RED SQUIRREL DEMOGRAPHY AND BEHAVIOUR IN A MANAGED INTERIOR
DOUGLAS-FIR FOREST OF BRITISH COLUMBIA

By
Jim R. Herbers

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We accept this thesis as conforming to the required standard

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Department of *Forest Sciences*

The University of British Columbia
Vancouver, Canada

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Abstract

I examined the affect of logging intensity and pattern on the North American red squirrel (*Tamiasciurus hudsonicus*) by measuring density and demography from zero to four years after logging, and by measuring territory size, habitat use, and behaviour of individual animals from three to five years after logging. This study was done in an interior Douglas-fir forest (IDF) near Kamloops, British Columbia, Canada. Patterns of tree removal ranged from small patch cuts (<1.6 ha) to individual tree selection (diameter-limit logging) and intensity of tree removal ranged from 20-50% by volume.

From two to four years after logging, red squirrel abundance declined in a 1:1 relationship with the volume of conifer tree removal. Absolute variation in squirrel abundance was highest in the uniform tree removal treatments and lowest in unharvested habitat. Red squirrel recruitment, survival, body weight, and reproduction was unrelated to pattern or intensity of tree removal. In general, these results are consistent with the predictions of the ideal free distribution model of habitat selection. I conclude that logging intensity had the greatest effect on red squirrels, but that uniform tree removal logging may result in poor quality habitat during years of conifer cone crop failure.

From three to five years after logging, red squirrel territory size was best explained by the density of Douglas-fir trees larger than 30 cm diameter-at-breast-height (DBH). Similarly, red squirrels prefered conifer trees larger than 15 cm DBH, with the strongest preference for trees between 30 and 44 cm DBH. Despite large differences in conifer tree density on individual territories, red squirrel activity budgets did not change. Further, red squirrels avoided canopy openings created by logging, but this did not affect their use of forest edge compared to interior forest habitat. I suggest that variation in conifer seed production may explain the relationship between Douglas-fir density and red squirrel territory size, habitat selection, and behaviour. I conclude that logging did not have a biologically meaningful effect on red squirrels, either overtime or across the range of habitats I sampled. However, diameter-limit logging may create poor habitat for red squirrels during years when little or no conifer seed is produced, or when logging dilutes conifer trees further than those sampled in this study. Individual tree selection treatments will likely not remain poor habitat for more than five years if greater than 50, 30 cm DBH Douglas fir trees are retained.

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This thesis is dedicated to my grandparents, Bernice and Jim Barber.

Chapter 1-

General Introduction

In 1960, Chitty outlined two decisive questions in the field of population limitation. First, why do populations not experience indefinite growth, and second, why do densities differ from one habitat to the next? The latter question has been and continues to be a central question in ecology (*e.g.*, Lack 1966, Brown 1969, Fretwell and Lucas 1970, Pulliam 1988, Boutin 1990, Krebs 1996) and wildlife management (*e.g.*, Van Horne 1983). Differences in food abundance and availability between habitats are often cited as important in limiting population densities (Boutin 1990, Sinclair 1989, Krebs 1996). Although there is still considerable debate over the relative importance of these two factors, Boutin (1990) suggests that many vertebrate populations are proximately limited by food abundance.

Logging is often assumed to have a direct negative affect on species that depend on forest resources such as conifer foliage and conifer seeds for food (*e.g.*, Benkman 1993a). Logging practices, however, are varied; thus it is difficult to generalize about the effects of forest harvesting on species that feed on these conifer resources. Two stand structure variables, when manipulated, are likely to affect the quality of habitat for species that feed on conifer foliage and conifer seeds: pattern and volume (intensity) of tree removal. The effects of pattern and intensity of tree removal on wildlife can be measured at the scales of populations and of individuals.

Conifer foliage and seeds can account for as much as 95% of the food items consumed by the North American red squirrel (*Tamiasciurus hudsonicus* Erxleben) during winter months (M. Smith 1968). Thus, the red squirrel is likely sensitive to structural changes in habitat caused by logging. Two studies have examined the effect of logging on squirrel abundance in North America. They reported declining densities that are approximately proportional to the volume of timber removed by the logging (Wolff and Zasada 1975, Patton *et al.* 1985). These descriptive studies suggest that logging negatively effects red squirrel numbers for the first two to three years after cutting (long term effects have not yet been examined). My thesis examines the effect of logging on the red squirrel by measuring density and demographic parameters at a population scale and territory size, habitat use, and behaviour at the scale of individual animals.

Study species

Red squirrels are territorial rodents (*Rodentia: Scuiridae*) that live in boreal and subalpine coniferous forests across most of Canada and Alaska, extending to the Southwest United States along the Rocky Mountains (Gurnell 1987). They vigorously defend sex-specific territories necessary for exclusive access to food resources (C. Smith 1968, M. Smith 1968, Kemp and Keith 1970). Throughout the year they forage on locally abundant foods such as fungi, conifer buds, and rose hips; however, the staple of their diet is conifer seed (C. Smith 1968, Rusch and Reeder 1978, Sullivan 1990). Previous research has demonstrated a positive relationship between conifer cone abundance and red squirrel densities (C. Smith 1968, Kemp and Keith 1970). During autumn, red squirrels in coniferous habitat collect and store conifer cones in central locations on their territories (C. Smith 1968). This cache of cones (a midden) contains food necessary for overwinter survival. Year-round defense of individual territories and their dependence on conifer seed may make red squirrels particularly sensitive to the structural changes in habitat caused by logging.

Opax Mountain Silvicultural Systems Project-Background

The Interior Douglas-fir forests (IDF) of British Columbia have traditionally been logged using individual tree selection (Klenner and Vyse 1998). Recently, several problems have been identified in these managed forests, including an increase in forest pests, insufficient tree regeneration, and a loss of stand structures necessary for biodiversity conservation (Klenner and Vyse 1998). Individual tree selection logging methods are being blamed. In an effort to diminish the magnitude of such problems, managers have begun exploring alternative logging strategies for this forest type.

In 1992, the Ministry of Forests in Kamloops, British Columbia began a long-term project designed to test several types of logging in IDF forests (Figures 1.1 and 1.2; Klenner and Vyse 1998). As one component of this research, populations of three common species of scuirids (*Tamiasciurus hudsonicus*, *Glaucomys sabrinus*, and *Tamias amoenus*) were monitored. Although data were collected on all three species, my thesis specifically examines the population and behavioural response of the red squirrel.
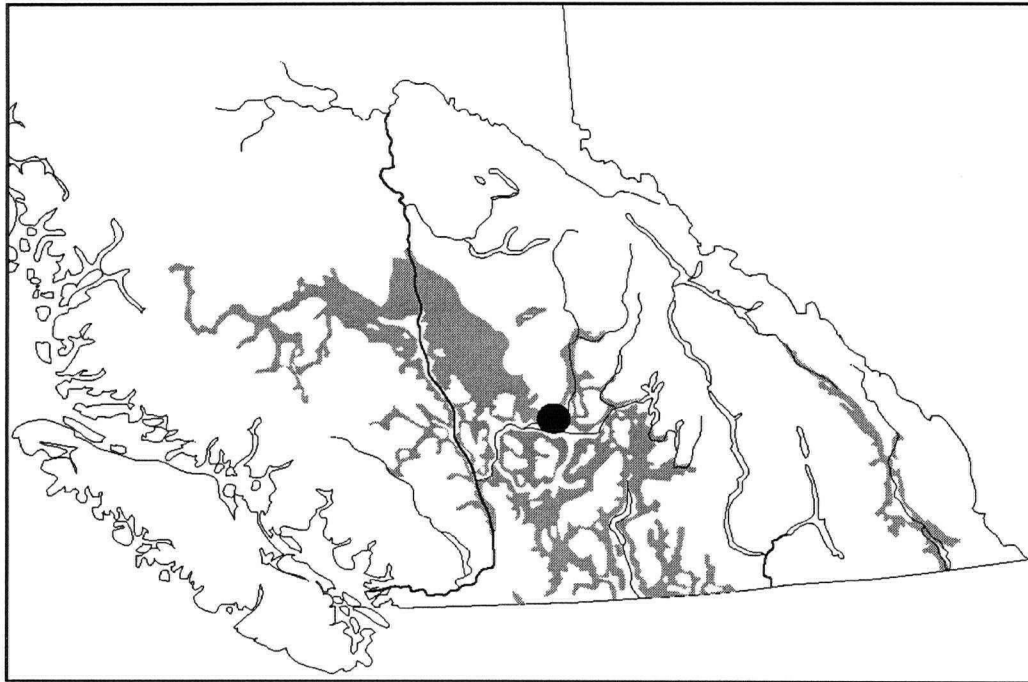
Figure 1.1. Location of the Interior Douglas-fir zone in British Columbia and the location (●) of the Opax Mountain Research Project.
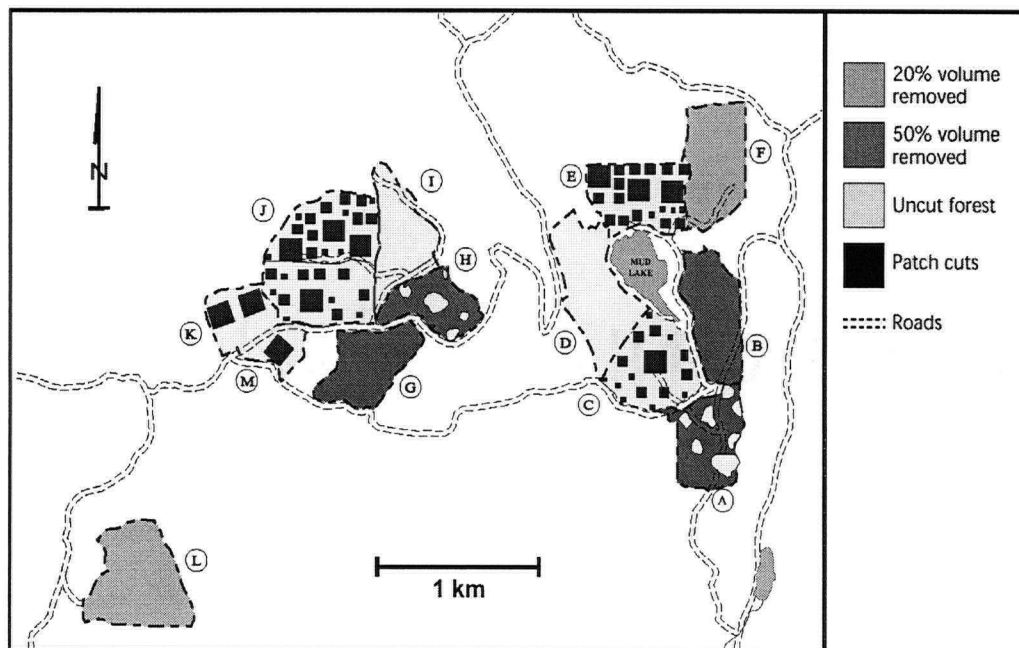
Figure 1.2. Harvesting treatments at the Opax Mountain research site: 20% volume removal using individual-tree selection (units F, L); 35% volume removal, consisting of 75% of the treatment unit area harvested as 50% volume removal using individual-tree selection, and 25% of the treatment unit area retained as uncut reserves (units A, H); 50% volume removal using individual-tree selection (units B, G); patch cuts of 0.1, 0.4, and 1.6 ha on 20% of the treatment unit area (units C, K); patch cuts of 0.1, 0.4, and 1.6 ha on 50% of the treatment unit area (units E, J); uncut controls (units D, I).

Statistical rationale

I have always struggled in university level statistics courses (courses in classical statistics are the only serious option for science students). When I took those courses, I thought that statistics were difficult. I have since come to believe that they are not difficult, but rather they are counter to the way that most ecologists think about the world, and, therefore, confusing. Deming (1975 in Johnson 1999) aptly synthesized this sentiment as follows: "The reason students have problems understanding hypothesis tests is that they may be trying to think". A discussion on hypothesis selection, testing, and interpretation follows.

In the paradigm of classical statistics, data are confronted with two hypotheses, a null hypothesis (or "everything else" hypothesis) and an alternative hypothesis (Cohen 1994). Confining the scientific method to a dual confrontation between a null hypothesis and an alternative hypothesis is at best an exceptionally narrow view of science (Hilborn and Mangel 1997). Chamberlain (1890 in Hilborn and Mangel 1997) first warns against this and argues that science is better served by considering multiple working hypotheses simultaneously. Chamberlain's views have received considerable support (Platt 1964, Lakatos 1978, Connor and Simberloff 1986). Of the advantages associated with outlining multiple hypotheses, the greatest may be to encourage researchers to abandon favorite theories and carefully consider all options and opinions (Platt 1964).

Null hypotheses typically predict no effect of an experimental treatment (*e.g.,* Hicks 1993, pg. 21). This prediction is too often trivial (*i.e.* a nil hypothesis, Cohen 1994) and obscures the question we are really interested in (*e.g.,* how big is the effect of x on species parameter y?). When a nil hypothesis is substituted for a null hypothesis and tested against an alternative it is always false (Cohen 1994). So, by default, researchers using this approach test whether their sample size was sufficient to detect the difference that they already knew existed (Johnson 1999). Although he was not the first, Cohen (1994) suggests as an option, to admit *a priori* that there is an effect of a treatment and develop multiple hypotheses to explain what that difference might be and how meaningful each of the outcomes would be (*e.g.,* Burnham and Anderson 1998).

Few people would argue against the importance of posing testable scientific hypotheses (*e.g.,* strong inference, Platt 1964). There is, however, controversy over how to choose between competing hypotheses. Classical statistics falsify hypotheses by

asking the probability of obtaining the data that have been collected assuming the null hypothesis to be true (Cohen 1994). This method of hypothesis testing results in a true-false dichotomy; however, true-false dichotomies are rarely useful in ecological science. A second method of choosing between competing hypotheses is to measure the degree of empirical evidence for each hypothesis (Burnham and Anderson 1998). This view of statistical confrontation explicitly acknowledges uncertainty in hypothesis selection and allows readers to make more informed decisions about the weight of evidence for each hypothesis.

For these reasons I chose to use alternative methods of statistical analysis that include posing multiple working hypotheses and using a tool that measures the degree of evidence for each hypothesis. In chapters 2 and 3 of this thesis I use means with two standard errors (approximate 95% confidence intervals) to illustrate differences between treatment groups. Where further statistical analysis was required I developed multiple hypotheses (models) and used Akaike's Information Criterion (A.I.C.) to measure the degree of empirical evidence for each.

Chapter 2-

Effects of Logging Pattern and Intensity on Red Squirrel Demography in an Interior Douglas-fir Forest of British Columbia.

Chapter Summary

Red squirrel (*Tamiasciurus hudsonicus*) demography was measured in relation to logging pattern and logging intensity in an interior Douglas-fir (*Pseudotsuga menziesii glauca*) forest at the Opax Mountain silvicultural systems site near Kamloops, British Columbia. Red squirrel populations were sampled with mark-recapture live trapping from one year pre-logging to four years post-logging to obtain estimates of density, recruitment, survival, body weight, and reproduction. Squirrel populations were monitored in two uniform partial cut treatments, two patch cut treatments, one uniform partial cut treatment with reserves, and an unlogged control.

After a lag of one-year and up to four years post-logging, red squirrel density declined in direct proportion to the volume of timber removed but was not affected by pattern of logging. Red squirrel recruitment, survival, weight and proportion of animals in reproductive condition did not appear to be affected by logging. From two to four years after logging, the intensity of tree removal was the primary determinant of red squirrel habitat quality. However, single tree selection harvesting (uniform harvesting) may result in lower quality habitat for red squirrels when compared to patch-cut methods.

In general, these results are consistent with the predictions of the ideal free distribution (IFD) model of habitat selection (Fretwell and Lucas 1970). Logging reduces the intrinsic quality of habitat for red squirrels such that fewer squirrels are supported in harvested areas, while appearing to have a negligible affect on the individual fitness of the animals that remain.

Introduction

Red squirrels (*Tamiasciurus hudsonicus*) are one of the most widely distributed forest vertebrates in North America. This territorial species is primarily associated with boreal and subalpine coniferous forests in the western portion of their range (Gurnell 1987), and is of particular interest in applied ecology for three reasons. First, they are an important component in the diet of less common avian and terrestrial predators, such as the northern goshawk (*Accipiter gentilis*) and the American marten (*Martes americana*), and are themselves predators on smaller vertebrate species (Gurnell 1987, Callahan 1993, Boonstra *et al.* 2001, Doyle and Smith 2001). Second, because conifer cones and buds can account for as much as 95% of the food items consumed during winter months (M. Smith 1968), red squirrels are likely sensitive to the changes in habitat caused by forest harvesting. Third, they have life-history characteristics that enable a detailed investigation of their response to changing stand attributes. In particular they function at a temporal and spatial scale that is practical for researchers and useful to resource managers. For these reasons the red squirrel may be a particularly useful surrogate for examining the effects of alternative methods of logging on vertebrates that require coniferous seed for survival.

