

UNIVERSITY OF CALGARY

The Effects Of Resource Distribution And Spatial Scale On The Distribution Of  
Two Species Of Bark Beetle: *Polygraphus rufipennis* (Kirby) And *Trypodendron*  
*lineatum* (Olivier) (Coleoptera: Scolytidae)

By

Jane Soo Hyun Park

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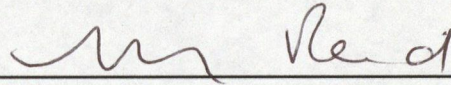
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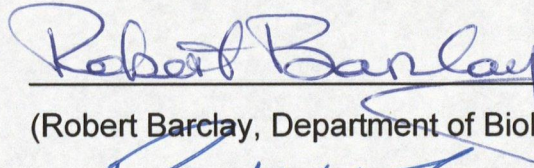


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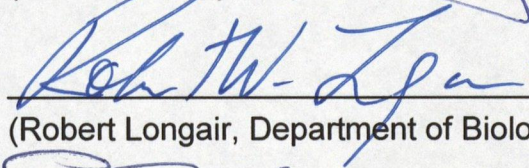
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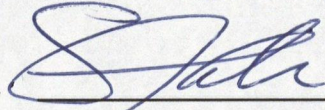
Supervisor (Mary Reid, Department of Biological Sciences)



(Robert Barclay, Department of Biological Sciences)



(Robert Longair, Department of Biological Sciences)



External Examiner (Shelley Alexander, Department of Geography)

20 Sept 2002

Date



## ABSTRACT

Bark and ambrosia beetles (Scolytidae) are forest insects that inhabit the bark and sapwood of many trees. The spatial scale at which bark beetles respond to environmental variation may affect their distributions. I examined the distribution of two bark beetles, *Trypodendron lineatum* (Olivier) and *Polygraphus rufipennis* (Kirby), in relation to different spatial scales of environmental variation. The abundance of both species in a stand increased with the proportion of host trees. However only *T. lineatum* responded to the changes in resource abundance following harvesting. Settlement of *T. lineatum* among stumps was not influenced by landscape variation, but instead stump diameter. *P. rufipennis* settlement among resources differed from *T. lineatum* in that settlement densities were primarily influenced by landscape level variation. This study shows that species with similar life history traits may be affected differently by environmental variation at different spatial scales.

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## 1.0 GENERAL INTRODUCTION

Because the environment in which organisms exist is not homogeneous, most animals must engage in habitat search and selection. Suitable habitat includes patches that vary in quality, and organisms may choose among these to maximize their fitness. Between patches of suitable habitat, a matrix of unsuitable habitat may exist through which organisms must move. This matrix may further influence habitat choice. Although the theory of the interactions of patches and matrices in determining animal distributions is recent, there has been increasing interest in this topic (Wiens, 1997). The effects of the heterogeneous matrix and the distribution of habitat patches on the distribution of organisms are of interest because of the continuing fragmentation of the landscape due to natural and anthropogenic changes. However, the distribution of organisms across the landscape and among habitat patches is dependent on the ability of organisms to detect environmental variation.

The dispersal of organisms in search of suitable habitat is poorly understood, but many models of animal dispersal have been proposed. Models of animal dispersal generally take two approaches (Lima and Zollner, 1996). First, the information-based approach assumes that organisms use information from the surrounding landscape to reach a goal (habitat selection), while taking into consideration stopping rules such as costs. The second approach, based on random walks and diffusion processes, considers organisms unable to utilize information from the landscape to make strategic decisions. Information-based models of animal movement are usually applied to vertebrate species such as

birds and mammals (Andren, 1994; Taborsky and Taborsky, 1995), whereas random walks and diffusion processes are typically applied to arthropods (Rogers, 1972; Helland et al., 1989; Turchin, 1991). However, empirical evidence shows that arthropods are able to strategically use information from the surrounding environment to find suitable habitat. For example, some insects adaptively alter their oviposition decisions in response to host plant density, shifts in life expectancy and habitat quality (Rausher, 1983; Stanton, 1983; Roitberg et al., 1992).

The question of how organisms are distributed among habitat patches has also led to many theories of habitat selection. The ideal free distribution (Fretwell and Lucas, 1970), source-sink theory (Pulliam, 1988), and other variations (Sutherland, 1983; Pulliam and Danielson, 1991; Parker and Sutherland, 1986; Danielson, 1992), attempt to explain the relationship between habitat quality and animal distribution.

### **1.1 Habitat Colonization and the Ideal Free Distribution**

Many models offered with regards to the settlement distributions of organisms are based on the idea of an ideal free distribution (IFD), where, at equilibrium, no individual can increase its fitness by being elsewhere (Fretwell and Lucas, 1970). An IFD assumes that habitat suitability declines with increased population density, and that individuals choose the habitat patch with the highest average suitability at the time of settlement. Organisms dispersing according to an IFD are assumed to incur no costs of searching for suitable

habitat, and are endowed with information concerning the available habitat such as the location and quality of habitat patches. In reality, however, organisms in search of suitable habitat incur costs of movement due to a heterogeneous landscape, and may gather information as they move. The disparities between the assumptions of the IFD and actual ecological situations have led to alternative hypotheses of distribution such as the theory of ideal pre-emptive distribution (Pulliam and Danielson, 1991), which assumes that habitat patches that become occupied are no longer available to other colonists; and the theory of ideal free distribution for unequal competitors (Parker and Sutherland, 1986). These alternatives take into consideration the differences inherent in the quality of both the patches of habitat as well as individuals. Specific factors that may cause organisms to settle in a pattern differing from an IFD include effects due to the matrix through which individuals must move (landscape heterogeneity, costs of movement), and patch distribution (habitat distribution, abundance, and quality). During habitat selection, organisms must face trade-offs between the costs of finding suitable habitat (travel costs), and the benefits to be gained from different habitat patches.

### **1.1.1 Matrix Effects**

Costs of dispersal may become relevant when high quality habitat becomes isolated within the landscape. If high quality patches are surrounded by heterogeneous or homogeneous matrix, the success of an individual's habitat search depends on its dispersal capabilities through the landscape, habitat

requirements and preference, and the rate of movement through different types of habitat. Gustafson and Gardner (1996) created a model including a heterogeneous matrix that predicted that the movement of organisms among patches of habitat may be largely due to landscape heterogeneity. Physical barriers in the matrix may actively funnel individuals towards one patch, or heterogeneity may create patches of preferred land cover (Ricketts 2001; Merriam and Lanoue, 1990). Areskoug (2001) showed that remnant forest corridors were used by native fauna, including birds, mammals, amphibians and reptiles as dispersal corridors between pastures. Tropical dung beetles and butterflies have been found to use linear strips of rain-forest vegetation as dispersal corridors (Hill, 1995). Furthermore, Hindmarch and Reid (2001) suggested that beetles prefer thinned forest-stands due to their physical structure. Therefore, a heterogeneous landscape matrix may cause asymmetrical transfers of organisms where individuals may settle disproportionately in certain areas despite higher suitability of other areas. In contrast, the IFD predicts that individuals would not aggregate if being in a different patch increases fitness.

### **1.1.2 Effects of Habitat Quality**

The IFD predicts that across all patches, the number of individuals should be proportional to habitat abundance in a particular patch. However, several studies have shown that the distribution and abundance of habitat patches of varying quality influence the spatial distribution and dispersal of organisms

(Andow, 1990; Coll and Botrell, 1994). In a source-sink model by Pulliam and Danielson (1991), the distribution of individuals occupying habitat patches was suggested to depend on population size and the distribution of patches of differing quality. They showed that when habitat fragmentation occurs, the proportions of source, sink and unusable habitat patches may change, affecting an individual's success. However, the net effect of the habitat patch loss depends on the quality of the patch and the ability of an individual to select patches. If a low quality patch is removed, the ability of the organism to detect habitat will play a less important role than if a high quality patch is lost. If there is a low proportion of source patches relative to both sink and unusable patches, then source patches will be difficult to locate. By increasing the effort needed for searching, habitat selection may become less efficient and individuals may be forced to settle in sink habitat. However, the ability to discern differences in habitat quality will allow an individual to better find remaining patches of high quality when they are scarce.

For organisms having a limited dispersal phase, it may be too costly to always reject suboptimal habitat. For time limited dispersers, Ward's (1987) model predicts that the optimal strategy is to accept only good habitat during initial search, but if unsuccessful, to then accept any habitat for the remainder of the search period. The time frame of an organism's initial discrimination phase is expected to depend on the probability of finding good quality habitat.

The models proposed by Pulliam and Danielson (1991) and Ward (1987) predict that organisms may be distributed unevenly among poor and good quality



habitat as with the IFD. In an ideal free distribution, all individuals eventually settle in patches with the same average fitness due to density dependent regulation, irrespective of search costs. However, the IFD ignores the costs of searching. Models proposed by Pulliam and Danielson (1991) and Ward (1987), point to the importance of the efficiency of searching for suitable habitat with respect to costs of movement, and an individual's ability to locate habitat. If individuals incur search costs, trade-offs may exist between selecting a habitat of high quality and potentially high search costs. Therefore, in some cases, habitat of sub-optimal quality but with relatively low search costs may have higher densities than expected by the IFD.

### **1.1.3 Insects and Habitat Search**

Previously it has been assumed that insects search for habitat randomly across the landscape (Rogers, 1972). However, more recently insect movement studies and models of insect movement have suggested that insects search non-randomly (Bell, 1990; Steinberg et al., 1993; Turchin, 1998). One group of insects that uses information obtained from the environment during dispersal is bark beetles (Coleoptera: Scolytidae). In particular, bark beetles locate suitable host tree species by using host and non-host kairomones and semiochemicals to direct search (Byers, 1989; Byers et al., 1989; Wilson et. al., 1996; Borden et. al., 1997). The habitat used by bark beetles is often sparse since it typically consists of freshly downed wood of particular host species (Atkins, 1966). Therefore, searching for habitat efficiently is extremely important. I expected that changes

in stand density, tree species' composition, and the abundance of habitat would be important to the distribution of bark beetles during search for suitable habitat, and the subsequent settlement patterns of these insects.

The resource concentration hypothesis proposed by Root (1973) states that herbivorous insects are more likely to find hosts that occur in dense or nearly pure stands. Furthermore, those individuals that arrive in an area containing many suitable hosts will remain in the area causing an increase in the population density in that area. In areas where host plants are concentrated, the ability of an organism to detect habitat will be less vital to successfully finding suitable habitat, than in areas where suitable habitat is interspersed with unsuitable habitat (Pulliam and Danielson, 1991). Moreover, restricting search to areas with large numbers of host plants would decrease both search costs and time spent searching for suitable habitat (Grunbaum, 1998), which may be important for time- or energy-limited dispersers (Ward 1987).

Many studies have shown that herbivorous insects alter their movement towards areas with higher densities of host plants (Douwes, 1968; Risch, 1981, Batch, 1984; Turchin, 1988; Andow, 1990). However, all of these studies have examined agricultural crop insect populations in relation to monocultures and polycultures. To date, no studies have examined the tendency for forest dwelling insects to follow the predictions of the resource concentration hypothesis. Unlike insects that feed on agricultural plants grown in large homogeneous crops or systematically mixed crops, forest dwelling insects inhabiting freshly dead wood must deal with highly variable and unpredictable habitat. Therefore, there is a

need to understand how host plant abundance and distribution affect wood dwelling insects in this larger and more diverse landscape.

## **1.2 Spatial Scale and the Distribution of Organisms**

The IFD, RCH as well as source-sink models rely heavily on the concept of habitat patches on the landscape. However, different species of organisms respond to variation across the landscape at different scales. With (1994) showed that among three different species of grasshoppers, recognition of variation in environmental characteristics varied by spatial scale, causing differences in rate of dispersal. Roland and Taylor (1997) showed similar results for four parasitoids of forest tent caterpillars. In their study, rates of parasitism were influenced by forest structure at differing spatial scales. These, and other studies by Morris (1987), Wiens (1989), Samu et al (1990), Orians and Wittenberger (1991), Doak et al. (1992), Huhta et al. (1998), and Ritchie (1998), emphasize the significance of examining multiple spatial scales when considering environmental effects on behavioural processes.

Spatial scale issues are particularly pertinent when testing ecological theories such as the IFD and RCH. Ray and Hastings (1996) conducted a meta-analysis on 79 papers of insect population studies and found that the detection of density-dependent population regulation was correlated to the scale at which the study was conducted. Therefore, empirical studies on population distributions must take into account different scales at which responses to environmental variation may occur.

### **1.3 Selective Logging/Silvicultural Thinning**

Anthropogenic disturbances such as logging alter the landscape and cause changes in the distribution and abundance of coarse woody debris. Silvicultural thinning and selective logging are two common practices resulting in lower stand density and periodic inputs of coarse woody debris (McCarthy and Bailey, 1994; Tinker and Knight, 2000). Following felling, quantities of host volatiles increase making logging debris left on site such as logs and stumps particularly attractive to bark beetles inhabiting dead wood (Lindelow et al., 1992). Furthermore, logging produces a landscape in which there are discrete areas where this habitat is clumped. The irregular distribution of this habitat may cause bark beetles to alter their movements based on habitat availability and abundance. However, the scale at which these anthropogenic changes occur is often smaller than the scale at which natural inputs of suitable habitat occur. If bark beetles are accustomed to detecting habitat that is unevenly and sparsely distributed across the landscape, responses to logging-induced changes in habitat abundance may not be easily detected.

The removal of standing trees during thinning also causes changes in the physical structure of a stand that may cause changes in the movement of bark beetles (Hindmarch and Reid, 2001). Moreover, the removal of trees causes gaps in the canopy, allowing an increase in sunlight reaching the forest floor, moisture and available nutrients. This increase in resources may result in an increase in the density of understory vegetation (McConnell and Smith, 1965;

Thysell and Carey, 2000). If these structural changes hinder or assist dispersal, individuals may prefer to disperse through areas that minimize travel costs.

If bark beetles accumulate in certain areas (e.g. those containing large amounts of habitat or facilitating dispersal), settlement patterns may differ from those predicted by the ideal free distribution. In these situations, beetles may accumulate in some patches of suitable habitat while others remain unnoticed.

#### **1.4 Study Objectives**

In this thesis, I test predictions of habitat search and selection models in two species of bark beetles that inhabit freshly dead wood: *Trypodendron lineatum* (Olivier) and *Polygraphus rufipennis* (Kirby). I examine the effects of host tree distribution, habitat abundance and physical structure on the movement and settlement of these species. More specifically, I determine whether stand composition, abundance of logs and stumps, and stand density influence the distribution *T. lineatum* and *P. rufipennis*. I used the EMEND (Ecosystem Management by Emulating Natural Disturbance) project to elucidate these effects in the context of forest harvesting regimes which alter the density of forest stands and the abundance of stumps and logs.

#### **1.5 Study Site**

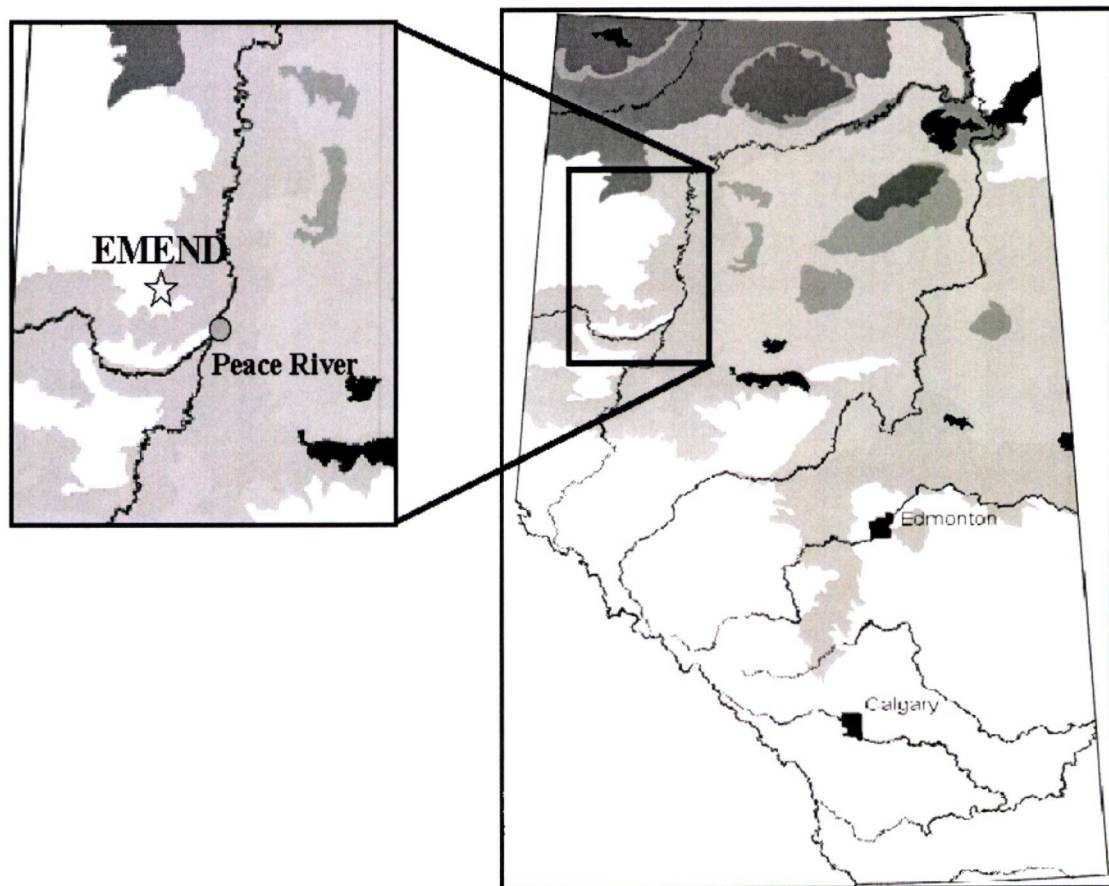
The EMEND project site is located approximately 90 km northwest of Peace River, Alberta (56° 40' N 118° W, Figure 1.1). The topography of the

region is relatively flat with a range in elevation from 667 m to 880 m. It lies within the Upper Boreal Cordilleran Ecoregion, which consists of mixed stands of white (*Picea glauca* (Moench)) and black spruce (*Picea mariana* (Miller)), trembling aspen (*Populus tremuloides* (Michx.)) and balsam poplar (*Populus balsamifera* (L.)). Forest stand age within the project ranged from 80 to 140 years. EMEND is a multidisciplinary project that aims to determine which forest harvest techniques are ecologically sustainable in maintaining biotic communities, spatial patterns of forest structure, and ecological integrity (Sidders and Spence, 2000). To this end, EMEND uses different harvest treatments to mimic natural disturbances such as fire.

