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Effects of Thinning of Mature Lodgepole Pine Stands on Diversity and Abundance of Bark Beetles (Coleoptera: Scolytidae).

by

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ABSTRACT

Thinning of mature lodgepole pine stands (*Pinus contorta* var. *latifolia* Engelm.) changed forest structure in ways that increased the diversity and abundance of secondary bark beetles (Coleoptera: Scolytidae). In particular, increased coarse woody debris and wind speeds in thinned stands relative to unthinned stands were associated with increased diversity and abundance. Thinned stands also enhanced dispersal in pine engraver bark beetles, *Ips pini* Say, measured as increased number of days above the temperature threshold for flight (19° C) and reduced dispersal costs in terms of fat consumption. Further, pine engravers in thinned stands had more mates, longer egg galleries, more eggs, and higher egg densities relative to unthinned stands. These multiple influences on bark beetles suggest that increased population sizes due to thinning may be reduced by minimizing the amount of coarse woody debris remaining after thinning, monitoring coarse woody debris input after thinning, and maintaining higher tree densities.

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CHAPTER 1
INTRODUCTION

To make predictions about biodiversity, the mechanisms determining the distribution of individuals must be known. These mechanisms can be deduced by manipulating habitat and determining the responses of species to these manipulations. In forested ecosystems, forestry is a large-scale manipulation of habitat. Since one goal of the forest industry is to maintain biodiversity following harvesting (Bondrup-Neilsen 1995), it is important to determine how a given harvesting practice affects biodiversity, and more importantly what mechanisms are responsible for any changes that are observed in the abundance of organisms.

Traditional harvesting methods such as clear-cutting have significant effects on biodiversity. Clear-cutting typically increases the number of large mammals (Wallmo 1969; Wallmo et al. 1972) while reducing the number of small mammals (e.g., Carey and Johnson 1995), and changing community structure of insects (e.g., Niemala et al. 1988, 1992, 1993), thereby also altering the diversity of these taxa. The mechanisms responsible for these changes can be managed for at the time of harvesting, as they are affected by the number of trees that are cut and tree density in residual stands. For example, there are more deer in clear-cuts because reduced tree density allows grass to grow, therefore providing more browse material for the deer (Wallmo 1969; Wallmo et al. 1972). However, changes in understorey vegetation are partly responsible for fewer small mammals in clear-cuts, as are changes in the amount of logging debris and number of fallen trees, both of which offer cover from predators (Carey and Johnson 1995). Finally, change in understorey vegetation towards grasses is also responsible for the switch from forest-specialist ground beetles (Coleoptera: Carabidae) to species that prefer open habitat (Niemala et al. 1988, 1992, 1993).

Alternative methods such as commercial thinning may have smaller effects on organisms because the forest remains somewhat intact. During commercial thinning, mature trees are selectively removed from a stand, resulting in an evenly spaced stand. Trees that are removed are topped and de-limbed in the stand, and this fresh coarse woody debris is left in the stand, thereby increasing this aspect of forest structure. Furthermore, thinned stands are warmer and windier than unthinned stands (Bartos and Amman 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994).

One taxon that is likely to be affected by thinning is bark beetles (Coleoptera:

Scolytidae). Bark beetles are of interest for several reasons. First, they may be important in forest ecosystem processes such as the decomposition of fallen trees or logging debris and, in turn, affect nutrient cycling (Harmon et al. 1986; Freedman et al. 1996). They are also food for other insects (Mills 1985; Reeve 1997) and birds (Shook and Baldwin 1970; Berryman 1976; Amman 1984; Murphy and Lenhausen 1998) and therefore may affect total biodiversity within the forest. Bark beetles also pose an economic threat as they sometimes kill trees (Mitchell et al. 1983; Bartos and Amman 1989; Schenk and Benjamin 1969) and attack and degrade harvested trees (Fisher et al. 1953; McMullan 1956; Kaila et al. 1997). Consequently, the forest industry has taken great measures to control bark beetles (Fisher et al. 1954; McMullan 1956; Mitchell et al. 1983; McGregor et al. 1987; Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994).

Because their life histories are closely linked to the forest environment, bark beetles are an excellent indicator group for evaluating alternative harvesting practices. The life history of the focal species of this thesis, the pine engraver (*Ips pini* Say), provides a representative example. Pine engravers typically form breeding aggregations on freshly dead or dying pine trees (Schenk and Benjamin 1969) or debris from logging (Reid 1955). The proportion of bark beetles that find breeding habitat is typically low, as indicated by low recapture rates in mark-recapture experiments (e.g., Weslien 1990; Thoeny et al. 1992; Zumr 1992; Turchin and Thoeny 1993; Zolubas and Byers 1995), and similar trends are expected for pine engravers since fresh breeding habitat is ephemeral. In pine engravers, males disperse through the forest in search of hosts, which they find using host kairomones (Miller and Borden 1990), visual cues (Seybert and Gara 1970), and pheromones (Miller et al. 1990; Teale et al. 1991; Seybold et al. 1992). At a host, males excavate nuptial chambers in the phloem layer, and produce pheromones that attract females, as well as other males which leads to the formation of breeding aggregations (Miller et al. 1990; Teale et al. 1991; Seybold et al. 1992). Typically, males mate with three females at one time (Reid 1955; Schenk and Benjamin 1969; Kirkendall 1989; Reid and Roitberg 1995). Females extend egg galleries that run parallel to each other from the nuptial chamber (Reid 1955). Offspring chew perpendicularly from the egg galleries (Reid 1955). Consequently, the phloem layer is consumed in one generation, and emerging adults must disperse in search of a new host.

These life history characteristics suggest several ways in which alteration of the forest environment by thinning will affect bark beetle diversity and abundance. Perhaps

most importantly, coarse woody debris dynamics will change following thinning. Although the effects of thinning on coarse woody debris dynamics are unknown, inferences can be made from studies on coarse woody debris dynamics after clear-cutting. Although the input of coarse woody debris may be high at the time of clear-cutting because crowns and limbs are left in the stands, it is significantly lower than natural conditions thereafter (Carey and Johnson 1995; Krankina and Harmon 1995). On the basis of species-area relationships (MacArthur and Wilson 1972; Connor and McCoy 1979), there should be more bark beetles in thinned stands immediately following thinning, and their abundance may decrease over time.

Dispersal costs for bark beetles will likely be affected by changes in tree density and microclimate associated with thinning. Bark beetles fly in the mid-bole region (Forsse and Solbreck 1985; Safranyik et al. 1992), suggesting that they seek uncluttered flight paths. Since there are fewer trees to maneuver around en route to a host in thinned stands than in unthinned stands, dispersal costs may be lower in thinned stands than unthinned ones. On the other hand. increased temperatures and wind speeds in thinned stands may increase dispersal costs because of higher energy expenditures while the beetles are flying (Seybert and Gara 1970) and during periods of inactivity between flights (Forsse and Solbreck 1985; Jactel and Gaillard 1991).

Thinning may also affect bark beetle reproductive success. Higher temperatures, such as are found in thinned stands relative to unthinned stands, generally result in longer egg galleries (Reid 1962; Amman 1972; Wagner et al. 1981; Wermelinger and Seifert 1999) with more eggs (Wagner et al. 1981; Wermelinger and Seifert 1999) at higher densities (Amman 1972; Wagner et al. 1981). Similar trends in egg gallery length and number of eggs are expected in large females retaining high energy reserves upon arrival at breeding sites (Clarke et al. 1979; Wagner et al. 1981; Anderbrant 1988). Consequently, dispersal costs may be important in determining bark beetle reproductive success, and may differ between thinned and unthinned stands.

In this thesis, I quantify the effects of commercial thinning of lodgepole pine stands (*Pinus contorta* var. *latifolia* Engelm.) on scolytid bark beetle diversity and abundance (Chapter 2). Given the many changes in forest structure and microclimate associated with thinning, I identify which aspects best explain diversity and abundance of these beetles (Chapter 2). I also experimentally investigate the effects of thinning on dispersal (Chapter 3) and reproduction (Chapter 4) to further deduce potential mechanisms by which thinning can influence bark beetles.

CHAPTER 2
EFFECTS OF THINNING OF MATURE LODGEPOLE PINE STANDS ON PATTERNS OF SCOLYTID BARK BEETLE DIVERSITY AND ABUNDANCE.

INTRODUCTION

Thinning has been proposed as a forest management tool to reduce the effects of bark beetles (Coleoptera: Scolytidae) that attack living trees (i.e., primary bark beetles; Mitchell et al. 1983; McGregor et al. 1987; Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994). The mechanisms responsible for the reduced success of these beetles in thinned stands have not been directly tested. Increased tree vigour as a result of reduced competition between the remaining trees (Mitchell et al. 1983), as well as higher temperatures and wind speeds due to reduced canopy closure and tree density (Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994) have been proposed as possible mechanisms. However, increased tree vigour and higher temperatures and wind speeds do not always have a negative effect on bark beetles. For example, once the potentially adverse effects of host tree active defenses are overcome, bark beetles have higher reproductive success in host trees that had been growing vigorously prior to death (Slansky and Haack 1986; Reid and Robb 1999). Also, higher temperatures and wind speeds do not always affect dispersal success in bark beetles (Safranyik et al. 1989; Chapter 3). Effects on dispersal are significant because bark beetles require previously unused hosts for each reproductive bout and therefore dispersal is a necessary part of their life histories. Here, I investigate the effects of thinning mature forests on patterns of diversity and abundance of bark beetles, as well as the mechanisms that may be responsible for these patterns. My focus here is on beetles inhabiting dying or freshly dead trees (i.e., secondary bark beetles) since they are more common than primary bark beetles (Raffa et al. 1993).

Thinning changes several aspects of the forest environment that are relevant to secondary bark beetles. During thinning, trees are selectively removed from a stand, resulting in an relatively open, evenly spaced stand. This makes thinned stands warmer and windier than their unthinned counterparts. Furthermore, trees that are removed are usually topped and de-limbed on site, resulting in a large input of fresh coarse woody debris that can be used as breeding sites by secondary bark beetles.

The tendency of most bark beetles to fly in the mid-bole region of the forest (Forsse and Solbreck 1985; Safranyik et al. 1992) suggests that bark beetles seek uncluttered flight

paths. Thinned stands may therefore be more attractive to bark beetles because flight is less costly than in unthinned stands because there is less clutter for beetles to maneuver around when searching for a host (Chapter 3). Furthermore, higher temperatures in thinned stands mean that temperature thresholds for flight are reached more often than in unthinned stands (Chapter 3). Together, these would likely increase beetle diversity and abundance in thinned stands. However, higher temperatures may result in faster fat depletion that may limit flight in thinned stands, while higher wind may deter flight (Seybert and Gara 1970; Salom and McLean 1991a,b). In this scenario, bark beetle diversity and abundance would be expected to be lower in thinned stands than in unthinned stands.

The large input of fresh coarse woody debris as a result of thinning is also expected to affect secondary bark beetles. This debris would release a large plume of host volatiles (kairomones) that attract bark beetles, thereby potentially attracting bark beetles from a large area into thinned stands. Upon arriving in thinned stands, bark beetles could readily find a host due to the large amount of coarse woody debris available. Reduced clutter in thinned stands may enhance the host finding process because bark beetles rely on visual cues (Seybert and Gara 1970; Billings et al. 1976; Hynum and Berryman 1980) as well as chemical cues to find a host. However, the long-term coarse woody debris dynamics in thinned stands are unknown. Input of coarse woody debris may remain high following thinning as the remaining trees are more exposed to wind and are not supported by surrounding trees like in unthinned stands (Quine et al. 1995), thereby perpetuating high levels of bark beetle activity in thinned stands. Conversely, input of coarse woody debris may quickly return to pre-harvest levels, forcing beetles to go elsewhere to find a host.

In this chapter, I quantify the effects of commercial thinning of mature lodgepole pine stands (*Pinus contorta* var. *latifolia* Engelm.) on scolytid bark beetle diversity and abundance. Given the many changes in forest structure and microclimate associated with commercial thinning, I identify which aspects of forest structure and microclimate best explain diversity and abundance of these beetles.

METHODS

Study Sites

This study was conducted in commercially thinned lodgepole pine stands and matched unthinned stands near Whitecourt, Alberta, Canada (54°8'N 115°42'W). Thinned stands were approximately 50 ha, and had a 1 ha unthinned control plot (internal control stand) on one side (Figure 2.1). A 1 ha unthinned control plot (external control stand) was

established in the continuous forest surrounding each thinned stand to control for possible edge effects in the internal control (Figure 2.1). A 1 ha plot was also established in the thinned stand to ensure equal sampling in thinned and unthinned stands (Figure 2.1). I sampled at three sites (stands aged 60, 70, 100 yr) from 15 June - 31 August 1996, 3 May - 12 August 1997, and 1 May - 30 June 1998, while a fourth (100 yr) was sampled in 1997 and 1998 only. The internal control at the fourth site was harvested between the first and second year of sampling and therefore comparisons in the second year of sampling for this site were between the thinned stand and external control only. At all sites, thinning occurred the winter before sampling began.

During thinning, approximately two-thirds of the trees were removed from each stand. Average tree densities ($\pm$ SE) were 841 + 171 trees$\cdot$ha^{-1} in thinned stands, 2703 $\pm$ 289 trees$\cdot$ha^{-1} in internal controls, and 2346 $\pm$ 371 trees$\cdot$ha^{-1} in external controls. The crowns and limbs of harvested trees were left in the stand.

