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Effects of clearcut logging on buffaloberry (*Shepherdia canadensis*) abundance and bear myrmecophagy in the Flathead River drainage, British Columbia.

by

Richard Eldon Knight ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

Department of Biological Sciences

Edmonton, Alberta

Spring 1999

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Effects of clearcut logging on buffaloberry (*Shepherdia canadensis*) abundance and bear myrmecophagy in the Flathead River drainage, British Columbia" submitted by Richard Eldon Knight in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

Understanding the impact of logging on habitat is a vital component of bear management. I investigated effects of logging on two summer bear foods. Clearcuts without post-logging treatment had more buffaloberry bushes than scarified clearcuts or unharvested areas. Bush abundance in scarified clearcuts did not exceed unharvested sites. Berry biomass partially reflected bush density but appeared more affected by factors such as weather patterns.

Clearcuts had more wood nesting ants than unharvested areas. Ants were used as a food source by bears which selectively attacked larger species. Relative abundance of ants, hardness of wood, and ant defense mechanisms were unrelated to selection of ant species by bears. Number of bear attacks on ant nests per hectare of clearcut decreased as distance to clearcut edge increased. 90% of attacks occurred within 50 m of clearcut edge and 96% occurred within 30m of cover.

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I. INTRODUCTION

Grizzly bear (*Ursus arctos*) numbers have declined and their distribution has narrowed during the last 150-200 years, primarily due to human settlement, resource extraction, and excessive mortality (Herrero 1972; Pearson 1975; Martinka 1976). Grizzly bears are currently restricted to national parks and remote and often mountainous regions of northwest North America (Martinka 1976; Zager 1980). Resource extraction industries are rapidly impinging upon these areas and timber harvesting is believed to have had the greatest impact on grizzly bear habitat in the last 25 years (Zager 1980). Industrial resource extraction is destined to continue and thus the integration of bear management with an understanding of the impact of logging on habitat is vital.

Optimal grizzly bear habitat consists of a blend of forested land and open habitats (Herrero 1972; Mundy and Flook 1973; Martinka 1976). Although black bears (*Ursus americanus*) are best adapted to forest habitat (Herrero 1978), they do feed in open areas (Lindzey and Meslow 1977). Optimal black bear habitat, therefore, also encompasses a mosaic of successional stages (Irwin and Hammond 1985).

Prior to the implementation of fire suppression policies, wildfire played an important role in creating habitat with diverse successional stages. There has been some suggestion that timber harvesting may be a viable replacement for wildfire. Telfer (1974) argued that logging can be used to provide the diversity of forest types and age classes that wildlife species require. Zager et al. (1983) noted that certain post-wildfire conditions, such as reduced tree canopy, altered soil moisture, and altered nutrition regimes, may be simulated by logging. The early seral plant communities that follow logging often produce bear foods (Lindzey and Meslow 1977; Irwin and Hammond 1985). Boileau et al. (1994) felt disturbances such as logging, burns, and insect epidemics are beneficial to black bears by increasing fruit and berry species. Davis (1977), however, argued that while both wildfire and logging increase diversity, it is unclear whether they affect the ecosystem in the same way.

The purpose of this study was to investigate the effects that logging and post-logging site preparation had on the abundance of bear foods in southeastern British Columbia. The study area is the North Fork of the Flathead River drainage in southeastern British Columbia (Figure 1-1). This area underwent extensive clearcutting from the late 1950s to 1960s and late 1970s to early 1980s in response to bark beetle (*Dendroctonus obesus, D. ponderosae*) infestations and resulting tree mortality.

The study area contains all major bear foods identified throughout the interior of western North America (McLellan and Hovey 1995). As a possible result, a large black bear population and one of the highest densities of grizzly bears on the continent occurred there (McLellan 1989). A pilot study (Knight 1993), investigating the effects of logging on eight bear foods, was conducted in the summer of 1992. The eight foods of interest were *Vaccinium membranaceum* Dougl. (huckleberry), *V. scoparium* Leiberg (whortleberry), *Shepherdia canadensis* Nutt., (buffaloberry),*Heracleum lanatum* Michx. (cow parsnip), *Lathyrus ochroleucus* Hook. (pea vine), *Hedysarum sulphurescens* Rydb., *Angelica arguta* Nutt. (white angelica) and ants (Formicidae). *H. lanatum* and *A. arguta* were dismissed from investigation because they were essentially absent from the sites sampled. *H. sulphurescens* was also dismissed from the study for two reasons; its response to disturbance had previously been investigated by Edge et al. (1990) and its patchiness did not facilitate sampling. The remaining items were included in the pilot study and two, *S. canadensis* and ants were chosen for the future research. These choices were made primarily by the

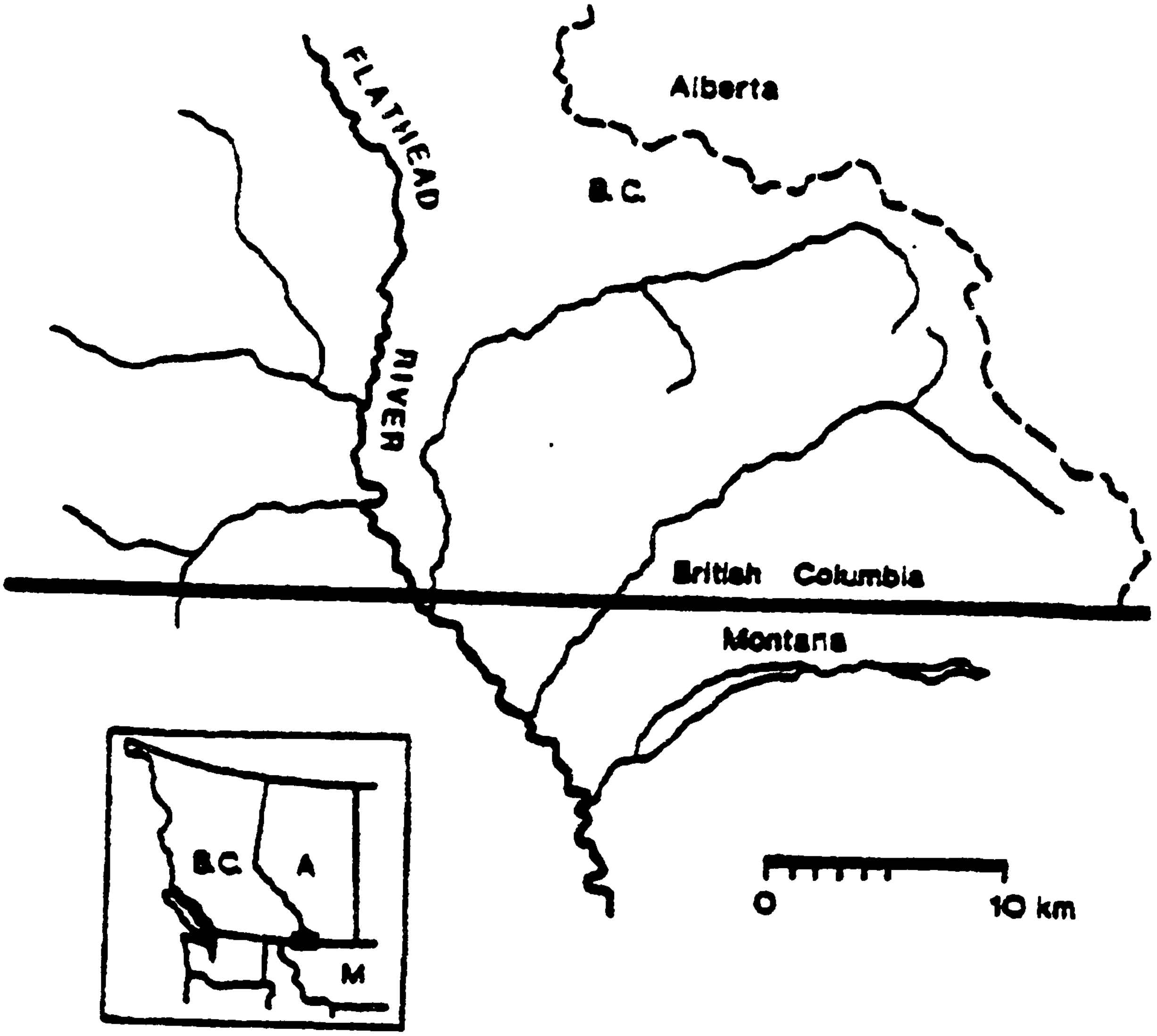

Figure 1-1. Map of study area (from McLellan 1989).

process of elimination. I was unable to develop an adequate method to sample *L. ochroleucus* during the pilot study. Sampling of *Vaccinium* spp. was also hampered by the inability to obtain enough sites to represent a sample size large enough to perform statistical analyses.

For the current research, *S. canadensis* and ants were sampled in clearcuts that had not received post-logging site preparation (unscarified) and clearcuts that were more heavily disturbed by post-logging mechanical scarification. Results from clearcuts were compared to those from unharvested reference areas to determine if there was a treatment effect.

All sites sampled were within an area of approximately 250 km^2 and were located within the Montane Spruce biogeoclimatic zone (Hope et al. 1991). Elevations of sites ranged from 1300m to 1600m. Within the limits imposed by the landscape, an attempt was made to use sites with similar aspects and slopes (Appendix A). Placement of the sites within the study area is shown in Appendix B.

Clearcuts were logged between 1978 and 1981 and mechanical scarification was completed in 1980 and 1982. Unharvested reference areas were dominated by lodgepole pine (*Pinus contorta* Dougl.). Larch (*Larix occidentalis* Nutt.), spruce (*Picea engelmanni* Parry x *glauca* (Moench) Voss) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) occurred less frequently.

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II. The long term effect of clearcut logging on *Shepherdia canadensis* (buffaloberry) bush density and berry biomass.

INTRODUCTION

Shepherdia canadensis Nutt. (common names include soapolallie, soapberry, and buffaloberry) is a 1-3 m tall dioecious shrub occurring across a wide geographical range and in a variety of community types (Noble 1985). Unfortunately, readily accessible information about *Shepherdia* spp. is sparse (Remlinger 1994) and the majority of the information that does exist concerns *S. argentea*.

Although preferring medium textured, well-drained soils, *Shepherdia* spp. are considered winter hardy, saline tolerant and drought resistant (Remlinger 1994). *Shepherdia* spp. exhibit a preference for sunlight over shade (Remlinger 1994) and Cody (1988) considers it characteristic of open woodlands and clearings. Wilkinson (1990) regards *S. canadensis* as characteristic of the dry, semi-open montane spruce and pine forests typical of the study area.

S. canadensis is a key component of bear habitat. Its yellow-red berries have been identified as a major food for both grizzlies (Hamer and Herrero 1987; Mattson et al. 1991; McLellan and Hovey 1995) and black bears (Irwin and Hammond 1985; MacHutchon 1989; Holcroft and Herrero 1991). During the summer months, a time critical for bears to gain weight (Noble 1985), up to 100% of the feeding activity of some bears is centered on *S. canadensis* (Noble 1985). Despite its importance to bears, the effect of disturbance, particularly logging, on *S. canadensis* is poorly understood.

Forest canopy cover is a variable that has previously been identified as affecting *S. canadensis* abundance. After a pilot study of *S. canadensis* in the study area, Noble (1985) suggested that the effects of canopy cover on total *S. canadensis* berry production warranted investigation. Hamer (1996) found a negative correlation between forest canopy cover and *S. canadensis* fruit production. In a multiple linear regression, forest canopy cover explained the greatest amount (67%) of variation in fruit abundance (Hamer 1996).

The effect of disturbance on *S. canadensis* is only somewhat understood based on equivocal results (Zager et al. 1983) or anecdotal observations (Bratkovich 1986). The purpose of this research was to quantify the effects of logging and post-logging site preparation on *S. canadensis* bush density and berry biomass and hence, on the quality of habitat for bears.

MATERIALS AND METHODS

TREATMENTS

I investigated differences in bush density and berry biomass between unharvested reference areas and 10 to 15 year old clearcuts that had either (i) no post-logging site preparation (unscarified), or (ii) had been further disturbed by mechanical scarification. None of the clearcuts had been broadcast burned. Two types of mechanical scarification were included; drag scarification and blade scarification. Drag scarification involves a chain with metal plates towed behind a tractor to agitate residual cones and distribute seeds allowing natural establishment of on-site conifer species (J. Davis, Silviculture, B.C. Ministry of Forests, pers. comm.) . Blade scarification uses the blade of a crawler tractor to remove slash and expose mineral soil on the forest floor. The objectives are to provide continuous trails for replanting seedlings and to remove competing vegetation, thus improving establishment of planted conifers (J. Davis, pers. comm.). Drag scarification is generally recognized as a lighter form of disturbance than blade scarification.

SITES

Twenty-five sites were used for the study. These included seven unscarified clearcuts, seven drag scarified clearcuts, four blade scarified clearcuts and seven unharvested reference areas. Physical characteristics and number of plots for each site are outlined in Appendix A. These sites represented all cutting units within the study area described that had unambiguous history records, were located in the montane spruce zone (Hope et al. 1991) and were similar in slope and aspect. Although some clearcuts were scarified in 1980 and some in 1982 (for both scarification methods), no differentiation was made between the two dates during data analysis. Sampling was conducted in the same sites in 1994 and 1995.

SAMPLING

Data were collected during 14-26 July 1994 and 11-19 July 1995 when *S. canadensis* berries were ripe. Within each site, 0.01 ha (5.64 m radius) circular plots were placed 50-100m apart (distance determined by random number) along parallel transects spaced 50-100m apart (distance determined by random number) across the whole site. Number of plots ranged from 5 to 20 depending on the size of the site (Appendix A). This method of incorporating randomness was used both years so that, although the same sites were used in both years, placement of plots in 1995 was largely independent of plot placement in 1994.

Within each plot, the total number of *S. canadensis* bushes was counted. All branches with berries were categorized into three groups, based on stem diameter (< 0.95 cm, 0.95 - 1.27 cm and 1.27 - 1.59 cm) after Vandehey (1991). If a branch was greater than 1.59 cm, it was counted as several branches with each branch forking off the >1.59 cm branch being categorized into its appropriate class. When there were five or fewer branches of a given size class in the plot, the number of berries on each branch was counted. Berries were counted on every third branch if the branch total for a given class was 6-20 branches, on every fifth branch for 20-100 branches and on every tenth branch for totals exceeding 100 branches. This was an arbitrary method chosen to sample dense bushes without requiring extensive time being spent on any single plot (e.g. for one plot containing 10 bushes it allowed an estimate to be calculated by counting 1436 berries as opposed to the estimate of 7216 if every berry in the plot was counted). This allowed all sites to be sampled in less than a two week period, thus minimizing variation introduced by drop-off or consumption of berries by animals. I made the assumption, however, that drop-off and consumption would be similar across all sites. Using the data collected, the total number of berries was estimated for each plot.

In 1994, all berries were picked from one branch of each size class in three unharvested areas, one unscarified, one drag scarified and one blade scarified clearcut. These berries were all combined and oven dried at 105^{o}C for 24 hours and weighed to estimate the mean dry weight of a single berry. That value was multiplied by the mean number of berries/plot to estimate the dry berry biomass per plot.

In 1995, a 100m line transect was placed randomly in three sites of each treatment type. All bushes touching the transect were clipped at ground level and aged by counting the annuli in the stem tissue (Looman 1984).

DATA ANALYSIS

Bush densities for 1994 and 1995 were pooled for data analysis since mortality and recruitment of *S. canadensis* between two consecutive years is likely minimal. Bush density, berry biomass for 1994 and berry biomass for 1995 were tested using nested ANOVAs. The treatment variable was not significant for any of the three ANOVAs but the site variable was highly significant for each test (Appendix C). Therefore, I attempted to determine if there were any other factors that might be causing differences among sites.

A factor of potential importance was location relative to the Flathead river. I categorized sites sampled in one of two location categories based on whether they were on the east or west side of the river. Location was used as a blocking variable because it was apparent from cursory examination that the sites on the west side of the river had much thicker vegetation growth (of all types, not just *S. canadensis*) than sites on the east side.

Bush density, berry biomass for 1994 and berry biomass for 1995 were then retested in a nested ANOVA with treatment and location as the variables. Treatment data were coded as one of the four treatment types and location was coded as east or west of the Flathead river. If the F-test was significant ($p<0.05$) the variables were tested with Fisher's LSD multiple comparison test (Dowdy and Wearden 1991) to determine where the differences were.

Data on bush age were also analyzed with a nested ANOVA followed by Fisher's LSD multiple comparison test.

Purely for exploratory purposes, bush density, berry biomass for 1994 and berry biomass for 1995 were each tested in a multiple regression which included treatment and location plus the three variables (slope, elevation and aspect) which were largely controlled for in the experimental design. Data for treatment (four treatment types) and location (east or west of Flathead River) were categorical and each treatment type and each location category were coded using dummy variables (Zar 1984). Data for slope, elevation and aspect were continuous and were obtained from the B.C. Ministry of Forests site history records.

RESULTS

For *S. canadensis* bushes, the F-test from the nested ANOVA was significant for both the treatment (p=0.03) and the location (p=0.01) variables. When Fisher's LSD multiple comparison test was used, mean bushes per 0.01 ha (Figure 2-1) in unscarified clearcuts were significantly greater than those in drag scarified (p=0.01) and blade scarified (p=0.05) clearcuts but did not differ from unharvested sites (p=0.12). Sites on the west side of the Flathead river had more bushes than those on the east side of the river (Appendix D).

