

**RESPONSE OF SMALL MAMMAL POPULATIONS
TO SPRUCE BARK BEETLE INFESTATION
AND LOGGING ON THE KENAI
PENINSULA, ALASKA**

By

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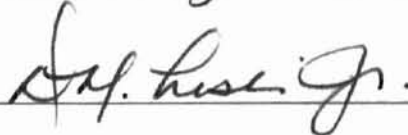
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PREFACE

Historically, Alaskan ecosystems have been shaped by natural disturbance events such as fire, earthquakes, wind, glacial retreat, and insect infestations. Concerns of scientists, land managers, and the public over past and current efforts to manage the Kenai Peninsula's forest resources have led to an attempt to understand and quantify impacts of anthropogenic and natural disturbances on wildlife and their habitats. Small mammals, as resident biomonitors of environmental change have the potential to be indicators of ecological health. To this end, we evaluated the influence of logging and spruce bark beetle (*Dendroctonus rufipennis* Kirby) infestations on small mammal population dynamics. This thesis includes three manuscripts formatted for submission to the *Journal of Mammalogy* (Chapter I), *Forest Ecology and Management* (Chapter II), and *The Canadian Field Naturalist* (Chapter III). The manuscripts are complete as written and need no supporting material.

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**RESPONSE OF *CLETHRIONOMYS RUTILUS* POPULATIONS TO
DISTURBANCE ON THE KENAI PENINSULA, ALASKA**

We examined differences between populations of northern red-backed voles (*Clethrionomys rutilus*) in unlogged, logged, and spruce bark beetle (*Dendroctonus rufipennis* Kirby) infested forests in pure white spruce (*Picea glauca*) habitat, and logged and spruce bark beetle infested forests in mixed hardwood-white spruce habitat. Small mammals were livetrapped in each habitat type four times between May and August 1998 to estimate population abundance, survivability, and recruitment. Capture rates of northern red-backed voles (*Clethrionomys rutilus*) differed among habitat types, treatments, and trapping sessions. Numbers of reproducing *C. rutilus* females and juvenile-adult ratios were also different among habitats, treatments, and trapping sessions. Populations of *C. rutilus* in all areas were similar in sex composition. Our results suggest that within the pure white spruce habitat, spruce bark beetle infestations positively influence *C. rutilus* numbers, while logging has a negative effect. However, within the mixed hardwood-white spruce habitat type neither logging nor spruce bark beetle infestation impacted *C. rutilus* population dynamics.

Key words: northern red-backed vole, *Clethrionomys rutilus*, *Picea glauca*, white spruce, *Dendroctonus rufipennis*, spruce bark beetle, logging

For at least the last century, outbreaks of the endemic spruce bark beetle (*Dendroctonus rufipennis* Kirby) have occurred in south central and interior Alaska (Fastie and Berg, 1997). Since the 1920's, greater than 6.6 million ha have been infested, with greater than 1.1 million ha of ongoing and new infestations reported in 1996 alone (United States Forest Service, 1997). Historically, spruce bark beetles attacked downed trees, mainly from recent windthrow or flood events. As beetle populations build and recent downed material becomes scarce beetles attack slow growing, usually large diameter, trees or trees weakened by drought stress or root damage (Holsten et al., 1991). Today, however, fire suppression and other human activities have created large tracts of old and slow growing forests that are uniformly susceptible to attack (Holsten et al., 1996).

These large tracts of old and weak, slow growing trees have created a food resource that has allowed *D. rufipennis* to reach epidemic proportions. The unprecedented large numbers of beetles and beetle killed trees have created concerns about increased risk of fire, loss of valuable timber resources, and diminished forest aesthetic value (Holsten et al., 1996; Reynolds and Hard, 1991). In response to these concerns, forest managers have prescribed intensive management (i.e., salvage logging) to control the spruce bark beetle infestation (United States Forest Service, 1997; Holsten et al., 1991; Reynolds and Hard, 1991). Some information exists about impacts of logging and *D. rufipennis* on white spruce forest vegetation (Holsten et al., 1995; Martell, 1983), but little is known about how these disturbance events affect habitat use and suitability for Alaskan wildlife in general and small mammals in particular.

The northern red-backed vole (*Clethrionomys rutilus*) is one of the most common and widespread small mammals on the Kenai Peninsula and displays a variety of life-

history traits that have allowed it to adapt and survive episodic disturbances that characterize the Alaskan landscape (Bourliere, 1975; West, 1979; West, 1974). This ability, coupled with the amount of energy *C. rutilus* represents in the system due to sheer numbers, enables *C. rutilus* populations to have a substantial impact on predator dynamics, vegetation consumption, and forest decomposition (Staples, 1995; Johnson et al., 1990; Bangs, 1984; Stoddart, 1979; Maser et al., 1978). Our objectives were to evaluate effects of logging and beetle infestation on *C. rutilus* demographics and determine differences in *C. rutilus* populations between pure white spruce and mixed deciduous-white spruce habitats.

MATERIALS AND METHODS

Study area.—The general location of the study area is the Kenai Peninsula, Alaska, USA (Fig. 1). It is located between 59°-61° N and 148°-152° W in what is considered south central Alaska. Cook Inlet forms the western boundary, Prince Williams Sound the east, and the Gulf of Alaska the south. The Kenai Mountain Range with elevations <2,000 m dominates the eastern two-thirds. The Kenai Lowlands, dominating the western one third, have elevations of 15-100 m and are occupied by numerous lakes left by retreating glaciers (Schwartz and Franzmann, 1991). The lowlands contain aspects of both continental and maritime climates and are the location of the study sites.

The primary forest composition of the northern one half of the Kenai Lowlands is a mixture of white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). Typical understory in these deciduous tree dominated stands includes shrubs such as willow (*Salix* spp.),

Labrador tea (*Ledum* sp.), low bush cranberry (*Vaccinium* spp.), rusty menziesia (*Menziesia ferruginea*), and American devilsclub (*Oplopanax horridus*). The percent of white spruce infested by *D. rufipennis* in northern stands tends to parallel the overall percent of white spruce in the stand composition (Boughten, 1996). The wider dispersion and fewer numbers of white spruce make them less available to insect attack. The southern one half of the Lowlands is dominated by mature stands of white spruce with mosses, lichens, and ferns in the understory (Oldemeyer and Regelin, 1987). Southern white spruce stands have $\geq 60\%$ of the total canopy infested with *D. rufipennis* (Boughten, 1996). Across the entire Lowland region, black spruce (*Picea mariana*) dominates poorly drained sites, open or disturbed areas often support an herbaceous layer of fireweed (*Epilobium angustifolium*) and bluejoint reedgrass (*Calamagrostis canadensis*).

Sampling.—The study examined two dry, upland habitats as designated by the Alaska Department of Fish and Game: pure white spruce and mixed deciduous (i.e., *Betula papyrifera*)-white spruce. Pure spruce habitat types (hereafter, spruce) are defined as having a stand composition of ≥ 90 percent or more white spruce. Mixed deciduous-white spruce (hereafter, mixed) habitat types have ≥ 10 percent deciduous trees. Forests infested with *D. rufipennis* (hereafter, infested) experienced canopy mortality by *D. rufipennis* ca. 3 years before the start of the study. Logged treatments were clearcut, ca. 3 years prior, in a way consistent with general forestry practices on the Kenai Peninsula. Unlogged, reference forests (hereafter, control) were undisturbed by any factor including fire for at least the last century. All treatments within each habitat type were at about the same elevation, aspect, age (≥ 100 years), and understory composition before disturbance.

Sampled areas were restricted to slopes of <5%. Within each habitat type, each treatment had three replicates. The infested treatment within the mixed habitat was restricted to two replicates. All sites were separated by ≥ 500 -m to prevent inter-site movements of small mammals (Rexstad, 1996). Populations were constant within each session and allowed us to

use (1). We used mark-recapture techniques to assess the influence of logging and *D.*

rufipennis infestation on small mammal population dynamics. Within each of the 14 sites, we established a 0.09-ha trapping grid. A 30-m buffer zone around each grid was maintained to control for possible habitat edge effect. Each trapping grid consisted of 100 Sherman live traps (8 by 9 by 23-cm) arranged in a 10 by 10 grid and separated by 10-m intervals. Traps were opened for 4, 5-day sessions every 2 weeks from 15 May to 9 August 1998. Four trapping sessions were used to characterize small mammal population dynamics throughout the entire season. Traps were baited with commercial rodent chow, supplied with bedding and checked twice daily (0600, 1800) for animals, and proper functioning of the trap. Passive integrated transponder (PIT) tags (Biomark Inc., Boise, ID; Schooley et al., 1993) were used to permanently mark individual voles. PIT tags caused no noticeable deleterious effects on marked individuals and subsequent identification was rapid and efficient. Species, sex, weight, and reproductive condition were determined for all animals.

Statistical analysis.—Population densities of small mammals were estimated using both relative abundance and the modified Lincoln-Peterson index (Chapman, 1951). Relative abundance was expressed as the number of captures per 100 trap-nights and was determined using the formula of Nelson and Clark (1973). That procedure corrected for closed traps that reduce number of animals that could be captured. Because we had

relatively low capture rates, program CAPTURE did not provide reliable density estimates (White et al., 1982). Therefore, we used Pollock's robust capture-recapture design that incorporates both open and closed population model components (Pollock et al., 1990). That design assumed that populations were constant within each session and allowed us to use Chapman's approximation of the Lincoln-Petersen index to estimate population densities (Krebs, 1989; Pollock et al., 1990).

All data were tested for homogeneity of variances using the likelihood ratio test (PROC MIXED, SAS Institute Inc., 1994). Data not meeting that assumption were transformed (square-root or arcsine) before further analysis (Steel et al., 1997). To account for time across sessions, a repeated-measures analysis of variance was used to test for effects of habitat type (mixed or pure) and treatment (logged, infested, or control) on population density of *C. rutilus*, proportion of males, proportion of juveniles, number of pregnant or reproducing (lactating) females, and relative abundance (PROC MIXED, SAS Institute Inc., 1994). If three-way interactions (habitat type by treatment by session) were found to be significant, simple effects were analyzed by performing multiple-comparisons using Fisher's least significant difference (LSMEANS, SAS Institute Inc., 1994). Simple effects were compared with the SLICE option for the LSMEANS statement. In the event of no significant three-way interactions main effects of session and the combined effects of habitat type and forest treatment were examined. Satterthwait's approximation was used to calculate degrees of freedom for the error term. The failure to reject the hypothesis that there is no difference between treatments when false (Type II error) would have serious consequences when examining effects of disturbance and its implications for management (Shrader-Frechette and McCoy, 1992). Due to our small sample size and in

consideration of Type II error, we felt strict adherence to $\alpha = 0.05$ was inappropriate (Scheiner, 1993; Shrader-Frechette and McCoy, 1993). For all tests, we used an alpha of 0.10. $F = 1.93$, $df = 12, 27$, $P = 0.0759$). The pure spruce infested treatment showed higher *rutilus* abundance than the spruce control in June and August and the spruce logged treatment for all sessions (Fig. 2). We

RESULTS

We captured 457 northern red-backed voles 2,227 times on 14 study sites. Other captures included 56 masked shrews (*Sorex cinereus*), 5 short-tail weasels (*Mustela erminea*), and 1 red squirrel (*Tamiasciurus hudsonicus*). The *S. cinereus* were caught mainly on the mixed and spruce logged treatments, with two individuals caught on each of the spruce and mixed infested treatments. Three of the *M. erminea* and the *T. hudsonicus* were caught on the spruce infested treatment, with the other two *M. erminea* caught on the mixed logged, and spruce control.

The combined interaction of habitat type, treatment and session had the greatest influence on the total number of individual *C. rutilus* ($F = 1.93$; $df = 12, 27$; $P = 0.0759$). Comparisons of total individual *C. rutilus* captures between the pure spruce logged, infested, and control treatments showed that the spruce-infested treatment had the greatest number of *C. rutilus* in June, July, and August. Within the mixed habitat type the infested treatment had the greatest total *C. rutilus* captures, except in June when the logged treatment had more *C. rutilus* captures. When total captures of *C. rutilus* were compared between mixed and pure spruce logged treatments, the mixed logged had greater numbers of animals until the last session in early August. After the initial trapping session in May, the pure spruce had higher numbers of *C. rutilus* than the mixed habitat type (Fig. 2).

The Lincoln-Peterson index indicated that the combined interaction between habitat type, treatment and session had the greatest influence on *C. rutilus* abundance ($F = 2.35$; $df = 12, 27$; $P = 0.0319$). The pure spruce infested treatment showed higher *C. rutilus* abundance than the spruce control in June and August and the spruce logged treatment for all sessions (Table 1). Within the mixed habitat type, the logged treatment had greater *C. rutilus* abundance only for the June session (Table 2). For logged treatments, *C. rutilus* abundance was higher in the pure spruce habitat for May, June, and July, but the mixed habitat had greater *C. rutilus* abundance in August (Table 3). The pure spruce infested treatment however, had higher *C. rutilus* abundance than the mixed infested treatment during all four sessions (Table 4).

Relative abundance of *C. rutilus* did not show a significant three-way interaction ($F = 1.77$; $df = 12, 27$; $P = 0.1059$). Both the main effect of session and a two-way interaction between habitat type and treatment influenced relative abundance of *C. rutilus* ($F = 7.49$; $df = 3, 27$; $P = 0.0008$ and $F = 13.06$; $df = 4, 9$; $P = 0.0751$; respectively). Both the spruce control and the spruce infested treatments experienced a *C. rutilus* population peak during July. In addition, the spruce infested treatment had the highest *C. rutilus* relative abundance in June and July, but was not higher than the spruce control in May or August. The spruce logged maintained fairly low *C. rutilus* numbers throughout the summer (Table 1). The logged treatment within the mixed habitat type had greater *C. rutilus* relative abundance than the mixed infested during July and August (Table 2). Relative abundance was not higher on the mixed logged than the spruce logged treatment until August (Table 3). Conversely, the spruce infested had higher *C. rutilus* relative abundance than the mixed infested during both July and August (Table 4).

Male to female ratios of *C. rutilus* were influenced by the main effect of session ($F = 2.72$; $d.f. = 3, 22.2$; $P = 0.0688$). Within the pure spruce habitat, there were more *C. rutilus* males than females on the control treatment during the July trapping session (Table 1). There were also greater numbers of *C. rutilus* males present on the pure spruce infested treatment than the mixed infested treatment during the July session (Table 4).

