree, but also its defensive capabilities, modulated by individual beetles' estimates of conspecific (attack) densities as well as beetles' internal energy reserves (see Atkins, 1966b, 1969; Wood, 1972; Elkin and Reid, 2005). Energy reserves are particularly important in determining the dispersal and search capabilities of individuals: individuals with limited reserves are expected to be less 'choosy' when selecting host trees. In this thesis, I used a combination of empirical, experimental, and theoretical approaches to explore the effects of energy- and time-limitation on influencing individual beetles' host choice behaviour and examine the impact of individual variation on the resulting population distributions of beetles on host trees.

The goals of Chapter 2 were two-fold: first, I characterized the individual variability present in a field population of beetles by assessing their timing of emergence and somatic energy (lipid) reserves at emergence; and second, I evaluate the role of beetles' lipid reserves on their host selection decisions using a field experiment. Demonstrating that substantial variation does exist in natural beetle populations and that differences in beetles' energy state do contribute to host selection decisions was important for the development of my theory of state-dependent habitat settlement decisions, and served as an important test of the fundamental predictions of the models developed in Chapters 3 and 4.

In Chapter 3 I developed, from first principles, a model of MPB habitat settlement and inter-stand dispersal decisions. I use a state-dependent modelling approach to account for the energy-state dependent processes beetles experience when selecting host trees. Specifically, I developed a dynamic state variable (DSV) using field- and lab- collected data for model parameterization, and evaluated the sensitivity of the model to various parameters. This model was published in *Ecological Modelling* (Chubaty et al., 2009), and serves as the basis for the dynamic game model I developed in the subsequent chapter.

Chapter 4 extends the model from the previous chapter by developing a dynamic state-dependent game model of MPB settlement decisions. This model solves the dynamic evolutionary stable strategy (ESS) decisions for beetle host choice for three species of pine (jack, lodgepole, and their hybrid), by coupling the DSV model previously developed with Monte Carlo simulations of beetle settlement and attack in forest stands comprised of each host species. These simulations model the population-level outcomes of beetles' host preferences, generating attack distributions within these simulated stands. I considered the differences between stands of each type on beetle performance in each stand, as well as the resulting attack distributions. In addition to predicting beetles' host settlement decisions, this model also predicts inter-stand dispersal rates, which I subsequently used in my final data chapter to incorporate individual beetle behaviour, and the variation therein, in a population-level model of bark beetle spread through a forest landscape.

The population dynamics model developed in Chapter 5 considered the spatial spread of genetically engineered beetles, from a central release point, and considers the roles of dispersal, resource depletion, and environmental heterogeneity on beetle outbreak dynamics. This model explored the theoretical potential for 'genetic control' of MPB, by assessing the circumstances which lead to beetle population suppression (rather than extirpation) across a landscape of interconnected forest stands, modelling dispersal as a diffusion process based on the outcome of the behavioural model developed in the previous chapter. In this chapter I developed a spatially explicit population dynamics and population genetics model of beetle infestation and spread of a homing endonuclease gene (HEG) (Burt, 2003) within a generalized bark beetle – conifer system. HEGs, when inserted into an essential target gene are very effective at suppressing population fitness because they result in substantial transmission ratio distortion and high genetic load. HEG-mediated genetic control operates through meiotic drive, such that the proportion of gametes produced that contain the inserted HEG element are skewed towards HEG homozygous genotypes (HEG^+/HEG^+), through the conversion of hemizygotes (i.e., those carrying only a single copy of the construct, HEG^+/HEG^-) to these homozygotes. Hemizygous genotypes do not suffer any serious deleterious effects, yet the relative fitness of HEG^+/HEG^+ genotypes is substantially reduced because insertion of this construct knocks out both copies of the target gene. This genetic control element is well suited for population control, particularly in insect systems, because of its quick spread through efficient gene conversion and its evolutionary stability (Burt, 2003; Gould, 2008).

Throughout my thesis I explore the intersection of individual- and population-level processes by examining the role of individual habitat settlement behaviour on population distributions. I mostly consider these effects using bottom-up individual-based approaches, rather than top-down phenomenological ones; however, I attempt to incorporate variability in individual behaviour into phenomenological models to account for more than simply describing behavioural averages, because individual behavioural variation is increasingly recognized as an important driver of population-level processes (e.g., Grimm, 1999; Nonacs, 2001; Alonzo, 2002).

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1.3 Connecting statement

I begin by demonstrating the substantial variation in beetle energy (lipid) reserves and timing of emergence, and experimentally assess the effect of energy-limitation on beetles' host acceptance decisions. I develop condition upon beetle emergence (CUBE) profiles for field-collected beetles, which describe the probability of an individual emerging on a particular day with a particular state. This CUBE profile is used in subsequent modelling chapters. Additionally, the host acceptance experiment serves as an important test of the theory developed in Chapters 3 and 4.

Chapter 2

The role of energy limitation on host tree acceptance in a bark beetle

2.1 Abstract

Energy and time constraints experienced by dispersing animals often limit dispersal and subsequent habitat selection. When substantial variation in individual dispersal capabilities is present, these constraints may have significant impact on populations. In this study, we 1) sample a population of mountain pine beetles to characterize the variation in individual somatic energy condition and time of emergence, and 2) test the effect of somatic energetic condition on habitat (host) selection decisions. We show that beetles' host selection decisions are influenced by both host tree nutritional quality and individuals' lipid reserves. Good nutritional quality trees are accepted sooner than poor nutritional quality trees, and beetles with high energy reserves wait longer to attack poor nutritional quality trees than low energy beetles. These results suggest that internal energy state and environmental conditions are important for habitat selection in this species, and they support the condition-matching hypothesis of beetle host tree selection. Thus, we highlight the importance of considering individual variation in energy reserves when examining population-level phenomena and developing population models.

Keywords: dispersal, host selection, state-dependent behaviour, condition-dependent behaviour, bark beetles, *Dendroctonus ponderosae*

2.2 Introduction

Understanding the drivers of population-level distribution patterns of organisms is important for the conservation and management of species. How organisms distribute themselves across habitats reflects the outcome of habitat selection decisions by individual organisms, and is driven by individuals' assessment and evaluation of available habitats. For many organisms, the location and productivity of habitats varies both spatially and temporally, which imposes additional challenges for dispersers as they search for and subsequently evaluate ephemeral habitat sites. Models of dispersal and habitat selection have generally considered populations of identical individuals, or used an 'average' behaviour extended to the whole population, thus ignoring the importance of individual behaviour, and individual variation, in determining population-level outcomes (Roitberg and Mangel, 1997; Patterson et al., 2008; Clobert et al., 2009).

In addition to site resources, several other important factors drive individuals' habitat settlement decisions. These decisions often account for both extrinsic, environmental factors such as mortality risk (i.e., due to predators or host plant defences), as well as intrinsic factors such as a dispersing organism's energetic or other physiological state. Dispersing individuals are often limited in their energetic reserves as well as the amount of time available for habitat search and colonization. Thus, in many dispersing organisms, habitat selection decisions are limited by both energy and time constraints during dispersal (e.g., Ward, 1987; Stamps et al., 2005). In species that disperse from their natal habitats, which includes many insect species, we observe substantial variation in both timing of emergence and somatic energetic condition at emergence. For such species, in order to predict population distributions, we must account for individual variation in energy stores and time available for search and the effects of these constraints on individual habitat selection.

This study examines the individual variation in energy (lipid) reserves at emergence, and the effect of lipid reserves on the host tree acceptance of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Mountain pine beetle (MPB) is a major forest pest, whose reproduction is contingent on successful attack and subsequent death of its primary host, lodgepole pine (*Pinus contorta* var *latifolia*). Adult MPBs overwhelm host tree defences (resin flows and monoterpene production) through the introduction of mutualistic blue-stain fungus, which is pathogenic to the tree, and by using a coordinated mass attack, which is initiated by individual beetles and mediated via pheromone cues produced by the attacking beetles. The timing of this attack is synchronous; early arrivers' entry into the host is slowed by the tree's defences (Raffa and Berryman, 1983), whereas beetles arriving mid-attack or later experience easier tree entry (Pureswaran et al., 2006). Beetles arriving too early, before the attack is well-underway, or who arrive too late, suffer reduced offspring production (Pureswaran et al., 2006). Selection for synchrony in the timing of attack may also drive the evolution of synchrony of timing of emergence.

The decision to initiate an attack is based, in part, on host tree nutritional quality, tree defensive capabilities, and the density of conspecifics (Safranyik and Carroll, 2006). Individuals base their decisions on the perceived (mortality) risk at the selected site (i.e., 'safe-site hypothesis' (Frank and Leggett, 1982)). In this case, individuals are expected to select host trees that are less well defended by resin or that can be more easily overcome by MPB mass attack. Additionally, an individual beetle's energy reserves may influence host attack (acceptance) decisions (e.g., Atkins, 1966), in that beetles with higher energy reserves could afford to be choosier when selecting a host tree whereas those with low reserves would be more likely to accept poorer nutritional quality hosts if host options are limited (Chubaty et al., 2009; Latty and Reid, 2010). This is because those individuals with higher lipid content are expected to survive longer (e.g., Safranyik, 1976), have higher capacity for flight (Williams and Robertson, 2008), and therefore dispersal, and be better able to deal with the host's defences. Consequently, they would be more likely to find and attack more suitable (i.e., higher nutritional quality) hosts.

The extent to which MPB host acceptance decisions are based on energy reserves has not previously been tested directly in a field setting. If individuals select low nutritional quality sites out of desperation, settling as a result of depleted energy reserves (i.e., poor somatic energetic condition), *cf.* the 'desperate larva' hypothesis for marine invertebrates (Knight-Jones, 1953), then we would expect to see beetles in poorer energetic condition accepting lower nutritional quality trees more often (and sooner) than beetles in better energetic condition, irrespective of the tree's defensive capabilities. Latty and Reid (2010) use the term 'condition-matching' to describe an integrated hypothesis of habitat selection in MPB which takes into account the influence of both host defences (i.e., site safety) and an individual's energetic state, whereby individuals in better energetic condition are more likely to attack better-defended trees, as also indicated in Chubaty et al. (2009).

The purpose of this study is twofold. First, we determine the extent of individual variation in somatic energetic condition present in a field-collected population of mountain pine beetles. We measure the energetic condition of newly emerged beetles in relation to the timing of emergence, which may be important in determining the energetic status of individuals (e.g., late emergence is often associated with low energy reserves). Second, we test the role of energy (lipid) reserves on the host tree acceptance of individual beetles in a field setting, and discuss the importance of considering individual variation and its impacts on individual behaviour and population dynamics.

2.3 Methods

2.3.1 Field sites

Two field sites were used: the first, during the summer of 2006, to collect beetles on which to perform lipid analyses to determine energetic condition upon emergence; the second, during the summer of 2010, to run host-acceptance experiments. The beetle-collection site, located $\sim 30\ km$ south of Merritt, BC, Canada $(49°50'15.00''N,\ 120°45'30.00''W)$ was a uniform, mature $(\geq 80\ a)$ lodgepole pine forest, in an area undergoing a widespread MPB infestation at the time. Experiments were conducted in Yoho National Park, near Field, BC, Canada $(51°22'45''N,\ 116°30'48''W)$, in an area previously impacted by mountain pine beetle outbreak. Work at both sites was conducted near the start of the beetles' emergence and flight period.

2.3.2 Energetic condition upon emergence

Three large (diameter at breast height, $DBH > 30\ cm$) beetle infested lodgepole pine trees were felled in June 2006 and cut into $50\ cm$ bolts. Bolts were stored in a refrigerated storage facility and kept near $4°C$, until they could be transported back to the lab at the end of the field season (late August). Once back in the lab, bolts were placed into individual emergence cages and kept at room temperature. Emergence cages were checked twice daily: in the morning and late afternoon, and all emerged beetles collected and immediately frozen. Cages were monitored for 6 weeks after emergence began to ensure all emerging adult beetles were captured.

Beetles were individually sexed (see Lyon, 1958), and had their right elytron carefully removed and placed beside a stage micrometer (OB-M-2/200; $d = 0.001mm$) under a dissecting microscope and photographed. The length (l) and width (w) of each elytron were then measured using imaging software (Rasband, 1997), and used to calculate a beetle size index using the formula for cylindrical volume $v = \pi w^2 l$, as beetles are approximately cylindrical in shape.

Beetles and their elytra were then individually sealed into filter paper envelopes and placed in a drying oven at $\sim 62°C$ for 72 hours, before being weighed (Mettler Toledo XP26, $d = 0.001\ mg$). Next, lipids were extracted using petroleum ether in a Soxhlet apparatus for 8 hours, after which time the samples were re-dried in the drying oven for 24 hours and reweighed, to determine the mass of lipids lost during the extraction. This corresponds to the lipid mass of the beetle (Elkin and Reid, 2005; Williams and Robertson, 2008).

2.3.3 Host acceptance experiment

Four lodgepole pine trees ($\sim 25 - 30\ cm$ diameter), heavily infested with mountain pine beetles, were felled, and several $\sim 40\ cm$ bolts were cut from the bottom $3\ m$ of each tree. These bolts were placed inside specially constructed containers to collect beetles as they emerged. These emergence containers were checked daily for beetles which were collected, brought back to the lab, and haphazardly assigned to one of the treatment groups: either in the fridge ($\sim 4°C$) or at ambient outdoor air temperature (up to $\sim 25°C$) for 48 hours (e.g. Latty and Reid, 2010) on a substrate of damp paper towel. Because insects are ectotherms, beetles at higher temperatures expend their energy reserves more quickly than those at cooler temperatures. Therefore, beetles kept at ambient temperatures comprised the ‘low energy’ group, and those stored in the fridge made up the ‘high energy’ group. Approximately twenty beetles from each group were used per experiment on each test tree (several beetles died during the trials and were excluded from analyses). Beetles of both sexes were used due to the difficulty of accurately sexing live beetles using auditory and morphological characteristics, and to ensure large enough experimental cohorts.

To prepare trees for the experiment, suitable lodgepole pine trees were first identified based on canopy volume, proximity to neighbouring trees, DBH, and phloem thickness (PT). PT was measured using a small circular punch and taken at breast height ($\sim 1.3\ m$) from the north and south sides of the tree. We selected four trees, from each of two classes. Poor nutritional quality trees were smaller trees with thinner phloem (DBH: $\sim 15 - 20\ cm$; PT: $\sim 1\ mm$), and good nutritional quality trees were larger and had thicker phloem (DBH: $\sim 25 - 30\ cm$; PT: $> 1.5\ mm$). This characterization of tree nutritional quality classes is consistent with the lodgepole pine distributions in a previous study (Chubaty et al., 2009). Trees within each class had approximately equal canopy volume and proximity to neighbouring trees based on visual assessment. Trees were girdled near the base $\sim 36 - 48\ h$ before the experimental trials began to elicit a chemical response to the damage (which beetles find more attractive (Gara et al., 1984)) and to partially mitigate the effect of host tree defences on beetles' choices. Approximately $1\ m^2$ area of the bark, above the girdle, was covered in mesh to prevent the experimentally introduced beetles from flying away, and to exclude non-experimental beetles. The mesh was wrapped loosely around the tree, tightly secured at the top and bottom using staples and duct tape, leaving a resealable flap through which observations could be made. Modelling clay was used to fill in gaps in the bark where the mesh was secured.

Prior to introducing the experimental beetles onto the trees, the rear portions of their elytra were coloured using brightly-coloured (fluorescent) water-based paint such that beetles from the two experimental treatments were a different colour. All beetles were placed in a flight cage in the sun for $\sim 2\ h$ to warm up and fly around in order to make them more receptive to attacking a tree. After this warm up period, beetles from each treatment were introduced onto the experimental trees via the resealable mesh flap at the bottom of the experimental area on the western side of the tree. The time to attack (i.e., the time until each beetle began burrowing into the bark to begin gallery construction) was measured, along with the vertical distance along the bark the beetle moved prior to initiating gallery construction. Experiments were run until all beetles had entered the tree, up to a maximum duration of $3\ h$.

Following termination of the experiment, beetles were recovered from the tree so that lipid extractions (as described above) could be performed to confirm the temperature treatment generated the desired differences in the beetles' somatic energy condition.

2.3.4 Data analyses

The goal of the preliminary analyses was to determine the relationship between lipid mass and beetle volume, so that a size- and sex-corrected measure of lipid content (*i.e.* energetic condition) could be used in subsequent analyses (e.g., Jakob et al., 1996; Elkin and Reid, 2010; Latty and Reid, 2010). Using a generalized linear model (GLM), lipid mass was examined as the response variable with beetle volume, beetle sex, a volume:sex interaction, and the tree from which the beetle emerged as the predictor variables. A GLM was used instead of a generalized linear mixed model (GLMM) because there were only three different levels for the $tree$, thus $tree$ could not be included as a random effect and was treated as a fixed effect in the model (Zuur et al., 2009). This GLM was modelled using gamma distributed errors with a log link function, and showed significant sex and tree effects (Figure 2.1; Table 2.1). The residuals from these models were used as a measure of beetle energetic condition for subsequent analyses for each sex.

To examine the relationship between date of emergence and energetic condition for each sex, we performed a bootstrapped ($N = 10000$) cubic polynomial regression using higher-order day terms. Beetle timing of emergence was fit to a Weibull distribution, which describes poikilotherm emergence patterns (Wagner et al., 1984). Additionally, by plotting these emergence patterns against the proportion of beetles that emerged each day we generated condition upon beetle emergence (CUBE) profiles, which represent the probability of a beetle emerging on a particular day with a particular energetic condition.

Experimental treatments were compared using ANOVA, to assess the efficacy of our temperature treatments. A GLM model was used to determine beetle energetic condition, as above but without including sex and $tree$ which were non-significant. Beetles that had died during the experiment were excluded from analyses.

Latency (time until host tree acceptance) was analyzed using a survival analysis and log-rank test with tree nutritional quality class and beetle treatment group as factors, and a Cox's proportional hazards test which included both of these factors and their interaction term. Distance travelled was rank-transformed and analyzed using a two-factor ANOVA with a Tukey's Honest Significant Differences test.

All analyses were performed using R Programming Language and Environment (v 2.14.0) (R Development Core Team, 2011).

2.4 Results

2.4.1 Energetic condition upon emergence

Despite a statistically asymmetric response between male and female beetles, both groups showed a qualitatively similar emergence pattern. Beetle energetic condition was higher near the start of the emergence period, subsequently dropping off at the end of the emergence period (table 2.2; Figure 2.2a); however, there was substantial variation present. Most beetles emerged during the first half of the emergence period, with males and females both following a Weibull distribution ($\alpha_f = 1.724872$; $\beta_f = 9.674882$; $\alpha_m = 1.82726$; $\beta_m = 9.94895$) (Figure 2.2d-e). CUBE profiles showing the probability of a beetle emerging on a particular day with a particular energetic condition are shown in Figures 2.2b-c.

2.4.2 Host acceptance experiment

Our temperature treatments produced beetles in relatively poor and good somatic energetic condition ($F_{1,211}$ = 4.81, p = 0.0294; Figure 2.3). Low energy beetles (L) accepted poor nutritional quality trees (P) sooner than did high energy beetles (H), and beetles on good nutritional quality trees (G) accepted sooner than beetles on poor nutritional quality trees (Figure 2.4; log-rank: $\chi^2 = 84$, $df = 3$, $p \ll 0.001$; Cox's proportional hazard: all $p < 0.01$ except interaction term NS). High energy beetles travelled further than those with low energy on poor nutritional quality trees (Figure 2.5; table 2.3).

2.5 Discussion

This is the first study to test, using a manipulative experiment, the effect of energy reserves on individual host selection decisions in mountain pine beetle, and to characterize the variation in individuals' timing of and energetic condition at emergence. Reduced choosiness as a result of a decline in individual state is a common theme in behavioural ecology, affecting a variety of behavioural decisions such as host selection (e.g., Roitberg et al., 1992, 1993; Wajnberg et al., 2006), foraging decisions (e.g., Nonacs, 2001), and mate selection (e.g., Hunt et al., 2005; Lynch et al., 2005). The results of this study (Figures 2.4 & 2.5) support the prediction that high-energy beetles are choosier (slower to enter) than low-energy beetles at selecting host trees, in a manner consistent with the condition-matching hypothesis. We did not observe a significant interaction between a beetle's somatic energetic condition and the nutritional quality of the host tree, suggesting that the effects of the tree's defences on beetles' decisions were mitigated. Low-energy beetles accepted poor nutritional quality trees sooner, and traversed the bark significantly less than did high-energy beetles. These results validate the basic predictions of previous work by Chubaty et al. (2009) who modelled MPB host selection decisions using a dynamic state variable model that based individuals' decisions on distribution and nutritional quality of host trees, conspecific attack densities, the time left in the season to find a suitable host, and individuals' energy reserves. While previous work with MPB host selection has suggested support for the safe-site hypothesis, the researchers could not exclude the condition-matching hypothesis (Latty and Reid, 2010). Our study does not support the safe-site hypothesis.

Our sample beetles used to generate CUBE profiles and our experimental beetles are from different populations, thus their residual-derived energetic conditions cannot be compared directly (Jakob et al., 1996), however our temperature treatments produced groups of beetles representative of those emerging relatively early in the season, but with either high or low lipid reserves. Beetles in the ambient temperature treatment had much lower lipid reserves than beetles stored in the fridge. As a result, we saw much higher mortality in the ambient temperature treatment (as indicated by the difference in sample sizes between the two groups). These two beetle groups likely represent the extremes of the range of somatic energetic conditions found in host-seeking beetles, yet their behavioural differences demonstrated the flexibility of their host-selection strategies.

Animal dispersal and habitat selection models are increasingly considering the role of individual variation and state-dependent decisions on behaviour, and their population-level outcomes. Models that account for individual variation/heterogeneity in behaviour make better predictions of resultant distributions at larger spatial scales than those that do not (e.g., Morales and Ellner, 2002). There are numerous examples of the importance of considering individual behaviour when modelling populations, including the spread of invasive species and disease, and conservation (reviewed in Patterson et al., 2008). Individual variation affects decisions in the current generation, and may also carry over into future generations if behaviours are heritable (e.g., Wallin et al., 2002) or in the presence of maternal effects (e.g., Stamps, 2006). Additionally, research into consistent individual differences (i.e., behavioural syndromes) is exploring how decisions made in one dimension of behaviour (e.g., habitat selection) may correlate with decisions made in other dimensions of behaviour across an individual's lifetime (e.g., 'choosiness' in general, or in mate choice) (Sih et al., 2004; Pruitt et al., 2011). Thus, understanding the extent of individual variation in natural populations and the role it plays in animal decision-making is an essential first step in developing more accurate models of dispersal and habitat selection, and of behaviour more generally.

In our present study, we quantitatively characterized the variation in energetic condition at and timing of emergence for beetles of both sexes. As previously mentioned, although there were statistically significant differences between female and male beetles, they exhibited qualitatively similar emergence patterns. Beetles emerging earlier during the emergence period were in better energetic condition than those emerging near the end, and beetle emergence followed a Weibull distribution with most beetles emerging during the first half of the emergence period. These patterns can be summarized as condition upon beetle emergence (CUBE) profiles, which describe the probability of a beetle emerging on a particular day with a particular energetic condition. CUBE profiles are useful for parameterizing individual based simulation models that incorporate beetle emergence. This work further enhances the development of MPB host selection models to understand better beetle outbreak dynamics within and among forest stands. Chapter 4 builds upon the Chubaty et al. (2009) model by developing a dynamic game model of MPB tree attack in a simulated forest stand as the next step in evaluating the role of energy constraints on population-level responses of MPB. These models could be further expanded and developed to assess disturbance patterns at the landscape level.

2.6 Acknowledgements

We would like to thank Chao Li and Larry Dill for comments and feedback on the planning of this work and on this manuscript; Margo Moore for helpful suggestions during the planning stages of this work; Allan Carroll and Doug Linton for field site access; Howard Thistlewood and Naomi DeLury for access to cold storage facility; Fred Davis for tree falling; Maxence Salomon and Elizabeth Nyboer for assistance in the field; Kristen Gorman, Amber Gigi Hoi, Jeremy Jackson and Roberto Trasolini for their assistance in the lab; Will Stein, Phil Molloy, Michelle Paddack, and Gi-Mick Wu for statistical advice. Special thanks also to Jane Park and Rick Kubian from Parks Canada for assisting with locating a suitable field site and for providing assistance falling trees; Gary Roke for providing data on mountain pine beetle attack locations within Yoho National Park; and the University of Calgary Biogeosciences Institute for providing accommodations and lab space. Funding was provided through a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant awarded to Bernard Roitberg.

2.7 Tables

Table 2.1: Generalized Linear Model of Lipids vs. Volume.