## 1.6 Study Design

The experimental design at EMEND is structured with respect to two main variables: stand type and residual level. Stand type refers to the composition of the forest canopy prior to harvest. The four different stand types examined at EMEND are: deciduous-dominated (DDOM) stands - greater than 70% mixture of trembling aspen and balsam poplar; deciduous-dominated with conifer understory (DDOMU)- conifer understory at least 50% canopy height; mixed (MX) stands 35-65% mixture of conifer and deciduous; and conifer-dominated (CDOM) greater than 70% mixture of white and black spruce. Three replicates of each stand type were randomly chosen from a range of candidate stands during the summer of 1997. Forest stands were chosen to be uniform and similar in age, canopy and understory vegetation composition. Although attention was



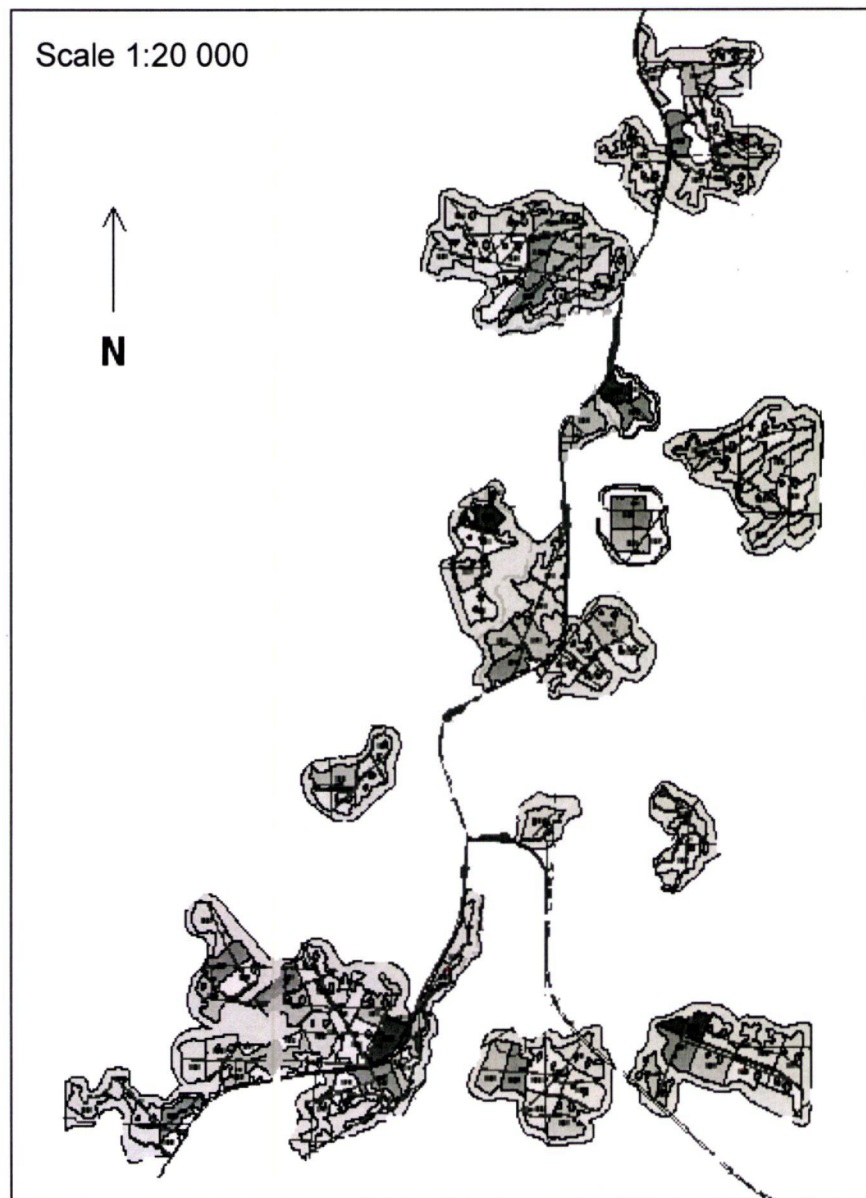


Source: Government of Alberta/Natural Heritage Information Centre 2001

**Figure 1.1.** EMEND study site located approximately 90 km northwest of Peace River, Alberta.

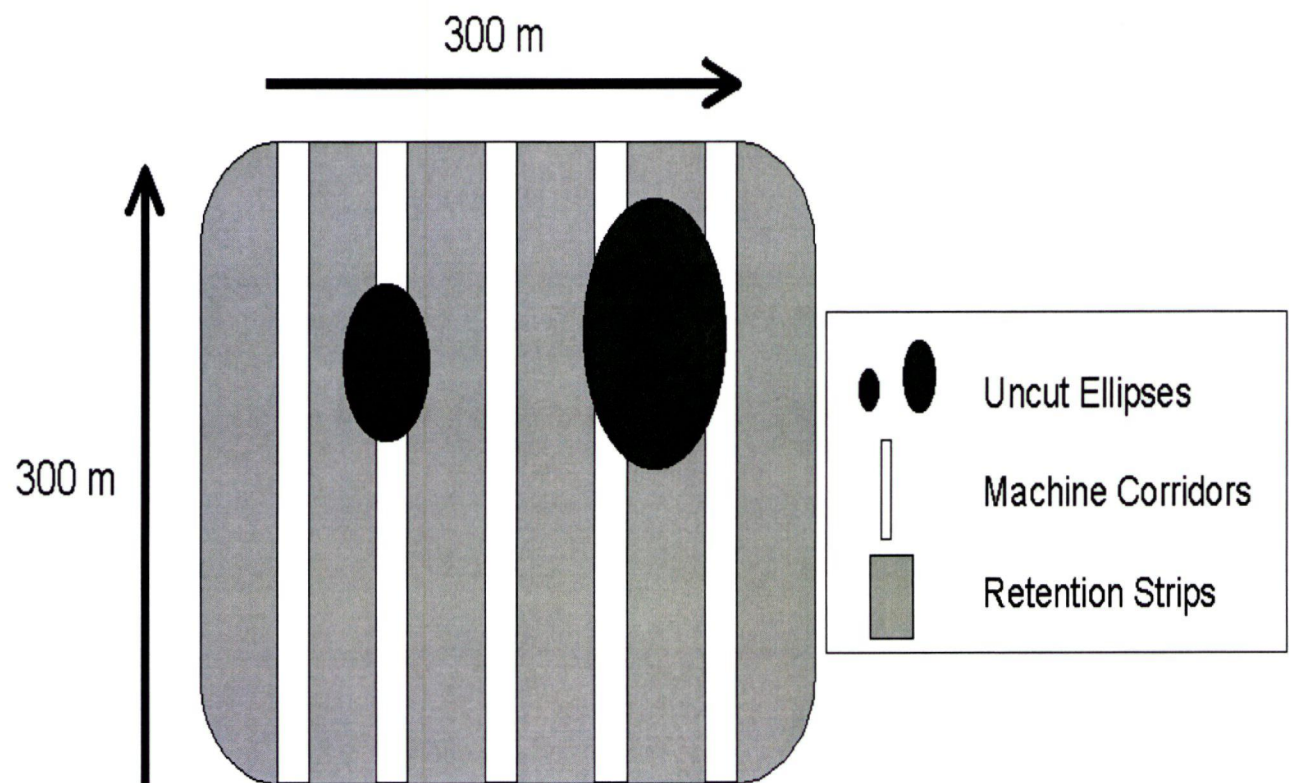
given to ensure that experimental stands and treatment compartments were uniform across the project, the large spatial extent (approximately 1000 ha) of the project resulted in minor differences in stand characteristics (age, composition) and treatment compartments (diameter of trees harvested, amount of logging debris remaining).

Within each replicate, several 10 ha (approximately) compartments were also established to receive harvest treatments in 1998 (Figure 1.2). During the winter logging season of 1998-1999, residual treatments were applied to all compartments. Retention level refers to the percentage of trees left standing post harvest, and includes six categories: 0% (Clearcut), 10%, 20%, 50%, 75% and uncut controls. Each treatment compartment was approximately 10 ha. All operations (felling and skidding) were conducted in 5 m wide machine corridors that were spaced 20 m (centre to centre) apart, leaving a 15 m wide retention strip. Machine corridors account for 25% of the tree removal from each compartment. Retention levels (10%, 20%, 50%) were achieved by systematic tree removal from the retention strips. The retention strip removal protocol consisted of removing 1 of 3 trees for the 50% residual level, 3 of 4 trees for the 20%, and 7 of 8 for the 10%. Machine corridors and retention strips were oriented perpendicular to the prevailing wind direction (north-south). 10%, 20% and 50% retention level compartments had two uncut ellipse-shaped patches (0.20 ha and 0.46 ha) to mimic old growth islands often left following fire (Figure 1.3). I examined all three replicates of the four stand types for the 10%, 20%, 50%, 75% and uncut control compartments in 1999 and 2000.



Source: <http://www.biology.ualberta.ca/EMEND>

**Figure 1.2.** Map showing layout of forest stands and harvest treatments. The large polygons represent forest stands of different stand types. The smaller shaded polygons within the forest stands represent retention level compartments. Each compartment is approximately 10 ha. The dark lines running north-south and from the southeast are access roads.



**Figure 1.3.** EMEND harvest treatment pattern.

## 1.7 Study Species

In this study, I chose to focus on bark beetles (Coleoptera: Scolytidae), with emphasis on two species, *Trypodendron lineatum* and *Polygraphus rufipennis*. Bark beetles are insects that generally inhabit the phloem and xylem of forest trees, especially conifers (Bright, 1976). These small insects can be classified into primary and secondary bark beetles. Primary bark beetles inhabit live trees of normal vigor, while secondary beetles such as *T. lineatum* and *P. rufipennis*, inhabit dead, dying or weakened trees. However, despite their preference for dead and dying wood, secondary insects are capable of attacking healthy trees when population densities become high.

Striped ambrosia beetles, *Trypodendron lineatum*, are wood borers that use the sapwood of dead and dying trees, bringing a symbiotic fungus which they use to assist in the digestion of the wood. This species overwinters as adults and emerges in the spring to disperse across the landscape in search of suitable habitat (Prebble and Graham, 1957). *T. lineatum* is an economically important pest to the forest industry (McLean, 1985), as can cause damage to stored wood in millyards (Lindelow et al., 1992). Although many studies have examined both dispersal and settlement of *T. lineatum* (Chapman and Kinghorn, 1958; Chapman, 1962; Rudinsky and Daterman, 1964; Dyer and Chapman, 1965; Salom and McLean, 1989, 1990; 1991a.b), no studies to date have examined the effect of stand composition, density and habitat distribution on the distribution of *T. lineatum*.

In addition to the wood borer *T. lineatum*, I examined the distribution and

settlement of the four-eyed spruce beetle, *Polygraphus rufipennis*. This species breeds in the inner bark of freshly dead white (*Picea glauca*) and black (*P. mariana*) spruce trees. Like *T. lineatum*, *P. rufipennis* overwinters as adults and requires a dispersal period to search for suitable habitat. *P. rufipennis* is also considered a pest species, due to its ability to take advantage of trees weakened by other forest pathogens such as spruce budworm, *Choristoneura occidentalis* (Freeman) (Bowers et al, 1996). However, studies on the dispersal behaviour of *P. rufipennis* have not been conducted.

Secondary bark beetles such as *T. lineatum* and *P. rufipennis* are ideal study organisms to examine the effects of spatial scale and landscape heterogeneity on population distributions. These organisms are common across Canada (Bright, 1970), and are easily examined because they inhabit distinct habitat patches (logs and stumps). Furthermore, the use of Lindgren funnel traps (Lindgren, 1983) with synthetic pheromones, is a widely used method for estimating beetle distributions.

By examining both of these species, I sought to elucidate potential differences in the scale at which environmental factors affect the distribution of bark beetles. Although members of this taxonomic group appear similar, they differ widely in ecology and biochemical adaptations to host trees (Byers, 1995). *T. lineatum* generally inhabits the xylem of conifer stumps up to two years old, while *P. rufipennis* inhabits the phloem freshly dead logs. These differences may lead to differences in the response to landscape and habitat patch variation. By examining each species separately, I was able to examine environmental factors



and spatial scales relevant to each species.

## Chapter 2

### **Distribution of a Bark Beetle, *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae) in a Harvested Landscape**

#### **2.1 Introduction**

Organisms in search of suitable habitat must have the ability to detect and locate suitable patches of habitat amidst a heterogeneous matrix of unsuitable habitat. Furthermore, there are likely strategies that improve search efficiency, or decrease the effort needed to locate suitable habitat during a searching episode. The resource concentration hypothesis (Root, 1973) was an early recognition that search costs may influence the distribution of individuals. This hypothesis suggests that herbivorous insects restrict the habitat search to areas with high densities of host plants. As predicted, several studies have shown that insects concentrate their search for habitat in areas of high habitat concentration, leading to higher insect abundance in these areas (Douwes, 1968; Risch, 1981; Batch, 1984; Turchin, 1988; Andow, 1990).

Even if insects restrict their search to areas with many host plants, they must still contend with the natural variation of habitat quality among individual plants (habitat patches). These differences in patch quality, and the relative abundance of patches of varying quality, should influence the propensity of a searching individual to accept a specific patch. The extent to which individuals discriminate among habitat patches may depend on the opportunity for choice. For organisms limited by time or energy, habitat specificity (i.e. the rejection of sub-optimal habitats) is expected to increase with the abundance and quality of

optimal habitat (Ward 1987, Danielson 1992). If a given area is comprised of large amounts of unusable habitat, then individuals may spend a long time searching for suitable habitat. In this case, poor quality habitat patches will become more important if good quality patches are difficult to locate, and individuals may select a low quality patch even if a better patch exists elsewhere (Ward 1987).

Even if optimal suitable habitat is abundant, high quality patches may be neglected if physical barriers or corridors of movement exist. Corridors of movement may effectively funnel individuals towards or away from particular patches: For example, dung beetles and butterflies use dispersal corridors caused by the physical structure of forest stands (Hill, 1995; Sutcliffe and Thomas, 1996). In these cases, strips of suitable forest cover promoted dispersal between forest stands. The physical structure of a forest stand may also cause differences in microclimate (wind, temperature) that in turn may hinder or aid the dispersal of individuals. For example, thinning of forest stands causes increases both in temperature and wind velocity (Bartos and Booth, 1994), both of which may assist the dispersal of bark beetles (Scolytidae; Hindmarch and Reid, 2001). However, other studies have suggested that increased wind and stand temperatures deter bark beetle dispersal (Amman et al. 1988; Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al., 1991; 1992a, b; Bartos and Booth 1994).

The ideal free distribution (IFD; Fretwell and Lucas, 1970) states that individuals will settle where their access to habitat is highest, dependent on both

intrinsic patch quality and the number of other individuals in the patch. As a result, high quality habitat will support larger numbers of individuals, but the fitness of individuals across all patches will be equal at equilibrium. If search by dispersers is affected by a combination of habitat patch abundance, habitat quality and physical structure of the landscape, then individuals will be distributed across the landscape in response to these variables, and their distribution based on these responses will likely deviate from the IFD. The IFD assumes that individuals searching for habitat are 'ideal' in their ability to search and detect habitat due to their perfect knowledge of the habitat available to them and lack of search costs. However, the alteration of behaviour to increase effectiveness of searching and minimize search costs may lead to deviations from the IFD since areas containing high quality patches in small quantities may be left unoccupied (Kennedy and Gray, 1993).

In this study I examine the effects of host plant distribution, habitat abundance, and physical structure of the landscape on the dispersal and settlement distribution of the ambrosia beetle, *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae). The habitat of *T. lineatum* is dead and dying coniferous wood particularly one or two years following tree death (Dyer and Chapman, 1965). Consequently, its habitat is normally rare, unpredictable and ephemeral, even though the host tree species may be abundant. These insects overwinter as adults in the duff and emerge in the spring when they fly in search of suitable breeding material from April through May (Chapman and Kinghorn, 1958; Chapman, 1962). During this dispersal flight, individuals lose approximately one

quarter of their stored lipids (Nijholt, 1967). Therefore, individuals must find their rare habitat quickly to minimize the loss of lipids needed to mate and reproduce.

While individual *T. lineatum* are capable of flying distances up to 40 km (Salom and McLean, 1991a), long distance flight is inefficient, especially if habitat is located nearby. Therefore, the ability to detect suitable habitat is likely important. *T. lineatum* are attracted to volatiles emitted by conifer logs and stumps (Moeck, 1970; Lindelow et al, 1992). It has been speculated that broad plumes of host kairomones emitted from areas with large quantities of habitat attract beetles, and subsequent settlement occurs in any suitable habitat encountered (Chapman, 1962; Dyer and Chapman, 1965; Chapman and Kinghorn, 1958; Chapman, 1966). *T. lineatum* can also bias their search to areas likely to contain high concentrations of habitat, such as coniferous forest stands, by avoiding volatiles emitted by deciduous trees (Borden et al., 1997). While *T. lineatum* has the chemosensory facilities to detect areas containing habitat, no studies have examined the propensity for *T. lineatum* to alter its search behaviour based on differences in the strength of these cues caused by the density of host trees.

The ability to detect habitat may be influenced by the matrix of unusable habitat through which individual beetles must fly. *T. lineatum* orient better to olfactory signals in the absence of wind and have been found to move through forested areas more often than open areas (Salom and McLean, 1989, 1991a). However, Hindmarch and Reid (2001) found that trap catches of *T. lineatum* were higher in areas with higher wind velocities associated with lower tree

densities. Therefore, the exact nature of the influence of the physical structure of the forest has not been resolved. Furthermore, many bark beetles, including *T. lineatum*, require a minimum temperature to fly (Rudinsky and Daterman, 1964). If this flight threshold is met more often in the less dense stands, then bark beetles would benefit from preferential dispersing through these stands.

The primary objective of this study was to determine if *T. lineatum* biases its movements towards forest stands likely to contain host trees (coniferous stands) as predicted by Root's (1973) resource concentration hypothesis. If landscape level attributes influence the distribution of bark beetles at the landscape scale, then it follows that the settlement of bark beetles among habitat patches may be influenced by landscape attributes as well. I sought to determine whether decisions based on stand attributes cause deviations from the predictions of the ideal free distribution. I examined the effects of habitat abundance and quality, and the physical structure of the forest on the distribution of beetles at the landscape and habitat patch level.

This study contributes to the elucidation of the relationship between individual habitat search and spatial scales. Traditionally, studies have examined population responses to variation at a single scale, but they have overlooked the effects at other scales. More recently, the effect of scale on population responses has been emphasized (Kotliar and Wiens, 1990; Doak et al., 1992; and Ritchie, 1998). However, most studies have focused only on one spatial scale. For example, Salom and McLean (1991) examined environmental influences such as wind and forest stand density on beetle dispersal. Similarly,



Chapman (1962) studied *T. lineatum* settlement among logs, but did not consider possible landscape level factors that may influence colonization of logs. This study will attempt to determine whether landscape level features affect distributions of *T. lineatum* at both the landscape level and the habitat level.

## **2.2 Methods**

### **2.2.1 Study site**

The study site was located at the EMEND (Ecosystem Management by Emulating Natural Disturbance) project site located in the boreal mixedwood forest northwest of Peace River, Alberta (Figure 1.1). In 1997, four forest stand types were identified: deciduous-dominated (DDOM) (70-95% deciduous: *Populus balsamifera* L., *P. tremuloides* (Michx), deciduous-dominated with conifer understory (DDOMU), mixed (MX) (35-65% deciduous and conifer), and conifer-dominated (CDOM) (70-95% conifer: *Picea glauca* (Moench), *P. mariana* (Miller), *Abies balsamea* (L.). Each stand type had 3 replicates. The replicates were divided into compartments of 8 – 10 ha that were subjected to the harvesting treatments. Harvest treatments used in this study consisted of five retention levels (retention referring to the proportion of standing trees remained after harvest): 10%, 20%, 50%, 75%, and 100% (controls). To apply the treatments, trees were harvested from 5 m machine corridors, where all vegetation was removed (75% compartments had only machine corridors), and 15m retention strips, where the remaining selected felling was carried out. Harvesting occurred in the winter of 1998-1999.

### 2.2.2 Bark beetle distribution and abundance

To examine the effect of conifer abundance alone on the distribution of *T. lineatum*, beetles were sampled during the summer of 1998, prior to harvesting. Thirty-two baited 12-funnel Lindgren traps (Lindgren, 1983) were erected in 6 deciduous-dominated stands, 6 deciduous-dominated with conifer understory, 12 mixed-wood, and 8 conifer-dominated stands. These 32 stands were candidate stands from which 3 replicates of each stand type were chosen for application of the harvest treatments in 1999. Traps were centrally located within a stand at a height of approximately 1.5m from the ground. Traps were baited with tree kairomones ethanol and alpha-pinene (release rates for both ethanol and alpha-pinene were 1 g/day; from Phero Tech Inc.). Previous studies have shown that *T. lineatum* are attracted to alpha-pinene (Bauer and Vité, 1975; Salom and M<sup>c</sup>Lean, 1988, Lindelow et. al, 1992) and ethanol (Moeck, 1970) during dispersal. Traps were emptied every two weeks between 31 May 1998 and 3 August 1998. Trap placement and sample collection was carried out by EMEND core crew prior to my involvement in the study.

Harvesting provided large differences in the actual abundance of habitat among stands, since *T. lineatum* inhabit stumps following harvest, and altered the physical structure of the forest matrix. In 1999 and 2000, I placed one baited 12-funnel Lindgren trap in each 10%, 20%, 50% and control compartment in all replicates of all stand types for a total of 48 traps. The same trap locations were used in both years. Each trap was baited with alpha-pinene released at a rate of

100-150 mg/day from Phero Tech Inc. Insecticide (Vapona™) was placed in each collection cup. Traps were placed within retention strips in the centre of each compartment. In 1999, traps were emptied every two weeks from 09 May to 08 August. In 2000, I collected *T. lineatum* from 09 May and 27 June, since 1999 data showed that this species' peak dispersal occurred between 09 May to 14 June. Samples were stored in plastic bags, frozen and counted in the laboratory.