The combined effect between habitat types, treatments, and trapping sessions had the greatest influence on juvenile to adult ratios of *C. rutilus* ($F = 3.01$; $d.f. = 11, 24.3$; $P = 0.0113$). No *C. rutilus* juveniles were caught on any of the 14 treatment during the May trapping session. However, more *C. rutilus* juveniles were present on the pure spruce control and infested treatment than the logged treatment in June (Table 1). The number of *C. rutilus* juveniles did not differ between any of the 4 sessions on the pure spruce logged treatment. There were no differences found in the number of *C. rutilus* juveniles on either the mixed infested or mixed logged treatment (Table 2). Numbers of *C. rutilus* juveniles were higher in July on the mixed logged treatment than the pure spruce logged treatment (Table 3). The pure spruce infested treatment had a greater proportion of *C. rutilus* juveniles than the mixed infested treatment during the June and July trapping sessions (Table 4).

The number of reproducing *C. rutilus* females was most influenced by the combined effect of habitat types, treatments and sessions ($F = 2.76$; $d.f. = 12, 36$; $P = 0.0091$). During the July session, the spruce infested had the highest number of *C. rutilus* pregnant females, while the spruce logged had the fewest for both July and August (Table 1). Numbers of *C. rutilus* pregnant females did not differ between the mixed logged and infested treatments. Both mixed treatments had the most reproducing *C. rutilus* females

during the June session (Table 2). During the June and July sessions, the mixed logged treatment had more reproducing *C. rutilus* females than the spruce logged (Table 3), but the spruce infested had more pregnant and reproducing *C. rutilus* females than the mixed infested treatment (Table 4).

DISCUSSION

Spruce bark beetle infestation and logging in pure white spruce habitat produced measurable effects on *C. rutilus* demographics in our study area. However, logged and infested treatments did not produce the same effects on population dynamics within the mixed hardwood-white spruce habitat, indicating differences in *C. rutilus* populations between habitat types.

The higher *C. rutilus* population densities, numbers of reproducing females and consequently high numbers of juveniles on the spruce infested treatment as compared with spruce control and logged treatment agree with other research that reductions in canopy caused by insect infestations have an initial positive effect on densities of small mammals (Clough, 1987; Stone, 1995). However, much of the positive response reported was attributed to non-forest species of small mammals.

By reducing overstory shade and competition, beetle infestation and salvage logging can increase understory density, and change structure and function of plants used by small mammals for food and cover (Holsten et al.; 1995, Interagency Forest Ecology Study Team, 1997). An increase in understory density resulting from beetle induced canopy mortality could reduce predation on small mammals by decreasing ocular detection and/or providing more opportunities for escape. Conversely, an increase in light to the

forest floor may decrease abundance of moss, fungi, and other important habitat variables. However, presence of *D. rufipennis* larvae in white spruce trees may provide an additional year-long high energy food resource for *C. rutilus*.

In contrast to beetle infestation, mechanical disturbance (logging and scarification) directly impacts the understory and soil layers, removes a greater portion of canopy cover, and can reduce berries, mosses, lichens and mushrooms, while increasing shrubs, grass and debris (Bangs, 1979; Martell 1981). Additional research (Martell, 1983; Nordstrom, 1995) showed scarification of a site after logging further reduced the moss and lower vegetation layer, which in turn reduced numbers of voles and shrews. The effects of scarification on the moss and understory vegetation layer help explain the low densities and reproductive success observed on our spruce logged treatment. The presence of a moss layer as important food and thermal cover requirements for small mammals in cold environments (Bangs, 1984; Prins, 1981; West, 1974) further supports our conclusion that removal of the moss layer through the process of logging or scarification in pure spruce habitat appears to have a negative impact on populations of *C. rutilus*.

To be used successfully by a small mammal, a clearcut must fall within the range of acceptable limits for food, moisture, cover and any other requirements that are unique to the individual species (Kirkland, 1990). Our study indicated that clearcut mixed hardwood-white spruce forests provide more acceptable habitat requirements than clearcuts in pure spruce forests. It is difficult to determine the pre-disturbance conditions of mixed forests without a treatment control, but the fact that there was very little difference in demographics between the mixed logged and infested treatment indicates that

neither of these treatments produce conditions that are initially detrimental to *C. rutilus* populations.

Recent burns and logged areas are considered habitat sinks where mortality exceeds reproduction for many small mammals (Pulliam, 1994; Sullivan, 1979). Habitats where reproduction exceeds mortality (source habitats) that contain as few as 10% of the total animal population, can be responsible for maintaining the 90% of the population found in sink habitats (Pulliam, 1988). While sinks provide an important dispersal area for juvenile or less dominant animals when densities in optimum habitat become too high (Sullivan, 1979). Both our spruce and mixed logged treatments indicated a pattern of spring colonization and subsequent fall abandonment that suggest poorer quality habitat.

Small mammal (particularly rodent) populations often vary according to cyclic patterns. Seasonal population patterns emerge as a function of breeding cycles. Yearly cycles are related to changes in weather, resource availability, and pressure from predators. Multi-annual cycles may occur due to lagged response to environmental changes or in response to density (Batzli, 1991; Flemming, 1979; French et al., 1975; Smith et al., 1975; Southern, 1979;). In Alaska, there appears to be a 3-year cycle for most arvicolines, *C. rutilus* in particular (Rexstad, 1996). Populations will reach a peak, crash, and then begin to rise again. Theories on the cause of the cycle are inconclusive and range from food shortage and overpopulation to snowless winters that prevent the animals from building tunnels to food caches (Furtsch, 1995; Rexstad, 1996; Staples, 1995; West, 1979). While our study did not span enough years to provide any clues as to yearly or multi-annual cycles, there appeared to be a similar seasonal cycle across all treatment. No measured population parameter helped to predict the number or timing of

peak densities from the uniformly low densities observed in May. An early spring population bottle-neck was also noted by West (1979). A year-round dietary study would provide important clues as to habitat quality and use in early spring.

Our results illustrate that populations of *C. rutilus* are responding to specific environmental variables that are not exclusive to either *D. rufipennis* infestation or logging. Ultimately, small mammal response to logging and beetle infestation on the Kenai Peninsula are most likely to be determined by the initial population, method of timber harvest, and subsequent plant succession. Year-round studies that examine the order in which optimal and sub-optimal habitats are filled and abandoned will help illuminate the source habitat needs of *C. rutilus*. The additional knowledge gained from year-round dietary and habitat occupation studies will help focus efforts on enhancing source habitat and prevent management efforts from inadvertently creating more sink habitat by focusing solely on total population numbers.

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Table 1. Means and standard errors for measures of population estimation parameters for *C. rutilus* in spruce habitat type forests in 1998. Means with the same capital letter do not differ across session within the same treatment at $\alpha > 0.10$. Means with the same lower case letter do not differ within a session, across treatments at $\alpha > 0.10$.

Session	Treatment	Lincoln - Petersen Est. of Abundance		Relative Abundance		Male / Female Ratio		Juvenile / Adult Ratio		Reproductive Females	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Session 1	Control	3.0 A,a	3.1	0.2 A,a	0.3	0.5 A,a	0.6	0.0 A,a	0.8	0.7 A,a	0.6
May 1998	Logging	0.0 A,a	3.1	0.0 A,a	0.3	0.0 A,a	0.9	0.0 A,a	N/A	0.0 A,a	0.6
	Infested	8.6 A,a	3.1	0.4 A,a	0.3	1.2 A,a	0.5	0.0 A,a	0.1	1.7 A,a	0.6
Session 2	Control	6.2 A,B,a	3.1	0.4 A,B,a	0.3	1.4 A,a	0.5	0.2 B,a,b	0.8	0.3 A,a	0.6
June 1998	Logging	1.0 A,a	3.1	0.2 A,a	0.3	0.9 A,a	0.9	0.1 A,a	0.1	0.0 A,a	0.6
	Infested	21.2 B,b	3.1	1.4 B,b	0.3	1.2 A,a	0.5	0.4 B,b	0.1	1.3 A,a	0.6
Session 3	Control	16.5 C,b	3.1	1.2 C,a	0.3	3.0 B,a	0.5	0.1 A,B,a	0.8	2.0 A,a	0.6
July 1998	Logging	8.0 A,a	3.1	0.5 A,a	0.3	1.5 A,b	0.5	0.1 A,a	0.1	0.3 A,b	0.6
	Infested	28.4 B,c	3.1	2.2 C,b	0.3	0.8 A,c	0.5	0.2 A,a	0.1	4.7 B,c	0.6
Session 4	Control	11.7 B,C,a	3.1	1.0 B,C,a,b	0.3	1.5 A,a	0.5	0.2 B,a	0.1	1.3 A,a,b	0.6
August 1998	Logging	5.7 A,a	3.1	0.4 A,a	0.3	2.3 A,a	0.6	0.2 A,a	0.1	0.0 A,a	0.6
	Infested	20.3 B,b	3.1	1.6 B,C,b	0.3	1.1 A,a	0.5	0.1 A,a	0.1	2.7 A,b	0.6

Table 2. Means and standard errors for measures of population estimation parameters for *C. rutilus* in mixed hardwood-white spruce habitat type forests in 1998. Means with the same capital letter do not differ across session within the same treatment at $\alpha > 0.10$. Means with the same lower case letter do not differ within a session, across treatments at $\alpha > 0.10$.

Session	Treatments	Lincoln - Petersen Est. of Abundance		Relative Abundance		Male / Female Ratio		Juvenile / Adult Ratio		Reproductive Females	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Session 1	Logging	13.0 A,B,a	3.1	0.7 A,a	0.3	1.6 A,a	0.5	0.0 A,a	0.1	0.0 A,a	0.6
May 1998	Infested	18.0 A,a	3.9	1.3 A,a	0.4	0.9 A,a	0.6	0.0 A,a	0.1	0.5 A,a	0.7
Session 2	Logging	13.2 A,B,a	3.1	0.9 A,a	0.3	1.1 A,a	0.5	0.1 A,a	0.1	3.3 C,a	0.6
June 1998	Infested	9.4 A,a	3.9	0.9 A,a	0.4	0.7 A,a	0.6	0.2 A,a	0.1	4.0 B,a	0.7
Session 3	Logging	20.5 B,b	3.1	1.2 A,B,a	0.3	1.0 A,a	0.5	0.3 A,a	0.1	2.3 B,a	0.6
July 1998	Infested	10.6 A,a	3.9	1.1 A,a	0.4	0.3 A,a	0.6	0.6 B,b	0.1	1.5 A,a	0.7
Session 4	Logging	6.1 A,a	3.1	1.6 B,a	0.3	1.7 A,a	0.5	0.1 A,a	0.1	1.3 A,B,a	0.6
August 1998	Infested	6.6 A,a	3.9	0.7 A,a	0.4	3.0 A,a	0.9	0.1 A,a	0.1	2.0 A,a	0.7

Table 3. Means and standard errors for measures of population estimation parameters for *C. rutilus* in logged forests in 1998. Means with the same lower case letter do not differ within a session, among habitat types (pure white spruce, mixed hardwood-white spruce) at $\alpha > 0.10$.

Session	Habitat Type	Lincoln - Petersen Est. of Abundance		Relative Abundance		Male / Female Ratio		Juvenile / Adult Ratio		Reproductive Females	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Session 1	Spruce	0.0 a	3.1	0.0 a	0.3	0.0 a	0.9	0.0 a	0.1	0.0 a	0.6
May 1998	Mixed	13.0 b	3.1	0.7 a	0.3	1.6 a	0.5	0.0 a	0.1	0.0 a	0.6
Session 2	Spruce	1.0 a	3.1	0.2 a	0.3	0.9 a	0.9	0.1 a	0.1	0.0 a	0.6
June 1998	Mixed	13.2 b	3.1	0.9 a	0.3	1.1 a	0.5	0.1 a	0.1	3.3 b	0.6
Session 3	Spruce	8.0 a	3.1	0.5 a	0.3	1.5 a	0.5	0.1 a	0.1	0.3 b	0.6
July 1998	Mixed	20.5 b	3.1	1.2 a	0.3	1.0 a	0.5	0.3 b	0.1	2.3 a	0.6
Session 4	Spruce	5.7 a	3.1	0.4 a	0.3	2.3 a	0.6	0.2 a	0.1	0.0 a	0.6
August 1998	Mixed	6.1 a	3.1	1.6 b	0.3	1.7 a	0.5	0.1 a	0.1	1.3 a	0.6

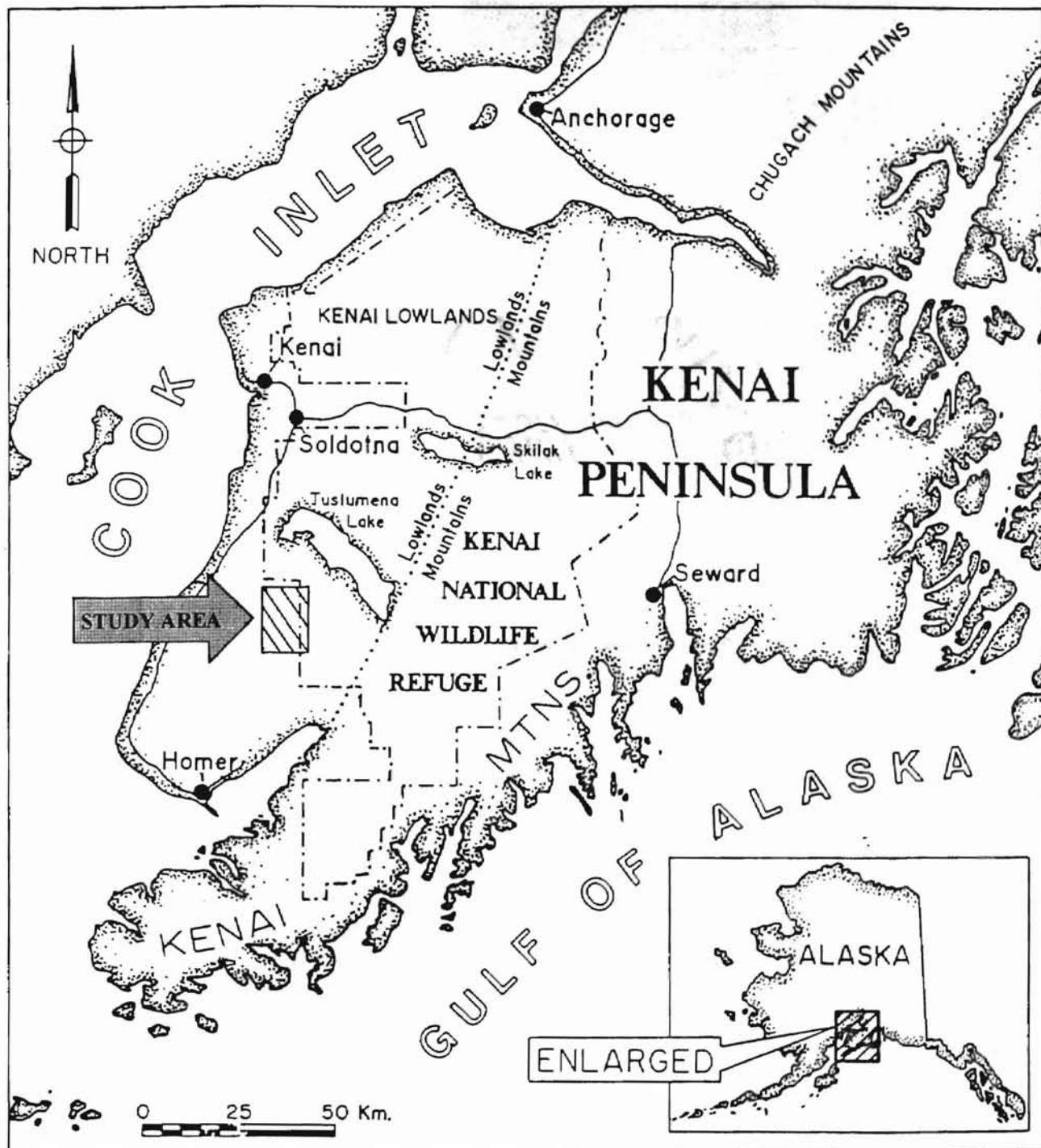
Table 4. Means and standard errors for measures of population estimation parameters for *C. rutilus* in spruce bark beetle infested forests in 1998. Means with the same lower case letter do not differ within a session, among habitat types (pure white spruce, mixed hardwood-white spruce) at $\alpha > 0.10$.