	Estimate	**Std. Error**	**t-value**	**p-value**
$(Intercept)$	0.9441	0.0357	26.46	$\ll 0.001$
$Volume$	0.0184	0.0019	9.78	$\ll 0.001$
$SexM$	-0.1389	0.0533	-2.61	0.0092
$TreeB$	0.0851	0.0160	5.32	$\ll 0.001$
$TreeC$	-0.0427	0.0160	-2.67	0.0075
$Volume : SexM$	0.0081	0.0033	2.42	0.0156

Table 2.2: Cubic polynomial regression models for beetle energetic condition vs. day of emergence.

	Estimate	**Std. Error**	**t-value**	**p-value**
$(Intercept)$	-0.1697	0.0262	-6.47	$\ll 0.001$
Day	0.0682	0.0081	8.39	$\ll 0.001$
Day^2	-0.0056	0.0007	-8.02	$\ll 0.001$
Day^3	0.0001	0.0000	6.01	$\ll 0.001$

$r^2_{adj.} = 0.07892; F_{3,2049} = 59.61; p \ll 0.001$

Table 2.3: Two-factor ANOVA of vertical distance traveled before accepting host for beetles with high or low energy reserves on host trees of good or poor nutritional quality.

Factor	**Sums of Squares**	**F-value**	**p-value**
$(Intercept)$	61.36	8.8489	$\ll 0.001$
$Beetle\ Energy\ Reserves$	0.48	0.0687	0.984
$Tree\ Quality$	524.53	75.6429	$\ll 0.001$
$Beetle\ Energy\ Reserves : Tree\ Quality$	105.23	15.1751	$\ll 0.001$

$F_{3,136} = 33.01; p \ll 0.001$

2.8 Figures

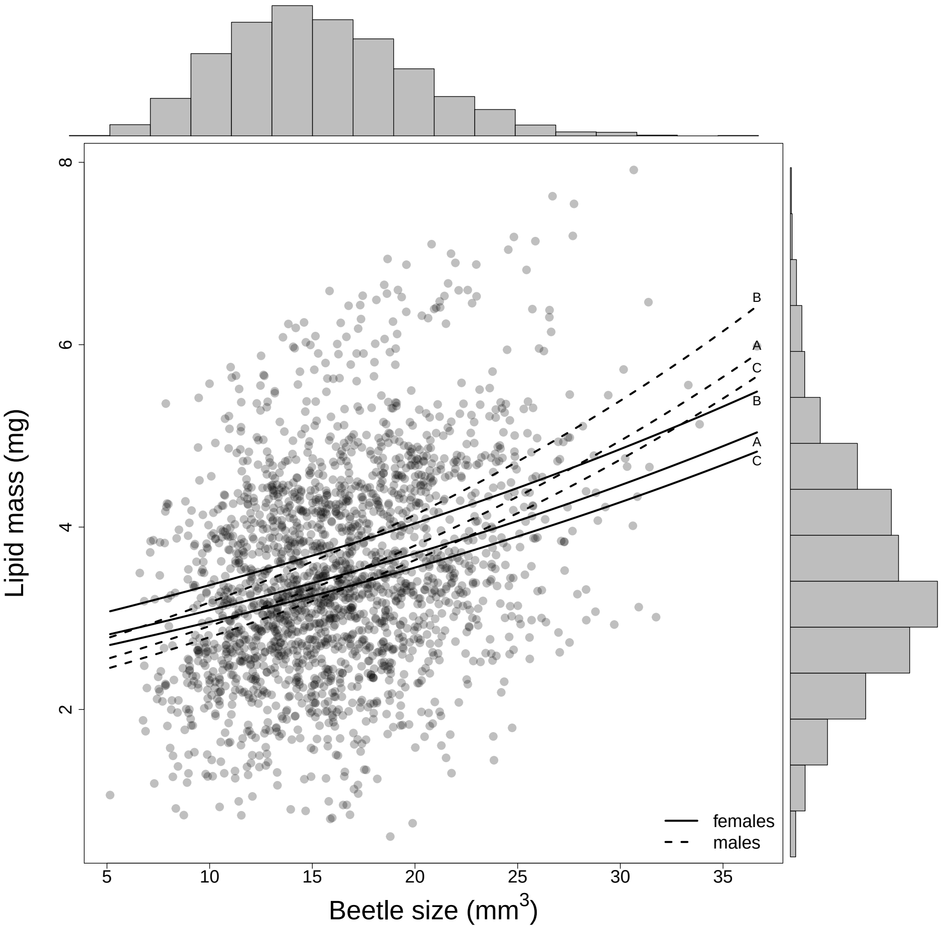

Figure 2.1: Generalized linear model of beetle lipid mass with beetle volume for beetle sex and tree from which the beetle emerged; modeled using gamma distributed errors with a log link function. Residuals from this model were used as a measure of beetle energetic condition for subsequent analyses. Letters label curves corresponding to each tree. Histograms along each axis show distributions of the data.

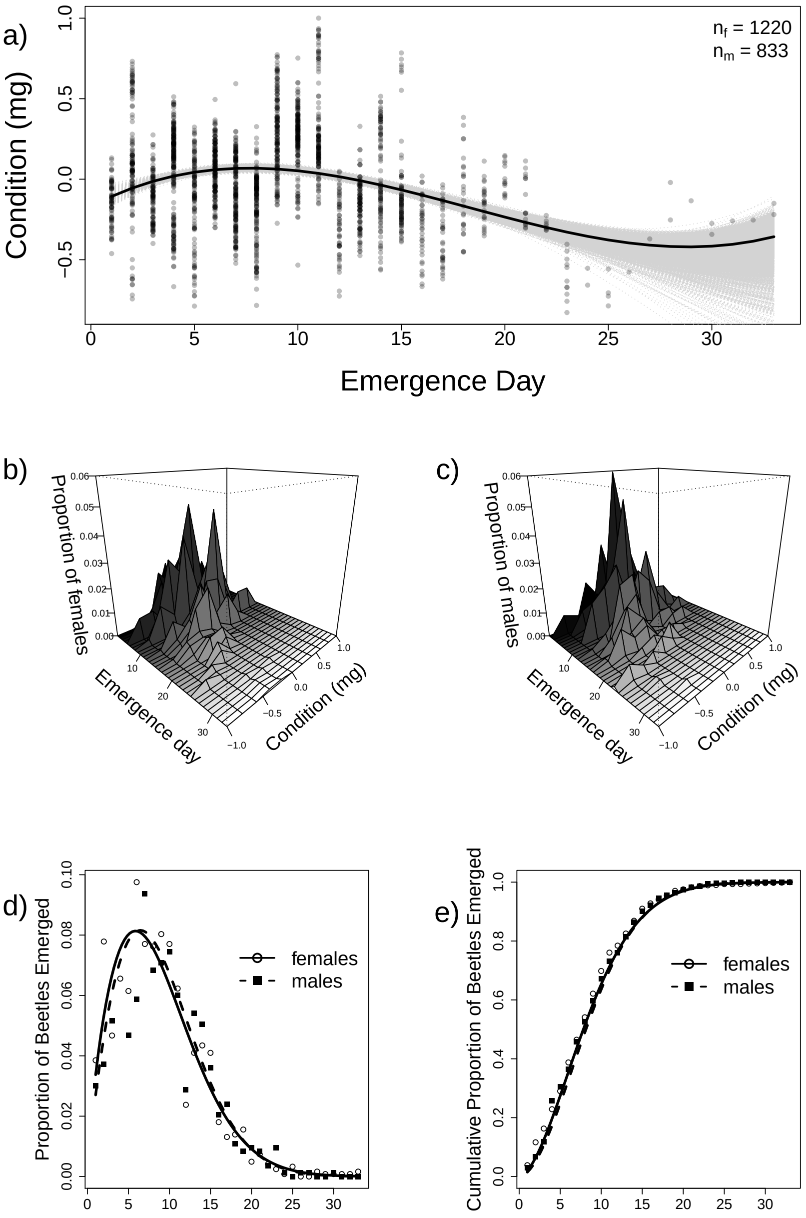

Figure 2.2: Beetle energetic condition upon emergence ($n_f = 1280$; $n_m = 833$): a) polynomial regression curve of date of emergence and energetic condition for both sexes (solid black) with bootstrapped regression curves (light grey) ($N = 10000$); b) proportion of female beetles with varying energetic condition emerging daily (female condition upon emergence profile); c) proportion of male beetles with varying energetic condition emerging daily (male condition upon emergence profile); d) proportion of female (open circles, solid line) and male (closed squares, dashed line) beetles emerging daily fit using Weibull distribution ($\alpha_f = 1.724872$; $\beta_f = 9.674882$; $\alpha_m = 1.82726$; $\beta_m = 9.94895$); e) cumulative proportion of female and male beetles emerging daily fit using Weibull distribution (parameters as in d).

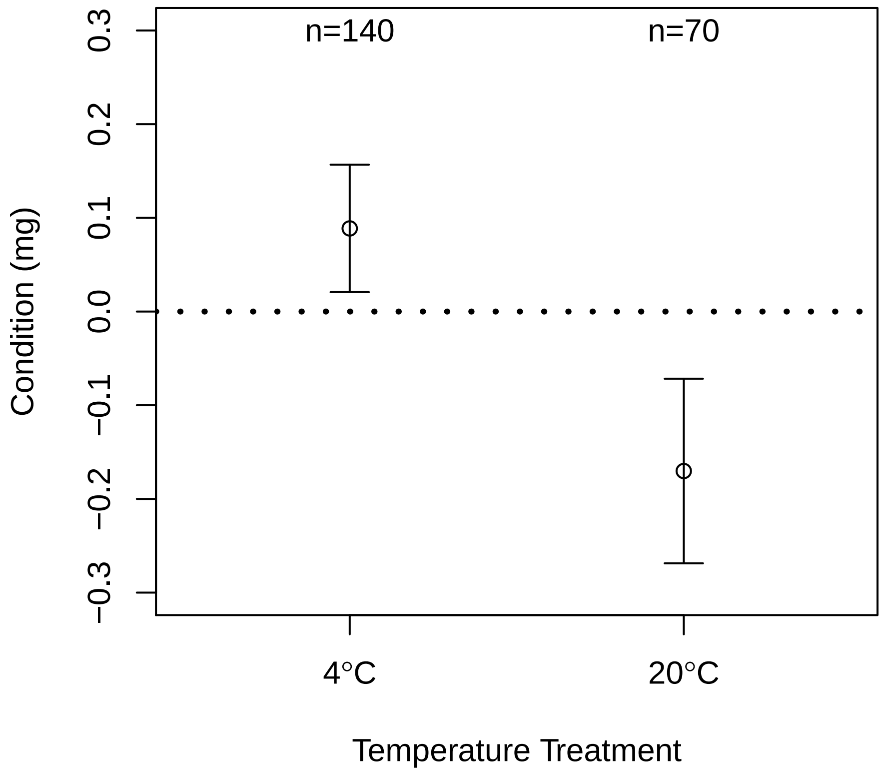

Figure 2.3: Effect of low and ambient temperature treatments on mean beetle energetic condition. Error bars indicate standard errors.

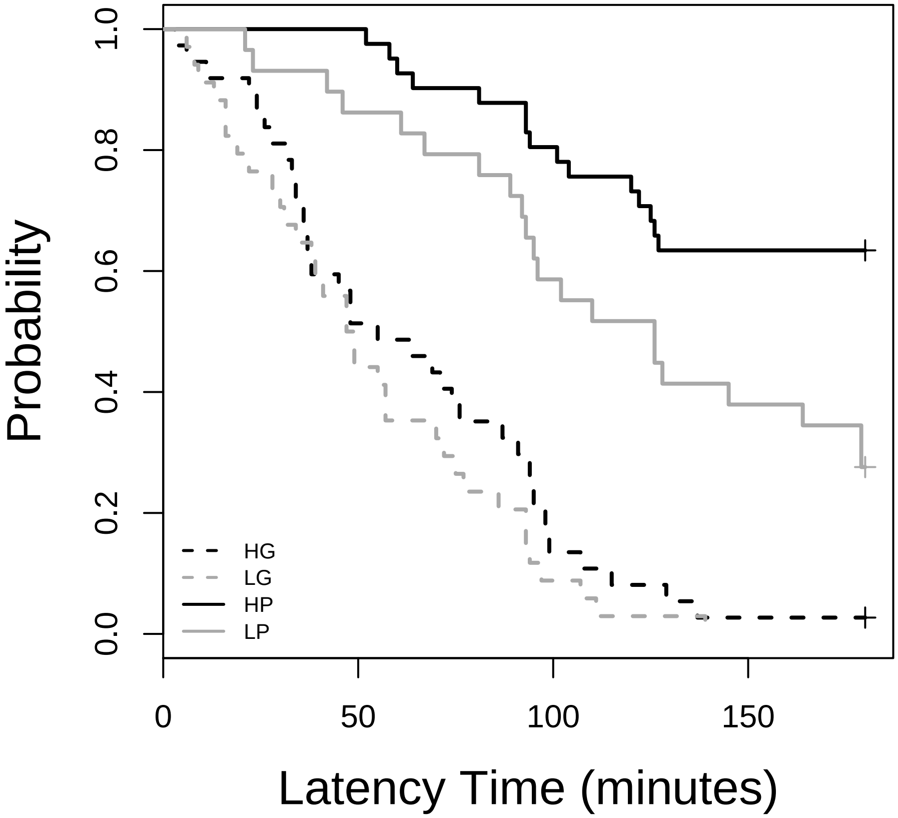

Figure 2.4: Kaplan-Meier survival plots showing latency time on poor and good nutritional quality hosts (time until acceptance) of beetles with high and low energy reserves. Steeper slopes indicate shorter delays accepting the host tree (i.e., beetles accept the tree more readily), whereas shallow slopes indicate longer delays before host acceptance.) HG denotes high energy beetles on good nutritional quality trees; HP denotes high energy beetles on poor nutritional quality trees; LG denotes low energy beetles on good nutritional quality trees; and LP denotes low energy beetles on poor nutritional quality trees.

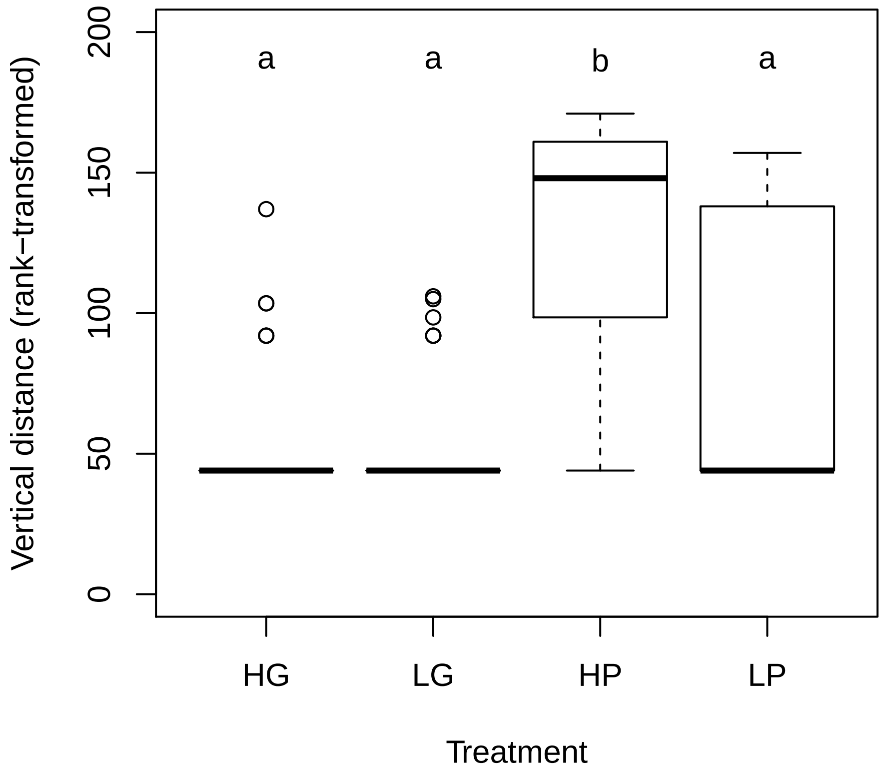

Figure 2.5: Box-and-whisker plot showing vertical distance traveled before accepting host for beetles with high or low energy reserves on host trees of good or poor nutritional quality. Bolded lines indicate the median; boxes denote the first and third interquartile range; whiskers indicate the data range within 1.5 times the interquartile range from the box; and open circles indicate data points outside the whisker range (i.e., outliers). Lowercase letters above each treatment's box highlight significant differences between treatments using an ANOVA with Tukey's Honest Significant Differences test. Symbols for treatments as in figure 2.4.

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2.10 Connecting statement

Having empirically determined characterized the individual variation in energy reserves and timing of emergence, and having shown that energy reserves do modulate beetles' host choice decisions, in the following two chapters I develop, from first-principles, a state-dependent model of habitat selection (host choice) by mountain pine beetle. Chapter 3 describes the development of the basic model for individual tree- and stand-level decisions based on a static background distribution of beetles in a lodgepole stand. I then extend this model in Chapter 4 to account for the decisions made by other beetles, and develop a dynamic-game model of habitat choice in multiple host species (lodgepole pine, jack pine, and their hybrid).

Although this experimental chapter was presented before the modelling chapters in my thesis, the modelling work in Chapter 3 was done prior to the experiments presented in this chapter (Chapter 2). These host-acceptance experiments served, in part, to test the basic predictions of the model in Chapter 3; and the CUBE profiles constructed here, characterizing the individual variation in energy reserves and timing of emergence, were used to parameterize the simulations in Chapter 4.

Chapter 3

A dynamic host selection model for mountain pine beetle, *Dendroctonus ponderosae* Hopkins

Previously published as Chubaty, A.M., B.D. Roitberg, C. Li (2009) A dynamic host selection model for mountain pine beetle, *Dendroctonus ponderosae* Hopkins. Ecological Modelling 220:1241-1250.

3.1 Abstract

The link between individual habitat selection decisions (i.e., mechanism) and the resulting population distributions of dispersing organisms (i.e., outcome) has been little-studied in behavioural ecology. Here we consider density-dependent habitat (i.e., host) selection for an energy- and time-limited forager: the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). We present a dynamic state variable model of individual beetle host selection behaviour, based on an individual's energy state. Field data are incorporated into model parameterization which allows us to determine the effects of host availability (with respect to host size, nutritional quality, and vigour) on individuals' decisions. Beetles choose larger trees with thicker phloem across a larger proportion of the state-space than smaller trees with thinner phloem, but accept lower nutritional quality trees more readily at low energy-

and time-states. In addition, beetles make habitat selection decisions based on host availability, conspecific attack densities, and beetle distributions within a forest stand. This model provides a framework for the development of a spatial game model to examine the implications of these results for attack dynamics of beetle populations.

Keywords: host selection, bark beetles, *Dendroctonus ponderosae*, energy reserves, dynamic state variable model, Allee effect.

3.2 Introduction

Modeling efforts describing population-level consequences of individuals' habitat use are typically individual-based simulation models (IBMs) (e.g., Fankhauser and Enggist, 2004; Charles et al., 2008). IBMs take a bottom-up approach to elucidate higher-level (i.e. population) patterns, whereas analytical state variable models take a top-down approach (e.g., Logan et al., 1998; Biesinger et al., 2000). While IBMs may provide added realism through the consideration of an individual's state (e.g., physiological), individual behaviour in these models is often represented as probabilities describing the likelihood of the behaviour occurring. On the other hand, analytical state variable models may be used to describe behavioural rules used by individuals, but these behavioural rules tend to describe behavioural averages and thus do not consider individual variation (Grimm, 1999), despite the importance of individual variation in many systems.

Dispersing organisms making habitat-selection decisions, evaluate habitat opportunities based on the availability of limited resources in these habitats, the level of competition for these resources, as well as the availability of alternative opportunities (Muller et al., 1997). Habitat selection theories, such as the ideal free distribution theory (Fretwell and Lucas, 1970), examine the distributions of organisms across habitats (i.e., the outcome of habitat selection behaviour) and are not generally designed to consider the mechanisms underlying these distributions (i.e., habitat selection behaviours themselves, but see Abrahams (1986)). Habitat selection can be considered a general optimal foraging problem: an organism making a decision between two (or more) habitats seeks to maximize the payoff (e.g., energy gains, fitness) relative to the costs of searching or travel (e.g., time, energy losses, missed opportunities). More realistic models of habitat selection necessarily become more complex and impose limitations (e.g., sequential search, time-constraints), which can affect the habitat selection decisions organisms make. Limiting an organism's search opportunities (e.g., short dispersal stage or high dispersal mortality) may result in higher individual fitness when accepting suboptimal habitats if the likelihood of finding optimal habitats is low. Similarly, imposing time constraints lowers acceptance thresholds for lower quality habitats (Ward, 1987; Stamps et al., 2005). Furthermore, environmental variability and interactions with other individuals require increased behavioural flexibility in making habitat selection decisions because what may be considered optimal under certain sets of conditions may be suboptimal under others (Komers, 1997; Elkin, 2004). Thus, organisms may exhibit flexible host selection behaviour in variable environments in response to these additional constraints.

Here we consider how constraints on individuals' habitat search influence behavioural decisions of habitat settlement by examining tactical habitat selection decisions of a time- and energy-limited forager. In such situations, and where mating is contingent upon successful habitat (i.e., host) selection, it is especially important to allow for and consider partial preferences, which may be flexible and change over time. We take into account that an organism's decision to reject a particular habitat at one point in time should not affect the possibility of accepting similar habitat in the future (Ward, 1987). Previous habitat selection models generally have not considered the impact of both time and energy states on individual decisions. These relationships are expected to play an important role in shaping the distributions of individuals in time and space, and thus, may have significant implications for species conservation and pest management.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae)(MPB), is an aggressive bark beetle species native to pine forests of North America, which primarily attacks lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) (Rudinsky, 1962; Wood, 1982; Safranyik and Carroll, 2006). Reproduction in bark beetles is contingent upon successful search for and attack of a suitable host tree, which, unlike most other phytophagous insects, results in tree death. Host search involves both visual and olfactory cues, including beetle-produced pheromones involved in coordinated 'mass attack' required to overcome host defences including toxic secondary compounds and resin secretions (Atkins, 1966a; Wood, 1982; Raffa and Berryman, 1983;

Berryman et al., 1985). The extent of these defences varies between individual trees, and they may only be overcome if a sufficiently high number of beetles attack an individual tree over a short period of time, thereby exhausting the defensive capabilities of the tree (Raffa and Berryman, 1983). At low attack densities, individual beetles face almost-certain death, especially against vigorous trees, and thus benefit from conspecifics joining the aggregation (i.e., an Allee effect, Allee, 1931). However, at very high beetle attack densities, larval competition for resources (phloem) increases substantially and can have significant deleterious effects on overall brood production (Reid, 1963; Raffa and Berryman, 1983; Safranyik and Carroll, 2006).

Individual beetles must therefore search for a host which will yield the greatest amount of resources for use toward reproduction relative to the individual risk and effort to overcome host defences. As alluded to above, beetles are choosy and discriminate among hosts based on size, nutritional quality, and defensive capability, as well as conspecific (attack) densities; and evaluate them based on gustatory cues (Raffa and Berryman, 1982). Beetles favour large diameter trees and those with thick phloem, as phloem thickness is positively correlated with brood production (Reid, 1963; Berryman, 1976; Safranyik and Carroll, 2006). However at low beetle population densities they will attack weakened or stressed trees (Rudinsky, 1962; Safranyik and Carroll, 2006).

The extent of this ‘choosiness’ is likely modulated by individual energy reserves (Atkins, 1966b). Bark beetles use lipids to power flight and beetles generally do not feed after emerging from their natal trees (Atkins, 1969; Wood, 1972; Elkin and Reid, 2005). Thus, they are limited in the duration and extent of their host-search period. Furthermore, beetles become more receptive to hosts after a minimum flight period (Shepherd, 1966; Safranyik and Carroll, 2006), suggesting that host acceptance is dependent on the energy state (i.e., lipid reserves) of the beetle. We take this energy state-dependent approach to explain what a bark beetle should do when it encounters a host tree.

Using a theoretical modelling approach, we examine beetles’ ‘choosiness’ as a complex interaction between the energy state of the individuals, and their environment (i.e., the trees available in a forest stand, as well as the number of other individuals). We develop a dynamic state variable (DSV) model, which is ideally suited for examining this behaviour at the individual level, and can be readily expanded upon to consider population-level processes and effects such as population and attack dynamics. Major impacts of MPB infestation include the effects on forest community dynamics, the economic impact on timber supplies, and the effects on climate change (Kurz et al., 2008). These impacts warrant explicit examination of how individual behaviour may shape population processes, thus, we construct a DSV model of individual MPB host selection, based on an individual's energy state, as a necessary first step toward the development of a strategic state-dependent model of host selection.