Microclimate

I monitored microclimate weekly at the centre of each stand. Maximum temperature over the sampling period was measured using a digital thermometer (Micronta 63-867) attached to the north side of a tree at breast height. Wind speed was measured using a hand-held anemometer (SIMS Model DIC) at 2 m above ground level. I determined microclimate differences in thinned and unthinned stands by comparing the residuals of the average maximum temperature and wind speed of all three stands at a site for each monitoring period. This controlled for seasonal variation in temperature and daily variation in wind. Residuals were analyzed as a function of stand type for each site and time since thinning using a Kruskal-Wallis test.

Habitat Availability

I measured fresh coarse woody debris > 3 cm diameter each year using the line intersect method (Van Wagner 1968). Fresh coarse woody debris was defined as any tree that had been cut or fallen in the winter before sampling. Five random transects were done in each stand. Each transect was an equilateral triangle with 30 m sides. I analyzed fresh coarse woody debris as a function of stand type (thinned versus unthinned) and time since thinning using a multiple regression model that controlled for differences between sites (a random effect).

Beetle Diversity and Abundance

I sampled beetles using three methods: commercially baited funnel traps (Lindgren 1983), acrylic window traps hanging above sections of recently felled pine trees, and by excavating coarse woody debris. These methods sample different aspects of beetle activity, and in combination provide the greatest insight into patterns of diversity and abundance. Funnel traps sample the beetles flying through a stand, acrylic barrier traps indicate the beetles arriving at hosts, and coarse woody debris excavations identify the beetles actually breeding in the stand.

Three 12-unit funnel traps were placed at least 20 m apart in each stand. This distance ensured independent trap catches (M. Reid, University of Calgary, pers. comm.). Two traps were baited with pine engraver (*Ips pini* Say) pheromones (ipsdienol and lanierone) and one was baited with a pine tree kairomone (α-pinene). All chemicals were supplied by Phero Tech Inc. I emptied traps weekly.

I sampled beetles arriving at hosts using acrylic window traps hanging from logs of freshly felled pine trees that were placed in each thinned stand and its external control. In 1996, four logs were placed in thinned and unthinned stands at two sites. In 1997, four new logs were placed in thinned and unthinned stands at all four sites (this was in addition to the four added in the previous year at two sites). All logs were 2 m long, and 16.57 $\pm$ 0.60 cm (mean $\pm$ SE) in diameter. Logs were baited with ipsdienol and lanierone (Phero Tech Inc.), and were placed at least 20 m from each other and from funnel traps to ensure independent catches. One acrylic window trap (20 cm wide x 30 cm high) was suspended over each log in 1997 and 1998. I collected beetles from window traps weekly.

I excavated coarse woody debris while sampling habitat availability to identify beetles actually breeding in stands. I included all coarse woody debris originating at the time of thinning or later. A 15 cm^2 area of bark was removed from pieces of debris that showed signs of beetle activity (apparent from frass piles on the bark surface). I collected all beetles from the 15 cm^2 area.

Shannon's H diversity index was used to describe diversity because it takes into account both species richness (number of species) and evenness (the equitable distribution of individuals among species results in high evenness; Krebs 1989). Shannon's H diversity index is also robust to differences in sample size (Krebs 1989). I calculated Shannon's H separately for all pheromone traps (using the mean of the two traps per stand), kairomone traps, and for the total number of beetles found during coarse woody debris excavations at each stand for each year (stand-years). I calculated Shannon's H for

each window trap for each year because logs of different ages were in each stand at any one time.

I analyzed diversity as a function of stand type and time since thinning using a multiple regression model controlling for differences between sites (a random effect). Log age was also included in the model for diversity in window traps. To determine the mechanism(s) responsible for the effects of stand type and time since thinning, I further analyzed diversity as a function of tree density, the current amount of fresh coarse woody debris, the amount of fresh coarse woody debris in the previous year (because of potential offspring effects), temperature, and wind. For the first year after thinning, the amount of fresh coarse woody debris in the previous year was estimated by averaging the amount of fresh coarse woody debris in control stands over the duration of the study (mean = 0.86 $m^3 \cdot ha^{-1}$).

Differences in sampling periods among years may have affected which beetles were captured in pheromone traps, kairomone traps, and window traps, and made comparisons of the absolute number of beetles captured in these traps over time difficult. Comparing the absolute number of beetles captured over time was also difficult because one stand was a year behind the others in terms of time of thinning. Therefore, to combine data from all years while focusing on within year differences among stand types, I standardized the number of individuals of a given species at each stand and for each year. I calculated the standardized number of individuals, Z, using:

$$Z = (X_i - \mu)/\sigma$$

where X_i = actual number of individuals of that species in that stand, μ = mean number of individuals of that species in all of the stands at that site, σ = standard deviation of the mean number of individuals of that species in all of the stands at that site (Zar 1984). The standardized number of individuals was a relative measure of beetle abundance, and was analyzed for treatment effects, time since thinning effects, and mechanism(s) as described above for diversity. The total number of beetles found during coarse woody debris excavations was not standardized because this represented the whole season's capture, but was also analyzed as a function of stand type, time since thinning, and for mechanism(s) as above.

Statistical Analyses

Analyses were conducted using JMP ® version 3.0 software (SAS Institute Inc.). Data were transformed to meet assumptions of multiple regression models where

necessary. Interactions among variables were included in initial models, and removed if non-significant. In all cases, means are reported ± SE.

RESULTS

Microclimate

In general, thinned stands were significantly warmer than their unthinned counterparts in all three years after thinning (Figure 2.2; Kruskal-Wallis test, $p < 0.05$). Similarly, thinned stands were windier than unthinned stands in all three years after thinning (Figure 2.3; Kruskal-Wallis test, $p < 0.05$). Actual temperatures and wind speeds are shown in Table 2.1.

Habitat Availability

Thinning significantly affected fresh coarse woody debris dynamics, as indicated by a significant interaction between stand type and time since thinning ($F_{4,20} = 9.76$, $p < 0.001$). In the first year after thinning, fresh coarse woody debris was at least an order of magnitude greater in thinned stands than in unthinned stands (Figure 2.4; $F_{2,6} = 78.03$, $p < 0.0001$). Input of fresh coarse woody debris did not differ in thinned stands and unthinned stands in the second year after thinning (Figure 2.4; $F_{2,5} = 1.98$, $p > 0.2$) and the third year (Figure 3; $F_{2,4} = 0.59$, $p > 0.5$). In all cases, there was no additional site effect (all $p > 0.1$).

Beetle Diversity

Twenty-one bark beetle species were captured in pheromone-baited funnel traps (Table 2.2). More species were captured in thinned stands (19) than in unthinned stands (13 and 11 in internal and external controls, respectively; Table 2.2). However, diversity of beetles captured in pheromone traps, as measured by Shannon's H, did not differ in thinned stands and unthinned stands in any year after thinning (Table 2.3a; Shannon's H in thinned stands: 0.58 ± 0.89, n = 11 stand-years; internal controls: 0.48 ± 0.13, n = 10 stand-years, external controls: 0.35 ± 0.049, n = 11 stand-years). Furthermore, diversity was not related to the current amount of fresh coarse woody debris, temperature, or wind speed, and only increased marginally with the amount of coarse woody debris in the previous year (Table 2.3b).

Eighteen species were captured in kairomone-baited funnel traps (Table 2.2). As with the pheromone traps, more species were captured in thinned stands (16) than in

internal controls (14) or external controls (10; Table 2.2). Diversity of beetles captured in kairomone traps did not differ in thinned stands and unthinned stands in any year after thinning (Table 2.3a; Shannon's H in thinned stands: 0.74 ± 0.16, n = 11 stand-years; internal controls: 0.67 ± 0.22, n = 10 stand-years; external controls: 0.34 ± 0.11, n = 11 stand-years). Not suprisingly then, diversity was not related to any of the mechanisms measured (Table 2.3b).

Twelve species were captured in window traps in both thinned and external control stands, for a total of 15 species (Table 2.2). Diversity was, however, higher in thinned stands than in unthinned stands, and decreased slightly over time (Table 2.3a; Shannon's H in thinned stands: 0.66 ± 0.066, n = 48 window traps; external controls: 0.40 ± 0.062, n = 48 window traps), and did not depend on the age of the log that the trap was suspended over ($F_{2,87}$ = 1.57, p > 0.2). Diversity was positively related to the current amount of fresh coarse woody debris and wind speed (Table 2.3b).

Six species of beetles were found during coarse woody debris excavations (Table 2.4). The beetles only attacked coarse woody debris less than two years old, and were only found in thinned stands. Therefore, diversity analyses focused on thinned stands only. In thinned stands, diversity decreased slightly over time (Shannon's H in first year after thinning: 0.80 ± 0.30, n = 4 stands; second year: 0.60 ± 0.091, n = 4 stands; third year: 0 ± 0, n = 3 stands). Diversity was positively related to the current amount of fresh coarse woody debris and wind speed, increased slightly with the amount of fresh coarse woody debris in the previous year, and decreased slightly with temperature (Table 2.5b).

Shannon's H for pheromone and kairomone traps was also calculated using only those species found during coarse woody debris excavations (i.e., those actually breeding in stands). These species were captured in all stand types. Diversity was higher in thinned stands than in unthinned stands (Table 2.5a; Shannon's H in thinned stands: 0.52 ± 0.053, n = 11 stand-years; internal controls: 0.19 ± 0.044, n = 10 stand-years, external controls: 0.13 ± 0.040 stand-years, n = 11), and increased over time (Table 2.5a; first year: 0.21 ± 0.061, n = 4 stands; second year: 0.37 ± 0.084, n = 4 stands; third year: 0.26 ± 0.057, n = 3 stands). Interestingly, diversity was positively related to the amount of fresh coarse woody debris in the previous year (Table 2.5b) even though the amount of coarse woody debris decreased over time (Figure 2.3). Diversity was also positively related to temperature and wind speed (Table 2.5b). For kairomone traps, diversity for this limited data set was also higher in thinned stands than in unthinned stands (Table 2.5a; Shannon's H in thinned stands: 0.49 ± 0.13, n = 11 stands; internal controls: 0.42 ± 0.14, n = 10

stands; external controls: 0.074 ± 0.58, n = 11 stands), and increased over time (Table 2.5a; first year after thinning: 0.25 ± 0.10, n = 4 stands; second year: 0.28 ± 0.13, n = 4 stands; third year: 0.48 ± 0.14, n = 3 stands). However, diversity was not related to any of the mechanisms measured (Table 2.5b).

Beetle Abundance

The number of individuals captured in pheromone traps (20,968) was higher in thinned stands (14,046) than in the internal controls (3,931) and external controls (2,991) combined (Table 2.2). Over ninety percent of the individuals captured were striped ambrosia beetles (*Trypodendron lineatum* Olivier) or pine engravers. The standardized number of striped ambrosia beetles was higher in thinned stands than in unthinned stands for all three years after thinning (Table 2.6a; standardized number of beetles in thinned stands: 0.90 ± 0.12, n = 11 stand-years; internal controls: -0.49 ± 0.12 , n = 10 stand-years; external controls: -0.45 ± 0.18, n = 11 stand-years). The standardized number of striped ambrosia beetles was positively related to wind speed (Table 2.6b). The standardized number of pine engravers was also higher in thinned stands than in unthinned stands for all three years after thinning (Table 2.6a; thinned stands: 1.10 ± 0.40, n = 11 stand-years; internal controls: -0.52 ± 0.41, n = 10 stand-years; external controls: -0.64 ± 0.033, n = 11 stand-years). Their presence was positively related to the current amount of fresh coarse woody debris, the amount of fresh coarse woody debris in the previous year, and wind speed (Table 2.6b).

For kairomone traps, the number of individuals captured in thinned stands (3,397) was lower than the number captured in internal controls (4,362), but higher than in external controls (787; Table 2.2). Once again, striped ambrosia beetles and pine engravers represented over ninety percent of the individuals captured. Here, the abundance of neither species was significantly affected by stand type (both $p > 0.1$) or time since thinning (both $p > 0.9$). Similarly, there were no relationships between their abundance and the mechanisms measured ($p > 0.1$ for all mechanisms measured for both species).

More individuals were captured in window traps in thinned stands (773) than in external control stands (312; Table 2.2). Three species were captured in sufficient numbers to analyze individually. More striped ambrosia beetles were captured in window traps set up in thinned stands than in external control stands (Table 2.6a; standardized number in thinned stands: 0.36 ± 0.29, n = 48 window traps; external control stands: -0.36 ± 0.20, n = 48 window traps). This result is initially surprising given that the overall number of

striped ambrosia beetles captured in window traps was higher in external control stands (Table 2.2). However, the majority of individuals captured in external control stands were the result of one trap (54 individuals). Overall, their numbers were positively related to the current amount of coarse woody debris, temperature, and wind speed (Table 2.6b). Similarly, more pine engravers were captured in thinned stands than in external control stands (Table 2.6a; standardized number in thinned stands: 1.02 ± 0.50, n = 48 window traps, external control stands: -0.56 ± 0.067, n = 48 window traps). Pine engravers slightly decreased over time (Table 2.6a). Pine engraver abundance was positively related to the current amount of coarse woody debris only (Table 2.6b). However, the number of *Hylurgops rugipennis* (Mannerheim) did not differ in thinned and unthinned stands in any year after thinning (Table 2.6a; standardized number in thinned stands: 0.054 ± 0.15, n = 48 window traps; external control stands: -0.054 ± 0.12, n = 48 window traps). Their abundance was somewhat dependent on the amount of coarse woody debris in the previous year and wind speed (Table 2.6b).