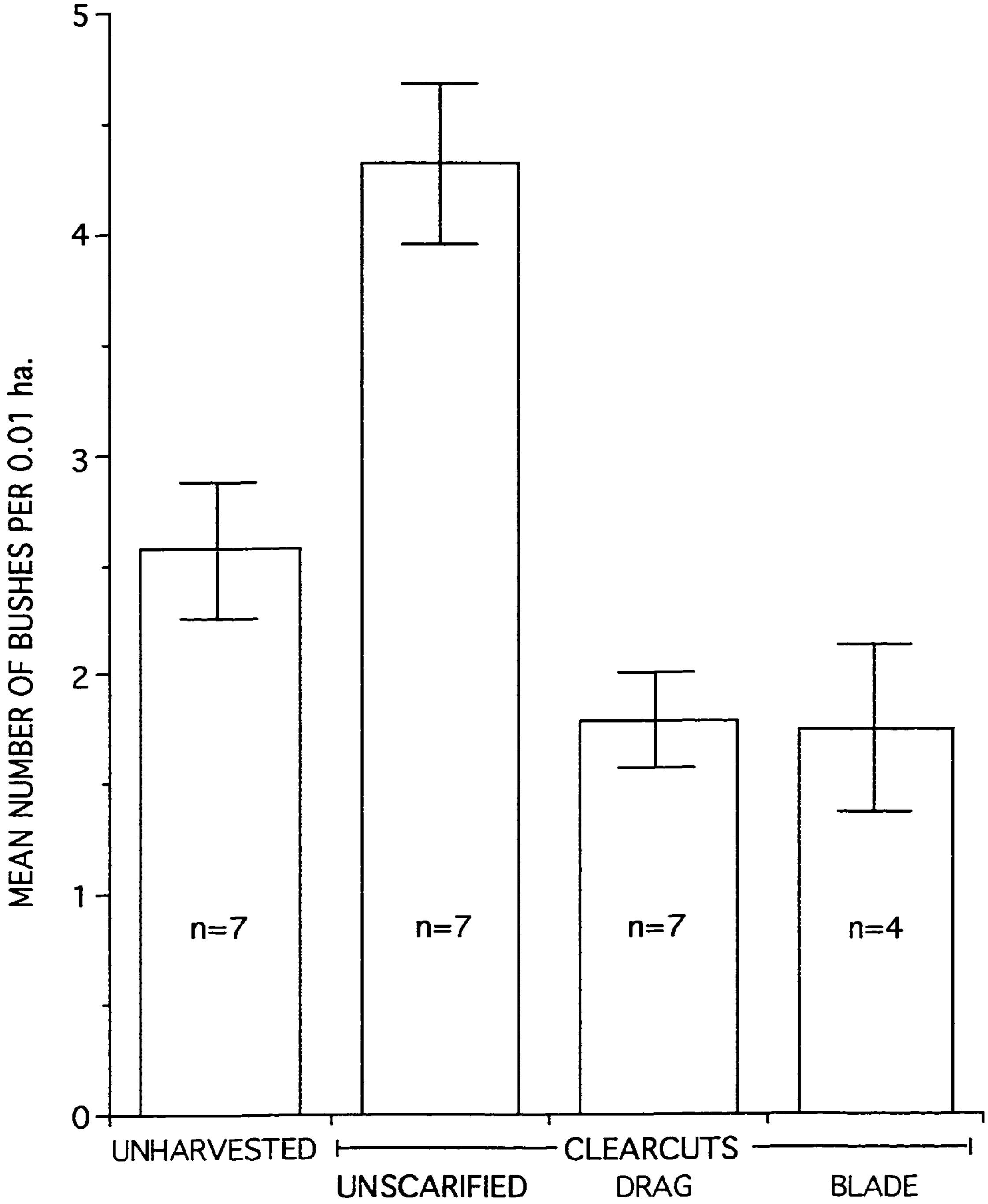

Figure 2-1. Mean (±SE) number of *Shepherdia canadensis* bushes in unharvested reference areas and unscarified, drag scarified and blade scarified clearcuts. Unscarified clearcuts have significantly more bushes than drag or blade scarified clearcuts.

The F-test for mean berry biomass (dry weight in grams) per 0.01 ha was not significant (p>0.05) for either the treatment (Figure 2-2) or location (Appendix C) variables for either 1994 or 1995.

S. canadensis stem age was a significant factor (p=0.004) in the nested ANOVA (Appendix D) and the multiple comparison test revealed that the age of stems (Figure 2-3) from unharvested sites were significantly older than those from unscarified (p=0.004), drag scarified (p=0.02) and blade scarified (p=0.007) clearcuts. There were no significant differences (p>0.85) between any of the clearcut types.

In the multiple regression for bush density (Appendix E), the overall regression was significant (p=0.025). Location (p=0.006) and unscarified clearcuts (p=0.045) were significant variables. Locations on the west side of the Flathead River (Appendix D) and unscarified clearcuts (Figure 2-1) had more bushes than other sites. Slope (Appendix E), elevation (Appendix G) and aspect (Appendix H) were not significant.

The multiple regression tests for berry biomass (Appendix E) were not significant for either 1994 or 1995.

Appendix I contains a regression between bush density and berry biomass.

Complete tables for all nested ANOVAs for these results are located in Appendix C. Mean bushes per 0.01 ha for each site are listed in Appendix J. Mean berry biomass (dry weight in grams) per 0.01 ha for each site are provided for both 1994 (Appendix K) and 1995 (Appendix L).

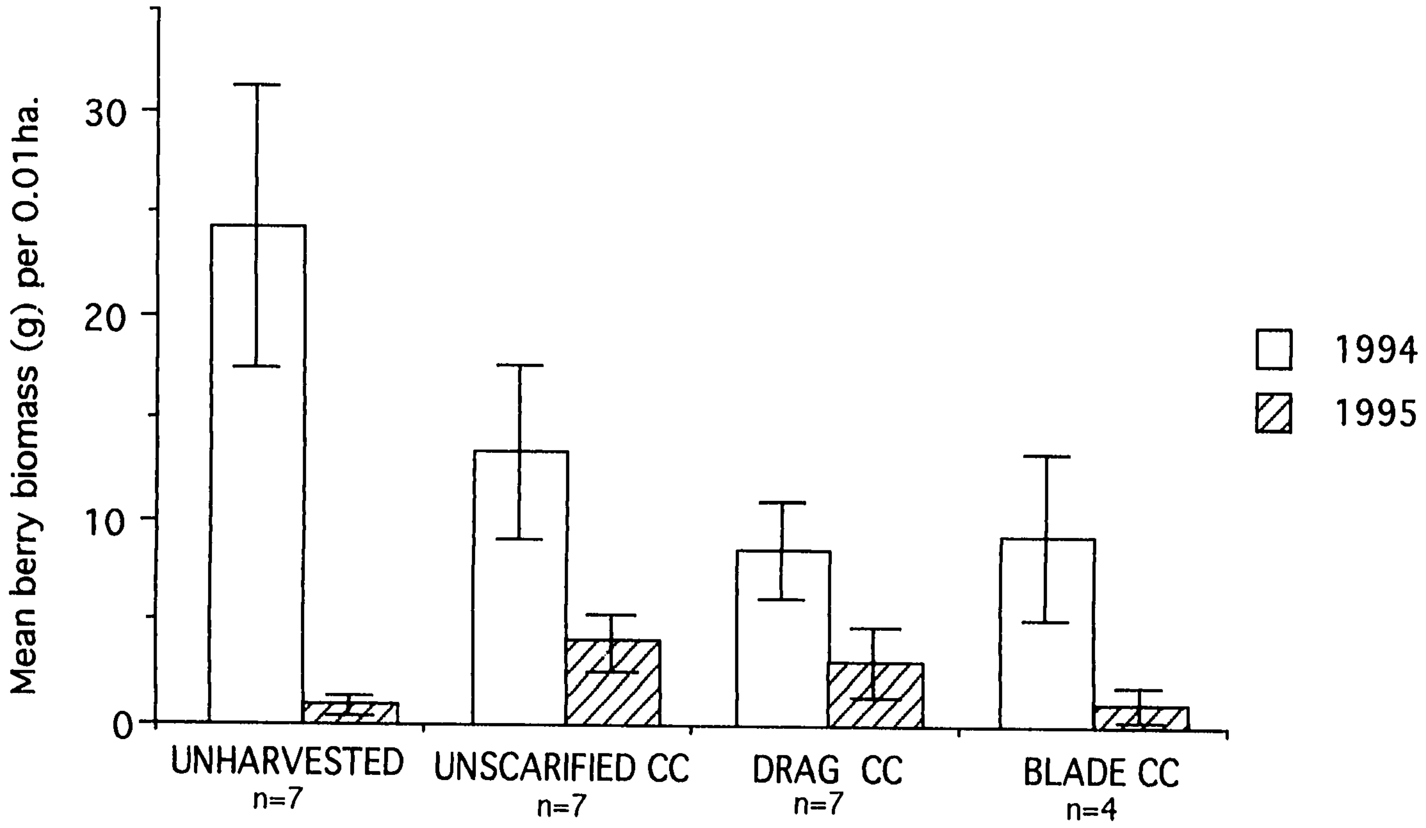

Figure 2-2. *Shepherdia canadensis* berry biomass in unharvested reference areas and unscarified, drag scarified, and blade scarified clearcuts. In neither 1994 nor 1995 were there significant differences ($p>0.05$) in berry biomass between treatment types. Bars indicate SE.

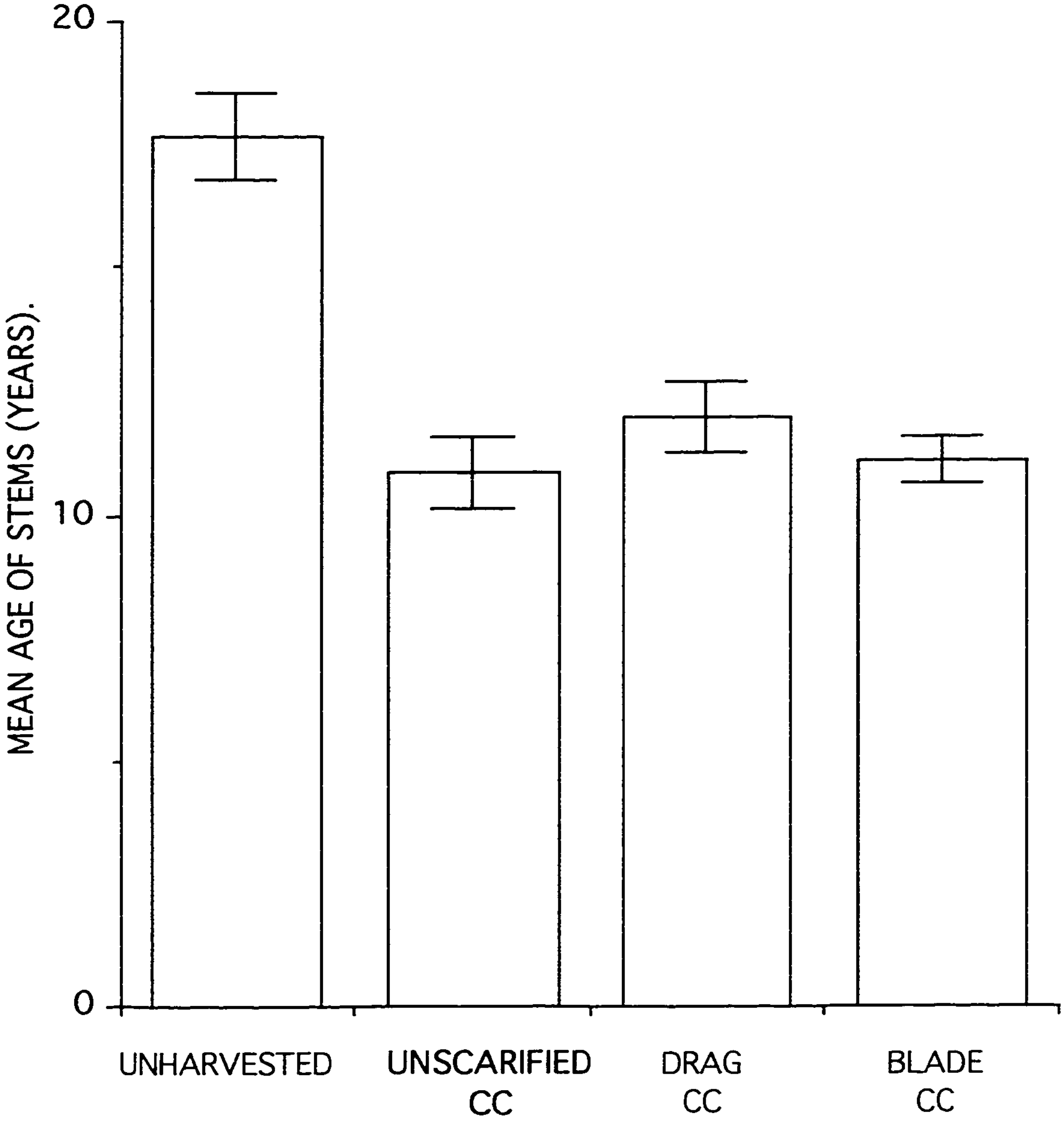

Figure 2-3. Mean (±SE) age of *Shepherdia canadensis* stems in unharvested reference areas and unscarified, drag scarified and blade scarified clearcuts. Ages in unharvested sites are significantly greater than ages in all clearcuts.

DISCUSSION

Clearcut logging and post-logging site treatment affected *S. canadensis* bush density. Although the difference was not statistically significant, clearcuts without post-logging treatment tended to have greater bush densities than unharvested sites. Clearcuts that received post-logging treatment, in the form of drag or blade scarification, had significantly fewer bushes than unscarified clearcuts and did not differ from unharvested sites or from each other. These results suggest that timber harvesting without post-logging scarification enhances the recruitment of *S. canadensis* bushes. This is compatible with the conclusions of Boileau et al. (1994) who stated that clearcuts produced more fruit and berry producing species than other habitats. Dzwonko and Loster (1997) reported that the number of species and the number and cover of shrubs increased along an ecocline of disturbance. When logging is followed by mechanical scarification, however, bush density does not increase, and may even decrease, regardless of the severity of the scarification. These results are consistent with Bratkovich's (1986) observations that *S. canadensis* increased in unscarified clearcuts and decreased in scarified clearcuts. Zager (1980) also found that *S. canadensis* declined following disturbance but suggested that this was an artifact of infrequent occurrence of *S. canadensis* on sample sites. His observations led Zager (1980) to postulate that scarification results in a decrease in *S. canadensis* cover. Thus, all evidence indicates that scarification following logging lowers *S. canadensis* bush density and destruction of root crowns likely delays recruitment.

S. canadensis reproduces vegetatively by means of shoot extensions that run just below the humus layer (Hayes et al. 1990). Both shoots and adventitious roots arise from these extensions (Hayes et al. 1990) and may allow regrowth of *S. canadensis* after surface bushes are damaged by logging. In sites that are scarified, these shoot extensions are likely to suffer mechanical damage. Such damage would result in slower recruitment and a lower bush density in scarified clearcuts than in unscarified clearcuts. Martin (1983) reported similar results for *Vaccinium globulare* Rydb. (globe huckleberry) in northwestern Montana; percent cover was lower in sites that received blade scarification than in unscarified sites. She felt this was because scarification damaged rhizomes by which the shrubs reproduce vegetatively.

My initial hypothesis was that bush densities in sites that received the lighter drag scarification would fall somewhere between those in unscarified clearcuts and those in the more severely disturbed blade scarified cuts. Yet, there was no difference between sites with the two scarification treatments. This suggests that, in regard to *S. canadensis*, the disturbance created by the two types of scarification is of equal severity and may last at least 10 to 15 years.

Results for berry biomass were not significant for either the 1994 or 1995 data. Despite the great variation in biomass within the four treatment types, as a general trend berry biomass appears to reflect bush density (Appendix I). Given the variation in berry biomass and resulting lack of significance of the measured variables, other unmeasured variables are of greater importance for fruit production. For example, soil type (Vandehey

1991), pH of soil, light and moisture levels, and time since disturbance may all influence berry production.

Weather may have a great effect on fruit production. There was a poor berry crop in the hot and dry summer of 1994 and a much lower crop (almost nonexistent) in the cooler and rainier summer of 1995. These conditions may explain the apparent difference in berry biomass in unharvested sites between 1994 and 1995. In 1994, unharvested sites had the greatest biomass of the four treatment types but the lowest berry biomass in 1995. *S. canadensis* is mesophilic (Noble 1985); in the hot and dry summer of 1994 the unharvested areas would be cooler and more mesic than clearcuts. In the cool, wet summer of 1995, however, clearcuts would have been warmer and dryer due to a lower canopy cover and may have provided better growing conditions for *S. canadensis* plants.

Stems from branches located in unharvested sites were significantly older than those from clearcuts. Age of stems in clearcuts was the same regardless of whether the site had received post-logging scarification. It must be noted that the stem ages reported should not be considered ages of the *S. canadensis* bushes. I expected ages of *S. canadensis* bushes in the unharvested areas to be much greater than 18 years as there was no disturbance at these sites for decades (McLellan pers. comm.) Looman (1984) found that, for *S. argentea*, because old stems may die and be replaced by young stems, age of the root crown is a more accurate measure of bush age. He reported that root crowns were older than stems and usually exceeded stem diameters. Looman (1984) found plants with 50-60 year old root crowns that had individual branches aged 20-25 years old. Therefore, the ages which I have reported should be considered stem ages rather than bush ages. Nonetheless, my data clearly indicate that, consistent with a 10-15 year old disturbance, mean age of stems in clearcuts were 11-12 years old while those in unharvested areas were significantly older. Combined with the results on bush density, this suggests that clearcut logging initially destroys *S. canadensis* bushes within the cut-block and subsequent scarification inhibits the regeneration of bushes.