To assist with parameterization of the model presented here, we collected data to assess the availability and distributions of potential host trees in a forest stand representative of suitable MPB habitat.

3.3 Methods

3.3.1 Model description

Dynamic state variable (DSV) models

DSV models are optimization models that have been used for a variety of applications, including behavioural ecology, where they have been employed to solve such problems as patch- and host selection and oviposition decisions in parasitoids (Li et al., 1993; Wajnberg et al., 2006; Roitberg and Bernhard, 2007). Unlike other types of models, DSVs explicitly consider one or more dynamic states. In general, DSV models calculate the expected fitness payoff associated with each of a possible set of outcomes (i.e., decisions), and select optimal decisions that maximize fitness. (Note, 'decision' in this case does not mean a conscious decision on the part of the organism.) Specifically, these optimal decisions are solved numerically using the process of 'backward iteration': fitness values at the end of time are computed first, and then working backwards through time, the remainder of the values are computed (Bellman, 1957; Mangel and Clark, 1988; Clark and Mangel, 2000). Furthermore, our choice of an economic model subsumes underlying genetic variation in habitat selection behaviour without specifying exact mechanisms (Grafen, 1984).

MPB-DSV model

Female mountain pine beetles take flight in late summer in search of suitable hosts in which to lay their eggs. They rely on lipid stores to power their flight and are not known to feed once leaving their natal tree. In addition, beetles have a limited amount of time to find a suitable host, begin gallery excavation, and lay their eggs, since their larvae must develop past the second instar stage to overwinter (Safranyik and Carroll, 2006). Given these constraints, this model considers two state variables, energy (x) and time (t), where fitness (F) is accrued only if a host is found and accepted before terminal time (T), and a beetle's energy state is greater than zero. We define fitness at terminal time as $F(x, T) = \Phi(x)$, where $\Phi(x)$ is the terminal fitness function representing total future reproduction (Appendix Equation A.1), and where x_{min} is the minimum energy level below which successful reproduction is not possible, yielding the equation

$$\Phi(x) \begin{cases} = 0 & \text{if } x \leq x_{min} \\ \in (0,1] & \text{if } x_{min} < x \leq x_{max}. \end{cases} \tag{3.1}$$

The model maximizes fitness over two behavioural decisions: the first is whether to stay in or leave the current (i.e., natal) stand, and the second is whether to accept or reject a particular new host with a certain density of beetles if it is encountered. There is no opportunity to return to the natal stand once the decision to leave is made, and a beetle cannot leave a host once a decision to accept that host has been made (i.e., we do not consider females that produce second broods).

Beetles encounter host trees that vary in size (as measured by diameter at breast height), nutritional quality (as measured by phloem thickness), and density of other beetles attacking the tree (n). For simplicity, hosts are described as belonging to specific size, nutritional quality, and attack density classes, denoted using the subscripts i, j, and k, respectively. Thus, the probability of encountering a particular host of particular size and nutritional quality, with a particular attack density of beetles, in the current timestep is described by λ_{ijk} (A.2), and the the probability of not finding a host in the current timestep is $1 - \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk}$. The baseline probability of encountering a host of size class i and nutritional quality class j is obtained by taking the product of the areas under empirically-derived host-size and -nutritional quality distribution curves (see Model parameterization:

host availability). This baseline probability is then multiplied by an additional term, $l_{ij}(n_k)$ which follows a logistic-like curve, describing the probability of encountering a specific host given its beetle attack density class, k (Appendix Equation A.3). It is further modified by the function, $L_{ij}(k)$, which follows a negative binomial distribution and describes the background distribution of beetles on each host type (Apeendix Equation A.4). Thus, the probability of encountering a particular host is a function of baseline empirical probability of encounter and the effects of beetle pheromones as a result of beetle attack density.

While in flight, searching for a host, a beetle's energy reserves are depleted at some rate, σ, which is described as the per unit time cost of searching. In the case where no host is found in the current timestep, the new energy state is calculated as

$$x^o = x - \sigma. \tag{3.2}$$

If a beetle leaves the stand, its new energy state is determined by the time required to leave (t_L) and cost of searching, whereby

$$x_L = x - \sigma t_L. \tag{3.3}$$

In addition to the search cost associated with finding a host, there is a further energetic cost of evaluating the suitability of any particular host (γ) encountered. We assume only an energetic cost when evaluating a host; any individual beetle can find, evaluate, and reject a host in a single unit of time without any additional time cost. Bark beetles have been shown to further modulate their host-acceptance behaviour based on experience with previously encountered hosts (Wallin and Raffa, 2002). Although we assume beetles have a priori knowledge of their environment (i.e., overall availability and suitability of hosts), we have not specified a mechanism by which beetles have obtained this information, and thus, our model is compatible with beetles sampling or learning about their environment in order to obtain this information. Rejecting an encountered host gives the new energy state

$$x' = x - \sigma - \gamma. \tag{3.4}$$

The decision to accept the host still incurs a cost of searching out that host and evaluating it for suitability, but now the beetle has a chance to feed on the phloem of the tree. Beetles have been shown to offset some of the energetic costs of dispersal through host-feeding during gallery construction (Elkin and Reid, 2005). The rate of energy intake, $\varepsilon_{ij}(n)$, will depend on the size and nutritional quality of the host itself as well as the number of other individuals present on the host, such that higher nutritional quality hosts yield higher energy intake than lower nutritional quality hosts. Energy intake decreases slightly as beetle densities increase, due to slight competition effects. These effects on adult beetles are small, but play a larger role at high densities, and thus follow the accelerating, asymptotic portion of an inverse logistic curve (Appendix Equation A.5).

Host size and nutritional quality also determine the likelihood of beetles overcoming host defences. This is dependent on the attack density of other beetles on the tree, since a larger number of beetles attacking a single host can more quickly overcome these defences and kill the tree. Although larger, higher nutritional quality hosts can yield higher energetic returns to colonizing beetles, these trees also secrete larger amounts of resin and defensive secondary compounds, making them a riskier choice for colonizing beetles that attack these high nutritional quality hosts at lower attack densities (Shrimpton, 1973; Safranyik and Carroll, 2006). The probability of successfully overcoming host defences and ensuring tree death is based on attack density and follows a logistic curve (Appendix Equation A.6) $\delta_{ij}(n)$ (adapted from Berryman et al., 1985). If the tree's defences are not overcome, we assume the beetle is killed and produces no offspring.

We consider the simple case where beetles only encounter host trees (i.e., no non-host trees are present). We further assume any beetle accepting a particular host commits itself to that host, with no opportunity to leave, and its future fitness is determined at terminal time (T). Net energetic gain is calculated additively per timestep for the time remaining until terminal time ($\tau = T - t_{accept}$) so that

$$x''_{ijk} = \Big[x - \sigma - \gamma + \tau \varepsilon_{ij}(n_k)\Big]\, \delta_{ij}(n_k). \tag{3.5}$$

For a beetle accepting a particular host, attack density is also an important determinant of larval survival, and thus of expected future fitness. At high attack densities, larval competition for resources becomes high and may result in high brood failure (Raffa and Berryman, 1983; Berryman et al., 1985). To account for this, we introduce $\Theta_{ij}(n)$ which describes the proportion of surviving larvae with respect to attack density, and follows an inverse logistic curve (A.7) (adapted from Raffa and Berryman, 1983). For simplicity, we do not consider female beetles' adjustment of oviposition behaviour with respect to colonization density or female condition (see Raffa, 2001; Elkin and Reid, 2005).

The fitness values calculated at each value of x at each timestep t are discounted by the probability of dying during that time period. Extrinsic mortality risk of searching for a host is denoted by the constant μ_s; whereas the risk for a beetle inside a host is modeled as an exponentially decreasing density-dependent function and denoted by $\mu_h(n)$ (A.8).

The overall fitness value for any particular combination of energy state and time is thus the weighted sum of maximized fitness from staying in or leaving the stand, and, if staying, the maximized fitness from accepting or rejecting a given host with a given beetle density. The expected future fitness for leaving the stand is calculated first for the entire state space; the formula for which mirrors that for staying in the stand. Thus, the following dynamic programming equation is constructed:

$$F(x,t) = \max \left[\begin{array}{l} (1-\mu_s)^{t_L} F(x_L, t+t_L); \\ (1 - \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk})(1-\mu_s) F(x^o, t+1) + \\ \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk} \max \left[\begin{array}{l} (1-\mu_s) F(x', t+1); \\ (1-\mu_s)(1-\mu_h(n_k))^{\tau} F(x''_{ijk}, T) \Theta_{ij}(n_k) \end{array} \right] \end{array} \right] \tag{3.6}$$

This equation describes optimum fitness accrued by the decision, at each time and energy state, to either leave the current stand (top line), or stay within it (bottom two lines). Within the stand, a beetle faces two possibilities: it may either not encounter a host (middle line), or may encounter one and decide to either reject or accept it (last line). Decisions are made across a variety of host sizes and qualities, as well at different beetle attack densities.

3.3.2 Model parameterization: host availability

To obtain realistic estimates of host availability we collected field data from a site representative of suitable MPB habitat. All field work was carried out at the study site located

$\sim 30\ km$ south of Merritt, BC, Canada ($49°50'15.00''N$, $120°45'30.00''W$). The site is a uniform, mature ($\geq 80\ a$) lodgepole pine forest, in an area currently undergoing a widespread MPB infestation. We systematically sampled all live lodgepole pine trees over a $1.42\ ha$ area (excluding very young trees, e.g., saplings), measuring circumference at breast height ($1.3\ m$) to determine diameter at breast height (DBH), which we use as a measure of tree size. Phloem samples were taken from the north- and south-facing sides of each tree using a circular punch ($\sim 1\ cm^2$ area) and phloem thickness (defined here as the live tissue between the outer bark and the wood) was measured immediately (to prevent desiccation) using digital calipers ($d = 0.01\ mm$). We use phloem thickness as a proxy measure for tree nutritional quality since beetles feed upon phloem tissue. We use the term ‘quality’ here to refer specifically to the nutritional quality of the tree, and ‘suitability’ to describe the interaction between nutritional quality, tree chemistry, and defensive vigour.

We examined the relationship between tree size and phloem thickness. To determine the frequency distributions of tree size and phloem thickness, we generated histograms and fit them to known theoretical distributions, estimating parameters using maximum log-likelihood analysis. Host quality distributions were also generated based on trees’ size class (small, DBH $< 15\ cm$; medium, $15\ cm \leq$ DBH $< 25\ cm$; large, DBH $\geq 25\ cm$). Each of these size classes was then further broken up by phloem thickness (PT) class (thin, $PT < 1.5\ mm$; intermediate, $1.5\ mm \leq PT < 2.5\ mm$; thick, $PT \geq 2.5\ mm$), yielding a total of nine host types. The proportion of each size and phloem thickness class (i.e., the area under each part of the curve) was used to parameterize baseline host-encounter probabilities within a stand in the model. All analyses were performed using R Programming Language and Environment (v. 2.4.1).

To simulate stands of different qualities (i.e., change host availability within the stands), we shift host frequency distribution curves to the left or right, effectively increasing or decreasing the number of large and thick-phloemed trees, by increasing and decreasing the mode of the distributions (see Equation A.2). Additionally, we simulate differences in beetle distribution in each stand by adjusting the mean and variance of a negative binomial distribution (Appendix Equation A.4 and Appendix Table A.1). Although we do not consider non-host trees in the environment, we could easily consider them by further changing host-availability distributions used in the model.

We performed a sensitivity analysis to test the effects of varying model parameters (see Appendix).

3.4 Results

3.4.1 Host availability

Phloem thickness correlated positively with DBH ($n = 979$, $R^2 = 0.2247$, $p \ll 0.001$), and the distributions of both tree size (Figure 3.1) and phloem thickness for each size class (Figure 3.2) were best fit by gamma distributions.

3.4.2 Model results

Overall, we found the beetles' decisions to accept or reject particular hosts (i.e., preferences) changed as energy state and time decreased, and as beetle densities changed. Beetles were more likely to accept hosts when they are running out of time to find another suitable host, as well as when energy reserves were low. However, beetles with extremely low energy reserves accept only large-diameter, high quality trees at higher attack densities. In addition, beetles choose higher quality sites with favourable beetle distributions, and the total proportion of decision space corresponding to 'accept' for each host type (across all densities) within the stand increases with both size and quality of the host.

Inter-stand decisions

In general, our results between stands showed that beetles only leave the current (natal) stand when stand quality was much higher or the distribution of beetles outside of the natal stand are better. Changing the variance of the host-size and -quality distributions (with mean held constant) produced overall stand qualities inside and outside of the natal stand which were either lower or higher than the stand quality from the collected data. When stand quality inside the stand was better than that outside the stand, (i.e., more large, high quality trees inside the stand), beetles stay in the stand (Figure 3.3a). Conversely, when stand quality outside of the natal stand was higher than that inside, most of the state-dependent decision space was made up of decisions to leave the stand, except when beetles had low energy reserves (Figure 3.3b). Likewise, changing the background distributions of beetles in each stand generated similar results. Increasing the number of larger, higher-quality trees with higher beetle attack densities generated more favourable conditions for beetles. When the beetle distributions across hosts were better inside the stand, beetles stay in the stand (Figure 3.4a), whereas when the beetle distributions were more favourable outside the stand, beetles made decisions to leave except when energy reserves were low and approaching the 'no choice threshold' (Figure 3.4b).

As more time is available for host search (i.e., moving backward through time from T), the decisions made at each time unit begin to converge on a stationary solution (i.e., the optimal decision does not change as one moves back from t to $t-1$). When the natal stand is either of higher quality (Figure 3.3) or has a more favourable beetle distribution (Figure 3.4) all decisions are to stay within the stand. However, when stand quality or beetle distributions are better outside the natal stand beetles leave, except when energy is low. Though, as time is running out they stay more readily at higher energy states than they do with lots of time remaining.

Intra-stand decisions

Examining beetles' decisions within the natal stand, the model shows a larger proportion of accept decisions for larger trees and for trees of higher quality, and also shows different decision patterns for each host type at different densities. Large trees and trees with thick phloem are accepted at much higher beetle attack densities than smaller trees and those with thinner phloem (Figures 3.5 and 3.6). Empty trees and trees with very low beetle attack densities are rejected by beetles in favour of trees with intermediate to high beetle densities. Beetles only accept small trees with densities above 30-40 beetles/m^2, they accept medium size trees at attack densities greater than 50-60 beetles/m^2, and large trees at attack densities greater than 60-70 beetles/m^2. For each size class, beetles more readily accept trees with thicker phloem, and do so at lower densities. Although beetles accept all tree size and quality classes at high beetle densities, the maximum proportion of accept decisions for each host class occurs at higher beetles densities as tree size and tree quality increase (Table 3.1).

In general, with increased time available for host search beetles are more likely to reject hosts they encounter, with the exception of medium and large hosts and those with thicker phloem, with medium to high beetle densities (Figures 3.5 and 3.6). Just like for stay-leave decisions, as one moves further back in time from T, the decisions made by beetles begin to converge. We see a similar trend for more 'accept' decisions as beetles run out of either energy or time; however, we also see that for some host types (especially smaller trees and those with thinner phloem) as energy or time continue to decrease, beetles are more likely to make 'reject' decisions.

3.5 Discussion

General habitat selection theory predicts that organisms make habitat settlement decisions optimally, and will reject suboptimal habitats when fitness in these lower quality habitats is low or availability of higher quality habitats is high, and when lots of time is available for search (Ward, 1987). Qualitatively, our results are consistent with these predictions, as well as settlement decisions made by naturally-occuring beetles (Raffa and Berryman, 1983; Berryman et al., 1985; Safranyik and Carroll, 2006). We were able to generate reasonable approximations of observed host selection behaviour and resulting distributions of beetles – both at the stand-level, as well as at the tree-level. As expected, attack densities needed to overcome host defenses increase with host vigour (in this case, with tree size and nutritional quality), and we have calculated 'optimal' attack densities consistent with observed optimum densities. Previous studies have estimated this optimum density of beetles at $\sim$60 beetles/m^2, but these estimates vary widely with host vigour (see Raffa and Berryman, 1983; Berryman et al., 1985; Safranyik and Carroll, 2006). We also determined that the distribution of available host trees in a mature, uniform lodgepole pine stand best fit a gamma distribution (Figures 3.1 and 3.2), which allowed us to simulate a realistic beetle environment: one with very few large, high nutritional quality trees. Although we do not have data for younger or mixed stands, our model framework could be generalized to incorporate other host availability distributions.

The sensitivity analysis demonstrated the robustness of the qualitative predictions generated by the model. As expected, the model is quite sensitive to changes to mortality and time-cost parameters. For example, increasing host-search or -assessment costs (e.g., γ, μ_s, σ , t_L) resulted in beetles making fewer 'leave' decisions, and accepting trees sooner and at higher energy states. In addition, increasing mortality costs in host (m) led to fewer 'leave' decisions, more 'reject' decisions, and much fewer 'accept' decisions: beetles searched for hosts as long as possible, finally accepting hosts only at low energy reserves or toward the end of the time available for search. Also as predicted, as the relative difference in stand quality (i.e., availability of highly suitable hosts) increases, such that the natal stand is increasingly poorer than the other stand, the number of 'leave' decisions generally increases and the number of 'accept' decisions decreases. Overall, general trends were consistent across parameterizations, with the exception of biologically unrealistic parameter sets, which were still included to test the range of suitable values. Values used, including those used in the sensitivity analysis, are presented in the Appendix (Table A.1).

This model of host selection behaviour for mountain pine beetle generates tactical decisions for an individual beetle across a range of energy and time states, and against different backgrounds of host size and nutritional quality classes and beetle attack densities (Figures 3.3 and 3.4). This interplay between an individual's internal state and the environment generates a flexible host-acceptance strategy and represents a multifaceted decision-making process in MPB. Our model predicts that beetles will accept larger trees with thick phloem at high energy levels at the beginning of the search period, thus suggesting that beetles do not require an initial flight period in order to become receptive to hosts. However, the model shows that beetles do accept hosts more readily later in the flight period. This is consistent with the idea of a 'discrimination period' (Ward, 1987), during which poorer nutritional quality hosts are rejected, but after which both high and low nutritional quality hosts may be accepted. Furthermore, our results show beetles exhibiting partial preferences for lower nutritional quality hosts, where beetles accept lower nutritional quality hosts more readily at lower time and energy states (see Ward, 1987). It is interesting to note how beetles' preferences changed for smaller hosts and those with thinner phloem, and those at higher beetle attack densities (i.e., those that are poorer nutritional resources and where larval competition would be especially high). As time and energy run out, beetles generally accept more readily up to some point; after which they reject the host. This may point toward the benefits of joining an aggregation earlier, toward the middle of the attack sequence (Pureswaran et al., 2006).

Beetles' density-dependent host selection decisions reflect conspecific attraction, which is especially high at low population densities, as the product of an Allee effect. Our model thus suggests the resulting Allee curves for this system would dynamically reflect tree size, nutritional quality, and vigour, and individual beetle lipid reserves, as well as conspecific density. This effect on beetles' decisions is expected to have serious implications for population dynamics (Courchamp et al., 1999; Stephens and Sutherland, 1999; Wallin and Raffa, 2004). For example, such effects could generate multiple equilibria (Berryman, 2003).

Having constructed this MPB-DSV and generated tactical individual behavioural decisions to describe bark beetles' interactions with their environment, we can further expand upon this theoretical framework and evaluate population-level phenomena, such as within-stand and outbreak dynamics, including aggregation behaviour. Our model provides the first step in this bottom-up approach to examine which hosts beetles will actually end up on (i.e., to determine attack patterns). Further development of our model must be spatially explicit, such that individual beetles, as well as individual trees, are tracked, and an individual beetle's expectation of future attack densities on a host is considered. Only by using this approach can we fully explain our results. This point is illustrated by the fact that the attack densities corresponding to the maximum proportion of accept-decisions for each host type are quite high, especially for small trees. In theory, larval competition at these high densities should cause more individuals to reject hosts, especially small trees and those with thin phloem. However, these trees (with high densities) might be so rare that beetles would accept them at some combinations of energy and time if encountered, but since these hosts would not be encountered frequently we would not actually see beetles aggregating on these trees in the simulation. Additionally, trees with no or very low beetle attack densities are never accepted by beetles – which on first glance seems counter-intuitive, in that it would appear that these 'empty' trees would never be attacked, yet we know that this is not the case. In this case, because we set up the environment in such a way that trees of all attack densities were present in some proportion, the decision to never accept 'empty' trees simply reflects a preference to attack trees already under attack: a result consistent with observed attack patterns (Raffa and Berryman, 1983; Berryman et al., 1985; Safranyik and Carroll, 2006). Furthermore, in this model, beetles' decision to reject 'empty' trees is based on the current density of beetles rather than on the expected density. Consider an early-emerging female seeking out a host: we expect her to make the decision to accept an empty tree if she can expect attracting enough beetles to overwhelm host defenses.

We see beetles distributing themselves optimally with respect to resources as well as conspecific densities; however, the assumption made in ideal free distribution theory that individuals are ‘free’ to settle in any habitat (i.e., host) is not met in our model because energy and time constraints directly relate individual fitness to individual preference, thus imposing limits on individual movement between habitats and resulting in competitively unequal individuals (Fretwell and Lucas, 1970; Rausher, 1984; Abrahams, 1986; Ward, 1987; Hugie and Grand, 1998). Our model thus provides a link between individual behavioural decisions as the mechanism to generate an outcome of how individuals distribute themselves across habitats. This bottom-up approach, while considering energy- and time-constraints on individual habitat selection, further provides the necessary framework for considering these decisions within a game context and generates beetle distributions consistent with general habitat selection theory.

Our model is one of the few habitat settlement models that incorporates state-dependent decisions, thereby bridging the gap between traditional IBMs and analytical state variable models by solving for the optimal habitat use policy. Traditional habitat (or patch) use models, based on the classic Marginal Value Theorem (Charnov, 1976), tend to be intake rate-maximizing models and ignore individual state. On the other hand, state-dependent habitat selection models, which typically focus on insect parasitoid systems, are generally concerned with patch time allocation and physiology state (e.g., energy) on short time scales (i.e. patch residency) (reviewed in Wajnberg, 2006). However, our model is concerned with long-term settlement decisions. An extensive literature search yielded very few studies of energy-state-dependent habitat selection per se. Nonetheless, energy state and individual variation have been shown to be important components of determining population distributions (Alonzo, 2002). Additionally, state-dependent foraging models also highlight the role of energy in more accurately predicting individual distributions across habitats (e.g., Nonacs, 2001). Thus, we underscore the importance of considering an organism’s habitat settlement decisions and the consequent population distributions using a state-dependent approach.

3.6 Acknowledgements

Our sincere thanks for all the assistance we've received with this work: Elizabeth Nyboer for her assistance with field work; Allan Carroll and Doug Linton for access to field sites and their helpful suggestions; Brian Ma, Conan Phelan, and Larry Dill for their feedback on an earlier version of this model and manuscript, and their assistance with the initial computer-implementation; Harinder Hans for his expertise and assistance with final computer-implementation; Maxence Salomon for his feedback on an earlier version of this manuscript; and Bill Nelson and Alex Potapov for their feedback and suggestions. This work was supported through funds from Simon Fraser University, Natural Resources Canada, and the National Science and Engineering Research Council of Canada. All research complies with current local laws.

3.7 Tables

Table 3.1: Beetle attack densities corresponding to the maximum proportion of accept decisions for each host type.