### **2.2.3 Habitat Abundance**

To determine the relative importance of host-tree abundance and habitat abundance in determining *T. lineatum* abundance, I compared the effects of the proportion of spruce in a compartment and the number of stumps found within a compartment. I used the proportion of both white and black spruce (*Picea glauca* and *P. mariana*, respectively) in a compartment as a measure of the abundance of host tree species in a forest stand. The proportion of spruce within a stand was estimated from ground surveys of species composition in each stand, obtained from the EMEND project core database. The estimated number of spruce stumps (i.e. habitat abundance) per compartment was calculated from the estimated number of conifers in each stand multiplied by the proportion of trees felled during harvest (retention level). Stumps can be assumed suitable for colonization in 1999 because all trees were felled in the 1998-1999 logging season.

#### **2.2.4 Matrix Assessment**

To further examine the influence of the physical structure of the forest on the movement of *T. lineatum*, I conducted a separate experiment in 2000 in which the abundance of beetles in machine corridors and retention strips were compared. To determine whether machine corridors acted as corridors or barriers for movement by *T. lineatum*, I placed baited (alpha-pinene) traps in the three conifer-dominated 75% retention compartments. In each compartment, 6 baited traps were erected, with 3 being placed within retention strips and 3 being placed in machine corridors from 09 May to 27 June 2000.

#### **2.2.5 Habitat Colonization Surveys**

To estimate the proportion of habitat colonized in each compartment in 1999, I measured 10 spruce stumps (diameter and height), and recorded the presence or absence of *T. lineatum*. Stumps were selected such that they were no closer than 50 m apart within a particular machine corridor or retention strip, to ensure uniform sampling across compartments. In compartments with fewer than 10 conifer stumps in total, all stumps were measured. Distinctive boring dust made by individuals as they enter the stump indicated presence of *T. lineatum*. I also excavated 10 individuals from each stump and verified that they were *T. lineatum*.

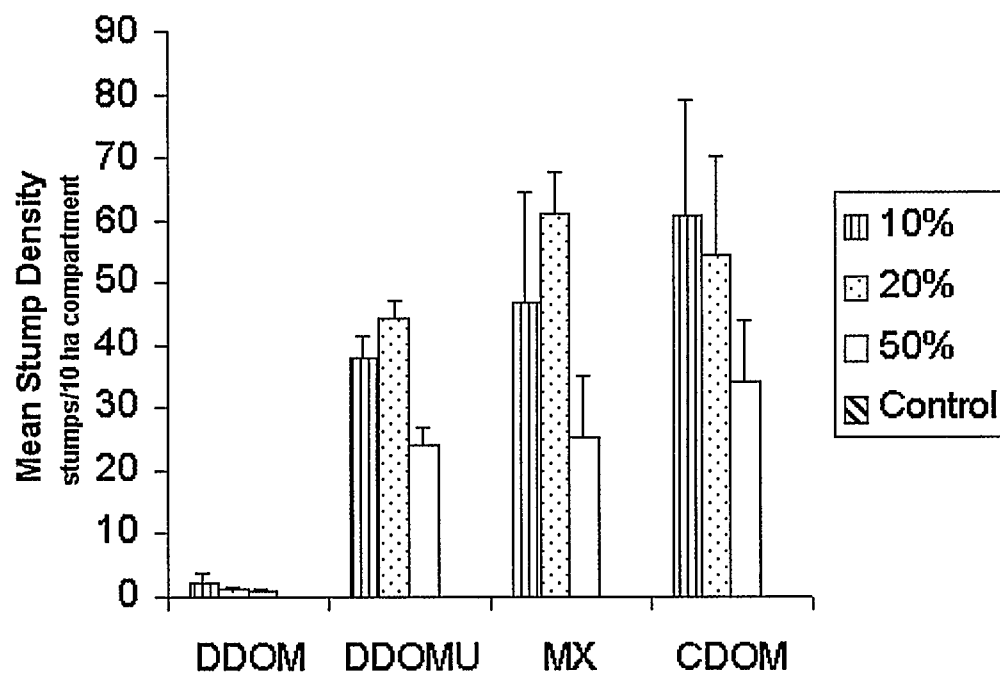
### **2.2.6 Analyses**

Analyses were performed using JMP® Version 3.0 (SAS Institute, 1995). I used an alpha of 0.05 for all analyses. I used the sum of all beetles caught in each compartment over the whole sample period. The sums from all sample dates were used since the objective of the study was not to examine temporal variations in insect abundance, which may be due to meteorological influences, but to examine overall changes in insect population density. Initial models included all interactions, but final models include significant interactions only. When variance inflation factors (VIFs) were greater than 10, a multicollinearity problem was identified and model variables with the highest VIFs were eliminated until all VIFs were less than 10. Least square means were used for the Tukey-Kramer Honestly Significant Difference (T-K HSD) tests to determine significant differences among treatments. All data were transformed if necessary to meet assumptions of normality. Means are reported  $\pm 1$  SE unless otherwise noted.

## **2.3 Results**

### **2.3.1 Description of the Environment**

Figure 2.1 shows that stump abundance was not uniform across all stand types and retention levels. To determine whether the abundance of conifer stumps varied according to stand type and retention level, I used a split plot ANOVA (stand type, retention level nested in stand type, and replicate nested in stand type). Stump abundance was significantly affected by both stand type and



**Figure 2.1.** Mean conifer stump density by stand type and retention level with standard error. Stand type abbreviations are as follows: DDOM (deciduous-dominated), DDOMU (deciduous-dominated with conifer understory), MX (mixed), CDOM (conifer-dominated).

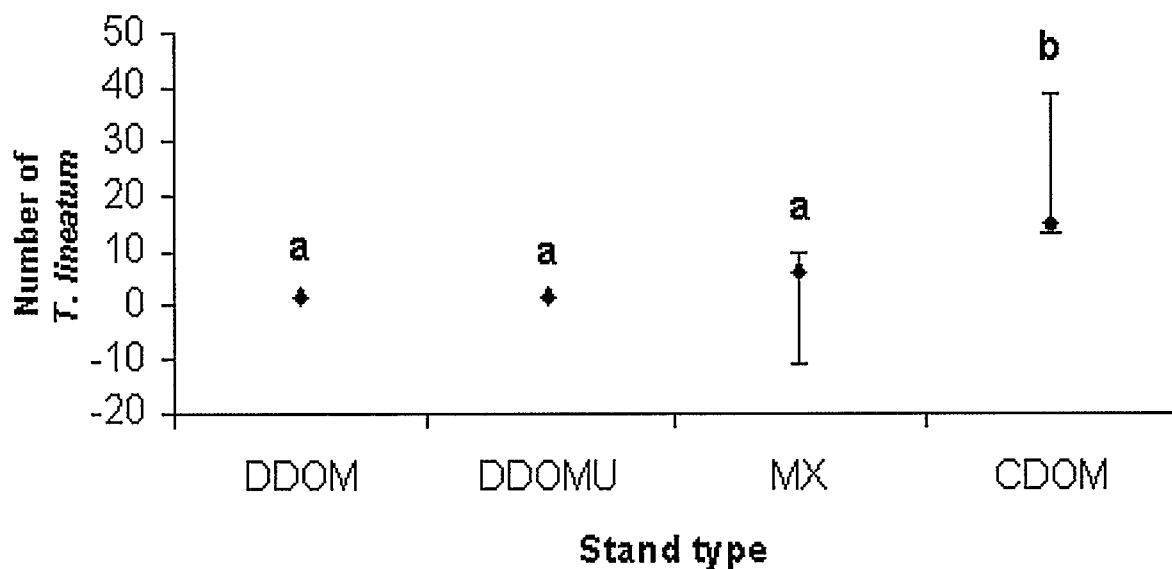
retention level (overall model:  $R^2=0.90$ ,  $F_{23,24}=9.50$ ,  $p<0.0001$ ; Figure 2.1).

Conifer stumps were least abundant in deciduous-dominated stands (T-K HSD  $p<0.05$ ). Stumps were also less abundant in control stands than 10% and 20% retention level stands (T-K HSD  $p<0.05$ ).

To determine whether diameter of stumps varied by stand type and retention levels (control stands were not included in analyses, since no stumps were measured), I conducted a split plot ANOVA (stand type, retention level nested in stand type and replicate nested in stand type). Stand type had a significant effect on stump diameter ( $F_{19, 269}=5.66$ ,  $p<0.0001$ ; overall model:  $R^2=0.28$ ;  $F_{3, 285}=8.36$ ,  $p<0.0001$ ) with CDM and MX stands having significantly larger stumps than DDOM and DDOMU stands (T-K HSD,  $p<0.05$ ) (least square mean  $_{CDM}=43.12\pm1.51$  cm;  $_{LSM_{MX}}=42.52\pm1.43$  cm;  $_{LSM_{DDOM}}=36.43\pm3.01$  cm;  $_{LSM_{DDOMU}}=33.97\pm1.48$  cm respectively). Retention level also had a significant effect on stump diameter ( $F_{8,280}=2.82$ ,  $p<0.006$ ), with the smallest diameter stumps being found in 20% retention stands. Replicate also had a significant effect ( $F_{8,280}=6.66$ ,  $p<0.0001$ ). The significant effects of stand type, retention level and replicate on diameter may be due to biases in the selection of trees during the harvesting process.

### 2.3.2 Stand type and Retention Level Effects on Beetle Distribution

To analyze the distribution of *T. lineatum* as a function of stand type prior to harvest (1998), I transformed the data using a reciprocal transformation to meet the assumptions of normality. Furthermore, since each stand type did not



**Figure 2.2.** Mean number of *T. lineatum* captured in funnel traps per compartment prior to harvest (1998) with 95% confidence limits as a function of stand type. Means and confidence limits were back-transformed from reciprocal transformed data. Stand abbreviations as in Figure 2.1. Similar letters indicate non-significant differences (Tukey-Kramer HSD-  $p > 0.05$ ).



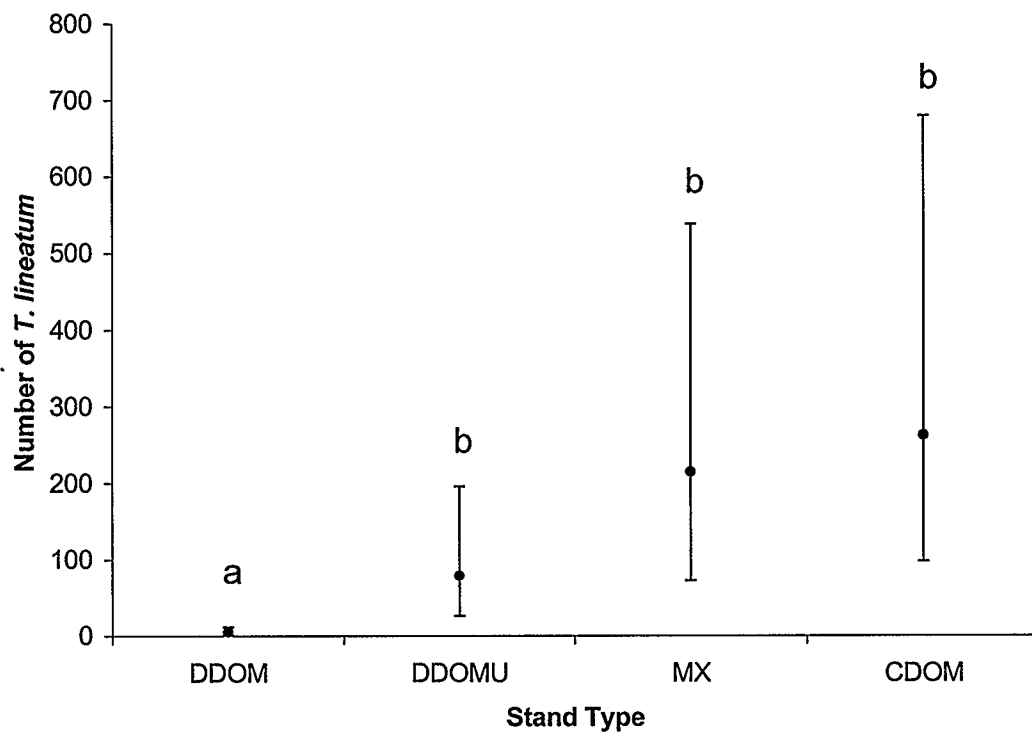
have equal numbers of traps, I used the means of all traps in each replicate.

Stand type had a significant effect on the number of *T. lineatum* caught (overall model:  $R^2=0.68$ ;  $F_{3,11}=5.61$ ,  $p<0.03$ ; Figure 2.2) Beetles were more abundant in conifer-dominated stands compared to stands with a significant deciduous component.

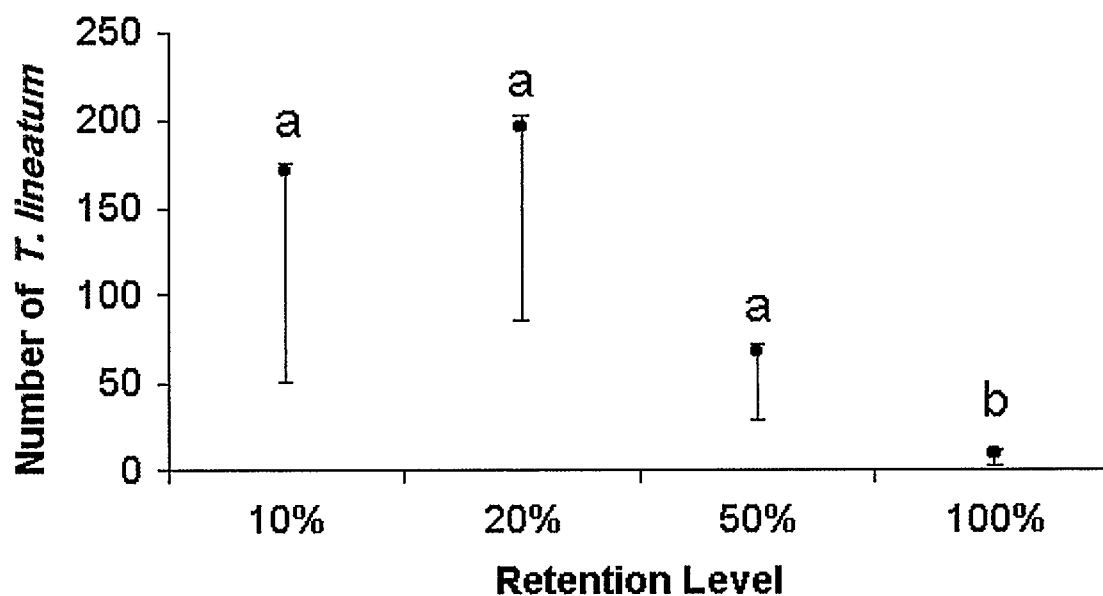
To examine the response of *T. lineatum* to the landscape following harvest (1999-2000), I used a four-way split plot ANOVA (Factors: stand type, retention level nested within stand type, replicate nested within stand type, year (random)). Trap catches were natural log transformed for analysis. Neither replicate nor year had an effect on the number of *T. lineatum* caught ( $p>0.05$ ). However, stand type had a significant effect on the number of beetles caught in a trap ( $F_{3,95}=9.85$ ,  $p<0.005$ ; overall model:  $R^2=0.62$ ,  $F_{24,71}=4.77$ ,  $p<0.0001$ ). Traps in deciduous-dominated stands caught fewer beetles than all other stand types (T-K HSD,  $p<0.05$ ) (Figure 2.3). Retention level also had a significant effect on the number of beetles caught in traps ( $F_{12,95}=4.47$ ,  $p<0.0001$ ). Trap catches were higher in harvested compartments compared to uncut controls (T-K HSD,  $p<0.05$ ) (Figure 2.4). Figure 2.5 shows trap catches for each stand type and retention level.

### 2.3.3 Habitat abundance

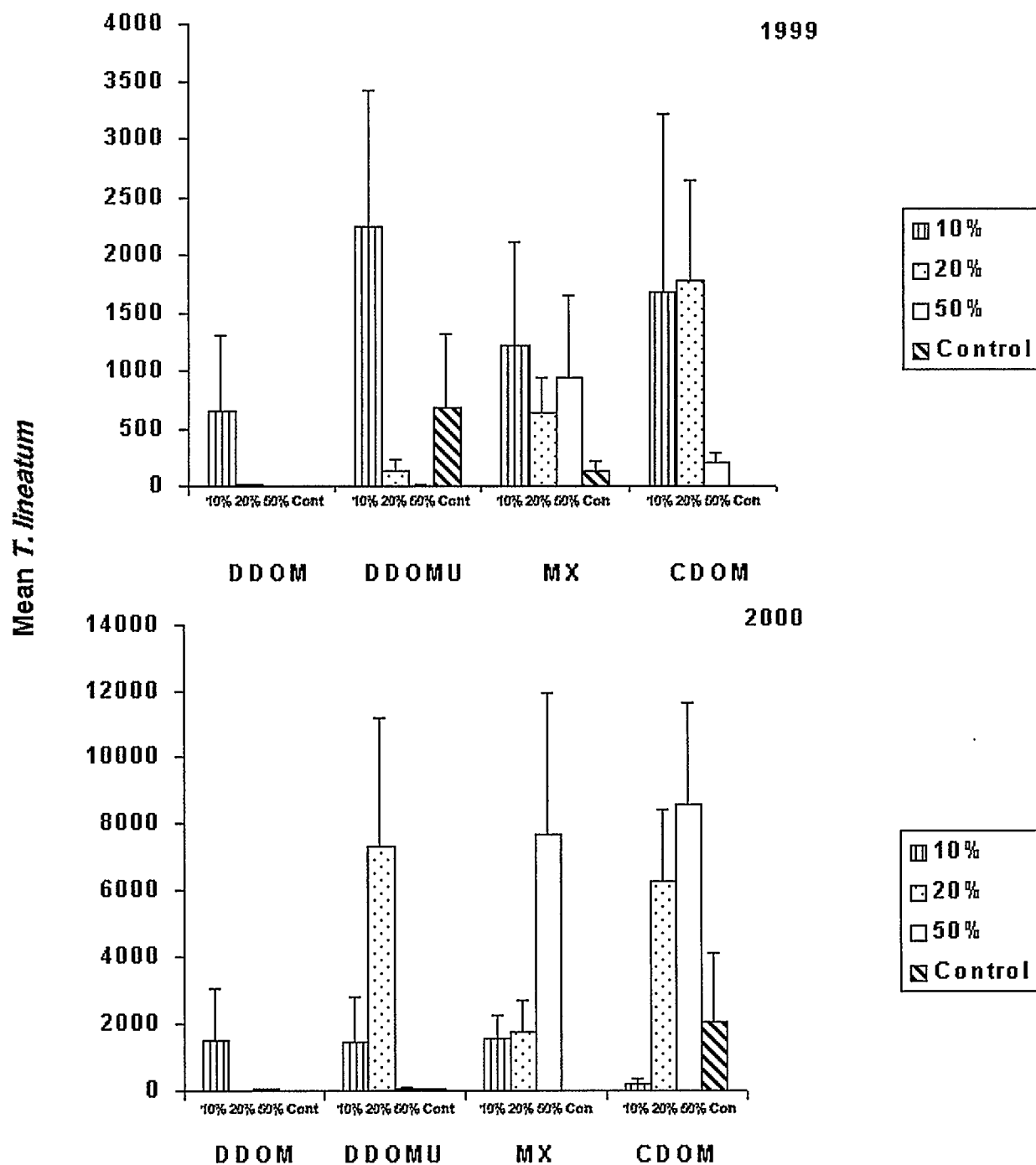
To test directly whether the distribution of *T. lineatum* was influenced by the increase in the abundance of suitable habitat following harvest, I used the density of spruce stumps as a measure of habitat abundance. Since stumps



**Figure 2.3.** Number of *T. lineatum* caught as a function of stand type following harvesting. Shown are least square means and 95% confidence intervals, back-transformed from natural log transformed data used in analyses. Stand abbreviations as in Figure 2.1. Similar letters indicate non-significant differences (T-K HSD,  $p > 0.5$ ).