When bush density was tested in a multiple regression with treatment, location, and the three factors controlled for in the experimental design (slope, elevation, aspect), slope had a $r^2 = 0.16$. This suggests that slope can affect *S. canadensis* density and should be considered an important variable in any future research on this plant.

Results from the multiple regression tests support the results from nested ANOVAs. When bush density was tested, location and unscarified clearcuts were the only variables of significance. The multiple regression tests for berry biomass were not significant for either 1994 or 1995 data. The fact that slope, elevation and aspect were not significant in the multiple regression tests suggests that the attempt to control for these variables in experimental design was successful.

The primary objective of this study was to quantify the long-term effect of logging and post-logging site treatment on *S. canadensis*. Fifteen years after disturbance by logging, *S. canadensis* located in clearcuts that were not scarified appeared to have more bushes than unharvested reference areas and had significantly more bushes than clearcuts receiving post-logging mechanical scarification. Bush densities in scarified clearcuts did not exceed those in unharvested sites.

In this study, no conclusion can be made on the effect of logging and post-logging mechanical scarification on *S. canadensis* berry biomass as both 1994 and 1995 were poor berry years. As a general trend, berry biomass appeared to at least partially reflect bush density. Successful sampling of berry biomass will require a large sample size in a year with a "good" berry crop. Other possible variables, such as weather and soil, may also have to be taken into account. Unless controlled for in experimental design, slope should be considered an important variable in research on *S. canadensis* (Noble 1985; Hamer 1996).

From a bear forage perspective, unscarified clearcuts provide significantly greater densities of *S. canadensis* bushes than do mechanically scarified clearcuts. They also appear to have greater *S. canadensis* densities than unharvested sites (although this result was not statistically significant.)

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III. Bear myrmecophagy 1: Wood-nesting ants in clearcuts utilized as a food source.

INTRODUCTION

A large proportion of the animal matter in diets of bears is insects, of which ants (Formicidae) are the most common (Hatler 1972; Graber and White 1983; Holcroft and Herrero 1991). MacHutchon (1989) reported that during June and July, ants were the most common animal food in the diet of black bears in the Pelly River Valley in the Yukon. Black bear populations in Alaska (Hatler 1972), southwestern Alberta (Holcroft and Herrero 1991) and Wyoming (Irwin and Hammond 1985) also included ants in their spring and summer diet. Ants were also a significant item in the diet of black bears in north-central Minnesota (Noyce et al. 1997). In that study, 60% of the bears foraging time in May was spent feeding on ants, rising to 80-100% during June. Ants were also common in the summer diet of some grizzly bear populations (Almack 1986; Hamer et al. 1991; Mattson et al. 1991).

Ants are frequently found in bear scats, but rarely make up a large proportion of the scat volume (Irwin and Hammond 1985; Holcroft and Herrero 1991). Even when ants only make up a small percentage of the diet, they may be a source of essential amino acids and other dietary requirements absent in vegetation (Eagle and Pelton 1983; Redford and Dorea 1984). Ants may be underrepresented in diet studies because scats containing ants are cryptic and wash away quickly. Bears also seem to prefer pupa and eggs which are more digestible than are adults and therefore do not show up in scats. Hatler (1972) found that when hymenopterans were present in bear stomachs, larvae and eggs constituted a large proportion of total insect volume. In scats, however, these items were rarely evident. Noyce et al. (1997) reported peak consumption of ants by black bears in Minnesota coincided with the highest abundance and largest size of pupae. According to Redford and Dorea (1984), larval and pupal forms of insects have substantially higher fat and lower chitin content than adults of the same species, and these immatures are less well defended and are easier to catch when detected. Noyce et al. (1997) reported that even worker ants contain more gross energy per gram dry mass than do fruits and vegetation.

Ants may be of greater importance during years when other bear foods fail (Mattson et al. 1991). Grizzly bear diets in Yellowstone National Park contained the greatest concentration of ants during years of poor growing conditions and low availability of pine nuts (Picton et al. 1986; Mattson et al. 1991).

In southeastern British Columbia, ants are an important summer food for black bears (Hovey pers. comm.) Although they commonly occur in grizzly bear scats, ants do not appear to constitute a large proportion of grizzly bear diet (McLellan and Hovey 1995).

Hatler (1972) felt that insects must be aggregated for bears to include them as food. His evidence for this was the fact that colonial hymenopterans, particularly ants, are the insects consistently taken across most areas. Using the same argument at a larger scale, I felt that a concentration of ant nests should provide better foraging for bears. The abundance of woody material created by logging provides the potential for large concentrations of ant nests. Therefore, the objectives of this part of my research were (i) to confirm quantitatively that stumps were being colonized by wood-nesting ants and (ii) if ants were indeed colonizing the stumps, to determine whether the ant nests were attacked by bears.

MATERIALS AND METHODS

Sampling was done in clearcuts with different post-logging treatments and unharvested reference areas to determine influences of logging practices on abundance of ants and foraging on ants by bears. Sampling was conducted in a total of 25 sites; 7 unscarified clearcuts, 7 drag scarified clearcuts, 4 blade scarified clearcuts and 7 unharvested reference areas. These represented all the clearcuts I could find within the study area with an unambiguous site history (corroborated by walking through the cut prior to sampling). Physical characteristics of the sites and the number of plots per site are listed in Appendix A. Although some clearcuts were scarified in 1980 and some in 1982 (for both scarification methods), no differentiation was made between the two dates during data analysis.

Of the 25 sites used, four of the unscarified clearcuts, four of the drag scarified clearcuts, all blade scarified clearcuts, and four of the unharvested reference areas were sampled from 3 June - 6 July 1994. Results from these locations are pooled for analysis with results obtained in July and August 1992 from the other three unscarified clearcuts, three drag scarified clearcuts, and three unharvested reference areas (Knight 1993).

Ant colonies were sampled using a stratified random sampling technique (Greig-Smith 1983). Each treatment site was divided into plots of 50m x 50m. A 10m x 10m quadrat was placed in each plot using random X and Y coordinates. Within each quadrat, the number of stumps was counted and all stumps were broken open using an ax. The number of stumps that contained, or had contained, ants was counted as were stumps that showed no sign of ever having been colonized by ants. I classified a stump as not being previously colonized if there were no chambers or tunneling.

Before the stumps were broken open, the number of stumps attacked by bears was counted. An attacked stump was obvious as a quarter to a third of the stump was knocked off (Figure 3-1a) and, occasionally evidence of further excavation (usually at the base) was present.

Data on attack numbers were analyzed using a nested ANOVA followed by Scheffe's multiple comparison procedure (Dowdy and Wearden 1991). Data on proportions of stumps attacked were analyzed using a log linear model.

RESULTS

Unharvested reference areas had significantly fewer ($p<0.05$) total stumps and bear attacked stumps than all types of clearcuts (Figure 3-2). Total number of stumps and the number of stumps attacked by bears did not differ significantly ($p>0.05$) between clearcuts with different site histories. Stumps with no evidence of previous colonization were rare and there were no significant differences ($p>0.05$) in stump occupation by ants between any of the four treatment types. Specific p-values for individual comparisons for all of these tests are in Appendix M.

There were no significant differences ($G=0.181$, $df=3$, $p=0.98$) in the proportion of stumps attacked in any of the treatment types (Figure 3-3). In general, stumps in unharvested reference areas had a relatively low proportion of attacks compared to those in clearcuts.

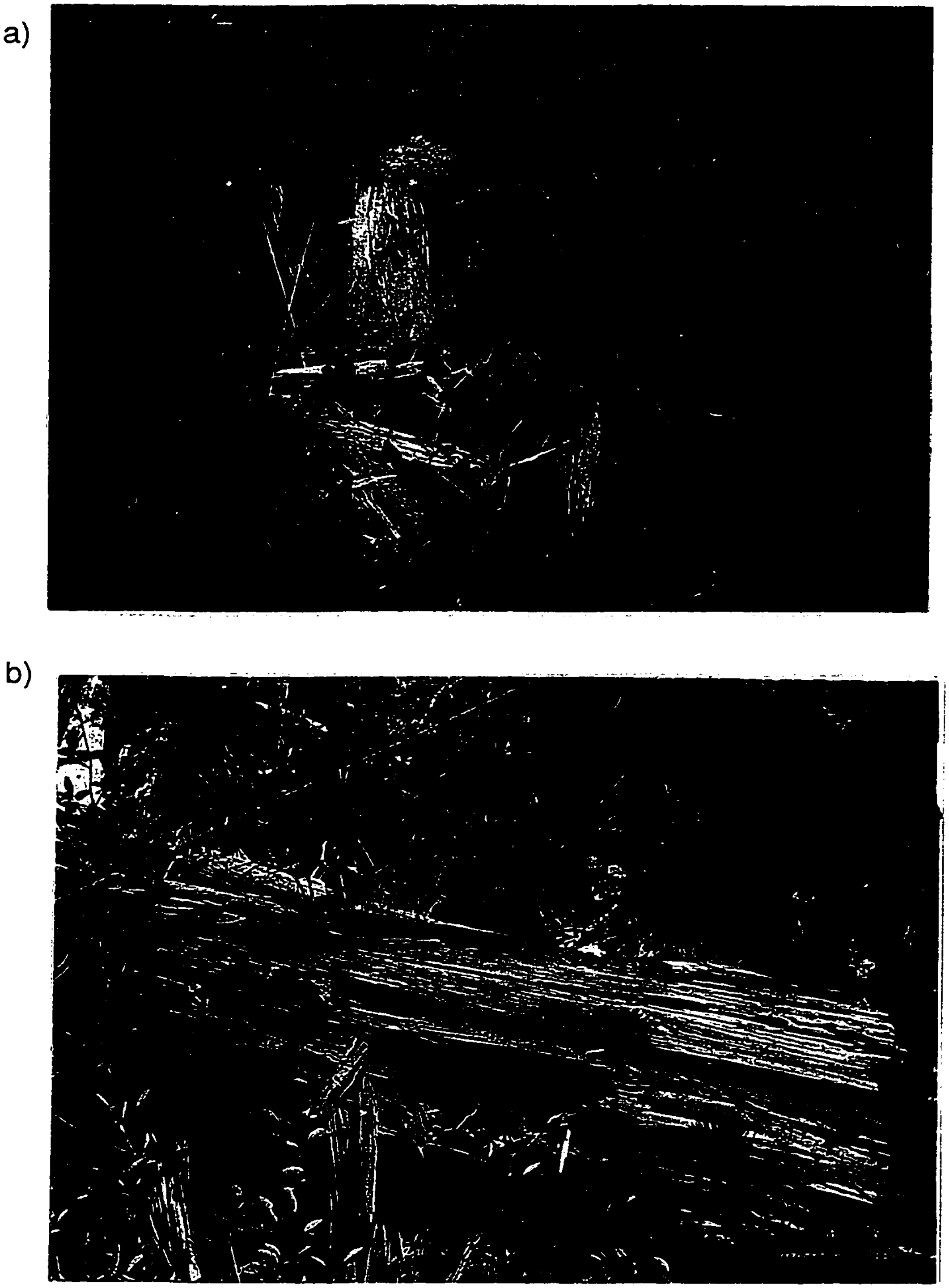

Figure 3-1. Examples of bear attacks on ants nesting in (a) a stump and (b) a log.

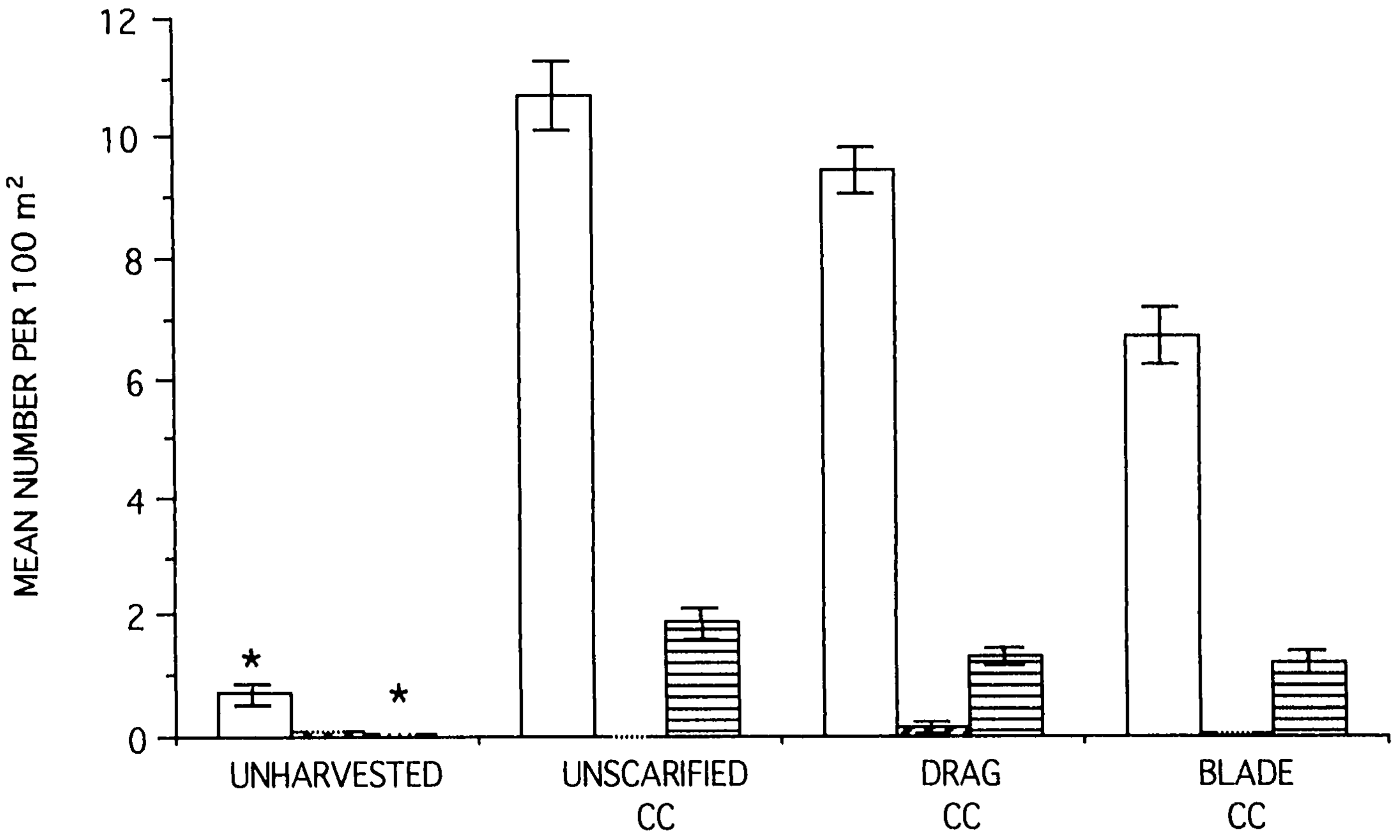

Figure 3-2. Mean (±SE) number of stumps □, number of stumps with no evidence of ant colonization ▨, and number of bear attacked stumps ▤ in unharvested reference areas (n=7) and unscarified (n=7), drag scarified (n=7), and blade scarified (n=4) clearcuts. * indicates means whose differences from other treatments are statistically significant ($p<0.05$). All data were tested with a nested ANOVA followed by Scheffe's multiple comparison procedure if the F-ratio was significant.

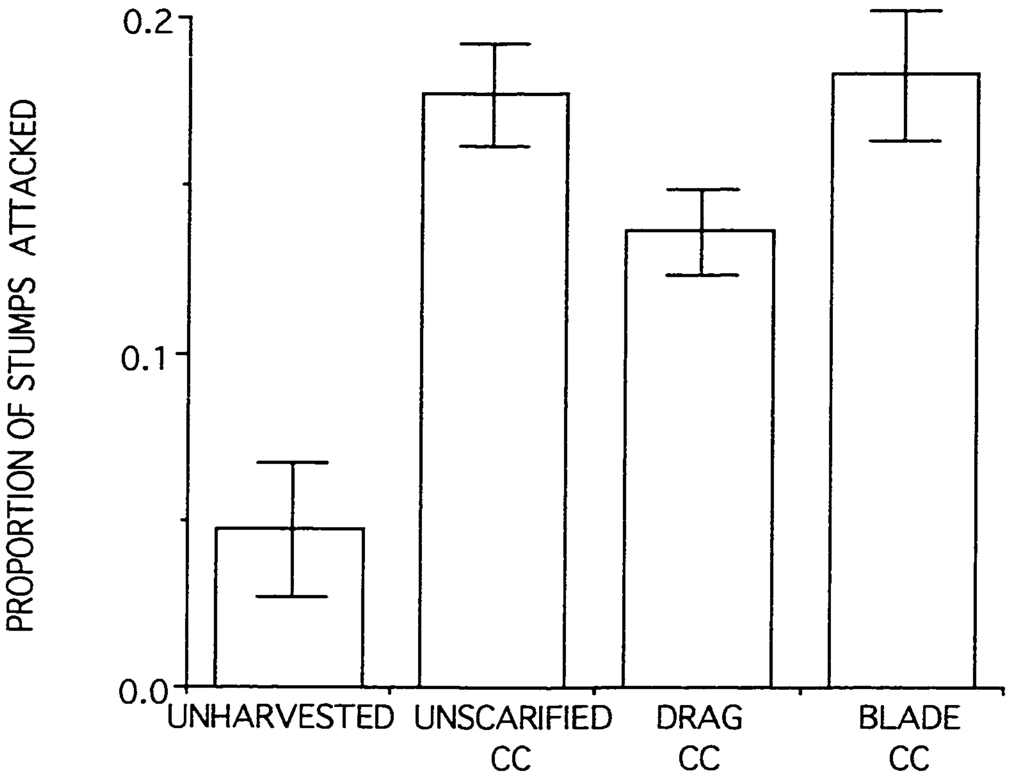

Figure 3-3. Proportion of stumps attacked by bears in unharvested reference areas and unscarified, drag scarified and blade scarified clearcuts. Sample sizes as presented in Fig. 3-2. There are no significant differences between categories (G=0.181, df=3, p=0.98).