In general, the total number of beetles found during coarse woody debris excavations was higher in thinned stands than in unthinned stands in all three years after thinning (Table 2.7a). The mechanism determining the total number of beetles found during coarse woody debris excavations varied by species (Table 2.7b). The total number of striped ambrosia beetles was positively related to the current amount of coarse woody debris, while the total number of pine engravers was positively related to the current amount of coarse woody debris and wind speeds. The total number of *P. rufipennis* was positively related to the amount of coarse woody debris in the previous year.

To determine whether the number of beetles in thinned stands decreased over time, I estimated the number of beetles per hectare and analyzed this number as a function of time since thinning using a multiple regression model that controlled for site (treated as a random effect). To estimate the total number of beetles per hectare, I multiplied the average number of beetles per 15 cm^{-2} by the sum of the amount of fresh coarse woody debris in the current year and the amount of coarse woody debris in the previous year (beetles use one and two year old debris). The estimated number of beetles per hectare in each thinned stand (mean $\pm$ SE: $21{,}542 \pm 9763$ striped ambrosia beetles, $10{,}249 \pm 7{,}632$ pine engravers, and $48{,}703 \pm 20{,}253$ *P. rufipennis*.) did not change over time (all $p > 0.1$).

DISCUSSION

Increased habitat abundance is expected to result in the presence of more species

(MacArthur and Wilson 1970; Connor and McCoy 1979). This has been observed in secondary bark beetles, as their diversity and abundance in a forest stand is determined by the amount of coarse woody debris (Vaisanen et al. 1993; Okland et al. 1996; Peltonen et al. 1998). I found that thinning resulted in a large one-time input of fresh coarse woody debris, followed by a return to pre-harvest input levels in the second and third years after thinning. Therefore, a short-lived increase in bark beetle activity was expected after thinning occurred.

Although the diversity of beetles captured in pheromone and kairomone traps was higher in thinned stands than in unthinned stands, diversity increased over time. Similarly, diversity of beetles captured in window traps suspended over logs was higher in thinned stands than in unthinned stands, a difference that persisted over time. In general, the number of beetles captured in all three types of traps was higher in thinned stands than in unthinned stands in all three years after thinning. Diversity and number of beetles in thinned stands could have been high in the second year after thinning as offspring from the first year that had overwintered in these stands were captured (Mason 1969). By this reasoning, the diversity and number of beetles in thinned stands should not have been high in the third year after thinning because there was a limited amount of coarse woody debris in the second year after thinning to produce beetles for the third year. Since diversity and abundance did not decrease in the third year after thinning, some change associated with thinning other than the abundance of coarse woody debris likely helped determine the diversity and number of beetles in a stand.

Microclimate differences between thinned and unthinned stands persisted through three years after thinning. Wind speeds partially explained the diversity of beetles captured in pheromone and window traps, with higher diversity associated with higher wind. The number of striped ambrosia beetles and pine engravers captured in these traps was likewise positively associated with wind speeds. These results contrast with other studies that have found negative effects of wind on bark beetle dispersal (Seybert and Gara 1970; Salom and McLean 1991a,b). It could be that negative effects of wind were masked in the current study by other correlated features. For example, tree density and temperature are expected to have a positive effect on dispersal (Chapter 3). Tree density did not, however, affect diversity or the abundance of beetles. Similarly, temperature significantly affected beetle activity only in two instances (see Tables 2.5 and 2.8). Therefore, rather than affecting dispersal, wind may positively affect host finding ability. Wind tends to focus kairomone and pheromone plumes relative to calm conditions (Fares et al. 1980). Consequently,

attractive smells from hosts, breeding aggregations, and traps would be more focused in thinned stands than in unthinned stands, perhaps making it easier for beetles to locate hosts in thinned stands (Salom and McLean 1991b).

However, kairomone trap catches do not support the importance of host finding to diversity and number of beetles in a stand. Diversity and number of beetles captured in kairomone traps could not be explained by any of the mechanisms measured. In fact, the number of beetles captured in thinned stands did not differ from unthinned stands. These results may have been due to a combination of the number and location of traps. Since trap locations were randomly chosen, some may have been in better spots for attracting beetles than others due to something as simple as differences in understorey vegetation around them (Dickens et al. 1992; Borden et al. 1997). Such variation would have been reduced in pheromone traps because there were two set up in each stand, whereas only one kairomone trap was set up in each stand.

For pheromone, kairomone, and window traps, standardizing the number of beetles captured may have affected abundance analyses. If the effects of thinning were mitigated over time, the standardized number of beetles captured in thinned and unthinned stands should converge. In this study, significant differences in the standardized number of beetles captured in thinned stands and their unthinned counterparts persisted over time. Since standardizing eliminates variation between years, it is difficult to compare absolute abundance as a function of time since thinning. It is similarly difficult to determine the mechanisms responsible for absolute abundance given that one of the suggested mechanisms (i.e., the amount of fresh coarse woody debris) does vary over time. Nonetheless, standardizing showed that differences existed between thinned and unthinned stands in all three years after thinning, and allowed reasons for the differences to be elucidated.

Coarse woody debris excavations overcame problems with trap location, number of traps, and standardizing data that were associated with pheromone, kairomone, and window trapping. Coarse woody debris excavations eliminated bias due to trap location and number because they covered large areas and sampled the same amount of area in each stand. It was not necessary to standardize data from coarse woody debris excavations because they were done once the main spring flight was over and before adults and offspring emerged to overwinter, so all of the beetles colonizing a stand were sampled in each year. Therefore, coarse woody debris excavations give the best indication of how thinning affects diversity and the number of beetles in a stand.

Coarse woody debris excavations, like the pheromone trap catches, suggest that host finding is important in determining diversity and number of beetles in a stand. During coarse woody debris excavations, beetles were only found in thinned stands, where they formed breeding aggregations on coarse woody debris less than two years old. Diversity in thinned stands decreased slightly over time, and was positively related to the current amount of fresh coarse woody debris, the amount of fresh coarse woody debris in the previous year, and wind speed. Depending on the species, the total number of beetles from excavations was positively related to the current amount of fresh coarse woody debris, the amount of coarse woody debris in the previous year, and wind speed. However, the estimated number of beetles per hectare did not change over time, perhaps due to large variation in the number found.

Overall, commercial thinning enhanced beetle activity relative to natural conditions, indicated by higher beetle diversity and abundance in thinned stands than in unthinned stands. This was likely the result of increased host finding ability due to the large, one-time input of fresh coarse woody debris in the first year after thinning and higher wind speeds that persisted after thinning. So, although thinning deters aggressive bark beetles that attack live trees (Mitchell et al. 1983; McGregor et al 1987; Bartos and Amman 1989; Schmitz et al. 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994), it creates a favourable situation for bark beetles that form breeding aggregations on fresh coarse woody debris. It may therefore be necessary to evaluate forest management in terms of residual tree density and input of coarse woody debris. The increased population sizes of beetles due to thinning may be reduced by removing fewer trees to maintain low wind speeds and by minimizing the amount of coarse woody debris remaining after thinning. Furthermore, if thinning increases tree vigour in the residual stand (Mitchell et al. 1983), then coarse woody debris input also needs to be monitored in the long-term because beetles make better use of coarse woody debris from vigorous trees, resulting in higher reproductive success (Slansky and Haack 1986; Reid and Robb 1999).

Table 2.1 Mean temperatures and wind speeds (± SE) in thinned and unthinned stands at each site and year after thinning.

a) Temperature (° C)

Year	Site	n (weeks)	Thinned	Internal Control	External Control
1	1	13	23.5 ± 1.5	22.2 ± 1.4	20.8 ± 1.4
	2	5	25.1 ± 1.3	23.2 ± 0.9	22.3 ± 0.8
	3	10	24.4 ± 1.5	22.9 ± 1.9	22.3 ± 1.4
	4	3	30.8 ± 0.5	28.2 ± 1.0	28.2 ± 0.6
2	1	9	23.9 ± 1.4	22.7 ± 1.4	21.7 ± 1.4
	2	14	24.9 ± 1.3	25.8 ± 1.0	22.3 ± 1.2
	3	11	26.8 ± 1.2	25.8 ± 1.0	25.9 ± 1.2
	4	8	24.1 ± 0.9	n/a	24.2 ± 0.8
3	1	5	25.4 ± 1.4	26.1 ± 1.4	25.0 ± 1.5
	2	8	24.4 ± 0.9	22.6 ± 0.9	21.5 ± 0.9
	3	4	26.5 ± 1.4	25.6 ± 1.3	25.4 ± 1.5

b) Wind ($m \cdot s^{-1}$)

Year	Site	n (weeks)	Thinned	Internal Control	External Control
1	1	4	0.8 ± 0.5	0.05 ± 0.03	0.3 ± 0.3
	2	5	1.4 ± 0.6	0.2 ± 0.1	0.0 ± 0.0
	3	3	3.0 ± 0.4	1.7 ± 1.2	0.5 ± 0.3
	4	3	1.0 ± 0.4	0.7 ± 0.4	0.5 ± 0.2
2	1	10	1.3 ± 0.3	0.5 ± 0.1	0.3 ± 0.1
	2	12	0.8 ± 0.2	0.2 ± 0.1	0.3 ± 0.1
	3	12	2.8 ± 0.8	1.0 ± 0.4	0.6 ± 0.2
	4	8	2.0 ± 0.5	n/a	0.6 ± 0.2
3	1	8	1.4 ± 0.3	0.4 ± 0.2	0.2 ± 0.1
	2	8	1.0 ± 0.3	0.2 ± 0.0	0.2 ± 0.1
	3	8	2.2 ± 0.7	0.3 ± 0.2	0.3 ± 0.1

n/a refers to no data because stand was harvested prior to year 2

Table 2.2. List of species captured in pheromone, kairomone, and window traps.

Species	Pheromone Traps			Kairomone Traps			Window Traps	
	Thinned	Internal Control	External Control	Thinned	Internal Control	External Control	Thinned	External Control
Cryphalus ruficollis	0	2	0	0	0	0	0	0
Crypturgus borealis	1	0	0	0	0	0	0	0
Dendroctonus rufipennis	1	0	2	0	0	0	0	1
Dendroctonus valens	9	7	3	4	4	2	12	6
Dryocetes affaber	15	6	2	2	2	1	10	5
Dryocetes autographus	18	4	1	5	2	0	27	34
Gnathotricus sp.	0	0	0	1	0	0	0	0
Hylurgops rugipennis	88	13	7	60	23	5	93	65
Ips latidens	4	5	0	2	0	0	1	1
Ips mexicanus	3	0	0	2	0	0	0	0
Ips perroti	0	0	0	0	0	0	1	0
Ips pini	5,899	1,378	658	82	56	109	500	101
Orthotomicus caelatus	0	0	0	1	0	0	0	0
Othotomides lasciocarpa	0	0	0	0	0	0	2	0
Phloeotribus annectans	0	0	0	0	1	0	0	3
Phloeotribus lecontei	3	4	1	1	4	2	0	0
Phloeotribus piceae	2	0	0	2	0	0	0	0
Pityogenes plagiatus knechteli	191	11	0	2	2	0	28	0
Pityopthorus sp.	1	0	0	0	0	0	0	0
Polygraphus rufipennis	77	7	3	31	6	1	54	8
Pseudohylesinus sp.	1	0	0	0	1	0	0	0
Scierus annectans	1	4	2	3	4	1	0	1
Scolytus unispinosis	1	0	0	0	0	0	0	0
Trypodendron lineatum	7,728	2,488	2,302	3,196	4,245	659	42	83
Xylechinus montanus	0	2	10	3	12	7	3	4
Total Individuals	14,046	3,391	2,991	3,397	4,362	787	773	312
Total Species	19	13	11	16	14	10	12	12

Table 2.3 Results of multiple regression models for diversity (Shannon's H) of all beetles captured in pheromone, kairomone, and window traps: a) effects of stand type and time since thinning, and b) mechanisms for diversity.

a)

	Pheromone Traps			Kairomone Traps			Window Traps		
	F	DF	p	F	DF	p	F	DF	p
Site[a]	3.84	3,24	< 0.05	1.03	3,24	> 0.3	2.00	3,87	> 0.1
Stand Type	2.25	2,24	> 0.1	1.83	2,24	> 0.1	8.94	1,87	< 0.01
Time Since Thinning	1.39	2,24	> 0.2	2.62	2,24	> 0.1	0.54	2,87	> 0.5

b)

	Pheromone Traps			Kairomone Traps			Window Traps		
	F	DF	p	F	DF	p	F	DF	p
Tree Density	0.11	1,26	> 0.7	0.83	1,26	> 0.3	0.19	1,90	> 0.6
Current CWD[b]	0.83	1,26	> 0.3	1.45	1,26	> 0.2	7.16	1,90	< 0.01
Last Year's CWD[b]	3.01	1,26	< 0.1	0.012	1,26	> 0.9	0.013	1,90	> 0.9
Temperature	0.14	1,26	> 0.8	0.73	1,26	> 0.4	1.54	1,90	> 0.2
Wind Speed	0.022	1,26	> 0.7	0.22	1,26	> 0.6	8.35	1,90	< 0.01

[a] Site was treated as a random effect
[b] CWD refers to coarse woody debris

Table 2.4. Species found during coarse woody debris excavations in thinned stands. Total number found (mean ± SE) shown.