**Figure 2.4.** Number of *T. lineatum* caught as a function of residual level following harvesting. Shown are least square means and 95% confidence intervals, back-transformed from natural log transformed data used in analyses. Similar letters indicate non-significant differences (Tukey-Kramer HSD-  $p < 0.05$ ).

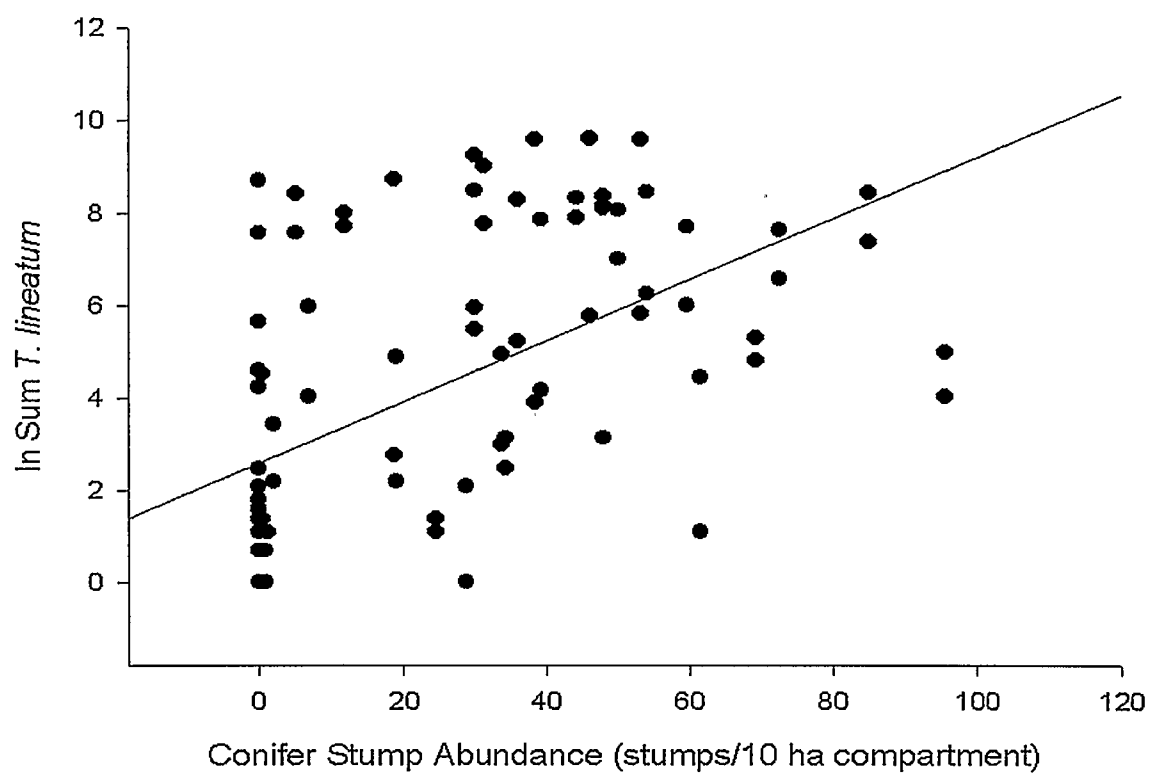


**Figure 2.5.** Mean  $\pm$  SE number of *T. lineatum* by stand type and retention level in **a)** the first year following harvest (1999) and **b)** in the second year following harvest (2000). Stand type abbreviations as in Figure 2.1.

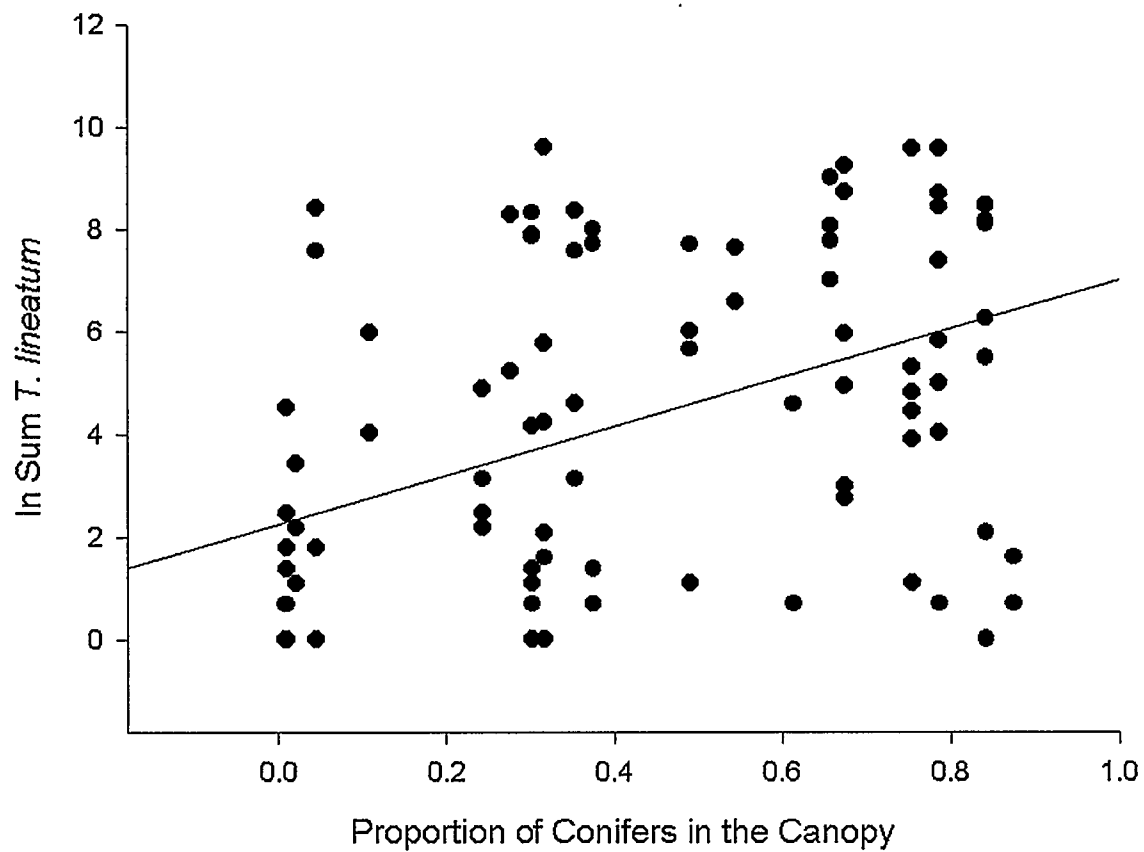
were only suitable in 1999, I included the variable year to determine whether effects in 2000 were from habitat abundance or from the previous year's beetle production. I examined trap catches with respect to the estimated number of spruce stumps in each compartment, the percentage of spruce in a compartment, tree density, replicate and year. Year had no effect on the trap catches ( $F_{1,95}=1.20$ ,  $p>0.3$ ). There was also no significant effect of tree density, or replicate on the number of *T. lineatum* caught (both,  $p>0.10$ ). However, there was a small but significant negative interaction between percentage of spruce and estimated number of stumps per compartment ( $R^2=0.40$ ,  $F_{1,95}=4.43$ ,  $p<0.04$ , Coefficient=-0.000918). All other interactions were eliminated due to high variance inflation factors. The negative coefficient indicates that as the percentage of spruce in the forest decreases, the effect of stump density on the number of *T. lineatum* increases. However, stronger, positive effects were detected for the main factors of stump abundance ( $F_{1,94}=13.96$ ,  $p<0.0004$ , Figure 2.6), and the proportion of conifers in the canopy ( $F_{1,94}=8.15$ ,  $p<0.006$ , Figure 2.7).

#### **2.3.4 Physical structure of the forest**

The previous analysis showed no effect of tree density on the number of *T. lineatum* captured. To further examine the potential role of physical structure of the forest on the movement and distribution of *T. lineatum*, I compared the number of beetles in machine corridors and retention strips of the 75% conifer-dominated stands. I used a 2-way ANOVA with trap location (machine



**Figure 2.6.** Number of *T. lineatum* as a function of conifer stump abundance per 10 ha compartment. Data were natural log transformed for normality.



**Figure 2.7.** Number of *T. lineatum* as a function of the proportion of conifers in the canopy. Data were natural log transformed for normality.

corridor/retention strip), replicate and the interaction between trap location and replicate. There was a significant interaction between trap location and compartment number on the number of *T. lineatum* caught ( $R^2=0.74$ ,  $F_{5,17}=6.97$ ,  $p<0.05$ ). Contrasting the least square means between trap location in each replicate individually, significant differences were found in two of the replicates. Trap catches were higher in retention strips than in machine corridors in one replicate (T-K HSD,  $p<0.05$ ) while in another replicate, machine corridor traps caught more beetles than retention strips (T-K, HSD  $p<0.05$ ). Traps in the third replicate 2 showed no difference between machine corridors and retention strips (T-K HSD,  $p>0.05$ ).

### 2.3.5 Habitat Use

The mean percentage of stumps per compartment that were colonized in 1999 by *T. lineatum* was  $88.32 \pm 2.67\%$  ( $n=48$ ). I used a split plot ANOVA (factors: stand type, retention level nested in stand type and replicate) to determine if landscape attributes influence settlement of *T. lineatum* among habitat patches. Results showed that none of these factors had a significant effect on the proportion of stumps colonized by *T. lineatum* (overall model:  $R^2=0.57$ ,  $F_{19,15}=1.06$ ,  $p>0.4$ ).

I also examined whether the proportion of stumps colonized in a compartment depended on continuous landscape variables (tree density, stump abundance, and the proportion of spruce in canopy) and the habitat level factor (mean stump diameter). None of these factors significantly influenced the



proportion of stumps colonized (overall model:  $R^2=0.08$ ,  $F_{4, 30}=0.61$ ,  $p>0.6$ ).

Therefore, the results indicate that *T. lineatum* colonized the majority of stumps regardless of where they were located.

To determine the relationship between settlement probability and individual stump characteristics, I examined the probability that a stump became colonized by *T. lineatum* as a function of stand type, retention level nested in stand type, and replicate nested in stand type as well as height of the stump above ground and the diameter of the stump. I used a logistic regression using data from the 1999 stump surveys. Stand type, retention level, replicate and height of stump had no significant effects on the presence of *T. lineatum* in stumps (all  $p>0.05$ ). However, the diameter of the stump did have a significant effect on the likelihood that a stump contained *T. lineatum* ( $R^2=0.15$ ,  $\chi^2=7.15$ ,  $p<0.03$ ). *T. lineatum* were more likely to be present in larger diameter stumps than in smaller stumps ( $\text{Mean}_{\text{colonized}}=39.52+0.97 \text{ cm}$ ,  $n = 252$ ;  $\text{Mean}_{\text{uncolonized}}=34.91+ 2.49 \text{ cm}$ ,  $n=37$ ).

## 2.4 Discussion

### 2.4.1 Habitat distribution and abundance

Previous models of insect habitat selection have assumed random search (Rogers, 1972; Turchin, 1998). However, searching for habitat randomly may lead to fewer encounters with habitat patches if habitat is spatially clumped. As early as 1935, Salt proposed non-random host search by parasitic insects, such

that parasites may seek areas with an abundant supply of hosts and ignore areas where hosts are rare or absent. This idea was reiterated in the resource concentration hypothesis (Root, 1973) that proposes that herbivorous insects accumulate where hosts are abundant. Many studies have supported this hypothesis (Chamberlain and Tenlet, 1926; Clausen, 1940; Doult, 1964; Varley, 1941; Monteith, 1960; Watt, 1964, 1965; Douwes, 1968; Schroder, 1969; Spradbury, 1969; Batch, 1984; Turchin, 1988; Hassell, 1986; Andow, 1990).

Prior to harvesting in 1998, *T. lineatum* were scarce in stands containing few host trees (deciduous-dominated) and were most abundant in stands with many host trees (conifer-dominated). In a pre-harvest landscape, heterogeneity on the landscape is primarily due to stand level differences such as stand composition. Since spruce stumps or logs are likely to be scarce in areas with more deciduous trees, areas with high deciduous content may be avoided. Borden et al. (1997) found a 63-78% reduction in trap catches of *T. lineatum* when deciduous volatiles were placed in traps. By concentrating dispersal in areas with many host trees, individuals maximize the likelihood of finding suitable habitat. Alternatively, these results may reflect the production of beetles in the different stand types rather than, or in addition to, biased movement.

Following harvest, there was a redistribution of beetles across the landscape. As in the pre-harvest landscape, beetles were more abundant in conifer-dominated stands than in deciduous stands. Beetles were also more abundant in harvested areas compared to unharvested areas following logging. This change in the distribution of beetles following harvest was related to the

abundance of conifer stumps in a compartment. The stumps remaining following logging are prime habitat for *T. lineatum* and represent a sudden increase in habitat in some areas. The pattern of beetles two breeding seasons following logging did not differ significantly from the previous year. This result is best explained by the local production of beetles that settled in the previous year.

Given that *T. lineatum* are able to detect volatiles from breeding habitat (Lindelow et al., 1992), it is likely that they were attracted in greater numbers to areas containing more habitat, resulting in higher trap catches. These results concur with the predictions of the resource concentration hypothesis (Root 1973). However, another potential cause for higher catches of beetles where habitat is abundant is increased search effort by beetles in these areas. If an area has a high concentration of potential breeding sites, individuals may spend more time searching for suitable habitat patches and thus be more apt to be caught in traps within such areas, compared to areas with little habitat. According to an encounter rate model tested by Byers (1996), as search time increases so does the percentage of beetles that detect suitable hosts. In addition, if movement is slower when potential habitat is more abundant, beetles will accumulate more in areas with more habitat than in areas with scarce habitat (Turchin 1998). It is therefore possible that higher catches in areas with more habitat reflects an increased likelihood of beetles encountering the traps rather than an increase in the number of beetles arriving in the stand. These two alternative processes are difficult to distinguish without actual movement data.

There was a weakly significant negative interaction between stump

abundance and conifer abundance in explaining the abundance of *T. lineatum* captured. The ability of searching *T. lineatum* to detect differences in the abundance of habitat following harvest seemed to be more acute in areas where overall stump abundance was low and differences in abundance were large. This interaction may be explained by the Weber-Fechner law (Fechner, 1860 in Driessen and Bernstein, 1999). The Weber-Fechner law describes a relationship between stimulus strength and sensory detection wherein the amount of change in the stimulus needed for an organism to detect the change increases proportionately with the initial intensity of the stimulus. Driessen and Bernstein (1999) used this law to describe the mechanism behind the ability of parasitoids to discriminate between host densities. They found that the tendency of an individual to leave a habitat patch was a decreasing function of kairomone concentration. Sensory thresholds for discerning differences in kairomone concentration may have evolved in *T. lineatum* due to the ephemeral nature of their habitat. If individuals are able to sense proportionately large differences in habitat abundance when habitat is scarce, the probability of finding rare habitat patches is increased. In areas or situations where habitat is abundant, this ability to discriminate between concentration of kairomones and the quantity of habitat is less crucial to successfully finding suitable habitat.

While trap catches of *T. lineatum* were correlated with the abundance of stumps in a stand, the presence of the interaction between stump abundance and the proportion of conifers in the canopy), is contrary to the prediction of the IFD. The IFD depends on individuals to be cognizant of other individuals in an

area, the mechanism for density dependent settlement. Beetles flying in an area searching for habitat are unlikely to know how many other beetles are also in the area. However, the number of beetles may be proportional to the number of stumps in a stand if there is a direct relationship between stump abundance and volatile concentration. Therefore, beetles would be attracted from a larger area surrounding stands with many stumps, resulting in proportionately more beetles in these stands. Stands with many stumps that were adjacent to each other may attract beetles from overlapping areas, which may cause the discrepancy in beetle abundance with stump abundance. This possibility requires a spatially explicit analysis not considered here.

#### **2.4.2 Physical Structure of the Forest**

The negative effect of retention level on *T. lineatum* abundance could be due to stand density in addition to habitat abundance. The influence of stand density on the movement of bark beetles has not been examined thoroughly. Data from Salom and McLean (1991a), and a study by Hindmarch and Reid (2001) produced conflicting results for *T. lineatum*. Salom and McLean found that *T. lineatum* avoided open areas and preferred closed forests possibly due to an increase in their ability to detect host chemical. Conversely, Hindmarch and Reid (2001) found that *T. lineatum* were more common in thinned forests (2/3 of trees removed) than in unthinned forests, apparently due to beneficial microclimatological attributes and wind-assisted search (increased ability to detect olfactory plumes). In the current study, I also found that *T. lineatum* were

more abundant in stands with lower retention levels. This result may have been caused by habitat abundance since tree density had no effect on beetle abundance. Examination of microclimatological effects would determine whether the effect of retention level was due to habitat abundance or microclimate differences, or both.

Major structural features such as machine corridors created by some partial cutting regimes have also been hypothesized to affect the movement of insects by either increasing wind-assisted movement, or hindering olfactory detection due to increased wind velocity. For example, ringlet butterflies (*Aphantopus hyperantus* (Linnaeus)) used open corridors as flyways between fields and glades (Sutcliffe and Thomas 1996). In contrast, Hill (1995) found that linear strips of intact rainforest acted as dispersal corridors for several insects.

Salom and McLean (1991a) studied the movement of *T. lineatum* along roads and found that there were no significant differences in beetle distribution along roads versus in the forest. However, as stated above, the same study showed that beetles preferred closed forest to open, clear-cut stands for dispersal. The narrow width of the roadway compared to those of open stands examined in the study may have been the cause of the discrepancy in results. Smaller open areas such as roads and machine corridors may have less wind turbulence than large open areas, allowing insects to respond to olfactory cues. The results of my study suggest that *T. lineatum* are not strongly affected by the physical structure of the landscape (barriers or corridors) as no significant differences in trap catches were found between machine corridors and retention

strips, and results from replicates were conflicting. Thus, these results, combined with the lack of a detectable effect of tree density on trap catches of *T. lineatum* within stands, suggest that the physical structure of the forest is not a key determinant in the dispersal and distribution of *T. lineatum*.

#### **2.4.2 Habitat Use**

Although the activity of *T. lineatum*, as measured by trap catches, varied according to habitat abundance in the area, *T. lineatum* colonized the majority of stumps regardless of the number of stumps in the surrounding vicinity. Moreover, their preference for larger stumps was evident regardless of stand characteristics. These patterns of colonization are consistent with the ideal free distribution (Fretwell and Lucas, 1970). This suggests that while *T. lineatum* may bias their search effort towards areas likely to contain more habitat, their search costs are low enough that they are able to avoid competition resulting in an even distribution across habitat patches.

Examination of settlement densities within habitat patches, rather than simply presence and absence, would provide a better test of the IFD. Higher densities in large diameter stumps would suggest that beetles were settling according to the ideal free distribution. Furthermore, if Ward's (1987) theory for time limited dispersers is supported, small diameter stumps in areas containing little habitat would contain higher densities of beetles than similar sized stumps in areas with abundant habitat. Therefore, further investigation into beetle densities within habitat patches is necessary to elucidate the true distribution of

populations of *T. lineatum* according to habitat quality and abundance.

## 2.5 Conclusion

In summary, *T. lineatum* distributions across the landscape were influenced by landscape characteristics such as stand type and retention level. This appeared to be related to host tree and habitat abundance rather than physical structure of forest stands, showing support for the resource concentration hypothesis with respect to both the host tree and stump abundance.

At the habitat patch level, the proportion of stumps colonized was not affected by stand level characteristics. Thus, the abundance of individuals searching for habitat in an area does not necessarily predict the use of habitat patches in an area. The fact that habitat quality (as estimated by stump diameter) influenced the probability that a stump was colonized suggests that beetle distributions among habitat patches possibly conform to the ideal free distribution. However, further examination of beetle settlement densities is required to confirm or refute support of the ideal free distribution.