DISCUSSION

As expected, all clearcuts had significantly more stumps than unharvested sites and, therefore, the availability of potential nest sites for cavity dwelling ants was higher.

Total number of stumps did not differ significantly among clearcuts with different site histories. My initial hypothesis was that scarified cutting units would have fewer stumps due to mechanical breakdown during the scarification process. I also felt that the heavily disturbed blade scarified sites would have fewer stumps than drag scarified sites. Although the general trend of the results supports these hypotheses, none of the differences were statistically significant.

My initial objective was to determine whether these potential nest sites were being colonized by ants. Stumps showing no sign of previous colonization were extremely rare in all sites regardless of the site's history. Given that clearcuts have significantly more stumps than unharvested sites, they also have significantly more ant colonies. This is consistent with results indicating that unforested areas support more ants than do forested areas (Welch 1978; Ewuim et al. 1997). Kidd (1994) reported that ants preferred regenerating habitats (5, 10, 15 year old stands) over new clearcuts and closed canopy forests. Sanders (1970) counted a higher number of total ants and colonies of *Camponotus herculeanus* in immature stands than in intermediate aged or overmature stands.

According to Holldobbler and Wilson (1990), ants are thermophilic and therefore are relatively abundant and diverse in hot and dry habitats. Decaying stumps and logs found in clearcuts have thermoregulatory properties; a rise in substrate temperature can result from only a small amount of solar energy (Holldobbler and Wilson 1990). Therefore, ant species nesting in wood are less vulnerable to low humidity and high temperatures than those species that nest exclusively in soil (Holldobbler and Wilson 1990). Clearcuts have more decomposing organic matter than the forest floor and invertebrates involved in the decomposition of this organic matter provide an abundant food source for predatory ants (Punttila et al. 1991).

The fact that clearcuts with different treatments did not differ in the number of uncolonized stumps would suggest that scarification neither encourages nor discourages ants from colonizing stumps. Alternatively, any effect of the treatment may have been obscured by habitat saturation (i.e., all available nest sites are taken in all types of clearcuts).

Once I had evidence that ants were indeed colonizing the stumps within clearcuts, my next objective was to determine if bears were using those ant colonies as a food source. Hatler (1972) suggested that a concentration of ants was necessary for their use as food by bears. He felt that the colonial nature of ants provided the necessary concentration of ants (within a single nest) required for bear predation. I predicted that if bears attacked single ant nests because of the concentration of individuals, they should feed in sites where there are concentrations of nests each containing a concentration of individuals.

My data support the hypothesis that bears use the concentration of ant nests in clearcuts as a food source. If bears were not using ants as a food source, there would be no bear attacks in any sites (clearcut or unharvested) regardless of the number of ant nests present. Bears attacked significantly more stumps in clearcuts (where nests were concentrated) than unharvested reference areas (where nests were few in number). Clearcuts with different treatments did not differ significantly in the number of stumps attacked.

If bears were attracted to clearcuts to forage on ants, one would expect a higher proportion of attacks than in unharvested sites. However, there was no difference in the proportion of stumps attacked (Figure 3-3) between any of the four treatments. Nevertheless, the proportion attacked in unharvested sites was less than half the proportion attacked in the clearcuts. Unharvested sites also had a very low number of stumps to be attacked and if this sample size could be increased significant differences may occur. The fact that there was no difference in proportion attacked between any of the three types of clearcuts suggests that bears are equally willing to prey on ants across all clearcuts regardless of any effects different site histories may have on the ecology of the clearcuts (e.g. differing berry production).

In summary, clearcut logging provides wood nesting ants with an abundance of potential nesting habitat. The colonization of stumps by ants in turn provides a concentration of ant nests which bears use as a food source. Although different types of post-logging site treatments may slightly influence the total number of ant colonies at a site, bears expend a consistent effort in preying on ants in clearcuts regardless of post-logging treatment.

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IV. Bear myrmecophagy 2: Selective predation on ant species.

Preliminary research (Knight 1993) suggested that bears in the study area selectively forage on particular ant species. Noyce et al. (1997) reported that black bears in north-central Minnesota showed strong selection for some ant species and strong avoidance of others. Onoyama (1988) found that the yezo brown bear (*Ursus arctos yeoensis*) showed preferences for some ant species.

Other mammals that feed on social insects also select for certain species. Giant anteaters (*Myrmecophaga tridactyla*) show marked preferences for certain species of ants and termites both in captivity and in the wild (Redford 1985); *Camponotus* spp. accounted for 71% of foraging time by giant anteaters in that study. The anteater *Cyclopes* eats only ants, selecting against termites, and also exhibits preferences for certain ant species over others (Montgomery 1985). Burrowing mice exhibited preferences among species of termite prey (Redford 1984). In contrast, aardvarks (*Orycteropus afer*) eat the most available species so their diets reflect the relative abundance of ants and termites (Willis et al. 1992).

The purpose of this research was to determine whether bears were foraging selectively on certain ant species, and, if so, which species were preferred. Some factors that may have been responsible for a preference were also investigated. It is important to remember that, unlike other studies involving the predation of ants by bears (Onoyama 1988; Noyce et al. 1997), there are two species of bears (grizzly and black bears) foraging on ants in this study area. It was impossible to determine which species of bear had attacked a specific ant nest. Ants made up only 3-5% volume of grizzly bear scats from the study area during periods of peak predation on ants (McLellan and Hovey 1995). Ants make up a more significant portion of the summer diet of black bears in the study area (F. Hovey pers. comm.).

Because approximately 75% of the bears in the study area are black bears, I assume this species accounts for the majority of attacks on nests.

MATERIALS AND METHODS

In 1994, ants were collected from all bear attacked stumps in randomly located plots (see Chapter 3 methods) regardless of the length of time since attack. Ants were identified to species using keys (Creighton 1950, Wheeler and Wheeler 1963, Wheeler and Wheeler 1986, Hansen and Akre 1985, and Holldobler and Wilson 1990).

Sampling methods were changed for 1995 because I felt that an ant colony could move out of a nest and be supplanted by another species in the time period between the attack and sampling. For example, Smallwood (1982) reported that colony movement is a common phenomenon occurring in ant species across a diversity of taxonomic groups and a wide range of habitats. Furthermore, Smallwood and Culver (1979) stated that colony movement does not require a trigger such as drastic environmental stress or serious nest disturbance. In their study, 61% of all observed colonies (including *Tapinoma sessile*, *Lasius* sp., *Myrmica* sp., *Camponotus* sp., *Formica* sp., and *Leptothorax* sp.,) moved within 21 days. Nest disturbance can act as an emigration trigger for some ants. Leaf cutting ants have been observed emigrating following nest disturbance (Fowler 1981). Even slight nest disturbances "i.e. turning over of stones by erosion or larger animals" (Moglich 1978:210) will trigger nest emigration in *Leptothorax* spp.

In the summer of 1995, 10 clearcuts were searched for recent attacks by bears on ant colonies. This involved systematically walking through the entire clearcut to ensure that all recent attacks were found. A recent attack was defined as one that had occurred no more than two weeks previously, as determined by a lack of bleaching of the broken off pieces of wood and by the presence of fresh "sawdust". In some cases this approach was so successful that ants were taken from nests where ants were still alarmed and very active around the nest. As this was the same behaviour I noticed when I broke nests open, I took it as evidence of a very recent bear attack.

Unlike 1994, sampling of nests was not restricted to stumps. Other possible nest sites, such as wood debris, were included. Dirt mound nests were also included in the rare instances in which they were found. A total of 1841 potential nest sites were examined. These included 769 stumps, 1065 wood debris/logs, 4 larch tree bark, and 4 dirt mounds. Of these 1841 potential nest sites, 416 (195 stumps, 220 wood debris/logs, 1 dirt mound) had been recently attacked.

When a recent attack was found, the nest was broken open to determine the species of ant inside. I then recorded whether the five closest potential nest sites were unattacked or recently attacked (old attacks were lumped with unattacked). These five potential nest sites were then broken open and the type of ant (if any) was determined. If there were no ants present, the potential nest site was recorded as "no ants". If one of the adjacent colonies was also recently attacked, it was recorded as attacked and the five potential nest sites closest to it were then broken open and ants removed from each. In all cases, however, only the five closest potential nest sites were examined for each attack and these five were coded as attacked or unattacked. If an unattacked potential nest site was one of the five closest sites to two attacked nests, the unattacked site was only counted once. Therefore, every potential nest site, attacked or unattacked, was only counted once. Attacks were located in close proximity to one another (one of the five closest) 118 times out of the 416 attacks. Familiar ant species were identified by sight in the field. Other species were collected and later identified as described above.

Total length of adult and pupal ants were measured for each species. Two ants were measured from each of twenty different colonies for each species (n=40 per species). Similar sampling was attempted for pupae but for some species I was unable to find twenty colonies with pupae. In these cases, pupae were measured from as many colonies as possible and sometimes more than two per colony were measured. Queens were not included when measuring ant length.

Additional measurements made during the 1995 sampling included the diameter (cm) of the stumps, hardness of stumps and wood debris (subjectively recorded using a five point scale), distance (m) to the edge of the cut and distance (m) to cover for the 416 attacked colonies.

Distance to cover was defined as the shortest distance a bear would have to travel to no longer be visible from the nest. This was measured by having one person remain at the attack while a second person walked towards the nearest cover until no longer visible. Both distance to cover and distance to clearcut edge were measured because distance to cover was rarely the same as distance to the clearcut edge. In some cases, distance to cover was less than the distance to edge, in other cases it was greater.

Data on ant species in nests, bear attacks on ant species, and nest hardness were each analyzed using log-linear models (Zar 1984). When the test for independence was significant, pairwise differences were tested. The effect of stump diameter on number of attacks and ant species in the nest was analyzed using a two factor ANOVA (Zar 1984). Differences in bear attack rates at increasing distance from clearcut edge and increasing distance from cover were evaluated using log linear models. For distance to clearcut edge, the number of attacks per unit area (ha) was used for statistical analysis. The area within each distance category was calculated using B.C. Ministry of Forests GIS maps (F. Hovey, pers. comm.) Due to the nature of the calculation, the first distance category is 10m wide (0-9m) and the remaining categories are 20m wide (F. Hovey pers. comm.) This did not affect data analysis, however, because number of attacks per unit area was tested rather than attacks per distance category.

Distribution of ant species as distance from clearcut edge increased was also tested using a log linear model with four distance categories.

RESULTS

The species of ant in a nest was a significant factor in determining whether or not the nest was attacked. Table 4-1 illustrates the ant species present in attacked and unattacked nests in 1994 (G=74.40, df=7, $p<0.001$) and Table 4-2 illustrates data for 1995 (G=648.84, df=8, $p<0.001$). Data from both years indicate that bears did not attack nests randomly. Data from both tables divided statistically into four homogeneous groups ranging from those species that were rarely, if ever, attacked to those for which approximately forty to fifty percent of nests were attacked. The sampling method used in 1995 produced markedly less overlap between homogeneous groups than in 1994. Data from 1995 produced a more marked demarcation between ant species that were attacked and those that were avoided and a higher proportion of attacks for targeted species. The only major difference in rank between the two years is that *Lasius sitkaensis* was attacked at a greater rate in the 1994 data than in the 1995 data. Two ant *species (Camponotus herculeanus* and *Formica subnitens/planipilis*) were attacked often, three species *(Formica neorufibarbis*, *Formica fusca/altipens*, and *L. sitkaensis*) were attacked at moderate rates, while three species (*Myrmica incompleta*[*], *Tapinoma sessile*, and *Leptothorax muscorum*) were avoided. The "no ants" category included in 1995 indicated that potential nest sites without ants were rarely attacked by bears (only 3 of 622 or 0.5% attacked).

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[*] M. incompleta = M. brevinodis (Wheeler and Wheeler 1986)

Table 4-1. Number and percentage of stumps occupied by each ant species that were attacked by bears in 1994. Letters indicate homogeneous groups for proportion of stumps attacked based on a G-test for heterogeneity followed by the Simultaneous Test Procedure (α of 0.05 for both tests).

Species	Total Stumps	# Attacked	% Attacked	Homogeneous Groups
T. sessile	46	0	0	a
L. muscorum	36	2	5.6	a,b
M. incompleta	161	14	8.7	a,b
F. neorufibarbis	99	15	15.1	b,c
F. fusca/altipens	48	9	18.1	b,c
C. herculeanus	91	22	24.2	c,d
L. sitkaensis	114	41	36.0	d
F. subnitens/planipilis	78	30	38.5	d

Table 4-2. Number and percentage of nests occupied by each ant species that were attacked by bears in 1995. Letters indicate homogeneous groups for proportion of nests attacked based on a G-test for heterogeneity followed by the Simultaneous Test Procedure (α of 0.05 for both tests). Relative abundance rankings (1=most common) are based on 1994 data (Table 4-1) which was randomly sampled.

Relative Abundance	Species	Total Nests	# Attacked	% Attacked	Homogeneous Groups
8	*L. muscorum*	37	0	0	a
7	*T. sessile*	21	0	0	a
	No. ants	622	3	0.5	a
1	*M. incompleta*	250	11	4.4	b
2	*L. sitkaensis*	138	32	23.2	c
6	*F. fusca/altipens*	61	17	28.3	c,d
3	*F. neorufibarbis*	121	46	38.0	d
5	*F. subnitens/planipilis*	407	209	51.4	e
4	*C. herculeanus*	182	98	53.8	e

The species of ant occupying nests varied greatly in size (Table 4-3). There was a strong positive correlation between the size of an ant species and the propensity of that species to be attacked by bears (Figure 4-1a). Similarly, species with large pupae were attacked more often (Figure 4-1b). As expected, an extremely high correlation ($y=0.297 + 0.807x$, $r^2=0.97$) existed between ant size and pupa size for any given species.

The two factor (attack, ant species) ANOVA used to determine any effect of stump diameter revealed that, although attacked stumps tended to be larger (Figure 4-2a), the difference was not significant ($F=2.296$, $df=1{,}748$ $p=0.13$). The ant species factor was significant ($F=2.302$, $df=8{,}748$ $p=0.02$) so Fisher's LSD multiple comparison test (Dowdy and Wearden 1991) was done on all species combinations. Stumps of *L. muscorum* were significantly smaller than those of all other ants except *T. sessile* (Figure 4-2b). *C. herculeanus* and *F. subnitens/planipilis* stumps were significantly larger than those of *M. incompleta* and the no ants category. *F. subnitens/planipilis* stumps were also significantly greater than those of *L. sitkaensis* (p value for *C. herculeanus* vs. *L. sitkaensis* = 0.055). No other significant differences occurred. The ant species by bear attack interaction was not significant ($F=1.174$, $df=6{,}748$ $p=0.32$). The ANOVA table is located in Appendix M.

Attack by wood hardness was significant ($G=87.99$, $df=4$, $p<0.001$). The number of bear attacks on differing hardness of wood statistically divided into four homogeneous groups (Table 4-4). The majority of attacks occurred on wood of intermediate hardness and no attacks occurred on the hardest category of wood.

Ant species by hardness (Table 4-5) was also significant ($G=58.77$, $df=21$, $p=0.002$). The question being addressed by this analysis was what hardness of wood different ant species nested in. Ants rarely nested in hardness category 1 so it was left out of the analysis. [Of the 1841 potential

Table 4-3. Mean size of ants and pupae in mm (with standard error and n values) for the eight species of ants collected.