Species	Number
Hylurgops rugipennis	9.09 ± 8.02
Ips pini	5.73 ± 4.58
Orthotomicus caelatus	0.73 ± 0.73
Pityogenes plagiatus knechteli	4.54 ± 3.19
Polygraphus rufipennis	28.27 ± 10.81
Trypodendron lineatum	23.91 ± 12.09

Table 2.5 Results of multiple regression models for diversity of beetles in pheromone traps, kairomone traps, and coarse woody debris (CWD) for only those species found during coarse woody debris excavations: a) effects of stand type and time since thinning on diversity, and b) mechanisms for diversity.

a)

	Pheromone Traps			Kairomone Traps			Window Traps		
	F	DF	p	F	DF	p	F	DF	p
Site[a]	1.18	3,24	> 0.3	1.87	3,24	> 0.1	1.04	3,5	> 0.4
Stand Type	25.07	2,24	< 0.0001	4.71	2,24	< 0.05		[b]	
Time Since Thinning	3.77	2,24	< 0.05	3.78	2,24	< 0.1	4.88	2,5	< 0.1

b)

	Pheromone Traps			Kairomone Traps			Window Traps		
	F	DF	p	F	DF	p	F	DF	p
Tree Density	0.92	1,26	> 0.3	0.071	1,26	> 0.7	2.29	1,5	> 0.1
Current CWD	2.43	1,26	> 0.1	0.12	1,26	> 0.7	24.86	1,5	< 0.001
Previous Year's CWD	18.90	1,26	< 0.001	0.02	1,26	> 0.8	6.03	1,5	< 0.1
Temperature	4.95	1,26	< 0.05	1.13	1,26	> 0.2	4.24	1,5	< 0.1
Wind	3.71	1,26	< 0.1	0.21	1,26	> 0.6	13.93	1,5	≈ 0.01

[a] Site was treated as a random effect

[b] Beetles were only found in thinned stands during coarse woody debris excavations, and therefore diversity for coarse woody debris excavations were only analyzed for thinned stands

Table 2.6 Results of multiple regression models comparing the standardized number of striped ambrosia beetles and pine engravers captured in pheromone traps: a) effects of stand type and time since thinning on diversity, and b) mechanisms for diversity.

a)

	Striped Ambrosia Beetles			Pine Engravers		
	F	DF	p	F	DF	p
Site[a]	0.062	3,24	> 0.9	0.89	3,24	> 0.4
Stand Type	30.46	2,24	< 0.0001	623.69	2,24	< 0.0001
Time Since Thinning	0.036	2,24	> 0.9	0.49	2,24	> 0.6

b)

	Striped Ambrosia Beetles			Pine Engravers		
	F	DF	p	F	DF	p
Tree Density	0.0019	1,26	> 0.9	0.21	1,26	> 0.6
Current Year's CWD[b]	3.35	1,26	< 0.1	11.59	1,26	< 0.01
Previous Year's CWD	1.28	1,26	> 0.2	7.73	1,26	≈ 0.01
Temperature	0.06	1,26	> 0.8	0.49	1,26	> 0.4
Wind	4.30	1,26	< 0.05	8.86	1,26	< 0.01

[a] Site was treated as a random effect
[b] CWD refers to coarse woody debris

Table 2.7. Results of multiple regression models comparing standardized number of striped ambrosia beetles, pine engravers, and *Hylurgops rugipennis* captured in window traps: a) effects of stand type and time since thinning on diversity, and b) mechanisms for diversity.

a)

	Striped Ambrosia Beetles			Pine Engravers			*Hylurgops rugipennis*		
	F	DF	p	F	DF	p	F	DF	p
Site*	0.092	3,56	> 0.9	0.56	3,79	> 0.6	0.014	3,87	> 0.9
Stand Type	4.36	1,56	< 0.05	27.87	1,79	< 0.0001	0.0024	1,87	> 0.9
Time Since Thinning	0.37	2,56	> 0.9	0.97	2,79	> 0.3	0.031	2,87	> 0.9
Log Age	0.78	1,56	> 0.3	1.17	2,79	> 0.3	0.035	2,87	> 0.9

b)

	Striped Ambrosia Beetles			Pine Engravers			*Hylurgops rugipennis*		
	F	DF	p	F	DF	p	F	DF	p
Tree Density	1.02	1,58	> 0.3	1.30	1,82	> 0.2	0.62	1,90	> 0.4
Current Year's CWD	10.99	1,58	< 0.01	4.28	1,82	< 0.05	1.29	1,90	> 0.2
Previous Year's CWD	1.87	1,58	> 0.1	0.0067	1,82	> 0.9	3.10	1,90	< 0.1
Temperature	7.69	1,58	< 0.01	1.95	1,82	> 0.1	0.33	1,90	> 0.5
Wind	4.30	1,58	< 0.05	2.49	1,82	> 0.1	3.62	1,90	< 0.1

* Site was treated as a random effect

Table 2.8. Results of multiple regression models comparing the number of striped ambrosia beetles, pine engravers, and *Polygraphus rufipennis* found during coarse woody excavations: a) effects of stand type and time since thinning on diversity, and b) mechanisms for diversity.

a)

	Striped Ambrosia Beetles			Pine Engravers			*Polygraphus rufipennis*		
	F	DF	p	F	DF	p	F	DF	p
Site*	0.50	3,24	> 0.8	1.04	3,24	> 0.3	0.24	3,24	> 0.8
Stand Type	3.81	2,24	< 0.05	1.66	2,24	> 0.2	10.18	2,24	< 0.001
Time Since Thinning	2.91	2,24	≈ 0.1	2.81	2,24	> 0.1	0.13	2,24	> 0.7

b)

	Striped Ambrosia Beetles			Pine Engravers			*Polygraphus rufipennis*		
	F	DF	p	F	DF	p	F	DF	p
Tree Density	0.19	1,26	> 0.6	0.50	1,26	> 0.4	0.026	1,26	> 0.8
Current Year's CWD	13.62	1,26	≈ 0.001	7.99	1,26	< 0.01	2.49	1,26	> 0.1
Previous Year's CWD	0.46	1,26	> 0.5	1.95	1,26	> 0.1	8.06	1,26	< 0.01
Temperature	0.42	1,26	> 0.5	1.75	1,26	> 0.1	0.71	1,26	> 0.4
Wind	0.93	1,26	> 0.3	11.29	1,26	< 0.01	2.00	1,26	> 0.1

*Site was treated as a random effect

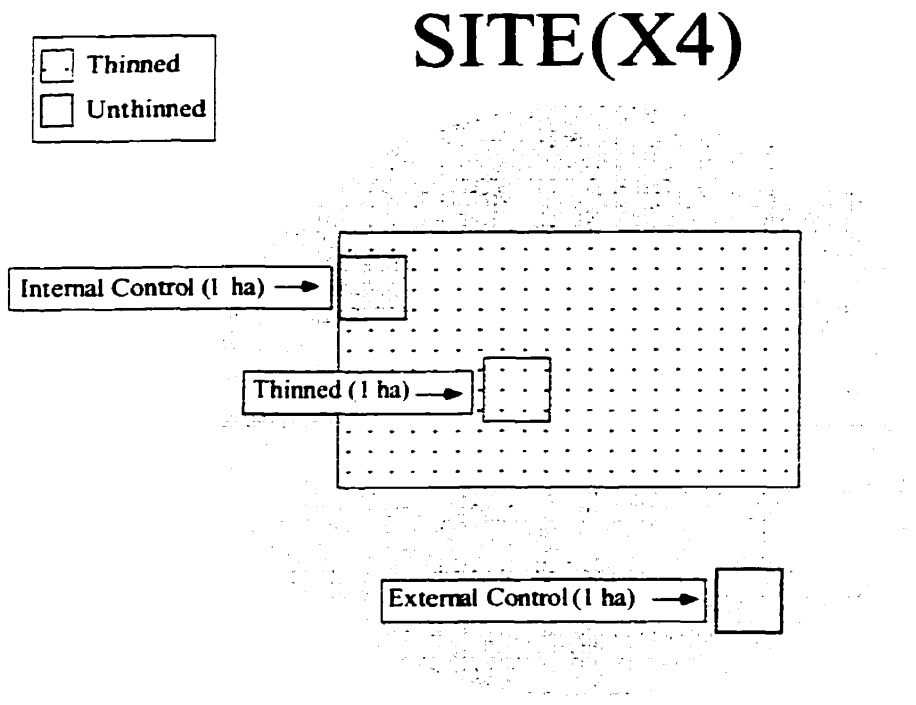

Figure 2.1 Schematic of study site. Each site consisted of a 50 ha thinned stand (not drawn to scale), with a 1 ha unthinned control stand (internal control stand) on one side. There was a 1 ha unthinned control stand (external control stand) in the continuous forest surrounding each thinned stand. A 1 ha plot was established in the thinned stand to ensure equal sampling in thinned and unthinned stands. Four sites were sampled.

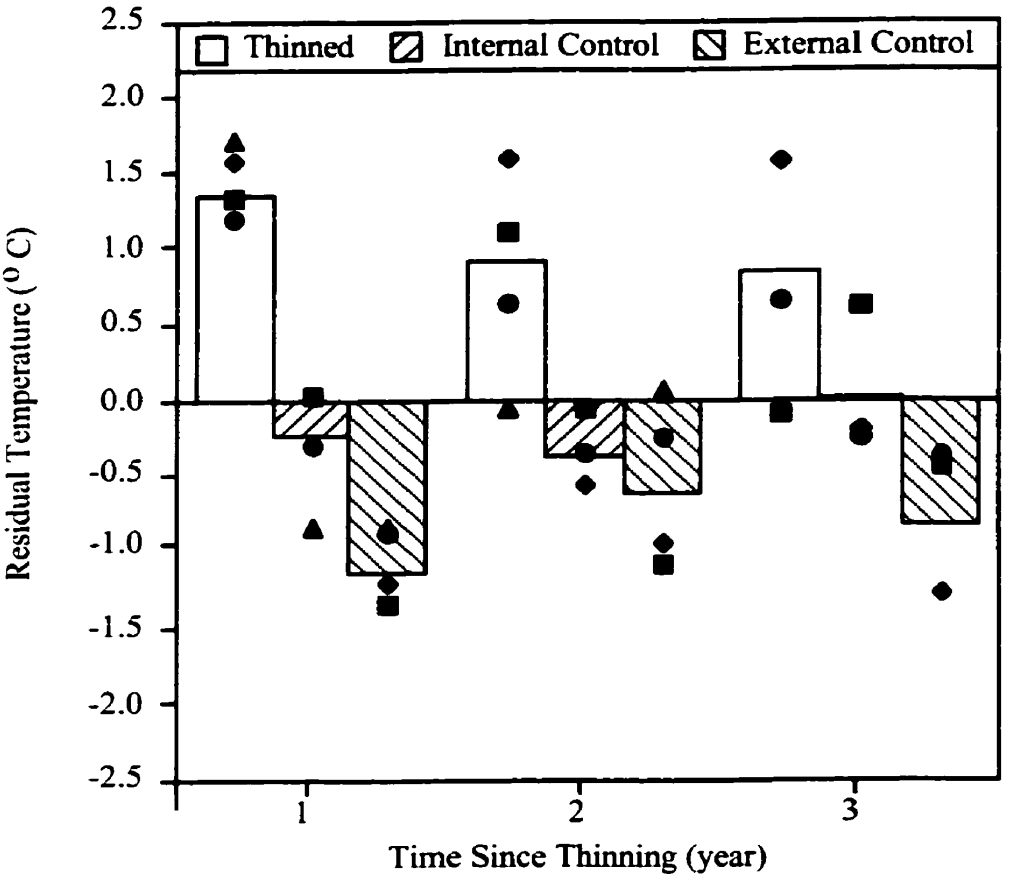

Figure 2.2 Residual temperatures in thinned and unthinned stands over time. Bars indicate means for all sites. Symbols indicate means for individual sites. Only three external control stands were sampled in year two, while only three sites (thinned, internal, and external control stands) were sampled in year three.