Results showed that major alterations to the distribution of bark beetle habitat due to logging result in a higher abundance of beetles in logged areas. Higher abundance of beetles in harvested areas in combination with *T. lineatum*'s ability to colonize habitat regardless of the surrounding landscape, suggest that harvested landscapes may promote the proliferation of *T. lineatum* populations. Since the abundance of this species was correlated to habitat



abundance, forest managers should consider manipulating the amount of available habitat remaining following harvesting as a method of reducing beetle abundance in certain areas.

This study emphasizes the importance of considering the spatial scale at which organisms respond to environmental variation across the landscape. It shows that responses at the landscape level are not always similar to responses at the habitat level, and suggests that individuals may use habitat specific cues to inform them about habitat quality.

## Chapter 3

### **The Effects of Spatial Scale on the distribution of a Bark Beetle, *Polygraphus rufipennis* (Kirby) (Coleoptera: Scolytidae)**

#### **3.1 Introduction**

Habitat selection and dispersal are two of the most important factors determining the distribution of organisms (Wiens, 1997). Habitat availability and quality, and the costs of dispersal are expected to be significant determinants of where and how an organism searches for and selects habitat (Danielson, 1992). However, the way in which organisms perceive variation in habitat abundance and quality across the landscape will affect how their search behaviour is influenced by these factors.

Traditionally, the focus of research on environmental effects on population distributions has been on habitat patches themselves, where quality, size and location of patches have been hypothesized to explain animal distributions (Arditi and Dacorogna, 1988; Thomas et al., 1992; Andren, 1994; Solbreck, 1995). More recently, the influence of environmental variation at the landscape scale, such as the spatial configuration of patches across the landscape, has gained attention in explaining the distribution of animals (McIntyre and Wiens, 1990; Bernstein et al., 1991; With and Crist, 1995; Wiens, 1997). Few empirical studies have examined both scales to determine the extent to which landscape effects alter the distribution of animals among habitat patches (Doak et al., 1992; Ritchie, 1998; Samu et al., 1999; Jonsen and Taylor, 2000).

Depending on the organism of interest, both the terms 'landscape' and

'patch' may take on different meanings. In general, patches can be defined as 'a surface area differing from its surroundings' (Kotliar and Wiens, 1990), whereas landscape is defined as a spatially heterogeneous area (Turner et al., 1989). Habitat that is relevant to searching organisms is necessary for the success of the organism.

*Polygraphus rufipennis* (Coleoptera: Scolytidae) is a secondary bark beetle that inhabits dead and dying conifer wood. These habitat patches are usually sparsely located across the landscape since natural inputs are primarily from trees killed by other insects or pathogens or broken by wind. The distribution of freshly dead conifer logs logically follows the distribution of living conifer trees.

At the landscape scale, beetles may focus on stands containing many conifers since these stands may represent areas more likely to contain suitable habitat logs. Many species of bark beetles have the ability to discern between host and non-host tree species through olfaction (Schroeder, 1992; Wilson et al., 1996; Borden et al., 1997; Byers et al., 1998, 2000). Such search behaviour is the basis of the resource concentration hypothesis (RCH) (Root, 1973), which proposes that herbivorous insects will be most abundant where host plants are concentrated. This hypothesis has been supported by many empirical studies, primarily involving crop insects in agricultural settings (Douwes, 1986; Risch, 1981; Batch, 1984; Turchin, 1988; Andow, 1990). Spending more time in areas containing more host trees may reduce the amount of energy needed for habitat patch (log) detection and increase the amount of energy remaining for

reproduction.

Forest stands can also represent the context within which habitat patches exist on the landscape. Forest tree density and understory vegetation density varies on a landscape scale and has the potential of influencing the distribution of forest dwelling insects such as bark beetles by altering dispersal behaviour. For example, the movement of some tropical insects is highly influenced by corridors of dispersal (Hill, 1995; Sutcliffe and Thomas, 1996).

At a smaller scale, individual logs represent habitat patches, and *P. rufipennis* may use habitat-specific cues concerning habitat quality. Because *P. rufipennis* rely on phloem as their sole source of nutrition, phloem represents an important resource to both breeding adults and developing broods. Reproductive success tends to be higher in trees with thicker phloem (Amman, 1972; Amman and Pace, 1976; Amman and Pasek, 1986; and Haack et al., 1987), which in turn tends to be correlated with log diameter (Berryman, 1976; Reid and Glubish, 2001). However, Reid and Robb (1999) found that phloem thickness was not consistently correlated with tree size. *P. rufipennis* may use phloem thickness to detect differences in habitat (log) quality, which in turn can be estimated experimentally using diameter.

High beetle densities within logs have negative effects on the fecundity of parents and the survival of offspring (e.g. Kirkendall, 1989; Rankin and Borden, 1991; Schlyter and Anderbrant, 1993; Robins and Reid, 1997). Therefore many beetles have evolved mechanisms to avoid competition from both conspecifics and heterospecifics (Byers and Wood, 1980; Borden et al., 1992; Miller and

Borden, 1992; Byers, 1993). However, established conspecifics or ecologically similar heterospecifics may provide another cue of habitat suitability (Wood, 1982; Danchin and Wagner, 1997; Mönkkönen et al. 1999; Stamps, 2001). Recent studies have indicated that heterospecific attraction may produce positive rather than negative consequences resulting in high settlement densities of multi-species aggregations within logs (Cane et al. 1990; Fox et al., 1991; Ayers et al., 2001). The use of conspecifics (or some heterospecifics) to detect habitat would be most beneficial in areas with low quantities of logs where the costs associated with competition are outweighed by the benefits obtained from actually finding habitat. Consequently, many searchers may aggregate in a few patches, while other patches may not be colonized at all. This habitat settlement strategy may result in higher variance in settlement densities in areas with little habitat than where habitat is sufficiently abundant that searchers ignore or avoid patches that are already colonized.

The extent to which the distribution of *P. rufipennis* matches stand- or log-level variation may depend on the scale of movement by individual beetles. Although no studies to date have examined the flight potential of this species, other beetles of similar size and habitat use are capable of flying up to 40 km (Salom and McLean, 1991a). In reality, while searching for habitat, beetle movements may be intricate and result in long flight distances with minimal displacement. Grain is defined as 'the smallest scale at which an organism responds to patch structure' (Kotliar and Wiens, 1990). If most movements are larger than variation in local habitat abundance and habitat quality, then small-

scale changes in the environment may not be detected as easily and individuals will respond most to coarse grain variation in patch quality across the landscape.

The scale at which organisms respond to landscape variation may influence the scale at which the ideal free distribution is demonstrated on the landscape. The ideal free distribution (IFD) (Fretwell and Lucas, 1970) is one in which, at equilibrium, the average fitness of individuals of all habitat patches is approximately equal. Danielson (1991) argues that the ideal free distribution is more suitable at smaller scales, where habitat selection is more likely to be 'ideal' since individuals are more likely to detect all suitable habitat patches. For insects such as *P. rufipennis*, that appear capable of honing into pieces of suitable habitat, the IFD may be demonstrated among individual logs. In this case, higher quality habitat logs will have higher densities of beetles.

The ideal free distribution may not hold at the habitat level for organisms that have a limited dispersal period (Ward, 1987) because it assumes that habitat selection incurs no costs. Danielson (1992) proposed that in landscapes with small amounts of high quality habitat, individuals should settle in sub-optimal habitat to avoid spending energy searching in areas with little habitat. In areas where suitable habitat is scarce, beetles may settle in any suitable log that is encountered or rely on conspecific or heterospecific pheromones to direct their settlement in logs.

Here, I examine the distribution of *P. rufipennis* at the landscape level (among forest stands), and at the patch scale (defined here as among logs). I begin at the larger scale by examining the effects of forest stand composition,

habitat abundance and structure (density, understory vegetation) on the abundance of beetles among stands. I then investigate the distribution of *P. rufipennis* among logs to determine whether *P. rufipennis* settlement at the log level is affected by landscape level influences (stand composition, tree density, log abundance), or whether it is more strongly affected by habitat-specific attributes such as phloem thickness (diameter). This study identifies the scale at which *P. rufipennis* responds to changes across the landscape. It also examines whether behaviour the landscape scale affects population distributions at the habitat patch level.

## **3.2 Methods**

### **3.2.1 Study site**

To examine the effects of environmental variation at different scales (landscape and habitat patch level) on the distribution of *P. rufipennis*, I conducted this study at the EMEND (Ecosystem Management by Emulating Natural Disturbance) project site northwest of Peace River, Alberta (56° 40' N 118° W). The project site covered an area of approximately 467 ha. In 1997, four forest stand types were identified: deciduous-dominated (DDOM: 70-95% deciduous), deciduous-dominated with conifer understory (DDOMU), mixed (MX: 35-65% deciduous and conifer mixed), and conifer-dominated (CDOM: 70-95% conifer). For each stand type, three replicates were chosen for use in the EMEND experiment. Within each replicate, compartments that were 8 – 10 ha were harvested, in which several retention treatments were applied. Retention

refers to the proportion of standing trees that remained post harvest, and those used in this study were 10%, 20%, 50%, 100% of trees retained. Within each retention treatment (except 100%), trees were cut from 5m 'machine corridors' in which all vegetation was removed, and 15m retention strips, where the remaining selected felling was carried out. Retention treatments were carried out in the winter logging season of 1998/1999.

### **3.2.2 Habitat Abundance and Stand Characteristics**

I examined the relationship between habitat (log) abundance and stand level characteristics for 1999 and 2000. In 1999, logging slash was suitable for breeding. In 2000, the slash was no longer suitable so habitat availability was expected to be much less, but harvested areas could retain higher habitat availability than unharvested areas because of increased windfall. In 1999, log abundance for each compartment was obtained from EMEND core data (EMEND core crew data, 1999). These data were derived from counts of coarse woody debris from six 2 x 40 m plots in each compartment. The diameter of all pieces of coarse woody debris was measured and categorized by the degree of decay. Only logs categorized by as decay class L1G and L1Y (freshly dead conifer logs with either green or yellow needles still present), and larger than 10 cm in diameter were used to calculate an estimate of total number of suitable logs for *P. rufipennis*. This diameter was used since *P. rufipennis* do not inhabit logs smaller than 10 cm (Bowers et al., 1996). I converted the number of logs from all six plots to the number of logs for a 10 ha compartment.



In 2000, all 48 compartments were surveyed in their entirety to detect inputs of suitable habitat due to natural mortality and windthrow. I determined that trees were freshly fallen if needles were intact and mostly green, and bark was moist. The diameter of all pieces of suitable habitat was measured and each log was inspected for the presence of bark beetles. If bark beetles were present, specimens were excavated and identified.

I estimated the percentage of conifer trees in the canopy, prior to harvest, using data obtained from the EMEND core database (EMEND core crew data, 1999). From these data, I calculated the estimated percentage of conifer (both white and black spruce, *Picea glauca* (Moench) and *P. mariana* (Miller), respectively in each experimental compartment. To obtain tree density following harvest in each compartment, I multiplied the pre-harvest tree density by the retention level. Preharvest tree density was determined from the number of stems counted in six 40 m by 2 m plots in candidate stands for each stand type (EMEND core crew data, 1999).

### **3.2.3 Bark Beetle Distribution Among Stands (Landscape Scale)**

During full compartment surveys of suitable habitat logs conducted in the summer of 1999, *P. rufipennis* was identified as the most common species of bark beetle within fallen logs. *P. rufipennis* occupied 22% of all logs examined in 1999. Therefore, in the summer of 2000, a baited 12-funnel Lindgren trap was placed in each treatment in all stand types and replicates for a total of 48 traps. Each trap was baited with the aggregation pheromone for *P. rufipennis*, 3-methyl-

3-buten-1-ol (from Phero Tech Inc.) with a release rate of 40-50 mg/d. Traps were placed near the centre of each compartment to avoid edge effects. I collected beetles from traps every two weeks between 04 June 2000 and 27 July 2000 resulting in 4 sample collections. However, the samples from the last two sample dates (4 July 2000 and 27 July 2000) were not analyzed due to water damage caused by heavy rain during the two-week intervals. Beetles in these samples had decomposed and an accurate measure of the number within each trap could not be made. The fact that the July samples were unable to be counted is not likely to have altered the results of this study since data from 1999 showed that the majority of beetles dispersed in June. Therefore, the two sample periods in June are the basis for this chapter.

Many samples contained more than 2000 beetles (up to 11 000 beetles). Therefore, I used sample mass to estimate abundance. Each sample was dried in a drying oven at 70-80 °C for 8-12 hours. Drying beetles assured that additional mass from water and moisture would not skew measurements. Upon drying, samples were examined and all debris (lichen, moss, soil etc.) and other insect species were removed. For each sample, I weighed the total sample as well as a sub-sample of 30 randomly selected beetles. The mean mass of a beetle from the sub-sample was used in estimating the total number of beetles in the whole sample. Estimates of beetle abundance using this method were accurate to approximately 5% of the actual number of beetles for samples of 2000 beetles or more, based on 10 samples in which all beetles were individually

counted. This method was used for all *P. rufipennis* samples of over 2000 beetles.

### **3.2.4 Physical Structure of the Forest**

The effect of the density of trees in forest stands on beetle distributions was examined using the density of trees in each stand from data obtained from the EMEND project core database. To determine whether the distribution of *P. rufipennis* varied with the density of understory vegetation, I measured the profile density (density of vegetation along a vertical axis) in each compartment in 2000. I used a 2-m profile pole that was divided into 25-cm coloured sections. The estimated proportion of a section that was obscured by vegetation was assessed from 10m away. These measurements were taken from a point in all four cardinal directions and at three heights (50 cm, 100 cm, and 150 cm). Profile pole measurements were taken adjacent to each *P. rufipennis* baited trap and a second trap used for another experiment, as well as at 5 other randomly chosen points, for a total of 7 points within each compartment. Measurements from all four cardinal directions for all points were averaged across all height intervals.

### **3.2.5 Colonization Patterns (Habitat Scale)**

To determine the settlement densities within habitat patches (logs); I conducted surveys of habitat logs surveys in 1999. Within each compartment, I measured the diameter of 10-20 spruce logs suitable for colonization by *P. rufipennis*. Logs were selected such that they were no closer than 30 m apart

and logs on adjacent machine corridors and retention strips were not chosen in order to ensure uniform sampling across all compartments. In each of these logs, I measured the density of all beetles. Since male *P. rufipennis* are the first to arrive at logs, and are responsible for creating gallery entrance holes (Bowers et al., 1996), the settlement densities of *P. rufipennis* were calculated estimated by counting the number of males excavated from each log within a 800 cm<sup>2</sup> area.

The data of settlement densities were also used to test whether trap catches in 2000 were influenced by the previous year's production of beetles from within stands. I calculated an index of brood production for each compartment in 1999 as follows. Surface area of logs, which is the portion that bark beetles use, was determined by using the measured diameter of each log sampled in 1999 and assuming 1 m logs. Logs were standardized to 1m since log length was not recorded during surveys. Brood production for each log was then estimated by examining the density of beetles in an 800 cm<sup>2</sup> area and determining the corresponding the number of broods for 1 m logs. The index of brood production of a compartment was then calculated by multiplying the mean brood number within logs by the number of logs in a compartment in 1999.

### **3.2.6 Analyses**

All ANOVAs, and regressions were performed on JMP® Version 3.0 (SAS Institute, 1995). A three-way split plot ANOVA (stand type, retention level nested in stand type, and replicate nested in stand type) was used to determine the effects of stand type and retention level. G-tests of independence of variables

were conducted using MS Excel. I used an alpha of 0.05 for all analyses. For the trap catch data analysis, I used the sum of all beetles caught in each compartment over the 2 sample dates. All data were appropriately transformed to meet assumptions of normality. I used Tukey-Kramer Honestly Significant Difference (T-K HSD) tests to determine significant differences among treatments. Means are reported  $\pm$  1 SE.

### **3.3 Results**

#### **3.1.1 Habitat Abundance**

To examine the distribution of habitat across the landscape, I examined log abundance as a function of compartment attributed using the three-way split plot model for stand type, retention level and replicate. The number of logs per compartment in 1999 varied significantly with stand type ( $F_{3,44}=81.02$ ,  $p<0.0001$ ; overall model:  $R^2=0.93$ ;  $F_{23,24}=14.17$ ,  $p<0.0001$ ) ( $F_{3,44}=81.02$ ,  $p<0.0001$ ), with log abundance in each stand type differing from other stand types (T-K HSD,  $p<0.05$ ). Logs were most abundant in conifer-dominated stands, followed by mixed stands. Logs were least abundant in deciduous-dominated and deciduous-dominated with conifer understory stands. Retention level also had a significant effect on logs abundance in 1999 ( $F_{12,35}=5.53$ ,  $p<0.0003$ ). All retention levels differed from each other (T-K HSD,  $p<0.05$ ). Stands with 20% retention had the most logs, 50% stands had intermediate numbers of logs and control followed by 10% stands had the lowest number of logs. The majority of logs available to beetles in the first year following harvest were a result of logging

debris left on site, thus explaining the fact that 10% stands had the lowest number of logs in 1999. Replicate had no effect on the number of logs in 1999.

I used the same split plot ANOVA design to examine log distribution in 2000. Log abundance in 2000 was significantly affected by stand type ( $R^2=0.77$ ,  $F_{3,44}=7.34$ ,  $p<0.002$ ), retention level ( $F_{12,35}=2.81$ ,  $p<0.02$ ), and replicate ( $F_{2,45}=2.97$ ,  $p<0.02$ ). All retention levels differed from the others (T-K HSD,  $p<0.05$ ). Logs were least abundant in deciduous-dominated stands compared to all other stand types (T-K HSD,  $p<0.05$ ). In 2000, 20% retention level stands had the highest number of logs, followed by 10% and 50% stands, with control stands having the fewest logs. Logs in 2000 were mostly caused by windthrow.

To determine whether the diameter of logs varied across the landscape, I used the same split plot ANOVA design. In both 1999 and 2000, none of the variables had significant effects on the diameter of logs in a compartment (overall model  $R^2=0.70$ ,  $F_{21,13}=1.44$ ,  $p>0.25$ ; and  $R^2=0.68$ ,  $F_{15,9}=1.30$ ,  $p>0.35$  respectively). Note that in 2000, only 25 compartments out of 48 contained any suitable habitat logs for this analysis.

### 3.3.2 Bark Beetle Distribution (Landscape Scale)

I used the split plot model for stand type, retention level and replicate to determine the effects of stand type and retention level on trap catches of *P. rufipennis* in 2000. Two traps of the 48 were omitted from the analysis due to problems with animal and wind disturbed traps. Stand type significantly affected the numbers of *P. rufipennis* caught ( $R^2=0.89$ ,  $F_{3,43}=37.09$ ,  $p<0.0001$ ). Fewer

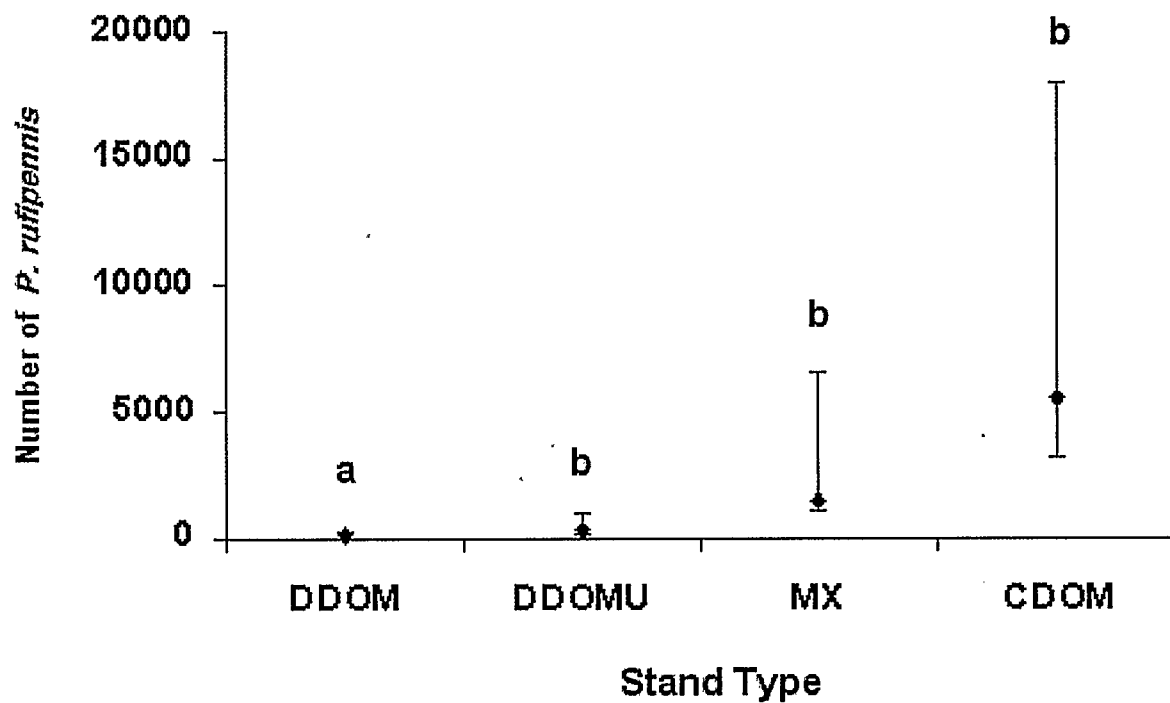
beetles were found in deciduous-dominated stands than in all other stand types (T-K HSD,  $p < 0.05$ ; Figure 3.1). Retention level also significantly affected trap catches ( $F_{8,37} = 3.34$ ,  $p < 0.007$ ) with the lowest trap catches in control compartments (Figure 3.2). Replicate also had a significant effect on trap catches ( $F_{8,37} = 3.46$ ,  $p < 0.01$ ).