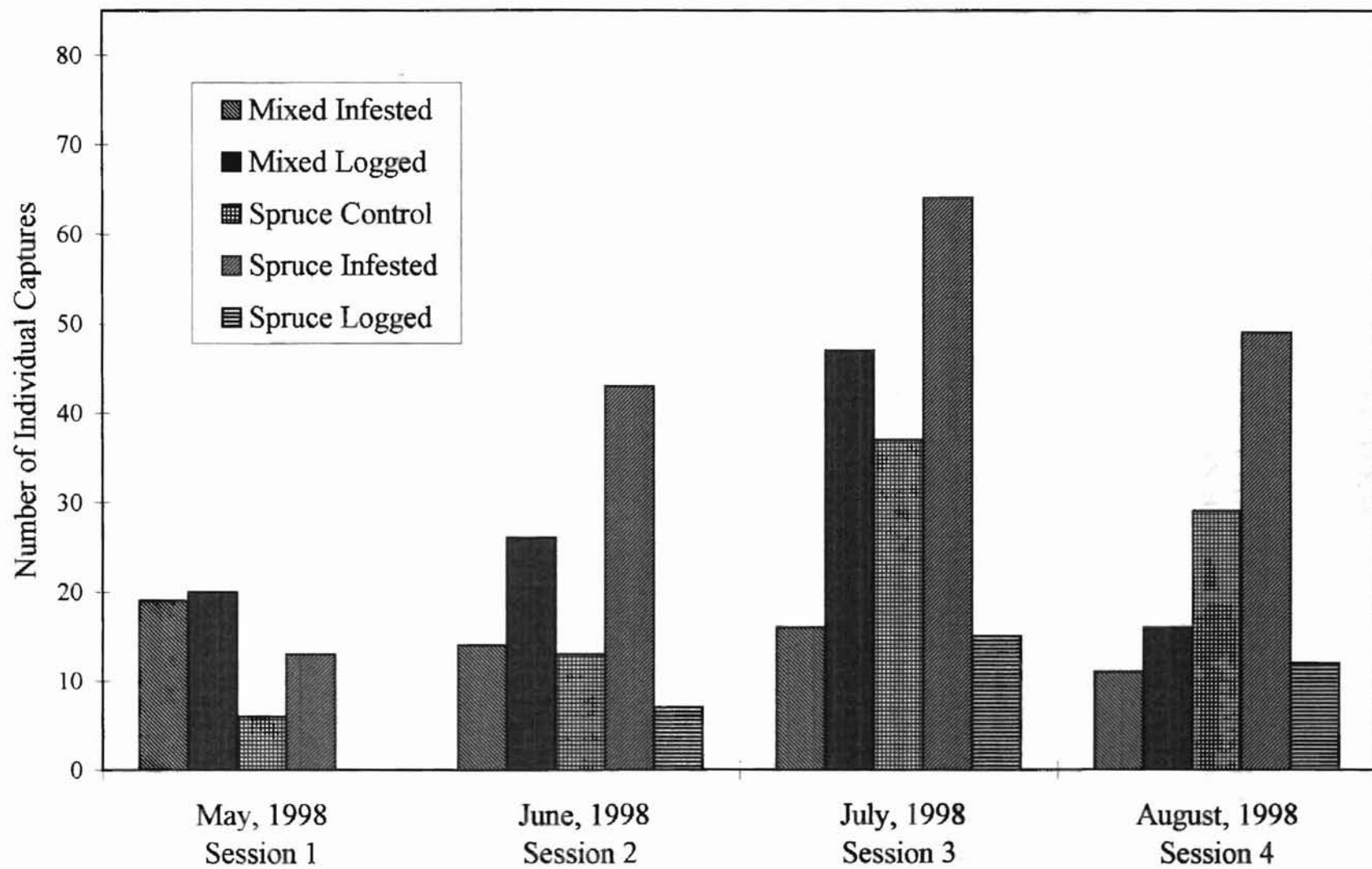
Session	Habitat	Lincoln - Petersen Est. of Abundance		Relative Abundance		Male / Female Ratio		Juvenile / Adult Ratio		Reproductive Females	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Session 1	Spruce	8.6 a	3.1	0.4 a	0.3	1.2 a	0.5	0.0 a	0.1	1.7 a	0.6
May 1998	Mixed	18.0 b	3.9	1.2 a	0.4	0.9 a	0.6	0.0 a	0.1	0.5 a	0.7
Session 2	Spruce	21.2 b	3.1	1.4 a	0.3	1.2 a	0.5	0.4 b	0.1	1.3 a	0.6
June 1998	Mixed	9.4 a	3.9	0.9 a	0.4	0.7 a	0.6	0.2 a	0.1	4.0 b	0.7
Session 3	Spruce	28.4 b	3.1	2.2 b	0.3	0.8 a	0.5	0.2 a	0.1	4.7 b	0.6
July 1998	Mixed	10.6 a	3.9	1.1 a	0.4	0.3 a	0.6	0.6 a	0.1	1.5 a	0.7
Session 4	Spruce	20.3 b	3.1	1.6 b	0.3	1.1 a	0.5	0.1 a	0.1	2.7 a	0.6
August 1998	Mixed	6.6 a	3.9	0.7 a	0.4	3.0 b	0.6	0.1 a	0.1	2.0 a	0.7

Figure Legends

Figure 1. Map of Alaska, showing location of Kenai Peninsula and the study area (after Schwartz and Franzmann 1990).

Figure 2. Plot of number of individual captures ($n = 457$) in the summer of 1998 for *C. rutilus* in pure white spruce forests and mixed hardwood-white spruce forests. Number of individuals captured illustrates seasonal variability in populations among habitat type and treatment.





CHAPTER II

RESPONSE OF WHITE SPRUCE FOREST VEGETATION TO LOGGING AND SPRUCE BARK BEETLE INFESTATION ON THE KENAI PENINSULA, ALASKA

Abstract

Spruce forests on the Kenai Peninsula are currently experiencing high rates of canopy tree mortality from a large-scale insect infestation. Intensive logging efforts have followed the path of the infestation in an attempt to reduce the risk of wildfires and salvage timber value. Our objectives in this study were to assess the impact of spruce bark beetle (*Dendroctonus rufipennis* Kirby) infestation and logging on vegetation and wildlife habitat. Plot locations corresponded to two habitat types: pure white spruce (*Picea glauca*) and mixed white spruce-deciduous (i.e., *Betula papyrifera*). Vegetation measurements included canopy tree composition and density, understory shrubs, and understory herbaceous species. The mixed white spruce-deciduous habitat retained a higher percentage of overstory canopy cover following logging and beetle infestation and had a more uniform composition of shrub species than the pure spruce habitat. Logging in both habitat types produced dense stands of *Calamagrostis canadensis* and a reduction in the abundance of many shrub and herbaceous understory species.

Keywords: *Picea glauca*, *Dendroctonus rufipennis*, *Betula papyrifera*, *Calamagrostis canadensis*

1. Introduction

Natural disturbance events such as fire, earthquakes, wind, glacial retreat, and insect infestations have long shaped Alaskan ecosystems (Fastie and Berg, 1997; Holsten et al., 1991). Of these natural disturbances, the spruce bark beetle (*Dendroctonus rufipennis* Kirby) is considered the most significant cause of mortality in mature spruce forests, with mature white spruce (*Picea glauca*), Sitka spruce (*P. sitchensis*), and Lutz spruce (*P. X lutzii*) the species most susceptible to attack (Reynolds and Hard, 1991; Werner and Holsten, 1990).

Early accounts of spruce bark beetle infestation document widespread and lethal outbreaks (80-100% tree mortality) of beetles as early as the 1920's, with annual tree-ring data showing outbreaks back to the 1850's (Fastie and Berg, 1997). Historically, spruce bark beetles preferred downed and stressed trees (e.g., windthrow, flood events) as hosts. After the 1930's, however, recorded outbreaks have originated from mining, logging, and seismic trail clearing activities (Holsten, 1984).

In 1996, approximately 1.1 million ha of new and ongoing spruce bark beetle infestation was detected on Alaska's Kenai Peninsula (USFS, 1997). Logging to remove all trees infested or susceptible to spruce bark beetles has been recommended to help control the infestation, reduce risk of wildfire, and offset loss of timber resources (Holsten et al., 1996).

Beetle infestation and logging impact forest habitats by releasing understory and early succession plants from overstory shade and competition. Beetle infestation, however, is unique from fire or logging disturbances in that: (1) large trees in older stands

are selectively killed; (2) the understory and soil layers are not directly impacted by the disturbance; (3) plant response and nutrient cycling respond gradually; (4) repeated epidemics help maintain a mosaic of uneven-aged stands; and (5) tree mortality is usually moderate with about 50% of the canopy cover altered (Stone and Wolfe, 1996).

In contrast to beetle infestation, mechanical disturbance (logging and scarification) directly impacts the understory and soil layers and removes a greater portion of canopy cover. This level of disturbance has been found to reduce berries, mosses, lichens, and mushrooms, while increasing shrubs, grass, and debris (Martell, 1983; Bangs, 1979).

After being logged, a site often needs to be scarified to provide a suitable seed bed for tree seedlings (Holsten et al., 1991). However, scarification has been shown to further reduce the moss and lower vegetation layer (Nordstrom, 1995; Martell, 1983). Mosses provide food and thermal cover for many small mammals and are an important habitat component in cold environments (Bangs, 1984; Prins, 1981; West, 1974). For example, habitat changes on the Kenai Peninsula related to the disturbance of moss and understory layers reduced the number of all small mammal species including the northern red-backed vole (*Clethrionomys rutilus*), the most abundant small mammal in the area (Bangs, 1979). The objectives of this study were to examine the relationships between disturbance and upland forest composition, structure, and function.

2. Methods

2.1. Site description

The general location of the study area is the Kenai Peninsula, Alaska, USA. It is located between 59°-61° N and 148°-152° W in what is considered south central Alaska.

Cook Inlet forms the western boundary, Prince Williams Sound the east, and the Gulf of Alaska the south. The Kenai Mountain Range with elevations <2,000 m dominates the eastern two-thirds. The Kenai Lowlands, dominating the western one third, have elevations of 15-100 m and are occupied by numerous lakes left by retreating glaciers (Schwartz and Franzmann, 1991). Annual precipitation occurs evenly throughout the year and averages between 40 and 50 cm. Temperatures range from -30 to 21 C. Winter thaws exposing bare ground are not uncommon, but average snow cover lasts from November through April with depths of 40-60 cm. The growing season is about 88 days from mid-June to early September (Schwartz and Franzmann, 1991). The lowlands contain aspects of both continental and maritime climates and are the location of the study sites.

The primary forest composition of the northern one half of the Kenai Lowlands is a mixture of white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). Typical understory in these deciduous dominated stands includes shrubs such as willow (*Salix* spp.), Labrador tea (*Ledum* sp.), low bush cranberry (*Vaccinium* spp.), rusty menziesia (*Menziesia ferruginea*), and American devilsclub (*Oplopanax horridus*). The percent of white spruce infested by *D. rufipennis* in northern stands tends to parallel the overall percent of white spruce in the stand composition (Boughten, 1996). The wider dispersion and fewer numbers of white spruce make them less available to insect attack. The southern one half of the Lowlands is dominated by mature stands of white spruce with mosses, lichens, and ferns in the understory (Oldemeyer and Regelin, 1987). Southern white spruce stands have $\geq 60\%$ of the total canopy infested with *D. rufipennis* (Boughten, 1996). Across the

entire Lowland region, black spruce (*Picea mariana*) dominates poorly drained sites, while open or disturbed areas often support an herbaceous layer of fireweed (*Epilobium angustifolium*) and bluejoint reedgrass (*Calamagrostis canadensis*).

2.2. Experimental design

The study examined two dry, upland habitats as designated by the Alaska Department of Fish and Game: pure white spruce and mixed deciduous (i.e., *Betula papyrifera*)-white spruce. Pure spruce habitat types (hereafter, spruce) are defined as having a stand composition of ≥ 90 percent or more white spruce. Mixed deciduous-white spruce (hereafter, mixed) habitat types have ≥ 10 percent deciduous trees. Forests infested with *D. rufipennis* (hereafter, infested) experienced canopy mortality by *D. rufipennis* ca. 3 years before the start of the study. Logged treatments were clearcut, ca. 3 years prior, in a way consistent with general forestry practices on the Kenai Peninsula. Unlogged, reference forests (hereafter, control) were undisturbed by any factor including fire for at least the last century. All treatments within each habitat type were at about the same elevation, aspect, age (≥ 100 years), and understory composition before disturbance. Sampled areas were restricted to slopes of less than five percent. Within each habitat type each treatment had three replicates. The infested treatment within the mixed habitat was restricted to two replicates. All sites were separated by at least 500-m to prevent inter-site movements of small mammals (Rexstad, 1996).