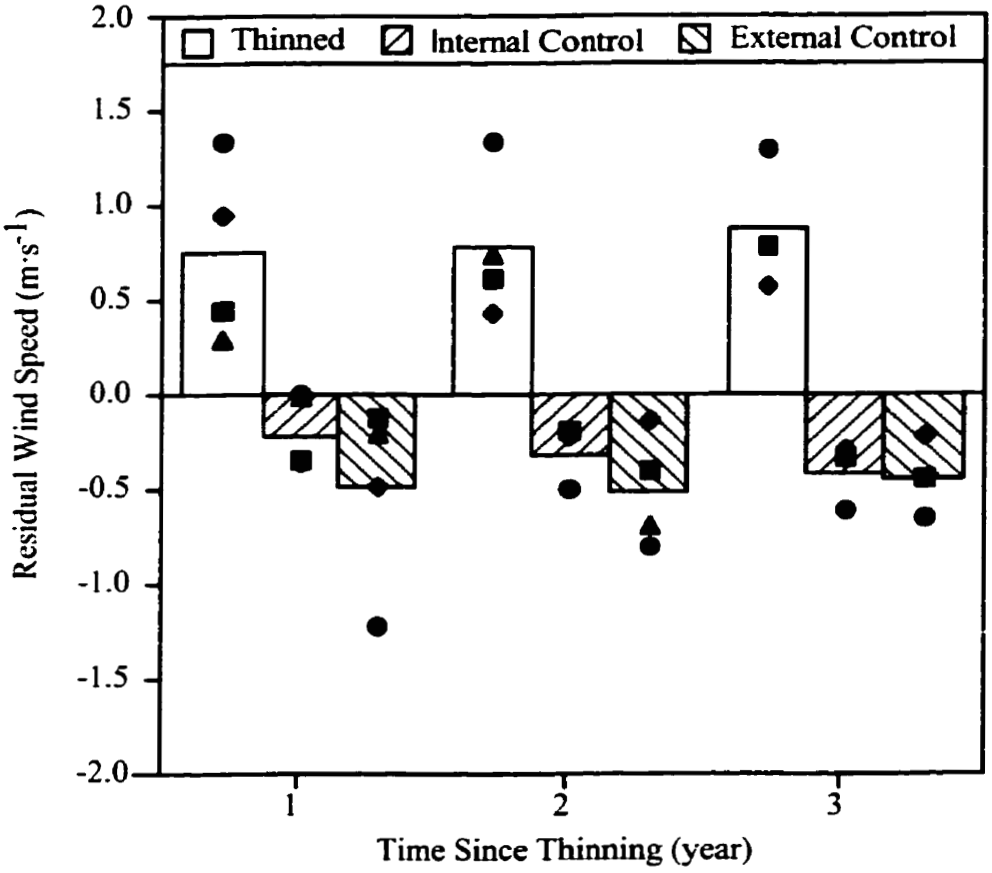

Figure 2.3 Residual wind speeds in thinned and unthinned stands over time. Bars indicate means for all sites. Symbols indicate means for individual sites.

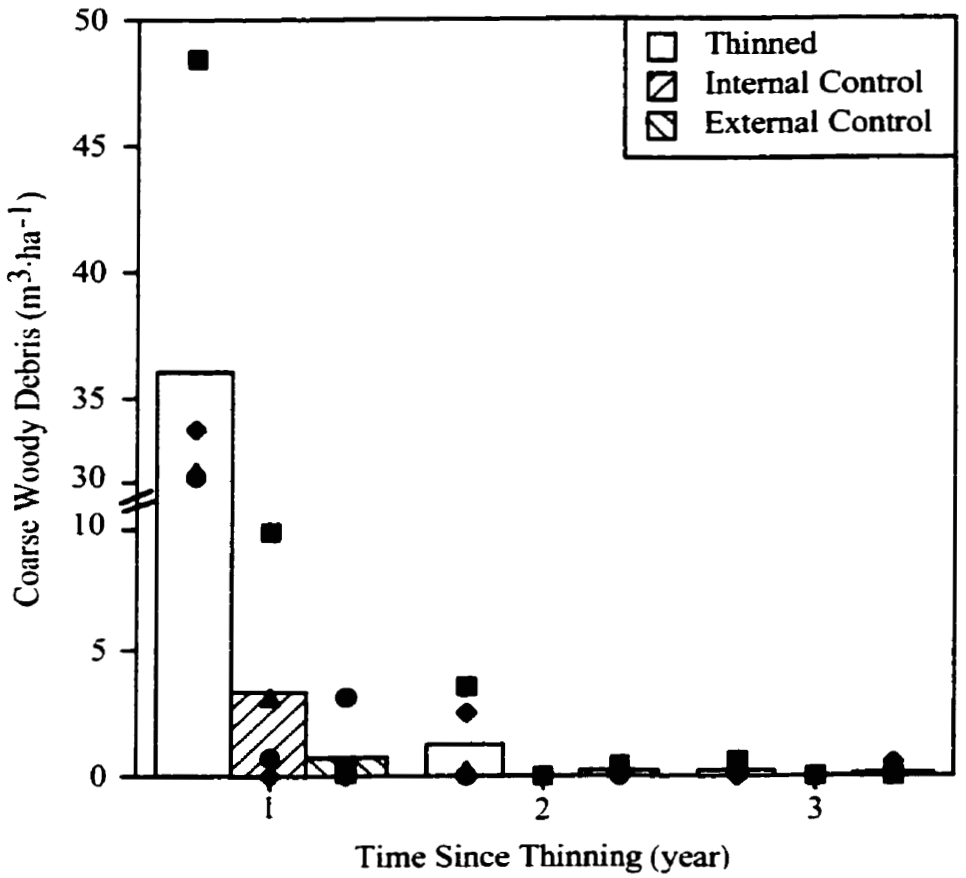

Figure 2.4 Input of fresh coarse woody debris in thinned and unthinned stands over time. Bars indicate means for all sites. Symbols indicate means for individual sites. Note break on y-axis.

CHAPTER 3
EFFECTS OF FOREST STRUCTURE ON DISPERSAL COSTS IN PINE ENGRAVER BARK BEETLES (COLEOPTERA: SCOLYTIDAE).

INTRODUCTION

Although dispersal between habitat patches is expected to influence population dynamics, the effects of inter-patch habitat (matrix) on dispersal success is often overlooked (Johnson et al. 1992; Wiens et al. 1993). Many aspects of matrix that influence dispersal are likely to be species specific, but some may be general. In particular, the structural complexity of the matrix should have two widespread effects on dispersal. First, vertical structure will affect microclimate variables by slowing wind speeds and providing shade. Second, clutter will impede the movement of organisms, requiring longer dispersal distances. In this chapter, I consider the effects of matrix complexity on dispersal success in bark beetles (Coleoptera: Scolytidae) in thinned and unthinned forests.

Both temperature and wind, which are known to affect bark beetle flight, increase due to the reduction of tree density and canopy closure associated with thinning (Bartos and Amman 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994). Temperature positively affects resting metabolic rate, and likely plays a role in dispersal in bark beetles given that dispersal is generally made up of many short duration flights separated by periods of inactivity (Forsse and Solbreck 1985; Jactel and Gaillard 1991). Wind affects the direction that bark beetles disperse, with most being captured upwind from where they are released (Schlyter et al. 1987; Salom and McLean 1990, 1991a; Safranyik et al. 1992). However, upwind flight decreases as wind speed increases (Seybert and Gara 1970) and flight may cease above certain wind speeds (Seybert and Gara 1970), suggesting that flying into the wind is costly. Temperature and wind also affect the diffusion of pheromone plumes (Fares et al. 1980; Bartos and Amman 1989), further complicating the effects of thinning on dispersal success in bark beetles. In sum, increased temperature and wind in thinned stands likely increase bark beetle dispersal costs relative to unthinned stands.

However, thinning may enhance bark beetle dispersal by reducing the amount of clutter in the stand that forces them to take indirect routes in search suitable hosts. This is likely given that most bark beetles fly in the mid-bole region of the forest (Forsse and Solbreck 1985; Schmitz et al. 1989; Safranyik et al. 1989, 1992), thereby making tree density important in determining the amount of flying needed to reach a suitable host.

Studies of bark beetle dispersal typically involve the release of marked beetles that

are recaptured in traps baited with pheromones (e.g., Safranyik et al. 1992; Thoeny et al. 1992; Zumr 1992; Turchin and Thoeny 1993; Zolubas and Byers 1995). These studies have focused on the number of marked beetles recaptured. This approach overlooks additional information about the costs of dispersal that may be evident in those individuals that are recaptured. Since dispersal requires lipid use (Atkins 1969), it may be possible to measure the fat content of recaptured beetles to determine dispersal costs. Body size is also likely to be important because large individuals tend to have absolutely more fat, and metabolize their fat reserves at a slower rate than do small individuals (Roff 1991). Both fat content and body size affect several fitness determining aspects of bark beetle life histories including host selection (Atkins 1969), pheromone production (Anderbrant et al. 1985; Gries et al. 1990), and reproductive ability (Anderbrant et al. 1985; Reid and Roitberg 1995).

Here, I investigate the effects of commercial thinning of mature lodgepole pine stands (*Pinus contorta* var. *latifolia* Engelm.) on the number, fat content, and body size of pine engraver bark beetles (*Ips pini* Say). To determine the mechanism by which thinning affects bark beetle dispersal, I examine the effects of changes in stand microclimate and structure on quantity and quality of recaptured beetles.

METHODS

Study Sites

This study was conducted in three pairs of commercially thinned and unthinned lodgepole pine stands (60, 100, and 100 yr). Mean tree densities (± SE) were 795 ± 102 trees·ha^{-1} and 2648 ± 181 trees·ha^{-1}, respectively. Two pairs of stands were used twice (60 yr and 100 yr).

Microclimate

I monitored microclimate at the centre of each stand during the mark recapture experiment (see below). I measured temperature hourly until dusk on the first day of each trial using a digital thermometer (Micronta 63-867) placed at breast height on the north side of a tree. I measured wind speed and direction hourly over this period using a mechanical anemometer (Wilh. Lambrecht KG, Woelfle Type) mounted on a 2 m pole. Temperature, wind speed, and wind direction were measured daily for the remainder of each trial, which lasted ten days.

Mark-Recapture Experiment

I collected pine engravers daily as they emerged from naturally attacked pine logs that were placed in rearing cages in the lab. Collected beetles were stored in vials lined with moist tissue paper, and were kept up to two weeks in the dark at 3° C. I marked beetles by dotting their pronotums with enamel paint. The number of beetles marked per trial ranged from 954 to 1640 (mean $\pm$ SE = 1132 $\pm$ 79 beetles).

Marked beetles were released from a platform at the centre of each stand. They were recaptured in 12-unit funnel traps (Lindgren 1983) placed at 50 m intervals up to 200 m away from the release point in four cardinal directions (i.e., 16 traps). Traps were baited with ipsdienol and lanierone (Phero Tech Inc.). Recaptured beetles were promptly killed by a piece of solid insecticide (Vapona ®) placed in the collecting cup of each trap. Traps were emptied hourly until dusk on the first day of each trial, and daily thereafter. I compared the number of marked beetles that were recaptured on the first day of each trial only and also the beetles recaptured over all days of a trial combined as a function of stand type (thinned versus unthinned) using a multiple regression model that controlled for differences between sites (a random effect).

Recaptured beetles were dried at room temperature and stored in the dark at 3° C prior to fat extraction. Fat extraction was accomplished using petroleum ether (60-80° C) in three separate 1 ml extractions at 38° C for each beetle (Anderbrant 1985, 1988). Pre- and post-extraction dry weights were taken after each beetle was dried at 60° C for 24 h (Anderbrant 1985, 1988). I calculated fat content as a percentage of each beetle's dry weight. I sexed each beetle and determined its body size by measuring its pronotum width using a stereomicroscope fitted with an ocular micrometer (40X). I compared fat content and size of recaptured beetles as a function of stand type and distance dispersed using regression models that controlled for trial effects (a random effect). Fat content analyses controlled for the sex and size of recaptured beetles, while size analyses controlled for sex only. Separate analyses were conducted for beetles recaptured on the first day of each trial only, and for beetles recaptured over all days of a trial combined.

Statistical Analyses

Analyses were conducted using JMP ® version 3.0 software (SAS Institute Inc.). Data were transformed to meet assumptions of tests where necessary. Actual means $\pm$ SE are reported.

RESULTS

The majority (> 71% per trial) of marked pine engravers initiated flight on the first day of each trial. However, beetles were only recaptured on the first day of seven of ten trials. These trials were distinguished by having maximum temperatures above 19° C on the first day (Figure 3.1). I determined whether thinned and unthinned stands differed in the number of weeks that the maximum temperature was above the flight threshold of 19° C by converting the distribution of maximum temperatures for all thinned and unthinned stands to a Z-distribution and finding the proportion of the distribution that was above the Z-value corresponding to 19° C. I used all stands sampled in this study (Chapter 2), not just the ones in which I conducted the dispersal experiments. I compared proportions as a function of stand type using a multiple regression model that controlled for differences between sites. The proportion of weeks that the maximum temperature was above 19° C was higher in thinned stands than in unthinned stands (Figure 3.2; $F_{2,6} = 5.35$, $p < 0.05$) and differed by site (Figure 3.2; $F_{3,6} = 20.72$, $p < 0.01$).

In trials with maximum temperatures above 19.0° C on the first day, temperature did not have a detectable effect on the percentage of beetles that were recaptured (linear regression, n = 7 trials, $r = 0.51$, $p > 0.2$). Similarly, wind speed (all < 1.2 $m \cdot s^{-1}$) did not have an effect on the percentage of beetles that were recaptured on the first day (linear regression, n = 10 trials, $r = -0.093$, $p > 0.7$), even when the flight threshold was taken into account (linear regression, n = 7 trials, $r = -0.48$, $p > 0.2$). Furthermore, beetles recaptured on the first day of each trial dispersed in random directions (Raleigh's z-test for trials with at least six beetles captured the first day, n = 4 trials, $p > 0.1$ for all trials), although the wind was significantly directional on the first day in all trials (Rayleigh's z-test, n = 7 trials, $p < 0.05$ for all trials). These data suggest that temperature and wind were not important to the beetles' dispersal behaviour and therefore did not significantly affect the costs of dispersal once the flight threshold temperature was achieved.