Species	Ant Size (mm)	S.E.	n	Pupa Size(mm)	S.E.	n
L. muscorum	3.84	0.07	40	3.47	0.10	6
T. sessile	3.35	0.07	40	2.78	0.14	40
M. incompleta	6.14	0.11	40	5.34	0.15	40
L. sitkaensis	5.37	0.09	40	4.79	0.11	40
F. fusca/altipens	7.83	0.13	40	5.85	0.08	22
F. neorufibarbis	7.61	0.11	40	6.82	0.25	40
F. subnitens/planipilis	8.83	0.19	40	7.81	0.28	23
C. herculeanus	11.52	0.32	40	9.47	0.27	40

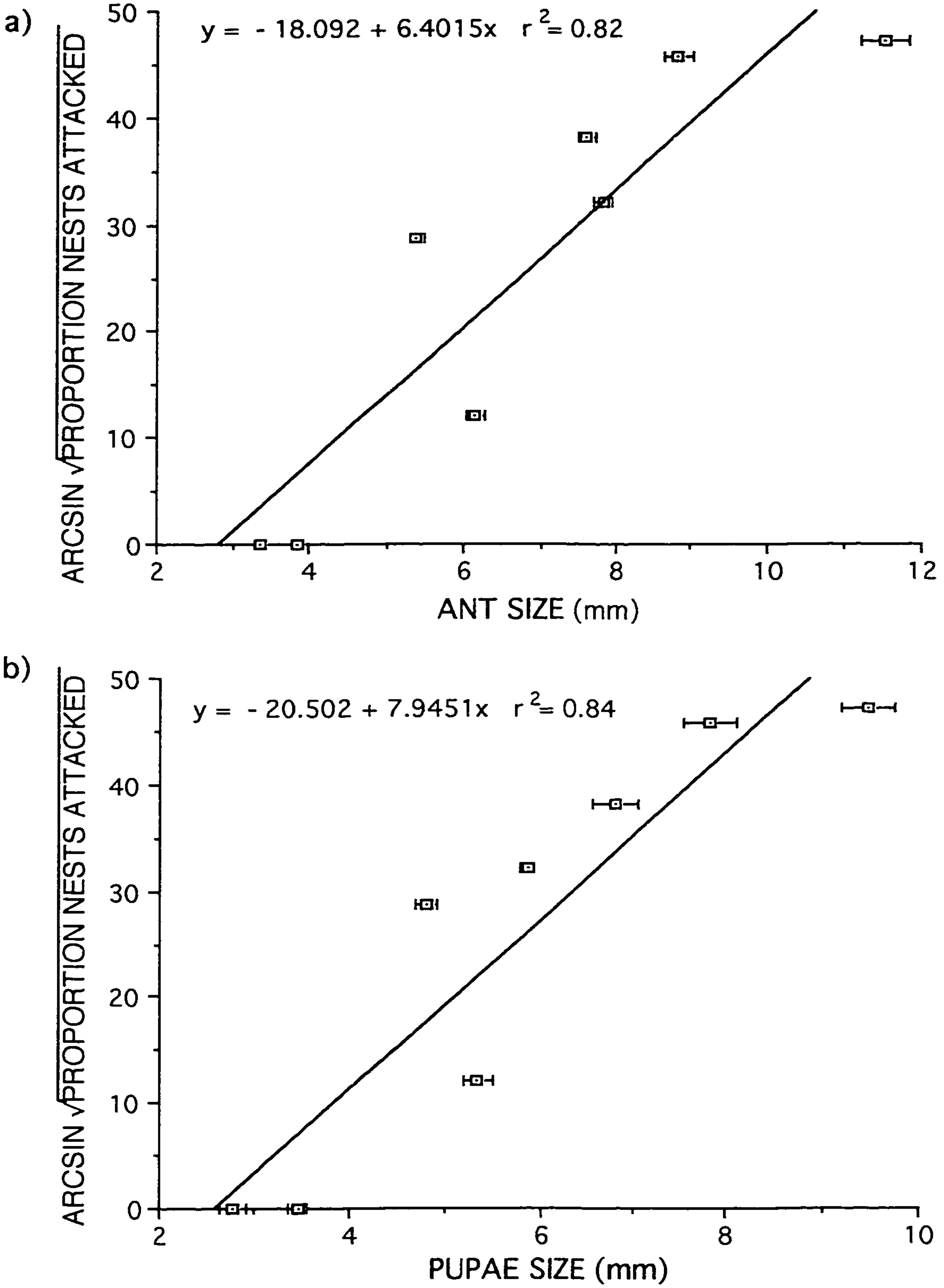

Figure 4-1. Relationship between proportion of nests attacked and (a) ant size and (b) pupae size.

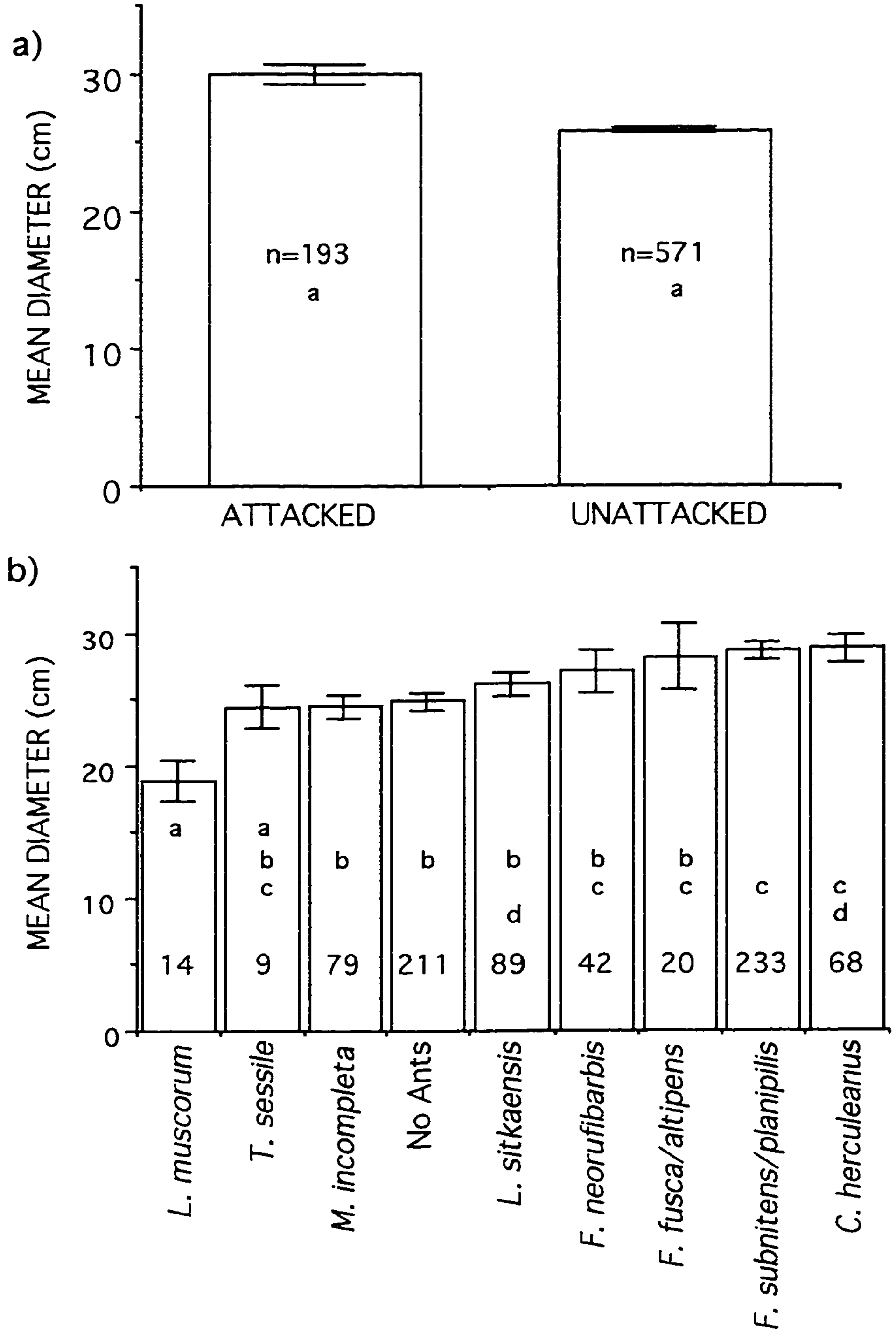

Figure 4-2. Mean diameter (±SE)of (a) attacked and unattacked stumps and (b) stumps in which different ant species were nesting. Letters indicate homogeneous groups.

Table 4-4. Number and percentage of potential nests (including "no ants") attacked by bears in different wood hardness categories. Hardness categories range from 1 (hardest) to 5 (softest). Letters indicate homogeneous groups for proportion of nests attacked based on a G-test for heterogeneity followed by the Simultaneous Test Procedure ($\alpha = 0.05$).

Hardness	Potential Nests	# Attacked	% Attacked	Homogeneous Groups
1	86	0	0	a
5	77	5	0.069	b
2	172	21	0.12	b
4	576	131	0.23	c
3	695	204	0.29	d

Table 4-5. Hardness of wood occupied by various ant species in this study. Numbers of nests per hardness category for each species is followed by % of nests for that species in parentheses. Hardness 1 was omitted because it was virtually uninhabited by ants. Letters indicate homogeneous groups based on G-test for heterogeneity followed by the Simultaneous Test Procedure ($\alpha = 0.05$).

	Hardness								
	2	%	3	%	4	%	5	%	Group
C. herculeanus	15	(10)	86	(58)	47	(32)	0	(0)	a
F. subnitens/planipilis	26	(8)	178	(53)	127	(37)	7	(2)	a,b
L. muscorum	1	(3)	17	(57)	12	(40)	0	(0)	a,b,c
T. sessile	1	(6)	11	(61)	4	(22)	2	(11)	b,c
F. neorufibarbis	4	(4)	48	(49)	43	(44)	3	(3)	b,c
L. sitkaensis	8	(5)	66	(49)	51	(38)	10	(7)	b,c
M. incompleta	18	(8)	81	(37)	100	(46)	17	(8)	c
F. fusca/altipens	1	(2)	21	(39)	29	(54)	3	(5)	c

nest sites investigated, only 86 (4.7%) were of hardness category 1 and of these, only 7 (0.4% of total, 0.6% of occupied) contained ants.] Although ant species divided statistically into 3 homogeneous groups based on the hardness of wood they nested in, there was considerable overlap in nest hardness between groups.

Table 4-6 illustrates the number of bear attacks on ant nests per unit area (ha) as distance from the edge of the cut increased. The overall test for independence was significant ($G=159.21$, $df=5$, $p<0.0001$) and the data divided into four homogeneous groups. The number and rate of bear attacks decreased as the distance from the edge of the cut increased. Of the 416 attacks, 70% were less than 30 m from the edge of the clearcut and 90% occurred within 50 m of the edge. More importantly, the number of attacks per unit area declined significantly at distances greater than 50 m from the edge. The results are similar when the relationship between the number of bear attacks on ant nests and the distance of the nest from cover is considered (Table 4-7). Once again, bear attacks decreased as distance to cover increased ($G=521.35$, $df=5$, $p<0.0001$). Although the data divided into four homogeneous groups, 89% of attacks occurred less than 20 m from cover.

A test of independence for the distribution of nests of the eight ant species in the four distance categories was significant ($G=48.79$, $df=21$, $p=0.002$). The data however, split into only two homogeneous groups (Table 4-8). The significance of the results can be attributed solely to one species, *C. herculeanus*. Removing *C. herculeanus* from the analysis resulted in a p-value of 0.08 ($G=31.26$, $df=18$).

Table 4-6. Number of attacks, area of distance category, and attacks per hectare at increasing distances from clearcut edge. Letters indicate homogeneous groups for attacks/ha based on a G-test for heterogeneity followed by the Simultaneous Test Procedure ($\alpha = 0.05$). Note that the first distance category is 10 m narrower than other distance categories.

Distance to edge (m)	Number of Attacks	Category area (ha)	Attacks per hectare	Homogeneous Groups
0-9	89	32	2.78	a,b
10-29	205	63	3.25	a
30-49	84	46	1.82	b
50-69	34	35	0.97	c
70-89	3	28	0.11	d
90+	1	48	0.02	d

Table 4-7. Number of attacks and proportion of total attacks at increasing distance from cover. Letters indicate homogeneous groups based on a G-test for heterogeneity followed by the Simultaneous Test Procedure (α for both 0.05).

Distance to cover (m)	Number of Attacks	% of Total Attacks	Homogeneous Groups
0-9	185	44.5	a
10-19	185	44.5	a
20-29	30	7.2	b
30-39	11	2.6	c
40-49	2	0.5	d
50-59	3	0.7	d

Table 4-8. Number and percentage of nests for each ant species in four categories of distance from clearcut edge. Letters indicate homogeneous groups of species based on a G-test for heterogeneity followed by the Simultaneous Test Procedure (α of 0.05).

	0-19 m # of nests	%	20-39 m # of nests	%	40-59 m # of nests	%	60+ m # of nests	%	Homogeneous groups
C. herculeanus	65	(36)	77	(42)	26	(14)	14	(7)	a
F. neorufibarbis	48	(40)	53	(44)	15	(12)	5	(4)	b
L. muscorum	18	(49)	15	(41)	3	(8)	1	(3)	b
T. sessile	10	(48)	11	(52)	0	(0)	0	(0)	b
L. sitkaensis	68	(49)	49	(35)	14	(10)	7	(5)	b
F. fusca/altipens	32	(52)	25	(41)	4	(7)	0	(0)	b
M. incompleta	126	(50)	78	(31)	38	(15)	8	(3)	b
F. subnitens/planipilis	197	(48)	153	(38)	53	(13)	4	(1)	b

DISCUSSION

Results from both 1994 and 1995 provided statistically significant evidence that bears selectively attack certain ant species. Given the different sampling methods and possibility of ant nest movement, results were markedly similar in 1994 and 1995. The overall ranking is similar in both years and the only major discrepancy (*L. sitkaensis*) could result from nest emigration/immigration. The data from 1995 with a larger sample size and emphasis on recent attacks produced less overlap between homogeneous groups. Because the sampling method in 1995 was more indicative of the species attacked than the method used in 1994, inferences will be drawn from the 1995 results.

If bears were randomly attacking nests in clearcuts, (i.e. bears had no preference for one species of ant over the other) it would be expected that ant species would be attacked in proportion to their abundance in the clearcuts. This did not occur. *C. herculeanus* and *F. subnitens/planipilis* were attacked most often. Although approximately 50% of nests containing these ants showed evidence of being attacked, these species ranked only fourth and fifth (out of 8 species) in relative abundance (Table 4-1). Nests containing *M. incompleta* ranked first in relative abundance yet only a small proportion (4%) of these were attacked by bears. Other ant species were also attacked disproportionately to their relative abundance; none of the nests containing *L. muscorum* or *T. sessile* had been attacked. The greatest evidence that bears were not randomly attacking potential nest sites was the fact that only 3 of 622 potential nest sites that did not contain ants showed evidence of bear attack. These data provide strong evidence that bears are aware of both whether or not a potential nest site is occupied by ants and, if it is occupied, which ant species is present.

In other studies, bears have been reported to prey on the ant species I found to suffer the greatest attack rates. Graber and White (1983), Maehr and Brady (1984) and Irwin and Hammond (1985) all reported black bears feeding on *Camponotus* sp. Almack (1986) observed grizzly bears feeding on *Camponotus* sp. in Idaho, and *C. herculeanus* and *F. neorufibarbis* were identified in scats from grizzly bears in Banff National Park (Hamer and Herrero 1987). During a drought year in Yellowstone National Park, grizzly bears consumed large volumes of ants (Mattson et al. 1991); the majority of those ants belonged to the genera *Camponotus* and *Formica* with the most common species being *C. pennsylvanicus modoc* and *F. neorufibarbis.* Onoyama (1988) found ants to be the most common animal food for Yezo brown bears and they were consumed throughout the bears' active season. Yezo brown bears showed a preference for ants from subfamily Formicinae. Specifically, ants from the genus *Camponotus* ranked number 2 in number of individuals present in scats and stomachs. In general, species of the genus *Camponotus* are the most common ants in the world and are the most frequently preyed upon of all ant species by mammalian predators (Redford 1987).

Noyce et al. (1997) reported that black bears in Minnesota exhibited strong selection for *Lasius umbratus* and *Acanthomyops* spp. In my study area, only two potential nest sites of 1841 contained a species of *Acanthomyops* and neither of these nests was attacked. *L. umbratus* does not occur in my study area (Wilson 1955). Bears from the Minnesota study avoided *Lasius alienus, Formica fusca*, and *Myrmica* spp. The only species of *Myrmica* that I found nesting in wood was also avoided by bears. *F. fusca* ranked fourth in proportion of nests attacked in my study and was attacked in greater proportion than its abundance. The only species of *Lasius* in my study appeared to suffer a high proportion of attacks in the 1994 data but when only fresh attacks were examined a much smaller proportion of nests were attacked.

I examined four factors which Onoyama (1988) suggested to be possible explanations of bears' preference for certain ant species: 1) relative abundance, 2) habitats and nest sites easy to find and handle, 3) soft integuments, and 4) larger size. Two additional factors, size of stumps and hardness of wood, were also considered as possible factors in explaining the non-random nature of bear attacks on ants in this study. Those two factors focused on the possibility that bears were keying in on characteristics of the nest material rather than the ants within the nest.

The first explanation put forth by Onoyama was relative abundance. Hatler (1972:25) also considered this important stating that, for black bears, "simple food availability is one of the most important factors governing food habits." Nonetheless, relative abundance does not provide an adequate explanation for the preferences exhibited by bears in this study. Because plot placement in 1994 was determined randomly, the data should reflect the relative abundance of various ant species. When compared to the number attacked in 1995, it is evident that the ant species attacked the most were not those ant species that were in greatest numbers. *C. herculeanus* and *F. subnitens/planipilis* were attacked the most but rank fourth and fifth, respectively, in relative abundance. *M. incompleta* was the most abundant ant but ranked very low in proportion attacked. *L. sitkaensis* was also attacked disproportionately less than its relative abundance. It was the second most abundant ant but ranked fifth in proportion attacked. Relative abundance was, therefore, not the main factor determining attack rate at the sites investigated.

The second explanation, regarding ease with which ants are found and handled, is not an adequate explanation for bear preference for certain ant species in this study area. Nests are easily found; clearcuts are scattered throughout the study area and each contains numerous ant colonies. Since practically all ant nests investigated were in stumps and wood debris, ease of handling and handling time should be similar for all species. One factor possibly related to handling time, hardness of wood, will be discussed later.

According to Onoyama (1988), because formicine ants have softer integuments than other subfamilies they are more easily digested and are, therefore, selected for by Yezo brown bears. There is some evidence for integument hardness being a factor in dietary preferences of other animals. Small dasyurids studied by Fisher and Dickman (1993) avoided beetles with hard cuticles, presumably because they did not have the jaw muscle strength that larger dasyurids possessed and which was necessary to crack beetle cuticles. I do not have data to support or refute the hypothesis that integument hardness is a factor in bears selecting or avoiding ant species. If, however, bears are feeding primarily on pupae rather than adult ants, the hardness of the ant integument is not a relevant consideration for digestibility.

Data from this study indicate that the size of the ants influences attack rates, with bears preferentially attacking large ants and ignoring smaller ones. A problem with this hypothesis is the suggestion that bears are not feeding on adult ants but rather on the pupae. Ant species that are being selectively attacked by bears, however, have both the largest ant size and the largest pupae. Preferentially attacking ants/pupae of larger size would allow bears to obtain the greatest amount of biomass for the energy expended in breaking open the nest. Echidnas also select ant and termite species on the basis of size (Abensperg-Traun et al. 1991). They, however, select for smaller ants due to the difficulty in subduing larger ants (≈15mm) and a narrow gape which hinders ingestion of larger prey. In that study, >80% of ants in echidna diets were 2-4mm long while those ≥7mm were avoided.