Phloem thickness	**Tree size**		
	Small	**Medium**	**Large**
Thin	$\sim$90 beetles/m^2	90–110 beetles/m^2	90–110 beetles/m^2
Medium	80–90 beetles/m^2	90–100 beetles/m^2	80–120 beetles/m^2
Thick	$\sim$100 beetles/m^2	80–120 beetles/m^2	70–130 beetles/m^2

3.8 Figures

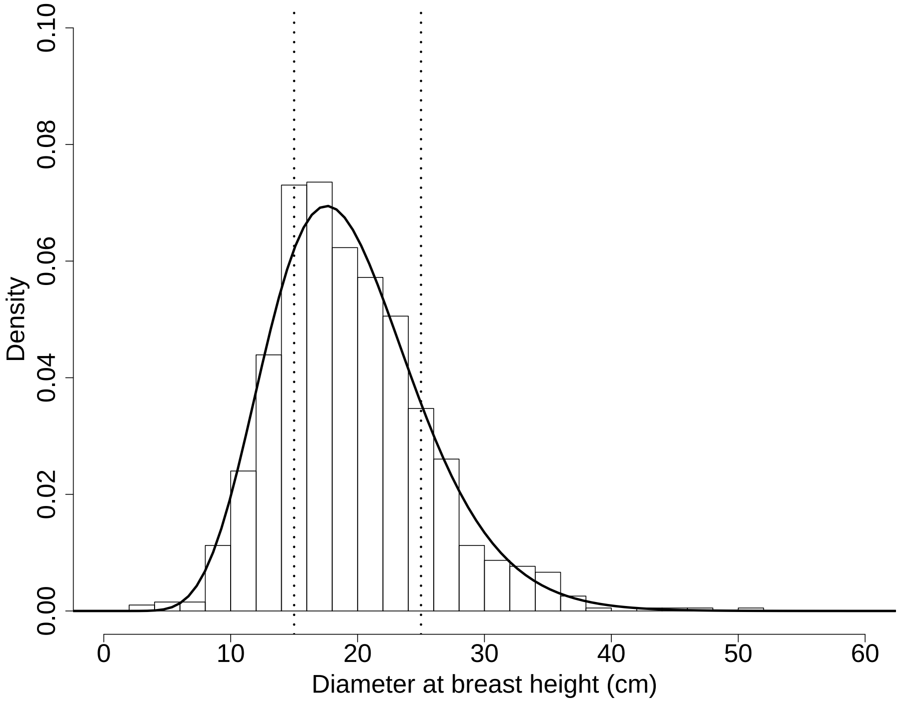

Figure 3.1: Size distribution of lodgepole pine trees ($n = 979$) at study site. This distribution follows a gamma distribution, $g(s; \alpha, \beta)$, with $\alpha = 10.5231$, $\beta = 0.5421$.

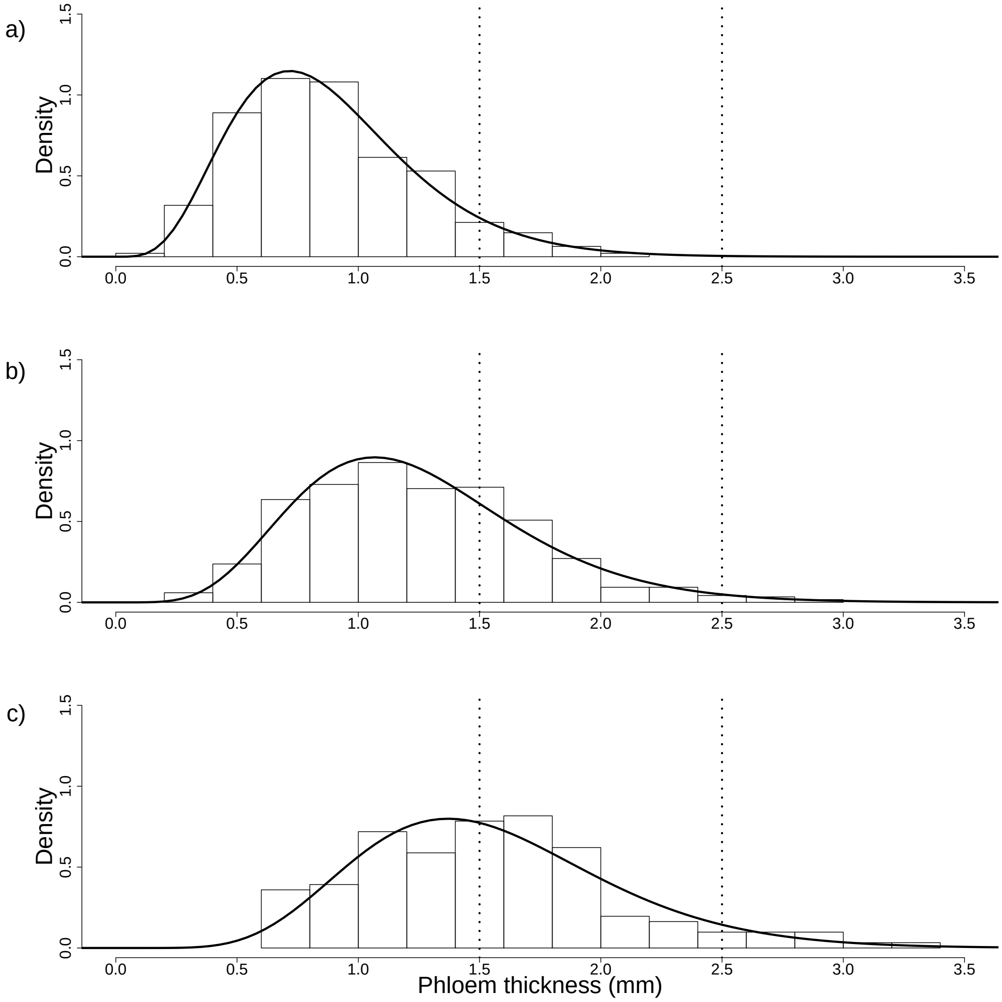

Figure 3.2: Phloem thickness distribution of (a) small ($n = 236$), (b) medium ($n = 590$), and (c) large ($n = 153$) lodgepole pine trees at study site. Each distribution follows gamma distribution, $g(q; \alpha, \beta)$, with parameters $\alpha_{small} = 5.4223$, $\beta_{small} = 6.1688$; $\alpha_{medium} = 6.9190$, $\beta_{medium} = 5.5450$; $\alpha_{large} = 8.7073$, $\beta_{large} = 5.6209$.

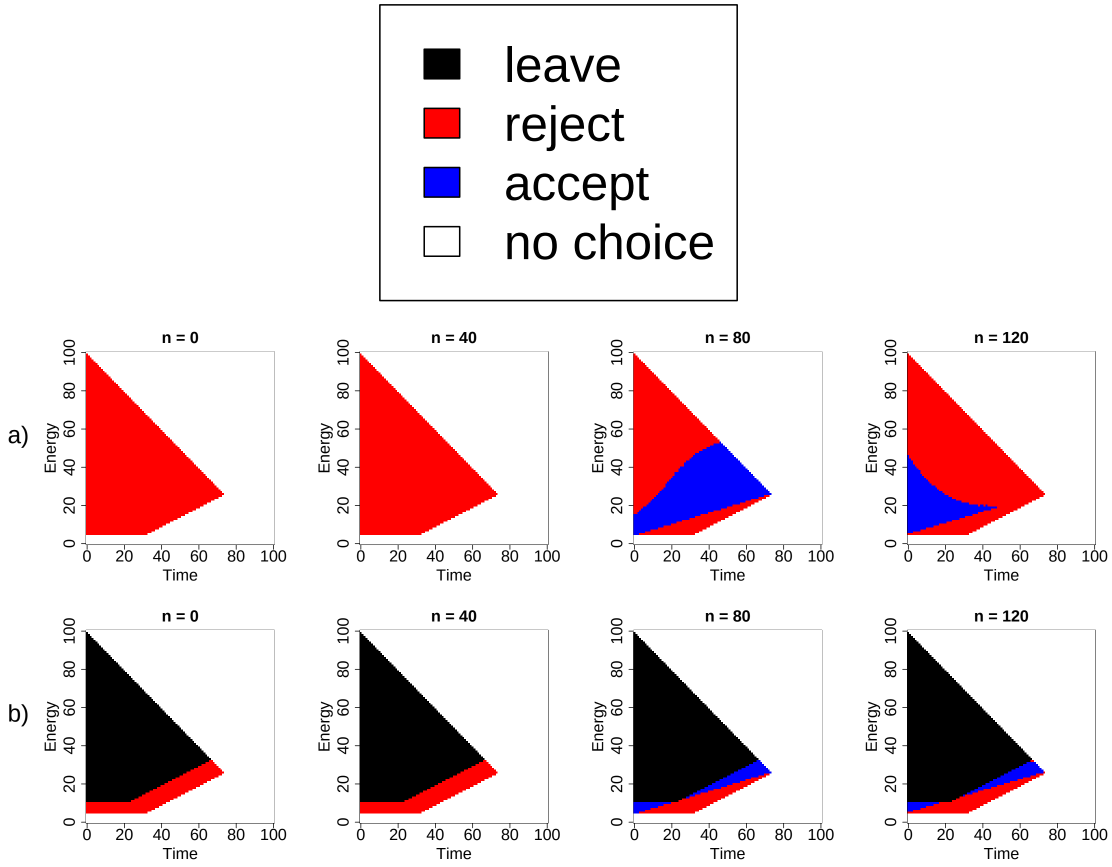

Figure 3.3: Stay-Leave and Accept-Reject decisions for a medium size, medium nutritional quality tree at different beetle attack densities (n). (a) Decisions when the stand quality inside the natal stand is higher than that outside the stand. (b) Decisions when the stand quality outside the natal stand is higher than inside. For clarity of explanation, we present the complex, multi-dimensional decision space as a series of two-dimensional plots. Each panel shows decisions across energy and time states, and each panel corresponds to a particular host size/quality and beetle attack density ranging from $0 - 120$ beetles/m^2. Coloured regions show optimal decisions: black corresponds to leaving the natal stand; red to staying within the stand but rejecting that particular host; and blue to staying within the stand and accepting the host. Uncoloured (i.e., white) regions of the decision space correspond either to 1) state combinations for which the expected fitness gain is 0, regardless of the decision made, or 2) impossible state combinations (e.g., the regions corresponding to high energy and low time: since beetles do not feed while searching for a host). In other words, they represent a regions of non-choice or those which are unreachable. We therefore do not consider decisions in these regions.

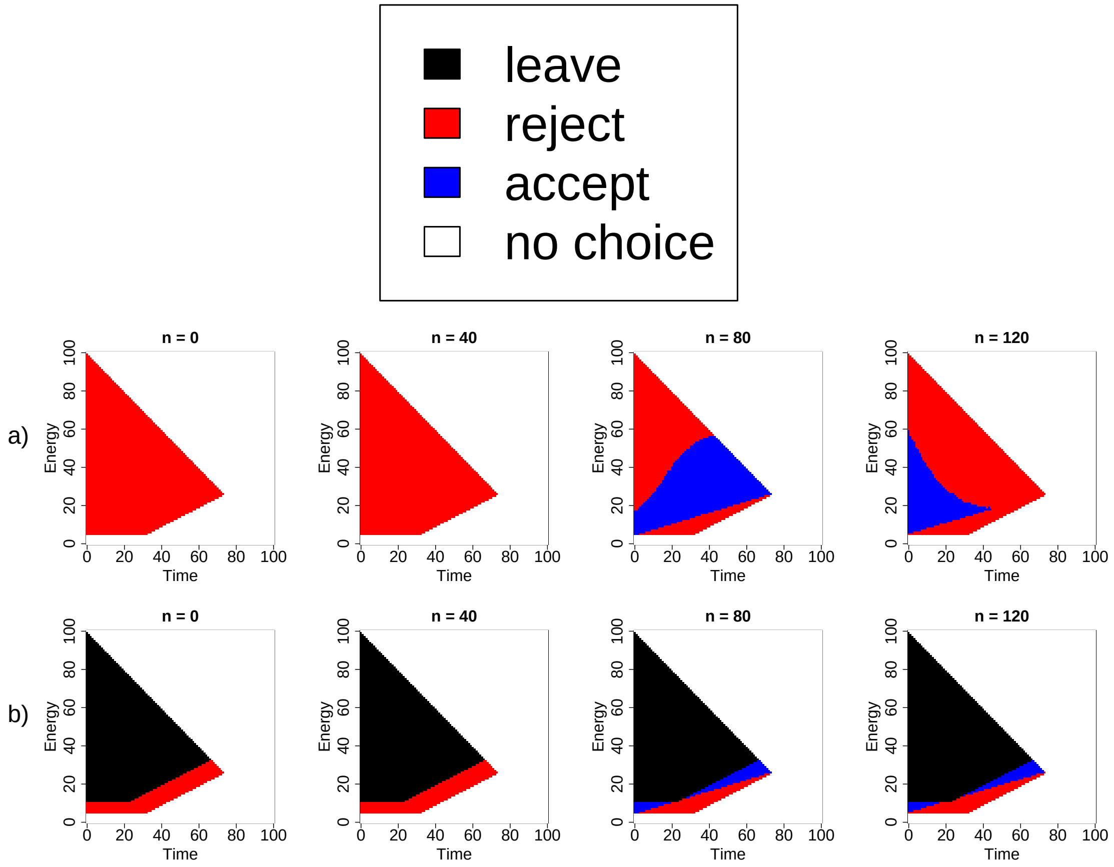

Figure 3.4: Stay-Leave and Accept-Reject decisions for a medium size, medium nutritional quality tree at different beetle attack densities (n). (a) Decisions when the background beetle distributions on host trees inside the natal stand is more favourable (i.e., higher beetle attack densities on larger, higher nutritional quality trees) than that outside the stand. (b) Decisions when the beetle distribution outside the natal stand is more favourable than inside. (See fig. 3.3 for figure explanation.)

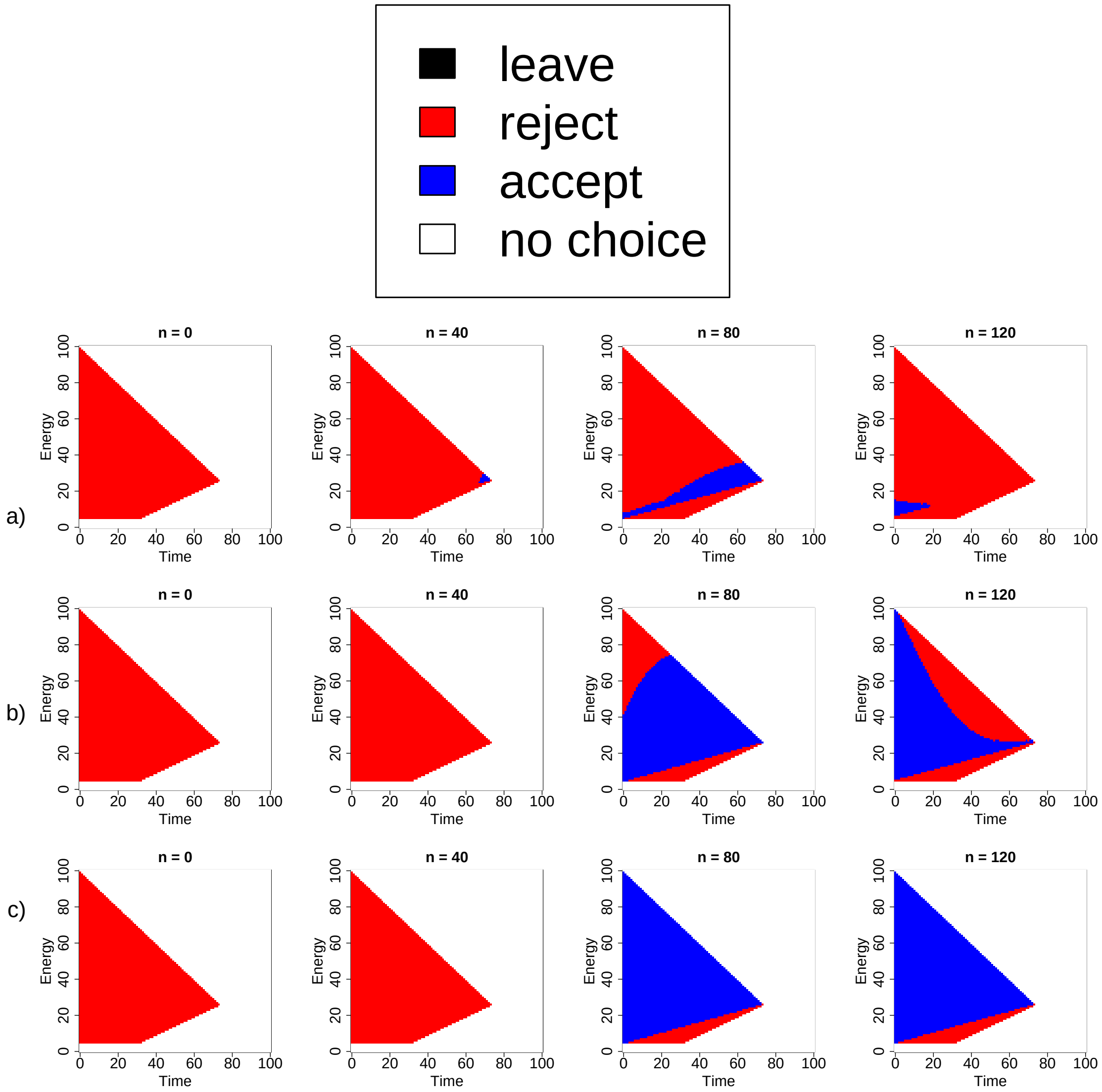

Figure 3.5: Within-stand Accept-Reject decisions for medium nutritional quality trees of (a) small, (b) medium, and (c) large size at different beetle attack densities (n). (See fig. 3.3 for figure explanation.)

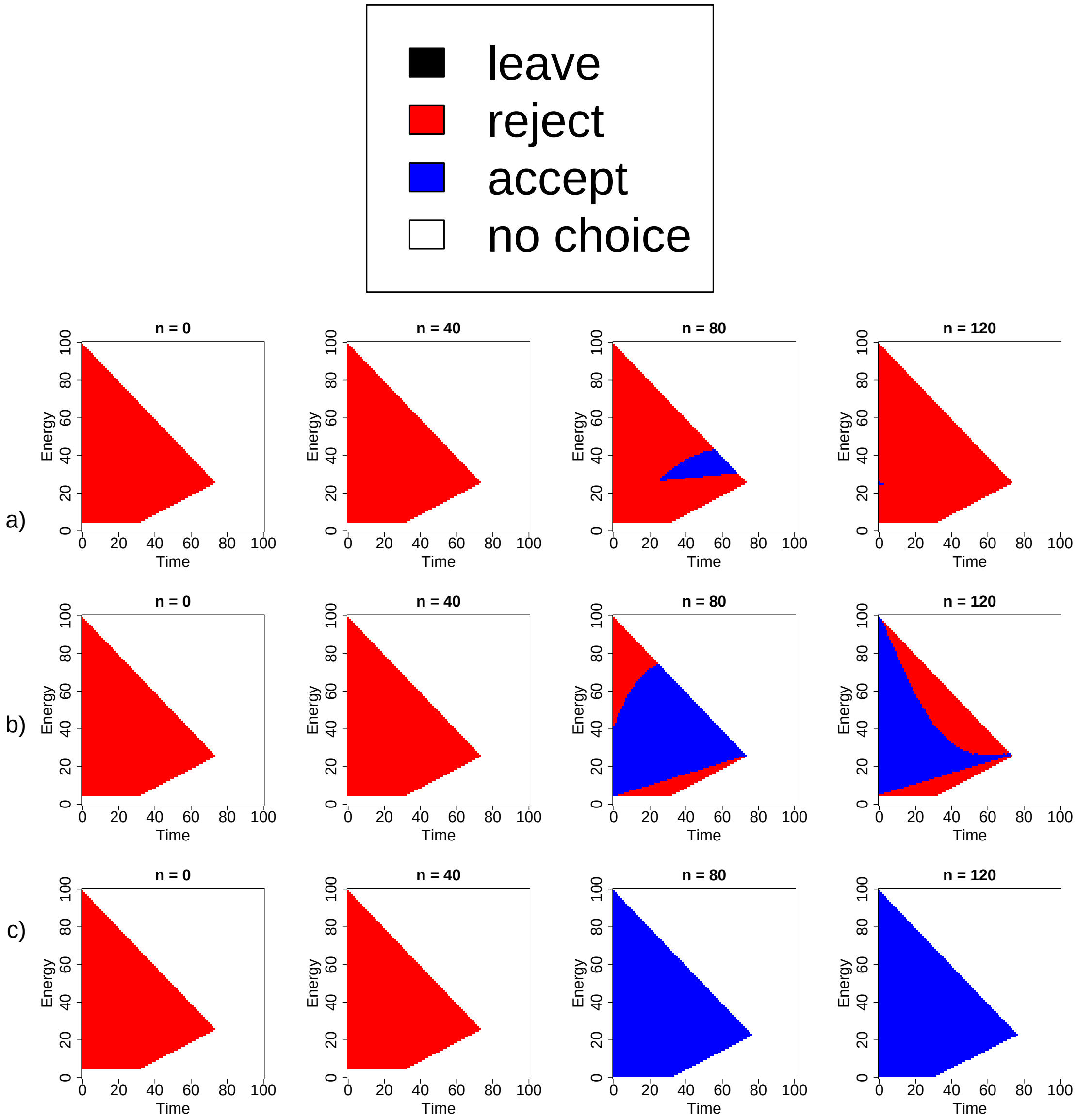

Figure 3.6: Within-stand Accept-Reject decisions for medium size trees of (a) low, (b) medium, and (c) high nutritional quality at different beetle attack densities. (See fig. 3.3 for figure explanation.)

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3.10 Connecting statement

In the subsequent chapter, I extend the state-dependent habitat selection model for mountain pine beetle to account for the decisions made by other beetles in the environment, thus developing a dynamic habitat selection game model. Using this dynamic game model, I simulate beetle populations attacking forest stands composed of multiple host tree species, to evaluate the performance of mountain pine beetle host selection strategies on non-lodgepole pine hosts. I subsequently use this model to assess the potential for the current beetle outbreak to establish itself in the boreal forests of Canada, which are dominated primarily by jack pine.

Chapter 4

A dynamic game model of differential host selection strategies for a bark beetle on multiple host species

4.1 Abstract

Canada's recent mountain pine beetle (MPB) outbreak has devastated lodgepole pine forests in British Columbia and continues to spread northward as well as eastward through Alberta, which has raised concerns that this outbreak could establish itself and continue to spread through the jack pine dominated Boreal forests of eastern Canada. Attacking beetles employ complex and flexible host selection strategies, and although they are capable of exploiting a range of pine species, it is unclear whether MPB, which have co-evolved with lodgepole pine, can sustain outbreaks in less suitable yet naïve host species. Here we extend a previously developed model of state- and condition-dependent host choice in MPB by incorporating the decisions made by other beetles in the environment, thus developing a dynamic habitat selection game for MPB. Using Monte Carlo simulations, we evaluate the evolutionary stable [host selection] strategy (ESS) at the tree- and stand-levels for multiple host pine species (lodgepole pine, jack pine, and their hybrids). These simulated stands were parameterized using field data and the greatest differences among host availability and host nutritional quality distributions and corresponding beetle dispersal and host selection decisions occurred between lodgepole pine and jack pine. Beetles reached slightly lower attack densities on lodgepole pine (which were larger and better defended on average) than jack pine, and typically beetles attacked more small and medium sized jack pine trees with thinner phloem than lodgepole pine. On average, beetles performed best in jack pine stands. These results suggest that jack pine stands face increased susceptibility to beetle attack as a direct result of their preference for smaller and medium-diameter trees, which are more common in these stands than in mature lodgepole pine stands.

Keywords: host selection, *Dendroctonus ponderosae*, energy reserves, dynamic state variable model, dynamic game, population dynamics.

4.2 Introduction

Animal dispersal and habitat selection decisions are typically made at the individual level based upon an individual's perceptions of resource availability, competition for these resources, and the suitability of alternative habitats (Muller et al., 1997), and thus individual-based modelling approaches are frequently employed when evaluating the population-level consequences of individuals' habitat selection decisions (e.g., Fankhauser and Enggist, 2004; Charles et al., 2008). Individual-based models (IBMs) take a bottom-up approach to modelling animal populations, which makes them well-suited for considering an individual's physiological state a well as the variation among individuals, when evaluating the impacts of individual behaviours at the population level. By contrast, analytical state variable models, including many classic habitat selection models based on ideal free distribution theory (Fretwell and Lucas, 1970), typically take a top-down, phenomenological approach whereby specific mechanisms underlying individuals' behaviours are not developed, and only 'average' behaviours are considered (e.g., Logan et al., 1998; Biesinger et al., 2000). Such analytical models are not well equipped to consider individual variation (Grimm, 1999), and the use of IBMs has become increasingly widespread, in part to account for variation among individuals.

Individual-based habitat selection models, in general, consider an organism making a decision to utilize one (of many) particular habitats, based on maximising the fitness payoff associated with a particular habitat choice relative to search and travel costs. Costs of an individual's search, such as increased dispersal mortality or time limits to search, increase the likelihood that an individual will select lower-quality habitat sites (Ward, 1987; Stamps et al., 2005). Flexible habitat selection strategies become increasingly important when environments are increasingly variable or when performance outcomes from decisions depend on interactions with other organisms, especially conspecifics (Komers, 1997; Elkin, 2004). The effects of search, travel, and settlement costs on individual habitat selection strategies may have important implications at the population level, in particular for wildlife conservation or management of invasive or pest species.