Because temperature and wind did not significantly affect dispersal behaviour of marked beetles recaptured on the first day of each trial, dispersal could be examined in terms of stand type (thinned versus unthinned) itself. There was no detectable difference in the percentage of marked beetles that were recaptured in thinned stands and unthinned stands on the first day of each trial (thinned stands: 1.04 ± 0.47 percent of flyers were recaptured, n = 5 trials; unthinned stands: 0.48 ± 0.36 percent recaptured, n = 5 trials; $F_{1,9} = 0.90$, $p > 0.3$). Thinning also did not influence the percentage of marked beetles that were recaptured over the entire duration of each trial (thinned stands: 2.65 ± 0.76 percent

recaptured, n = 5 trials; unthinned stands: 2.79 ± 0.73 percent recaptured; $F_{1,9} = 0.015$, $p > 0.9$).

However, beetles were recaptured farther from the release point in thinned stands than in unthinned stands (thinned stands: 92 ± 3.9 m, n = 162 beetles; unthinned stands: 81.2 ± 3.8 m, n = 136 beetles; $\chi^2_{[3]} = 7.98$, $p < 0.05$). This analysis included all beetles captured over the duration of each trial as there was no change in distance at which beetles were recaptured over time ($\chi^2_{[12]} = 11.14$, $p > 0.5$).

The fat content of beetles recaptured on the first day in thinned stands was slightly higher than those recaptured in unthinned stands (thinned stands: 13.2 ± 0.9 % dry weight, n = 69; unthinned = 11.8 ± 1.3 %, n = 31). This effect depended on the distance at which beetles were recaptured, as indicated by the significant interaction between stand type and distance (Table 3.1a). Fat content slightly increased with distance in thinned stands (Table 3.1b), and did not vary with distance in unthinned stands (Table 3.1b). There was also a significant interaction between stand type and distance when considering the fat content of beetles recaptured over the duration of each trial (Table 3.1c, thinned stands: 10.1 ± 0.6 %, n = 162; unthinned stands: 9.3 ± 0.6 %, n = 136). In this case, fat content did not vary with distance in thinned stands (Table 3.1c), but significantly decreased in unthinned stands (Table 3.1c). In general, males had higher fat content than females on the first day of each trial and over all days ($p < 0.01$, except in unthinned stands on the first day where $p > 0.4$). Overall, it appears fat loss was lower during dispersal in thinned stands than in unthinned stands, particularly as distance increased.

Body size of marked beetles that were recaptured on the first day of each trial did not differ in thinned and unthinned stands (Table 3.2a; thinned stands: 1.56 ± 0.026 mm, n = 69; unthinned: 1.57 ± 0.038 mm, n = 31), or vary with distance (Table 3.2a). Differences in body size among stand types did, however, become apparent over the duration of each trial, once again signified by an interaction between stand type and distance (Table 3.2a, thinned stands: 1.56 ± 0.0069 mm, n = 162; unthinned stands: 1.54 ± 0.077 mm). Body size of recaptured beetles slightly increased with distance in thinned stands (Table 3.2b), and did not vary with distance in unthinned stands (Table 3.2b). In all cases, males were larger than females (all $p < 0.01$).

DISCUSSION

Temperature was observed to affect dispersal behaviour in pine engravers, as they appeared unable to sustain dispersal at temperature below 19° C judging by the lack of

recaptures of beetles that initially flew from the release platform. The release platform may have had more direct sunlight than the forest floor or bark crevices where pine engravers may rest between bouts of flight. Temperature thresholds for flight activity have been reported for other species (e.g., 16° C for the mountain pine beetles, Safranyik et al. 1992). These thresholds should be met more often in thinned stands than in unthinned stands due to significant differences in temperature between these two types of stands (Chapter 2). This prediction was upheld for this study. Thus, beetles in thinned stands should be able to search for breeding sites more often than those in unthinned stands.

However, I found no relationship between temperature and the proportion of marked beetles that were recaptured in trials with temperatures above 19° C. Thus, while temperature ultimately determined when the marked pine engravers were able to disperse, it did not appear to affect dispersal activity once they were able to fly. Wind also did not appear to affect dispersal activity in the marked pine engravers. The proportion of beetles that were recaptured did not vary with respect to wind speed on the day of release with wind speeds below 1.2 $m \cdot s^{-1}$. Moreover, the marked beetles dispersed in random directions, despite directionality in wind. This is in contrast to field and lab studies that have shown that the similarly sized striped ambrosia beetle (*Trypodendron lineatum* Olivier) dispersed in specific directions at wind speeds below 0.9 $m \cdot s^{-1}$ (Salom and McLean 1990, 1991a).

Although I did not detect microclimate differences between thinned and unthinned stands that influenced pine engraver dispersal above the temperature threshold, there were differences among recaptured beetles that may be attributable to changes in stand complexity that require larger dispersal distances. Differences in fat content of recaptured beetles were indicated by significant interaction terms between stand type and the distance at which beetles were recaptured. For beetles recaptured on the first day of each release as well as those recaptured over the duration of each trial, fat content tended to be higher in thinned stands than in unthinned stands. Furthermore, fat content decreased with distance dispersed over the duration of each trial, significantly so for unthinned stands. These results, combined with the fact that pine engravers tended to be recaptured farther from the release point in thinned stands than in unthinned stands, suggest that dispersal was less expensive in terms of fat consumption in thinned stands than in unthinned stands despite higher temperatures and wind speeds.

Body size tended to be larger in thinned stands than in unthinned stands when considering beetles recaptured over the duration of the mark-recapture experiment. This

suggests that smaller beetles were less able to disperse in thinned stands than in unthinned stands, implying that dispersal was more costly in thinned stands than in unthinned stands. However, body size of beetles recaptured over the duration of the experiment did not vary with distance, suggesting that the effect of stand type on body size was not very strong. Furthermore, it is important to note that there was no difference in body size of beetles recaptured in thinned and unthinned stands on the first day of each trial when such a difference was expected to be most easily detected.

Effects of stand density on dispersal were detected over distances of 200 m. This will likely have implications for forest management given that the changes in forest structure investigated here were at a relatively small spatial scale (the stand level) compared to the size of the areas managed in the boreal forest (often thousands of square kilometers). Furthermore, these findings are also likely to hold for larger bark beetle species, which are expected to have larger dispersal capabilities than pine engravers (Roff 1991), but tend to disperse less than 200 m when given the choice of going farther. For example, the majority of mountain pine beetles (length 3.7-7.5 mm versus 3.5-4.2 mm for pine engravers) were captured within 30 m of their release point (Safranyik et al. 1992). Most spruce beetles (*Ips typographus*, 4.2-5.5 mm long) are recaptured less than 200 m (Zolubas and Byers 1995) and at only 10 m (Zumr 1992) from where they were released. Both of these species are more aggressive than pine engravers, killing large numbers of trees in epidemic situations (Vite 1989). The consequence of having larger energy reserves after dispersing through thinned stands may be increased reproductive success in these stands, thereby increasing the effects of these bark beetles on the forest.

I discovered that forest structure influenced dispersal in pine engravers by affecting both microclimate and dispersal path complexity. The changes in inter-patch habitat were relatively subtle in that tree density was reduced while maintaining a forest environment, and the organism is expected to have good dispersal abilities (Atkins 1966). This suggests that the effects of habitat structure on dispersal activity and costs may be ubiquitous as there are reports that habitat use in several taxa is affected by ease of movement (e.g., Paynter and Brady 1992; MacMillan and Kaufman 1995; Adams 1997). Thus, matrix structure may be a good predictor of dispersal patterns.

Table 3.1 Results of multiple regression models determining the effects of stand type on fat content of individual beetles: a) whole models on the first day of each trial and for the duration of each trial (all days), b) in thinned and unthinned stands on the first day, and c) in thinned and unthinned stands for all days.

a) Whole Model

	First Day			All Days		
	F	DF	p	F	DF	p
Trial*	2.15	5,86	< 0.1	7.64	9,268	< 0.001
Stand Type	2.17	1,86	> 0.1	0.37	1,268	> 0.8
Sex	9.40	1,86	< 0.0001	20.98	1,268	< 0.001
Size	0.039	1,86	> 0.8	2.47	1,268	< 0.1
Distance	0.41	1,86	> 0.5	1.82	1,268	> 0.2
Stand Type*Distance	6.81	1,86	< 0.05	5.07	1,268	< 0.05

b) First Day

	Thinned			Unthinned		
	F	DF	p	F	DF	p
Trial*	2.22	3,59	< 0.1	1.45	2,25	> 0.2
Sex	9.97	1,59	< 0.01	0.68	1,25	> 0.4
Size	0.018	1,59	> 0.8	0.0011	1,25	> 0.9
Distance	2.96	1,59	> 0.5	2.51	1,25	> 0.1

c) All Days

	Thinned			Unthinned		
	F	DF	p	F	DF	p
Trial*	12.23	4,146	< 0.001	2.96	4,120	< 0.05
Sex	14.26	1,146	< 0.001	6.79	1,120	< 0.01
Size	3.88	1,146	< 0.1	0.0012	1,120	> 0.9
Distance	0.36	1,146	> 0.5	5.35	1,120	< 0.05

* Trial was treated as a random effect

Table 3.2 Results of multiple regression models determining the effects of stand type on body size of individual beetles: a) whole models on the first day of each trial and for the duration of each trial (all days), and b) in thinned and unthinned stands for all days.

a) Whole Model

	First Day			All Days		
	F	DF	p	F	DF	p
Trial*	4.96	5,88	< 0.001	12.77	9,280	< 0.001
Stand Type	0.049	1,88	> 0.8	00.66	1,280	> 0.4
Sex	12.68	1,88	< 0.001	24.85	1,280	< 0.001
Distance	0.48	1,88	> 0.4	0.017	1,280	> 0.8
Stand Type*Distance		n/a		5.35	1,280	< 0.05

b) All Days

	Thinned			Unthinned		
	F	DF	p	F	DF	p
Trial*	8.53	4,151	< 0.001	17.80	4,128	< 0.001
Sex	16.46	1,151	< 0.001	8.54	1,128	< 0.01
Distance	3.45	1,151	< 0.1	1.83	1,28	> 0.1

* Trial was treated as a random effect

n/a represents non-significant interaction term that was removed from model

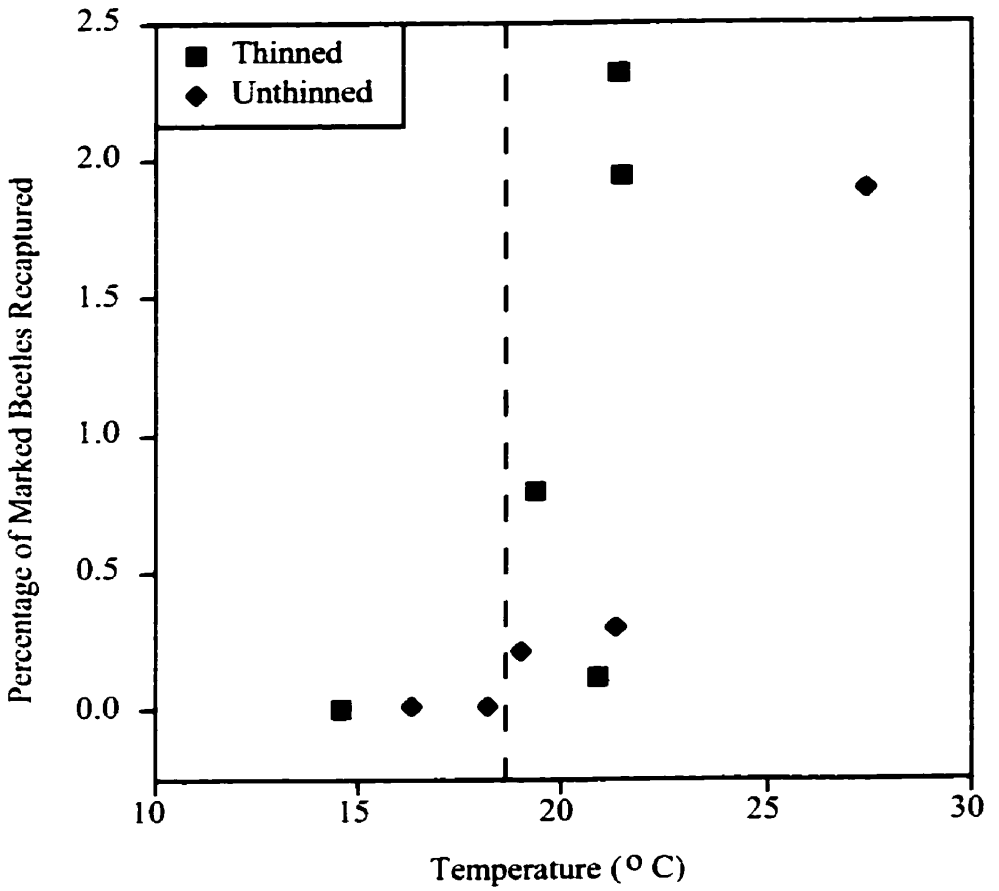

Figure 3.1 Percentage of marked beetles that were recaptured in thinned and unthinned stands on the first day of each trial. Dotted line suggests a flight temperature threshold of 19° C.