One factor I did not consider when measuring ant size was polymorphism. However, I do not believe this to be of major importance when considering the results. Only one ant species (*C. herculeanus*) of the eight identified exhibits polymorphism (Holldobler and Wilson 1990). The higher standard error associated with the lengths of *C. herculeanus* (Table 4-3) is probably a result of this polymorphism. When collecting *C. herculeanus*, it was difficult to capture a large number of individuals from each colony due to the rapid flight response of this species. Therefore, my measurements reflect the individuals I was able to obtain. I assume that bears would also take whatever individuals were available to them and not select larger individual ants over smaller individuals. It should also be noted that even the smallest *C. herculeanus* individuals are still larger in size than individuals from the ant species that were not attacked (Wheeler and Wheeler 1963).

The other two factors considered, size of stumps and hardness of wood, did not explain bear preference for certain ant species. Diameter of attacked stumps was roughly 4.5 cm larger than unattacked stumps although this difference was not statistically significant (Figure 4-2a). There were some statistical differences in the diameters of stumps that different ant species nested in (Figure 4-2b). Stumps containing *L. muscorum*, one of the two smallest ants, were significantly smaller than stumps occupied by all other ant species except *T. sessile* (the other smallest ant). Stumps of the two largest ants, *C. herculeanus* and *F. subnitens/planipilis* were also larger than stumps occupied by *M. incompleta, L. sitkaensis* and the "no ants" category. Stump size alone, however, cannot explain all differences in attack rate observed (i.e. *F. neorufibarbis* and *L. sitkaensis* nested in the same size stumps but differed significantly in attack rate.

One component of stump size that should be considered is the possible relationship between stump size and colony size. Considering Hatler's (1972) hypothesis that an aggregation of insects is required for bears to prey on them, a large colony would be expected to be attacked sooner and more often than a smaller one. Size differences amongst colonies can be quite dramatic; Sanders (1970) counted 13,376 individuals and 10,280 larvae in a single colony of *C. herculeanus* compared to minor colonies of the same species which he classified as those having less than 2000 individuals. Noyce et al. (1997) observed that bears fed longer at large colonies than small ones. I have no measure of colony size other than the magnitude of the wood being nested in. I did notice, however, that the largest colonies I encountered were located in the largest stumps and the ants present were invariably *F. subnitens/planipilis* or *C. herculeanus*. These observations coupled with the data indicating that those two species inhabit stumps significantly larger than some of the other ant species and are attacked at a significantly higher rate than other species suggests that colony size as well as individual ant size may be a factor influencing nest attack by bears.

Hardness of wood was a significant factor in the statistical analysis but does not appear to be an adequate explanation for why bears preferentially forage on certain ants. The effect of hardness on attack was significant; some categories of wood hardness were more likely to be attacked than others (Table 4-4). Unoccupied wood (hardness category 1, containing only 0.6% of ant colonies) is not attacked by bears providing evidence that the significant differences in bear attacks on other hardness categories are more likely a reflection of the presence of ants inside rather than hardness of the wood. Further evidence of this is that the two species attacked the most (*C. herculeanus* and *F. subnitens/planipilis*) and the species attacked the least (*L. muscorum*) nest in the same hardness of wood (Table 4-5). Furthermore, *T. sessile* had the greatest proportion of nests almost exclusively in the hardness group attacked most but was never (Table 4-1, Table 4-2) attacked.

Another factor to consider when discussing predation on ants is the defense mounted by the ant colony. In general, ants have three aggressive defense mechanisms: biting, stinging, and/or chemical secretions (Lubin 1983). Some colonies exhibit a swarming antipredator strategy in which large numbers of ants are recruited to the site of the disturbance. Others exhibit a flight response, carrying their brood deeper into the nest. The type of mound or nest is also important in defense. Some nests are too difficult to penetrate for some anteaters (Redford 1985). For some mammals, ant colony defense is the most important factor in determining which species are attacked. Preferences of burrowing mice (*Orymycterus roberti*) for certain termite species are based on termite defense and not size or nutritional quality (Redford 1984). Echidnas will tolerate chemical and mechanical attacks longer if high energy eggs are available than if they are not (Abensperg-Traun et al. 1991).

Noyce et al. (1997) felt that colony defense had some importance to selective foraging on ants by black bears in Minnesota. The two species that bears strongly selected for in that study mounted a passive defense and were slow to evacuate brood. In my study, the two ant species that suffered the highest proportion of attacks had contrasting defense mechanisms suggesting that ant defense was not a significant factor in bear predation. *C. herculeanus* collected brood and rapidly disappeared farther into the nest. This same type of defense by *Camponotus* spp. was observed by Lubin (1983) and Noyce et al. (1997). Lubin (1983) noted that *Camponotus* ants secrete formic acid and have strong jaws capable of piercing human skin. However, I did not notice the smell of formic acid and was rarely bitten by *C. herculeanus* ants while smashing open nests and collecting. By contrast, the red wood ants *F. subnitens/planipilis* mounted a very aggressive swarming attack in which thousands of ants rapidly appeared, often entirely covering the wood in which they were nesting. Concurrently, workers collected the brood and carried them deeper into the nest. There were so many ants moving that there was often an audible hum coming from the nest. The smell of formic acid was very strong and being bitten while collecting these ants was common. Redford (1987) felt that, regardless of whether an aggressive defense was mechanical (biting) or chemical, it would be relatively ineffective in preventing mammalian predation. He suggested it could, however, decrease the length of time spent feeding. Echidnas (Abensperg-Traun 1991) and banded tamanduas (Lubin 1983) are capable of assessing soldier:worker ratios and discontinue feeding or will not attack when soldier ratios are high.

Noyce et al. (1997) observed that bears stopped feeding long before consuming all the ants in a nest. They felt that bears' tendency to feed for short periods at a large number of nests maximized nutritional returns at each nest by ingestion of more ants per unit time and/or a higher ratio of brood to adults. Lubin (1983) also observed banded tamanduas moving from nest to nest feeding for a short time at each. This type of feeding behavior would be compatible with the defenses mounted by the preferred ant species in my study. A brief attack and feeding period would allow the bears to move on once the *C. herculeanus* and brood disappeared deeper into the nest and before *F. subnitens/planipilis* bites became too annoying.

Both Lubin (1983) and Noyce et al. (1997) felt that leaving the majority of the ants behind was also beneficial to the predator as it preserved the nest for future use. This might make sense for a strictly territorial species but partial consumption at a nest could also be the result of optimal foraging (Begon et al. 1996). As ants are consumed, the rate of energy intake gradually drops and at some point it will be more beneficial for a bear to move on to an unattacked nest. Eight of nine nests that Noyce et al. (1997) checked several days after disturbance by bears were still active. I noticed many stumps that showed evidence of having been attacked more than once. When rechecked one year later, of 100 stumps on which I had simulated a bear attack and foraging (ants and pupae removed), 65 had the same ant species in them, 12 had a different ant species, and 23 were unoccupied. In addition, 12 of the stumps had been attacked by bears since I had "attacked" them.

Bears attacked nests at greater numbers closer to the edge of clearcuts. As distance from the edge of the clearcut increased, the number of attacks per unit area decreased. The greatest attack rates and greatest number of attacks occurred within 50 m of the clearcut edge. Of the 416 attacks, 70% occurred within 30 m of the clearcut edge and 90% occurred within 50 m of the edge. Attack rates in these distance categories ranged from 1.82 attacks/ha to 3.25 attacks/ha and were significantly higher than attack rates at distances greater than 50 m. Attacks declined dramatically at 70 m from the clearcut edge; only 1% of the attacks occurred beyond 70 m from the edge and the attack rate dropped to 0.11 attacks/ha. Attacks were virtually nonexistent at distances of 90 m or more from the clearcut edge despite the fact that there were 48 ha of clearcut area in this distance category.

When distance to edge is replaced with distance to cover, the results are similar. 89% of all nests attacked were within 20 m of cover and 96% of all attacks were within 30 m of cover. Results produced four homogeneous groups in terms of number of attacks in different distance categories. In some cases, the distance to cover was less than the distance to edge, in other cases the distance to cover was actually farther than the distance to the edge of the clearcut.

The above results are consistent with previous literature suggesting that grizzly bears spend a disproportionate amount of time feeding close to forest cover (see Mattson 1997). As mentioned previously, the results from my study combine both grizzly bear and predominantly black bear nest attacks. This suggests that black bears in the study area forage primarily on ant nests that are within 50 m of the clearcut edge and 30m of cover. Behavior of this nature is an example of the tradeoff between foraging and the risk of predation (Cuthill and Houston, 1997). Especially for the black bears presumed to be responsible for most of the attacks on ants, forested areas provide trees which they use as escape routes. The farther they move from the forest edge the greater the risk of being killed by other bears or, to a lesser extent, hunters and poachers. Observations have been made, in the study area, of black bears killed in open habitat by grizzly bears (McLellan pers. comm.). Mattson et al. (1992) have also documented instances of adult grizzly bears preying on black bears and younger grizzly bears in Yellowstone. My data suggest that at about 50 m from the edge of the clearcut the returns from feeding on ants are not worth the risk of being killed.

One further factor must be considered. When bears feed closer to clearcut edges, preferences for certain ant species may simply be a reflection of a gradation in ant species as distance from clearcut edge increases. A log linear model was used to test this hypothesis, with nests of different species divided into four distance categories. The results indicate that decrease in bear attacks as distance increased was not the result of a gradation of ant species. The data divided into two homogeneous groups (Table 4-8) with the significance of the data attributed to only one species, *C. herculeanus.* This ant was one of the two species attacked the most yet it had the greatest proportion of nests at farther distances from clearcut edge. Although all *T. sessile* nests were located within 39 m of cover, none of them were attacked. These trends are the opposite of what would be expected with the hypothesis that a gradation of ant species is the cause of decreasing bear attacks as distance from the edge of the clearcut increases. If anything, these data provide further evidence of bears selectively attacking particular ant species.

Throughout this chapter, the assumption has been made that ants from attacked nests were consumed by bears. I had no way of ensuring this actually occurred. In previous diet studies from the area, ants were not identified when they occurred in scats (B. McLellan pers. comm.) Two statements can be made with certainty. First, ants which were not attacked were not consumed and were therefore, selectively avoided by bears. Secondly, bears selectively attacked nests of certain ant species. Ants were reported in scats in previous studies from this area (McLellan and Hovey

1995). Ants are being consumed, therefore, and these ants must belong to one of the species attacked. It is also important to remember, as previously mentioned, that the literature clearly states that the ant species attacked in this study area have been consistently reported to be consumed by both black and grizzly bears in a variety of other study areas (Graber and White 1983, Maehr and Brady 1984, Irwin and Hammond 1985, Hamer and Herrero 1987, Onoyama 1988, Mattson et al. 1991).

In summary, the fact that (i) ant species were attacked disproportionately to their relative abundance and (ii) uninhabited nests were not attacked provides strong evidence that bears do not randomly attack potential nests but preferentially attack certain ant species. Of the factors examined, size of ants/pupae provides the best explanation for this preference. Consistent with other studies, large ants of the genera *Camponotus* and *Formica rufa* group appeared to be preferred by bears while small sized ants from genera such as *Leptothorax*, *Tapinoma*, and *Myrmica* were ignored. For nests located in stumps, ants species attacked the most tended to nest in larger stumps. This result in and of itself is inadequate in explaining all differences in attack rates on different ant species. Larger sized colonies may also be susceptible to higher attack rates by bears.

Hardness of wood did not account for preferential attack rates. Ant defense does not appear to prevent bears in the study area from attacking nests but could limit the duration of feeding. The number and rate of bear attacks on ant nests declined as distance from the edge of the clearcut increase. 90% of all attacks occurred within 50 m of the clearcut edge and 96% occurred within 30 m of cover sufficient to hide a bear.

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V. General Discussion and Conclusions

Results from this study provide evidence that clearcut logging without post-logging site preparation resulted in a greater density of *Shepherdia canadensis* bushes than clearcut logging followed by mechanical scarification. An attempt to determine if there was a treatment effect on *S. canadensis* berry biomass was unsuccessful due largely to a poor berry crop the first year and a failure of the berry crop the second year. Weather patterns were markedly different the two years with the first being hot and dry and the second cool and rainy. Minore et al. (1979 in Martin 1983) reported that weather influenced huckleberry (*Vaccinium membranaceum*) crops more than any site characteristic and recommended that no conclusions on site production be based on 1 or 2 years of sampling. Martin (1983) concurred with this recommendation based on the yearly variation she noted in cover, height and percent cover of *V. globulare* during a two year study in northwestern Montana. Based on the results I obtained, it would appear that the same caution should be applied to sampling of *S. canadensis* berry biomass. It should also be noted that Pearson (1975) reported major variations in *S. canadensis* berry production between years during a six year study in Kluane Game Sanctuary in southwestern Yukon. In addition to multiple seasons, future attempts to quantify *S. canadensis* berry biomass should also include close attention to variables such as soil type (Vandehey 1991), canopy cover (Hamer 1996), time since disturbance (Vandehey 1991) and slope (Noble 1985; Hamer 1996; and this study) which all affect berry production.

All clearcuts sampled during this study had more ant colonies than unharvested sites. These ant colonies provided an aggregation of individuals which were used as a food source by bears. Of particular interest was the fact that bears selectively attacked nests of certain ant species and showed strong avoidance of other species. These preferences were not based on relative abundance. Large ant/pupae size, and perhaps large colony size, appeared to provide the best explanation for the ant preferences exhibited by bears in this study. Black bears in north-central Minnesota also show strong preference and avoidance of certain ant species (Noyce et al. 1997).

One area of interest for future research would be determining how bears are able to determine the species of ant located in a nest prior to attacking it. Noyce et al (1997) reported that bears appeared to first locate nests by visual cues such as logs or stumps and then used smell to determine where to break into the nest. The possibility that bears can discriminate between ant species of the same genus solely on the basis of smell is intriguing.

Combining current results with previous research on disturbance in the study area, clearcut logging generally resulted in an increase in summer food for bears. Post-logging site treatment had a significant negative effect on potential berry production in clearcuts in the study area. Clearcuts that received no post-logging treatment had more buffaloberry (*S. canadensis*) bushes (this study) and greater huckleberry (*V. globulare*) production and percent cover (Martin 1983) than unharvested areas. When logging was followed by scarification, however, buffaloberry bush densities did not exceed those in unharvested areas (this study) and production and percent cover of huckleberry plants was reduced (Martin 1983). Edge et al. (1990) found that *Hedysarum sulphurescens*, an important grizzly bear spring and autumn food source, was associated with some form of disturbance (fire, logging, or road cuts) in 94% of plots in the study area.

From a bear management perspective, therefore, clearcuts without post-logging treatment provide a better food source for bears than scarified clearcuts or unharvested areas. Factors other than simple food availability, however, are important in determining the extent to which bears will utilize clearcuts for food. The availability of cover is important as evidenced by the fact that 96% of all bear attacks on ant nests in this study occurred within 30 m of cover. The number and rate of attacks decreased as distance from clearcut edge increased. Attacks per hectare were significantly higher within 50 m of the clearcut edge than at distances beyond 50 m. Attacks were virtually nonexistent beyond 90 m from the clearcut edge. Lindzey and Meslow (1977) also reported that availability of cover and distance to edge affected black bears feeding in clearcuts in southwestern Washington. In addition, roads are an integral part of the timber harvesting industry. Road access must be controlled following logging if bears are to utilize clearcuts for food. McLellan and Shackleton (1988) found that grizzly bears in the study area used habitats within 100 m of roads less than expected regardless of food availability or traffic volume.

It is important to remember that habitat types other than clearcuts are important to bears. Black bears use timber as bedding sites (Unsworth et al. 1989) and riparian sites provide grizzly bears with a source of important spring forage (Servheen 1983; McLellan and Hovey 1995). Thus, as noted in chapter 1, properly managed clearcuts can be an integral component in the mosaic of habitat types which comprise optimal grizzly and black bear habitat.