During autumn, red squirrels collect and cache conifer cones in middens that are centrally located on their territories (M. Smith 1968). In many of North America's coniferous forests, red squirrels may hoard enough food each autumn to supply resources for the following two winters (M. Smith 1968). Hoarding an overabundance of conifer seed appears to have evolved in response to the fluctuating seed crops that occur in spruce, Douglas-fir and subalpine fir forests (M. Smith 1968, Gurnell 1987). On a large scale, comparative studies have consistently found that red squirrel abundance is related to conifer seed availability (C. Smith 1968, M. Smith 1968, Kemp and Keith 1970, Wheatley 1999). M. Smith (1968) describes a 67% reduction in squirrel abundance following two years of white spruce seed failure, while Kemp and Keith (1970) demonstrate a positive regional correlation between annual red squirrel fur returns and conifer cone crop production. Experimental studies have found a similar relationship between food availability and red squirrel density (Sullivan 1990, Klenner and Krebs 1991, Sullivan and Klenner 1993, Ransome and Sullivan 1997). There is little doubt that red squirrel populations are limited by food availability. However, without

understanding the numerical response of red squirrels to changing stand structure, this information provides limited guidance for future forest management.

Three studies have used territory size to examine the relationship between food availability and red squirrel abundance. C. Smith (1968) and Rusch and Reeder (1978) report a close inverse relationship between seed availability and territory size. Gurnell (1984) failed to find the same association, stating only that most squirrels appeared to have sufficient seed supplies to last a year or longer. Relating territory size directly to food availability is time consuming and difficult. In addition, research that examines the relationship between territory size and food availability is difficult to replicate due to the numerous sources of error involved in quantifying variables such as the number of cones per tree, the number of seeds per cone, the availability of non-coniferous food sources, and interspecific competition. A practical alternative is to relate squirrel demography directly to changes in stand structural attributes such as stand density and tree size.

The association between stand structure and red squirrel demography remains poorly understood because few researchers provide quantitative measurements of the stands they are working in. Mature conifer stands are generally considered optimal habitat for red squirrels, but "mature" is rarely defined (e.g., Brink and Dean 1966, C. Smith 1968, M. Smith 1968, Rusch and Reeder 1978). Further, two studies report no difference in red squirrel density between 20 year-old and greater than 100 year-old lodgepole pine stands, suggesting that these assumptions need further examination (Sullivan and Moses 1986, Ransome and Sullivan 1997). Similarly, Gurnell (1984) states that "low density lodgepole pine is apparently poor quality habitat for squirrels", but does not define what low density is in lodgepole pine forests. Predicting the effect of logging on habitat quality for red squirrels will remain difficult without quantitative descriptions of the habitat being discussed.

Only one study to date has specifically examined the effect of changing tree density on red squirrel density or demography. Wolff and Zasada (1975) report that red squirrel densities in Alaskan white spruce stands decreased by 100% and 66% in clearcut and shelterwood (83 % trees removed: 472 to 81 stems/ha), respectively. However, their study lacked spatial control sites. Kaibab squirrel (*Sciurus aberti kaibabensis*) density in Arizona ponderosa pine forests decreased by 50% with 28% tree removal (240 to 173 trees/ha, Patton *et al.* 1985). These two studies suggest that squirrel densities decline

following the removal of conifer trees, but the role of logging pattern and intensity of tree removal on red squirrel density has not yet been quantified.

In 1992, the B.C. Ministry of Forests began a long-term project designed to test several alternative silvicultural applications in interior Douglas-fir (IDF) forests near Kamloops, British Columbia (Klenner and Vyse 1998). As one component of this research, populations of the North American red squirrel were monitored. This chapter examines how changes in stand structure due to logging affect red squirrel density and demography. The specific goals of this research are to assess the effects of logging pattern and logging intensity on red squirrel density, recruitment, survival, body weight and reproduction in an IDF forest in British Columbia.

Methods

Study area

This study was conducted at the Opax Mountain silvicultural systems research site 20 km NW of Kamloops, British Columbia (Latitude: 120°28'00", Longitude: 50°40'30"). The Opax research site is located in the dry Douglas-fir forest, with an upper-elevation block (1200-1370 m) in the IDF Dry Cool (IDFdk1) biogeoclimatic variant and a lower-elevation block (950-1100 m) in the IDF Very Dry (IDFxh2) variant (Lloyd *et al.* 1990). The sites were originally harvested in 1956-57, likely using a diameter-based single-tree selection (Bealle-Statland, 1998). The upper block is 127 ha, with approximately two-thirds Douglas-fir (*Pseudotsuga menziesii glauca*), and one-third lodgepole pine (*Pinus contorta*) by basal area. The lower block is 132 ha and consists mainly of Douglas-fir with minor components of lodgepole pine, trembling aspen (*Populus tremuloides*) paper birch (*Betula papyrifera*) and hybrid spruce (*Picea glauca* x *engelmannii*). Forest cover is generally open and patchy, resulting from microsite variation and repeated small disturbances such as fire, insects, isolated root rot infections, wind-throw, cattle grazing, and irregular harvest entries (Bealle-Statland, 1998).

Bealle-Statland (1998) provides estimates of post-harvest stand structure for the Opax Mountain Silvicultural site. Average stand volume was highest in the controls (173.0 m³/ha) and lowest in the 50% uniform treatments (71.5 m³/ha), while average stand density was highest in the 20% uniform treatments (4594 stems/ha) and lowest in the 50% patch cuts (2677 stems/ha, Table 2.1).

Table 2.1. Summary of post-harvest stand structure for Opax Mountain Silvicultural Systems Site. Estimates are taken from Bealle-Statland (1998).

	Volume (m3/ha)	Volume Relative to Control (%)	Stems (No./ha)	Stems Relative to Control (%)
Control	173.0	-	1974	-
20%unif.	100.8	-41.7	2297	16.4
20%p.c.	135.8	-21.5	1863	-5.6
35%resv.	91.7	-47.0	1697	-14.0
50%unif.	71.5	-58.7	1502	-23.9
50%p.c.	83.2	-51.9	1339	-32.2

Experimental design and silvicultural systems

The study design is a twice-replicated randomized block design. Each block contains six treatments of approximately 20 ha. The treatments are as follows: 20% mature tree volume removal as uniform partial cuts (20% Uniform); 50% mature tree volume removal as uniform partial cuts (50% Uniform); 35% mature tree volume removal as 50% uniform removal partial cuts with uncut reserves (35% Reserve); 20% removal as patch cuts of 0.1 ha, 0.4 ha and 1.6 ha (20% Patch Cut); 50% removal as patch cuts of 0.1 ha, 0.4 ha and 1.6 ha (50% Patch Cut), and uncut controls. In the uniform partial cut treatments, the largest diameter trees were logged to achieve the volume removal objectives. For a detailed overview of site prescriptions see Bealle-Statland (1998). Collection of pre-treatment data began in the fall of 1993. Harvesting occurred during the winter of 1993-1994. Post-treatment data were collected from 1994 through 1997.

Red squirrel sampling

To monitor scuirid populations, 9-ha trapping grids (300 x 300 m) were established in each of the twelve treatment units. Trapping grids uniformly sampled all site conditions and were representative of the treatment in which they were located. For example, on the 20% patch cut removal treatment, approximately 80% of the trapping grid was in forested habitat, while 20% was in patch cut habitat. One hundred trap stations were systematically established on each of the 9-ha grids with 30 m separating each station. At alternate stations, a single Tomahawk live-trap (model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) was set on the ground, for a total of 50 trap-

stations with an average of 5.5 traps/ha. Traps were baited with a small amount of sunflower seed (approx. 10 g) and a slice of apple, which provided moisture. Each trap contained an insulated nest chamber (a 1-L plastic jar with a small entrance in one end, and half filled with coarse brown cotton). Captured animals readily consumed sunflower seed and apple slices, and squirrels captured during the evening used the nest chambers. Traps were covered with a 50 x 50 cm piece of heavy roofing paper to protect captured animals from wind and rain.

During each trapping session, traps were set for two overnight periods (approximately 1 hour before sunset to 4 hours after sunrise the following morning) on consecutive nights. Overnight trapping was used to sample flying squirrels (*Glaucomys sabrinus*), which are nocturnal, and the early morning trapping was used to sample red squirrels and chipmunks (*Tamias amoenus*). Captured animals were individually ear-tagged, identified to species, and their weight, sex, and reproductive condition recorded before they were released at the point of capture. Each grid was trapped for one session every 4 weeks during the snow-free period of the year (May to October). Twenty-five trapping sessions were conducted from 1993 to 1997. Trapping occurred from October to November in 1993 (2 sessions), from May to October in 1994 (6 sessions), from May to November in 1995 (7 sessions) and 1996 (7 sessions), and from May to July in 1997 (3 sessions).

Data Analysis

General

I examined population density, recruitment, survival, weight, and the proportion of squirrels reproducing to assess the effects of harvesting on red squirrel density and demography. Due to their year-round territorial behaviour, squirrels captured only one time were likely dispersing juveniles or transient adult squirrels that may not reflect the treatment conditions in which they were captured. I defined residents as animals that were captured more than once, and I excluded transients from the demographic analysis. When an animal was identified as resident to more than one treatment in a single year it was assigned to the treatment where it was most frequently captured.

Recruitment for each treatment is expressed as the number of resident squirrels in the population divided by the number of newly enumerated animals. Jolly-Seber (JS) estimates (Seber 1982) of density were calculated using the program JOLLY-88 (Krebs

1988). Yearly treatment density estimates were calculated as an average of monthly JS estimates and standardized for between year variation. The average monthly JS survival rates were calculated for each treatment using the program MEANPHI (Krebs 1989). These estimates were then averaged to derive an overall estimate of monthly survival for each treatment by year. Between-year variation in survival was not corrected for due to lack of variation in control estimates. Individual average weights of adult squirrels (>170 g) were used to calculate mean treatment weights for each sex. The effect of logging on reproduction was examined using data from 1994-1996. Reproduction is calculated as the proportion of adult squirrels reaching breeding condition each year. Scrotal males squirrels, and pregnant or lactating female squirrels were considered to be in breeding condition.

With the exception of density, pre-harvest data were not used for parameter estimation. Pre-harvest estimates of recruitment and reproduction were not available, while sample sizes used to estimate survival and weight were too small to provide accurate information. The remaining demographic parameters were compared between years, and when differences were not found data were combined within treatments. Estimates of recruitment, weight and reproduction were analyzed separately by sex.

Models

Following Burnham and Anderson (1998), I developed a set of candidate models to explain sources of variation between the treatments for each demographic parameter. For each demographic parameter I hypothesize that red squirrel populations:

1. are not affected by intensity or pattern of logging (M_{null})
2. are affected by intensity of logging only ($M_{\%}$)
3. are affected by pattern of logging only (M_{patt})
4. are affected by intensity of logging that interacts additively with pattern of logging ($M_{\%+patt}$)
5. are affected by both intensity and pattern of logging ($M_{\%*patt}$)
6. are best described by a linear regression ($M_{regress}$) with intensity of logging
7. response is described by a linear regression with intensity of logging that interacts additively with pattern ($M_{regress+patt}$)

These hypotheses were tested for each demographic parameter with the exception of red squirrel density. For this parameter, I added two additional models:

8. a negative 1:1 relationship between squirrel density and logging intensity (M_{prop})
9. a negative 1:1 relationship between squirrel density and logging intensity that interacts additively with pattern ($M_{prop+patt}$)

A global model ($M_{\%*patt}$) was developed that allows for complete interaction between harvesting pattern (M_{patt}) and intensity ($M_{\%}$). The null model (M_{null}), M_{patt}, $M_{\%}$, and $M_{\%+patt}$ are all nested in this global model. The remaining models ($M_{regress}$, $M_{regress+patt}$, M_{prop} and $M_{prop+patt}$) were derived independently of the global model. Regression models were developed using a simple linear regression. For all parameters in the regression models (density, recruitment, survival, weight and reproduction) the independent variable is intensity of harvest (0%, 20%, 35% and 50%) and the Y-intercept was fixed at the control estimate of a given parameter. $M_{regress}$ is a continuous and $M_{\%}$ a categorical representation of the same parameter, harvesting intensity. Proportional decline models were derived theoretically from the resource availability literature (*e.g.*, Brown 1964, Hixon *et al.* 1983, and Boutin 1990). These papers suggest that home range or territory size is often a function of resource (commonly food) availability. Territorial hummingbirds have been shown to decrease territory size by 50% when food was doubled (Hixon *et al.* 1983). In a review of terrestrial vertebrates, Boutin (1990) reported a negative relationship between home range/territory size and food availability in 19 of 23 species examined. The numeric functions of these relationships are rarely reported, due in large part to difficulties in quantifying food availability in natural systems. Changes in territory size can result in a corresponding shift in population density (Brown 1969). Here I test for a negative 1:1 relationship between volume of conifer tree removal and red squirrel density. For example, the proportional model predicts a 25% reduction in red squirrel density following 25% removal of timber.

Statistical Analysis

Models are a simplification of reality and therefore necessarily wrong. Given this, I set out to find the model(s) that "best" predict the relationship between logging and each parameter. I define the "best" model(s) as that which is the most parsimonious representation of the data, where parsimony is a compromise between bias (too few parameters) and variance (too many parameters, Burnham and Anderson 1998). This

definition of "best" is used in the following text. The best model(s) were then selected using Akaike's Information Criterion for small sample sizes (AICc), given as

$$AICc = n \log(\hat{\sigma}^2) + 2K + (2K(K+1))/(n-K-1),$$

where

$$\hat{\sigma}^2 = \Sigma \hat{e}_i^2/n \text{ (the maximum likelihood estimate of } \sigma^2)$$

and K is the number of parameters used in the model (Burnham and Anderson 1998). The model with the smallest AICc is considered to best represent the data. The ΔAICc values were calculated as the absolute difference between a given model and the most parsimonious model (ΔAICc=0). Using these values, I then calculated Akaike weights (ω_i), which were used as an index of relative plausibility. The ratio of ω_i between any two models is the relative weight of support of any particular model over another (Burnham and Anderson 1998). Akaike weights were calculated as

$$\omega_i = \exp(-\Delta AICc/2)/\Sigma(\exp(-\Delta AICc/2))$$

Proportions were tested for normality and when not normally distributed were arc-sin transformed to approximate normality (Zar 1984).

Results

General

In 29,800 trap nights, 640 individual red squirrels were captured, for a total of 3,038 capture events. Of the 640 red squirrels captured, 13 (2%) were captured more than once on two treatments within a single year. Ninety eight percent of squirrels were considered resident to one treatment. Ten red squirrels died in the traps as a result of exposure during this study, with juveniles suffering the highest mortality (n=6).

Density

Resident red squirrel abundance[1] did not change from one year pre-harvest (1993) to one year post-harvest (1994). The absolute abundance of red squirrels increased from eight animals per 9 ha in 1993 to 17 animals per 9 ha in 1996. However, relative to controls, squirrel abundance declined on harvested treatments from 1995-1997 (Figure 2.1). Overall, red squirrel densities reached a high of 19 animals (2.1 animals/ha) on a control replicate and a low of two animals (0.2 animals/ha) on a 50% patch cut replicate. From 1995 to 1997, red squirrel density was highest on the controls and consistently low on both 50% removal treatments. Estimates of density in the 20% and 35% removal treatments were generally intermediate between control and 50% treatment densities. There was no consistent relationship between spatial pattern of tree removal and squirrel abundance.

From 1995 to 1996, abundance increased across all treatments, then decreased in 1997 on all treatments except the 50% patch cut (Figure 2.1). However, the magnitude of change in density from 1995 to 1997 varied considerably with the different treatments (Figure 2.2). The lowest yearly variation in density was measured on the controls, with an average difference of 1.5 animals/year, and the greatest variation was measured on the 20% uniform (6.5 animals/year) and 50% uniform treatments (4.2 animals/year). Squirrel abundance on patch cut treatments increased from 1995 to 1996 but remained virtually unchanged from 1996 to 1997.

The best description of these data is that there was no difference in squirrel density between treatments for 1993 and 1994, and a negative 1:1 relationship between harvesting intensity and squirrel density from 1995-1997 (Table 2.2). The next best description of the data is less than one-fourth as likely in all cases and deserves little consideration (Burnham and Anderson 1998). Red squirrel abundance was not affected in the first year after logging, then declined approximately in proportion to the volume of timber removed in subsequent years. Figure 2.3 shows the model that best describes the effect of harvesting on red squirrel density from two to four years post-harvest at the Opax Mountain study site and includes the observed data for comparison.

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[1] Density values are reported as # of Red Squirrels per 9 ha trapping grid unless otherwise noted.

Recruitment

Of the 715 squirrels newly captured (animals could be new captures in more than one treatment) in this study, 348 (49%) were non-resident squirrels. Fifty-seven (16%) of the non-resident squirrels were considered to be resident on an adjacent treatment showing that red squirrels moved between treatments and presumably between the treatments and unharvested habitat adjacent to the study site. Juvenile red squirrels (<170 g) accounted for 19% of all single capture events.