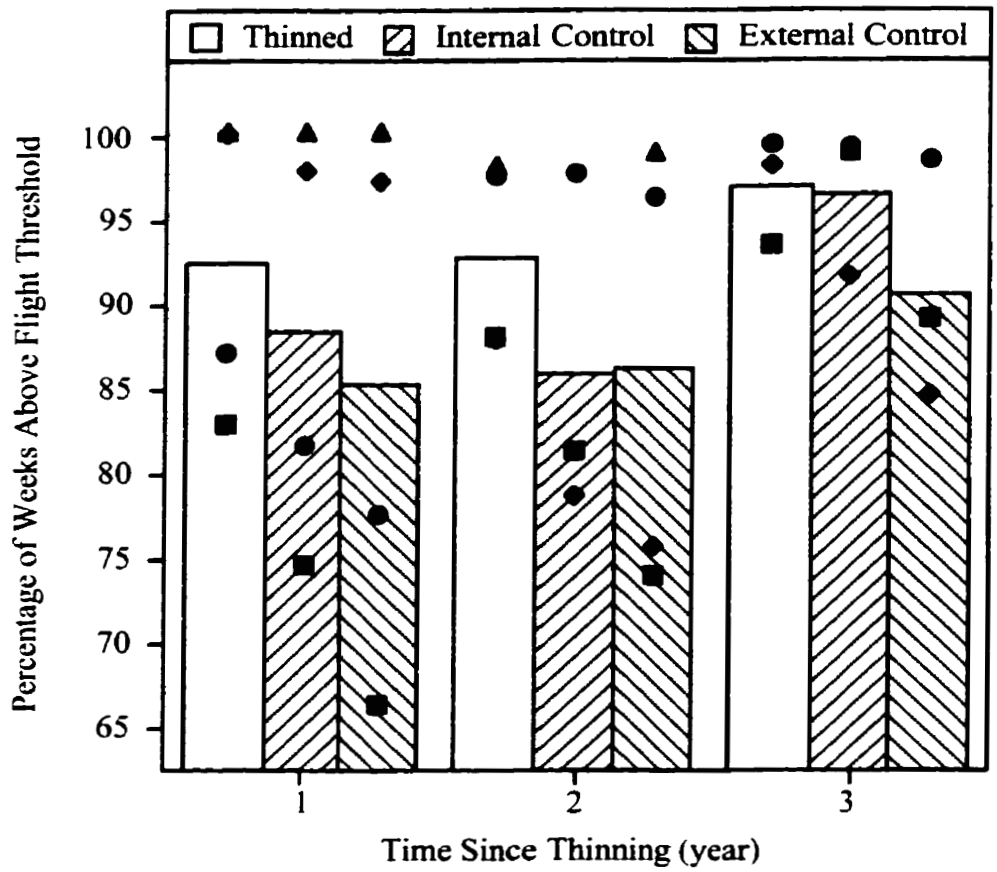

Figure 3.2 Percentage of weeks with at least one day above the flight temperature threshold of 19° C in thinned and unthinned stands at each site. Symbols indicate different sites.

CHAPTER 4
FOREST STRUCTURE AND REPRODUCTION IN PINE ENGRAVER BARK BEETLES (COLEOPTERA: SCOLYTIDAE).

INTRODUCTION

Changes in forest structure due to thinning are likely to affect reproduction in bark beetles (Coleoptera: Scolytidae) in several ways. Reduced tree density and canopy closure makes thinned stands warmer than their unthinned counterparts (Bartos and Amman 1989; Schmid et al. 1991, 1992a,b; Bartos and Booth 1994; Chapter 2), which is important because temperature is known to affect reproduction in bark beetles in controlled lab experiments. As temperature increases, female bark beetles extend their egg galleries farther (Reid 1962; Sahota and Thomson 1979; Wagner et al. 1981), lay more eggs (Wagner et al. 1981; Wermelinger and Seifert 1999), have higher egg densities (Amman 1972; Wagner et al. 1981), and lay their first egg earlier (Sahota and Thomson 1979). However, these patterns have never been tested under natural conditions.

Thinning may also affect reproduction in bark beetles indirectly by reducing dispersal costs in terms of fat content of individual beetles relative to costs in unthinned stands (Chapter 3). Large females, which typically have higher fat content than do small ones (Wagner et al. 1981; Anderbrant 1988), extend their galleries farther (Clarke et al. 1979; Wagner et al. 1981) and lay more eggs (Amman 1972; Clarke et al. 1979; Wagner et al. 1981) than small females.

However, density effects also influence reproduction in bark beetles regardless of temperature or fat content of beetles. At high densities, females do not extend their egg galleries as far as in less crowded situations (Knight 1969) and lay fewer eggs (Knight 1969; Amman 1972). In turn, the number of offspring produced at high densities is much lower than at low densities (Anderbrant et al. 1985; Kirkendall 1989; Robins and Reid 1997), as are offspring size and fat content (Botterweg 1983; Anderbrant et al. 1985; Anderbrant and Schlyter 1989).

In this chapter, I compare reproduction in pine engraver bark beetles (*Ips pini* Say) in thinned and unthinned lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) forests in light of the density of breeding aggregations they experience in these stands. The breeding biology of this species was outlined in Chapter 1. I considered five reproductive processes: number of females per male, female gallery length, number of eggs, egg density, and distance to the first egg in a gallery.

METHODS

This study was conducted at four sites that each consisted of one commercially thinned mature lodgepole pine stand and a matched unthinned stand. Tree densities (± SE) were 841 ± 171 trees·ha^{-1} and 2346 ± 371 trees·ha^{-1} for thinned stands and unthinned stands, respectively.

To provide a breeding substrate for pine engravers, I placed four logs (length = 2 m, average diameter (± SE) = 16.57 ± 0.60 cm) from recently felled pine trees in each stand. Two logs from each tree were placed in the thinned stand and unthinned stand at a site. Therefore, log and tree effects should be equal in thinned and unthinned stands at a site, and did not need to be controlled for in analyses. To make them more attractive to pine engravers, all logs were all baited with the pheromones ipsdienol and lanierone (supplied by Phero Tech Inc.).

To determine differences in pine engraver reproductive strategies in thinned and unthinned stands, I excavated a subset of approximately 25 gallery systems (i.e., a male with females) on each log at the end of the breeding season after most beetles had left. Sometimes the number of gallery systems on logs in unthinned stands was lower than 25, in which case I excavated all of the gallery systems. To check for the possibility of density dependence in thinned and unthinned stands, I calculated density of males for the area excavated.

I counted the number of females mated to each male to determine how thinning affects male breeding success. Stand averages for male density and the number of females mated to each male were analyzed as a function of stand type using a multiple regression model that controlled for differences between sites (a random effect).

To determine the effects of thinning on female reproduction, I measured gallery length, number of eggs, egg density, and the distance to the first egg in a gallery where it was possible to do so. Due to the many combinations of male density and the number of females mated to each male, there was the potential for a great number of situations that might uniquely influence female reproduction. Therefore, I considered each female to be an experimental unit. I then analyzed gallery length, number of eggs, egg density, and the distance from where a gallery started to where the first egg was laid as a function of stand type, male density and number of females mated to each male using a multiple regression model that controlled for differences between sites (a random effect).

All analyses were conducted using JMP ® version 3.0 software (SAS Institute Inc.). Data were transformed to meet assumptions of normality and homoscedasticity

where necessary. In all cases, actual means are reported ± SE.

RESULTS

Two bark beetle species were found during excavations: pine engravers and *Hylurgops rugipennis* (Mannerheim). The presence of *H. rugipennis* probably did not affect the pine engravers because of different habitat requirements: I found *H. rugipennis* typically attacked the bottom of logs, whereas pine engravers preferred the top.

The density of male pine engravers did not differ in thinned and unthinned stands ($F(\text{Stand Type})_{1,3} = 0.71$, $p > 0.4$; $F(\text{Site})_{3,3} = 0.94$, $p > 0.5$; male density in thinned stands: 7.08 ± 5.53 males·100 cm^{-2}, n = 4 sites; unthinned: 2.34 ± 0.19 males·100 cm^{-2}, n = 4 sites). However, males in thinned stands attracted slightly more females than their counterparts in unthinned stands (Figure 4.1; $F(\text{Stand Type})_{1,3} = 6.39$, $p < 0.1$; $F(\text{Site})_{3,3} = 1.25$, $p > 0.4$). Therefore, the total density of beetles (males plus females) was expected to be higher in thinned stands than in unthinned stands. The total density of beetles was analyzed as a function of stand type using a multiple regression model that controlled for differences between sites (a random effect). There was no difference in the total density of beetles in thinned and unthinned stands ($F(\text{Stand Type})_{1,3} = 0.17$, $p < 0.7$; $F(\text{Site})_{3,3} = 1.26$, $p > 0.4$; total density in thinned stands: 5.92 ± 0.70 beetles·100 cm^{-2}, n = 4 sites; unthinned: 5.27 ± 1.53 beetles·100 cm^{-2}, n = 4 sites).

Female galleries were significantly longer in thinned stands than in unthinned stands (Figure 4.2a; $F_{1,1362} = 46.53$, $p < 0.0001$), and varied by site ($F_{3,1362} = 17.98$, $p < 0.0001$). Gallery length decreased with the number of females mated to each male ($F_{1,1362} = 11.56$, $p < 0.001$), but was not affected by male density ($F_{1,1362} = 1.33$, $p > 0.2$).

The number of eggs laid by each female was higher in thinned stands than in unthinned stands (Figure 4.2b; $F_{1,924} = 18.29$, $p < 0.001$), and varied by site ($F_{3,924} = 11.83$, $p < 0.0001$). The number of eggs slightly increased as male density increased ($F_{1,924} = 2.73$, $p < 0.1$), but did not change as a function of the number of females in a gallery system ($F_{1,924} = 0.053$, $p > 0.8$). Egg density was also higher in thinned stands than in unthinned stands (Figure 4.2c; $F_{1,924} = 13.76$, $p < 0.001$), and varied by site ($F_{3,924} = 10.82$, $p < 0.0001$). Egg density was positively affected by both male density ($F_{1,924} = 8.84$, $p < 0.01$) and the number of females ($F_{1,924} = 4.76$, $p < 0.05$).

Since transforming the distance to the first egg did not result in assumptions of normality and homoscedasticity being met, the distance to the first egg needed to be analyzed for each site separately. At three sites, the distance to the first egg was not

affected by stand type, male density, nor the number of females mated to each male (all $p > 0.2$). At the fourth site, the distance to the first egg was not different in thinned and unthinned stands ($F_{1,226} = 2.47$, $p > 0.1$), but was negatively related to male density ($F_{1,226} = 13.03$, $p < 0.001$) and positively related to the number of females mated to each male ($F_{1,226} = 10.45$, $p < 0.01$). Overall, the distance to the first egg in thinned stands was 6.66 $\pm$ 0.15 mm (n = 693 galleries), while in unthinned stands it was 7.73 $\pm$ 0.50 mm (n = 110 galleries).

DISCUSSION

The reproduction of both male and female pine engravers was affected by thinning. Since the density of males and the total density of beetles were not significantly different in thinned and unthinned stands, the differences in male and female reproduction seen here are not likely due to density dependence. Furthermore, the effects of male density and the number of females mated to each male were inconsistent in explaining gallery length, number of eggs, egg density, and distance to first egg in a gallery. Therefore, male and female reproduction are likely determined by differences in the forest environment associated with thinning.

Many of the differences in female reproduction in thinned stands and their unthinned counterparts were consistent with increased temperature in thinned stands. Females had longer galleries, and laid more eggs at a higher density in thinned stands than in unthinned stands, as seen in laboratory studies on the effects of increased temperature for other bark beetle species (Reid 1962; Amman 1972; Sahota and Thomson 1979; Wagner et al. 1981; Wermelinger and Seifert 1999). However, many of these studies investigated the effects of temperature at a very coarse scale of five degree increments (Reid 1962; Amman 1972; Wagner et al. 1981; Wermelinger and Seifert 1999). Temperature differences in thinned and unthinned stands are generally small (1 or 2° C), albeit significant (Chapter 2). Furthermore, the effects of increased temperature in thinned stands may be mitigated by the lower night time temperatures experienced in these stands due to the lack of thermal cover resulting from reduced crown closure (Schmid et al. 1991). Therefore, increased temperature may not be the only change in forest structure associated with thinning that influenced reproduction in pine engravers.

Differences in female reproduction in thinned and unthinned stands may also be attributable to differences in individual quality (i.e., fat content and size) resulting from easier dispersal in thinned stands than in unthinned stands (Chapter 3). Long galleries with

more eggs are expected from high quality females (Atkins 1972; Clarke et al. 1979; Wagner et al. 1981). Similarly, the increased number of females mated to each male in thinned stands may be due to differences in individual quality (i.e., size and fat content). High quality males produce more pheromones than low quality males (Anderbrant 1985; Gries et al. 1990), thereby increasing their attractiveness.