### 3.3.3 Physical Structure of the Forest

I also examined trap catches as a function of continuous stand variables, rather than treatment categories, using multiple regression. Independent variables were habitat abundance (fallen fresh logs), host (conifer) abundance, stand density, profile density and beetle brood production from the previous year. Consistent with the effect of stand type shown previously, higher numbers of beetles were caught in traps located in stands with higher proportions of conifer trees ( $F_{1,45} = 18.62$ ,  $p < 0.0001$ ; Figure 3.3). Variables associated with retention level (stand density, log abundance, profile density) had no significant effect on quantity of trap catch (all  $p > 0.26$ ). Trap catches of *P. rufipennis* did not vary significantly with brood production ( $p > 0.36$ ), indicating that traps were not primarily influenced by within -stand contributions to catches and could be considered an indication of the abundance of beetles entering an area.

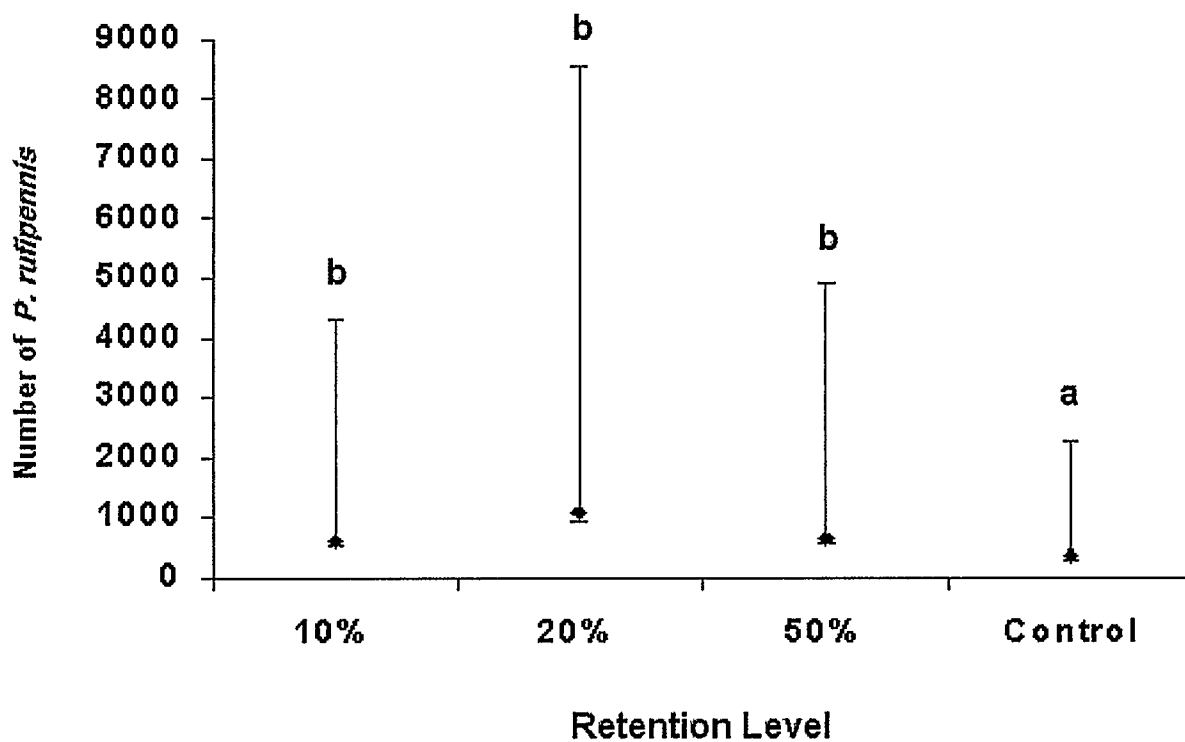
### 3.3.4 Colonization Patterns (Habitat Scale)

I examined the effects of stand type and retention level on male *P. rufipennis* densities in 1999 to determine whether landscape level attributes also



**Figure 3.1.** Number of *P. rufipennis* caught as a function of stand type following harvesting. Shown are least square means and 95% confidence intervals, back-calculated from natural log transformed data used in analyses. Similar letters indicate non-significant differences. Stand type abbreviations are as follows: deciduous-dominated (DDOM), deciduous-dominated with conifer understory (DDOMU); mixed (MX); conifer-dominated (CDOM).

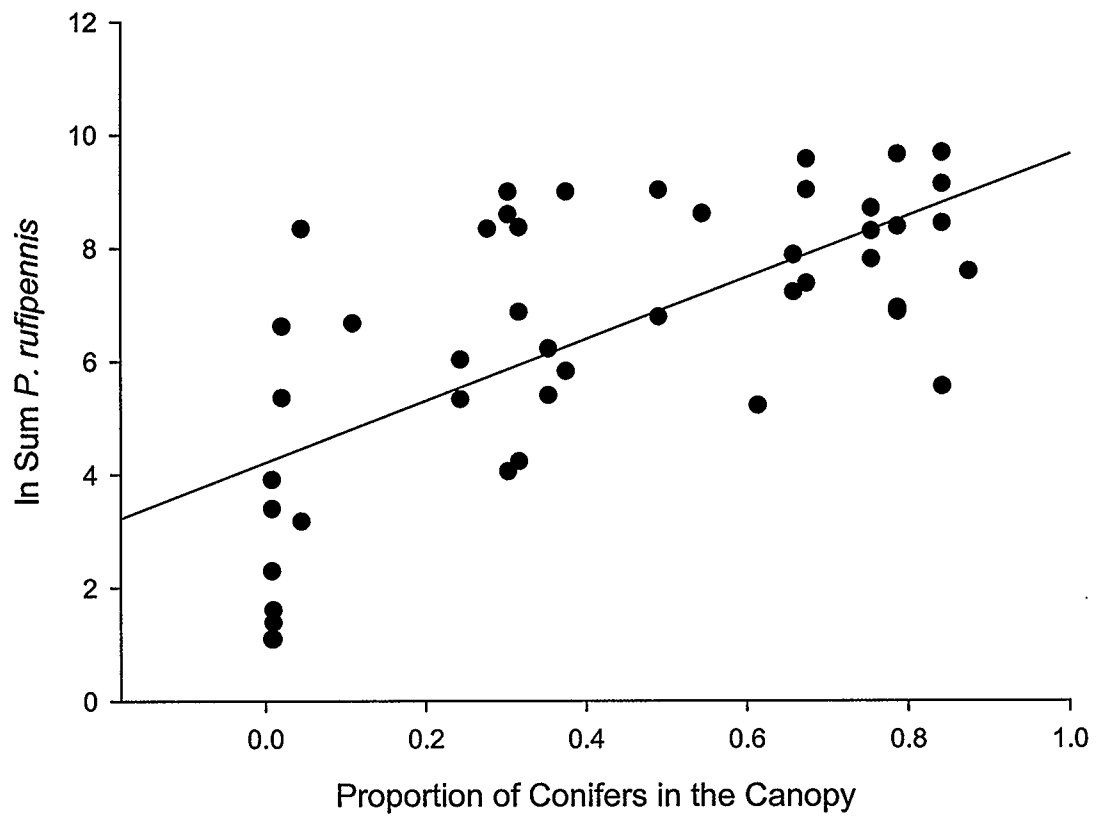




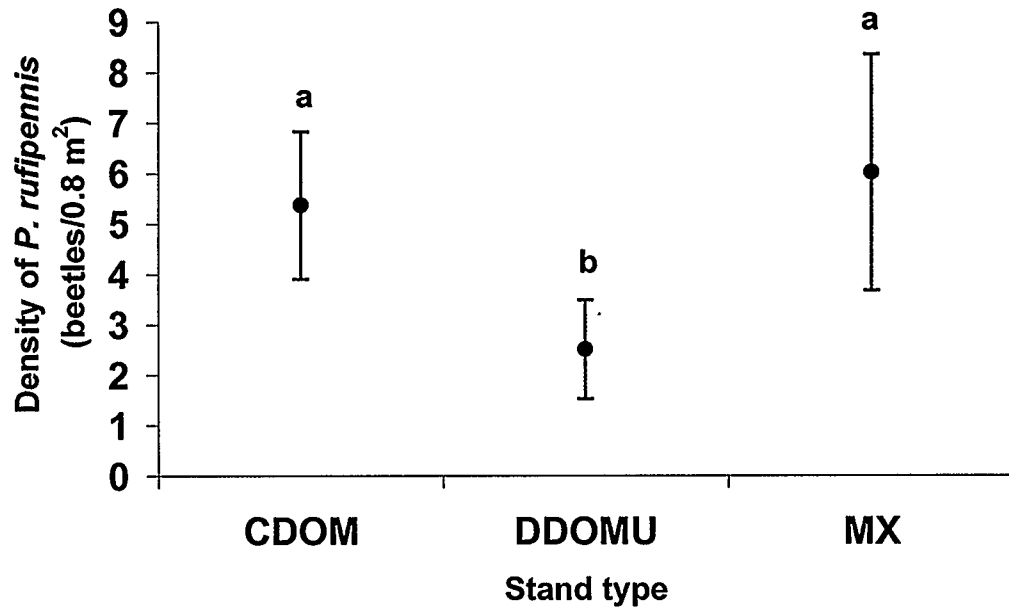
**Figure 3.2.** Number of *P. rufipennis* caught as a function of retention level following harvesting. Shown are least square means and 95% confidence intervals, back-calculated from natural log transformed data used in analyses. Similar letters indicate non-significant differences.

influenced habitat level distributions among habitat patches (conifer logs) using the split-plot ANOVA design used previously. Stand type had a significant effect on settlement densities of *P. rufipennis* ( $F_{2,128}=2.88$ ,  $p<0.06$ ; overall model:  $R^2=0.22$ ,  $F_{14,117}=2.33$ ,  $p<0.008$ ). Deciduous-dominated with conifer understory stands had lower settlement densities than both mixed and conifer-dominated stands (T-K HSD  $p<0.05$ ; Figure 3.4). Retention level also had a significant effect on the density of *P. rufipennis* ( $F_{6,125}=2.91$ ,  $p<0.01$ ), with 50% retention level stands having higher settlement densities than 10% and 20% retention levels (T-K HSD,  $p<0.05$ ; Figure 3.5). Replicate did not have a significant effect on settlement densities ( $p>0.2$ ). I also examined continuous variables such as (log diameter, tree density, proportion of conifers in canopy, and log abundance) using a multiple regression to determine if landscape variables were responsible for the effects of stand type and retention level. None of the variables in the model had a significant effect on settlement densities (overall model:  $R^2=0.05$ ,  $F_{4,127}=1.51$ ,  $p>0.2$ ).

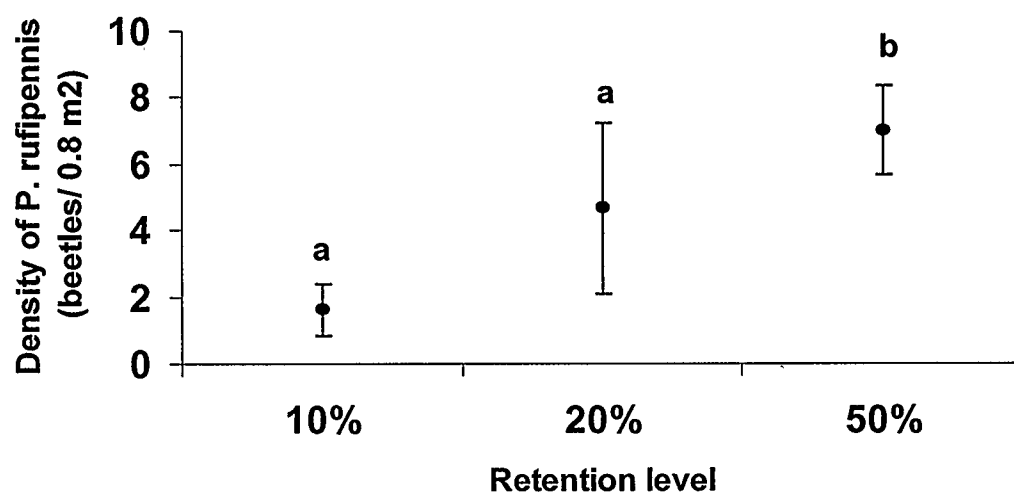
To determine if the variation in settlement density was significantly different across the landscape, I examined the coefficient of variation (CV) of *P. rufipennis* settlement density for each compartment using a split plot ANOVA as before. None of the variables (stand type, retention level, replicate) had a significant effect on the CV ( $R^2=0.82$ ,  $F_{15,9}=1.3032$ , all  $p>0.17$ ). I further examined the relationship between the coefficient of variation for *P. rufipennis* density as a function of log abundance, tree density and the proportion of conifers in the canopy using multiple regression. None of these variables had a



**Figure 3.3.** Total trap catches of *P. rufipennis* per compartment as a function of the proportion of conifers in the canopy following harvest (2000). Data were natural log transformed to meet assumptions of normality.



**Figure 3.4.** Settlement densities of *P. rufipennis* as a function of stand type following harvesting. Shown are untransformed means and standard errors. Data were natural log transformed to meet assumptions of normality for analysis. Similar letters indicate non-significant differences.



**Figure 3.5.** Settlement densities of *P. rufipennis* as a function of retention level following harvesting. Shown are untransformed means and standard errors. Data were natural log transformed to meet assumptions of normality for analysis. Similar letters indicate non-significant differences.

significant effect on the coefficient of variation for beetle density ( $R^2=0.056$ ,  $F_{3,14}=1.87$ ,  $p>0.25$ ) (Overall mean coefficient of variation:  $90.13 \pm 49.03$ ).

To determine whether distributions of beetles among logs was uniform, random or aggregated, I calculated the index of dispersion ( $I$ ) (Krebs, 1989). Calculation of the index showed that populations in all but one compartment containing logs with beetles were aggregated. The distribution of beetles in one deciduous-dominated with conifer understory 50% retention stand was found to be uniform.

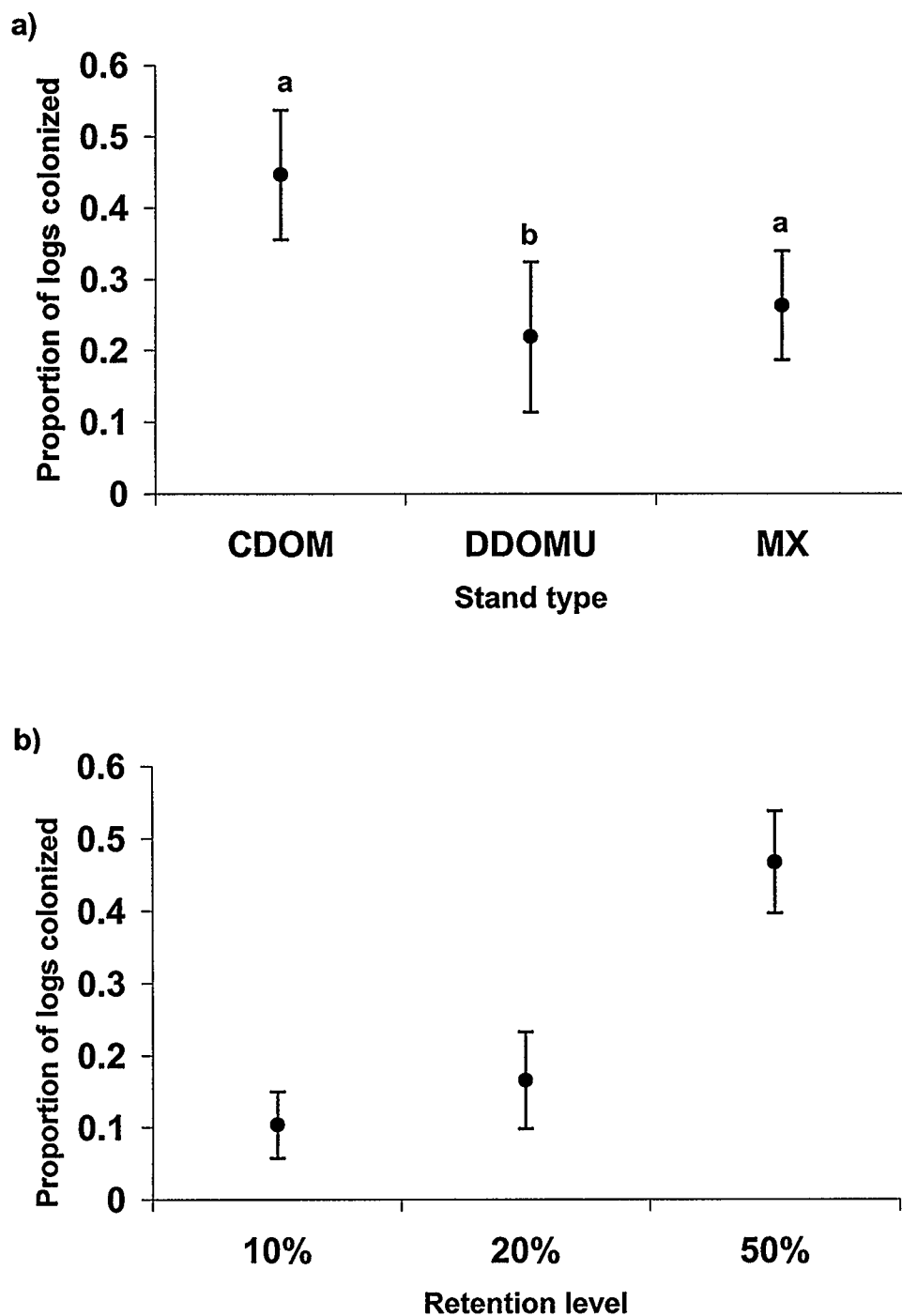
As another measure of habitat use, I examined whether the proportion of logs colonized by *P. rufipennis* in 1999 varied across the landscape, using the split-plot ANOVA design. Stand type had a significant effect on the proportion of logs colonized in 1999 ( $F_{2,24}=10.96$ ,  $p<0.003$ ; overall model:  $R^2=0.89$ ,  $F_{14,12}=7.26$ ,  $p<0.008$ ). Deciduous-dominated with conifer understory stands had the lowest proportion of logs colonized in 1999, followed by mixed and conifer-dominated stands, which had the highest proportions of logs colonized (T-K HSD,  $p<0.05$ ; Figure 3.6a). Retention level also had a significant effect on the proportion of logs that were colonized in 1999 ( $F_{6,20}=10.18$ ,  $p<0.0005$ ). 10% and 20% stands had lower proportions colonized than 50% and control stands (T-K HSD,  $p<0.05$ ; Figure 3.6b). Replicate had a significant effect on the proportion of logs colonized ( $F_{6,20}=3.11$ ,  $p<0.05$ ).