During the 1997 field season, vegetation data were collected for five forest treatments (spruce control, logged, and infested and mixed logged, and burned). In 1998, we sampled the 12 original sites and replaced the mixed burned sites with a mixed infested

forest treatment. Measurements were taken for each site using 4 line transects 140-m long and approximately 40-m apart. Five belt transects 30-m long and 2-m wide extended off each line transect at random angles (0-45°) for 20 vegetation belt transects per site.

Vegetation data were collected after the peak in growing season for both 1997 and 1998.

2.3. *Overstory sampling*

Vegetation was measured by layer. The overstory layer included all trees ≥ 5.0 cm diameter at breast height (dbh, 1.37-m above ground); the understory layer included woody species <15.0-cm tall and all herbaceous species. Overstory canopy cover was measured using a single point densitometer. Densitometer readings were taken every third meter of each belt transect. Diameter at breast height of overstory trees was measured to the nearest 0.1-cm and recorded by species. Density was determined by recording the number and species of all trees within each belt transect.

2.4. *Midstory sampling*

The midstory layer included all woody and berry producing stems ≥ 15.0 -cm tall and <5.0-cm dbh. Stem densities were counted using a 1-m by 30-m subplot and recorded by species. Berry production for shrubs was determined by counting all berries produced on shrubs for each belt transect in 1998.

2.5. *Understory-layer sampling*

Percent cover of understory-layer species was estimated similar to Daubenmire (1959) with visual cover classes assigned to all species found within one 0.25-m² frame randomly located along each belt transect. The six cover used were: 1 (0-5%), 2 (5-25%), 3 (25-50%), 4 (50-75%), 5 (75-95%), 6 (>95%). Midpoint values of each cover class were used in the analyses. Total number of downed logs (>5.0-cm dbh) were also

counted for each belt transect. We also estimated number of berries produced by understory shrubs in 1998 by counting the number of berries per plant within each 0.25-m² frame.

2.6. Data analysis

All data were tested for homogeneity of variances using the likelihood ratio test (PROC MIXED, SAS Institute Inc., 1994). Data not meeting this assumption were transformed (square-root or arcsine) prior to further analysis (Steel et al., 1997).

To account for time between years, a repeated-measures analysis of variance was used to test for effects of habitat (mixed or spruce) and forest treatment (logged, infested, or control) among measures of vegetation (PROC MIXED, SAS Institute Inc., 1994). If three-way interactions (habitat type by forest treatment by year) were significant, simple effects were analyzed by performing multiple-comparisons using Fisher's least significant difference (LSMEANS, SAS Institute Inc., 1994). The simple effects were compared with the SLICE option for the LSMEANS statement. In the event of no significant three-way interactions main effects of year and the combined effects of habitat type and forest treatment were examined. Satterthwait's approximation was used in calculating degrees of freedom for the error term. Understory cover data were in estimated percent values, and were arcsine square root transformed prior to testing (Steel et al., 1997). The failure to reject the hypothesis that there is no difference between treatments when false (Type II error) would have serious consequences when examining effects of disturbance and its implications for management (Shrader-Frechette and McCoy, 1992). Due to our small sample size and in consideration of Type II error, we felt strict adherence to $\alpha = 0.05$ was

inappropriate (Scheiner, 1993; Shrader-Frechette and McCoy, 1993). For all tests, we used an alpha of 0.10.

3. Results

3.1 Overstory layer

Canopy cover was significantly greater for the spruce control than all other treatments. The mixed habitat type had greater canopy cover than the spruce habitat within the infested or logged treatments. Both logged treatments had the lowest percent canopy cover overall (Fig. 1). Densities of live and beetle-killed spruce were greater for the spruce habitat than the mixed within the infested treatment. However, densities of live spruce and birch were greater for the mixed habitat within the logged treatment (Fig. 2). Average diameter at breast height (dbh) was greatest for live spruce on the control. Average dbh for beetle-killed and live spruce, and dead and live birch were greater in the mixed habitat than the spruce for infested the treatment (Fig. 3).

3.2 Midstory layer

In 1997, *Ribes laxiflorum* had significantly higher numbers in the spruce habitat than the mixed in the logged treatment. No other significant differences in shrub abundance were observed in 1997. In 1998 however, numerous differences occurred between habitat types. The spruce habitat had more *Betula papyrifera* and *Picea glauca* seedlings than did the mixed habitat in the logged treatment, but the mixed had greater numbers of *Viburnum edule*. The spruce habitat showed significantly greater numbers of *Streptopus amplexifolius*, *Spirea Beauverdiana*, *Menziesia ferruginea*, *Ribes laxiflorum*,

Ribes triste, and *Salix* species than the mixed in the infested treatment, while the mixed only showed significantly higher numbers of *Rubus idaeus* (Table 1).

Within the spruce habitat type, the infested treatment had greater numbers of *Spirea Beauverdiana* and *Ribes triste* than either the control or the logged for both 1997 and 1998. The logged treatment had the greatest abundance of *Betula papyrifera* and *Picea glauca* seedlings in 1998. The control had more *Streptopus amplexifolius* in 1997 and 1998 than either the logged or infested treatments. Within the mixed habitat, only *Rubus idaeus* was more abundant on the infested than the logged treatment (Table 2)

Berry abundance was uniform across habitat types and treatments, except *Viburnum edule*, which showed higher numbers on the mixed logged than mixed infested treatment (Table 3).

3.3. Understory layer

In 1998, *Calamagrostis canadensis* increased on the logged treatment for both habitat types. In 1998, *Epilobium angustifolium* and moss species abundance decreased on the spruce logged, but increased on the mixed logged. Conversely, the spruce habitat had more *Epilobium angustifolium*, woody litter, *Equisetum* species, and *Linea borealis* in 1997, and more herbaceous litter in 1998 within the logged treatment (Table 4).

Within the spruce habitat, the logged treatment had more *Calamagrostis canadensis*, *Epilobium angustifolium*, and woody litter in 1997 than either the control or infested treatments. The spruce control had greater coverage of moss species, *Gymnocarpium dryopteris*, and *Rubus pedatus* in 1997 than either the logged or the infested. In 1998, the logged had more herbaceous litter and *Calamagrostis canadensis*, while the control had the greatest coverage of moss species, *Rubus pedatus*, and *Linea*

borealis. Also in 1998, the infested treatment had greater moss coverage than the logged, but there was no significant difference in moss cover within the mixed habitat type. The logged treatment in the mixed habitat also had more *Calamagrostis canadensis* and *Epilobium angustifolium* than the infested, but the infested had greater amounts of *Rubus pedatus* and *Equisetum* species. Within the mixed habitat in 1997, the logged had more *Calamagrostis canadensis* and *Rubus pedatus*, but the burn had more *Epilobium angustifolium* and *Sanguisorbum stipulata* (Table 5). There were no significant differences observed in the number of downed logs for any of the measured interactions.

The number of *Cornus canadensis* berries were higher on the mixed logged than either spruce logged or the mixed infested treatments. Within the spruce habitat, the spruce control had a greater abundance of *Rubus pedatus* berries than either the logged or infested treatments.

4. Discussion

Of all the factors studied, fire had the most influence on species composition. This is not surprising considering that, at the sampling date, the burned area was in its first growing season while the logged sites were in their third. Consequently, the burned area was at a very early successional stage. The burned sites were characterized by near total removal of canopy and substantial loss of shrub and understory species. Initial species composition appears to be similar to that of other burn studies on the peninsula (West, 1974; Holsten et al., 1995). Of the remaining factors, logging had the greatest influence on species composition. Logged areas had little to no canopy cover and varying amounts of shrub and understory species. Disturbance from spruce bark beetle infestation also

impacted canopy structure and understory species composition, yet did not cause the same level of change as either the burn or logged factors.

4.1. Overstory

Our results agree with Reynolds and Hard (1991) and Werner and Holsten's (1983) research, that large diameter spruce trees are the most susceptible to attack by *D. rufipennis*. Of the areas containing infestation, the mixed habitat had greater mean beetle-killed dbh than in the spruce habitat. However, greater over all densities of spruce trees allow for higher levels of beetle infestation within the spruce habitat. As populations build and large diameter trees become scarce, they begin to attack smaller diameter trees. This explains the lower dbh in the spruce for beetle killed spruce trees than in the mixed habitat.

The mixed habitat had significantly higher percent canopy coverage in the infested and logged treatments than the spruce habitat. This difference is most likely influenced by the presence of live birch trees in the mixed habitat, which tend to have larger canopies than spruce trees. In addition, similar canopy coverage between treatments appears to explain the lack of variability in the response of vegetation to beetle infestation and logging within the mixed habitat type.

4.2. Midstory layer

Variability within the shrub layer was greatest for the logged forest treatments. The greater abundance of *P. glauca* and *B. papyrifera* seedlings on the spruce logged treatment was due to scarification and planting of the sites two years prior. It is uncertain if differences observed between the mixed and spruce logged sites were a result of this additional site treatment, or if it was also a function of habitat type.

In general, shrubs on these study sites tended to be highly aggregated, or clumped, which may explain part of the variability observed. However, the densities of shrub stems on the infested treatments suggest that many of these species prefer the moister/shadier conditions of the spruce habitat. Our results agree with the lack of significant differences in shrub abundance following beetle infestation and fire observed by Holsten et al. (1995).

4.3. Understory layer

With current *D. rufipennis* infestations reaching epidemic levels, there is growing concern on the Kenai Peninsula that formerly economically viable spruce forests will convert to hardwood forests or open stands of *Calamagrostis canadensis* (INFEST, 1997). This phenomenon does not seem to apply to the spruce habitat type, as *C. canadensis* coverage was similar between infested and control treatments for both 1997 and 1998. Our findings were not consistent with previous results that showed *C. canadensis* dominating beetle killed forests north-east of our study area (Holsten et al., 1995). However, Holsten's study spanned a six-year period and was conducted on sites that had been infested ten years prior to the start of vegetation sampling. This could indicate that, similar to reports from Stone (1995), plant response and nutrient cycling are occurring more slowly on our beetle killed sites than on the logged or burned sites.

Logging in both habitat types, on the other hand produced dense stands of *C. canadensis*. These dense stands are of concern because *C. canadensis* is a tall (≥ 1 -m), fast growing species that produces a considerable litter layer. In a relatively short time this litter layer can accumulate, prohibiting light and nutrients access to other species. The litter layer has also been shown to significantly lower the mean soil temperature below the temperature threshold for many plant species (INFEST, 1997; Lieffers et al., 1993).

Furthermore, the lower soil temperature associated with dense stands of *C. canadensis* have been shown to increase spruce susceptibility to *D. rufipennis* infestation (Holsten, 1984). Natural regeneration is also inhibited when the dense litter layer prevents *P. glauca* seed from contacting bare mineral soil (Werner and Holsten, 1983; Zasada and Viereck, 1970).

5. Conclusions

Spruce bark beetles are one of the most significant agents of mortality in mature spruce forests. Large-scale bark beetle outbreaks and logging have various effects on vegetation succession and wildlife habitat. Many of these effects are dependent on the density and diversity of plant species present before the disturbance and the habitat requirements of different wildlife species. For example, elk (*Cervus elaphus*) and moose (*Alces alces*) browse steadily declined over time, while grasses and forbs increased in heavily beetle infested forests in the Rocky Mountains, and the north-central portion of the Kenai Peninsula (Holsten et al., 1995; Schmid and Frye, 1977). Work done on Kenai Peninsula breeding bird populations (Quinlan, 1979) showed the lowest breeding bird density in the grass-forb successional stage, with the highest occurring in the tall shrub-sapling stage.

It was predicted that reduced canopy coverage from logging and beetle infestation would increase light and reduce competition for nutrients, allowing shade intolerant shrub species such as *Salix* spp. to increase. However, this did not appear to occur on our logged sites, or the beetle infested north-central Peninsula and Rocky Mountain sites. Similar to the two aforementioned studies, the increased competition from *C. canadensis*

seemed to be the most significant factor in suppressing the growth of early succession plant species on our study area.

It cannot be assumed that bark beetle infestations are detrimental to wildlife and their habitat. The key to managing forests with high levels of bark beetle infestation is creating a large-scale mosaic of treatments. These could include: logging in areas of high resource value or high fire danger due to urban/wildland interface; letting some areas of beetle infested forest stand to provide habitat for forest interior species until logged areas have sufficiently regenerated; and preventing further infestation using available pest management techniques. A heterogeneous forest with a mosaic of tree ages and health would no longer be uniformly susceptible to future bark beetle infestations.

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Table 1. Means and standard errors for shrub species abundance (number of shrubs per 30-m²) in spruce and mixed habitat types for 1997 and 1998. Means in the same row with the same capital letter do not differ within year across habitat types at $\alpha > 0.10$.

Species	1997				1998				1998			
	Spruce Logged		Mixed Logged		Spruce Logged		Mixed Logged		Spruce Infested		Mixed Infested	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
<i>Streptopus amplexifolius</i>	2.3A	1.2	0.7A	1.3	1.1A	1.2	2.4A	1.2	4.6B	1.2	1.2A	0.5
<i>Spirea Beauverdiana</i>	0.4A	2.3	3.3A	2.4	0.5A	2.3	2.5A	2.3	8.9B	2.3	1.9A	2.9
<i>Menziesia ferruginea</i>	2.3A	2.4	1.1A	2.5	1.4A	2.4	1.6A	2.4	5.3A	2.4	0.6A	3.0
<i>Betula papyrifera</i>	1.0A	2.7	1.5A	2.8	13.7B	2.7	3.2A	2.7	0.3A	2.7	0.2A	3.3
<i>Viburnum edule</i>	1.8A	1.2	2.3A	1.2	0.3A	1.2	4.6B	1.2	1.8A	1.2	3.4A	1.4
<i>Salix spp.</i>	0.4A	1.5	0.2A	1.6	0.5A	1.5	0.4A	1.5	5.8B	1.5	0.2A	1.9
<i>Ribes triste</i>	1.1A	0.6	0.5A	0.7	0.1A	0.6	0.9A	0.6	2.1B	0.6	0.0A	0.7
<i>Picea glauca</i>	0.0A	0.4	0.0A	0.5	2.8B	0.4	0.3A	0.4	1.3A	0.4	0.3A	0.5
<i>Ribes laxiflorum</i>	3.75B	0.5	0.0A	0.5	0.1A	0.5	0.0A	0.5	0.0A	0.5	0.1A	0.6
<i>Rubus idaeus</i>	0.0A	0.2	0.0A	0.2	0.0A	0.2	0.0A	0.2	0.0A	0.2	2.1B	0.3

Table 2. Means and standard errors for shrub species abundance (number of shrubs per 30-m²) in spruce and mixed habitat types for 1997 and 1998. Means in the same column with the same capital letter do not differ within year across habitat types at $\alpha > 0.10$. Means with the same lower case letter in the same row do not differ within a year, across treatments at $\alpha > 0.10$.