The current outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae)(MPB), has destroyed hundreds of millions of trees across western Canada and the United States and continues to spread both northward and eastward into Alberta and Saskatchewan. This outbreak has been driven through a combination of global climate change resulting in more favourable conditions for the beetle, and forest management practices such as fire suppression resulting in increased availability of susceptible forest stands (Safranyik et al., 2010). Although MPB primarily attacks lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) it is capable of attacking a variety of other pine species, including jack pine (*Pinus banksiana* Lambert) and others (Rudinsky, 1962; Wood, 1982; Safranyik and Carroll, 2006; Safranyik et al., 2010). There is concern that the beetle could sustain its outbreak out of the lodgepole pine dominated western forests and into the jack pine dominated eastern boreal forests (Nealis and Peter, 2008; Safranyik et al., 2010). In making the transition to jack pine, MPB may be assisted by trees in the intermediate zone where hybrid lodgepole-jack pines are common (see Figure 4.1; Safranyik et al., 2010). Although this bark beetle can utilize both jack and hybrid pines, it is unclear how their host selection strategies (which evolved with lodgepole pine) would fare against a non-preferred host, and whether the outbreak could sustain itself and continue to spread eastward.

Search for and colonization of host trees involves a combination of visual, olfactory, and gustatory cues and is largely driven by beetle-produced aggregation pheromones that are used to coordinate a 'mass attack' in response to the host tree's secreted defensive resins and toxic secondary compounds (Atkins, 1966a; Wood, 1982; Raffa and Berryman, 1982, 1983; Berryman et al., 1985). There is substantial variation in both host tree suitability and in defensive capabilities among trees, and beetles must carefully regulate the intensity of mass attack so as to ensure the conspecific attack density is high enough to overcome the tree's defensive capabilities yet not so high as to result in high larval competition for the phloem resource, which may result in total brood failure (Reid, 1963; Raffa and Berryman, 1983; Safranyik and Carroll, 2006). Thus, mating and reproduction in MPB are dependent upon successful habitat (i.e., host) selection, and understanding individual-level decisions can provide critical insight into the outbreak dynamics and other population-level outcomes of host selection and dispersal in MPB.

Previous work by Chubaty et al. (2009) considered the effects of energy- and time-constraints on individual habitat settlement decisions in this bark beetle–conifer system. Under these constraints, evolved habitat preferences are flexible over time, such that hosts which were rejected at one point in time may be accepted at another, and vice versa (Ward, 1987; Chubaty et al., 2009). Additionally, in this system, an individual's host preferences are also contingent upon the density of conspecifics at a host tree, thus beetles' host selection decisions are both state- and density-dependent. Beetles were more likely to accept trees at low energy states and as the time available for host search decreased, and beetles were more likely to accept trees with higher beetle attack densities (Chubaty et al., 2009).

Optimal host selection in MPB typically comprises search for and selection of host trees based on large size, thick phloem, diminished defensive capabilities, and suitably high beetle population and attack densities (Reid, 1963; Berryman, 1976; Rudinsky, 1962; Safranyik and Carroll, 2006). Beetles' host preferences are further modulated by internal (somatic) energy reserves, in particular by their lipid reserves (Atkins, 1966b, 1969; Wood, 1972; Elkin and Reid, 2005). Beetles do not feed during host search, are limited in flight (and therefore host search) duration, and will more readily accept hosts after an initial flight period (Shepherd, 1966; Safranyik and Carroll, 2006). As shown in Chapter 2, beetles with low energy reserves accept poor nutritional quality trees sooner than high energy beetles (see also Latty and Reid, 2010).

Here we extend the state-dependent habitat selection model of Chubaty et al. (2009) by developing a dynamic state-dependent habitat selection game to evaluate the optimal host selection strategies for a bark beetle when it encounters host trees of different species. Bark beetle population and outbreak dynamics are driven primarily by bottom-up processes such as host availability, defenses, and beetle performance (Reeve, 1997; Marini et al., 2013), which warrants an IBM approach. Dynamic games are ideally suited to examining both behaviour at the individual level and the population-level outcomes, including attack distributions and population outbreak dynamics. Beetles' range expansion and spread into boreal regions necessitates greater understanding of endemic and outbreak dynamics within both lodgepole and jack pine stands. MPB outbreaks are of particular interest because of their substantial economic and ecological impacts, and their effects on climate change (Kurz et al., 2008).

4.3 Methods

4.3.1 Model description

Dynamic state variable models

Dynamic state variable (DSV) models are optimization models that explicitly consider one or more dynamic states. In general, DSV models calculate the utility associated with each of a possible set of outcomes (i.e., decisions), and select optimal decisions based on maximizing (or minimizing) this utility function. Specifically, these optimal decisions are solved numerically using the process of 'backward iteration': fitness values at the end of time are computed first, and then working backwards through time, the remainder of the values are computed (Bellman, 1957; Mangel and Clark, 1988; Clark and Mangel, 2000). In behavioural ecology, DSV models are typically used to model individual behavioural decisions that arise from organisms' maximizing their reproductive output (i.e., evolutionary fitness), and have been applied to a variety of biological problems, including patch selection, habitat settlement, and oviposition decisions (e.g., Li et al., 1993; Wajnberg et al., 2006; Roitberg and Bernhard, 2007; Chubaty et al., 2009). When employed in these behavioural contexts, DSV models sufficiently assume genetic variation underlying behaviour without necessarily considering exact mechanisms (Grafen, 1984).

The MPB-DSV model

Our model builds upon the DSV model of mountain pine beetle (MPB) host choice developed by Chubaty et al. (2009). The MPB-DSV model calculates the optimal host settlement decision for every combination of somatic energy and time states of the beetle, based on the availability and encounter rate of host trees and beetle conspecific attack densities, by maximizing the expected fitness associated with the decisions to (1) stay in the natal patch or leave it, and (2) to accept or reject a particular host tree with a certain number of beetles already present. We provide a summary of the model below, and provide more detailed descriptions in Appendix B.1.

At each timestep in this model, a female beetle may encounter a host tree of a particular size (measured by diameter at breast height, DBH), nutritional quality (measured by phloem thickness, PT), and conspecific beetle attack density (n) class. These host classes are denoted using the subscripts i, j, and k, respectively. The probabilities of encountering a particular host is described by λ_{ijk} (B.4), and the the probability of not finding a host in the current timestep is $1 - \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk}$. The probabilities of encountering a host of size class i and nutritional quality class j were obtained using empirically-derived host-size and -nutritional quality distribution curves (see model parameterization below). Further details are provided in B.1.1.

During the host search phase beetles rely on their previously accumulated lipid reserves to power flight, landing occasionally on host trees to assess their suitability as hosts. Thus, a beetle's energy state x is depleted at rate σ, and when no host is found in the current timestep t the new energy state is calculated as

$$x^o = x - \sigma. \tag{4.1}$$

A beetle may leave the current forest stand, and its new energy state is calculated based on the time it takes to leave (t_L) and cost of searching

$$x_L = x - \sigma t_L. \tag{4.2}$$

If a host is encountered in the current timestep, there is an additional energetic cost (γ) of sampling the host to gauge its suitability. If the host is rejected, the new energy state is calculated as

$$x' = x - \sigma - \gamma. \tag{4.3}$$

When a host is accepted the decision is assumed to be permanent, such that for the duration of the host search period ($\tau = T - t_{accept}$) the female works to overcome host defences, initiates gallery construction, feeds upon the phloem under the tree's bark, and begins oviposition. A host's size and nutritional quality class, as well as the attack density of beetles determine how easily beetle attack overwhelms its defences. Larger, higher nutritional quality trees are better defended than smaller, lower nutritional quality trees (Shrimpton, 1973; Safranyik and Carroll, 2006). The likelihood of successfully overcoming a tree's defences goes up dramatically with beetle attack density, following a logistic curve (Appendix Equation B.6) $\delta_{ij}(n)$ (adapted from Berryman et al., 1985). The rate of energy intake while feeding ($\varepsilon_{ij}(n)$) depends on the size and nutritional quality class of the host and the beetle attack density. Energy intake rates are higher for higher nutritional quality hosts than for lower nutritional quality hosts, and decrease modestly with increased beetle densities due to competition (Appendix Equation B.5). The new energy state for a beetle accepting a host tree she encounters is calculated as

$$x''_{ijk} = \Big[x - \sigma - \gamma + \tau \varepsilon_{ij}(n_k) \Big] \, \delta_{ij}(n_k). \tag{4.4}$$

Additionally, the model considers the effects of larval crowding and competition($\Theta_{ij}(E(n))$ in trees with high beetle attack densities, where total brood failure can result from overcrowded conditions (Raffa and Berryman, 1983; Berryman et al., 1985). This follows an inverse logistic curve (Appendix Equation B.7) (adapted from Raffa and Berryman, 1983).

Fitness values are calculated for each combination of energy state and time, and are discounted by the risk of mortality during that time period. Beetles experience different mortality risks (μ) during the host search (denoted s) and host attack (denoted h) stages. There is a constant rate of mortality associated with host search; whereas mortality risk during attack is modelled as an exponentially decreasing density-dependent function (Appendix Equation (B.8)). The calculated fitness value for every value of x at each timestep t is the weighted sum of the maximum fitness from either staying in or leaving the stand, and if staying, the maximum fitness from either accepting or rejecting a particular host.

$$F(x,t) = \max \left[\begin{array}{l} (1-\mu_s)^{t_L} F(x_L, t+t_L); \\ (1-\sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\lambda_{ijk})(1-\mu_s)F(x^o, t+1) + \\ \sum_{i=1}^{I}\sum_{j=1}^{J}\sum_{k=1}^{K}\lambda_{ijk} \max \left[\begin{array}{l} (1-\mu_s)F(x', t+1); \\ (1-\mu_s)(1-\mu_h(n_k))^{\tau} F(x''_{ijk}, T)\Theta_{ij}(n_k) \end{array} \right] \end{array} \right] \tag{4.5}$$

Although this DSV model is useful in examining a beetle's preference for various hosts undergoing various levels of attack, it assumes a static distribution of beetles in the environment. A more useful examination of beetles' tree preferences would treat within-tree conspecific density as a variable rather than a parameter associated with a particular tree type. In other words, rather than simply treating habitat settlement decisions as a simple "1-player game" against the background environment, we extend this approach to find the n-player dynamic ESS, by developing a dynamic game model of MPB habitat-selection. This dynamic evolutionarily stable strategy (ESS) offers a more complete analysis of habitat selection problem, and is likely to yield different predictions than the static solution (Mangel, 1990).

The MPB dynamic game model

In this model, rather than assuming a fixed distribution of beetles across a range of host types, we consider habitat choice as a 'game against the field', whereby an individual's host selection strategy depends on the strategy employed by the population as a whole. Using the optimal decision matrix calculated using the DSV model, we calculate the expected distribution of beetles in the population using a forward iteration approach (Mangel and Clark, 1988). We use Monte Carlo forward iteration to simulate individual beetles in a forest searching for hosts, while explicitly tracking beetles' energy and time states. Each beetle behaves according to the optimal decision matrix previously calculated, and may or may not encounter and subsequently accept a host tree. We cycle through our population of beetles and determine whether they stay or leave the patch, and, if they stay, in which trees they choose to settle. The optimal decision matrix is then recalculated based on this new distribution of beetles. This procedure of determining beetle distributions and recalculating the optimal decisions is repeated until the decisions are stable (i.e., there is $> 99\%$ congruence between the current and previous decision matrices). Thus, the resulting decision matrix represents a beetle's state-dependent evolutionary stable strategy (ESS) (Mangel and Clark, 1988).

The resulting equations used in our dynamic game model are based on equation 6 of Chubaty et al. (2009), modified to reflect the expected ESS number of conspecifics, $E(n_k)$ in density class k.

$$F(x,t,T) = \max \left[\begin{array}{l} (1-\mu_s)^{t_L} F(x_L, t+t_L); \\ (1 - \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk})(1-\mu_s) F(x^o, t+1) + \\ \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{k=1}^{K} \lambda_{ijk} \max \left[\begin{array}{l} (1-\mu_s) F(x', t+1); \\ (1-\mu_s)(1-\mu_h(E(n_k)))^{\tau} F(x''_{ijk}, T) \Theta_{ij}(E(n_k)) \end{array} \right] \end{array} \right] \tag{4.6}$$

This equation describes optimum fitness accrued by the decision, at each time and energy state, to either leave the current stand (top line), or stay within it (bottom two lines). Within the stand, a beetle faces two possibilities: it may either not encounter a host (middle line), or may encounter one and decide to either reject or accept it (last line). Decisions are made across a variety of host sizes and qualities, as well as different beetle attack densities.

4.3.2 Model parameterization

Chubaty et al. (2009) did not consider decisions corresponding to high energy and little time remaining (see Chubaty et al., 2009, Figures 3-6), because (1) beetles do not feed during host search and (2) beetles were assumed to be starting with high energy reserves at the beginning of the season. In this dynamic game, we relax this second assumption and allow beetles to emerge at any combination of energy and time states, based on condition upon beetle emergence (CUBE) profiles developed in Chapter 2. CUBE profiles, which describe the probability of emerging on a particular day with a particular somatic energy condition, were scaled to fit the dimensions of the maximum energy and time states

(E_{max} and T_{max}). Simulated beetles in the forward iterations were randomly assigned initial (emergence) energetic and time states based on a female CUBE profile.

ESS habitat settlement requires an expectation or estimate of habitat quality; in this case, host tree availability and suitability. Chubaty et al. (2009) measured diameter at breast height (DBH) and used phloem thickness (PT) as a proxy measure for tree nutritional quality in a uniform, mature lodgepole pine stand. Likewise, using forest transect data (Langor and Williams 2006, unpublished) for various lodgepole pine, jack pine, and lodgepole-jack hybrid forest stands across Alberta and Saskatchewan (Figure 4.2), we determined the frequency distributions of each tree species based on DBH and PT, fitting these distributions to a gamma distribution, estimating parameters using maximum log-likelihood analysis (see Table 4.1). Following Chubaty et al. (2009), host nutritional quality distributions were based on trees' size class (small, DBH $< 15\ cm$; medium, $15\ cm \leq$ DBH $< 25\ cm$; large, DBH $\geq 25\ cm$). Each of these size classes was then further broken up by phloem thickness (PT) class (thin, $PT < 1.5\ mm$; intermediate, $1.5\ mm \leq PT < 2.5\ mm$; thick, $PT \geq 2.5\ mm$), for a total of nine host types. We determined the area under each curve, which corresponded to the proportion of each size and phloem thickness class representing host-encounter probabilities within a stand in the model.

Preliminary assessments of MPB performance in jack pine have shown that jack pine is as good of a host as lodgepole pine, and that jack pine stands are as susceptible (or maybe more so) to beetle outbreak as lodgepole pine stands. Beetle reproductive output is similar in both tree species, and differences in stand susceptibility are due primarily to differences in stand densities and host availability (Nealis and Peter, 2008; Safranyik et al., 2010). Thus, in this study, we parameterized all trees species similarly with respect to defensive capabilities and energy gain functions. Although these are likely to differ between species in real life (especially defences since jack pine isn't a co-evolved host), the model is largely insensitive to changes in energy gain and defensive capabilities. However, we did explicitly consider differences in the distributions and availability of hosts for each tree species.

To simulate stands of different qualities (i.e., change host availability within the stands), we shift host frequency distribution curves to the left or right, effectively increasing or decreasing the number of large and thick-phloem trees, by increasing and decreasing the mode of the distributions (see Equation (B.4)). Additionally, we simulate differences in beetle distribution in each stand by adjusting the mean and variance of a negative binomial distribution (Appendix Equation B.2; Table B.21). Although we do not consider non-host trees in the environment, we could easily consider them by further changing host-availability distributions used in the model.

Simulations were run using 1000 trees, which is approximately the number of trees present in the $1\ ha$ stand sampled by Chubaty et al. (2009), and used 10000 beetles. Additional simulations were performed with up to 50000 beetles; however, at these higher population densities the simulated stands became saturated with beetles, which swamped out many of the host settlement differences among hosts. Baseline model parameters follow those in Chubaty et al. (2009) and we additionally performed sensitivity analyses to test the effects of varying model parameters (see Appendix B.2).

4.3.3 Effect of tree species on decisions

Range distributions of lodgepole and jack pine do not generally overlap, except for narrow regions in Alberta and the North West Territories (Figure 4.1) where hybrids are also found. Thus, throughout most of the range of MPB, mature stands are dominated by a single pine species, namely lodgepole pine, and most infestation of jack pine to date has been incidental in mixed stands. Range expansion of MPB into jack pine and lodgepole-jack hybrid stands is a recent phenomenon and it is not clear whether MPB can sustain outbreak (or even endemic) populations in stands dominated by jack pine. Therefore, we assume forest stands comprise a single tree species: either lodgepole, jack, or hybrid pine.

We ran the model fifty times for each stand type and calculated the ESS solution for each species. We compared the resulting expected distributions of beetles on each host type, as well as the proportion of beetles that died while attacking a host tree and the proportion that died while searching.

4.3.4 Effect of patch differences on leaving rates

To simulate stands of different qualities, the modes of each host distribution, $\nu = (\alpha - 1)/\beta$, were either increased or decreased by adjusting α while holding β constant. Baseline estimates for ν values were derived from field data (Chubaty et al., 2009), and denoted ν_0. We constructed host size distributions using ν_0, $\nu_0 - 5cm$, and $\nu_0 + 10cm$, and host phloem thickness distributions using ν_0, $\nu_0 - 0.5mm$, and $\nu_0 + 0.5mm$.

We took the mean proportion of beetles leaving the natal patch during the forward iteration using the ESS solution under each scenario to get a mean dispersal rate for beetles under different patch quality scenarios.

All analyses were performed using R Programming Language and Environment (R Development Core Team, 2011).

4.4 Results

The proportions of each decision in the dynamic game model (i.e., the ESS decisions) were dramatically different than the proportions in the non-ESS DSV model (Figures 4.3 and 4.4). A much smaller proportion of the ESS decision space consisted of leave decisions compared to the DSV, and more of the ESS decision space consisted of reject and accept decisions than the DSV decisions. The proportion of 'no choice' decisions (i.e., state combinations for which the expected fitness gain is 0, regardless of the decision made) remained the same. Unsurprisingly, when the current (natal) patch was of lower quality than the other patch, the proportion of leave decisions increased for both the DSV and ESS solutions, albeit much more in the DSV solution than the ESS (Figure 4.4). This increase in leave decisions corresponded to a decrease in the proportion of reject decisions in the DSV solution, but not in the ESS one, where the proportions of each decision changed little in response to changes in relative qualities of the natal and non-natal patches.

4.4.1 Effect of tree species on decisions

Across all simulations, there was higher beetle mortality in the lodgepole pine and hybrid stands than in the jack pine stands (see Figure 4.8). For each host species, the majority of beetles ended up at a host tree of some type. However, a smaller proportion of beetles accepted the trees in which they ended up, compared to those that had no choice but accepting a host tree, either due to low energy reserves or running out of time (or both).

In other words, most beetles ended up in the lower-right region of the decision space (see Figure 4.3).

In general, the greatest differences in host attack among host species occurred between jack pine and lodgepole pine, with the hybrid lying somewhere between the two. The changes in the overall proportion of ESS decisions were similar across host species, with only a slight increase in the proportion of accept decisions in jack pine, with a corresponding decrease in the proportion of jack pine reject decisions (Figure 4.5). Despite these seemingly small differences in the overall decision matrices, the results of the forward iterations suggest these differences in ESS strategies manifested in more substantial ways with respect to the resulting attack distributions on trees. These simulation results showed that beetles attack more of the medium and small sized jack pine trees with thinner phloem than lodgepole pine (Figure 4.7). Comparing resultant beetle attack densities showed similar mean proportions of trees attacked for each species, with lower attack densities more prevalent for lodgepole pine trees than for jack pine. There was substantial variation across simulations, although there was considerably more variation in attack densities for jack pine than for lodgepole pine (Figure 4.6).

Mean fitness values for beetles utilizing jack pine stands were highest in lodgepole pine and lowest in hybrid pine stands (Figure 4.9).

4.4.2 Effect of patch differences on leaving rates

As mentioned above, the proportion of leave decisions was very low in the ESS solution. Likewise, the mean proportion of beetles that left the natal stand in the forward iterations was also very low, and beetle mortality during interstand dispersal was low (Figure 4.8). The proportion of beetles leaving the stand varied only slightly for each different forest type (see Figure 4.4). When the focal (natal) stand was of higher quality than the outside patch, the mean proportion of beetles leaving $p_{leave} = 0.00895$ ($sd = 0.0011$), whereas when the two stands were equal or the outside patch was of better quality than the natal stand the proportions of beetles leaving were both higher ($p_{leave} = 0.01130$; $sd = 0.0000$ for both).

4.5 Discussion

The current expansion of mountain pine beetle (MPB) into host ranges that have not historically encountered beetle infestation, coupled with beetle's ability to utilize naïve host species, has raised concern that the ongoing outbreak could extend beyond the lodgepole pine forests of western Canada and sustain itself in the jack pine dominated boreal forests. Beetles exhibit flexible host selection preferences that are dependent not only on the attack densities of conspecifics but are also energy- and time-dependent. This behavioural flexibility allows them to exploit a range of host tree size and nutritional quality classes, although it is unknown whether these host selection strategies could be successfully extended to other host tree species. Using a dynamic state variable game model, we explored beetles' optimal dynamic ESS host selection strategies in three species of pine.

Flexible state-dependent host selection strategies allow beetles to readily exploit other pine hosts. Beetles' ESS host selection decisions varied with host tree species, yielding substantially different attack distributions across each species. Beetles attacked more of the medium and small sized jack pine trees with thinner phloem than lodgepole pine, and tended to reach slightly higher attack densities on jack pine than on lodgepole pine trees. Additionally, beetles in hybrid stands, on average, performed most poorly; beetles in jack pine performed better, on average, than those in both lodgepole and hybrid pine stands.

Although the parameterization of each host species assumed similar energetic costs and benefits to colonizing and ovipositing females, it is likely that there are differences in phloem quality or defensive capabilities among lodgepole, jack and hybrid pines. However, despite this possibility, we feel that our characterizations of different host trees are generally representative of the differences between the species. Due to the long co-evolutionary history of MPB with its primary host, lodgepole pine, it is likely that this tree species has evolved better constitutive and inducible defences against beetle attack. Our model partially accounts for this, albeit indirectly, based on the positive relationship between host size and nutritional quality class and defensive capabilities. On average, the host availability distributions used in this model (which were based upon empirically collected field data) have more large lodgepole pines and those with thicker phloem, than jack pines (and hybrids). These larger, higher nutritional quality trees are also better defended, thus on average in our model an individual jack pine tree is less well defended than the average lodgepole pine tree.

Among host tree species, beetles' dynamic ESS host acceptance decisions and their outcomes (attack distributions) varied the most as a result of differences in host availability and host nutritional quality distributions, rather than with changes to host defensive characteristics. Although there have been few empirical studies comparing lodgepole pine to jack pine stands, our results here are consistent with what is expected to drive MPB outbreak dynamics (Safranyik et al., 2010). This suggests that stand-level features such as species composition and tree density, as well as landscape features, such as forest contiguity or fragmentation are likely to play important roles in determining the extent to which beetles' eastward expansion will proceed, especially as new latitudinal and altitudinal regions become available due to warmer temperatures brought about by climate change.

Additionally, although reproductive output is similar among host species, beetles emerging from jack pine trees tend to be smaller than those emerging from lodgepole pine (Safranyik et al., 2010). Smaller beetles may, in turn, be limited to attacking smaller trees by their reduced energy reserves relative to larger beetles. This may thus enhance jack pine stand susceptibility through beetles' preference for smaller and medium-diameter trees, which are more common in those stands than in mature lodgepole pine stands.

Jack pine stands may be further susceptible to beetle infestation due to elevated levels of beetle-attractant chemicals produced by stressed trees. Clark (2008) showed that α-pinene concentrations are higher in jack pine than in lodgepole pine. Higher α-pinene levels can contribute to increased attack risk, as this chemical is a precursor for the production of beetle aggregation pheromone (Safranyik et al., 2010).

Habitat selection and dispersal are two sides of the same coin, and our models considered both tree settlement decisions within stands as well as dispersal between stands (i.e., patch leaving). Both of these underlie population-level patterns predicted by our model, as well as those observed in natural systems. Our model predicted the proportions of inter-stand dispersers to be quite low despite similar performance to non-dispersers. This outcome is generally expected when travel costs between habitats are high (e.g., Hamilton and May, 1977; Waser et al., 2013). MPB has been shown to undergo two main types of dispersal: most commonly, short-distance dispersal which occurs below the canopy within a forest stand; and occasionally a long distance dispersal aided by wind currents above the canopy (Safranyik et al., 1992, 2010). Although our model did not explicitly consider the latter, the possibility exists that the small subset of beetles seeking to leave their natal stands may contribute to the numbers of long distance dispersers.