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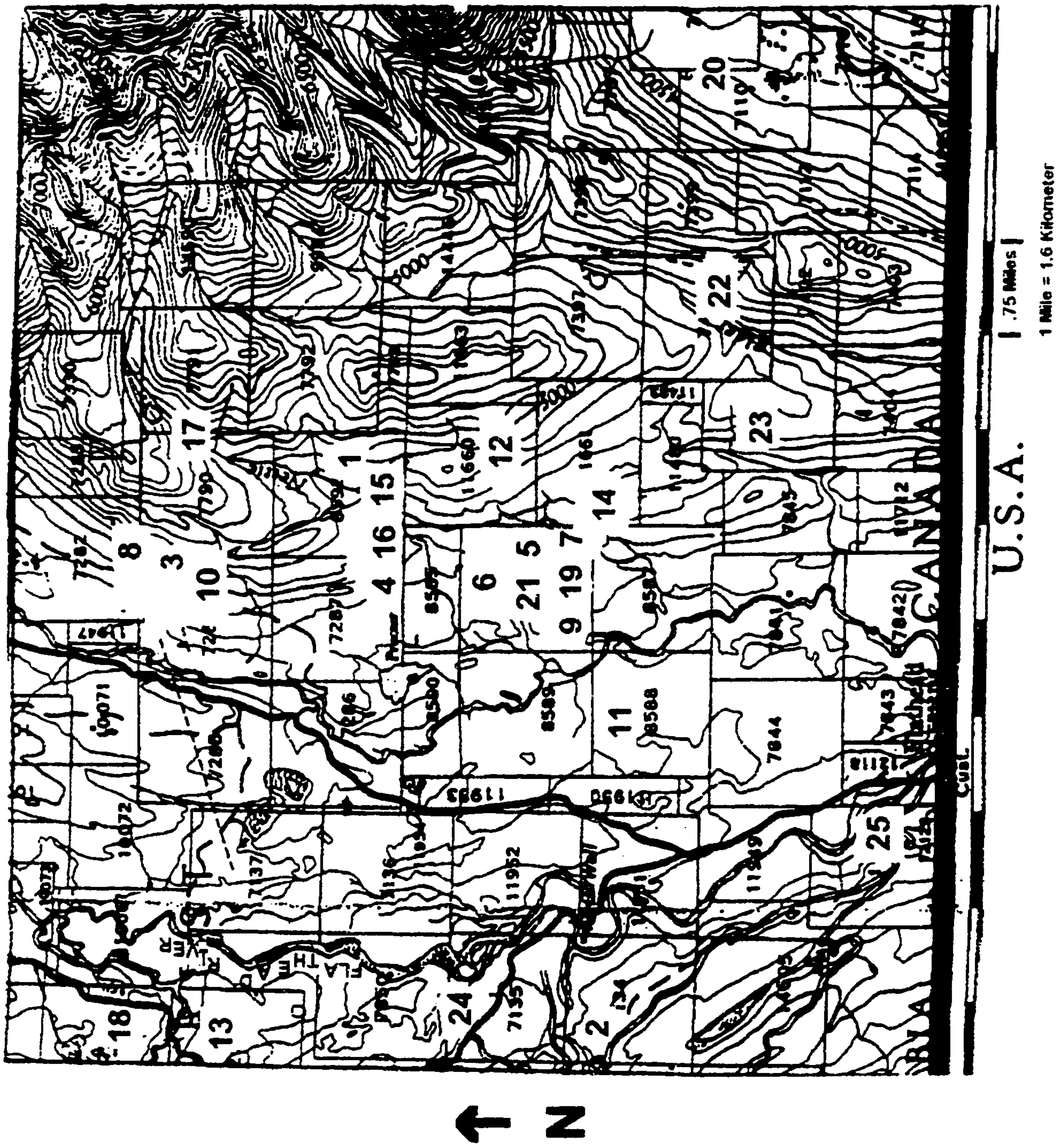
Appendix A. Selected physical characteristics of sites sampled for chapter 2 and chapter 3 data. Site numbers correspond to those in Appendix B.

SITE #	TREATMENT	ELEVATION (m)	ASPECT	SLOPE	YEAR LOGGED	YEAR TREATED	SIZE (ha)	NUMBER OF PLOTS	
								CH. 2 DATA	CH. 3 DATA
1	Forest control	1290	SE	10	-	-	NA	8	10
2	Forest control	1250	SE	15	-	-	NA	7	10
3	Forest control	1350	SW	10	-	-	NA	7	10
4	Forest control	1400	SW	10	-	-	NA	6	10
5	Forest control	1375	SW	5	-	-	NA	6	14
6	Forest control	1375	SW	10	-	-	NA	6	16
7	Forest control	1375	SW	10	-	-	NA	5	16
8	Unscarified	1350	SW	10	1978	-	48	10	10
9	Unscarified	1400	SW	10	1981	-	5	6	8
10	Unscarified	1350	SW	10	1978	-	28	8	10
11	Unscarified	1250	E	5	1977	-	42	12	12
12	Unscarified	1400	SE	10	1978	-	50	10	11
13	Unscarified	1310	SE	10	1980	-	22	6	10
14	Unscarified	1400	SW	15	1978	-	22	14	13

Appendix A. Selected physical characteristics of sites sampled for chapter 2 and chapter 3 data. Site numbers correspond to those in Appendix B.

SITE #	TREATMENT	ELEVATION (m)	ASPECT	SLOPE	YEAR LOGGED	YEAR TREATED	SIZE (ha)	NUMBER OF PLOTS	
								CH. 2 DATA	CH. 3 DATA
15	Drag scarified	1400	SE	10	1978	1980	12	14	12
16	Drag scarified	1400	SW	10	1978	1980	14	12	10
17	Drag scarified	1300	SE	5	1978	1980	50	14	11
18	Drag scarified	1380	S	10	1980	1982	12	6	10
19	Drag scarified	1375	SW	5	1978	1982	15	7	15
20	Drag scarified	1400	SE	10	1980	1982	80	20	10
21	Drag scarified	1350	SW	15	1978	1980	25	20	14
22	Blade scarified	1600	SW	20	1979	1980	24	12	10
23	Blade scarified	1400	SW	10	1978	1982	22	6	10
24	Blade scarified	1250	SE	20	1981	1982	12	6	10
25	Blade scarified	1250	SW	10	1980	1982	99	6	10

Appendix B. Location of sampling sites relative to one another. Numbers correspond to site numbers in Appendix A. Modification of Sheet 82 G/SE, Geographic Division, Surveys and Mapping Branch, Department of Lands, Forests and Water Resources, Victoria B.C. 1963.



Appendix C. *S. canadensis* nested ANOVA tables

1. Treatment variable only

(i) Dependent: *S. canadensis* bushes

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	535.217	178.406	1.874	.1650	Site
Site	21	1999.412	95.210	13.248	<.0001	Plots
Plots	431	3097.475	7.187			

(ii) Dependent: *S. canadensis* berry dry weight 1994

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	7127.803	2375.934	.644	.5953	Site
Site	21	77469.282	3689.013	5.044	<.0001	Plots
Plots	194	141878.908	731.335			

(iii) Dependent: *S. canadensis* berry dry weight 1995

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	395.718	131.906	.466	.7094	Site
Site	21	5949.614	283.315	2.144	.0035	Plots
Plots	212	28011.522	132.130			

Appendix C. *S. canadensis* nested ANOVA tables

2. Treatment and Location as variables

(i) Dependent: *S. canadensis* bushes

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	736.953	245.651	4.014	.0249	Site
Location	1	529.452	529.452	8.651	.0091	Site
Treat. * Loc.	3	400.498	133.499	2.181	.1277	
Site	17	1040.429	61.202	8.516	<.0001	Plots
Plots	431	3097.475	7.187			

(ii) Dependent: *S. canadensis* berry dry weight 1994

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	6545.821	2181.940	0.668	.5833	Site
Location	1	3506.447	3506.447	1.073	.3147	Site
Treat. * Loc.	3	19043.165	6347.722	1.943	.1610	
Site	17	55544.294	3267.311	4.468	<.0001	Plots
Plots	194	141878.908	731.335			

(iii) Dependent: *S. canadensis* berry dry weight 1995

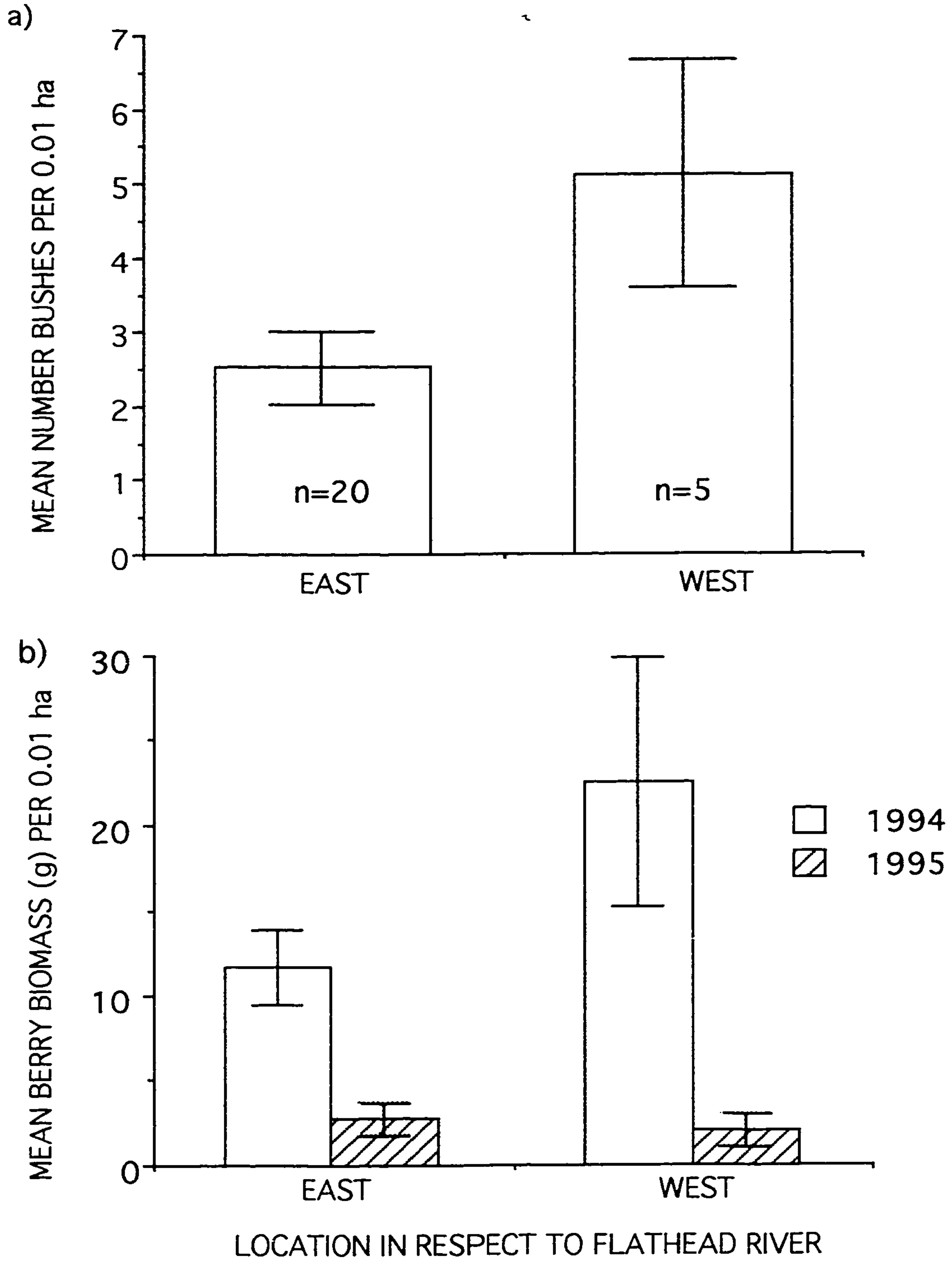
Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	254.392	84.797	0.253	.8583	Site
Location	1	0.038	0.038	1.132E-4	.9916	Site
Treat. * Loc.	3	271.184	90.395	0.269	.8465	
Site	17	5703.833	335.520	2.539	.0010	Plots
Plots	212	28011.522	132.130			

Appendix C. *S. canadensis* nested ANOVA tables

3. Age

Dependent: Bush Age

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	492.785	164.262	10.039	.0044	Site
Site	8	130.895	16.362	1.619	.1356	Residual
Residual	68	687.206	10.106			



Appendix D. Mean (±SE) number of *Shepherdia canadensis* bushes (a) and berry biomass (b) on sites located on the east vs. the west side of the Flathead River, B.C.

Appendix E. Multiple regression tables.

1. Y = *S. canadensis* bush means

	df	SS	MS	F-Value	p-Value
Model	7	90.00	12.86	3.155	0.025
Error	17	69.29	4.076		
Total	24	159.29			

Count = 25, R = 0.752, R^2= 0.565

Sums of Squares

Source	df	SS	MS	F-Value	p-Value	Beta	S.E.
Elevation	1	1.16	1.16	0.28	0.601	0.004	0.008
Slope	1	14.37	14.37	3.52	0.078	-0.259	0.138
Aspect	1	1.02	1.02	0.25	0.623	0.006	0.011
Location	1	40.83	40.83	10.01	0.006	-4.477	1.414
Treatment							
unscarified	1	19.01	19.01	4.66	0.045	-2.358	1.092
drag scar.	1	0.32	0.32	0.08	0.783	0.322	1.150
blade scar.	1	2.34	2.34	0.58	0.459	1.107	1.460
Residual	17	69.29	4.08				
Intercept						3.060	9.883

Appendix D. Multiple regression tables.

2. Y = Berry biomass in 1994

	df	SS	MS	F-Value	p-Value
Model	7	2315.36	330.77	0.529	0.801
Error	17	10632.80	625.46		
Total	24	12948.17			

Count = 25, R = 0.423, R^2= 0.179

Sums of Squares

Source	df	SS	MS	F	p	Beta	S.E.
Elevation	1	162.8	162.8	0.260	0.616	0.050	0.098
Slope	1	286.8	286.8	0.458	0.507	-1.157	1.709
Aspect	1	230.4	230.4	0.368	0.551	0.084	0.139
Location	1	1084.3	1084.3	1.734	0.205	-23.071	17.522
Treatment							
unscarified	1	305.5	305.5	0.488	0.494	9.455	13.529
drag scar.	1	738.1	738.1	1.180	0.293	15.474	14.245
blade scar.	1	841.8	841.8	1.346	0.262	20.989	18.092
Residual	17	10632.8	625.5				

Intercept -72.557 122.43

Appendix E. Multiple regression tables.

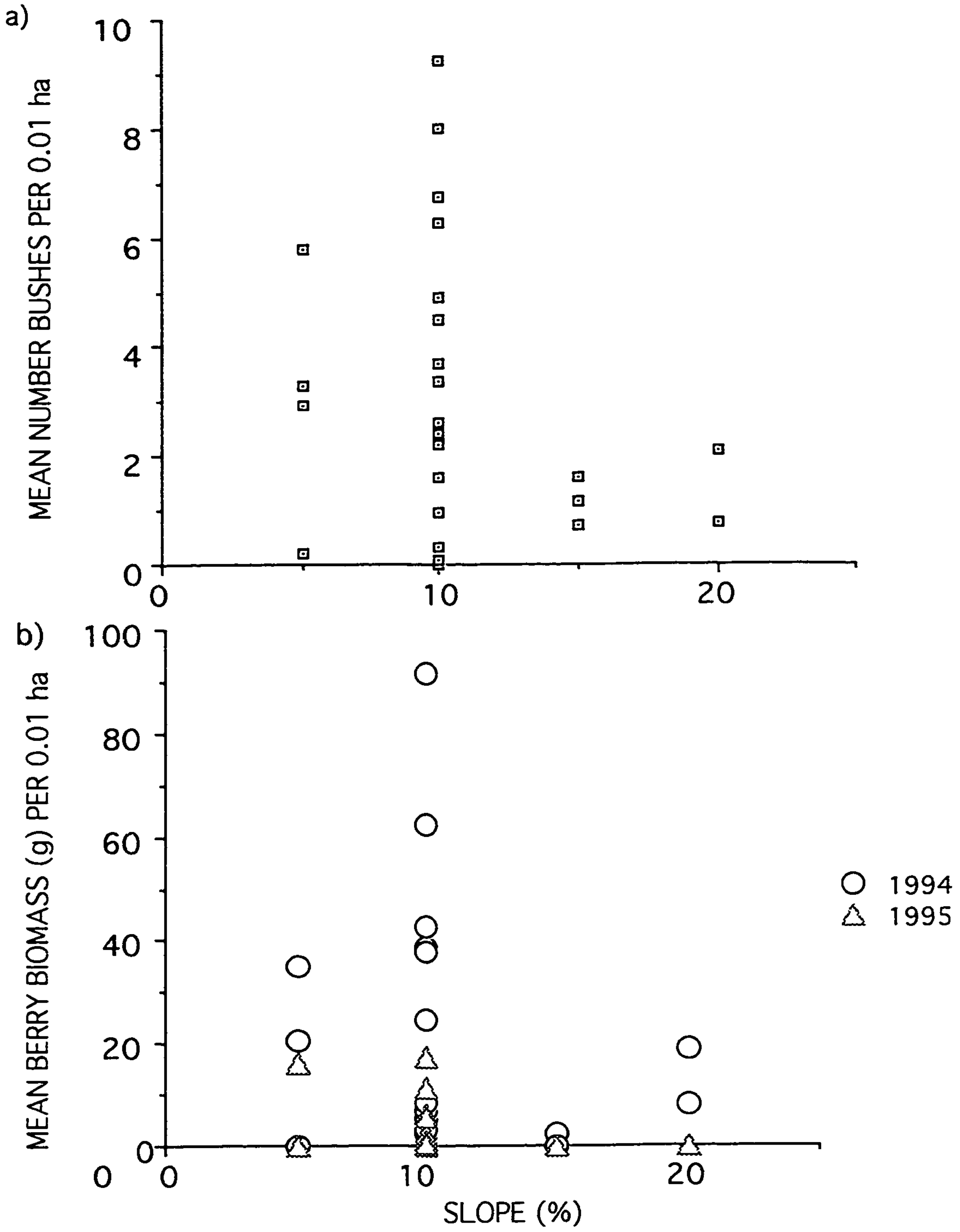
3. Y = Berry biomass in 1995

	df	SS	MS	F-Value	p-Value
Model	7	114.26	16.32	0.595	0.751
Error	17	466.28	27.43		
Total	24	580.54			