Of 573 squirrels newly captured after harvesting (1994-1997), 341 (60%) were recaptured on the same trapping grid and thus considered to be residents (recruited), while the remaining 40% were single captures and were considered transient. As harvesting intensity increased, there was a pattern of decline in the number of newly captured squirrels (Figure 2.4). Relative to the control, I observed a mean reduction in newly captured squirrels of 12%, 30% and 23% in the 20%, 35% and 50% removal treatments.

Overall the probability of recruitment into a treatment was constant at 60% (Figure 2.4). However, there were sex differences in recruitment rate. The probability of females recruiting into a treatment population was 65.8% (90% C.I. ± 6.8) and for males 54.0% (90% C.I. ± 6.7). The null model describes the recruitment probability between treatments approximately 3 times better than the next best model for females and approximately 4 times better than the next best model for males (Table 2.2).
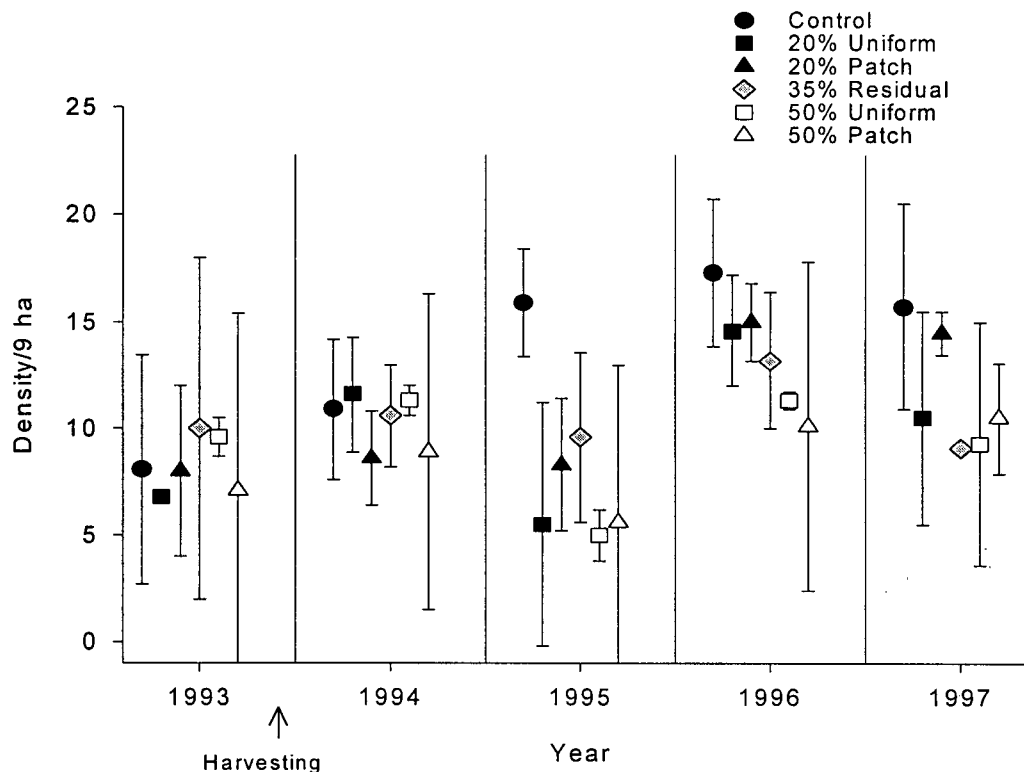
Figure 2.1. Mean Jolly-Seber density (# animals/9 ha trapping grid) estimates for red squirrels at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. Treatment means and standard errors were calculated using 2 replicates (Opax Mountain and Mud Lake). Density estimates for individual replicates were calculated using 1 sample in 1993, 6 in 1994, 7 in 1995 and 1996, and 2 in 1997. Error bars are 2 standard errors.
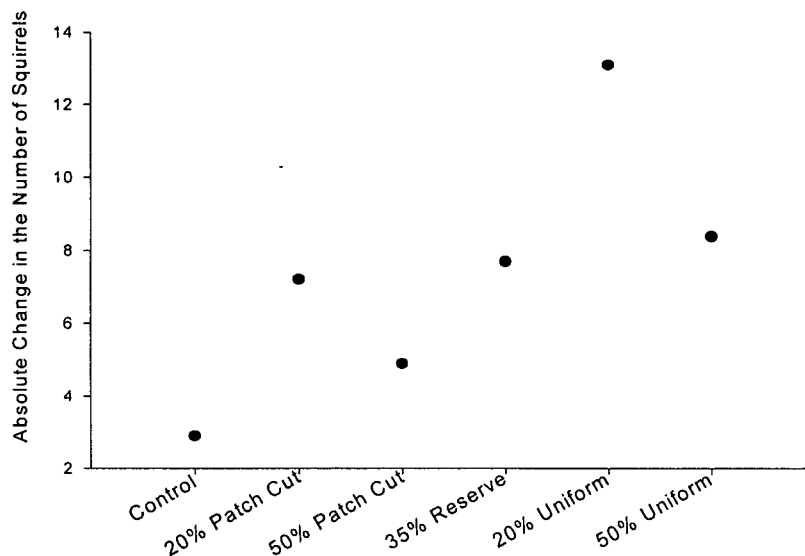
Figure 2.2. Absolute change in estimates of red squirrel density from 1995 to 1997 at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia.
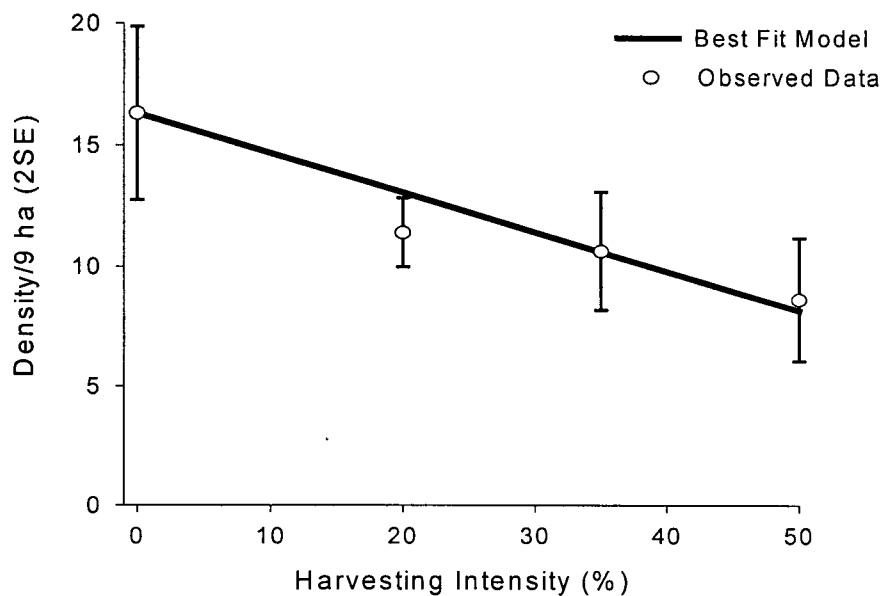
Figure 2.3. Best explanation of the relationship between forest harvesting intensity (% volume removed) and red squirrel density from 1995-1997 at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia (2-4 years post-harvest). Data are included for comparison. Error bars are 2 standard errors.
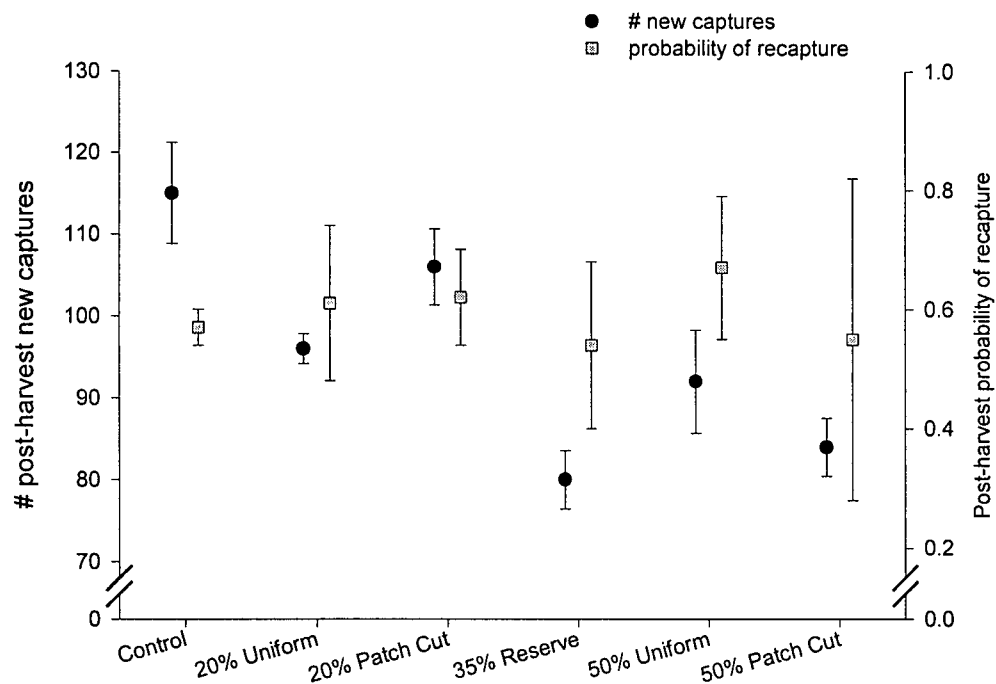
Figure 2.4. Total number of newly captured red squirrels and the proportion of red squirrels recruited (caught >1 times/# new captures) into treatment populations at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia from 1994-1997. Error bars are 2 standard errors.

Table 2.2. Summary of model testing for red squirrel density, survival, weight, reproduction, and recruitment at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia.[*]

		Model	K	AICc	ΔAICc	AICc Wts
Recruitment 1994-1997	Female	**M_{null}**	**2**	**-44.5**	**0**	**0.68**
		$M_{regress}$	3	-42.7	1.8	0.28
		$M_{\%*patt}$	7	-10.8	33.7	0.00
	Male	**M_{null}**	**2**	**-44.9**	**0**	**0.84**
		$M_{regress}$	3	-41.3	3.6	0.14
		$M_{\%*patt}$	7	-22.3	22.6	0.00
Density	1993 Pre-harvest	**M_{null}**	**2**	**31.4**	**0**	**0.84**
		$M_{regress}$	3	35.2	3.8	0.13
		$M_{\%*patt}$	7	66.1	34.7	0.00
	1994 Post-harvest	**M_{null}**	**2**	**24.3**	**0**	**0.79**
		$M_{regress}$	3	27.9	3.6	0.13
		$M_{\%*patt}$	7	57.1	32.8	0.00
	1995-1997	**M_{prop}**	**2**	**21.7**	**0**	**0.79**
		$M_{prop+patt}$	3	24.4	2.8	0.20
		$M_{\%*patt}$	7	52.7	31.0	0.00
Survival	1994-1996	**M_{null}**	**2**	**-91.1**	**0**	**0.83**
		$M_{\%*patt}$	7	-63.4	27.7	0.00
Weight	Female	**M_{null}**	**2**	**36.3**	**0**	**0.92**
		$M_{\%*patt}$	7	64.3	28.0	0.00
	Male	**M_{null}**	**2**	**38.7**	**0**	**0.56**
		$M_{regress}$	**3**	**39.4**	**0.7**	**0.39**
		$M_{\%*patt}$	7	70.0	31.2	0.00
Reproduction	Female 1994	**$M_{regress+patt}$**	**3**	**72.5**	**0**	**0.59**
		M_{patt}	**4**	**73.7**	**1.2**	**0.32**
		$M_{\%*patt}$	7	84.5	12.0	0.00
	Female 95/96	**M_{null}**	**2**	**69.5**	**0**	**0.79**
		$M_{regress}$	3	72.9	3.4	0.15
		$M_{\%*patt}$	7	102.1	32.6	0.00
	Male 1994	**M_{null}**	**2**	**73.53**	**0**	**0.87**
		$M_{regress}$	3	77.86	4.330	0.10
		$M_{\%*patt}$	7	102.09	28.56	0.00
	Male 95/96	**M_{null}**	**2**	**63.1**	**0**	**0.88**
		$M_{regress}$	3	67.5	4.5	0.10
		$M_{\%*patt}$	7	84.2	21.1	0.00

[*] Models are sorted by increasing number of parameters with $M_{\%*patt}$ being the global model. Only models that have $\geq$ 0.10 AICc weights are shown, with the global model included for comparison. Parameters include volume of timber removed (%), pattern of timber removal (patt) with "+" denoting additive effects and "*" denoting complete interaction. The most parsimonious model(s) are shown in bold.

Survival

Due to low sample sizes, precise estimates of survival (losses were due to both deaths and emigration) for 1993 and 1997 were not possible to generate. Little variation in monthly survival rates was observed between treatments or between years from 1994 to 1996 (Figure 2.5). Estimates of monthly survival were over 90% in all treatments. Average overwinter survival (December to April) was 92%, as was the average monthly survival (May to November) of resident red squirrels from 1994 to 1996. Overall, annual survival was approximately 51%, and appeared not to be affected by harvesting.

Of the candidate models tested for the effects of harvesting on red squirrel survivorship, the null model best described the data (Table 2.2). No other models of survival used in this analysis should be considered.

Body Weight

The average body weight for adult resident red squirrels was 213.2 g for females and 218.0 g for males. There was no consistent pattern in mean female body weight between harvesting treatments (Figure 2.6). Mean male body weights declined from 223.5 g on controls to 217.1 g on the 35% reserve and 50% patch cut treatments; however, variation in the data make this trend uncertain. The null model best describes female body weight while the null and regression models deserve equal consideration for male body weight (Table 2.2).

Reproduction

The overall proportion of female red squirrels in reproductive condition was 31% (2SE = 11.7) in 1994 and increased to 83% (2SE = 8.1) for 1995/1996 (Figure 2.7a). There appeared to be no treatment effect in 1995/1996. However, the $M_{regression+pattern}$ and $M_{pattern}$ models are good explanations of female reproductive condition in 1994 (Table 2.2). In 1994, the regression model with an additive term for the pattern of harvest predicts separate responses for uniform (y=(-0.2017x + 65) + 22.9%) and patch-cut (y=(-0.2017x + 65) - 22.9%) logging while holding reserve harvesting constant. In the absence of an additive term, the linear regression for both uniform and patch-cut logging had an intercept at 65% and a slope of –0.2. The additive term shifts the regression intercept to 88% and 42% for uniform and patch-cut harvesting respectively.

This model suggests that female reproductive rates were 46% lower in patch-cut treatments than in uniform treatments for the first year after harvesting. The $M_{pattern}$ model predicts the same difference (46% lower in patch-cut treatments) in reproductive rates for the first year after harvesting.

The overall proportion of male red squirrels that were reproductively active was high (94%, 2SE = 3.4) during all three years of this study (Figure 2.7b). The null model is four to five times better than any other model at describing the proportion of male squirrels in reproductive condition for all years of this study (Table 2.2).