Dynamic ESS habitat settlement strategies allow for increased behaviour flexibility, which is important in variable environments, especially when individuals are faced with constraints on habitat search and dispersal ability, or uncertainty when outcomes of these decisions depend on those made by conspecifics (Ward, 1987; Komers, 1997; Elkin, 2004; Stamps et al., 2005). By taking a bottom-up approach to modelling individual behavioural decisions constrained by energy- and time-limitations on host search and attack, in a frequency-dependent manner, we laid the necessary framework to determine the optimal attack densities in forest stands. We further compared the resultant population-level distributions of individuals across different habitat types and evaluated the performance of these dynamic habitat selection strategies across changing environments.

This modelling approach links analytical habitat selection models based on optimal foraging theory and individual-based state-dependent models in making long-term (i.e., 'permanent') habitat settlement decisions. Despite the paucity of energy-state-dependent habitat selection studies, energy state and individual variation have both been shown to contribute to population distribution outcomes (Alonzo, 2002). Furthermore, modelling studies of state-dependent foragers also emphasize the need to consider energy state to better predict distributions of individuals across habitats (e.g., Nonacs, 2001). Thus, our study emphasizes the utility of employing a state-dependent approach to evaluate the population outcomes of individuals' habitat settlement decisions.

4.6 Acknowledgements

We would like to extend our thanks to David Langor and Daryl Williams for providing stand data for Alberta and Saskatchewan. This work was supported through funds from Simon Fraser University, Natural Resources Canada, and the National Science and Engineering Research Council of Canada.

4.7 Tables

Table 4.1: Estimates and standard deviations of α and β values for gamma-fitted host distributions of lodgepole, jack, and hybrid lodgepole-jack pine stands, based on diameter at breast height (DBH) and corresponding phloem thickness (PT) measures for each DBH size class. Description of host size and phloem thickness classes follows Chubaty et al. (2009): small ($DBH < 15\ cm$), medium ($15\ cm \leq DBH < 25\ cm$), large ($DBH \geq 25\ cm$); thin ($PT < 1.5\ mm$), intermediate ($1.5\ mm \leq PT < 2.5\ mm$), thick ($PT \geq 2.5\ mm$).

Species	**Measure**	α	$\mathbf{sd}_\alpha$	β	$\mathbf{sd}_\beta$
lodgepole	DBH	10.51	1.33	0.40	0.05
jack	DBH	11.74	1.10	0.55	0.05
hybrid	DBH	11.80	1.15	0.48	0.05
lodgepole	PT_S	5.46	2.65	3.83	1.95
lodgepole	PT_M	6.58	1.31	3.34	0.69
lodgepole	PT_L	10.53	1.82	4.53	0.80
hybrid	PT_S	2.95	1.02	4.36	1.65
hybrid	PT_M	6.51	0.90	5.00	0.72
hybrid	PT_L	7.32	1.08	3.69	0.56
jack	PT_S	6.23	1.59	8.99	2.40
jack	PT_M	4.49	0.53	4.39	0.55
jack	PT_L	8.72	1.60	5.66	1.07

Table 4.2: Host availability probabilities based on the area under the curves derived from fitted gamma distributions, with shape α and rate β parameterized as per Table 4.1. Description of host size and phloem thickness classes follows Chubaty et al. (2009): small $(DBH < 15\ cm)$, medium $(15\ cm \leq DBH < 25\ cm)$, large $(DBH \geq 25\ cm)$; thin $(PT < 1.5\ mm)$, intermediate $(1.5\ mm \leq PT < 2.5\ mm)$, thick $(PT \geq 2.5\ mm)$.

Species	**Phloem thickness**	**Tree size**		
		Small	**Medium**	**Large**
lodgepole	all	0.0599	0.4172	0.5230
hybrid	all	0.0720	0.4924	0.4355
jack	all	0.1471	0.5931	0.2598

Species	**Phloem thickness**	**Tree size**		
		Small	**Medium**	**Large**
lodgepole pine	thin	0.6039	0.3396	0.0565
	intermediate	0.2952	0.4817	0.2231
	thick	0.1107	0.5212	0.3681
hybrid	thin	0.9605	0.0382	0.0012
	intermediate	0.6909	0.2857	0.0233
	thick	0.2756	0.5044	0.2200
jack pine	thin	0.9902	0.0098	0.0000
	intermediate	0.8458	0.1453	0.0090
	thick	0.5135	0.4382	0.0483

4.8 Figures

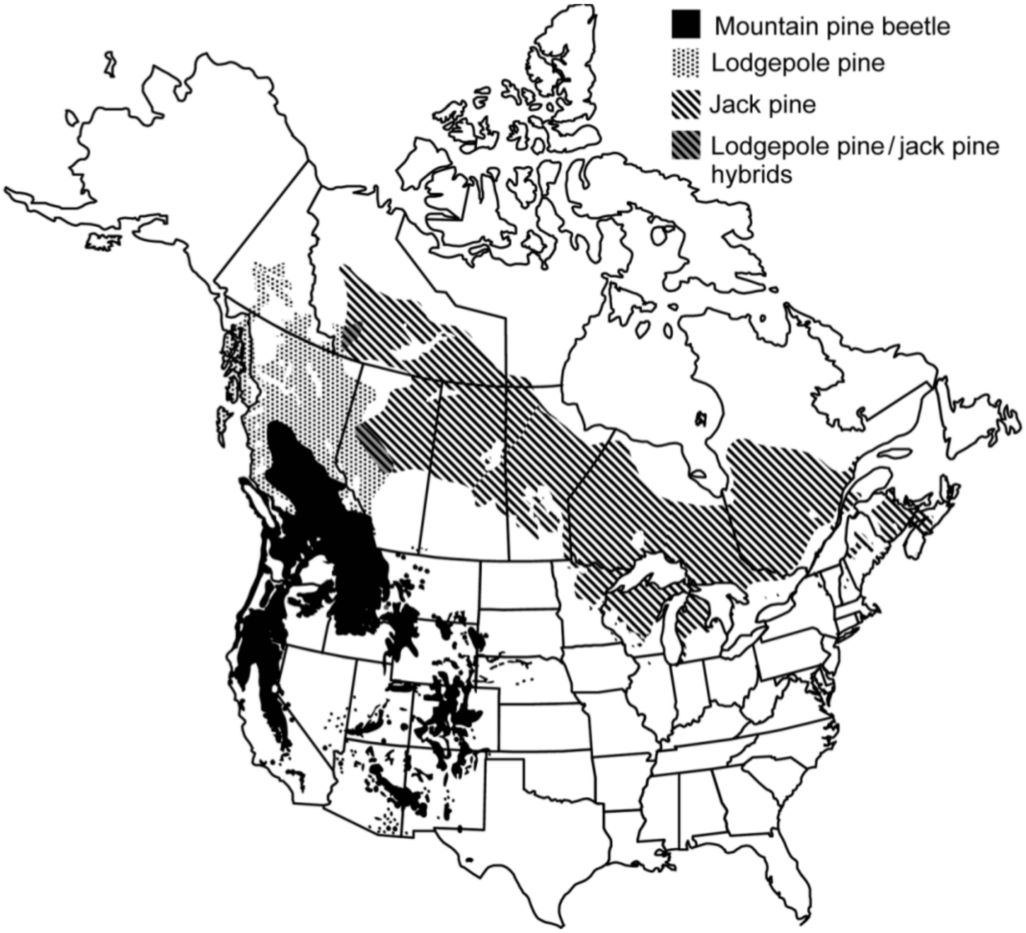

Figure 4.1: Range distributions of mountain pine beetle, its primary host tree species lodgepole pine, and alternate host species jack pine. Regions where hybrid lodgepole-jack pines occur are also highlighted. From Fig. 1 of Safranyik et al. (2010).

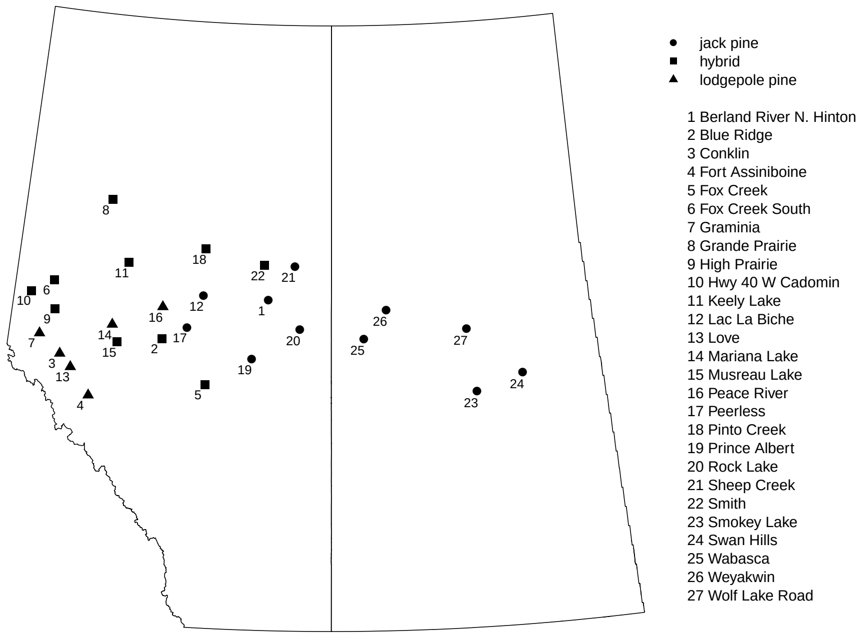

Figure 4.2: Map of lodgepole, jack, and hybrid lodgepole-jack pine stands sampled across Alberta and Saskatchewan provinces, Canada. Data provided by David Langor and Darryl Williams (unpublished).

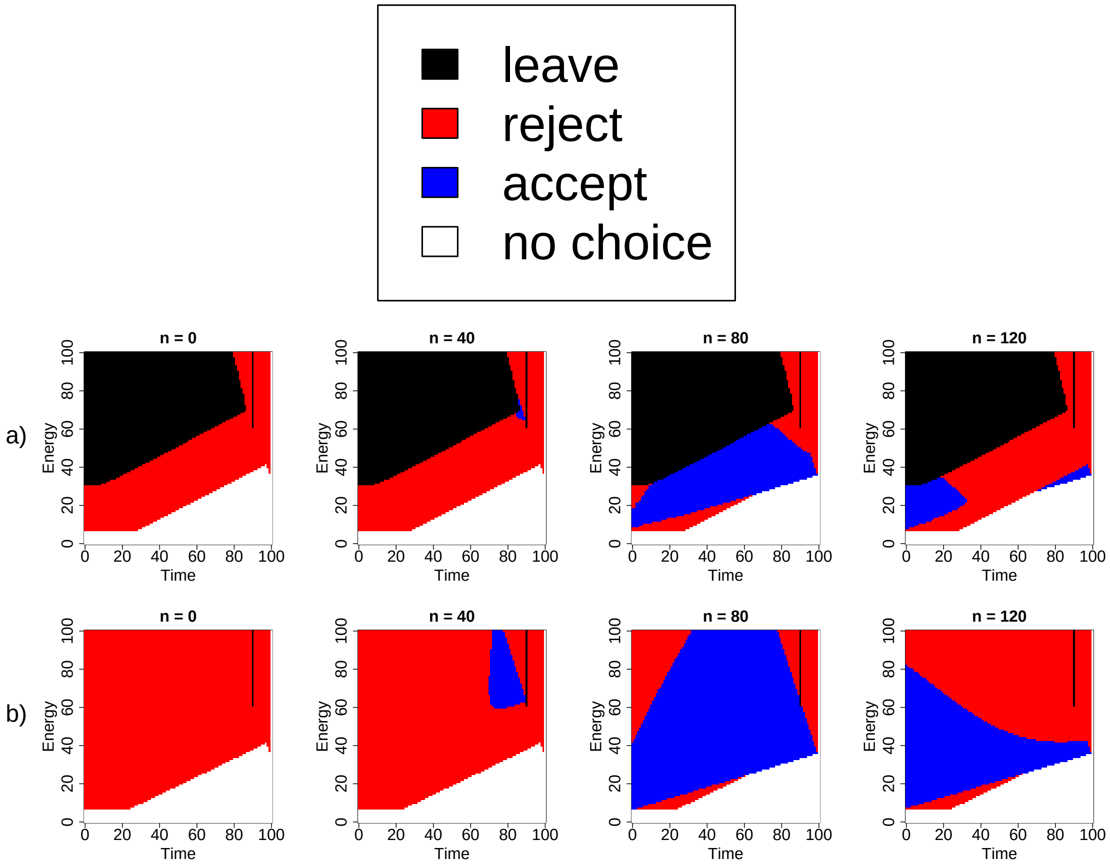

Figure 4.3: Stay-Leave and Accept-Reject decisions for a medium size, medium nutritional quality tree at different beetle attack densities (n). (a) Non-ESS DSV decisions; (b) ESS decisions. For clarity of explanation, we present the complex, multi-dimensional decision space as a series of two-dimensional plots. Each panel shows decisions across energy and time states, and each panel corresponds to a particular host size/quality and beetle attack density ranging from $0 - 120$ beetles/m^2. Coloured regions show optimal decisions: black corresponds to leaving the natal stand; red to staying within the stand but rejecting that particular host; and blue to staying within the stand and accepting the host. Uncoloured (i.e., white) regions of the decision space correspond to state combinations for which the expected fitness gain is 0, regardless of the decision made. In other words, they represent regions of non-choice. We therefore do not consider decisions in these regions.

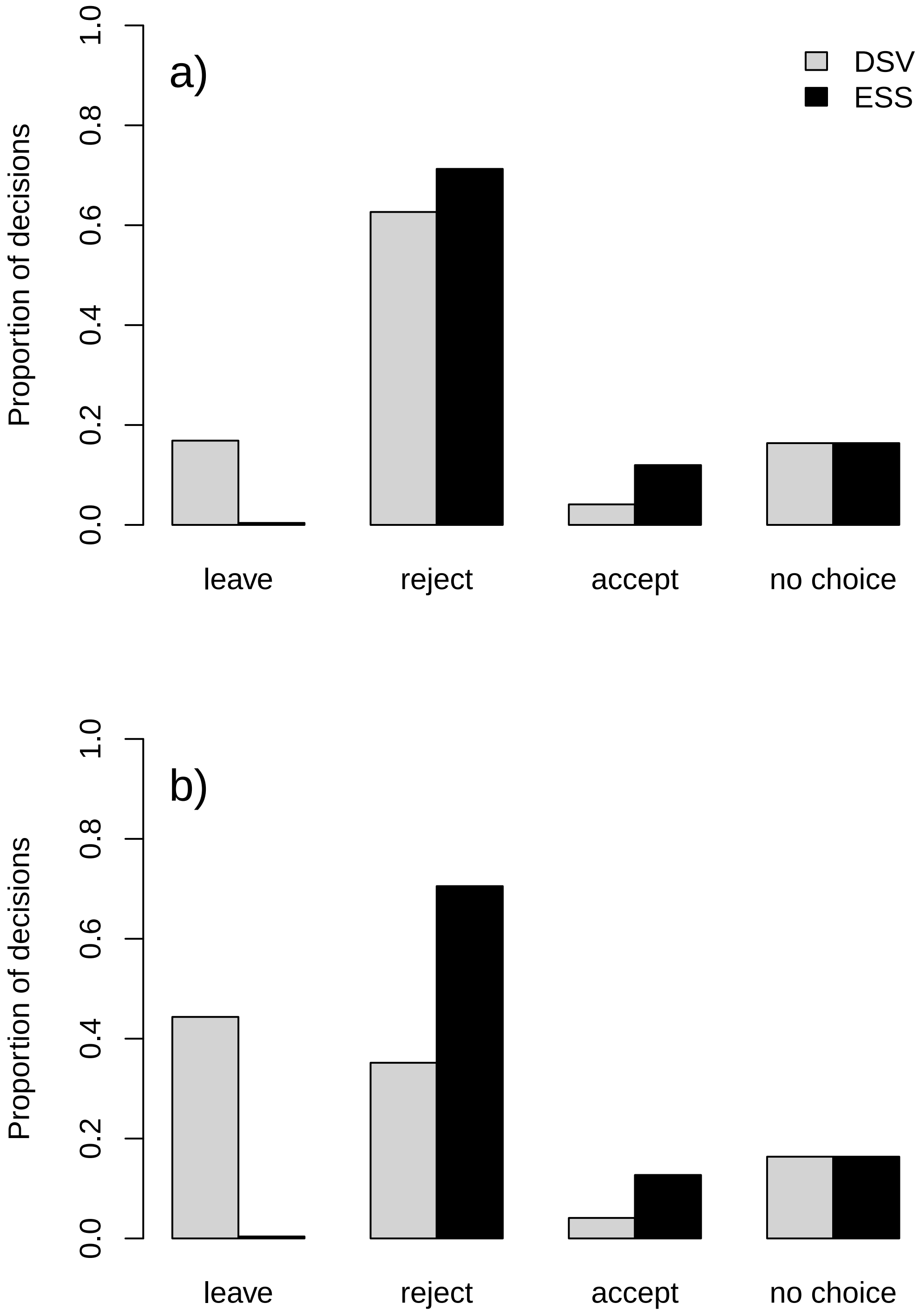

Figure 4.4: Proportion of optimal decisions corresponding to patch leave, host reject, host accept, and no choice, for the tactical DSV model (Chubaty et al., 2009) and the strategic dynamic game model. a) outer patch and inner patch are of similar quality; b) outer patch is better than inner patch.

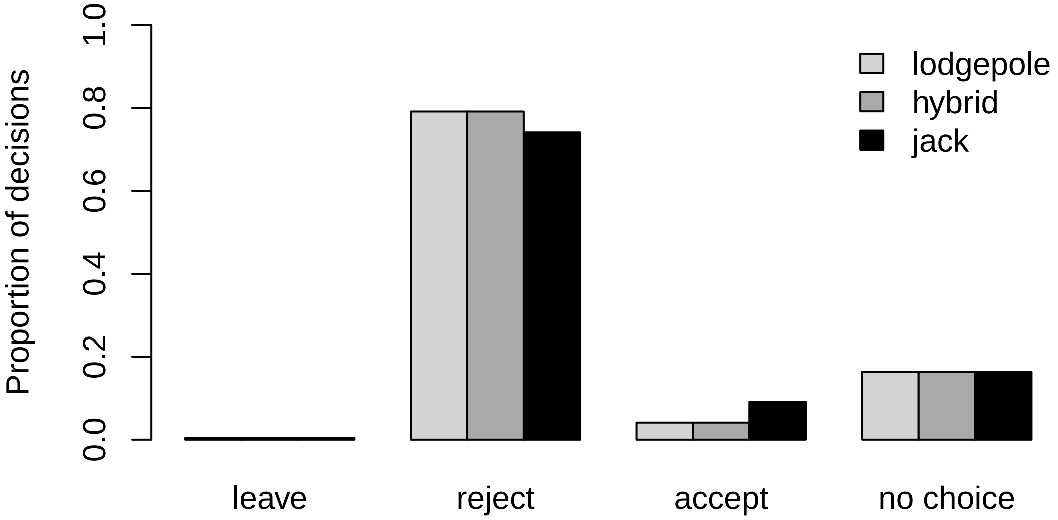

Figure 4.5: Proportion of optimal decisions corresponding to patch leave, host reject, host accept, and no choice, for ESS solutions for each pine species.

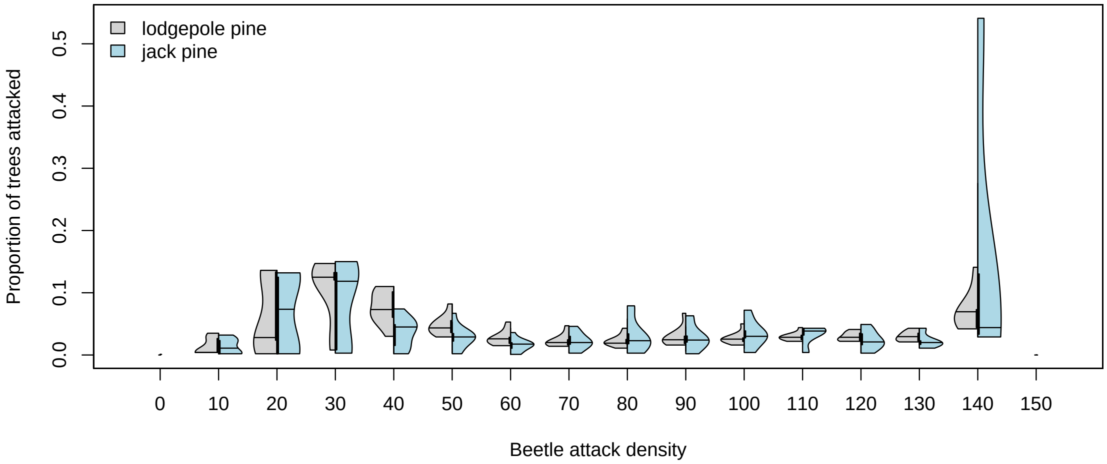

Figure 4.6: Split-violin plots showing the proportions of trees attacked across all attack density classes, summed across all host classes. For each attack density, the left side of the plot shows the distribution for lodgepole pine (grey), and the right side jack pine (blue). Values for hybrid pines were generally intermediate between these two species, and are not shown. Thin horizontal bars indicate mean proportions of trees attacked across all simulations, and thick vertical black bars indicate the inter-quartile range for the middle 50% of data. Shaded areas show the range of the data (vertical) and the kernel density estimates of the data (horizontal).

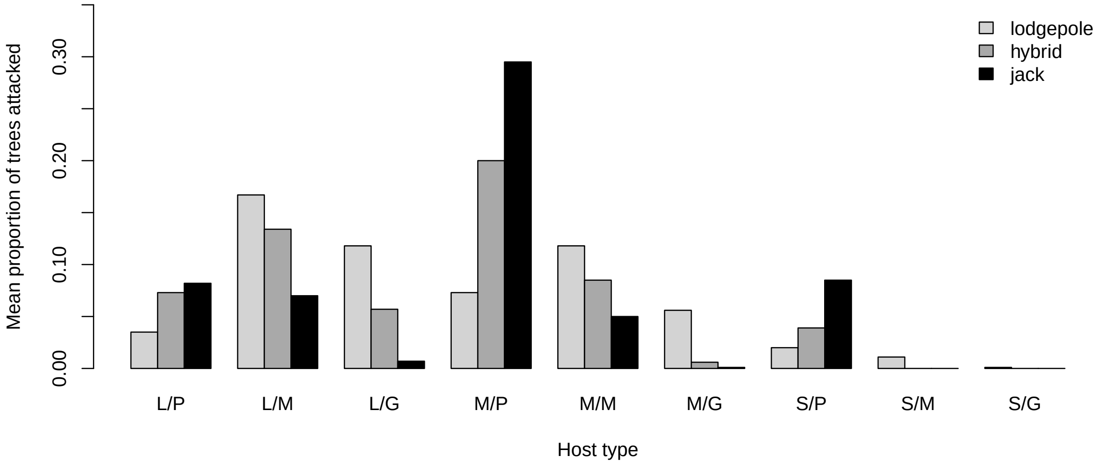

Figure 4.7: Mean proportion of trees of each species attacked (summed across all beetle attack densities), grouped by host size class (L = large diameter; M = medium diameter; S = small diameter) and phloem thickness class (P = thin phloem, i.e., poor nutritional quality; M = intermediate-thickness phloem, i.e., medium nutritional quality; G = thick phloem, i.e., good nutritional quality). Descriptions of each host class are provided in text.