Spruce Habitat Type Species	Treatments, 1997						Treatments, 1998					
	Logged		Infested		Control		Logged		Infested		Control	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
<i>Streptopus amplexifolius</i>	2.3Aa	1.2	2.9Aa	1.2	11.7Ab	1.19	1.1Aa	1.2	4.6Ab	1.2	9.2Ac	1.2
<i>Spirea Beauverdiana</i>	0.4Aa	2.3	8.9Ab	2.3	0.0Aa	2.3	0.5Aa	2.3	8.9Ab	2.3	0.9Aa	2.3
<i>Menziesia ferruginea</i>	2.3Aa	2.4	5.4Aa	2.4	0.0Aa	2.4	1.4Aa	2.4	5.3Aa	2.4	5.2Aa	2.4
<i>Betula papyrifera</i>	1.0Aa	2.7	0.5Aa	2.7	0.7Aa	2.7	13.7Bb	2.7	0.3Aa	2.7	0.5Aa	2.7
<i>Viburnum edule</i>	1.8Aa	1.2	1.3Aa	1.2	4.7Aa	1.2	0.3Aa	1.2	1.8Aa	1.2	2.4Aa	1.2
<i>Salix spp.</i>	0.4Aa	1.5	4.4Aa	1.5	0.4Aa	1.5	0.5Aa	1.5	5.8Ab	1.5	0.4Aa	1.5
<i>Fibes triste</i>	1.1Aa	0.6	3.3Ab	0.6	3.0Ba	0.6	0.1Aa	0.6	2.1Ab	0.6	1.3Aab	0.6
<i>Picea glauca</i>	0.0Aa	0.4	0.0Aa	0.4	0.0Aa	0.4	2.8Bb	0.4	1.3Ba	0.4	1.1Ba	0.4
<i>Ribes laxiflorum</i>	3.8Bb	0.5	0.0Aa	0.5	0.1Aa	0.5	0.1Aa	0.5	0.0Aa	0.5	0.0Aa	0.5
<i>Rubus idaeus</i>	0.0Aa	0.2	0.0Aa	0.2	0.0Aa	0.2	0.0Aa	0.2	0.0Aa	0.2	0.0Aa	0.2

Mixed Habitat Type Species	Treatments, 1997				Treatments, 1998			
	Logged		Burn		Logged		Infested	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
<i>Streptopus amplexifolius</i>	0.7Aa	1.3	0.1a	1.5	2.4Aa	1.2	1.2a	0.5
<i>Spirea Beauverdiana</i>	3.3Aa	2.4	1.4a	2.5	2.5Aa	2.3	1.9a	2.9
<i>Menziesia ferruginea</i>	1.1Aa	2.5	0.0a	2.7	1.6Aa	2.4	0.6a	3
<i>Betula papyrifera</i>	1.5Aa	2.8	0.4a	2.9	3.2Aa	2.7	0.2a	3.3
<i>Viburnum edule</i>	2.3Aa	1.2	0.1a	1.2	4.6Aa	1.2	3.4a	1.4
<i>Salix spp.</i>	0.2Aa	1.6	6.3a	1.6	0.4Aa	1.5	0.2a	1.9
<i>Fibes triste</i>	0.5Aa	0.7	0.0a	0.7	0.9Ab	0.6	0.0a	0.7
<i>Picea glauca</i>	0.0Aa	0.5	0.0a	0.5	0.3Aa	0.4	0.3a	0.5
<i>Ribes laxiflorum</i>	0.0Aa	0.5	0.0a	0.6	0.0Aa	0.5	0.1a	0.6
<i>Rubus idaeus</i>	0.0Aa	0.2	0.0a	0.3	0.0Aa	0.2	2.1b	0.3

Table 3. Means and standard errors for berry abundance of understory (number per 0.25m²) and shrub species (number per 30m²). Capital letters in the same row denote comparisons between habitat types, and lower case letters in the same row indicate comparisons within habitat types.

Species	Spruce Habitat Type						Mixed Habitat Type			
	Logged		Infested		Control		Logged		Infested	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Understory										
<i>Rubus pedatus</i>	0.1Aa	1.3	0.7Aa	1.3	6.4b	1.3	0.9Aa	1.3	0.0Aa	1.6
<i>Fungi</i>	0.0Aa	1.0	1.5Aa	1.0	0.4a	1.0	0.0Aa	1.0	3.8Aa	1.2
<i>Cornus canadensis</i>	0.0Aa	0.8	0.0Aa	0.8	0.0a	0.8	4.1Bb	0.8	0.0Aa	0.9
<i>Streptopus amplexifolius</i>	0.0Aa	0.9	3.2Aa	0.9	0.4a	0.9	0.0Aa	0.9	0.0Aa	1.1
<i>Vaccinium vitis idaea</i>	0.0Aa	0.4	0.0Aa	0.4	0.0Aa	0.4	0.8Aa	0.4	0.0Aa	0.4
<i>Ribes triste</i>	0.0Aa	0.1	0.1Aa	0.1	0.0a	0.1	0.0Aa	0.1	0.0Aa	0.1
Shrub										
<i>Streptopus amplexifolia</i>	11.9Aa	8.1	35.6Bb	8.1	62.0c	8.1	14.7Aa	8.1	8.4Aa	9.9
<i>Viburnum edule</i>	0.0Aa	7.9	0.5Aa	7.9	1.1a	7.9	20.6Aa	7.9	0.8Aa	9.7
<i>Sambucus racemosa</i>	0.0Aa	4.6	0.0Aa	4.6	0.0a	4.6	2.3Aa	4.6	15.3Aa	5.6
<i>Ribes triste</i>	0.0Aa	0.5	1.9Aa	0.5	0.3a	0.5	0.1Aa	0.5	0.0Aa	0.7
<i>Vaccinium ovalifolium</i>	0.0Aa	0.6	0.0Aa	0.6	1.6a	0.6	0.0Aa	0.6	0.0Aa	0.7

Table 4. Means and standard errors for understory species abundance (number per 0.25m²) in spruce and mixed habitat types in 1997 and 1998. Means with the same capital letter do not differ within year across habitat types at $\alpha > 0.10$. Values represent the arcsin-square root transformation of the midpoint of percent cover classes.

Species	1997				1998				1998			
	Spruce Logged		Mixed Logged		Spruce Logged		Mixed Logged		Spruce Infested		Mixed Infested	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Herbaceous litter	1.1A	0.1	1.2A	0.1	0.8B	0.1	1.1A	0.1	0.3A	0.1	1.2B	0.1
<i>Calamagrostis canadensis</i>	0.4A	0.1	0.7B	0.1	0.7A	0.1	0.9A	0.1	0.3A	0.1	0.4A	0.1
<i>Gymnocarpium dryopteris</i>	0.3A	0.1	0.1A	0.1	0.3A	0.1	0.4A	0.1	0.6A	0.1	0.5A	0.1
Moss spp.	0.3A	0.1	0.3A	0.1	0.2A	0.1	0.4B	0.1	0.5A	0.1	0.5A	0.1
<i>Epilobium angustifolium</i>	0.5B	0.0	0.3A	0.0	0.3A	0.0	0.5B	0.0	0.3B	0.0	0.1A	0.0
<i>Rubus pedatus</i>	0.2A	0.0	0.2A	0.0	0.1A	0.0	0.1A	0.0	0.4A	0.0	0.3A	0.0
<i>Sanguisorbum stipulata</i>	0.2A	0.1	0.2A	0.1	0.1A	0.1	0.2A	0.1	0.2A	0.1	0.1A	0.1
Wood litter	0.4B	0.0	0.1A	0.0	0.2A	0.0	0.2A	0.0	0.2B	0.0	0.1A	0.0
<i>Equisetum spp.</i>	0.2B	0.1	0.1A	0.1	0.1A	0.1	0.1A	0.1	0.1A	0.1	0.3B	0.1
<i>Linea borealis</i>	0.2B	0.0	0.0A	0.0	0.1A	0.0	0.1A	0.0	0.1A	0.0	0.2A	0.0

Table 5. Means and standard errors for understory species abundance (number per 0.25m²) in spruce and mixed habitat types in 1997 and 1998. Means with the same capital letter in the same column do not differ across year within the same treatment at $\alpha > 0.10$. Means with the same lower case letter in the same row do not differ within a year, across treatments at $\alpha > 0.10$. Values represent the arcsin-square root transformation of the midpoint of percent cover classes.

Spruce Habitat Type	Treatments 1997						Treatments 1998					
	Logged		Infested		Control		Logged		Infested		Control	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Herbaceous litter	1.1Aa	0.1	1.0Ba	0.1	0.8Ba	0.1	0.8Ab	0.1	0.3Aa	0.1	0.4Aa	0.1
<i>Calamagrostis canadensis</i>	0.4Ab	0.1	0.2Aa	0.1	0.2Aa	0.1	0.7Bc	0.1	0.3Ab	0.1	0.2Aa	0.1
Moss spp.	0.3Aa	0.1	0.3Aa	0.1	0.7Ab	0.1	0.3Aa	0.1	0.6Bb	0.1	0.8Ac	0.1
<i>Gymnocarpium dryopteris</i>	0.3Aa	0.1	0.3Aa	0.1	0.6Ab	0.1	0.2Aa	0.1	0.5Ab	0.1	0.6Ab	0.1
<i>Epilobium angustifolium</i>	0.5Bb	0.0	0.1Aa	0.0	0.1Aa	0.0	0.3Ab	0.0	0.3Bb	0.0	0.1Aa	0.0
<i>Rubus pedatus</i>	0.2Ba	0.0	0.5Bb	0.0	0.6Bc	0.0	0.1Aa	0.0	0.4Ab	0.0	0.5Ac	0.0
<i>Sanguisorbum stipulata</i>	0.2Aa	0.1	0.3Aa	0.1	0.2Aa	0.1	0.1Aa	0.1	0.2Aa	0.1	0.2Aa	0.1
Wood litter	0.4Bc	0.0	0.0Aa	0.0	0.2Ab	0.0	0.2Aa	0.0	0.2Ba	0.0	0.1Aa	0.0
<i>Equisetum spp.</i>	0.2Ab	0.1	0.2Ab	0.1	0.0Aa	0.1	0.1Aa	0.1	0.1Aa	0.1	0.1Aa	0.1
<i>Linea borealis</i>	0.2Bb	0.0	0.1Aa	0.0	0.2Ab	0.0	0.1Aa	0.0	0.1Aa	0.0	0.2Ab	0.0

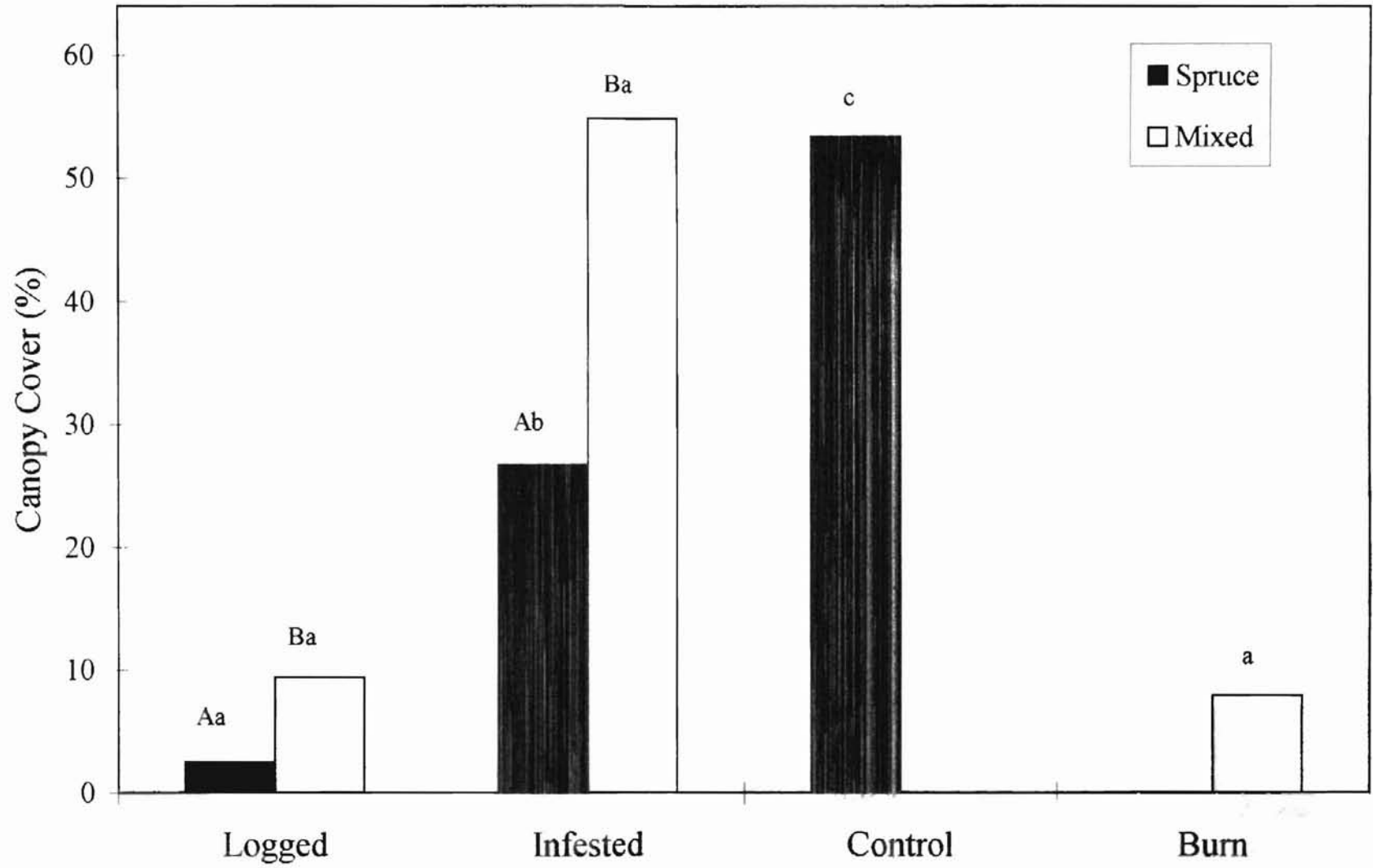
Mixed Habitat Type	Treatments 1997				Treatments 1998			
	Logged		Burn		Logged		Infested	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Herbaceous litter	1.2Aa	0.1	1.3a	0.1	1.1Aa	0.1	1.2a	0.1
<i>Calamagrostis canadensis</i>	0.7Ab	0.1	0.4a	0.1	0.9Bb	0.1	0.4a	0.1
Moss spp.	0.1Aa	0.1	0.0a	0.1	0.4Ba	0.1	0.5a	0.1
<i>Gymnocarpium dryopteris</i>	0.3Ab	0.1	0.0a	0.1	0.4Aa	0.1	0.5a	0.1
<i>Epilobium angustifolium</i>	0.3Aa	0.0	0.4b	0.0	0.5Bb	0.0	0.1a	0.0
<i>Rubus pedatus</i>	0.2Ab	0.0	0.1a	0.0	0.1Aa	0.0	0.3b	0.0
<i>Sanguisorbum stipulata</i>	0.2Aa	0.1	0.4b	0.1	0.2Aa	0.1	0.1a	0.1
Wood litter	0.1Aa	0.0	0.1a	0.0	0.2Ba	0.0	0.1a	0.0
<i>Equisetum spp.</i>	0.1Aa	0.1	0.1a	0.1	0.1Aa	0.1	0.3b	0.1
<i>Linea borealis</i>	0.0Aa	0.0	0.0a	0.0	0.1Ba	0.0	0.2a	0.0