An overall summary of the results is given in Table 2.3.
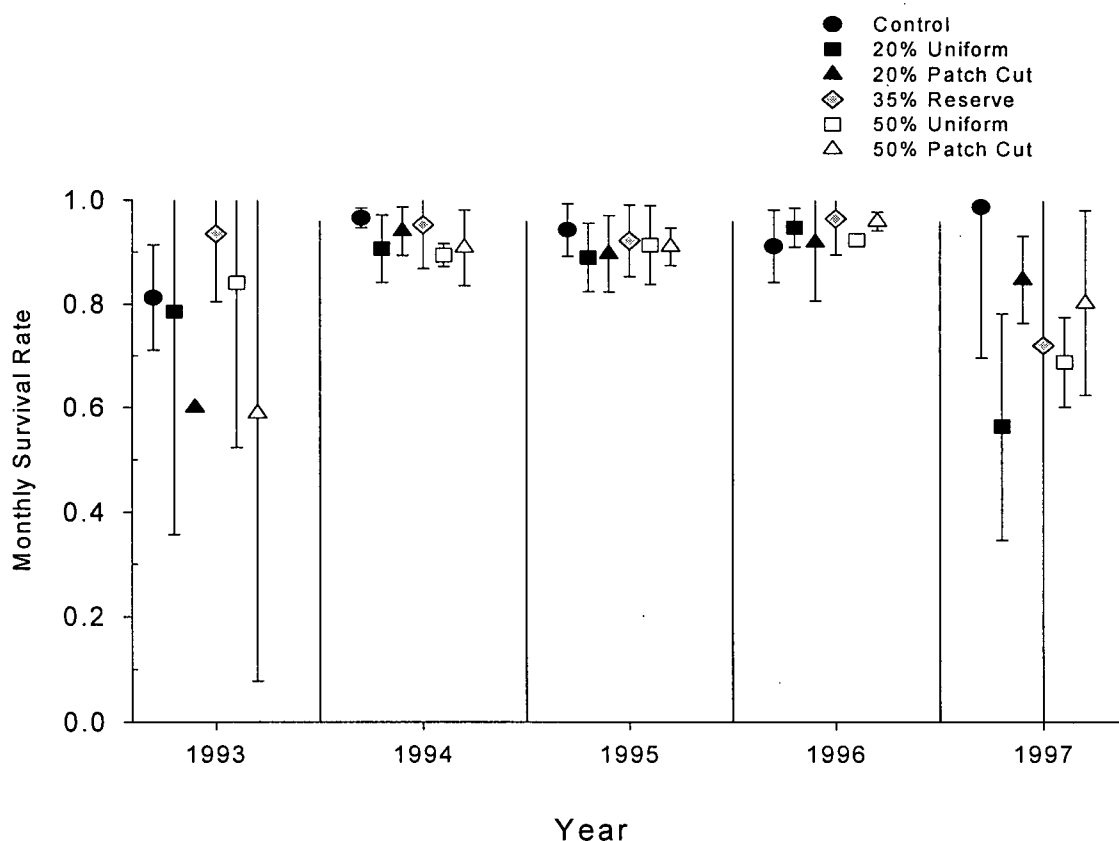
Figure 2.5. Mean Jolly survival estimates for red squirrels at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. Treatment means and standard errors were calculated using 2 replicates. Monthly survival estimates for individual replicates were calculated using 1 sample in 1993, 6 in 1994, 7 in 1995 and 1996, and 1 in 1997. Error bars are 2 standard errors.
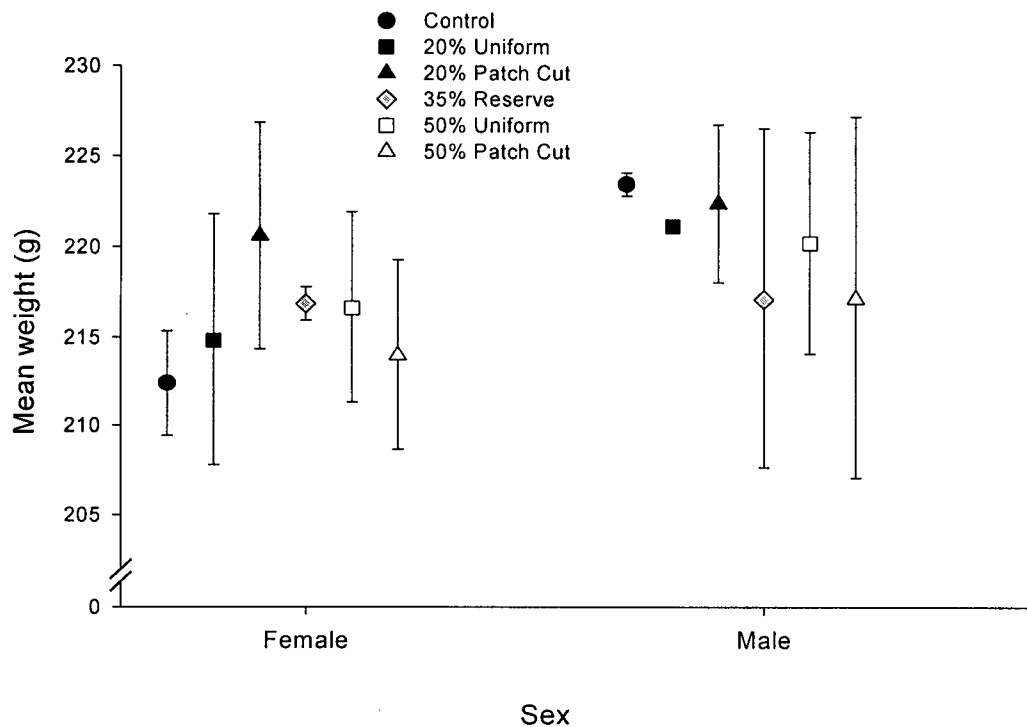
Figure 2.6. Mean body weight for adult red squirrels at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. Values are calculated using a mean body weight for each individual animal caught from 1994-1997. Juvenile weights are excluded (<170g) and pregnant females are included. Error bars are 2 standard errors.
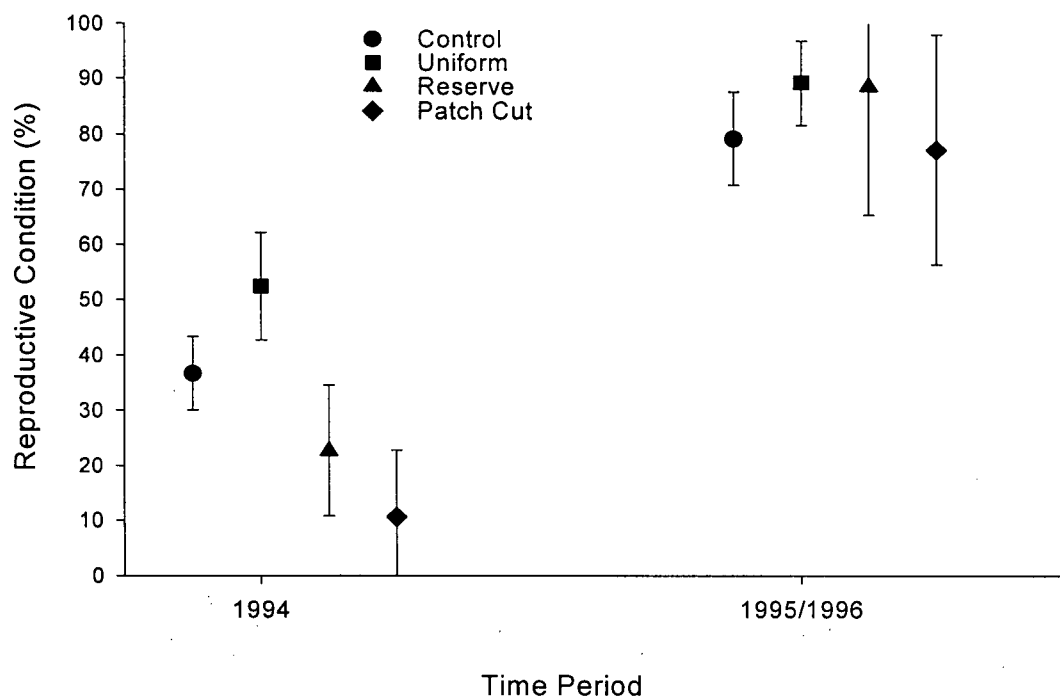
Figure 2.7a. Percent of adult female red squirrels in reproductive condition at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. Error bars are 2 standard errors.
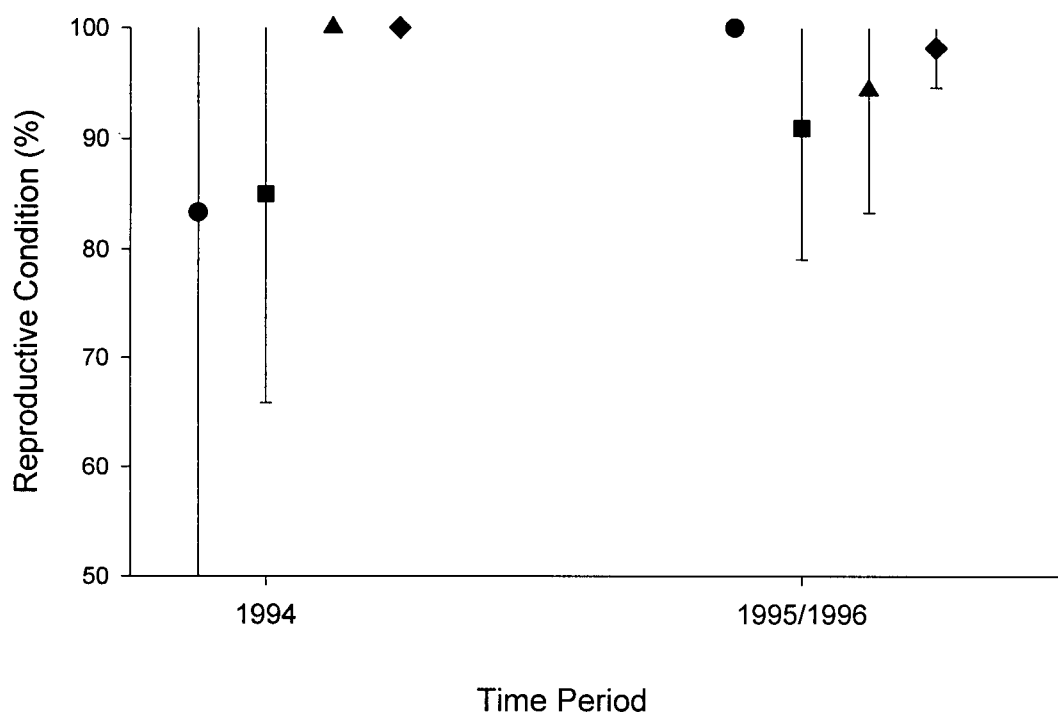
Figure 2.7b. Percent of adult male red squirrels in reproductive condition at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. Error bars are 2 standard errors.

Table 2.3. Summary of red squirrel demography for Opax Mountain Silvicultural Systems Site.

	Density (No./9ha)	Absolute change in Density	Recruitment New Cps.	Prob. of Recp.	Monthly Survival	Body Weight (g) Female	Male	Reproduction Female	Male
Control	16.3	2.9	115	0.57	0.94	212.4	223.5	0.79	1.00
20%unif.	10.2	13.1	96	0.61	0.91	214.8	221.1	0.87	0.82
20%p.c.	12.6	7.2	106	0.62	0.92	220.6	222.4	0.72	0.96
35%resv.	10.6	7.7	80	0.54	0.95	216.9	217.1	0.88	0.94
50%unif.	8.5	8.4	92	0.67	0.91	216.6	220.2	0.92	1.00
50%p.c.	8.7	4.9	84	0.55	0.93	214.0	217.1	0.82	1.00

Discussion

My results indicate that red squirrel abundance declined in response to forest harvesting after a lag of one-year. Immediately after logging, the abundance of squirrels remained unchanged, likely as a result of animals surviving on previously stored food. Squirrel abundance then declined in direct proportion to the volume of timber removed. Annual variation in abundance increased in treatments after logging, particularly in

uniformly harvested habitat. This variation in abundance likely resulted from differences in food availability and suggests differential rates of habitat occupancy and abandonment. Red squirrel demography (including recruitment, survival, weight and reproduction) was otherwise unaffected by forest harvesting. In general, these results are consistent with the predictions of the ideal free distribution (IFD) model of habitat selection (Fretwell and Lucas 1970). Thus, logging reduces the quality of habitat for red squirrel populations such that fewer squirrels are supported in harvested areas, while appearing to have a negligible effect on individual fitness of the squirrels that remain.

Density

Intensity of harvest (measured as the proportion of timber removed) is the best predictor of squirrel density from two to four years after tree removal. Initially however, squirrels showed no response to forest harvesting. The absence of a density response in the first year after harvesting is likely due to the presence of conifer seed stores on the harvested treatments. In most North American coniferous forests, red squirrels cache conifer cones in a single hoard (M. Smith 1968). These seed hoards may aid in survival for up to two consecutive winters, particularly if no new seed is produced (M. Smith 1968). I speculate that once the conifer seed became depleted, approximately one year after harvesting, red squirrel densities then adjusted to the post-harvest habitat conditions as animals died or emigrated off the treatment areas. By year two after harvesting, red squirrel density had responded to the post-harvest habitat conditions by declining in proportion to the volume of timber removed. The harvesting likely removed some necessary resource from these habitats, almost certainly conifer seed. Although little research has been conducted on the response of squirrel density to food deletion, a positive relationship between conifer seed availability and red squirrel density has been well established in the ecological literature (C. Smith 1968, M. Smith 1968, Kemp and Keith 1970, Wheatley 1999). Two studies have examined the response of tree squirrels to changes in conifer stand density and both report lower densities following the removal of trees (Wolff and Zasada 1975, Patton et al. 1985). Results from my research generally agree with those reported by Wolff and Zasada (1975), and Patton et al. (1985), but predict a response across a broader range of timber removal.

Variation between annual estimates of squirrel abundance was lowest in the controls, and increased in the patch-cut and uniformly harvested treatments. Increasing variability in density estimates on harvested treatments was likely caused by differences in food availability. Territorial behaviour in red squirrels evolved to defend caches of conifer seed for overwinter survival and for survival during years of seed crop failure (M.C. Smith 1968, Gurnell 1987). The volume of stored seed necessary to ensure against starvation varies between conifer habitats (Gurnell 1987). However, the level of seed stores necessary for survival are less likely to be achieved when seed distribution becomes diffuse as seen following uniform harvesting. C. Smith (1968) speculated that the energetic costs of holding a larger, resource-diffuse territory may be considerable for squirrels, and can include an increase in time spent traveling to sequester necessary resources, leading to fewer overwinter food stores. When faced with insufficient conifer seed stores, red squirrels have shorter periods of habitat occupancy or reduced survival (M. C. Smith 1968, Gurnell 1983 and 1987). The increasing variation in squirrel abundance observed in this study, particularly on uniform treatments, suggests that conifer seed hoards may not have been sufficient to provide food for more than a single winter. Thus, squirrels residing in uniformly harvested habitat may have little buffer against adverse circumstances such as a seed crop failure or seed pest infestation, resulting in higher rates of habitat occupancy and abandonment.

Recruitment

Consistent with the observed reduction in density, I found that the number of new squirrels captured declined as harvesting intensity increased. There are a number of possible explanations for this trend, including: 1) fewer non-resident animals making forays into the harvested treatments, 2) fewer offspring being produced, and therefore captured, in harvested treatments because densities of resident breeding females are lower or, 3) reduced catchability among investigating squirrels. Explanation 3 would hold if movement patterns among investigating squirrels are altered by harvesting, thereby causing the trap encounter rates to decrease (Winker et al.1995). The data are not sufficient to distinguish between these plausible explanations.

Even though the absolute number of recruits declined with increasing intensity of harvest, the proportion of squirrels recruited into the population remained constant at

approximately 60%. Although I was not able to distinguish between adult and juvenile recruitment in this study, most recruits were likely offspring of adults residing on or near the study site. Larsen and Boutin (1994 and 1995) reported that in response to vacant territories, 89% of recruited squirrels were juveniles and that 75% of all dispersing juveniles settled within 123 m of their natal territory. The consistent recruitment rate found in my study suggests that red squirrels were experiencing similar levels of intraspecific competition for territorial spaces and post-weaning mortality (a measure of territorial vacancy and reoccupation) across treatments.

Survival

There was no difference in survival rate among the treatments compared. Estimates of survival in this study are approximately 5 to 15% higher than those in other studies because single-capture squirrels were removed from the estimates. Despite this, estimates of monthly, overwinter and annual red squirrel survival generally agree with those previously reported (Kemp and Keith 1970, Rusch and Reeder 1978, Klenner 1990, Sullivan 1990, Ransome and Sullivan 1997, Larsen et al. 1997). Except during years of abundant conifer seed, juvenile red squirrels typically settle on territories that become vacant either through death or abandonment by the previous owner (Rusch and Reeder 1978, Larsen and Boutin 1994). The lack of a response in survival suggests that territorial vacancies occur at approximately the same rate in all treatments, which is consistent with the pattern of recruitment reported above. Even though there were fewer squirrels after logging occurred, residents appeared to have access to enough resources for survival. The resources most important for squirrels are food for over-winter survival (C. C. Smith 1968, Kemp and Keith 1970, Rusch and Reeder 1978, Larsen and Boutin 1994), and cover from predation (Lima et al. 1985, Lima and Valone 1986, Newman and Caraco 1987). These results imply that the changes in habitat structure brought about by harvesting were not measurably affecting rates of predation, or emigration in red squirrels and thus overall survival of red squirrels.

Weight and Reproduction

The body weight and proportion of red squirrels reaching reproductive condition were not affected by harvesting during this study. Humphries and Boutin (1996) showed that

body weight is a good indicator of stored energy in red squirrels. Despite this, red squirrel body weight in field studies has rarely proven to be an informative parameter (Sullivan 1990, Klenner and Krebs 1991, Sullivan and Klenner 1993, Ransome and Sullivan 1997, Larsen et al 1997). Neither food addition or deletion experiments have consistently produced changes in body weight. It is therefore not surprising that red squirrel body weight did not change in response to the harvesting treatments. Red squirrels in my study either had sufficient food resources in the logged habitat, or they travelled outside the boundaries of the treatments to gain additional foraging opportunities.