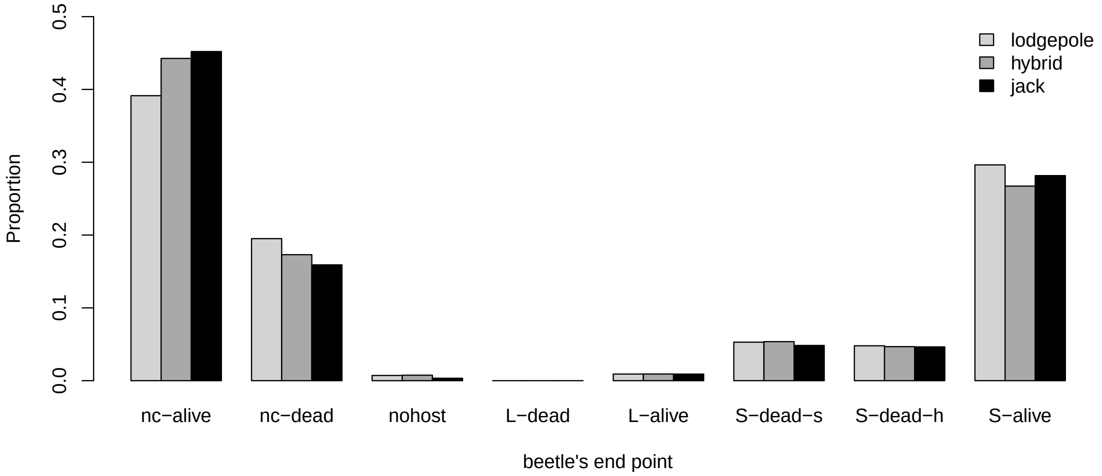

Figure 4.8: Beetles' patch-level decisions (no choice, leave, stay) and corresponding status (alive or dead) at the end of the simulation (nc = no choice; L = left stand; S = stayed in stand; dead-h = died in host; dead-s = died searching).

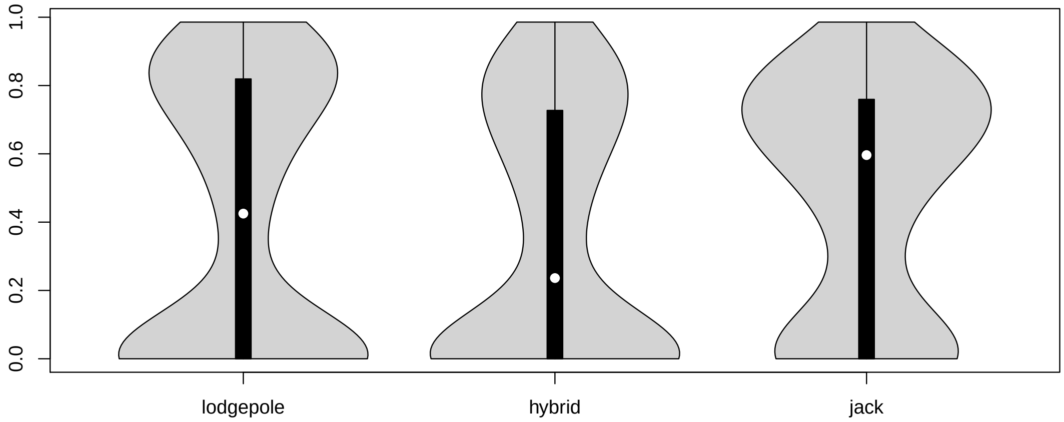

Figure 4.9: Violin plots showing beetle fitness values at the end of a simulation for each tree species. White points indicate the mean value and thick vertical black bars indicate the inter-quartile range for the middle 50% of data. Shaded areas show the range of the data (vertical) and the kernel density estimates of the data (horizontal).

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4.10 Connecting statement

In the next chapter, I evaluate the theoretical potential of using genetic control techniques to suppress bark beetle populations below outbreak thresholds. In so doing, I employ a population-level modelling approach to explore the spread of genetically engineered beetles across a forest landscape; however, I incorporate the outcomes of individual dispersal behaviour into this population model by including the inter-stand dispersal estimates derived from the dynamic game model. I also consider the impact of behavioural variation on these dispersal estimates, by including both mean and variance of these estimates.

Chapter 5

A genetic control model of bark beetle outbreak suppression in a forest landscape

5.1 Abstract

Numerous economically and medically important insect species have been targets of genetic control efforts to reduce or eliminate their negative impacts. Selfish genes (coupled with deleterious alleles) are one possible genetic mechanism that could be deployed to suppress pest populations. We develop a population dynamics model describing how such control may be effective from a theoretical perspective, using a bark beetle – conifer system as a case study. We consider a cellular automaton model, allowing diffusion of beetles between cells, and assess whether beetle populations can be suppressed and maintained below outbreak thresholds. We found, that for biologically-relevant parameter values, this selfish genetic element is maintained in the population and that local beetle populations become suppressed or extirpated without substantially depleting their conifer resource. Under certain conditions, beetle movements between cells were sufficient to maintain suppressed beetle populations, which suggests that genetic control of bark beetle pests may be possible.

Keywords: bark beetles, population dynamics, population genetics, outbreak suppression, genetic control, spatially-explicit model.

5.2 Introduction

Numerous economically and medically important insect species have been targets of genetic control efforts to reduce or eliminate their negative impacts on human societies. Various genetic approaches have been suggested, and a few of them implemented successfully for a few species (reviewed in Gould, 2008). However, a major limitation of many genetic methods of controlling pest populations has been the evolutionary stability of the genetic constructs (Burt, 2003; Gould, 2008). Burt (2003) describes several alternative genetic approaches which have the advantages of being evolutionarily stable as well as reversible. Site-specific selfish genes such as homing endonuclease genes (HEGs), group II introns, and site-specific LINE-like transposable elements, could all potentially be used as effective genetic mechanisms of population engineering and control (Chevalier and Stoddard, 2001; Belfort et al., 2002; Eickbush, 2002). HEGs are the simplest of these three genetic constructs and can quickly spread through populations via their 'super-Mendelian' inheritance as a result of gene conversion (Chevalier and Stoddard, 2001; Goddard et al., 2001; Burt, 2003).

HEGs code for an enzyme which cuts out a portion of the chromosome not containing the HEG (*i.e.*, HEG^-). The cell's own genetic repair mechanisms repair the cleaved HEG^- chromosome using the intact HEG^+ homologue as the template, thus converting a HEG^+/HEG^- hemizygote into a HEG^+/HEG^+ homozygote (Burt, 2003). By inserting a HEG into an essential gene, a knockout mutant would be created. Provided the knocked-out gene produces substantial deleterious effects in the homozygous recessive condition with little or no effect in the heterozygous condition, the resulting HEG construct can provide effective population control through transmission ratio distortion and high genetic load, leading to a substantial reduction in population fitness, the extent of which depends on the proportion of heterozygotes converted to homozygotes (e) (Burt, 2003).

Using a lethal HEG construct that has no effect on heterozygote fitness, introduced into 1% of the population (*i.e.*, $q = 0.01$) and assuming 90% conversion of heterozygotes ($e =$

0.90): the frequency of the allele construct quickly goes to 90% (e); and population fitness $(\overline{W})$ would be reduced by 80% in less than 15 generations (Burt, 2003). HEGs have thus received a lot of attention and are currently being explored as means of controlling insect pests, especially mosquitoes serving as disease vectors (Riehle et al., 2003; Windbichler et al., 2007; Gould, 2008). Although this genetic control system is theoretically possible (assuming homogeneous population, mass action, etc.) and potentially extremely effective, practical implementation in a pest population is at least several years away (Gould, 2008). Here we describe how such control may be effective from a theoretical perspective, using bark beetles as a case study, but we do not explore the practical or ethical considerations of its implementation (reviewed in Gould, 2008).

Unlike other phytophagous insects, reproduction in bark beetles (Coleoptera: Curculionidae: Scolytinae) is contingent upon successful search for and attack of a suitable host tree, which necessarily results in the tree's death. Population outbreaks of aggressive bark beetle species can have substantial impacts on timber supplies, resulting in serious negative economic impacts, thus the beetles are considered major forest pests (Rudinsky, 1962; Safranyik and Carroll, 2006).

Univoltine bark beetle species, such as mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, emerge from their natal trees in late summer and fly in search of a suitable host tree. This host search involves a combination of both visual and olfactory cues, including beetle-produced pheromones involved in coordinating a 'mass attack' required to overcome the host's defences, which include toxic secondary compounds and resin secretions (Atkins, 1966; Wood, 1982; Raffa and Berryman, 1983; Berryman et al., 1985). Beetles are choosy and discriminate between hosts based on their own internal energy state, conspecific beetle (attack) densities, and the size, quality, and defensive capability of such hosts (see Chapter 2 and Safranyik and Carroll, 2006; Safranyik et al., 2010). The extent of host defensive capabilities varies between individual trees and these defences may only be overcome if a sufficiently large number of beetles attack an individual tree over a short period of time, thereby exhausting its defensive capabilities (Raffa and Berryman, 1983). At low attack densities, individual beetles face near-certain death, especially against vigorous trees.

Thus, at low (*i.e.*, endemic) population densities, where beetles are unable to achieve the large attack densities sufficient to overcome the defences of large-diameter, well-defended hosts, they will typically attack smaller-diameter, low-quality, or stressed (e.g., fire- or lightning-damaged) trees. Conversely, at high (i.e., outbreak) population densities they are capable of and do go after larger diameter trees, which tend to have thicker phloem (Rudinsky, 1962; Safranyik and Carroll, 2006).

Previous models of genetic control rarely consider spatial structure and heterogeneity (but see Huang et al., 2011), and have not explicitly considered consumer-resource dynamics. Here we examine effects of dispersal (i.e., emigration and immigration), resource depletion, and environmental heterogeneity on the population dynamics and community dynamics of a bark beetle – conifer system, and explore the theoretical potential for an engineered genetic control element to suppress beetle outbreaks. This problem is approached in two stages: first, we develop a basic consumer-resource model to describe beetle/tree population dynamics in a homogeneous forest environment, incorporating the genetic control of the beetles; second, we examine the effect of dispersal on the system using a simple dispersal rule (diffusion) based upon dynamic-game-derived beetle inter-stand dispersal rates (from Chapter 4) and consider the impact of introducing environmental heterogeneity on beetle outbreak dynamics and spread of the genetic control element.

5.3 Methods

5.3.1 The basic model

Population dynamics models for diploid organisms experiencing selection have been previously developed (see Roughgarden, 1996, Chapter 3). The simplest models examine a single locus with two alleles (A and a), the frequencies of which are denoted by p and q, respectively. Each genotype (AA, Aa, aa) is treated as a subpopulation of the whole (N), and population growth is density-dependent such that the relative fitness (w) of each genotype corresponds to that genotype's subpopulation growth rate. Mean population fitness of all three genotypes is $\overline{w} = w_{AA}p_t^2 + 2w_{Aa}p_t(1-p_t) + w_{aa}(1-p_t)^2$. Combining the simplest population dynamics and population genetics models for a diploid organism yields the following system of difference equations:

$$p(t+1) = \frac{w_{AA}p(t)^2 + w_{Aa}p(t)(1-p(t))}{\overline{w}} \tag{5.1a}$$

$$N(t+1) = \overline{w}N(t) = w_{AA}N_{AA}(t) + w_{Aa}N_{Aa}(t) + w_{aa}N_{aa}(t) \tag{5.1b}$$

Burt (2003) developed the basic equations characterizing diploid selection in an engineered population using a HEG construct. Let A represent the natural non-engineered gene, a represent the HEG construct, p represent the frequency of A, and q represent the frequency of a. The HEG model differs from the basic model of diploid selection by conversion of some proportion of HEG^{+}/HEG^{-} hemizygotes to HEG^{+}/HEG^{+} homozygotes, denoted by the term e. It also assumes that the HEG construct only affects the fitness of homozygotes carrying it, and that hemizygous individuals are unaffected (i.e., $w_{AA} = w_{Aa} > w_{aa} > 0$). Note that we use both p and q notation at this point for clarity, and that because $q = 1 - p$ the equations can be written using only p notation.

$$p(t+1) = \frac{w_{AA}p(t)^2 + (1-e)w_{Aa}p(t)q(t)}{\overline{w}} \tag{5.2a}$$

$$q(t+1) = \frac{(e)w_{Aa}p(t)q(t) + w_{aa}q(t)^2}{\overline{w}} \tag{5.2b}$$

where, $\overline{w} = w_{AA}p_t^2 + 2w_{Aa}p_tq_t + w_{aa}q_t^2$

Combining (5.1) with (5.2) gives the basic form of a population dynamics model with selection incorporating HEG-mediated genetic control, where $\overline{w} = w_{AA}p_t^2 + 2w_{Aa}p_tq_t + w_{aa}q_t^2$.

$$p(t+1) = \frac{w_{AA}p(t)^2 + (1-e)w_{Aa}p(t)(1-p(t))}{\overline{w}} \tag{5.3a}$$

$$N(t+1) = \overline{w}N(t) = w_{AA}N_{AA}(t) + w_{Aa}N_{Aa}(t) + w_{aa}N_{aa}(t) \tag{5.3b}$$

Based on equations (5.3) we start with the following discrete-time system of equations describing a consumer-resource model incorporating beetle population genetics. We track resource (tree) biomass, R, allele frequency, p, and beetle population size, N, within a forest stand at the end of each year (generation, t).

Pine biomass dynamics are characterized by density-dependent growth and beetle-induced mortality. Growth follows a formulation of the Beverton-Holt model (Beverton and Holt, 1957) with rate λ, the area necessary to achieve λ is given by α, and sensitivity to crowding is described by b. Tree attack by beetles follows a type III functional response, characterized by the half-saturation constant (Q) and the maximum beetle per capita attack rate of trees (β).

$$R(t+1) = \frac{\lambda R(t)}{1+\alpha R(t)} - \frac{\beta N_t R(t)^2}{Q^2 + R(t)^2} \tag{5.4}$$

Beetle population growth is governed by the successful conversion of pine biomass towards offspring production, with the mean population conversion efficiency (i.e., per capita beetle production per tree) defined as $\overline{c} = c_{AA}p(t)^2 + 2c_{Aa}p(t)(1-p(t)) + c_{aa}(1-p(t))^2)$. Extrinsic beetle mortality occurs at a fixed rate d. Each genotype is modelled as a separate sub-population making up the whole, such that $N_t = N_{AA}(t)+N_{Aa}(t)+N_{aa}(t)$. We assume each genotype responds to density-dependent growth and mortality in the same way (a and β), but that they differ in their conversion rates (c), such that $c_{AA} = cAa > c_{aa} > 0$. Additionally, we substitute c_{xx} with χw_{xx} such that $c_{AA} = \chi(1)$, $c_{Aa} = \chi(1)$, and $c_{aa} = \chi(1-s)$, where s is the coefficient of selection against HEG.

$$N_{AA}(t+1) = \chi p(t)^2 \frac{\beta N_{AA}(t) R(t)^2}{Q^2 + R(t)^2} - dN_{AA}(t) \tag{5.5a}$$

$$N_{Aa}(t+1) = (1-e)\left[\chi p(t)(1-p(t))\frac{\beta N_{Aa}(t)R(t)^2}{Q^2+R(t)^2} - dN_{Aa}(t)\right] \tag{5.5b}$$

$$\begin{aligned} N_{aa}(t+1) = {} & e\left[\chi p(t)(1-p(t))\frac{\beta N_{Aa}(t)R(t)^2}{Q^2+R(t)^2} - dN_{Aa}(t)\right] \\ & + \chi(1-s)(1-p(t))^2\frac{\beta N_{aa}(t)R(t)^2}{Q^2+R(t)^2} - dN_{aa}(t) \end{aligned} \tag{5.5c}$$

Allele frequencies, based on p, are thus calculated by

$$p(t+1) = \frac{\chi p(t)^2 + \chi(1-p(t))(1-e)}{\chi \overline{w}} \tag{5.6}$$

5.3.2 The spatial model

We extend the basic model, making it spatially explicit using a cellular automaton model with no-flux boundaries, where each cell represents a forest stand, and individual stands are referenced by their Cartesian coordinates (i, j). Beetle population and allele frequencies dynamics change with the influx and efflux of beetles of each genotype (i.e., dispersal and gene flow). D is the diffusion rate, and if $n(t, i, j) < 0$ then $n(t, i, j) = 0$. As individuals move into or out of the current cell at (i, j), we simply add or subtract the numbers arriving or leaving, respectively. Likewise, because $p(t + 1)$ depends on $N(t)$, we update p based on the numbers of arriving and leaving individuals, such that

$$p^*(t,i,j) = \frac{N_{AA}(t,i,j) + 0.5N_{Aa}(t,i,j)}{n(t,i,j)} \tag{5.7}$$

We thus produce the following system of equations:

$$R(t+1) = \frac{\lambda R(t,i,j)}{1+\alpha R(t,i,j)} - \frac{\beta N_{AA}(t,i,j)R(t,i,j)^2}{Q^2 + R(t,i,j)^2} \tag{5.8a}$$

$$\begin{aligned} N_{AA}(t+1,i,j) &= \chi p(t,i,j)^2 \frac{\beta N_{AA}(t,i,j)R(t)^2}{Q^2+R(t)^2} - dN_{AA}(t,i,j) \\ &+ D\nabla^2 N_{AA}(x) \end{aligned} \tag{5.8b}$$

$$\begin{aligned} N_{Aa}(t+1,i,j) &= (1-e)\left[\chi p(t,i,j)(1-p(t,i,j))\frac{\beta N_{Aa}(t,i,j)R(t,i,j)^2}{Q^2+R(t,i,j)^2}\right. \\ &\left. - dN_{Aa}(t,i,j) + D\nabla^2 N_{Aa}(x)\right] \end{aligned} \tag{5.8c}$$

$$\begin{aligned} N_{aa}(t+1,i,j) &= e\left[\chi p(t,i,j)(1-p(t,i,j))(e)\frac{\beta N_{Aa}(t,i,j)R(t,i,j)^2}{Q^2+R(t,i,j)^2}\right. \\ &\left. - dN_{Aa}(t,i,j) + D\nabla^2 N_{Aa}(x)\right] \\ &+ \chi(1-s)(1-p(t,i,j))^2 \frac{\beta N_{aa}(t,i,j)R(t,i,j)^2}{Q^2+R(t,i,j)^2} - dN_{aa}(t,i,j) \\ &+ D\nabla^2 N_{aa}(x) \end{aligned} \tag{5.8d}$$

$$p(t+1)(i,j) = \frac{\chi p^*(t,i,j)^2 + \chi(1-p^*(t,i,j))(1-e)}{\chi \overline{w}} \tag{5.8e}$$

where,

$$\overline{w} = w_{AA}p^*(t,i,j)^2 + 2w_{Aa}p^*(t,i,j)(1-p^*(t,i,j)) + w_{aa}(1-p^*(t,i,j))^2 \tag{5.9}$$

We release engineered beetles in the center of the forest, at the beginning of the simulation, which is likely the easiest release protocol to implement. We model dispersal (gene flow) using a simple (linear) diffusion model. Movement of individual beetles occurs to and from the four nearest-neighbouring cells, following Bascompte and Solé (1994).

$$\begin{aligned}\nabla^2 N_{AA}(x) &= N_{AA}(t,i+1,j) + N_{AA}(t,i-1,j)\\ &\quad + N_{AA}(t,i,j+1) + N_{AA}(t,i,j-1)\\ &\quad - 4N_{AA}(t,i,j)\end{aligned} \tag{5.10a}$$

$$\begin{aligned}\nabla^2 N_{Aa}(x) &= N_{Aa}(t,i+1,j) + N_{Aa}(t,i-1,j)\\ &\quad + N_{Aa}(t,i,j+1) + N_{Aa}(t,i,j-1)\\ &\quad - 4N_{Aa}(t,i,j)\end{aligned} \tag{5.10b}$$

$$\begin{aligned}\nabla^2 N_{aa}(x) &= N_{aa}(t,i+1,j) + N_{aa}(t,i-1,j)\\ &\quad + N_{aa}(t,i,j+1) + N_{aa}(t,i,j-1)\\ &\quad - 4N_{aa}(t,i,j)\end{aligned} \tag{5.10c}$$

Diffusion parameter estimates were obtained based on outcomes of decisions previously modelled with a dynamic habitat selection game in Chapter 4. This dynamic game model calculates both optimal evolutionary stable strategy (ESS) tree-level accept/reject decisions, as well as stand-level stay/leave decisions using a state dependant dynamic programming approach. That model predicts that only a small proportion of the ESS decision space corresponds to leaving the natal stand, and only a small percentage of beetles ($\sim 1\%$) disperse between stands. We used this figure as a guideline to parameterize the inter-stand diffusion (dispersal) rates of beetles. A sensitivity analysis showed that the reaction-diffusion model was insensitive not only to changes in this dispersal parameterization, but also to stochastic variants of this dispersal term which included variance around the mean value.

The model was solved using numerical simulations because analytical solutions were intractable. We ran two sets of simulations, assuming either homogeneous forest stands whereby each stand is equivalent and has the same carrying capacity ($K_{i,j} = K$), or a heterogeneous forest stands that differ in their carrying capacities for tree populations. In the homogeneous parameterization of the model, the results are expected to closely match those of the non-spatial mass-action model. In the heterogeneous condition, the environment is initialized by randomly assigning a carrying capacity to each cell, drawn from a uniform probability distribution where $K_{i,j} = \mathbb{U}(0, K_{max})$.

Under both sets of environmental scenarios, we evaluated the dynamics of the system based over $t_{max} = 1000$ timesteps and identified parameter combinations which produced suppression, but not extirpation, of beetle populations. In particular, we explored the effects of HEG hemizygote-to-homozygote conversion efficiency (e) and HEG-induced fitness costs (s) on the viability of HEG as a population suppression mechanism to mitigate or prevent bark beetle outbreaks.

5.4 Results

The release of genetically modified beetles carrying the HEG-construct from the centre of each of the simulated forests resulted in a series of advancing waves of genetically engineered beetles moving outward from the centre and eventually spreading throughout the entire forest landscape. Beetle populations in stands at the wave front typically experienced rapid declines, followed by rebounding dynamics that varied depending on the outcome of the simulations and which population equilibrium was reached. Beetles were either extirpated ($N(t, i, j) = 0$), reached a stable maximum population size based on $R(t, i, j)$, or were suppressed at some intermediate population size.

In general, consumer-resource dynamics were closely linked, such that large beetle populations resulted in reduction of tree biomass. In many cases where the frequency of the HEG-construct went to fixation in the population, the beetle population crashed, resulting in extirpation of beetles and subsequent maximization of tree biomass. Only under conditions where the frequency of the HEG-construct reached an intermediate equilibrium value (i.e., $0 < q < p < 1$) were beetle populations suppressed and maintained at lower values within a stand.

Under homogeneous forest stand simulations, HEG-carrying beetles dispersed evenly in all directions outward from the central release point, whereas spatial heterogeneity resulted in much more complex waves of spread that had uneven margins (i.e., spread was not symmetrical across the landscape).

Across most simulations, HEG was maintained in the population (Figure 5.2), and under some combinations of e and s was able to successfully suppress beetle population densities (Figure 5.1); however, beetle populations were easily extirpated. In both homogeneous and heterogeneous forest landscapes, low values of HEG hemizygote-to-homozygote conversion efficiency (e) were associated with beetle population suppression across a wide range of values of HEG-induced fitness costs (s). Additionally, in homogeneous landscapes only, beetle population suppression was achieved at low s values across a full range of e values. Thus, beetle suppression in heterogeneous environments occurred in fewer of the simulations than under homogeneous conditions, and was more likely to result in extirpation of beetle populations than in homogeneous conditions. In many cases where beetles were extirpated within stands, incoming dispersal from neighbouring stands was sufficient to maintain low beetle numbers. In all stands where beetle populations were effectively suppressed, tree biomass reached its maximum and remained stable.

5.5 Discussion

We developed a spatially explicit consumer-resource model of HEG genetic control of a pest species, where system dynamics were characterized by resource depletion and consumer dispersal across both homogeneous and heterogeneous environments. We explored the effects of HEG hemizygote-to-homozygote conversion efficiency (e) and HEG-induced fitness costs (s) on the viability of HEG as a population suppression mechanism to mitigate or prevent bark beetle outbreaks. We found that although total extirpation of beetle populations was common across simulations, successful suppression is possible under a limited combination of e and s values.

Low e or low s values were associated with beetle population suppression in homogeneous forest landscapes, in which all stands were equally parameterized. However, a much smaller portion of the model parameter space resulted in beetle population suppression in heterogeneous forest landscapes, where stand carrying capacities varied. In these simulations, suppression was only achieved for low values of e. This suggests that resource heterogeneity, regardless of the fitness costs associated with the HEG-construct, plays an important role in the underlying dynamics of HEG spread through a landscape.

We emphasize that the goal of this study differs from most other studies of genetic control (e.g., Burt, 2003; Huang et al., 2011), in that our aim was to suppress pest populations rather than eliminate or extirpate them. Although bark beetles, and mountain pine beetle in particular, can be extremely devastating during population eruptions, their ecological role as a disturbance agent in conifer forests is a critical one. Historically, outbreaks of mountain pine beetle have been much more localized in scale, and the recent ongoing outbreak has been driven by additional factors, in particular, warmer winters due to climate change, which have resulted in much lower overwinter beetle mortality and have enabled range expansion of the beetle into previously uninfested forest regions (Safranyik and Carroll, 2006; Safranyik et al., 2010).