Using multiple regression, I also examined whether the proportion of logs occupied by *P. rufipennis* in a compartment in 1999 varied with landscape features such as tree density, proportion of conifers, habitat abundance (number

of logs in 1999), and habitat quality (mean log diameter). None of the variables in the model had a significant effect on the settlement densities of *P. rufipennis* (overall model:  $R^2=0.14$ ,  $F_{4,22}=0.92$ ,  $p>0.4$ ).

I repeated these analyses for the proportion of logs colonized in 2000. In the split plot ANOVA none of the variables (stand type, retention level, replicate) had a significant effect on the proportion of logs colonized by *P. rufipennis* in 2000 (overall model:  $R^2=0.49$ ,  $F_{15,9}=0.57$ ,  $p>0.57$ ). The multiple regression contained the same variables as for the 1999 analysis, with the addition of the index of brood production in 1999, log abundance in 2000, trap catches in 2000 and profile density. None of the variables in the model had significant effects on the proportion of logs occupied by *P. rufipennis* in 2000 (overall model:  $R^2=0.28$ ,  $F_{1,14}=0.79$ ,  $p>0.6$ ).

Surveys of logs in 1999 showed that 29 of 100 logs containing bark beetles contained two or more species. Of these 29 logs, 25 contained *P. rufipennis* and *Ips tridens*. Logs occupied by *P. rufipennis* alone and *I. tridens* alone did not differ significantly in mean diameter from each other ( $13.75 \pm 0.74$  cm,  $n=90$ , and  $14.42 \pm 2.36$  cm,  $n=10$  respectively;  $F_{1,97}=4.61$ ,  $p<0.04$ ). The diameter of logs containing both species was significantly larger than logs void of bark beetles (with both species: mean =  $17.13 \pm 1.41$  cm,  $n=25$ ; void:  $12.17 \pm 0.47$  cm,  $n=227$ ), but not significantly different than those with either *P. rufipennis* or *I. tridens* alone. A chi-square test of independence showed that these two species occurred together more frequently than expected by chance ( $\chi^2=19.71$ ,  $df = 1$ ,  $p<0.0001$ ).



**Figure 3.6.** Proportion of logs colonized (mean and standard error) by *P. rufipennis* in 1999 as a function of a) stand type and b) retention level. Data shown are untransformed data. Data were arcsin square root transformed for analysis. Stand type abbreviations as in Figure 2.1.



To determine if habitat type had a significant effect on the association of *I. tridens* and *P. rufipennis*, I conducted G-tests of independence based on the null hypothesis that the association was independent of habitat type. Logs were classified into logs containing *P. rufipennis* and logs containing both species together. Because of the low number of logs occupied by these two species in each stand type and retention level, I classified stand types into four categories based on stand type and density. These habitat types were: conifer/high density (conifer-dominated and mixed stands combined; 50% and 100% retention), conifer/low density (conifer-dominated, mixed; 10% and 20%), deciduous/high density (deciduous-dominated, deciduous-dominated with conifer understory; 50% and 100%), deciduous/low density (deciduous-dominated, deciduous-dominated with conifer understory; 10% and 20%). The occurrence of these two species together differed among stand classifications ( $G = 19.33$ ,  $df = 3$ ,  $p < 0.01$ ). Inspection of the contingency table expected values showed that in the deciduous/low class had observed values that were lower than expected, while all other classes had observed values that were higher than expected (Table 3.1).

To determine if the association between these two species depended on habitat abundance, I conducted a G-test based on the null hypothesis that the probability of the two species sharing a log is independent of habitat abundance by comparing logs containing *P. rufipennis* alone and logs with both species. Habitat abundance was categorized by looking at the distribution of log abundance among stands and dividing the distribution into thirds with equal

numbers of compartments. The abundance categories were 21 to 188 logs (13 compartments), 189 to 667 logs (13 compartments), and over 667 logs per 10 ha compartment (13 compartments). Logs containing both species were found to be independent of habitat abundance in the area ( $G=2.57$ ,  $df=2$ ,  $p>0.05$ ).

### 3.4 Discussion

#### 3.4.1 Bark Beetle Distribution (Landscape Scale)

Data from trap catches indicate that *P. rufipennis* responded to landscape scale rather than habitat scale information concerning habitat availability. Trap catches of *P. rufipennis* were strongly predicted by stand type and the percentage of conifers in the overstory, with trap catches being lowest in deciduous-dominated stands among all stand types, and increasing with the percentage of conifer in the canopy. Habitat abundance varied significantly with stand type, but it did not significantly explain the number of beetles caught. Therefore, it appears that *P. rufipennis* direct their search towards areas likely to contain habitat in an unharvested environment rather than in areas actually containing more habitat. Large-scale heterogeneity in habitat distribution, such as differences in the abundance of host species, can affect the selection behaviour since many bark beetles can detect habitat suitability from a distance. For example, *Trypodendron lineatum*, *Ips typographus*, and *Dendroctonus ponderosae* (Hopkins) have the ability to detect non-host odours and avoid them, presumably in order to search more efficiently (Schroeder, 1992; Wilson et al.,

**Table 3.1.** Observed and expected frequencies of logs containing both *I. tridens* and *P. rufipennis*. The association between *I. tridens* and *P. rufipennis* was dependent on stand classification (G-test of association  $p < 0.05$ ).

Stand Classification	Observed	Expected
Conifer/High	10	7
Conifer/Low	9	6
Deciduous/High	7	6
Deciduous/Low	0	7

1996; Borden et al., 1997; Byers et al., 1998, 2000). These results indicate that *P. rufipennis* may also be using host and non-host olfactory cues to find habitat.

Retention level had a weaker, though significant, effect on trap catches. Again, while habitat abundance varied with retention level, habitat abundance did not predict trap catches. The effect of retention level could also not be attributed to changes in the physical structure of the forest. Trap catches were not significantly affected by stand density or understory vegetation density (profile density).

Responses of other species of bark beetles to reductions in stand density are mixed. Both mountain pine beetles (*Dendroctonus ponderosae* (Hopkins)) (Priesler and Mitchell, 1993) and southern pine beetles (*Dendroctonus frontalis* (Zimmermann)) (Brown et al., 1987) prefer unthinned stands over thinned stands. Conversely, both *Ips pini* (Say) and *Trypodendron lineatum* are captured more in thinned stands than unthinned stands (Hindmarch and Reid, 2001; Chapter 2). The fact that both species that appear to prefer thinned areas are secondary beetles suggest that habitat availability may be an explanation for preferences for thinner stands. However, while habitat abundance associated with low retention explained *T. lineatum* distributions (Chapter 2), it did not explain differences in *P. rufipennis* distributions. Microclimate effects associated with thinning may also explain the response of beetles to thinning (Schmid et al., 1992; Bartos and Booth, 1994; and Hindmarch and Reid 2001). However, in this study, the effects of microclimate were not investigated.

### 3.4.2 Colonization Patterns (Habitat Scale)

Settlement densities of *P. rufipennis* were significantly influenced by landscape level factors such as stand type and retention level. However, none of the continuous variables examined significantly affected settlement densities.

The results of this study are consistent with the notion that *P. rufipennis* uses stand level cues rather than actual habitat abundance. If fewer beetles search for habitat in stands with fewer conifers, such as deciduous-dominated with conifer understory stands, then densities of beetles among logs in these stands can be expected to be lower. Furthermore, if fewer beetles are searching in these areas, then a lower proportion of suitable logs would be colonized. Densities of *P. rufipennis*, as well as the proportion of logs colonized, were found to be lower in DDOMU stands.

In harvested areas, log availability is higher than would be expected based on conifer abundance in unharvested stands. Therefore, if beetles used conifer abundance to direct search, the abundance of searching beetles would not necessarily be proportional to the amount of suitable habitat in harvested areas, resulting in lower settlement densities and lower proportions of logs colonized in harvested areas. These results differ from those of *T. lineatum* where settlement among habitat patches did not differ across the landscape (Chapter 2). However, Orians and Wittenberger (1991) showed similar results to *P. rufipennis* for yellow headed blackbirds, *Xanthocephalus xanthocephalus*, in which habitat selection was correlated with prey densities at the landscape scale (in marshes), but not at smaller scales (among territories).

### 3.4.3 Habitat Patch Quality

The IFD predicts that the density of individuals within a patch should be proportional to patch quality. For *P. rufipennis*, settlement density did not vary with log diameter. If phloem resources increased with log diameter, as is typical (Berryman, 1976; Reid and Glubish, 2001; but see Reid and Robb, 1999), then these results do not support the IFD. One possible explanation is that search costs are significant for *P. rufipennis*, contrary to the assumption for the IFD. Search costs for secondary bark beetles such as *P. rufipennis* are considerable given that their habitat is normally scarce and unevenly distributed, resulting in many individuals failing to find habitat (Atkins, 1962). If searching is costly, then individuals may be forced to occupy suboptimal habitat rather than continue to search for higher quality habitat.

Alternatively, beetles may not be able to obtain information concerning the quality of phloem within logs as they search for habitat across the landscape. If *P. rufipennis* is unable to respond to differences in habitat quality, then beetle distributions would not follow habitat quality.

Analysis of the coefficient of variation (CV) for the density of *P. rufipennis* among logs showed that landscape effects (stand type, retention level, habitat abundance, stand density) had no effect on the CV. These results indicate that searching individuals use the same acceptance criteria regardless of the quantity of habitat in an area. Real (1990) proposed that as search costs increase, the threshold for acceptance decreases. Search costs in *P. rufipennis* may be

significant enough that time and energy spent on discerning habitat of differing quality outweigh the benefits of potentially finding a higher quality habitat patch.

The index of dispersion showed that distributions of *P. rufipennis* were aggregated across the landscape. The aggregation of beetles across the landscape reiterates the absence of the IFD, but indicates the use of conspecifics and heterospecifics by *P. rufipennis* to detect habitat. Many studies have shown that bark beetles avoid aggregations of conspecifics and heterospecifics to decrease competition (Birch et al., 1980; Byers et al., 1984; Byers, 1989; 1993; Poland and Borden, 1998). However, if search costs are high, then joining aggregations of beetles among logs would facilitate habitat detection and decrease search costs. Therefore, the benefits of easier habitat detection could outweigh the costs of increased competition in aggregations.

*Polygraphus rufipennis* may use cues from conspecifics or heterospecifics to detect habitat, resulting in aggregations of one or more species within a log despite the costs of competition (Robins and Reid, 1997). In this study, *P. rufipennis* was found in association with *Ips tridens* more frequently than expected by chance in all habitat classifications except in high density deciduous-dominated stands.

Although attraction to heterospecific aggregation pheromones has not been documented between *P. rufipennis* and *I. tridens*, *I. tridens* is attracted to ipsdienol, it is interesting to note that the aggregation pheromone for *P. rufipennis*, 3-methyl-3-buten-1-ol, is an isoprene alcohol. Isoprene alcohols have been reported in only two other bark beetle species, both of which are *Ips* spp. (*I.*

*cembrae* (Heer) and *I. typographus* (Linnaeus)) (Bowers et al., 1991). *I. tridens* is attracted to the aggregation pheromone of *I. typographus* (Moeck and Safranyik, 1984).

### 3.5 Conclusion

Insects have the ability to detect habitat at a variety of spatial scales, which then allows them to search efficiently for habitat. However, how landscape and habitat scale features affect distributions at both scales may vary between species. In *P. rufipennis*, preferred habitat is normally scarce across the landscape and landscape-level cues such as stand composition appear to be used to search for habitat more efficiently. These results indicate that although individuals of this species respond to large-scale variation on the landscape, knowledge of smaller scale distributions of habitat is not complete. Changes in settlement distributions among habitat patches due to landscape scale influences have been shown in other systems. For example, Roland and Taylor (1997) found that parasitism by four insect parasitoid species was strongly influenced by landscape structure at different spatial scales.

For *P. rufipennis*, the predictions of both the IFD and the RCH hold at the landscape level, with larger numbers of beetles searching in more where host trees species are more abundant. However, closer inspection of distributions of beetles at the habitat patch level shows that settlement densities do not correspond to the IFD. The knowledge of the distribution of habitat patches (conifer logs) is not ideal. Furthermore, results indicate that *P. rufipennis*



augment their abilities to detect habitat by using cues from a heterospecific species (*I. tridens*).

The distribution of suitable habitat for secondary bark beetles following logging is vastly different than natural distributions of freshly dead wood (Atkins, 1962), with large quantities of suitable logs being concentrated in relatively small areas compared to the wide spread natural distribution of logs. Because of the discrepancy between human and natural processes, the cues that organisms naturally use to allow them to detect areas likely to contain habitat may not be appropriate for landscapes altered by humans. Therefore, organisms have imperfect knowledge of habitat distribution.

This study shows the importance of studying population distributions at varying spatial scales. The applicability of certain ecological theories such as the ideal free distribution and the resource concentration hypothesis to different species may vary depending on the perceptive capabilities of the study organism. If the appropriate spatial scale is not examined the complicated mechanisms that influence population distributions may be overlooked.

## 4.0 GENERAL CONCLUSIONS

Distributions of organisms across the landscape are inherently affected by habitat distribution. Habitat important to the breeding and reproduction of individuals are usually arranged unevenly across the landscape, and organisms have evolved to respond to a variety of cues to determine where resources are located. Spatial scale can have different effects on foraging and patch-selection behaviour, depending on the ability to respond to environmental variation and habitat specifications of a particular species (With, 1994; Ritchie, 1998).

Insects searching for suitable habitat by dispersing across the landscape are likely to use larger scale, general cues to detect areas likely to contain habitat and then use more specific cues to locate individual habitat patches (Bell, 1990). Although many studies have examined the ability of bark beetles to use olfactory cues to locate mates and habitat, few have considered the scale at which beetles respond. I have shown that both *T. lineatum* and *P. rufipennis* respond to different scales of variation across the landscape. O'Neill et al. (1988) suggested that organisms in landscapes with sparse resources use resources at a larger scale than when resources are abundant.

In *T. lineatum*, beetles appeared to use coarse-grained cues (stand composition) to detect habitat availability prior to harvest. However, following harvesting, the response to stand level cues was linked directly to distribution of habitat (stumps). Beetles were able to detect changes in habitat (stump) distribution and abundance following logging. The accumulation of beetles in areas where more host trees and more habitat was located supports the

resource concentration hypothesis at the landscape level. The abundance of host trees and habitat likely attracted beetles to the area, or alternatively caused beetles to spend more time searching in these areas.

At the habitat patch level, landscape influences did not affect the settlement of *T. lineatum* among habitat patches. Instead, beetles were able to detect and colonize most habitat patches in all areas. Rather than landscape level influences affecting settlement in *T. lineatum*, settlement appeared to be dependent on habitat quality. Larger stumps were more likely to be colonized, indicating that *T. lineatum* may be using phloem thickness as a measure of habitat quality.

The distribution of *P. rufipennis* at the landscape scale was similar to *T. lineatum*, in that beetle distributions were influenced by host tree abundance in the canopy. However, unlike *T. lineatum*, *P. rufipennis* was unable to respond to differences in habitat abundance following harvesting. Therefore, *P. rufipennis* distributions support the resource concentration hypothesis, but only with respect to host tree distributions and not to habitat log distributions.

At the habitat patch level, *P. rufipennis* again differed from *T. lineatum*. Neither settlement densities, nor the proportion of logs colonized, were affected by habitat quality (diameter). Landscape level characteristics seemed to override any influences that habitat patch level attributes may have had. Instead, settlement at the habitat patch level was significantly affected by stand type and retention level. Densities of beetles were lower and a lower proportion of logs was colonized in harvested areas (10% and 20% compartments) and areas with

few conifer trees (DDOMU stands). These results indicate that beetles may avoid areas with a significant deciduous component, or that beetles spend less time searching in these areas. Furthermore, lower densities and lower proportions of logs being colonized in harvested areas confirms that beetles are not able to respond to large fluctuations in habitat abundance following harvest. Settlement densities in logs indicated that beetles may have underestimated habitat log abundance following harvesting, resulting in under-use of abundant logs following harvesting.

This study shows that despite similar responses to stand level attributes, responses of *T. lineatum* and *P. rufipennis* were not the same at the habitat patch scale. Previous studies have also found differential responses to varying spatial scales between species with similar life history traits. Samu et al. (1999) showed that different spider species behave differently with respect to varying spatial scales. Similarly, four parasitoids of forest tent caterpillars responded differently to forest structure at different spatial scales (Roland and Taylor, 1997).

This and previous studies (Morris, 1987; Wiens, 1989; Orians et al., 1991) stress the importance of examining population responses at different spatial scales. Heterogeneity occurs at many scales across the landscape, and the ability to perceive this heterogeneity differs as well (Morris, 1987; With, 1994). Therefore, in testing the predictions of ecological theories, one must be careful about the scale at which behaviour is studied. The consequence of studying habitat selection behaviour at an inappropriate scale is that effects of variation at a different scale of examination may not be detected. Ray and Hastings (1996)

found that the detection of density-dependent population regulation was correlated with the scale at which the study was conducted.

The testing of theories such as the ideal free distribution and the resource concentration hypothesis at different scales helps to determine the perceptive ability of individual species. Theories such as the RCH (Root, 1973) and the IFD (Fretwell and Lucas, 1970) may not be relevant across taxa. Therefore, empirical studies on the effects of spatial scale on the distributions of organisms are valuable tools to test predictions of ecological theories. In addition to testing well known ecological theories, relatively unexamined processes such as the Weber-Fechner law can be used to interpret variations in the distribution of organisms.

In an applied forest management context, the results from my study may be used to identify characteristics of the landscape, such as stand composition and habitat abundance, that may hinder or facilitate the dispersal and colonization of potential pest species such as *T. lineatum* and *P. rufipennis*. Human disturbances are continually changing the landscape within which organisms need to locate suitable habitat, and many anthropogenic changes such as logging, occur at a smaller scale than natural events that are pertinent to forest pest insects (Atkins, 1962). Therefore, attempts by forest managers to manipulate the landscape at small scales to manage for forest pests may not be adequate to deter pest outbreaks. However, by understanding the spatial scale relevant to the species in question, an accurate indication of the effects of human disturbance can be determined, and forest management practices developed to

suit the attributes of a particular pest species.

In a conservation ecology context, this study shows that the abundance of individuals searching for habitat in an area does not necessarily predict the use of habitat in an area. Therefore, conservation efforts must consider the possible mismatch between population abundance and habitat use. Conservation of certain areas with high population densities may not lead to increased protection of areas actually used by individuals.

## 5.0 Literature Cited

- Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology* 65: 138-140.
- Amman, G. D. and V. E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Service INT-209.
- Amman, G. D. and J. E. Pasek. 1986. Mountain pine beetle in ponderosa pine: effects of phloem thickness and egg gallery density. U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station. INT-367.
- Andow, D.A. 1990. Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology* 71:1006-1017.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- Arditi, R. and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *The American Naturalist* 131:837-846.
- Areskoug, V. 2001. Utilisation of remnant dry forest corridors by native fauna in a pastoral landscape in the Paraguayan Chaco. *Skrifterie* 3:25-38.
- Atkins, M.D. 1966. Behavioural variation among scolytids in relation to their habitat. *The Canadian Entomologist* 98:285-288.

- Atkinson, W.D. and B. Shorrocks. 1984. Aggregation of larval diptera over discrete and ephemeral breeding sites: the implications for coexistence. *American Naturalist* 124:336-351.
- Ayers, B.D., M. P. Ayres, M.D. Abrahamson and S.A. Teale. 2001. Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). *Oecologia* 128:443:453.
- Bartos, D.L. and G.D. Amman. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. USDA Forest Service Research Paper INT-400.
- Bartos, D.L. and G.D. Booth. 1994. Effects of thinning on temperature dynamics and mountain pine beetle activity in a lodgepole pine stand. USDA Forest Service Research Paper INT-RP-479.
- Batch, C.E. 1984. Plant spatial pattern and herbivore population dynamics: Plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). *Ecology* 65: 170-195.
- Bauer, J. and J.P. Vité, J.P. 1975 Host selection by *Trypodendron lineatum* *Naturwissenschaften* 62:539.
- Bell, W.J. 1990. Searching behaviour patterns in insects. *Annual Review of Entomology* 35:447-467.
- Bernstein, C., A. Kacelnik and J.R. Krebs. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology* 60: 205-225.