The proportions of adult male red squirrels reaching reproductive condition did not change as a result of logging, but adult females show a less conclusive response. Female reproduction may have been affected by the pattern of logging in 1994, but then appears not to be affected in subsequent years. One year after harvesting, uniform harvesting may result in more females reaching reproductive condition than reserve or patch cut logging methods. It is not clear why this response was seen in uniform and not in reserve or patch cut treatments. Reserve and uniform harvesting both employed diameter limits based on volume of timber removal and any reproductive advantages for red squirrels should be experienced in both habitats. The longer-term (2-3 years) effects of harvesting on reproduction appear not to be substantial for male or female squirrels, and are consistent with patterns reported in past studies. Research in British Columbian conifer forests has shown that the proportion of squirrels in reproductive condition ranges from 77.6% to 100% for adult male and from 52.9% to 100% for adult female red squirrels (Sullivan 1990, Ransome and Sullivan 1997). Larsen et al. (1997) reported little effect of food additions or deletions on any indices of female reproduction beyond parturition date. The addition of supplemental food brought about parturition earlier in one year of their two-year study. They concluded that female red squirrels were not experiencing food shortages even after >1000 conifer cones were removed from middens. In my study, it appears that food resources were abundant enough on logged treatments for resident squirrels to reach reproductive condition. However, the measure of reproductive success used in this study says nothing about length or initiation of breeding season, number of offspring produced or the number of offspring weaned, all of which may be affected by logging.

General Discussion

Forest harvesting reduces the abundance of red squirrels, increases the variation in annual abundance, and has little affect on recruitment, survival, weight or reproduction. These results are consistent with the IFD model of habitat selection which generally predicts that individuals will distribute themselves across habitats that are variable in quality so that the mean fitness across habitats is constant (Fretwell and Lucas 1970). Specifically, "poor quality" habitats are predicted to have lower densities and be the last occupied and the first abandoned by animal species (Fretwell and Lucas 1970, O'Connor 1986). The IFD further predicts no difference in individual fitness between habitat types. Therefore, while harvesting negatively affects red squirrel habitat quality to the extent that squirrel abundance is reduced, densities adjust among habitats so that the mean fitness is similar. From two to four years after logging, the size of the decline in squirrel density will be best predicted by the intensity of timber removal.

Conclusion

Although logging intensity is the primary determinant of red squirrel habitat quality, I found that single tree selection harvesting (uniform harvesting) may lower the habitat quality for red squirrels when compared to patch-cut methods of logging. One assumption of the IFD is that "poor quality" habitats will experience the highest variation in animal abundance over time (O'Connor 1986, Krohn 1992). In my study, uniform harvesting showed the highest variation in squirrel abundance, suggesting a lower habitat quality in these habitats. However, differences in quality may become biologically meaningful only during years when conifer seed production is low or absent, and a low seed-production year did not occur during my study. During years when conifer seed availability is low, red squirrels residing in diffuse conifer habitat may experience higher rates of mortality or emigration, as large portions of habitat become unsuitable.

My results apply only to managed lands where ≤50% by volume of the timber is removed and only from one to four years after logging. When >50% by volume of timber is removed the disparity between uniform and patch-cut logging methods is likely to increase, and the magnitude of the response will depend largely on the volume of timber in the stand before harvesting. Future research should be directed toward the following questions. First, relative to other forest harvesting methods, how unsuitable

does uniformly-logged habitat become during years of cone crop failure? Second, for what length of time is there a disparity in habitat quality between uniform and patch-cut logging methods? It is possible that differences in habitat quality between logging methods is erased after 15 to 20 years, when regenerating conifer trees begin producing conifer seed. Both of these questions should be a priority for future research.

Chapter 3-

Red Squirrel Territory Size, Habitat Selection, and Behaviour in a Managed Interior Douglas-fir Forest of British Columbia

Chapter Summary

Use of interior Douglas-fir (*Pseudotsuga menziesii glauca*) forests by red squirrels (*Tamiasciurus hudsonicus*) was measured in relation to stand density and forest canopy openings at the Opax Mountain silvicultural systems site near Kamloops, British Columbia. Red squirrel territory size, habitat use, and behaviour were monitored in two uniform partial cut treatments, two patch cut treatments, and an unlogged control.

Red squirrel territory size was not affected by logging in areas where tree density was above 50-60, ≥30 cm diameter at breast height (DBH) stems per ha. Below this threshold red squirrel territory size expanded to include increasingly diffuse conifer resources. Changing red squirrel territory size is best explained by the density of conifer trees ≥30 cm DBH. Patterns of within-territory habitat selection show that red squirrels prefer living conifer trees greater than 15 cm, with trees in the 30-44-cm size class being the most preferred. Total activity budgets were not altered by changing stand structure and showed little variation between years. In contrast, red squirrel feeding and gathering behaviour was affected by stand density, and showed large yearly variation that was likely due to variation in cone production.

Logging had little effect on red squirrels during the years and across the range of habitats sampled in my study. However, logging practices that dilute Douglas-fir stands further than those sampled in this study will likely increase territory size further or cause territories to be abandoned altogether.

These results are discussed in relation to spatial and annual variation in stand, tree, and cone seed production. The seed-producing ability of a Douglas-fir stand is likely related more to the total photosynthetic surface area exposed to direct sunlight than to density of conifer trees.

Introduction

Research on the effects of logging on wildlife species often correlates stand level attributes with population measures such as species presence/absence, abundance, or simple demographic estimates; these estimates can be misleading (Van Horne 1983). The effects of logging on individuals within a population, for example, shifts in home-range size or changes in behaviour, remain largely unexamined. Yet, behaviour often provides insight into the mechanisms responsible for changing population parameters, and, therefore, has potential to reduce the uncertainty associated with wildlife and resource management (Martin 1998).

Two effects of logging on wildlife that can be measured at the scale of individual animals include habitat dilution (Huggard 1994 in Ehrlich 1996, Ganzhorn et al. 1997) and edge effects (see Yahner 1988). Habitat dilution in managed forests occurs when the home range of an animal contains a fixed amount of a resource that decreases in concentration as a result of logging. For example, animals that depend on conifer seeds are likely to experience habitat dilution when logging removes mature conifer trees (e.g., Benkman 1993a). The effects of habitat dilution are predicted to be most severe when individuals travel in a random-walk or central-place pattern, have a large home range relative to resource removal, and spend a high proportion of their time travelling between foraging sites (D.J. Huggard pers. comm.). Two of the most likely consequences of habitat dilution are a decrease in foraging efficiency and an increase in territorial defence behaviour, both of which may increase energy expenditure (e.g., Hixon et al. 1983) and ultimately reduce fitness.

Additionally, many methods of logging create a "hard edge" between habitat types. Historically, forest-openings and edges were considered positive features in forested landscapes because wildlife species diversity is generally high where two ecotypes meet (Yahner 1988, Paton 1994). More recently, research has focused on the negative effects of forest edge on wildlife. The creation of forest edge can modify patterns of wildlife distribution and dispersal, result in increased brood parasitism and predation for many bird species, and negatively affect species that require contiguous tracts of closed canopy forest (Yahner 1988, Murcia 1995). For these reasons, increasing amounts of forest edge have increasingly become a wildlife management concern.

It is clear that species interact with the environment at different scales. Identifying species that are likely to interact with the forest environment at a scale appropriate for measuring the effects of habitat dilution and edge is required to examine the causal mechanisms driving changing population parameters, such as density. The North American red squirrel (*Tamiasciurus hudsonicus*) is such a species. Red squirrels are territorial, forage in a central-place pattern, have a large home range relative to individual tree selection logging, and spend a considerable amount of time travelling between suitable foraging locations (C. Smith 1968, Ferron et al. 1986, Pelech 1999). In boreal and temperate coniferous forests, conifer seed has been identified as the most important food resource for the red squirrel (C. Smith 1968, M. Smith 1968, Rusch and Reeder 1978). As the production of conifer seed is thought to be positively correlated with tree age and size (Carey 1995), red squirrels are likely to be sensitive to the density of seed-bearing conifer trees (Gurnell 1983). Thus, logging practices that remove seed-bearing conifer trees at a spatial grain near 0.5 ha (the approximate median size of red squirrel territories) are likely to affect squirrel territory size and behaviour.

The energetic costs of holding a larger territory are thought to be high for red squirrels (C. Smith 1968). These costs include increased travelling time to gather food and defend territories. Few studies have investigated the effects of logging on individual red squirrels. Previous research has established that logging reduces squirrel abundance (Wolff and Zasada 1975, Patton *et al.* 1985, Chapter 2 of this thesis). Red squirrel densities in Alaska decreased by 66% after 83% tree removal (Wolff and Zasada 1975), and Kaibab squirrels (*Sciurus aberti kaibabensis*) declined by 50% after 32% tree removal (Patton *et al.* 1985). Authors from both studies suggest that squirrels increase their territory sizes to incorporate additional conifer seed resources. There is a lack of information describing the effect of logging on the behaviour of individual squirrels.

In 1992, the Ministry of Forests in Kamloops, British Columbia began a long-term project at Opax mountain designed to test several alternative silvicultural applications in interior Douglas-fir (IDF) forests (Klenner and Vyse 1998). As one component of this research, North American red squirrels were monitored. This chapter examines how red squirrel territory size and behaviour changed in response to conifer tree dilution and distance from forest edge at the Opax Mountain silvicultural systems site. To quantify the effects of forest harvesting on red squirrels, I measured territory

size, resource selection within territories, resource selection related to edges between forest and patch cuts, activity budgets, and foraging budgets during a three to five year period after logging.

Methods

Study area

This study was conducted on the lower elevation site at the Opax Mountain silvicultural systems research site 20 km northwest of Kamloops, British Columbia (Latitude: 120°28'00", Longitude: 50°40'30"). The lower set of replicates is 132 ha, 950-1100 m in elevation and located in the IDF Very Dry (IDFxh2) variant (Lloyd *et al.* 1990). The site was originally harvested in 1956-57 likely using a diameter method of single-tree selection (Bealle-Statland 1998). The site consists mainly of interior Douglas-fir (*Pseudotsuga menziesii glauca*) with minor components of lodgepole pine, trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and hybrid white spruce (*Picea glauca* x *engelmannii*). Forest cover is generally open and patchy resulting from microsite variation and repeated small disturbances such as fire, insects, isolated root rot infections, wind-throw, cattle grazing, and irregular harvest entries (Bealle-Statland 1998).

Experimental design and silvicultural systems

This study contains five logging treatments, each of approximately 20 ha, that were cut in the winter of 1993-1994. The treatments are: 20% mature tree removal as uniform partial cuts (20% unif.); 50% mature tree removal as uniform partial cuts (50% unif.); 20% removal patch cut of 0.1 ha, 0.4 ha and 1.6 ha (20% p.c.); 50% removal patch cut of 0.1 ha, 0.4 ha and 1.6 ha (50% p.c.), and an unlogged control. The uniform partial cut treatments were logged using a diameter method of single-tree selection. For a detailed overview of site prescriptions see Bealle-Statland (1998).

Estimates of post-harvest stand structure are taken from Bealle-Statland (1998). Average stand volume was highest in the control (174.0 m³/ha) and lowest in the 50% uniform treatment (67.5 m³/ha), while stand density was highest in the 20% patch cut (2455 stems/ha) and lowest in the control (1646 stems/ha, Table 3.1).

Red squirrel sampling

I collected information on red squirrel territory size and behaviour from September to October in 1996, 1997 and 1998. I trapped and ear-tagged squirrels with territories inside treatment boundaries at the midden using a Tomahawk live-trap (model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin). Traps were baited with 10 g of sunflower seed. I recorded the sex, weight, tag numbers, and reproductive condition of resident squirrels. Once squirrels on the study site were identified, a subsample of resident animals was fitted with radio transmitters to aid in collecting detailed spatial and behavioural information. Territory boundaries of the radio tagged animals were determined and reference points established on the territories using a 10-m x 10-m grid system (100-m^2 cells). I located squirrels approximately once daily and followed them for a 20-minute observation period after animals had acclimated to the presence of the observer. I collected the following data during these "focal" periods: spatial location; all behaviours; species, diameter and condition of trees used; duration spent in each 100-m^2 cell; and behaviour was recorded every 30 seconds. Red squirrels were followed between dawn and 1100 hours and between 1600 hours and dusk to coincide with the peak activity periods of the squirrels.

Habitat sampling

I recorded habitat variables for 4300 100-m^2 cells. The variables measured were: tree species and diameter-at-breast-height (DBH) using 5 size^2 classes (saplings, 7.5 - 15 cm, 15 - 29 cm, 30 - 44 cm and ≥45 cm). I recorded all standing dead trees separately without regard for tree size.

Conifer cone counts were used to estimate seed production on Douglas-fir trees ≥7.5 cm in the unharvested control, the 20% uniform partial cuts, and the 50% uniform partial cuts. I collected these data using linear transects that started at a random location inside each treatment boundary, and were oriented in a randomly selected direction. I collected data from starting point to the treatment boundary. Each transect was composed of two nested transects. The first transect was 8 m wide (4 m on either side of the observer) and censused living conifer trees greater than 7.5 cm. The second transect

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^{2} Future reference to tree size or size class will mean diameter-at-breast-height.

was 60 m wide and censused living conifer trees greater than 25 cm. I counted cones on only the south facing aspect of each tree.

Data Analysis

General

I examined territory size, tree density with respect to territory size, resource selection within territories, and activity budgets. The sampling unit was the individual squirrel; however, I summarized results by treatment type where suitable. There is no treatment replication in this study.

Territory Size

Territory sizes were calculated using 90% minimum convex polygon (M.C.P.) (Mohr 1947) and 80% fixed kernel (Worton 1989) estimators. Program HOME RANGE (Ackerman et al. 1991) was used to calculate 90% M.C.P. estimates and are included for comparison with previously published red squirrel research. To determine the minimum number of points needed to generate consistent area estimates, I calculated the cumulative M.C.P. territory size for eight squirrels using sequential point addition. These curves generally reached an asymptote between 70 and 100 points. Therefore, I excluded all squirrels that did not have 100 points collected over a minimum of 2 weeks. As M.C.P estimates of territory size increase with increasing sample size (White and Garrot 1990), all M.C.P. territory estimates were calculated using 100 randomly chosen data points.

Using HOME RANGER (Hovey 1999), I calculated 80% fixed kernel territories with an h=0.9 (except for animals in the 50% uniform treatment in 1998, where h=1.5). I used all data points to calculate fixed kernel area estimates. This was done because the fixed kernel method is less sensitive to sample size.

Models

Following Burnham and Anderson (1998), I developed a set of 20 candidate models to explain variation in the size of red squirrel territories based on habitat characteristics (Table 3.2). These analyses assume that red squirrel territory size is largely determined by conifer seed availability on the territory, which is primarily a function of conifer tree size and density. Generally, model development was hierarchical and assumed that larger conifer trees were more likely to influence territory size than

smaller trees. I present a detailed description of statistical analysis used for model selection in Chapter 2 of this thesis.

The null model (M_{null}) predicts no relationship between total conifer tree density and squirrel territory size. Eight candidate models were developed using a linear or inverse polynomial ($y = y_o + (a/x)$) regression with 4 classes of conifer tree size. $M_{\geq 45 linear}$ and $M_{\geq 45 inverse}$ predict that squirrel territory size is best explained by the density of conifer trees ≥ 45 cm. Similarly, $M_{\geq 30 linear}$ and $M_{\geq 30 inverse}$ predict that the density of conifer trees ≥ 30 cm will best explain territory size, $M_{\geq 15 linear}$ and $M_{\geq 15 inverse}$ use density of conifer trees ≥ 15 cm, and $M_{live-linear}$ and $M_{live-inverse}$ use density of all conifer trees greater than 7.5 cm. Three multiple regression models ($M_{45\&30}$, $M_{45\&30\&15}$ and $M_{45\&39\&15\&7.5}$) predict a relationship between territory size and the density of conifer trees in the 4 size classes.

Six models use estimates of conifer seed production to explain territory size. Greene and Johnson (1994) developed an equation to estimate mean annual seed production of individual trees based on basal area and average seed mass. Using this equation, models $M_{Greene-linear}$ and $M_{Greene-inverse}$ predict the annual seed production of individual trees in the 7.5-cm class as 212, in the 15-cm class as 764, in the 30-cm class as 1967 and in the ≥ 45 cm as 3872. Garman (1955), working on Vancouver Island, published the only comprehensive work on Douglas-fir seed production in a non-plantation environment. I used data from Garman (1955) to estimate the seed "value" of individual Douglas-fir trees by multiplying the expected annual number of seeds produced by the probability of producing seed in a given year. Models $M_{Garman-linear}$ and $M_{Garman-inverse}$ predict annual seed production of individual trees in the 7.5 cm class as 58, in the 15 cm DBH class as 268, in the 30 cm class as 1169 and in the ≥ 45 cm as 1914. Finally, the production of conifer cones by individual trees was estimated from data collected in my study ($M_{Herbers-linear}$ and $M_{Herbers-inverse}$). Again, the seed "value" of individual Douglas-fir trees was estimated by multiplying the expected number of cones produced in 1997 by the probability of producing cones in 1997 for each tree class. Results from my research suggest a difference in cone production between 20% uniform (7.5 cm=0 cones, 15 cm=34 cones, 30 cm=142 and ≥ 45 cm=242), 50% uniform (7.5 cm=0 cones, 15 cm=56 cones, 30 cm=140 and ≥ 45 cm=239), and all other treatments (7.5 cm=0 cones, 15 cm=21 cones, 30 cm=108 and ≥ 45 cm=183). Finally, two models

($M_{basal-linear}$ and $M_{basal-inverse}$) predict that conifer basal area will best explain variation in squirrel territory size.