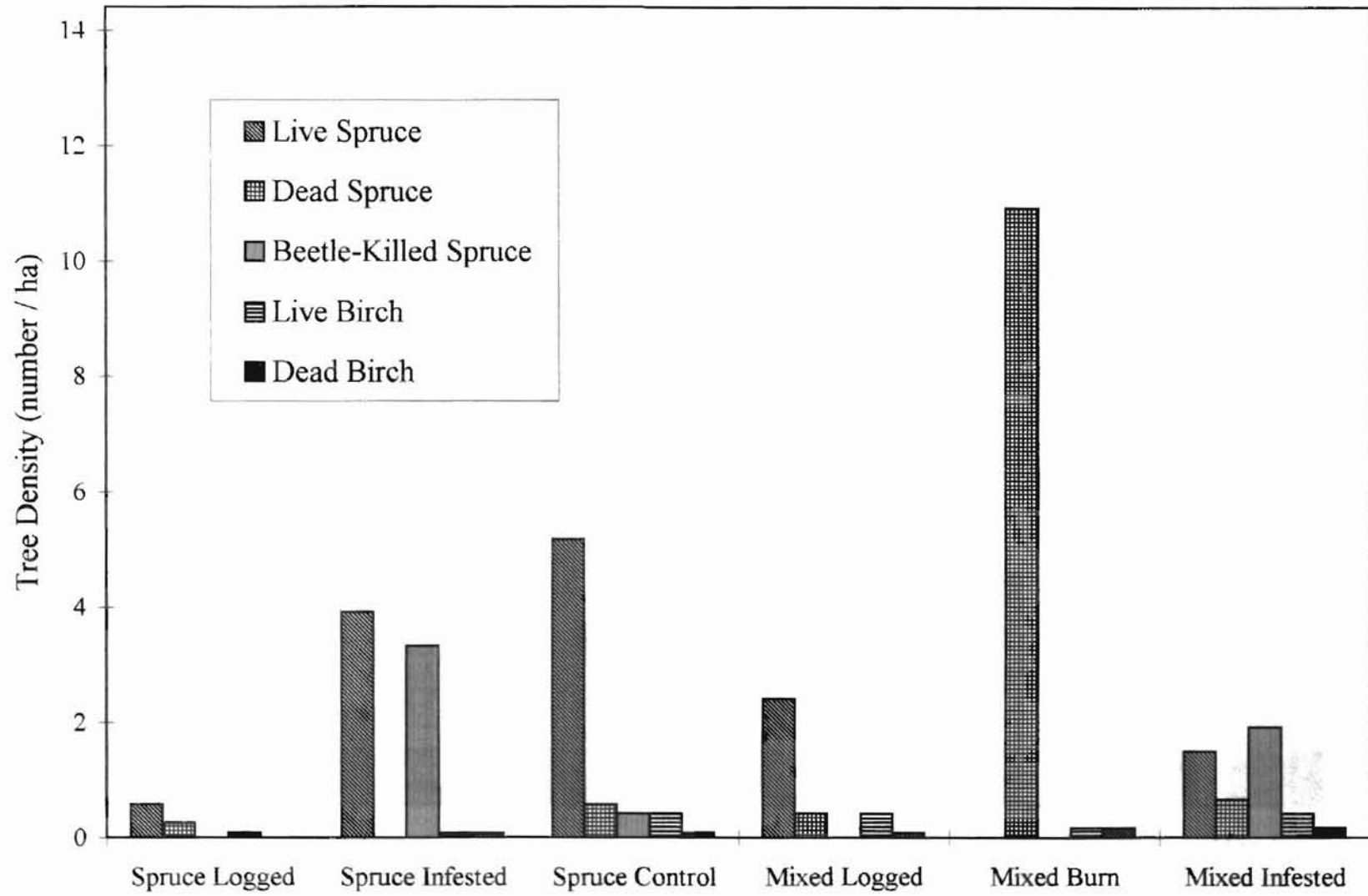
Figure Legends

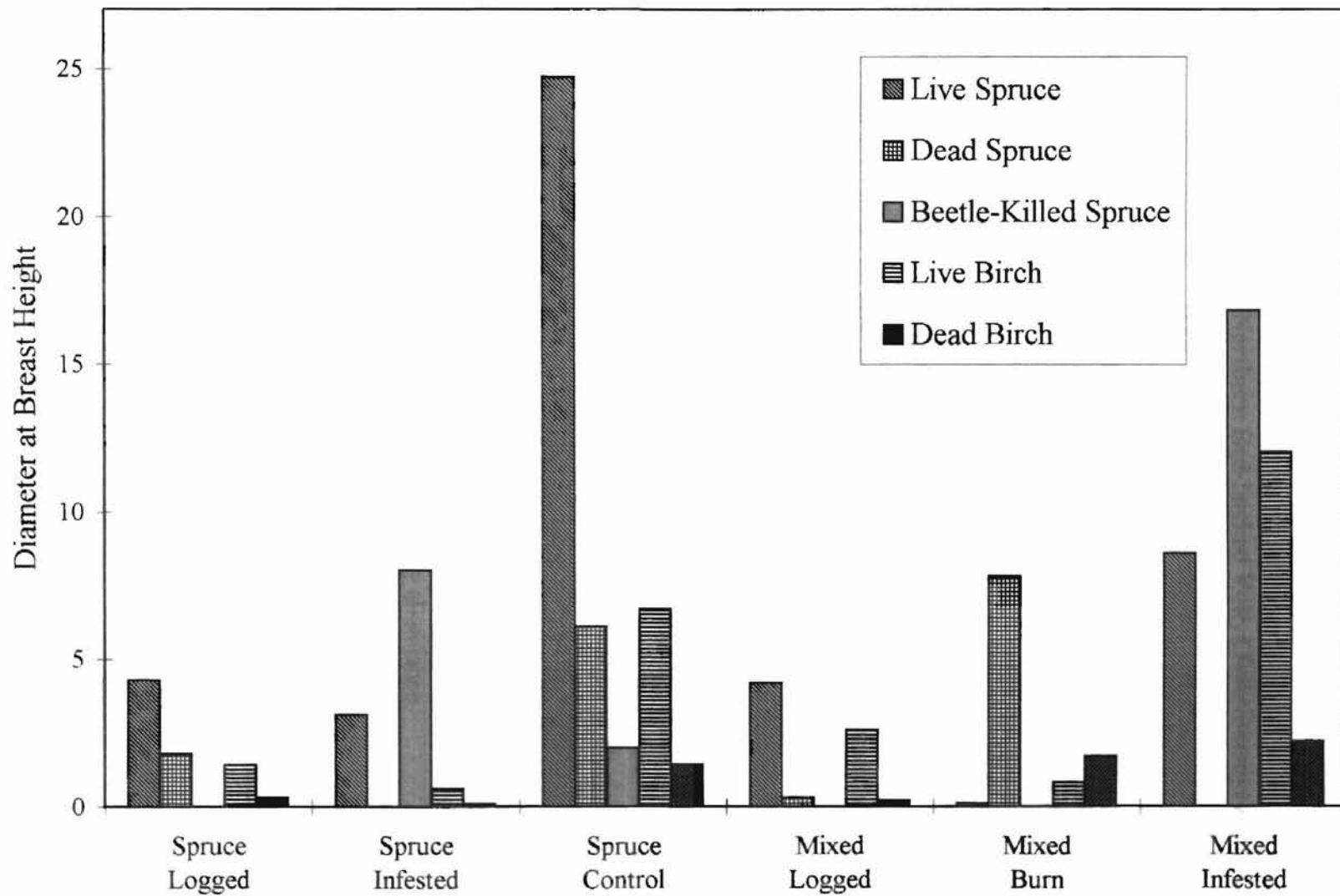
Figure 1. Average canopy coverage in logged, *D. rufipennis* (Kirby) infested, burned, and control forest types on the Kenai Peninsula, Alaska. Columns with the same capital letter do not differ across forest types within the same habitat type at $\alpha > 0.10$. Means with the same lower case letter do not differ within a forest type, across habitat types at $\alpha > 0.10$

Figure 2. Average tree density (number per hectare) for live white spruce, dead white spruce, beetle-killed white spruce, live paper birch, and dead paper birch trees in logged, *D. rufipennis* (Kirby) infested, burned, and control forest types on the Kenai Peninsula, Alaska.

Figure 3. Average diameter at breast height (cm) for live white spruce, dead white spruce, beetle-killed white spruce, live paper birch, and dead paper birch trees in logged, *D. rufipennis* (Kirby) infested, burned, and control forest types on the Kenai Peninsula, Alaska.







CHAPTER III

Habitat Factors Affecting Northern Red-backed Vole, *Clethrionomys rutilus*, Populations on the Kenai Peninsula, Alaska

We examined differences between populations of northern red-backed voles (*Clethrionomys rutilus*) in unlogged, logged, and spruce bark beetle (*Dendroctonus rufipennis* Kirby) infested forests in pure white spruce (*Picea glauca*) habitat, and logged and spruce bark beetle infested forests in mixed hardwood-white spruce habitat. Small mammals were livetrapped on each habitat type and forest treatment 4 times between May and August 1998 to estimate relative population abundance. Capture rates differed significantly among habitats, forest treatments, and trapping sessions. Numbers of reproducing females were also significantly different among habitats, forest treatments, and trapping sessions. Relative abundance was negatively correlated to bluejoint reedgrass (*Calamagrostis canadensis*), while number of reproductive females showed a positive relationship with moss abundance. Relative abundance and numbers of reproducing females were positively correlated with berry abundance.

Key words: Northern Red-backed Vole, *Clethrionomys rutilus*, white spruce, *Picea glauca*, bluejoint reedgrass, *Calamagrostis canadensis*, small mammals, Kenai Peninsula, Alaska

Introduction

There have been outbreaks of the endemic spruce bark beetle (*Dendroctonus rufipennis* Kirby) in south-central and interior Alaska for at least the last century (Fastie and Berg, 1997). Since the 1920's more than 6.6 million ha have been infested, with over 1.1 million ha of ongoing and new infestations reported in 1996 alone (USFS, 1997). Historically, spruce bark beetles attacked downed trees, mainly from recent windthrow or flood events. As populations build, and recent downed trees become scarce, they attack slow growing (usually large diameter) trees or those weakened by drought stress or root damage (Holsten et al., 1991). Today, however, fire suppression and other human activities have created large tracts of old and slow growing forests that are uniformly susceptible to attack (Holsten et al., 1996).

These large tracts of old and weak, slow growing trees have created a food resource that has allowed *D. rufipennis* to reach epidemic proportions. The unprecedented large numbers of beetles and beetle killed trees have created concerns about increased risk of fire, loss of valuable timber resources, and diminished forest aesthetic value (Holsten et al., 1996; Reynolds and Hard, 1991). In response to these concerns, forest managers have prescribed intensive management such as salvage logging, to control the spruce bark beetle infestation (USFS, 1997; Holsten et al., 1991; Reynolds and Hard, 1991). In addition, scarification following logging is often needed to prepare a suitable seed bed for white spruce (*Picea glauca*) seedlings.

The northern red-backed vole (*Clethrionomys rutilus*) is one of the most common and widespread small mammals on the Kenai Peninsula and displays a variety of life history traits that have allowed it to adapt and survive the episodic disturbances that

characterize the Alaskan landscape (Bourliere, 1975; West, 1979; West, 1974). This ability, coupled with the amount of energy they represent in the system due to sheer numbers, enables them to have a substantial impact on predator dynamics, vegetation consumption, and forest decomposition (Staples, 1995; Johnson et al., 1990; Bangs, 1984; Stoddart, 1979; Maser et al., 1978). Our objectives were to assess the effects of disturbance upon the structure of plant communities and associated small mammal populations on the Kenai Peninsula, Alaska.

Materials and Methods

Study area

The general location of the study area is the Kenai Peninsula, Alaska, USA (Fig. 1). It is located between 59°-61° N and 148°-152° W in what is considered south central Alaska. Cook Inlet forms the western boundary, Prince Williams Sound the east, and the Gulf of Alaska the south. The Kenai Mountain Range with elevations <2,000 m dominates the eastern two-thirds. The Kenai Lowlands, dominating the western one third, have elevations of 15-100 m and are occupied by numerous lakes left by retreating glaciers (Schwartz and Franzmann, 1991). The lowlands contain aspects of both continental and maritime climates and are the location of the study sites.