- Berryman, A. A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. *Environmental Entomology* 5: 1225-1233.
- Birch, M.C., P. Srihara, T.D. Paine and J.C. Miller. 1980. Influence of chemically mediated behaviour on host tree colonization by four cohabiting species of bark beetles. *Journal of Chemical Ecology* 6:395-414.
- Borden, J.H., L. Chong, A. Savoie, and I.M. Wilson. 1997. Responses to green leaf volatiles in two biogeoclimatic zones by striped ambrosia beetle, *Trypodendron lineatum*. *Journal of Chemical Ecology* 23:2479-2491.
- Borden, J.H., D.R. Devlin, and D.R. Miller. 1992. Synomones of sympatric species deter attack by the pine engraver *Ips pini* (Coleoptera: Scolytidae). *Canadian Journal of Forest Research* 22:381-387.
- Bowers, W.W. and J.H. Borden. 1992. Attraction of *Lasconotus intricatus* Kraus. (Coleoptera: Colydiidae) to the aggregation pheromone of the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby) (Coleoptera: Scolytidae). *The Canadian Entomologist* 1214:1-5.
- Bowers, W.W., J.H. Borden and A. Raske. 1996. Incidence and impact of *Polygraphus rufipennis* (Coleoptera: Scolytidae) in Newfoundland. *Forest Ecology and Management* 89:173-187.
- Bowers, W.W., G. Gries, J.H. Borden and H.D. Pierce, Jr.. 1991. 3-methyl-3-buten-1-ol: Pheromone of the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby) (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 17:1989-2002

- Bright, D.E. 1976. The insects and arachnids of Canada, Part 2. Canadian Department of Agriculture Publication #1576. 241 pp.
- Brown, M.W., T.E. Nebeker, and C.R. Honea. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. *Southern Journal of Applied Forestry* 11:28-31.
- Byers, J.A. 1989. Behavioural mechanisms involved in reducing competition in bark beetles. *Holarctic Ecology* 12:466-476.
- Byers, J.A. 1993. Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Experientia* 49:272-275.
- Byers, J.A. 1995. Host tree chemistry affecting colonization in bark beetles, in R.T. Cardé and W.J. Bell (eds.). *Chemical Ecology of Insects* 2. Chapman and Hall, New York, pp. 154-213.
- Byers, J.A. 1996. An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modeling* 91:57-66.
- Byers, J.A. and D.L. Wood. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. *Journal of Chemical Ecology* 6:149-164.
- Byers, J.A., B.S. Lanne and J. Löfqvist. 1989. Host tree suitability recognized by pine shoot beetles in flight. *Experientia* 45: 489-492.
- Byers, J.A., D.L. Wood, J. Craig, and L.B. Hendry. 1984. Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: Regulation of inter- and intraspecific competition. *Journal of Chemical Ecology* 10:861-877.

- Byers, J. A., Q., Zhang, and F. Schlyter. 1998. Volatiles from non-host birch trees inhibit pheromone response in spruce bark beetles. *Naturwissenschaften* 89:557-561.
- Byers, J.A., Q.H. Zhang, and G. Birgersson. 2000. Strategies of a bark beetle, *Pityogenes bidentatus*, in an olfactory landscape. *Naturwissenschaften* 87:503-507.
- Cane, J.H., D.L. Wood, and J.W. Fox. 1990. Ancestral semiochemical attraction persists for adjoining populations of sibling *Ips* bark beetles (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 16:993-1013.
- Chamberlain, F.S. and J.N. Tenlet. 1926. *Cardiochiles nigriceps* Vier., and important parasite of the tobacco budworm, *Heliothis virescens* Fab. *Journal of Agricultural Research* 33:21-27.
- Chapman, J.A. 1962. Field studies on attack flight and log selection by the ambrosia beetle *Trypodendron lineatum* (Oliv.) (Coleoptera: Scolytidae). *The Canadian Entomologist* 99:1132-1137.
- Chapman, J.A. 1966. The effect of attack by the ambrosia beetle *Trypodendron lineatum* (Olivier) on log attractiveness. *The Canadian Entomologist* 98:50-59.
- Chapman, J.A., and J.M. Kinghorn. 1958. Studies of flight and attack activity of the ambrosia beetle, *Trypodendron lineatum* (Oliv.) and other scolytids. *The Canadian Entomologist* 90:362-372.
- Clausen, C.P. 1940. Entomophagous insects. McGraw-Hill, New York.

- Coll, M., and D. G. Bottrell. 1994. Effects of non-host plants on an insect herbivore in diverse habitats. *Ecology*. 73:723-731.
- Danchin, E. and R.H.G. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology and Evolution* 12:342-347.
- Danielson, B. J. 1992. Habitat selection, interspecific interactions and landscape composition. *Evolutionary Ecology* 6:399-411.
- Doak, D.F., P.C. Marino, and P.M. Karieva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: Implications for conservation. *Theoretical Population Biology* 41:315-336.
- Doutt, R.L. 1964. Biological characteristics of entomophagous adults. *Biological Control of Insect Pests and Weeds*. P. DeBach, ed. Chapman and Hall, London.
- Douwes, P. 1968. Host selection and host finding in the egg laying female *Cidaria albulata* L. (Lep, Geometridae). *Opuscula Entomologica* 33:233-279.
- Driessen, G., and C. Bernstein. 1999. Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *Journal of Animal Ecology* 68:445-459.
- Dyer, E.D.A. and J.A. Chapman. 1965. Flight and attack of the ambrosia beetle, *Trypodendron lineatum* (Oliv.) in relation to felling date of logs. *The Canadian Entomologist* 97:42-57.

- Fox, J.W., D.L. Wood and J.H. Cane. 1991. Interspecific pairing between two sibling *Ips* species (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 17:1421-1435.
- Fretwell, S.D., and H.L. Lucas Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, 19:16-36.
- Greene, C.M, and J.A. Stamps. 2001. Habitat selection at low populations densities. *Ecology* 82:2091-2100.
- Grunbaum, D. 1998. Using spatially explicit models to characterize foraging performance in heterogeneous landscapes. *American Naturalist* 151:97-115.
- Gustafson, E.J. and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77:94-107.
- Haack, R. A., R. C. Wilkenson and J. L. Foltz. 1987. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. *Oecologia* 72: 32-38.
- Hassell, M.P. 1986. Detecting density dependence. *Trends in Ecology and Evolution* 1:90-93.
- Helland, I.S., O. Anderbrandt, and J.M. Hoff. 1989. Modeling bark beetle flight: a review. *Holarctic Ecology* 12:427-431.
- Hill, C.J. 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. *Conservation Biology* 9:1559-1566.

- Hindmarch, T. D. and M. L. Reid. 2001. Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity. *Canadian Journal of Forest Research* 31:1502-1512.
- Huhta, E., J. Jokimaki, and P. Rahko. 1998. Distribution and reproductive success of the Pied Flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics; the effect of scale. *Ibis* 140: 214-222.
- Jonsen, I. and P.D. Taylor. 2000. *Calopteryx* damselfly dispersions arising from multiscale responses to landscape structure. *Conservation Ecology* 4:4. [online] URL: <http://www.consecol.org/vol4/iss2/art4>.
- Kennedy, M., and R.D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. *Oikos* 68:158-166
- Kirkendall, L.R. 1983. The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). *Zoological Journal of the Linnean Society* 77:293-352.
- Kotliar, N.B. and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *OIKOS* 59:253-260.
- Krebs, C. J. 1989. *Ecological Methodology*. Harper and Row. New York.
- Lima, S.L. and P. A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131-135.
- Lindelow, A., B. Risberg, and K. Sjodin. 1992. Attraction during flight of scolytids

- and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. *Canadian Journal of Forest Research* 22:224-228.
- Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *The Canadian Entomologist* 115:299-302.
- McCarthy, B.C., and R.R. Bailey. 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. *Canadian Journal of Forest Research* 24:1317-1329.
- McConnell, B.R. and J.G. Smith. 1965. Understory response three years after thinning pine. *Journal of Range Management* 18:129-132.
- McIntyre, N.E., and J.A. Wiens. 1990. Interactions between landscape structure and animal behaviour the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* 14:437-447.
- McLean, J.A. 1985. Ambrosia beetles: a multi-million dollar degrade problem of sawlogs in coastal British Columbia. *Forestry Chronicles* 61:295-298.
- Merriam, G. and A. Lanoue. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. *Landscape Ecology* 4:123-131.
- Miller D.R, and J.H. Borden. 1992. (s)-(+)-ipsdienol interspecific inhibition of *Ips latidens* (Leconte) by *Ips pini* (Say) (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 18:1577-1582.
- Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). *The Canadian*

- Entomologist 102:985-995.
- Moeck, H.A. and L. Safranyik. 1984, Assessment of predator and parasitoid control of bark beetles, Canadian Forest Service, Info. Rep. BC-X-248
- Moeck, H.A. , L. Safranyik, C.S. Simmons and Lawko, C.M. 1985. *Ips tridens* (Coleoptera: Scolytidae) attracted by ipsdienol plus cis-verbenol. Canadian Entomologist. 117: 955-960.
- Monkkonen, M., R. Hardling, J.T. Forsman and J. Tuomi. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evolutionary Ecology 13:91-104.
- Monteith L.G. 1960. Influence of plants other than the food plants of their host on host-finding by tachinid parasites. The Canadian Entomologist 92:641–645.
- Morris, D.W. 1987. Ecological scale and habitat use. Ecology 68:362-369.
- Nijholt, W.W. 1967. Moisture and fat content during the adult life of the ambrosia beetle *Trypodendron lineatum* (Oliv). Journal of the Entomological Society of British Columbia 64:51-55.
- D.A. Nordlund and W.J. Lewis. 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. Journal of Chemical Ecology 2:211-20.
- O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2:63-69.
- Orians, G.H., and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29-S49.



- Parker, G.A. and W.J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* 34:1222-1242.
- Poland, T.M., and J.H. Borden. 1998. Semiochemical-induced competition between *Dendroctonus rufipennis* and two secondary species, *Ips tridens* and *Dryocetes affaber* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 91:1142-1149.
- Prebble, M.L., and K. Graham. 1957. Studies of attack by ambrosia beetles in softwood logs on Vancouver Island, British Columbia. *Forest Science* 3:90-112.
- Preisler, H.K., and R.G. Mitchell. 1993. Colonization patterns of the mountain pine beetle in thinned and unthinned lodgepole pine stands. *Forest Science* 39:528-545.
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *American Naturalist* 132:652-661.
- Pulliam, H.R. and B.J. Danielson. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137: S51-S66.
- Rankin, L.J. and J.H. Borden. 1991. Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Canadian Journal of Forest Research* 21:1029- 1036.
- Rausher, M. D. 1983. Alteration of oviposition behavior by *Battus philenor* butterflies in response to variation in host plant density. *Ecology* 64: 1028-

1034.

- Ray, C. and A. Hastings. 1996. Density dependence: Are we searching at the wrong spatial scale? *Journal of Animal Ecology* 65:556-566.
- Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist* 136:376-405.
- Reid, M. L. and S. S. Glubish. 2001. Tree size and growth history predict breeding densities in Douglas-fir beetles (Scolytidae) in fallen trees. *The Canadian Entomologist* 133: 697-704.
- Reid, M. L. and T. Robb. 1999. Death of vigorous trees benefits bark beetles. *Oecologia* 120: 555-562.
- Ricketts, T. H. 2001. The matrix matter: Effective isolation in fragmented landscapes. *American Naturalist* 158:87-99.
- Risch, S.J. 1981. Herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* 62:1325-1340.
- Ritchie, M.E. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* 12:309-330.
- Robins, G.L. and M.L. Reid. 1997. Effects of density on the reproductive success of pine engravers: is aggregation in dead trees beneficial? *Ecological Entomology* 22: 329-334.
- Rogers, DJ 1972. Random search and insect population models. *Journal of Animal Ecology* 41: 369-383.

- Rohlf, W.M. and L.L. Hyche. 1984. Observations on activity and development of *Lasconotus pusillus* and *Lasconotus referendarius* (Coleoptera: Colydiidae) following arrival at *Ips. spp.* infested southern pines. Journal of the Georgia Entomological Society 19:114-119.
- Roitberg, B.D., J. Sircom, C.A. Roitberg, J.J.M Van Alphen, L. Ver. 1992. Seasonal dynamic shifts in patch exploitation by parasitic wasps. Behavioural Ecology 3:156-165.
- Roland, J., and P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710-713.
- Root, R.B. 1973. Organization of a plant arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95-124.
- Rudinsky, J.A. and G.E. Daterman. 1964. Field studies on flight patterns and olfactory responses of ambrosia beetles in douglas-fir forests of western Oregon. The Canadian Entomologist 96:1339-1352.
- Salom, S.M. and J.A. McLean. 1988. Semiochemicals for capturing the ambrosia beetle, *Trypodendron lineatum*, in multiple-funnel traps in British Columbia. Journal of the Entomological Society of British Columbia 85:34-39.
- Salom, S.M. and J.A. McLean. 1989. Influence of wind on the spring flight of *Trypodendron lineatum* (Oliver)(Coleoptera: Scolytidae) in a second-growth coniferous forest. The Canadian Entomologist 121: 109-119.

- Salom, S.M. and J.A. McLean. 1990. Flight and landing behaviour of *Trypodendron lineatum* (Coleoptera: Scolytidae) in response to different semiochemicals. *Journal of Chemical Ecology* 16:2589-2604.
- Salom, S.M. and J.A. McLean. 1991a. Environmental influences on dispersal of *Trypodendron lineatum* (Coleoptera: Scolytidae). *Environmental Entomology* 20:565-576.
- Salom, S.M. and J.A. McLean. 1991b. Flight behaviour of scolytid beetle in response to semiochemicals at different wind speeds. *Journal of Chemical Ecology* 17:647-662.
- Salt, G.W. 1967. Predation in an experimental protozoan population (*Woodruffia-Paramecium*). *Ecological Monographs* 37:113-144.
- Samu, F., K.D. Sunderland, and C. Szinetár. 1999. Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: A review. *The Journal of Arachnology* 27:325-332.
- SAS Institute, Inc. 1995. *JMP User's Guide*, Cary, NC. SAS Institute, Inc.
- Schlyter, F., and O. Anderbrant. 1993. Competition and niche separation between two bark beetles: Existence and mechanisms. *Oikos* 68:437-447.
- Schlyter, F., G. Birgersson, J.A. Byers, and A. Bakke. 1992. The aggregation pheromone of *Ips duplicatus* and its role in competitive interactions with *I. typographus* (Coleoptera: Scolytidae). *Chemoecology* 3:103-112.

- Schmid, J. M., S. A. Mata, and R. A. Schmidt. 1991. Bark temperature patterns in ponderosa pine stands and their possible effects on mountain pine beetle behaviour. *Canadian Journal of Forest Research* 21: 1 439-1446.
- Schmid, J. M., S. A. Mata, and D. C. Allen. 1992a. Potential influences of horizontal and vertical air movement in ponderosa pine stands on mountain pine beetle dispersal. USDA Forest Service Research Note RM-516.
- Schmid, J. M., S. A. Mata., and R. A. Schmidt. 1992b. Bark temperature patterns in mountain pine beetle susceptible stands of lodgepole pine in the central Rockies. *Canadian Journal of Forest Research* 22:1669:1675.
- Schmitz, R. F., M. D. McGregor, G. D. Amman, and R. D. Oakes. 1989. Effect of partial cutting treatments of lodgepole pine stands on the abundance and behaviour of dying mountain pine beetles. *Canadian Journal of Forest Research* 19:566-574.
- Schroder, D. 1969. *Lypha dubia* (Fall.)(Dip.: Tachinidae) as a parasite of the European pine shoot moth, *Rhyacionia buolinana* (Schiff.) (Lep.: Eucosmidae) in Europe. Technical Bulletin of the Commonwealth Institute for Biological Control 12:43-60.
- Schroeder, L.M. 1992. Olfactory recognition of non-hosts aspen and birch by conifer bark beetles *Tomicus piniperda* and *Hylurgops palliatus*. *Journal of Chemical Ecology* 18:1583-1593.

- Shields, W.M., J.R. Crook, M.L. Hebblethwaite, and S.S. Wiles-Ehmann. 1988. Ideal free coloniality in the swallows. *Ecology of Social Behavior*. C. N. Slobodchikoff. ed., Academic Press, NY, pp 189-228.
- Shore, T. L. and J. A. McLean. 1995. Ambrosia beetles. *Forest insect pests in Canada*. J. A. Armstrong and W. G. H. Ives eds. Ottawa, Natural Resources Canada, Canadian Forest Service.
- Sidders, D., and J. Spence. 2000. Ecosystem management emulating natural disturbance: Research Study and Field Guide. Canadian Forest Service-Northern Forestry Centre.
- Solbreck, C. 1995. Variable fortunes in a patchy landscape- the habitat templet of an insect migrant. *Researches on Population Ecology* 37:129-134.
- Spradbury, J.P. 1969. The biology of *Pseudorhyssa sternata* Merrill (Hym., Ichneumonidae), a cleptoparasite of Siricid woodwasps. *Bulletin of Entomological Research* 59:291-297.
- Stanton, M.L. 1983. Spatial patterns in the plant community and their effects upon insect search. *Herbivorous Insects: host-seeking behavior and mechanisms*. Ahmad, S. ed. pp, 125-157. Academic Press.
- Steinberg, S., M. Dicke, and L.É.M. Vet. 1993. Relative importance of infochemicals from first and second trophic level in long-range host location by the larval parasitoid *Cotesia glomerata*. *Journal of Chemical Ecology* 19:47-59.

- Sutcliffe, O.L., and C.D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* 10:41359-1365.
- Sutherland, W.J. 1983. Aggregation and the 'ideal free' distribution. *Journal of Animal Ecology* 52:821-828.
- Stamps, J. 2001. Habitat selection by dispersers: proximate and ultimate approaches. *Dispersal*. Clobert J, E. Danchin, A. Dhondt and J. Nichols eds. pp, 230-242. Oxford University Press.
- Taborsky, B. and M. Taborsky. 1995. Habitat use and selectivity by the brown kiwi (*Apteryx australis mantelli*) in a patchy environment. *Auk* 112:680-689.
- Thomas, C.D., J.A. Thomas, and M.S. Warren. 1992. Distributions of occupied and vacant butterfly habitats. *Oecologia* 92:563-567.
- Thysell, D.R. and A.B. Carey. 2000. Effects of forest management on understory and overstory vegetation: a retrospective study. USDA General Technical Report PNW-GTR-488.
- Tinker, D.B., and D.H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* 3: 472-483.
- Tommeras, B.A. 1985. Specialization of the olfactory receptor cells in the bark beetle *Ips typographus* and its predator *Thanasimus formicarius* to bark beetle pheromones and host tree volatiles. *Journal of Comparative Physiology and Sensory Neural and Behavioural Physiology* 157:335-342.

- Turchin, P. 1988. The effect of host-plant density on the numbers of Mexican bean beetles *Epilachna varivestit*. *American Midland Naturalist* 119:15-20.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72: 1253-1266.
- Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Sunderland, MA.
- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197.
- Varley, G.G. 1947. The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*). *Journal of Animal Ecology* 16:139-187.
- Ward, S.A. 1987. Optimal habitat selection in time limited dispersers. *American Naturalist* 129:568-579.
- Watt, K.E.F. 1964. Comments on fluctuations of animal populations and measures of community stability. *The Canadian Entomologist* 96: 1434-1442.
1965. Community stability and the strategy of biological control. *The Canadian Entomologist* 97:887-895
- Werner, R.A., and E.H. Holsten. 1984. Scolytidae associated with felled spruce in Alaska. *The Canadian Entomologist* 116:465-471.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.



- Wiens, J.A. 1997. Metapopulation dynamics and landscape ecology. Pp.43-62. *Metapopulation Biology: Ecology, Genetics and Evolution*. Hanski, I. & M.E. Gilpin (eds.), Academic Press, New York.
- Wilson, I.M., J.H. Borden, R. Gries, and G. Gries. 1996. Green leaf volatiles as anti-aggregants for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Journal of Chemical Ecology* 22:1861-1875.
- With, K. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* 9:25-36.
- With, K. and T. O. Crist. 1995. Critical thresholds in species responses to landscape structure. *Ecology* 76:2446-2459.
- Wood, D. L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behaviour of bark beetles. *Annual Review of Entomology* 27:411-446.