It was further assumed that a territory size greater than 3 ha could not exist for red squirrels in this study.

Table 3.1. Summary of post-harvest stand structure for Opax Mountain Silvicultural Systems Site. Estimates are taken from Bealle-Statland (1998)

	Volume (m3/ha)	Volume Relative to Control (%)	Stems (No./ha)	Stems Relative to Control (%)
Control	174	-	1646	-
20%unif.	108.2	-37.8	1827	11.0
20%p.c.	145.5	-16.4	2455	49.1
50%unif.	67.5	-61.2	1938	17.7
50%p.c.	73.4	-57.8	1769	7.5

Table 3.2. Summary of hypotheses used to examine red squirrel territory size.

1. no relationship with conifer tree density (M_{null})
2. a linear relationship with density of conifer trees ≥ 45 cm ($M_{\geq 45linear}$)
3. an inverse relationship with density of conifer trees ≥ 45 cm ($M_{\geq 45inverse}$)
4. a linear relationship with density of conifer trees ≥ 30 cm ($M_{\geq 30linear}$)

5. an inverse relationship with density of conifer trees ≥ 30 cm ($M_{\geq 30inverse}$)
6. a linear relationship with density of conifer trees ≥ 15 cm ($M_{\geq 15linear}$)
7. an inverse relationship with density of conifer trees ≥ 15 cm ($M_{\geq 15inverse}$)
8. a linear relationship with density of conifer trees ≥ 7.5 cm ($M_{live-linear}$)

9. an inverse relationship with density of conifer trees ≥ 7.5 cm ($M_{live-inverse}$)
10. a multiple regression model with the ≥ 45 cm and 30-44 cm size classes ($M_{45\&30}$)
11. a multiple regression model with the ≥ 45 cm, 30-44 cm and 15-29 cm size classes ($M_{45\&30\&15}$)
12. a multiple regression model with all four size classes ($M_{45\&39\&15\&7.5}$)

13. a linear relationship with Greene and Johnson's seed production equation ($M_{Greene-linear}$)
14. an inverse relationship with Greene and Johnson's seed production equation ($M_{Greene-inverse}$)
15. a linear relationship with Garman's seed value equation ($M_{Garman-linear}$)
16. an inverse relationship with Garman's seed value equation ($M_{Garman-inverse}$)

17. a linear relationship with Herbers' seed value equation ($M_{Herbers-linear}$)
18. an inverse relationship with Herbers' seed value equation ($M_{Herbers-inverse}$)
19. a linear relationship with basal area ($M_{basal-linar}$)
20. an inverse relationship with basal area ($M_{basal-inverse}$)

Selection and Behaviour

Resource selection was analyzed in 3 ways: at the scale of 100-m^2, selection of individual trees, and selection as a function of distance from edge. Analyses compared

use and availability within red squirrel territories, with the assumption that all resources within territorial boundaries were equally available. For selection of 100-m^2 cells and forest-patch cut edge selection, I defined use as the total amount of time spent in each cell. I recognized six categorical variables for these analyses: canopy openings; cells containing dead and deciduous trees only; cells containing living conifer trees with a maximum size of ≥45 cm; cells containing living conifer trees with a maximum size of 30-44 cm; cells containing living conifer trees with a maximum size of 15-29 cm, and cells containing living conifer trees with a maximum size of 7.5-14 cm. Further, cells with middens were excluded from analysis to reduce bias toward habitat characteristics associated with midden sites. For analysis of individual tree selection, I defined use as the frequency with which trees in each size class were used. With the exception of canopy openings, I used the same categorical variables that are described above. Only red squirrels with canopy openings greater than 0.2 ha available to them were used to measure habitat selection related to forest-patch cut edge. I used 8 forest-patch cut edge categories: 40-m forest, 30-m forest, 20-m forest, 10-m forest, edge, 10-m opening, 20-m opening, and 30-m opening.

Red squirrel activity budgets are based on within-territory behaviour. Similar to Ferron et al. (1986), I recognized 7 behavioural categories (Table 3.3). Three behaviour budgets were summarized in detail: a total activity budget, a foraging location budget, and a feeding and food gathering budget.

Table 3.3. Description of behavioural patterns recognized for *Tamiasciurus hudsonicus* at Opax Mountain Silvicultural Systems site near Kamloops, British Columbia.

Behaviour	Description
Foraging	All short-term and long-term feeding behaviours associated with food gathering and ingestion
Searching activities	Behaviours associated with locating food
Feeding and food handling	Activities associated with the manipulation and ingestion of food
Gathering and hoarding	Clipping conifer cones and fungus, locomotion with food held in teeth
Locomotion	All locomotory activities not associated with transporting food, nesting material, or territorial disputes
Resting	All stationary behaviours on the ground or in trees that involve observing surroundings
Resting	Lying down on the ground or in trees while observing surroundings
Alert	Sitting on the ground or in trees while observing surroundings
Grooming activities	Stretching, scratching, licking, or chewing fur.
Social Activities	All behaviours related to conspecific interactions
Aggressive	Territorial disputes including fighting and chasing
Vocal	Vocal communication
Other	Less common behaviours not covered elsewhere including gathering nest material, spending time in nest and cheek rubbing
Unknown	Location known but behaviour was not observed

Results

General

    Seventy-three hours of observation data were collected on 11 animals in 1996, 99 hours on 12 animals in 1997, and 101 hours on 24 animals in 1998. Approximately 10% of all the squirrels that I radio-collared did not acclimate to observer presence and were not included in the data analysis.

Territory Size

    M.C.P. and fixed kernel territory size were estimated for 38 of 47 red squirrels. The 90% M.C.P. and the 80% fixed kernel estimates of territory size showed similar results in this study although M.C.P. estimates were consistently more variable

(Figure 3.1). As M.C.P. estimates do not estimate irregular territory shapes well (White and Garrot 1990), they were not used in any additional analyses. Red squirrel territory sizes ranged from 0.50 ha to 2.2 ha and showed no consistent differences between sexes or years. All squirrels were observed actively defending territorial boundaries. Figure 3.2 provides a schematic representation of territory sizes and shapes in three of the study areas.

Territory Resources

The relationship between conifer tree resources and territory size was best explained by the inverse $\geq$30-cm model (Table 3.4). No other models used in this analysis should be considered. Figure 3.3 shows the relationship between red squirrel territory size and conifer trees $\geq$30 cm. In general, territory size decreases from 10 to 50-60 stems per ha, then remains stable from 50-60 to 110 stems per ha.

Habitat Selection (100-m^2 Cells)

Red squirrels consistently preferred cells characterized by 30-44-cm conifer trees, while avoiding forest openings, cells characterized by dead or deciduous trees, and cells characterized by 7.5-14-cm conifer trees (Figure 3.4). Squirrels selected cells characterized by 15-29 cm and $\geq$45-cm conifer trees approximately in proportion to their availability. When $\geq$45-cm habitat cells were available, squirrels showed little difference in selection patterns compared to when these cells were not available.

Habitat Selection (Individual Trees)

Selection of individual trees showed similar results to the selection of 100-m^2 cells (Figure 3.5). Dead and deciduous trees were avoided as were conifer trees smaller than 15 cm. Conifer trees between 15 and 29 cm, and $\geq$45 cm were selected more than expected, while conifer trees between 30 and 44 cm were preferred. There were no obvious differences in selection patterns between squirrels that had $\geq$45-cm trees available to them and those that did not.
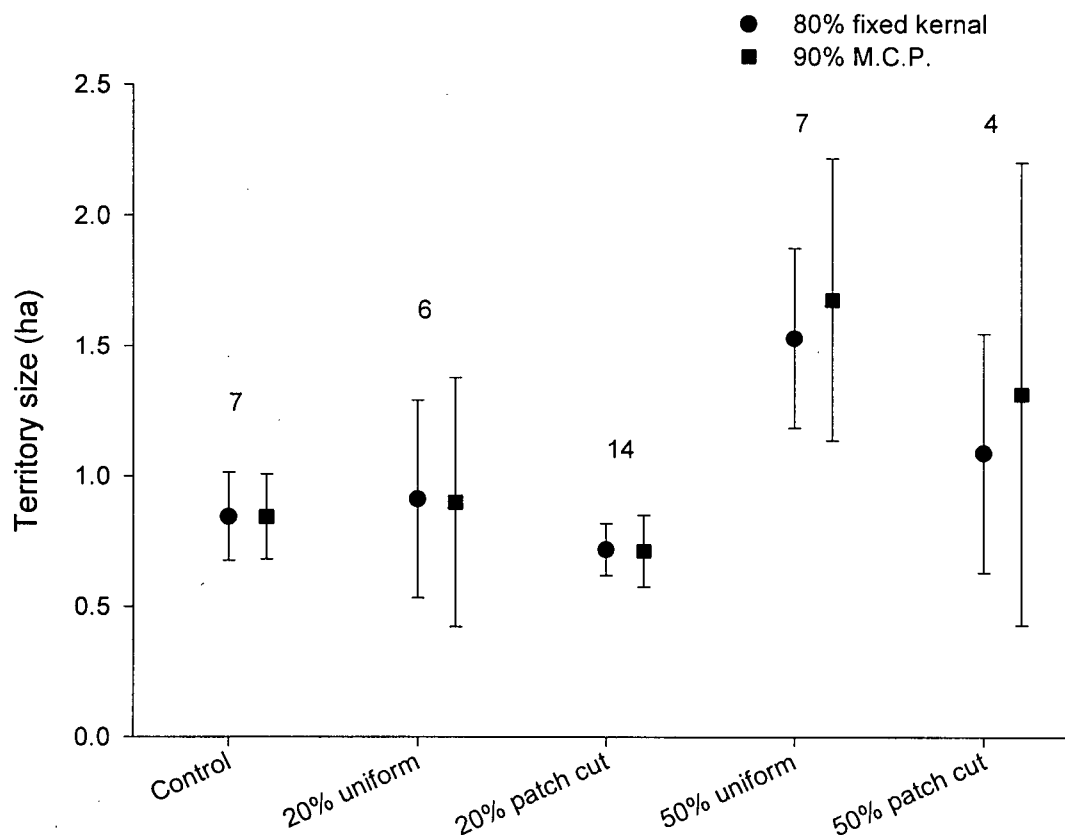
Figure 3.1. Comparison of red squirrel territory size estimators (80% fixed kernel with h=0.9-1.5 and 90% M.C.P.) in 5 treatments at the Opax Mountain silvicultural systems site. Sample size shown above the plots.

Table 3.4. Summary of model testing for red squirrel territorial resources at Opax Mountain Silvicultural Systems Site near Kamloops, British Columbia. The four models with the highest A.I.C. weights are shown with the null model included for comparison. The most parsimonious model is shown in bold.

Model	K	ΔAICc	AICc Wts
M_{null}	2	11.0	0.00
$M_{>30\text{-linear}}$	3	1.7	0.02
$M_{>30\text{-inverse}}$	**4**	**0.0**	**0.84**
$M_{Garman\text{-inverse}}$	4	0.3	0.08
$M_{basal\ area\text{-inverse}}$	4	2.0	0.02

Control

50% uniform
treatment

20% patch cut
treatment

Mud
Lake

approx. 250 m.

approx. 350 m.

C-12

C-11

C-1

Road

Patch Cut
C-15 (1 ha)