The primary forest composition of the northern one half of the Kenai Lowlands is a mixture of white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and black cottonwood (*Populus trichocarpa*). Typical understory in these deciduous dominated stands includes shrubs such as willow (*Salix* spp.), Labrador tea (*Ledum* sp.), low bush cranberry (*Vaccinium* spp.), rusty menziesia (*Menziesia*

ferruginea) and American devilsclub (*Oplopanax horridus*). The percent of white spruce infested by *D. rufipennis* in northern stands tends to parallel the overall percent of white spruce in the stand composition (Boughten, 1996). The wider dispersion and fewer numbers of white spruce make them less available to insect attack. The southern portion of the Lowlands is dominated by mature stands of white spruce with mosses, lichens, and ferns in the understory (Oldemeyer and Regelin, 1987). Southern white spruce stands have at least 60% of the total canopy infested with *D. rufipennis* (Boughten, 1996). Across the entire Lowland region, black spruce (*Picea mariana*) dominates poorly drained sites, while open or disturbed areas often support an herbaceous layer of fireweed (*Epilobium angustifolium*) and bluejoint reedgrass (*Calamagrostis canadensis*).

Study sites

The study examined two dry, upland habitats, as designated by the Alaska Department of Fish and Game: pure white spruce and mixed deciduous (i.e., *Betula papyrifera*)-white spruce. Pure spruce habitat types (hereafter, spruce) are defined as having a stand composition of ≥ 90 percent or more white spruce. Mixed deciduous-white spruce (hereafter, mixed) habitat types have ≥ 10 percent deciduous trees. Forests infested with *D. rufipennis* (hereafter, infested) experienced canopy mortality by *D. rufipennis* ca. 3 years before the start of the study. Logged treatments were clearcut, approximately 3 years before in a way consistent with general forestry practices on the Kenai Peninsula. Unlogged, reference forests (hereafter, control) have been undisturbed by any factor including fire for at least the last century. All treatments within each habitat type were at about the same elevation, aspect, age (≥ 100 years), and understory composition before disturbance. Sampled areas were restricted to slopes of less than five percent. Within

each habitat type each treatment had three replicates. The infested treatment within the mixed habitat was restricted to two replicates. All sites were separated by at least 500-m to prevent inter-site movements of small mammals (Rexstad, 1996)

Small mammals

We used mark-recapture techniques to assess the influence of logging and *D. rufipennis* infestation on small mammal population dynamics. Within each of the 14 sites we established a 0.09-ha trapping grid. A 30-m buffer zone around each grid was maintained to control for possible habitat edge effect. Each trapping grid consisted of 100 Sherman live traps (8 by 9 by 23-cm) arranged in a 10 by 10 grid and separated by 10-m intervals. Traps were opened for 4, five-day sessions every 2 weeks from 15 May until 9 August 1998. Four trapping sessions were used to characterize small mammal population dynamics throughout the entire season. Traps were baited with commercial rodent chow, supplied with bedding, and checked twice daily (0600, 1800) for animals, and proper functioning of the trap. Passive integrated transponder (PIT) tags (Biomark Inc., Boise, ID; Schooley et al., 1993) were used to permanently mark individual voles. PIT tags caused no noticeable deleterious effects on marked individuals and subsequent identification was rapid and efficient. Species, sex, weight, and reproductive condition were determined for all animals.

Vegetation

During the 1997 field season, vegetation data was collected for four forest treatments (spruce control, logged, and infested and mixed logged). In 1998, we sampled the 12 original sites and added two sites in a mixed infested forest treatment. Each site had one vegetation grid overlapping the corresponding small mammal trapping grid.

Measurements were taken for each vegetation grid using 4 line transects, 140-m long and approximately 40-m apart. Five belt transects 30-m long and 2-m wide extended off each line transect at random angles ($0-45^{\circ}$) for a total of 20 vegetation belt transects per site. Vegetation data was collected after the peak in growing season for both 1997 and 1998.

Vegetation was measured by layer. The overstory layer included all trees ≥ 5.0 -cm diameter at breast height (dbh, 1.37-m above ground); the understory layer included woody species < 15.0 -cm tall and all herbaceous species. Overstory canopy cover was measured using a single point densitometer. Densitometer readings were taken every third meter of each belt transect. Diameter at breast height of overstory trees was measured to the nearest 0.1-cm and recorded by species. Density was determined by recording the number and species of all trees within each belt transect.

The midstory layer included all woody and berry producing stems ≥ 15.0 -cm tall and < 5.0 -cm dbh. Stem densities were counted using a 1-m by 30-m subplot and recorded by species. Berry production for shrubs was determined by counting all berries produced on shrubs for each belt transect in 1998.

Percent cover of understory-layer species was estimated similar to Daubenmire (1959) with visual cover classes assigned to all species found within one 0.25-m^2 frame randomly located along each belt transect. The six cover classes used were: 1 (0-5%), 2 (5-25%), 3 (25-50%), 4 (50-75%), 5 (75-95%), 6 ($> 95\%$). Midpoint values of each cover class were used in the analyses. Total number of logs (> 5.0 -cm dbh) were also counted for each belt transect. We also estimated number of berries produced by understory shrubs in 1998 by counting the number of berries per plant within each 0.25-m^2 frame.

Data analyses

Population densities of small mammals was estimated using relative abundance. Relative abundance was expressed as the number of captures per 100 trap-nights and was determined using the formula of Nelson and Clark (1973). This procedure corrects for closed traps that reduce the number of animals that can be captured. Because we had relatively low capture rates, program CAPTURE did not provide reliable density estimates (White et al., 1982).

All data were tested for homogeneity of variances using the likelihood ratio test (PROC MIXED, SAS Institute Inc., 1994). Data not meeting this assumption were transformed (square-root or arcsine) prior to further analysis (Steel et al., 1997).

To account for time across sessions, a repeated-measures analysis of variance was used to test for effects of habitat (mixed or pure) and forest treatment (logged, infested, or control) on *C. rutilus* relative abundance, and the mean number of reproductive (lactating, or pregnant) *C. rutilus* females (PROC MIXED, SAS Institute Inc., 1994). To account for time between years, a repeated-measures analysis of variance was used to test for effects of habitat (mixed or pure) and forest treatment (logged, infested, or control) among measures of vegetation (PROC MIXED, SAS Institute Inc., 1994). If three-way interactions (habitat type by forest treatment by session) for *C. rutilus* relative abundance or (habitat type by forest treatment by year) for vegetation were found to be significant, simple effects were analyzed by performing multiple-comparisons using Fisher's least significant difference (LSMEANS, SAS Institute Inc., 1994). The simple effects were compared with the SLICE option for the LSMEANS statement. In the event of no significant three-way interactions main effects of session and the combined effects of

habitat type and forest treatment were examined. Satterthwait's approximation was used in calculating degrees of freedom for the error term. Because understory cover data were in estimated percent values they were arcsine square-root transformed prior to testing (Steel et al., 1997).

Pearson correlation coefficients (PROC CORR) were calculated for relationships between *C. rutilus* abundance, canopy cover, understory and shrub species. The failure to reject the hypothesis that there is no difference between treatments when false (Type II error) would have serious consequences when examining effects of disturbance and its implications for management (Shrader-Frechette and McCoy, 1992). Due to our small sample size and in consideration of Type II error, we felt strict adherence to $\alpha = 0.05$ was inappropriate (Scheiner, 1993; Shrader-Frechette and McCoy, 1993). For all tests, we used an alpha of 0.10.

Results

We captured 457 northern red-backed voles 2,227 times on 14 study sites. Other captures included 56 masked shrews (*Sorex cinereus*), 5 short-tail weasels (*Mustela erminea*), and 1 red squirrel (*Tamiasciurus hudsonicus*). The *S. cinereus* were caught mainly on the mixed and spruce logged treatments, with two individuals caught on each of the spruce and mixed infested treatments. Three of the *M. erminea* and the *T. hudsonicus* were caught on the spruce infested treatment, with the other two *M. erminea* caught on the mixed logged, and spruce control.

Relative abundance of *C. rutilus* did not show a significant three-way interaction ($p = 0.1059$). Both the main effect of session and a two-way interaction between habitat

type and treatment influenced relative abundance of *C. rutilus* ($p = 0.0008$ and $p = 0.0751$; respectively). Both the spruce control and the spruce infested experienced a population peak of *C. rutilus* during July. In addition, the infested treatment had the highest *C. rutilus* relative abundance in June and July, but were not greater than the control in May or August. The spruce logged maintained fairly low *C. rutilus* numbers throughout the summer. The logged treatment within the mixed habitat type had greater *C. rutilus* relative abundance than the mixed infested during July and August. Relative abundance of *C. rutilus* was higher on the spruce logged than the mixed logged until August. Conversely, the spruce infested had higher *C. rutilus* relative abundance than the mixed infested during both July and August (Fig. 1).

The combined interaction of habitat type, treatment and session had the greatest influence on the number of reproducing *C. rutilus* ($p = 0.0091$). During the July session, the spruce infested had the highest number of *C. rutilus* pregnant females, while the spruce logged had the fewest for both July and August. Numbers of *C. rutilus* pregnant females did not differ between the mixed logged and infested treatments. Both treatments had the most reproducing *C. rutilus* females during the June session. During the June and July sessions, the mixed logged treatment had more reproducing *C. rutilus* females than the spruce logged. However, the spruce infested had more pregnant and reproducing *C. rutilus* females than the mixed infested treatment (Fig 2).

Relative abundance of *C. rutilus* was positively correlated with abundance of *Ribes triste* berries (Fig. 3b), but was not correlated with *R. triste* stem density ($r = 0.3946$, $p = 0.2204$). *Calamagrostis canadensis* was negatively associated with *C. rutilus* abundance (Table 1), while canopy cover had no correlation ($r = 0.2685$,

$p = 0.3533$). The mean number of reproductive *C. rutilus* females was positively correlated with the abundance of mosses (Fig. 3d), but had no correlation with canopy cover ($r = -0.36251$, $p = 0.2027$). Mosses however, were positively associated with canopy cover (Fig. 3c).

Discussion

Overall, the spruce infested and mixed logged treatments had the greatest relative abundance of *C. rutilus*. However, when the pattern of abundance is broken down by session, *C. rutilus* colonized the mixed logged treatment later in the spring and did not achieve as great a population peak in mid-summer. This, combined with the consistently low numbers on the spruce sites would indicate that the logged treatments are a sink habitat where mortality exceeds reproduction (Pulliam, 1994) for young, or less dominant animals. This pattern was also documented in a recently burned site that provided a suitable summer habitat for dispersing but, was subsequently abandoned in fall (West, 1979). The high levels of *C. canadensis* on the mixed logged sites may have provided adequate cover from predators during summer but did not provide suitable thermal cover in winter.

The spruce infested treatment, while having a higher abundance of *C. canadensis* than the spruce control, still maintained a deep moss layer, which would provide the thermal cover necessary in winter. *Clethrionomys* is a generalist feeder capitalizing on available food sources throughout the year (Bangs, 1984; West, 1982; Martell, 1981; Whitney, 1976). Early spring has been shown as population bottle-neck for *C. rutilus* (West, 1979; Whitney 1976) in south-central Alaska, possibly due to the sudden decrease

in food supply, as over-wintered berries begin to decay and the new berries have yet to mature. *D. rufipennis* over-wintering as larvae and adults and the base of mature spruce trees (Holsten et al., 1991) could explain the high colonization and population peak that occurred on the spruce infested treatment.

On the other hand, consistent population levels on the mixed infested and spruce control sites might indicate a source habitat where reproduction exceeds mortality (Pulliam, 1988). Female *Clethrionomys* exhibit territorial aggression with the onset of the breeding season (West, 1982; Turner et al., 1975; Murie and Dickinson, 1973). This aggressive defense of optimum habitat would force young, or less dominant females into less suitable, or sink habitats. Consequently, the total relative abundance of animals in source habitats would not necessarily increase over time but, their reproductive contribution to the overall population would be significant. Source that contain as few as 10% of the total animal population, can be responsible for maintaining the 90% of the population found in sink habitats (Pulliam, 1988). After the breeding season, intra-specific aggression is reduced, allowing animals to aggregate in higher quality habitat during the winter months. The presence of deep moss layers, both as insulation against cold, and as a food source have been used as indicators of high winter populations and quality habitat (Bangs, 1984; Prins, 1981; West 1979). This agrees with our observations of a high correlation between moss and reproductive females. Moss abundance was also significantly lower on the logged treatments.

In addition, logged treatments had significantly lower abundance of berries. Berries are utilized by *C. rutilus* as an important year round food source (Bangs, 1979; West 1982; Rexstad, 1996). Shrubs such as *Ribes triste* and *Vaccinium ovalifolium*

produce berries that persist on the shrub throughout the winter and early spring, when food resources are lowest. Berry persistence is a key to explaining why berry abundance of *Ribes triste* and *Vaccinium ovalifolium* are positively associated with *C. rutilus* abundance, while stem densities alone do not have a significant effect.

No previous study has examined the relationship between effects of beetle infestation and logging on small mammals on the Kenai Peninsula. This study demonstrates that small mammals do not necessarily respond as predicted to secondary succession following the removal of overstory canopy. The distribution of *C. rutilus* populations among habitat types seem to correspond to localized adaptive requirements rather than general environmental factors. Populations found in pure spruce forests respond negatively to logging disturbance, while seeming to increase with beetle infestation. Further study is needed to determine if the increase on the infested treatment is a function of successful exploitation of a sink habitat, or if it functions as a source habitat. Populations in the mixed habitat showed less overall change in response to disturbance. This appears to be directly related to localized environmental adaptations, rather than a general response predicted of *Clethrionomys*. It appears that until more specific response variables are identified, a large-scale mosaic of logging and standing infestation treatments would provide the best balance between offsetting loss of timber value and retaining important components of *C. rutilus* source habitat.

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Table 1. Pearson's correlation coefficients and p-values for correlations between abundance^a of *Calamagrostis canadensis* and abundance of herbaceous litter, abundance of *Calamagrostis canadensis* and abundance of *Rubus pedatus*, abundance of *Calamagrostis canadensis* and abundance of *Betula papyifera*, abundance of *Calamagrostis canadensis* and abundance of *Sanguisorba stipulata*, and abundance of *Calamagrostis canadensis* and relative abundance of *C. rutilus* populations on the Kenai Peninsula, Alaska (May, 1998 to August, 1998).

Response Variable	Correlation Coefficient (r)	p-value
Herbaceous Litter	0.7380	0.0026
<i>Rubus pedatus</i>	-0.8937	0.0001
<i>Betula papyifera</i>	0.7124	0.0043
<i>Sanguisorba stipulata</i>	-0.5316	0.0504
<i>C. rutilus</i> relative abundance	-0.4849	0.0788
Percent Canopy Cover	-0.3411	0.0001

^a Species abundance is the angular transformation of the mean Daubenmire cover class midpoint.