The results of our model were largely insensitive to inter-stand dispersal rates of beetles, nor were they greatly affected by stochastic dispersal parameterizations. This is a surprising result, because previous studies have suggested that habitat selection (and therefore dispersal) depends on the energetic condition of dispersing beetles (Chubaty et al., 2009; Latty and Reid, 2010) and that there is substantial individual variation among dispersing beetles (Chapter 2 and Latty and Reid, 2010). This variation is expected to play an important role in intra-stand dynamics, and may also contribute to inter-stand dispersal and attack dynamics, especially when beetles disperse through highly variable resource environments such as those simulated by heterogeneous stands in our model.

Most dispersal in MPB occurs over short distances between trees within a forest stand, although a small percentage of beetles ($< 2\%$) will travel long-distances above the canopy, usually carried by wind currents (Safranyik et al., 1992, 2010). Although this represents a small proportion of the beetle population, and may be insignificant during endemic level of beetle attack, during large scale outbreaks long distance dispersal is likely an important factor in extending the range of the outbreak area (Safranyik et al., 2010). Although in the present model, and in the dynamic game model presented in Chapter 4, we did not explicitly consider such long distance dispersal events, the model can be adapted to account for greater dispersal distances.

Long-distance dispersal among patches may ensure that a single central release point is effective at facilitating the spread of the genetic control construct through the landscape, and would likely speed up its spread (Huang et al., 2011). A single, large release area, while often the easiest to deploy, may limit the spread of a genetic control construct if inter-stand migration is low, or if the fitness cost is too high (Huang et al., 2011). If the pest population in a given patch collapses before enough individuals can migrate into neighbouring patches, thus spreading the genetic control construct, then the release may not be successful. Thus it will be important to carefully engineer the genetic control construct to meet the exact requirements for the biological system.

Genetic control is still many years away from being implemented in natural systems, and a number of practical considerations including ethical concerns (reviewed in Gould, 2008) still need to be addressed. However, the potential exists for such approaches to be implemented successfully, especially as the gaps between general models and system-specific models are explored further. Genetic control models that take into account the complex spatiotemporal dynamics present in natural systems bring us closer to developing effective and safe genetic control programs (Huang et al., 2009, 2011). For mountain pine beetle, forest fragmentation and stand heterogeneity are key to understanding how the current outbreak continues to spread eastward (Chapter 4 and Safranyik et al., 2010; Bone et al., 2013), and our genetic control model here further suggests that landscape heterogeneity plays an important role in determining the successful outcome of potential genetic control efforts.

5.6 Acknowledgements

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5.7 Tables

Table 5.1: Description of parameters and variables used

Symbol	**Value**	**Description**
D	0.01–0.05	diffusion rate
e	0.1–0.9	proportion of $HEG^{+/-}$ hemizygotes converted to $HEG^{+/+}$ homozygotes (i.e., proportion of Aa heterozygotes converted to aa homozygotes)
β	0.001	replacement rate
λ	1.15	replacement rate
χ	1.25	replacement rate
f	0.01	introduction frequency of HEG-construct
K	–	stand carrying capacity (i.e., stand quality)
N	–	beetle population size
p	–	allele frequency of A
q	$(1-p)$	allele frequency of a (HEG complex)
R	–	tree biomass
s	0.1–0.9	fitness cost of aa genotype
t	–	time (i.e., generation)
w_{AA}	1	genoptype AA's relative fitness
w_{Aa}	1	genoptype Aa's relative fitness
w_{aa}	$1-s$	genoptype aa's relative fitness
$\overline{w}$	–	mean population fitness

5.8 Figures

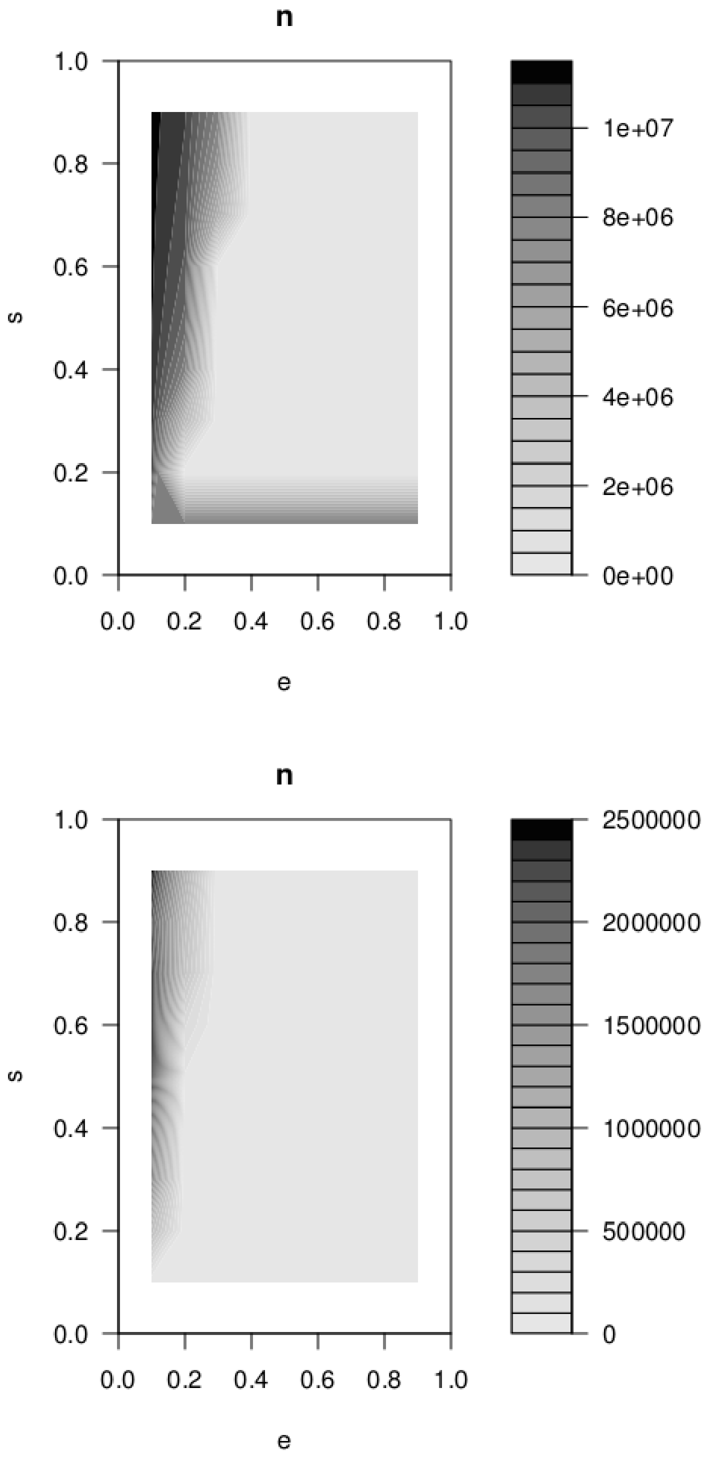

Figure 5.1: Total beetle population sizes at the end of simulations across a range of e and s values. a) homogeneous forest landscapes; b) heterogeneous forest landscapes.

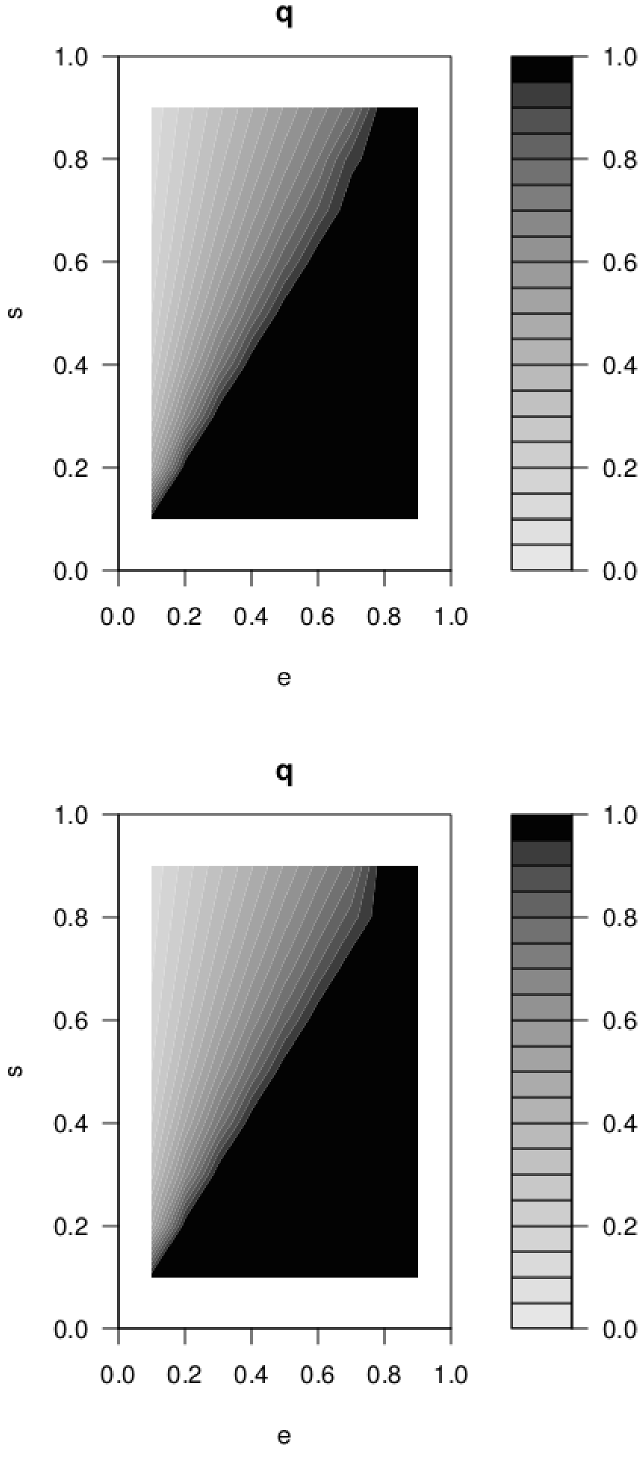

Figure 5.2: Allele frequencies p at the end of simulations across a range of e and s values. a) homogeneous forest landscapes; b) heterogeneous forest landscapes.

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Chapter 6

Concluding Remarks

6.1 Beyond individual behaviour

A central theme of my thesis has been explaining population-level phenomena, in particular the distribution of individuals across habitats, by examining behaviour at the individual level. I examined the role of energy- and time-limitation on the host selection behaviour of mountain pine beetle (MPB), with the aim to better elucidate the resulting patterns of beetle attack across trees within forest stands and among stands. I highlighted the importance of considering individual behaviour, especially where flexibility and variability in individual behaviours have direct impacts on the outcomes of these decisions, as they do in MPB where beetles base host settlement decisions not only on host tree characteristics but also on conspecific densities. The context for this work is the ongoing MPB outbreak in western Canada that continues to spread and may pose a threat to the Canadian boreal forests (Nealis and Peter, 2008; Safranyik et al., 2010).

The current MPB outbreak is the result of increased susceptibility of forest stands to beetle attack, driven primarily by global climate change, which has reduced beetle overwintering mortality as well as released beetles from climatic barriers that had previously limited their latitudinal and altitudinal ranges (Safranyik et al., 2010). As a result, the beetle has expanded its range eastward and northward, and has additionally benefited from reduced defensive capabilities of naïve tree populations that have not previously co-evolved with this threat. In order to begin to address this shift in habitat availability and use, I advocate for using a bottom-up approach to inform population-level phenomena such as the outbreak distributions of beetles in forest stands.

A beetle's lipid reserves determine the dispersal and search capabilities, and I showed in Chapter 2 that beetles with high lipid reserves were more 'choosy' (i.e., they could afford to and did delay accepting poor nutritional quality trees in a no-choice experiment) compared to beetles with low lipid reserves. This result was predicted by the models developed in Chapters 3 and 4. Furthermore, I showed there is substantial variation in the timing of beetle emergence as well as the lipid levels of newly emerged beetles. This variation in beetle energy states, together with beetles' flexible host selection behaviour need to be considered when examining population-level phenomena.

Chapters 3 and 4 described the development of a pair of MPB habitat selection models for MPB using a dynamic state variable approach to explicitly consider the role of energy and time in influencing beetles' decisions, in addition to host tree characteristics, availability, and conspecific densities. The basic model developed in Chapter 3 predicted that beetles preferentially select larger trees with thicker phloem over smaller trees with thinner phloem, accepting lower nutritional quality trees more readily at low energy- and time-states. Chapter 4 extended this model through the development of a spatial game to examine the implications of beetles' decisions on attack dynamics and beetle distributions. I used this dynamic game model to assess the decisions (and outcomes of these decisions) in stands comprised of lodgepole, jack, and their hybrid pine, to explore how beetle outbreaks may be facilitated in jack pine stands. This model showed that jack pine stands, like those found in the boreal forests of Canada, may be more susceptible to MPB attack due to the increased availability of trees of medium size with thinner phloem (and lower defensive capabilities) than in lodgepole pine stands. The model in Chapter 4 also predicted inter-stand dispersal rates, which were incorporated in a model of bark beetle genetic control in Chapter 5.

In my final data chapter I modelled the spatial spread of genetically engineered beetles in a forest landscape and examined the effects of dispersal, resource depletion, and environmental heterogeneity on beetle outbreak dynamics and the theoretical potential for genetic control of MPB. Inter-stand dispersal of beetles was based on the estimates of beetle dispersal from the dynamic game model of Chapter 4. The results of the genetic control model show that beetle population suppression is possible for a narrow region of the parameter space explored, but that, in general, the genetic control mechanism is so successful at reducing beetle population fitness that beetle populations become extirpated in many cases. Surprisingly, the parameterization of inter-stand dispersal rates of beetles had little effect on the results of the model, despite previous work (including this thesis) which suggests that habitat selection and dispersal depend on the energetic condition of dispersing beetles (Chubaty et al., 2009; Latty and Reid, 2010).

Due to the complexity of models I developed in this thesis, I was constrained to using numerical solutions to evaluate each model and to perform exploratory and sensitivity analyses. This limitation meant that I was unable to fully explore the entire parameter space for each model, and certainly in the case of the genetic control model, had to limit my analyses to a few key parameters that were suggested to be the most important. Although dispersal rates had little effect on the results of the model under the narrow set of parameter combinations explored, it difficult to evaluate whether dispersal would have larger effects under different parameterizations. Although impractical from a computational standpoint, I had hoped to more fully explore other regions of the parameter space, in particular how differences in vital rates in each beetle metapopulation affected the landscape-level dynamics.

Future work could further scale up the level at which beetle habitat selection and dispersal decisions are examined, especially as they relate to current forest stand and landscape level assessments of susceptibility to beetle outbreak. In particular, I'm interested in exploring the role of long-range versus short-range dispersal, and the importance of variation in dispersal behaviour as it relates to continued spread of the beetle outbreak (e.g., Safranyik et al., 1992, 2010).

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Appendix A

Parameter values and equations for DSV model

A.1 Detailed equations

Terminal fitness function

$$\Phi(x) = 1 - exp\left(-0.05(x - x_{min})\right) \tag{A.1}$$

Baseline host encounter rate

$$\lambda_{ijk} = \int_{i-1}^{i} g(s; \alpha_{s_i}, \beta_{s_i}) \times \int_{j-1}^{j} g(q; \alpha_{q_j}, \beta_{q_j}) \times l_{ij}(n_k) \times L_{ij}(k) \tag{A.2}$$

$g(x; \alpha, \beta)$ denotes gamma distribution with shape α and rate β. To simulate stands of different qualities the modes of each distribution, $\nu = (\alpha - 1)/\beta$, were either increased or decreased by adjusting α while holding β constant. Baseline estimates for ν values are derived from field data, and denoted ν_0. Host size distributions used ν_0, $\nu_0 - 5cm$, and $\nu_0 + 10cm$. Host phloem thickness distributions used ν_0, $\nu_0 - 0.5mm$, and $\nu_0 + 0.5mm$. (See fig. 3.1 and 3.2 for α and β values derived from field data.)

Density-dependent host encounter rate modifier

$$l_{ij}(n) = 1 - \frac{(1 - c_{ij})R_{ij}^{\omega}}{R_{ij}^{\omega} + n^{\omega}} \tag{A.3}$$

Baseline probability of encountering a host with attack density n_k. (Follows negative binomial distribution with mean u and variance v).

$$L_{ij}(k) = NegBinom(k; u_{ij}, v_{ij}) \tag{A.4}$$

Energy intake rate

$$\varepsilon_{ij}(n) = a_{ij}\left(1 - \frac{2}{1 + exp\left(-\psi_{ij}(n - N_{ij})\right)}\right) \tag{A.5}$$

Probability of overcoming host defenses

$$\delta_{ij}(n) = \frac{1}{1 + exp\left(-\xi_{ij}(n - M_{ij})\right)} \tag{A.6}$$

Larval survival function

$$\Theta_{ij}(n) = 1 - \frac{1}{1 + exp\left(-r_{ij}(n - Q_{ij})\right)} \tag{A.7}$$

Mortality in host

$$\mu_h(n) = m + (1 - m)exp(-\zeta n) \tag{A.8}$$

Table A.1: Description of parameters and values used in sensitivity analyses.

Greek Symbol	'Base' value(s) used in model	Range of values used in sensitivity analysis	Definition
γ	3	1 – 10	Energetic cost of evaluating host
ζ	0.050	0.001 – 1.000	Shape parameter of $\mu_h(n)$
μ_s	0.50	0.01 – 0.99	Mortality risk associated with searching for a host
σ	1	1 –10	Rate of energy expenditure while searching for host
ξ	0.25	0.10 – 0.50	Shape parameter in $\delta_{ij}(n)$
ψ	0.025 – 0.035	$-0.010 \leq \Delta\psi_{ij} \leq 0.010$	Shape parameter in $\varepsilon_{ij}(n)$
ω	10	5 - 30	Shape parameter in $l_{ij}(n)$

Roman Symbol	'Base' value(s) used in model	Range of values used in sensitivity analysis	Definition
a	0.1 – 0.5	$0.25a - 4.00a$	Maximum energy gain in $\varepsilon_{ij}(n)$
c	0.30	0.00 – 0.30	Affects minimum probability of encounter host in $l_{ij}(n)$
m	0.10	0.01 – 0.99	Minimum risk of mortality in host in $\mu_h(n)$
M	20 – 60	$-40 \leq \Delta M_{ij} \leq 40$	Inflection point in $\delta_{ij}(n)$
N	250	$-40 \leq \Delta N_{ij} \leq 40$	Inflection point in $\varepsilon_{ij}(n)$
Q	13 – 60	$-20 \leq \Delta Q_{ij} \leq 20$	Inflection point in $\Theta_{ij}(n)$
R	80	$-10 \leq \Delta R_{ij} \leq 20$	Inflection point in $l_{ij}(n)$
r	0.20	$0.05 - 0.20$	Shape parameter in $\Theta_{ij}(n)$
t_L	5	1 – 20	Time required to leave the current stand
u	2	0 – 4	Mean in negative binomial distribution describing $L_{ij}(k)$
v_{ij}	10 – 25	5 – 40	Variance in negative binomial distribution describing $L_{ij}(k)$
x_{min}	30	0 – 60	Minimum energy required for successful reproduction

Appendix B

Details of the MPB DSV and game models

B.1 The MPB-DSV model

The Chubaty *et al.* (2009) model maximizes the reproductive fitness of a female mountain pine beetle based upon her expectation of successfully finding a suitable host tree, initiating or joining a mass attack, and laying her eggs inside the host tree. The model considers two state variables, energy (x) and time (t). There is limited time in the season to find and accept a suitable host (T), and fitness ($F(x,t,T)$) is accrued only if a host is found and accepted before the end of this host search phase. Fitness at the end of the season is non-negative, and is non-zero only above a minimum energy level (x_{min}).

$$F(x,T,T) \begin{cases} = 0 & \text{if } x \leq x_{min} \\ \in (0,1] & \text{if } x_{min} < x \leq x_{max}. \end{cases} \tag{B.1}$$

B.1.1 Detailed Equations

Host encounter rate

The baseline probability of encountering a host with attack density n_k follows a negative binomial distribution with mean u and variance v, and describes the background distribution of beetles on each host type.

$$L_{ij}(k) = NegBinom(k; u_{ij}, v_{ij}) \tag{B.2}$$

Host encounter rate is further modified in a density-dependent manner, and follows a logistic-like curve describing the probability of encountering a specific host given its beetle attack density class, k.

$$l_{ij}(E(n)) = 1 - \frac{(1-c_{ij})R_{ij}^{\omega}}{R_{ij}^{\omega} + E(n)^{\omega}} \tag{B.3}$$

The baseline probability of encountering a host of size class i and quality class j is obtained by taking the product of the areas under empirically-derived host-size and -quality distribution curves, denoted by a gamma distribution, $g(x; \alpha, \beta)$, with shape α and rate β. To simulate stands of different qualities the modes of each distribution, $\nu = (\alpha - 1)/\beta$, were either increased or decreased by adjusting α while holding β constant. Baseline estimates for ν values are derived from field data.

Thus, the encounter probabilities for a particular host tree class is a function of a baseline empirical probability of encounter and the (attack) density-dependent effects of beetle pheromones.

$$\lambda_{ijk} = \int_{i-1}^{i} g(s; \alpha_{s_i}, \beta_{s_i}) \times \int_{j-1}^{j} g(q; \alpha_{q_j}, \beta_{q_j}) \times l_{ij}(E(n_k)) \times L_{ij}(k) \tag{B.4}$$

Energy intake rate

$$\varepsilon_{ij}(E(n)) = a_{ij}\left(1 - \frac{2}{1 + exp\left(-\psi_{ij}(E(n) - N_{ij})\right)}\right) \tag{B.5}$$

Mortality and survival functions

Probability of overcoming host defences

$$\delta_{ij}(E(n)) = \frac{1}{1 + exp\left(-\xi_{ij}(E(n) - M_{ij})\right)} \tag{B.6}$$

Larval survival For simplicity, we assume there is no adjustment of oviposition behaviour with respect to attack density or female condition (but see Raffa 2001; Elkin and Reid 2005).

$$\Theta_{ij}(E(n)) = 1 - \frac{1}{1 + exp\left(-r_{ij}(E(n) - Q_{ij})\right)} \tag{B.7}$$

Mortality in host

$$\mu_h(E(n)) = m + (1 - m)exp(-\zeta E(n)) \tag{B.8}$$

B.2 Sensitivity Analyses

Table B.21: Description of parameters and values used in sensitivity analyses.

Greek Symbol	**'Base' value(s) used in model**	**Range of values used in sensitivity analysis**	**Definition**
γ	3	1 – 10	Energetic cost of evaluating host
ζ	0.050	0.001 – 1.000	Shape parameter of $\mu_h(n)$
μ_s	0.50	0.01 – 0.99	Mortality risk associated with searching for a host
σ	1	1 –10	Rate of energy expenditure while searching for host
ξ	0.25	0.10 – 0.50	Shape parameter in $\delta_{ij}(n)$
ψ	0.025 – 0.035	$-0.010 \leq \Delta\psi_{ij} \leq 0.010$	Shape parameter in $\varepsilon_{ij}(n)$
ω	3	3 - 30	Shape parameter in $l_{ij}(n)$

Roman Symbol	**'Base' value(s) used in model**	**Range of values used in sensitivity analysis**	**Definition**
a	0.1 – 0.5	$0.25a$ – $4.00a$	Maximum energy gain in $\varepsilon_{ij}(n)$
c	0.50	0.00 – 0.50	Affects minimum probability of encounter host in $l_{ij}(n)$
m	0.10	0.01 – 0.99	Minimum risk of mortality in host in $\mu_h(n)$
M	20 – 60	$-40 \leq \Delta M_{ij} \leq 40$	Inflection point in $\delta_{ij}(n)$
N	250	$-40 \leq \Delta N_{ij} \leq 40$	Inflection point in $\varepsilon_{ij}(n)$
Q	13 – 60	$-20 \leq \Delta Q_{ij} \leq 20$	Inflection point in $\Theta_{ij}(n)$
R	30	$-10 \leq \Delta R_{ij} \leq 30$	Inflection point in $l_{ij}(n)$
r	0.20	$0.05 - 0.20$	Shape parameter in $\Theta_{ij}(n)$
t_L	5	1 – 20	Time required to leave the current stand
u	2	0 – 4	Mean in negative binomial distribution describing $L_{ij}(k)$
v_{ij}	10 – 25	5 – 40	Variance in negative binomial distribution describing $L_{ij}(k)$
x_{min}	30	0 – 60	Minimum energy required for successful reproduction