C-10

C-2

Road

C-4

○   100-m^2 canopy opening

—— Squirrel territorial boundary

—— Opening boundary

├─── 120 m ──┤
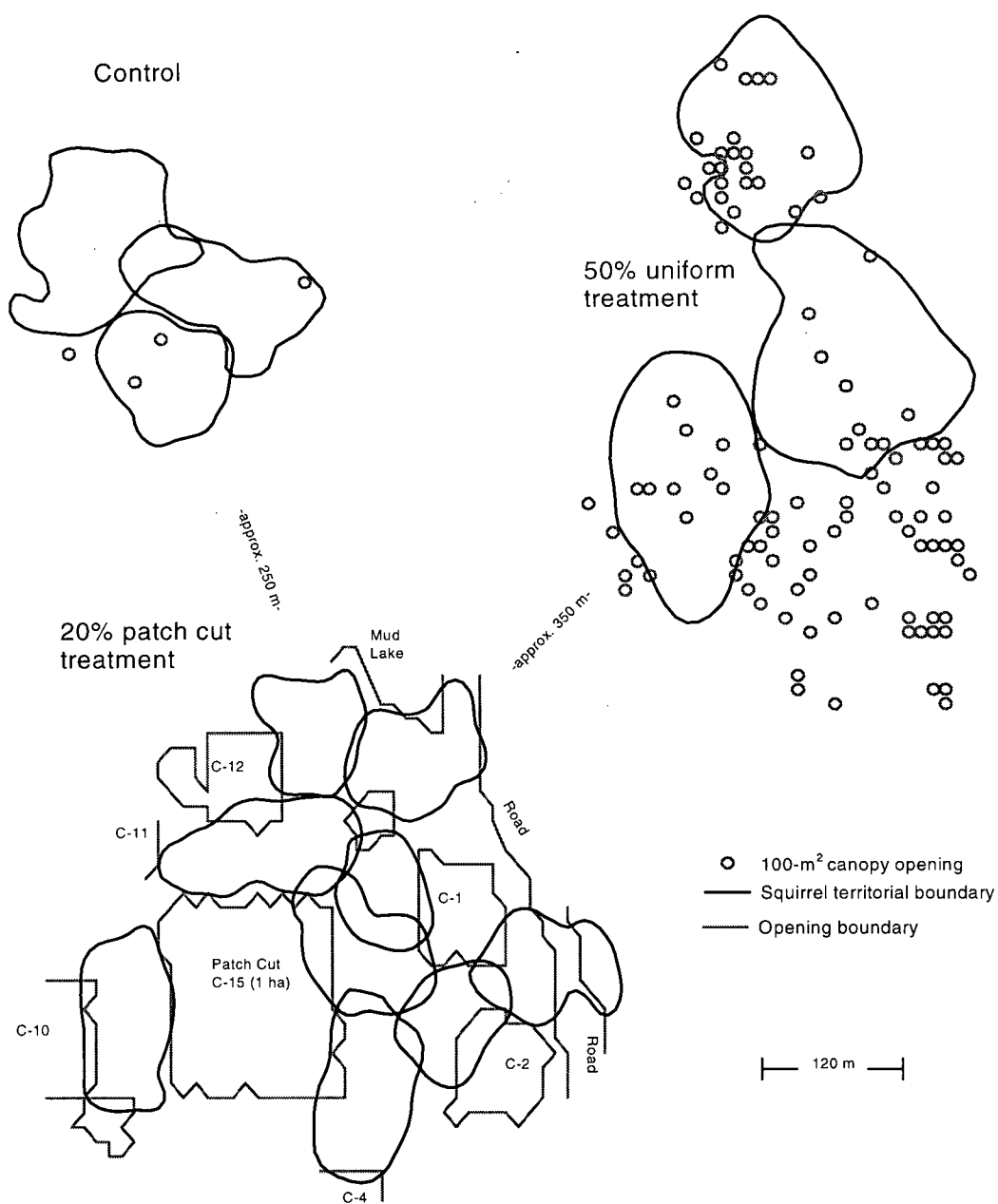
Figure 3.2. Example of red squirrel territory size (80% fixed kernel, h=0.9-1.5) in three study areas at the Opax Mountain silvicultural systems site. Scales shown in this diagram are consistent between all sites
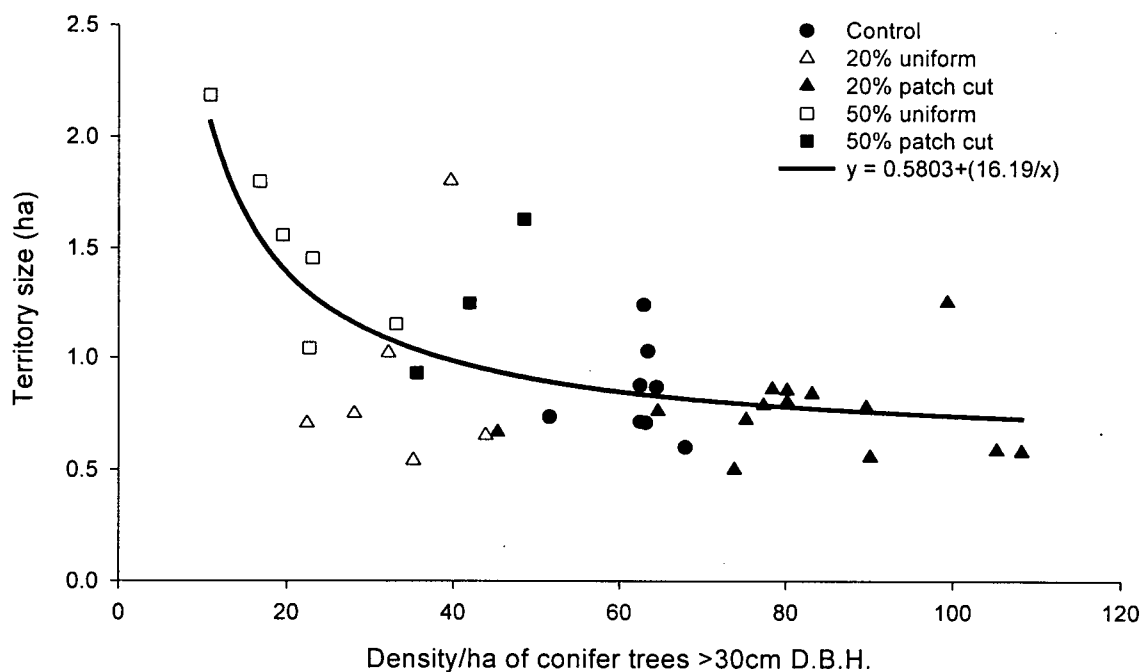
Figure 3.3. Relationship between density of Douglas fir trees larger than 30 cm DBH and red squirrel territory size. Data were collected from 1996-1998 and are expressed by treatment with the inverse (AICc Wt. =0.84) model shown.
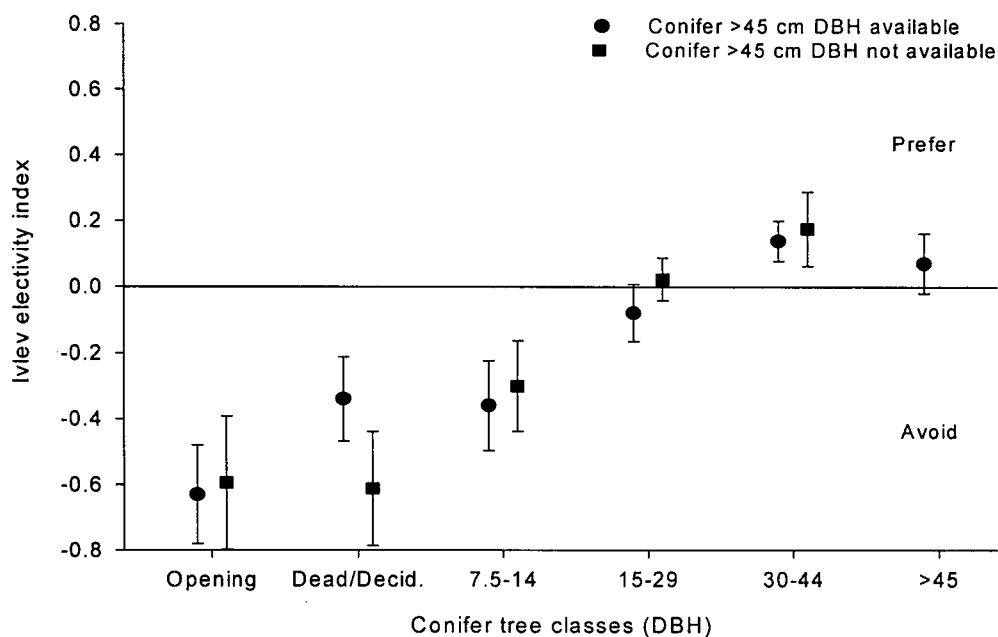
Figure 3.4. Red squirrel selectivity for habitat characteristics (100-m^2 cells) within territorial boundaries. An Ivlev electivity value of 0 indicates use proportional to availability; a positive value indicates preference while a negative value indicates avoidance. Error bars are 2 standard errors.
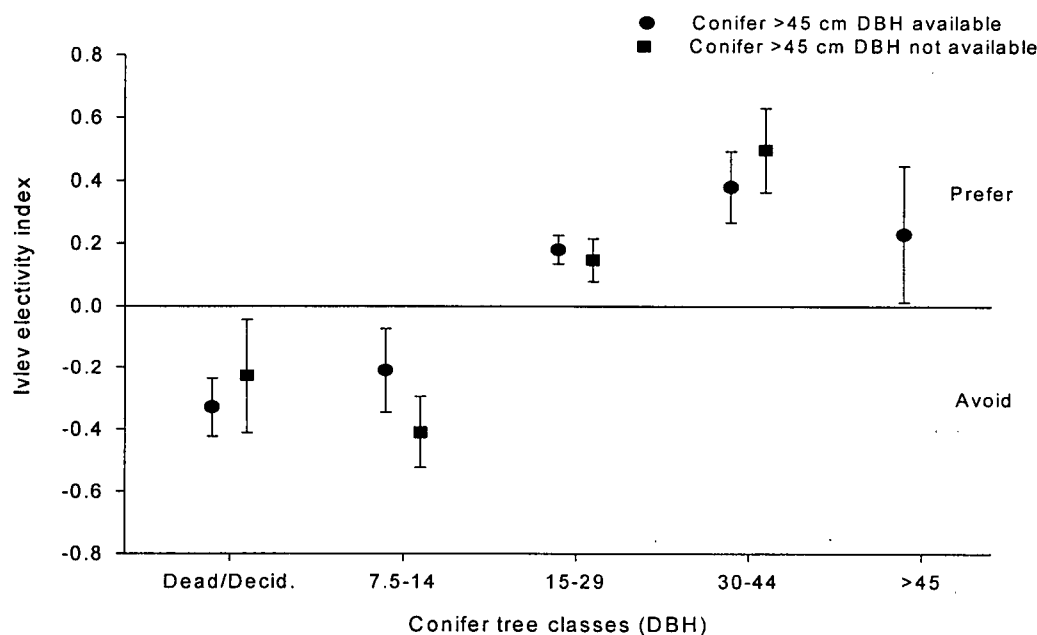
Figure 3.5. Red squirrel selectivity for individual trees within territorial boundaries. An Ivlev electivity value of 0 indicates use proportional to availability; a positive value indicates preference while a negative value indicates avoidance. Error bars are 2 standard errors.

Activity Budgets

Total time spent active showed no consistent patterns by sex, year, or density of conifer resource. Results are summarized by treatment (Table 3.5). On average, squirrels spent 80% of their time feeding, travelling, and resting.

The location of squirrels while foraging did not differ by sex or density of conifer resources but differed between years (Table 3.6). Red squirrels in 1996 and 1997 spent a similar amount of time foraging on the midden but, in 1997, shifted much of their activity from trees to the ground. In 1998, squirrels shifted their foraging effort toward the midden site, spent less time foraging in trees, and spent the majority of their time on the ground.

Feeding and gathering activity showed no difference by sex, but showed strong differences by year and consistent trends with changing density of conifer trees. In 1996 and 1997, red squirrels spent most of their feeding and gathering activity budget eating and gathering conifer cones (Table 3.7). In 1998 there was a shift away from these behaviours, toward feeding on conifer buds, fungi, and other food sources (*e.g.*, rose hips and paper birch catkins). Overall, increasing tree density led to an increase in time spent feeding on conifer cones (Figure 3.6).

Table 3.5. Red squirrel activity budget (%) summarized by treatment with 2 standard errors shown in brackets.

Treatment	n	Foraging	Locomotion	Resting	Grooming	Social	Other	Unknown
Control	7	53.4 (6.2)	13.9 (2.6)	10.7 (3.2)	2.6 (1.9)	0.8 (0.3)	13.4 (5.2)	5.2 (2.3)
20%unif.	6	61.1 (7.7)	13.9 (5.5)	8.4 (3.2)	2.2 (1.2)	1.4 (0.8)	7.5 (4.9)	5.6 (3.1)
20%p.c.	14	57.6 (6.5)	13.0 (1.6)	12.4 (3.9)	2.0 (1.0)	1.2 (0.3)	7.2 (2.1)	6.6 (2.3)
50%unif.	7	45.7 (14.4)	12.8 (3.1)	18.3 (9.8)	1.6 (1.8)	1.1 (0.3)	16.4 (9.2)	4.2 (3.2)
50%p.c.	4	46.2 (22.7)	15.5 (3.9)	11.4 (8.7)	0.9 (1.0)	0.9 (0.9)	22.5 (13.7)	· 2.7 (3.3) ·
Overall	38	54.0 (4.7)	13.5 (1.3)	12.4 (2.6)	1.9 (0.6)	1.1 (0.2)	11.7 (3.0)	5.3 (1.3)

Table 3.6. Location of foraging (% of foraging time) by year.

Year	n	Ground	Trees	Midden
1996	10	47.9 (9.4)	50.2 (9.2)	1.9 (2.7)
1997	9	72.3 (11.2)	26.9 (10.8)	0.8 (1.5)
1998	19	57.9 (6.6)	30.8 (7.9)	11.3 (4.8)

Table 3.7. Feeding and food gathering activities (% of foraging observations) by year.

Year	n	Conifer Cones	Conifer Buds	Fungus/lichen	Other	Clipping and Hoarding
1996	10	58.3 (6.2)	5.6 (2.0)	10.1 (3.8)	5.3 (4.7)	20.8 (8.3)
1997	9	69.2 (7.2)	0.3 (0.3)	3.4 (1.1)	2.6 (2.3)	24.5 (8.0)
1998	19	24.0 (7.9)	21.2 (9.7)	36.7 (8.2)	13.6 (7.8)	4.6 (2.4)

Table 3.8. Red squirrel activity budget (%) summarized by distance from edge with 2 standard errors shown in brackets.

	n	Feeding	Locomotion	Resting	Grooming	Social	Other	Unknown
Opening	14	57.9 (18.9)	20.9 (14.9)	10.5 (7.1)	1.6 (1.6)	0.2 (0.4)	6.8 (8.3)	2.0 (2.0)
Edge	16	55.8 (9.0)	15.5 (3.0)	12.4 (4.9)	1.8 (0.8)	1.0 (0.5)	6.7 (5.3)	6.8 (2.9)
10m Forest	16	55.0 (8.4)	17.3 (3.1)	12.0 (6)	1.9 (1.1)	1.4 (0.4)	4.9 (3.2)	7.5 (3.1)
20m Forest	16	53.7 (8.2)	19.1 (4.0)	11.7 (6.7)	2.3 (1.5)	1.2 (0.6)	7.5 (5.7)	4.5 (1.7)
30m Forest	12	55.5 (10.0)	15.4 (4.4)	10.3 (5.1)	3.1 (1.5)	1.6 (0.8)	6.7 (5.2)	7.3 (5.7)
40m Forest	7	58.6 (17.8)	21.3 (9.4)	6.4 (3.7)	1.7 (2.5)	2.0 (2.4)	3.1 (3.9)	6.9 (6.0)
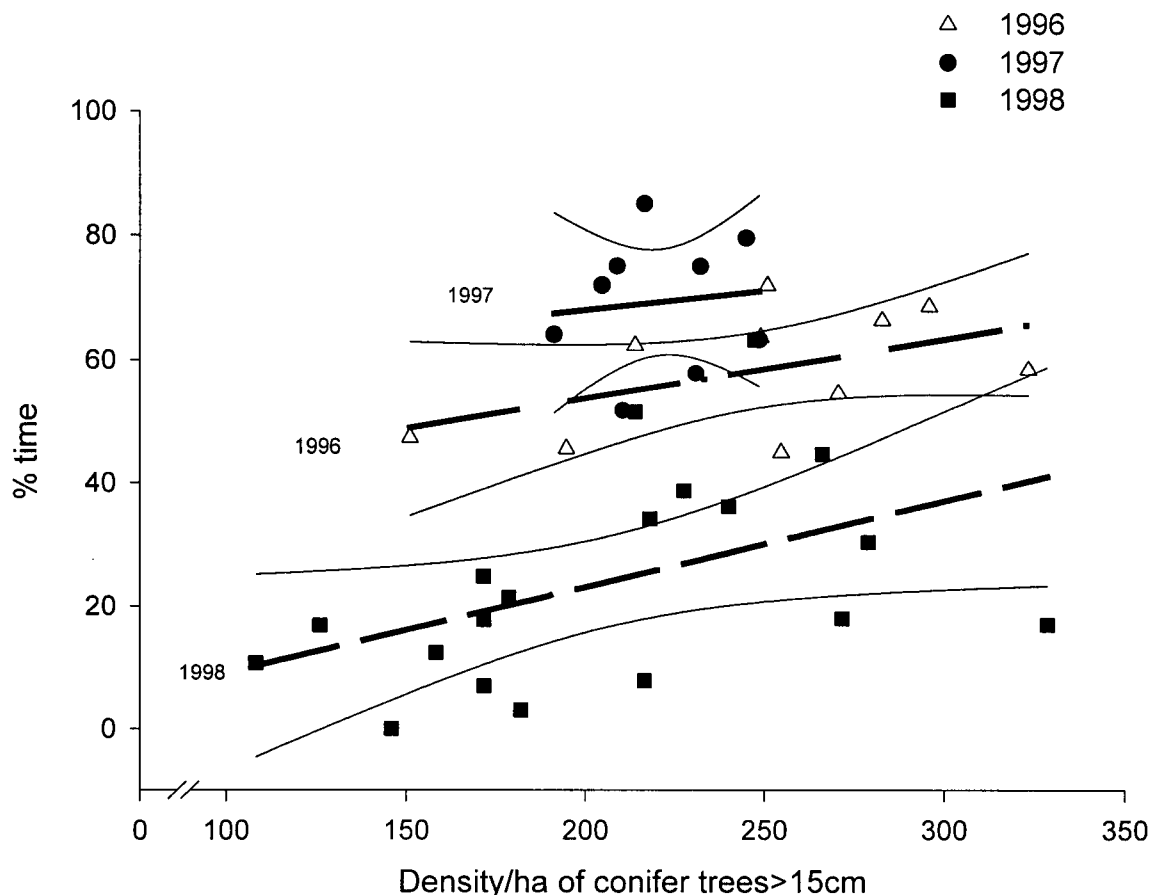
Figure 3.6. Percent of feeding time spent eating conifer cones with 95% confidence intervals.

Forest-Patch Cut Edge

Eighteen red squirrels had territories that bordered on canopy openings larger than 0.2 ha. Squirrels strongly avoided habitat ≥10 m into an opening and selected habitat in proportion to its availability from the edge up to 30 m into the forest (Figure 3.7). When available, habitat at 40 m into the forest appeared to be avoided. Red squirrel behaviour did not appear to be affected by proximity to edge (Table 3.8).

Conifer Cone Availability

A quantitative assessment of the 1996 cone crop was not done; however, it appeared to be considerably larger than the crop in 1997. A moderate cone crop was produced in 1997, and no cones were produced in 1998.

In 1997, a total of 134 Douglas-fir trees were surveyed in the control, 124 in the 20% uniform partial cut treatment, and 165 in the 50% uniform partial cut treatment.

Douglas-fir trees <15 cm did not produce any cones (Table 3.9). Although sample sizes were not large, the 15-29 cm and 30-44 cm size classes in the 20% and 50% uniform partial cut treatments consistently had a greater proportion of trees producing cones and consistently produced more cones per tree when compared to unlogged areas.
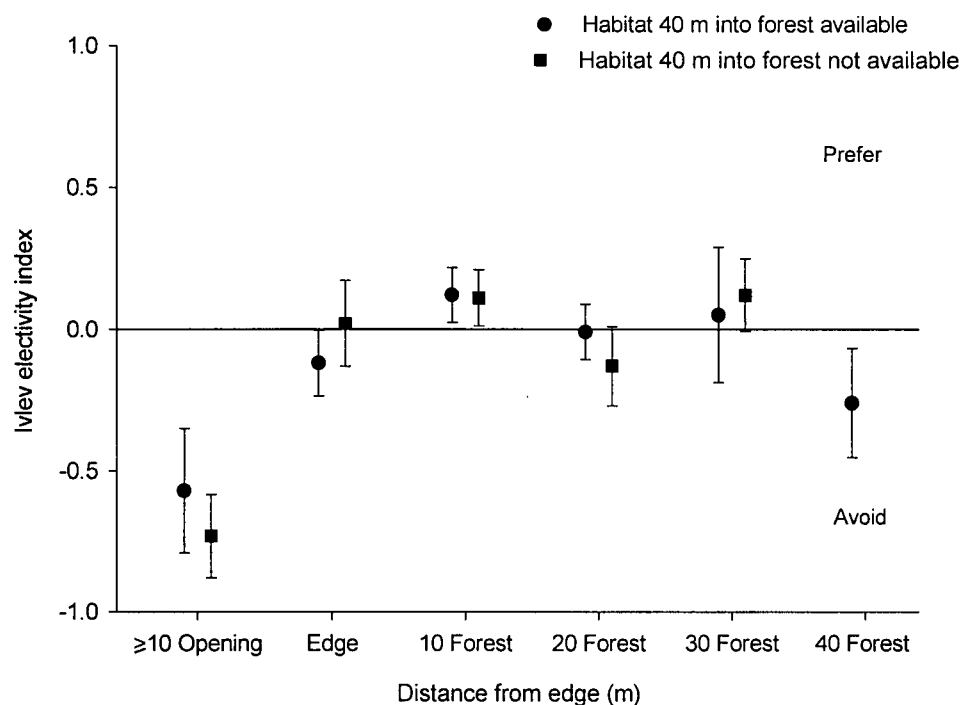
Figure 3.7. Red squirrel selectivity for habitat (100-m^2 cells) as a function of distance from edge. An Ivlev electivity value of 0 indicates use proportional to availability; a positive value indicates preference while a negative value indicates avoidance. Error bars are 2 standard errors.