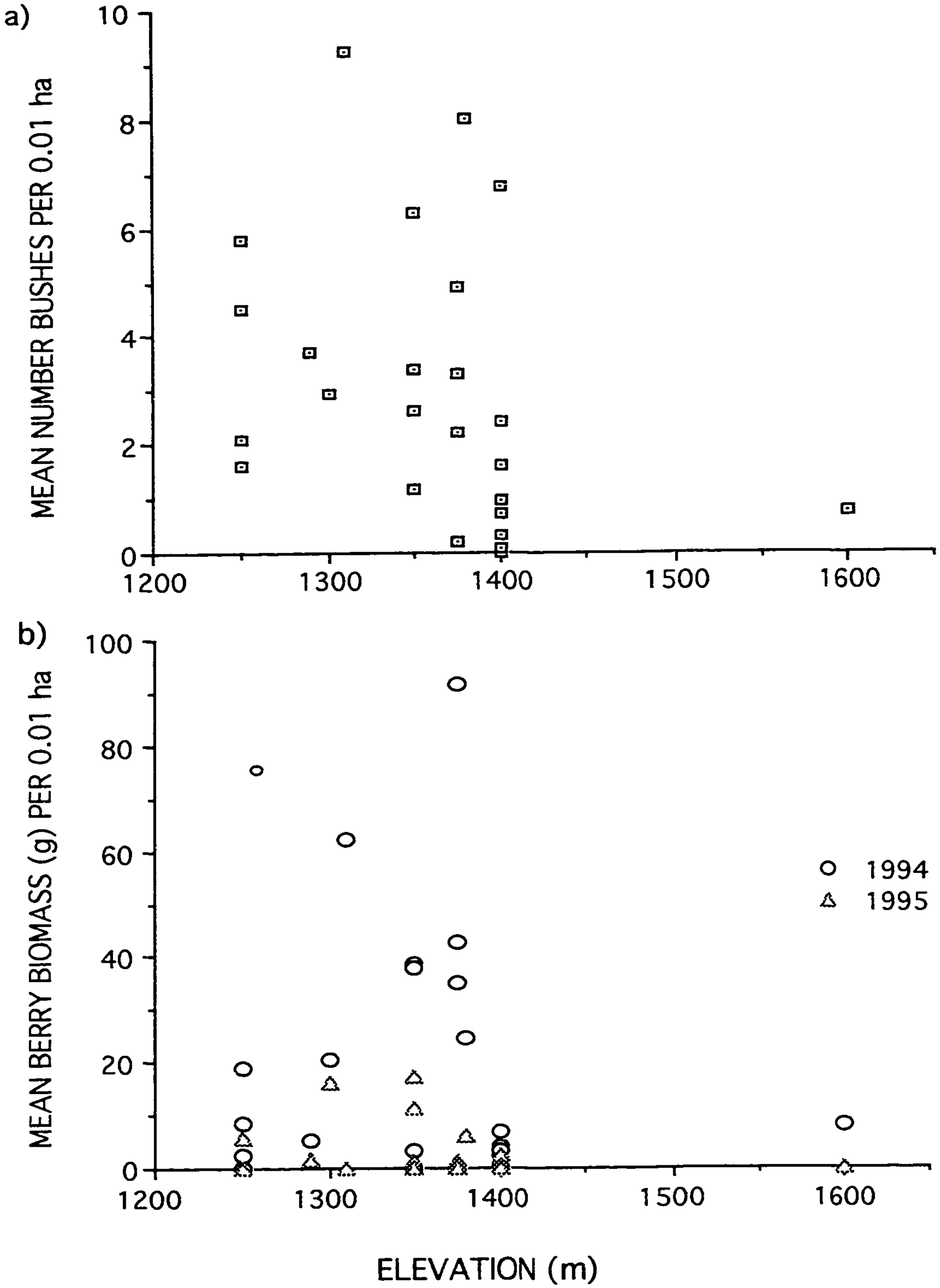
Count = 25, R = 0.444, R^2= 0.197

Sums of Squares

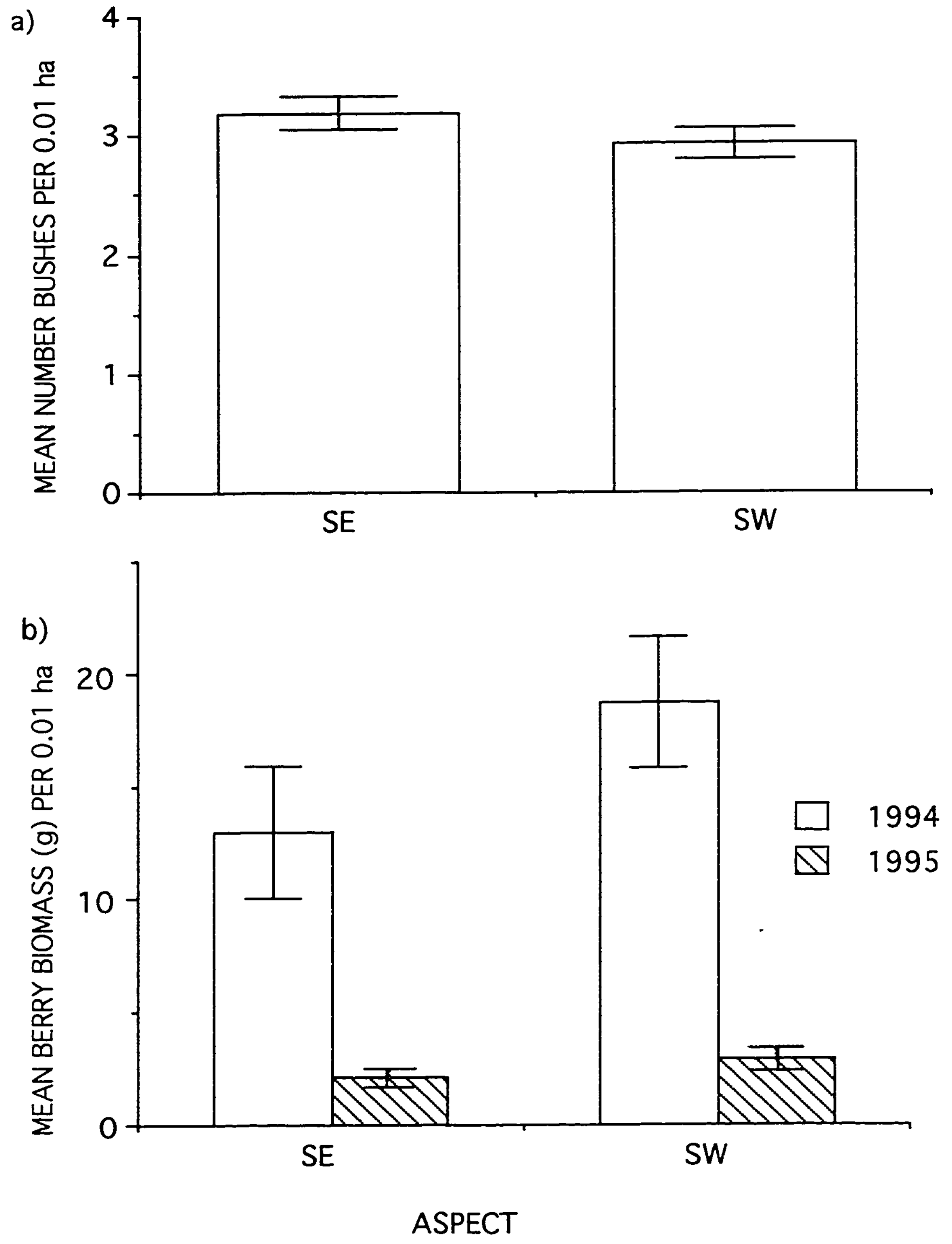
Source	df	SS	MS	F	p	Beta	S.E.
Elevation	1	21.2	21.2	0.774	0.391	-0.018	0.021
Slope	1	9.8	9.8	0.358	0.558	-0.214	0.358
Aspect	1	19.7	19.7	0.720	0.408	0.025	0.029
Location	1	0.4	0.4	0.014	0.907	0.118	3.669
Treatment							
unscarified	1	52.2	52.2	1.903	0.186	-3.909	2.833
drag scar.	1	31.8	31.8	1.159	0.300	-1.077	2.983
blade scar.	1	8.8	8.8	0.319	0.580	-2.141	3.789
Residual	17	466.3	27.4				
Intercept						31.418	25.639



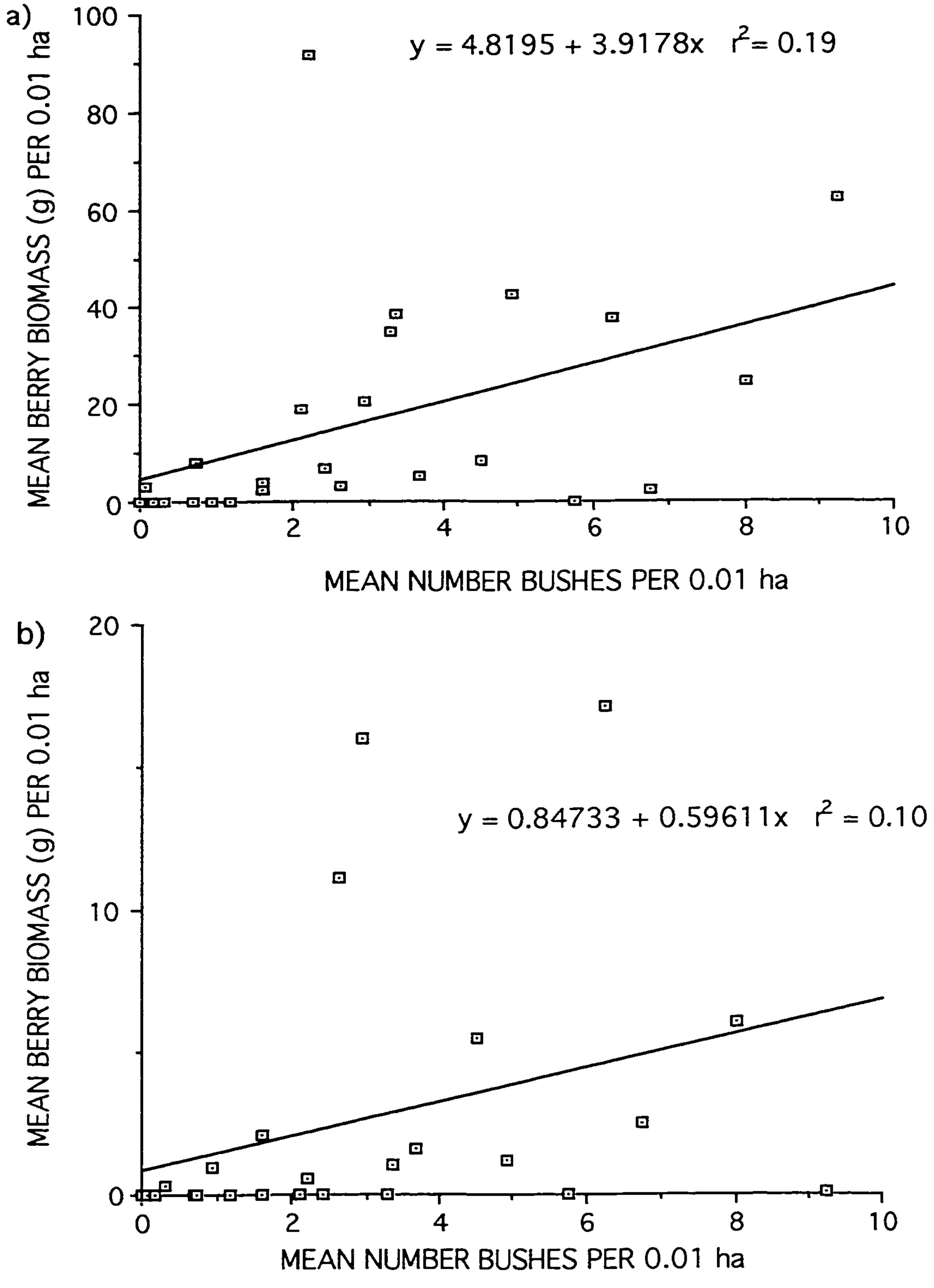
Appendix F. Mean number of *Shepherdia canadensis* bushes (a) and berry biomass (b) on different slopes.



Appendix G. Mean number of *Shepherdia canadensis* bushes (a) and berry biomass (b) at different elevations.



Appendix H. Mean number of *Shepherdia canadensis* bushes (a) and berry biomass (b) at two aspects.



Appendix I. Regression between *Shepherdia canadensis* bushes and berry biomass in (a) 1994 and (b) 1995.

Appendix J. Mean number of *Shepherdia canadensis* bushes per 0.01 ha. for 25 sites. (Sites are in the same order as they occur in Appendix A).

Treatment	**Count**	**Mean**	**Std. Error**
Unharvested	16	3.688	.530
Unharvested	15	1.600	.456
Unharvested	14	3.357	.970
Unharvested	13	1.615	.836
Unharvested	11	0.182	.182
Unharvested	12	4.917	.874
Unharvested	10	2.200	.593
Unscarified cc	20	6.250	1.277
Unscarified cc	12	6.750	0.986
Unscarified cc	16	2.625	0.455
Unscarified cc	23	5.783	0.717
Unscarified cc	20	2.400	0.467
Unscarified cc	13	9.231	1.316
Unscarified cc	28	0.714	0.229
Drag scarified cc	22	0.000	0.000
Drag scarified cc	23	0.304	0.132
Drag scarified cc	28	2.929	0.433
Drag scarified cc	12	8.000	1.376
Drag scarified cc	14	3.286	0.794
Drag scarified cc	40	0.950	0.304
Drag scarified cc	34	1.176	0.265
Blade scarified cc	24	0.750	0.271
Blade scarified cc	12	0.667	0.355
Blade scarified cc	12	2.083	1.069
Blade scarified cc	12	4.500	1.154

Appendix K. Dry weight of *Shepherdia canadensis* berries (g / 0.01 ha) for 25 sites in 1994. (Sites are in the same order as they occur in Appendix A.)

Treatment	**Count**	**Mean**	**Std. Error**
Unharvested	8	5.385	4.063
Unharvested	7	2.311	1.429
Unharvested	7	38.487	20.632
Unharvested	6	4.043	4.043
Unharvested	5	0.000	0.000
Unharvested	6	42.437	19.403
Unharvested	5	91.756	31.209
Unscarified cc	10	37.745	18.234
Unscarified cc	6	2.382	1.082
Unscarified cc	8	3.296	2.440
Unscarified cc	11	0.193	0.118
Unscarified cc	10	6.931	2.645
Unscarified cc	6	62.330	25.685
Unscarified cc	14	0.029	0.029
Drag scarified cc	8	0.000	0.000
Drag scarified cc	11	0.000	0.000
Drag scarified cc	14	20.531	7.354
Drag scarified cc	6	24.460	12.355
Drag scarified cc	7	34.876	17.396
Drag scarified cc	20	0.132	0.132
Drag scarified cc	14	0.047	0.046
Blade scarified cc	12	7.901	4.750
Blade scarified cc	6	3.235	3.235
Blade scarified cc	6	18.872	18.488
Blade scarified cc	6	8.342	3.265

Appendix L. Dry weight of *Shepherdia canadensis* berries (g / 0.01 ha) for 25 sites in 1995. (Sites are in the same order as they occur in Appendix A.)

Treatment	**Count**	**Mean**	**Std. Error**
Unharvested	8	1.634	1.478
Unharvested	8	0.000	0.000
Unharvested	7	1.016	1.016
Unharvested	7	2.065	2.065
Unharvested	6	0.000	0.000
Unharvested	6	1.197	0.858
Unharvested	5	0.583	0.583
Unscarified cc	10	17.106	7.331
Unscarified cc	6	2.503	1.896
Unscarified cc	8	11.096	4.831
Unscarified cc	12	0.007	0.007
Unscarified cc	10	0.032	0.032
Unscarified cc	7	0.067	0.046
Unscarified cc	14	0.008	0.008
Drag scarified cc	14	0.000	0.000
Drag scarified cc	12	0.284	0.280
Drag scarified cc	14	16.021	10.615
Drag scarified cc	6	5.989	2.027
Drag scarified cc	7	0.021	0.021
Drag scarified cc	20	0.957	0.700
Drag scarified cc	20	0.003	0.002
Blade scarified cc	12	0.034	0.034
Blade scarified cc	6	0.000	0.000
Blade scarified cc	6	0.000	0.000
Blade scarified cc	6	5.481	4.313

Appendix M. ANOVA tables for ant data.

A. Nested Anovas, Chapter 3.

(i) Dependent: Number of Stumps

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	4686.927	1562.309	23.277	.0001	Site
Site	21	1412.538	67.264	9.473	.0001	Plots
Plots	257	1824.840	7.101			

Scheffe's

	Vs.	Difference	Critical Diff.	P-Value
Unharvested	Unscarified	9.931	3.948	.0001
	Drag	8.719	3.843	.0001
	Blade	5.956	4.765	.0106
Unscarified	Drag	1.212	3.992	.8369
	Blade	3.976	4.887	.1399
Drag	Blade	2.763	4.802	.4048

(ii) Dependent: Number of attacked stumps

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	135.499	45.166	11.360	.0001	Site
Site	21	83.496	3.976	2.949	.0001	Plots
Plots	257	346.488	1.348			

Scheffe's

	Vs.	Difference	Critical Diff.	P-Value
Unharvested	Unscarified	1.857	.960	.0001
	Drag	1.258	.934	.0057
	Blade	1.190	1.159	.0426
Unscarified	Drag	.599	.971	.3445
	Blade	.667	1.188	.4263
Drag	Blade	.068	1.168	.9985

(iii) Dependent: Stumps with no previous ant colonization

Source	df	Sum of Squares	Mean Square	F-Value	P-Value	Error Term
Treatment	3	.979	.326	1.354	.2841	Site
Site	21	5.061	.241	1.980	.0076	Plots
Plots	257	31.283	.122			

B. Two factor ANOVA, Chapter 4.

(i) Dependent: Stump diameter

Source	df	Sum of Squares	Mean Square	F-Value	P-Value
Ant Species	8	1267.470	158.434	2.302	.0193
Bear Attacks	1	158.021	158.021	2.296	.1301
Species * Attacks	6	484.756	108.441	1.174	.3180
Residual	748	51471.299	68.812		