Not all of the reproductive trends that I measured can be explained in terms of differences in temperature or individual quality of beetles in thinned and unthinned stands. The distance to the first egg in a gallery did not differ between thinned and unthinned stands. Sahota and Thomson (1979) found that the distance to the first egg decreased as temperature rises. Similarly, the distance to the first egg is expected to decrease with fat content because energy reserves are readily available for egg production. However, the increased number of females mated to each male may have resulted in these trends being minimized because females wait longer to lay their first egg in crowded conditions (Kirkendall 1989; Reid and Robb 1999). Yet, the number of females mated to each male did not have a significant effect on the distance to the first egg in the majority of cases in this study.

Overall, it appears that reproduction in pine engravers may be influenced by changes in temperature and dispersal costs in the forest environment due to thinning. To my knowledge, this is the first study to document different breeding patterns in forests of different structure. Future work should focus on the reproductive success of pine engravers in thinned and unthinned stands so that population dynamics in these stands can be predicted.

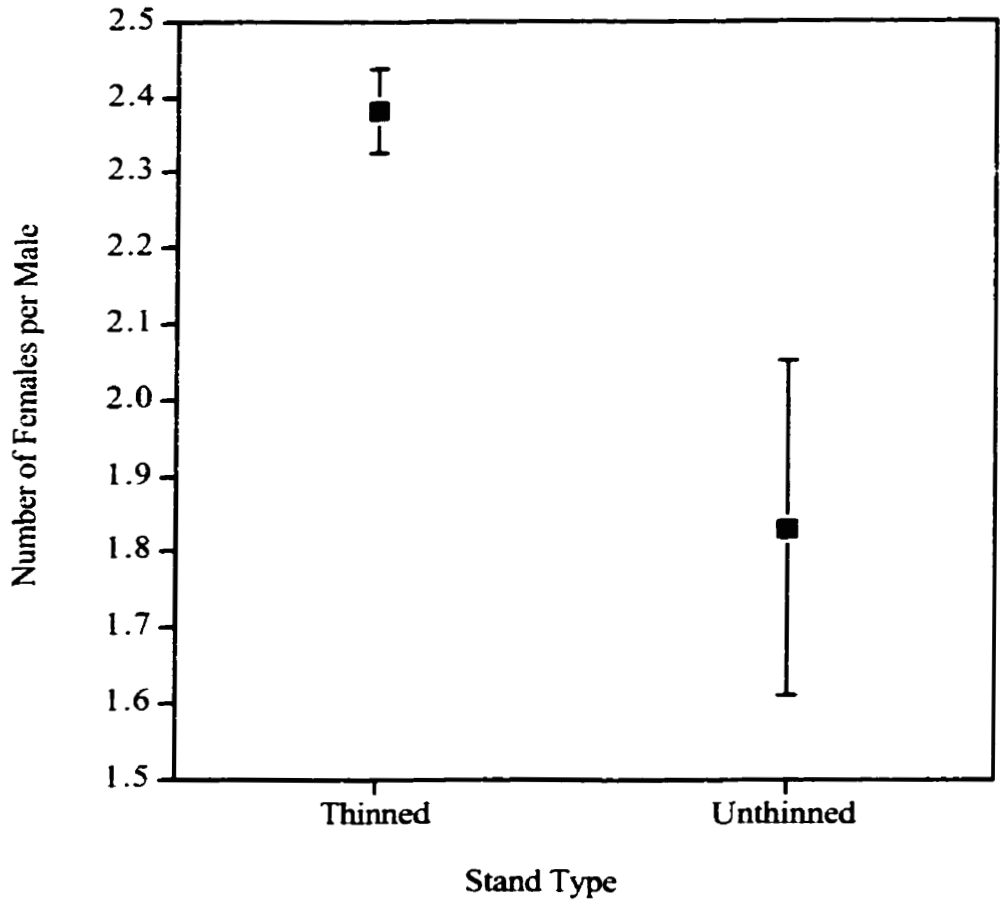

Figure 4.1 Number of females mated to each male in thinned and unthinned stands. Actual means ± SE are shown.

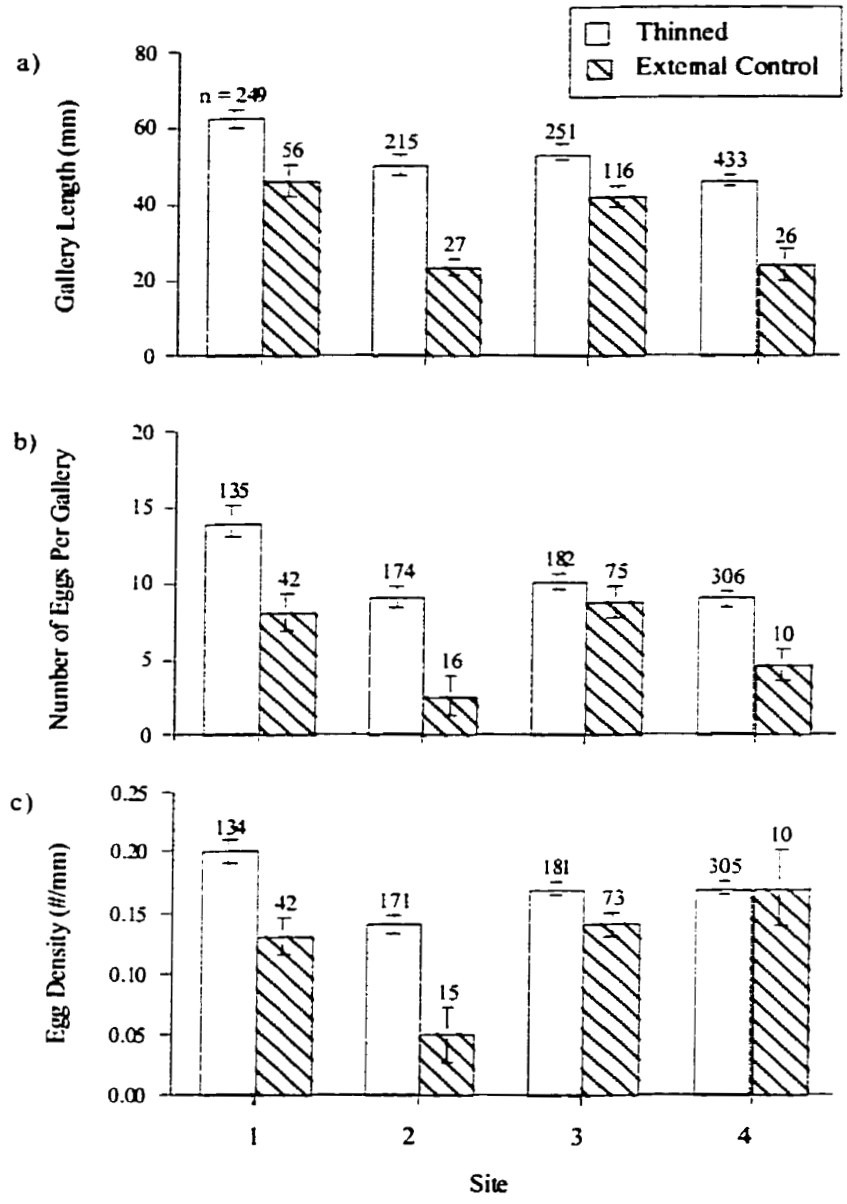

Figure 4.2 Comparison of reproductive traits of females in thinned and unthinned stands at each site: a) egg gallery length, b) number of eggs per gallery, and c) egg density within a gallery. Actual means ± SE are shown.

CHAPTER 5
CONCLUDING DISCUSSION

Commercial thinning had a significant effect on secondary bark beetles. Diversity and abundance were higher in thinned stands than in unthinned stands (Chapter 2). These patterns were related to the amount of coarse woody debris and wind speed, suggesting that they resulted from increased host finding ability in thinned stands (Chapter 2). Beetles could also fly on more days and do so more easily in thinned stands than in unthinned stands (Chapter 3), further indicating that finding a host is easier in thinned stands than in unthinned stands.

Upon arrival at a host, reproduction was further affected by increased temperatures and reduced dispersal costs in thinned stands. In thinned stands, males attracted more females than in unthinned stands (Chapter 4). Also, females extended their egg galleries farther, laid more eggs, and had higher egg densities than in unthinned stands (Chapter 4). There is reason to believe that these changes in reproduction are adaptive and result in increased individual fitness, as male and female pine engravers leave poor situations in search of breeding prospects elsewhere. Therefore, the observed increases likely reflect higher reproductive success in thinned stands than in unthinned stands. Consequently, population sizes are expected to grow faster in thinned stands than in unthinned stands.

The effects of increased pine engraver abundance in thinned stands does not warrant immediate concern to forest managers. They prefer horizontal silhouettes to vertical ones (Seybert and Gara 1970), suggesting that they prefer coarse woody debris to living trees. Although they sometimes attack living trees (Schenk and Benjamin 1969, C. Elkin and K. Hodnett, University of Calgary, pers. comm.), there are no reports of pine engraver epidemics in the boreal forest. Regardless of whether they form breeding aggregations on coarse woody debris or attack living trees, their gallery systems are largely confined to the phloem layer, and probably do not affect timber quality.

However, increased striped ambrosia beetle abundance in thinned stands is a concern. Ambrosia beetles bore into the sapwood, depositing ambrosia fungus along their gallery walls (Fisher et al. 1953; McMullan 1956). The galleries, with their black-staining fungus reduce timber quality (Fisher et al. 1953; McMullan 1956). Ambrosia beetles pose a significant threat to trees that have been harvested (Fisher et al. 1953; McMullan 1956), especially trees that were felled in the previous year (Dyer and Chapman 1965). The economic significance of ambrosia beetles is obvious and methods to control their numbers

range from quickly removing logs from stands, de-barking logs that have been attacked, and covering logs in oil solutions to prevent attack (see Fisher et al. 1954 and McMullan 1956 for review).

Although bark beetles affect forest ecosystem processes (Harmon et al. 1986; Freedman et al. 1996) and influence the diversity of other organisms in the forest (Shook and Baldwin 1970; Berryman 1976; Amman 1984; Mills 1985; Reeve 1997; Murphy and Lenhausen 1998), forest managers may want to limit bark beetle population sizes because of their effects on timber quality. Short-term increases in bark beetle diversity and abundance after thinning may be limited by controlling the amount of fresh coarse woody debris present in thinned stands.

If thinning increases tree vigour (Mitchell et al. 1983), then coarse woody debris input also needs to be monitored over the long term. Beetles breeding in coarse woody debris from vigorous trees have higher reproductive success (Slansky and Haack 1986; Reid and Robb 1999). Combined with easier flight and host finding in thinned stands, this could allow bark beetle activity to remain higher than in unthinned stands. It may be necessary to quickly remove fallen trees before they are attacked. This would be especially true after large fall-down events due to wind storms or heavy snow fall in which the amount of coarse woody debris is particularly high and therefore capable of attracting a large number of beetles to a stand.

Long-term effects of thinning on beetle activity may be mitigated by reducing the number of trees removed during thinning. Tree density will remain relatively constant after thinning. Consequently, wind speeds will remain higher in thinned stands than in unthinned stands (Bartos and Amman 1989; Schmid et al. 1991, 1992b; Chapter 2). Since both pine engravers and striped ambrosia beetles appeared drawn to stands with relatively high wind speeds, their increased activity in thinned stands relative to unthinned stands is likely to persist. They may do well in thinned stands because it is much easier to find suitable hosts (Seybert and Gara 1970; Billings et al. 1976; Fares et al. 1980; Hynum and Berryman 1980), even though coarse woody debris input levels are the same as in unthinned stands. Furthermore, reduced flight costs in thinned stands relative to unthinned stands, as well as a larger window of flight opportunity due to higher temperatures, may result in greater reproductive success in thinned stands. This would, in turn, have an effect on overall beetle activity in a stand.

This study shows that bark beetles make good indicators for evaluating the effects of harvesting practices because several aspects of their life histories are affected by changes

in the forest environment. Commercial thinning represents a small change in the forest environment compared to clear-cutting, yet bark beetle activity is significantly affected by the changes. Bark beetle activity will likely affect decomposition and nutrient cycling within the forest (Harmon et al. 1986; Freedman et al. 1996), and, in turn, other animals in the forest (Shook and Baldwin 1970; Berryman 1976; Amman 1984; Mills 1985; Reeve 1997; Murphy and Lenhausen 1998). Therefore, monitoring their activity following disturbance such as harvesting, or natural disturbances such as fire and windthrow, may give a good indication of forest ecosystem processes.

This study also makes a contribution to landscape ecology. Traditionally, landscape ecology has focused on how habitat patch connectivity affects dispersal success of organisms, and has largely neglected the role of inter-patch ("matrix") in determining dispersal success (Johnson et al. 1992; Wiens et al. 1993). This study has shown that even small changes in the tree density has significant effects on bark beetle dispersal (Chapter 3). These effects may ultimately affect reproductive success (Chapter 4), suggesting that it is worth considering matrix structure when landscape level process affecting the distribution of organisms (e.g., Hanski and Gilpin 1991; Hansson 1991).

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