Table 2. Pearson's correlation coefficients and p-values for correlations between abundance^a of moss species and abundance of herbaceous litter, abundance of moss species and abundance of *Sanguisorba stipulata*, abundance of moss species and abundance of *Epilobium angustifolium*, and abundance of moss species and the mean number of reproductive *C. rutilus* females on the Kenai Peninsula, Alaska (May, 1998 to August, 1998).

Response Variable	Correlation Coefficient	p-value
Herbaceous Litter	-0.6991	0.0054
<i>Sanguisorba stipulata</i>	0.8444	0.0001
<i>Epilobium angustifolium</i>	-0.5794	0.0299

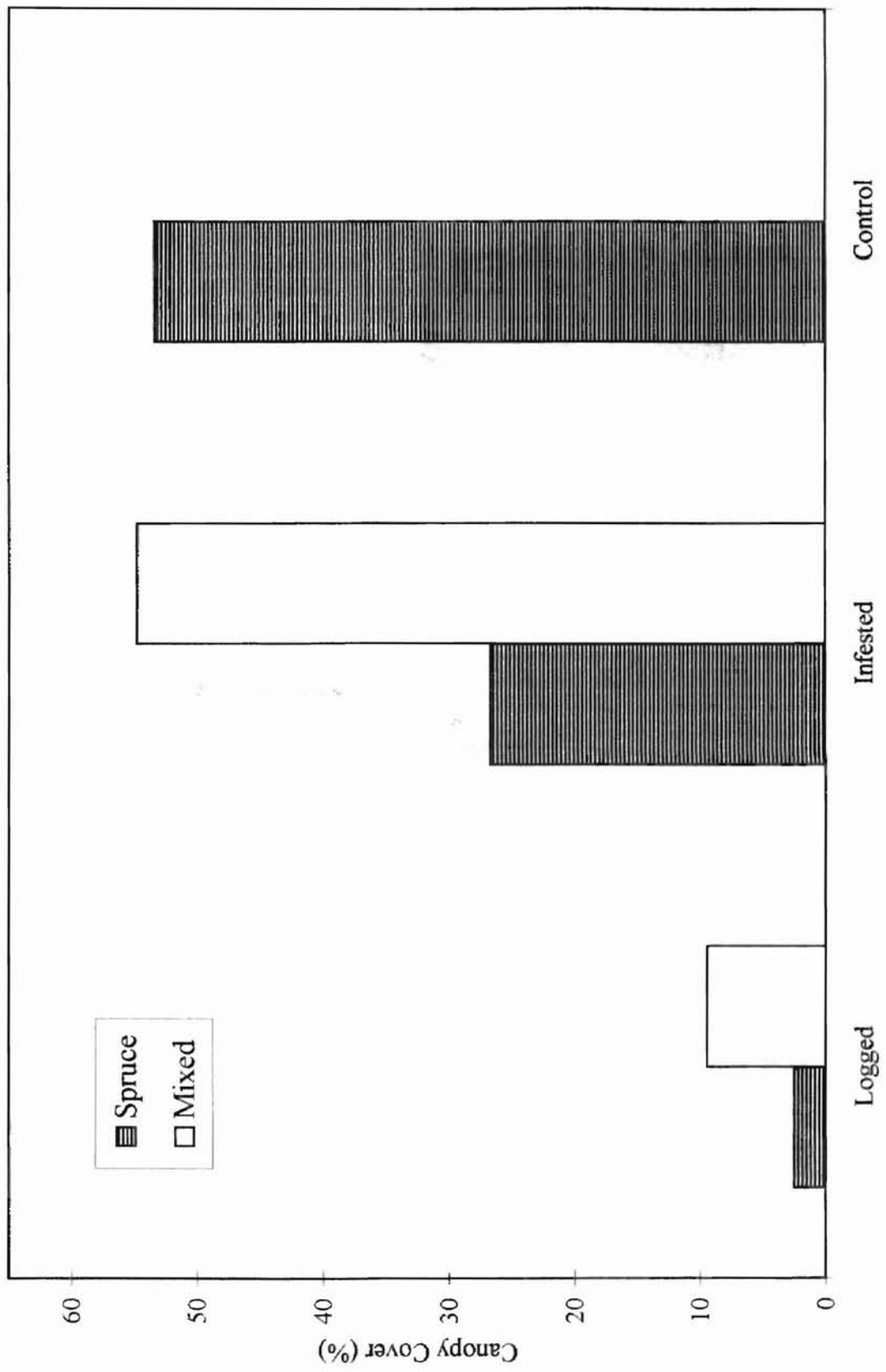
^a Species abundance is the angular transformation of the mean Daubenmire cover class midpoint.

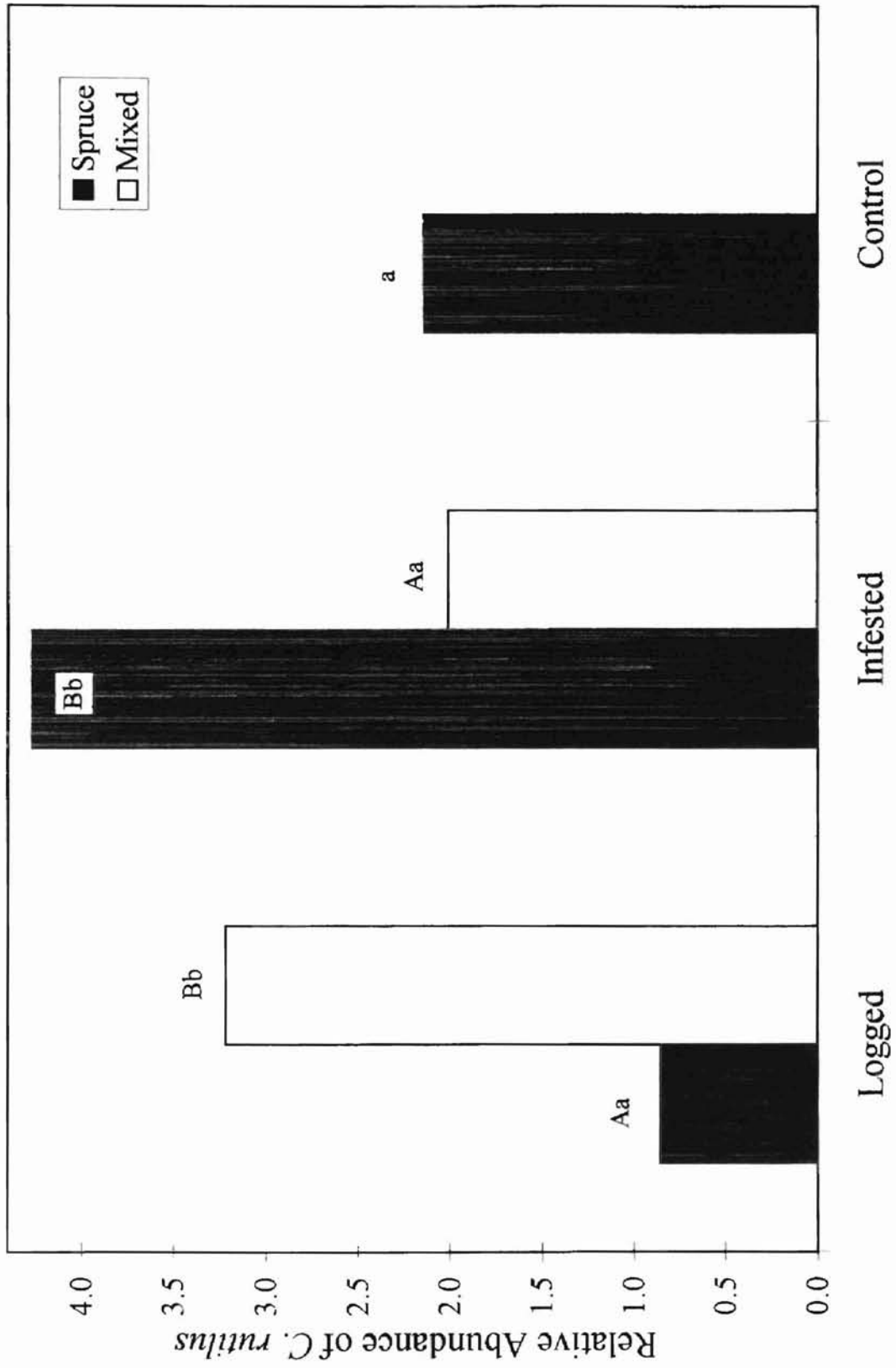
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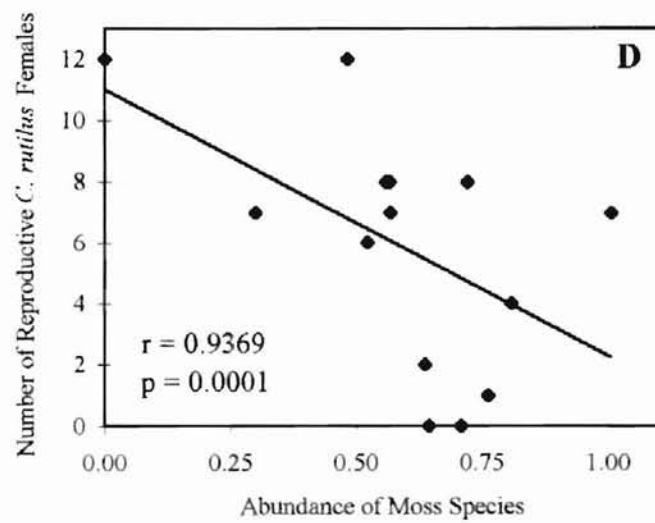
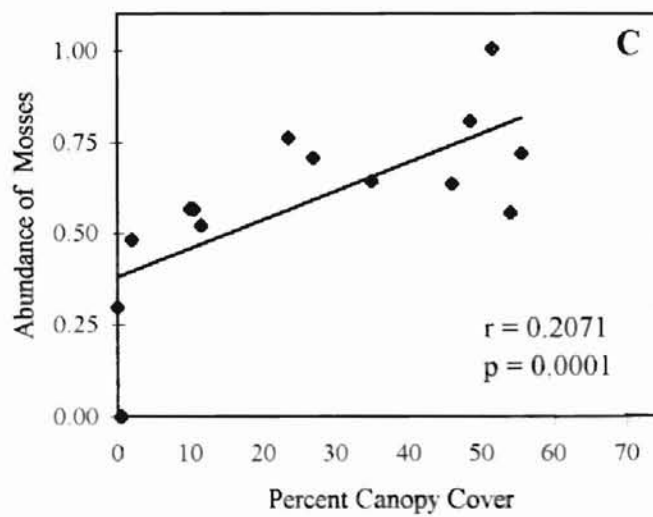
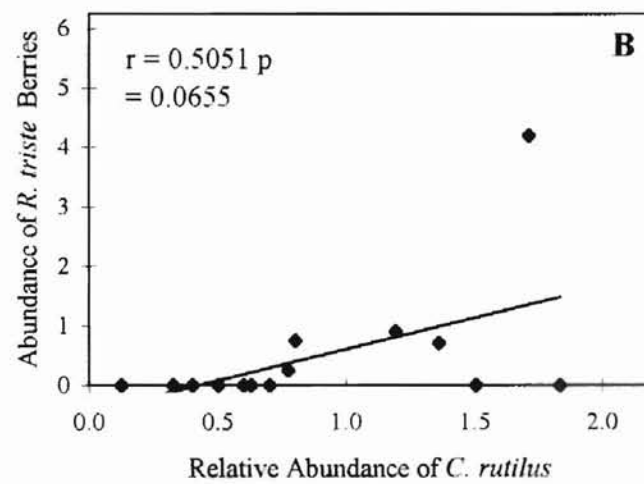
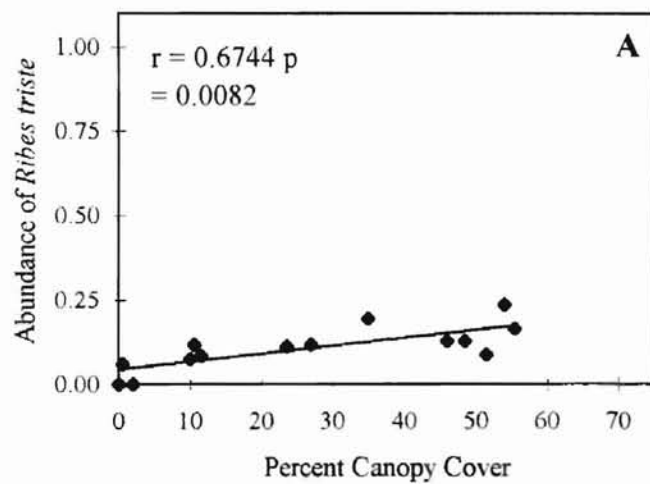
Figure 1. Mean percent canopy coverage in logged, *D. rufipennis* (Kirby) infested, and control forest types on the Kenai Peninsula, Alaska. Columns with the same capital letter do not differ across forest types within the same habitat type at $\alpha > 0.10$. Means with the same lower case letter do not differ within a forest type, across habitat types at $\alpha > 0.10$.

Figure 2. Relative abundance of *C. rutilus* in logged, *D. rufipennis* (Kirby) infested, and control forests on the Kenai Peninsula, Alaska for May, 1998 - August, 1998. Columns with the same capital letter do not differ across forest types within the same habitat type at $\alpha > 0.10$. Means with the same lower case letter do not differ within a forest type, across habitat types at $\alpha > 0.10$.

Figure 3. Correlations of species abundance, environmental variables and relative abundance of *C. rutilus* in logged, *D. rufipennis* (Kirby) infested, and control forest types on the Kenai Peninsula, Alaska. Abundance of midstory and understory species is the angular transformation of the mean Daubenmire cover class midpoint. (A) Correlation of mean percent canopy cover with *Ribes triste* ($r = 0.6744$, $p = 0.0082$) in mixed white spruce-hardwood and pure white spruce habitat types. (B) Correlation of relative abundance of *C. rutilus* (May, 1998 - August, 1998) with abundance of *Ribes triste* berries ($r = 0.5051$, $p = 0.0655$) in mixed white spruce-hardwood and pure white spruce habitat types. (C) Correlation of abundance of mosses with mean percent canopy cover in mixed white spruce-hardwood and pure white spruce habitat types ($r = 0.2071$, $p = 0.0001$). (D) Correlation of moss species abundance with mean number of reproductive *C. rutilus* females in mixed white spruce-hardwood and pure white spruce habitat types ($r = 0.9369$, $p = 0.0001$).







VITA²

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Master of Science

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