Table 3.9. Douglas-fir cone counts and the proportion of trees that produced seed in the unharvested control, 20% uniform partial cut treatment, and 50% uniform partial cut treatment in 1997. The mean number of cones per tree represents only cones counted on the south-facing crown of each tree. Garman (1951) suggests a conversion factor to derive estimates of cone production per tree.

DBH size class (cm)	Control			20%			50%		
	n	Mean # cones/tree	Proportion	n	Mean # cones/tree	Proportion	n	Mean # cones/tree	Proportion
7.5-14	37	0	0.00	34	0	0.00	33	0	0.00
15-29	56	47	0.45	64	53	0.64	110	77	0.73
30-44	32	119	0.91	25	155	0.92	21	147	0.95
45+	9	206	0.89	1	164	1.00	1	390	1.00

Discussion

My study suggests that red squirrel territory size is not affected by logging as long as tree density does not fall below a threshold of 50-60, large ($\geq$30 cm) stems per ha. At densities above 50-60, large stems per ha, squirrel territory sizes remained at approximately 0.5-1.0 ha. The density of large live conifer trees was the best explanation of territory size. Similarly, patterns of within-territory habitat selection show that red squirrels prefer living conifer trees greater than 15 cm, with trees in the 30-44 cm size class being the most preferred. Total activity budgets were not altered by changing stand structure and showed little variation between years. In contrast, red squirrel feeding and gathering behaviour was affected by stand density, and showed large yearly variation that was likely due to variation in cone production. Red squirrels spent more time foraging on conifer cones and less on fungi when conifer tree density increased. Red squirrel behaviour is discussed in relation to spatial and annual variation in stand, tree, and cone seed production.

Territory Size and Conifer Resources

Red squirrel territory sizes in this study ranged from 0.50 ha to 2.2 ha. The lower range of red squirrel territory size in my study is similar to that reported by Klenner (1990). He reports a mean autumn territory size of 0.55 ha for squirrels (adult and juvenile) in Douglas-fir forests. Red squirrel territory sizes exceeding 1 ha have rarely been found (Gurnell 1987), and no studies have previously reported active defence of territories exceeding 1.5 ha. The most parsimonious explanation of red squirrel territory size was the $M_{\geq30\text{inverse}}$ (Table 3.4). The relationship between large trees and squirrel territory size is expected for two reasons. In boreal and temperate coniferous forests, conifer seed is the most important food resource for red squirrels (C. Smith 1968, M. Smith 1968, Rusch and Reeder 1978), and the production of conifer seed appears to be positively correlated with increasing tree age and size (Carey 1995). Therefore, the density of trees able to produce seed (*e.g.*, $\geq$30 cm) is expected to affect squirrel territory size (Gurnell 1983) as it did in this study.

The influence of large conifer trees ($\geq$30 cm) on red squirrel territory size seems particularly important when tree density falls below 50 to 60 stems per ha because

territory sizes begin to increase below this threshold (Figure 3.3). This is likely to be a consequence of habitat dilution (Huggard 1994 in Ehrlich 1996). Similarly, Patton *et al.* (1985) found that the Kaibab squirrel doubled its home-range size after logging, while Wolff and Zasada (1975) speculate that red squirrel territory size increased after logging to incorporate diffuse resources. Other territorial species show similar patterns. For example, hummingbird territory size is inversely correlated with energy production within an environment (Gass *et al.* 1976, Gass 1979). When food resource was uniformly halved, the territory size of birds approximately doubles (Hixon *et al.* 1983). The energetic and ultimately fitness costs associated with defending dilute resources remains unknown but may be substantial (Hixon 1980). Red squirrels appear to experience habitat dilution when the density of large Douglas-fir falls below 50 to 60 stems per ha. Below this threshold, red squirrel territory size increases likely to encompass additional conifer resources.

In contrast, there was little change in squirrel territory size in areas where tree densities ranged from 50-60 stems per ha up to 110 stems per ha. Territory size varied between 0.5 and 1.0 ha and did not decline below 0.5 ha (Figure 3.3). These results are similar to those of Klenner (1990), who observed a mean territory size of 0.65 per ha for adult red squirrels in Douglas-fir stands. There are two plausible explanations for why territory size does not continue to decline as conifer tree density increases. First, intraspecific territorial interactions may be regulating red squirrel populations in high density Douglas-fir stands. This, however, is inconsistent with red squirrel natural history. Under both natural and experimental conditions, red squirrels decrease territory sizes to 0.2-0.4 ha when food is abundant (Rusch and Reeder 1978, Price et al. 1986, Klenner 1990). An alternative explanation for stable red squirrel territory sizes is that food availability is limiting. Two important variables that influence the availability of conifer seed in a stand are the number of conifer cones produced by individual trees and the proportion of trees in the stand that produce any seed at all.

Foresters have long realized the benefits of "releasing" individual conifer trees on seed production (Bilan 1960). "Open grown" trees can produce between 2 and 12 times more conifer cones compared to trees growing in dense stand conditions (Issac 1943, Garman 1951 and 1955, Bilan 1960, Allen and Trousdell 1961, Reukema 1961, Owens and Blake 1985, Karlsson 2000). The mechanism responsible for this pattern is not

known, but seed production is likely influenced strongly by the temperature during bud differentiation (approx. 17-18 months prior to cone maturation in Douglas-fir) and the amount of crown surface area exposed to direct sunlight (Allen and Owens 1972, Owens and Blake 1985). Further evidence for increased conifer cone production on sun exposed crowns can be inferred from information collected at three scales. Cone production in conifer species is higher on south facing slopes when compared to north facing slopes (Owens and Blake 1985). Pelech (1999) reports 1.7 to 3 times higher white spruce cone production on south facing forest edge when compared to north facing edge. At a finer scale, Douglas-fir cone production is approximately 20% higher on southern aspects of individual trees (Garman 1955, Owens and Blake 1985). With increasing stand density, the total crown surface area and total crown surface area exposed to direct sunlight for individual trees will decrease. Thus, the seed-producing ability of a Douglas-fir stand is likely related more to the total surface area exposed to direct sunlight rather than to the total number of trees. For species that depend on conifer seed, the quality of the habitat (assuming seed is the most important resource) will be similar when individual trees begin competing for access to direct sunlight. Red squirrels in my study may thus be limited by conifer seed production above a threshold of 50 to 60, $\geq$30 cm Douglas-fir stems per ha.

In addition to the number of cones produced per tree under different stand densities, the total number of trees that produce any conifer seed at all will also influence red squirrel habitat quality. There is little quantitative information available to describe this variable. Bilan (1960) found that 100% of "released" loblolly pine (*Pinus taeda*) in North Carolina produced seed compared to only 80% of "unreleased" trees. Results from my study suggest that the proportion of trees in the 15-29 cm size class that produce any seed at all increases from 45% in the control to 73% in the 50% uniform partial cut treatment (Table 3.9). Future studies should incorporate this variable into study designs when quantifying conifer seed production between heterogeneous stands.

Within-territory resource selection

Within-territory resource selection at both the scale of 100-m^2 cells and individual trees supports the relationship described between $\geq$30-cm Douglas-fir trees and territory size. Red squirrels consistently selected conifer trees in the 30-44-cm size class, even

above conifer trees ≥45 cm when they were available. Squirrels selected living conifer trees between 15-29 cm in proportion to their availability, while avoiding canopy openings, dead and deciduous trees, and small living conifers. The selection of 30-44-cm trees over ≥45 cm is unexpected as other researchers have often assumed that older conifer trees produce the most conifer seed (*e.g.,* Burns and Honkala 1990, Benkman 1993a). However, there is evidence that this assumption is incorrect. For example, European red squirrels (*Sciurus vulgaris*) living in Scots pine (*Pinus sylvestris*) forests preferred foraging in smaller trees growing in dry soils at high densities rather than large trees growing in wet, open stand conditions (Summers and Proctor 1999). Isaac (1943) reported that a typical 15-year-old coastal Douglas-fir (*P. m. menziesii*) tree produces 4 000 seeds annually, an average 100-200-year-old tree produces 40 000 seeds annually, while an average 600-year-old tree produces 7 000 seeds annually. This suggests that older conifer trees do not necessarily produce the most seed, and, therefore, may not be preferred foraging sites for red squirrels. Unfortunately, tree cone data collected in my study was not sufficient to test cone production as a function of tree size beyond 44 cm. This information further suggests that habitat quality for red squirrels in my study was influenced most by the availability of 30-44-cm Douglas-fir trees.

Activity Budgets

Red squirrels in my study spent most of their time foraging, travelling, and resting (Table 3.5). These results are consistent with those previously reported for the North American red squirrel (C. Smith 1968, Ferron et al. 1986, Pelech 1999) and other forest rodents (Wauters et al. 1992). The time and energy budget of an animal may be stressed for three main reasons: 1) a reduction in prey density leading to an increase in time spent travelling for food (habitat dilution), 2) a reduction in time available to forage, and 3) an increase in metabolic requirements (Norberg 1977). I found no evidence that red squirrels living in diffuse conifer habitat were experiencing time or energy stresses related to increased travel or decreased time to forage. Additional shifts in red squirrel metabolic requirements resulting from changing stand structure are more likely to occur during the winter and not in the autumn when I conducted my study.

The location of red squirrel foraging was not affected by the sex of the squirrel or the density of conifer trees but showed large annual variation (Table 3.6). Feeding and

food gathering behaviour similarly showed no pattern by sex but did show large annual variation (Table 3.7). The annual variation in these behaviours was likely related to conifer seed production. In 1996, a good cone crop was produced and squirrels spent an average of 50% of their foraging effort in conifer trees and 80% of their feeding activities eating and hoarding conifer resources. In 1997, an intermediate cone crop was produced, and squirrels shifted their foraging effort to the ground (72% of their foraging time) and their feeding activities toward eating and hoarding conifer resources (94% of their feeding and hoarding time). In 1998, there was a conifer cone crop failure. Squirrels again spent much of their foraging effort on the ground (58%), however, there was a five-fold decrease in the time spent gathering food and a five-to-ten fold increase in the time spent foraging on the midden compared to the previous two years. The increased activity on the midden was presumably spent searching for stored conifer cones. In addition, squirrel feeding activities shifted strongly away from feeding and hoarding conifer cones in 1998 and toward feeding on conifer buds and fungus.

Independent of annual conifer cone production, the time spent feeding on conifer cones was positively correlated with increasing conifer tree density (Figure 3.6). Thus, squirrels with a higher density of conifer trees on their territory spent more time feeding on conifer cones. Counter to the relationship described between conifer tree density and red squirrel territory size, these results suggest that conifer cone availability increases with increasing stand density. Although conifer cone availability will almost certainly decline with decreasing stand density below some threshold, the interaction between conifer seed production and stand density may be considerably more complex than previously described in wildlife literature.

A third variable that influences the availability of conifer seed in a stand is seed production per cone and the factors that influence successful pollination and seed maturation. Red squirrels appear to be sensitive to this variable and will select trees that produce the highest number of conifer seeds per cone (Smith 1970). Douglas-fir can potentially produce 70-80 seeds per cone (Colangeli et al. 1989). However, the number of seeds actually produced per cone varies between years and between habitats, typically ranging from 20-60% of the maximum (Colangeli et al. 1989). Colangeli et al. (1989) showed that the most important variables responsible for low Douglas-fir seed production per cone were inadequate pollination (30% of seeds per cone were empty for this reason),

and pollen inviability or low vigour (14% of seeds per cone). Pollen production is thought to decrease in conifer stands with increasing stand density (Owens and Blake 1985) and this pattern may be related to light exposure (Allen and Owens 1972). Although the mechanism is not known, conifer trees appear to increase the proportion of seed cones and decrease the proportion of pollen cones produced as stand density increases (Owens and Blake 1985). For example, the production of sound conifer seed per cone in loblolly pine was as much as 67% lower in high density stands (Bilan 1960). However, Reukema (1961) did not find any effect of stand density on conifer seed production. It is possible that red squirrels in my study spent more time feeding on conifer cones as stand density increased, because the number of seeds produced per cone was lower when compared to low density conifer stands. This result has important implications for management as it again challenges the assumption that dense conifer stands are high quality seed production habitat, and, therefore, high quality red squirrel habitat. This relationship should to be examined further before concluding that older conifer stands produce more seed.

Selection of Forest Edge

Squirrels in my study avoided habitat openings and selected equally for edge and interior habitat (Figure 3.7). In addition, red squirrels showed no change in activity at any distance from the forest-patch cut edge (Table 3.8). These results are consistent with previous behavioural research on red squirrels. Pelech (1999) examined the behavioural response of red squirrels to forest-opening edge and found that they avoided habitat openings. Red squirrels likely avoid habitat openings for two reasons: limited foraging opportunities and an increased risk of predation (Lima et al. 1985, Lima and Valone 1986, Pelech 1999). When red squirrels in my study were in habitat openings, they spent approximately 60% of their time foraging on fungus, rosehips and other locally abundant resources. These openings appeared to contain a considerable amount of unused food (per. ob.). I suggest that a perceived increase in the risk of predation is the primary reason that red squirrels avoid forest openings created by logging.

Red squirrel avoidance of habitat openings did not appear to affect the use of adjacent forest edges. Squirrels selected equally for forest edge and habitat from 10 m to 30 m into the forest. Similarly, Pelech (1999) reports that red squirrels selected for edge

habitat from late spring to early summer, but showed neutral selection for edge in late summer. Unfortunately I did not have sufficient data to examine foraging behaviour in habitat openings or along forest edges. Future research should consider conifer cone gathering and conifer cone feeding behaviour along edge habitat, and particularly on south facing aspects.

Conclusion

There appears to be three phases of Douglas-fir seed production with respect to tree density: a habitat dilution phase, a constant seed production phase, and a declining seed viability phase. I suggest that there is a threshold stand density in mature Douglas-fir forests below which habitat quality for red squirrels declines and above which habitat quality is approximately constant but may decline as seed production per cone falls off (Figure 3.8).

Habitat dilution in my study occurred only in low density Douglas-fir stands (<50-60, ≥30 cm stems per ha) and did not appear to affect squirrels during the years and across the range of habitat sampled in this study. Although squirrels spent less time feeding on conifer cones in dilute conifer habitat, this result may not accurately reflect that availability of conifer seed. In addition, resource selection and total activity budgets did not change in low-density stands. These results are consistent with those reported in Chapter 2, where I showed that red squirrel recruitment, survival, body weight, or reproduction were not affected by logging. However, the effect of habitat dilution on squirrels during years when there is a seed crop failure remains unknown and will likely become most apparent during winter. Logging practices that dilute Douglas-fir stands further than those sampled in this study will likely result in further increases in territory size or the abandonment of territorial behaviour altogether. To quantify the effect of habitat dilution on red squirrels, future studies should include sampling during the winter in at least one year of cone crop failure and in forest stands with a lower density than sampled in this study.

When there are at least 50, ≥30 cm Douglas-fir trees per ha, red squirrels appear not to be affected by changing stand density. Across this range of stand density, there is evidence suggesting that seed production remains approximately constant. As stand density increases, seed production per tree may decline such that changes in stand level

seed production are relatively small. Finally, there is weak evidence that seed production per cone may decline at high stand densities. Red squirrels continued to increase the proportion of time they spent feeding on conifer cones under conditions of high stand density.

The perceived risk of predation may be constant from the forest-patch cut edge into the forest interior as red squirrel habitat selection and activity patterns showed little variation across this gradient. However, canopy openings created by logging were strongly avoided and the likely cause of this behaviour may be an increase in the perceived risk of predation. The number of years that red squirrels avoid using forest openings after logging is likely less than 20 (Sullivan and Moses 1986, Sullivan and Klenner 1993, Ransome and Sullivan 1997).

Red squirrels are only one of at least 50 North American species that use conifer seed as a food resource during one or more life history phases (Smith and Balda 1979). Of these species, crossbills (*Loxia spp*) are perhaps the most sensitive to changes in seed production and among the most likely to become locally extirpated as a result of forest practices in conifer stands (Benkman 1993a, Benkman 1993b, Summers and Proctor 1999). My results suggest that forest managers may have a considerable range of options to choose from when managing for species that depend on conifer seed. Environmental variables such as stand density, tree age, soil moisture, and stand aspect are all likely to affect conifer seed production and can be incorporated into management plans. Since the early 1960's when manual planting with nursery stocks became the dominant form of restocking stands after logging, research on natural seed production has steadily declined. There is considerable opportunity for future research to examine the effect of environmental gradients on seed production at a variety of scales and under experimental and observational conditions.
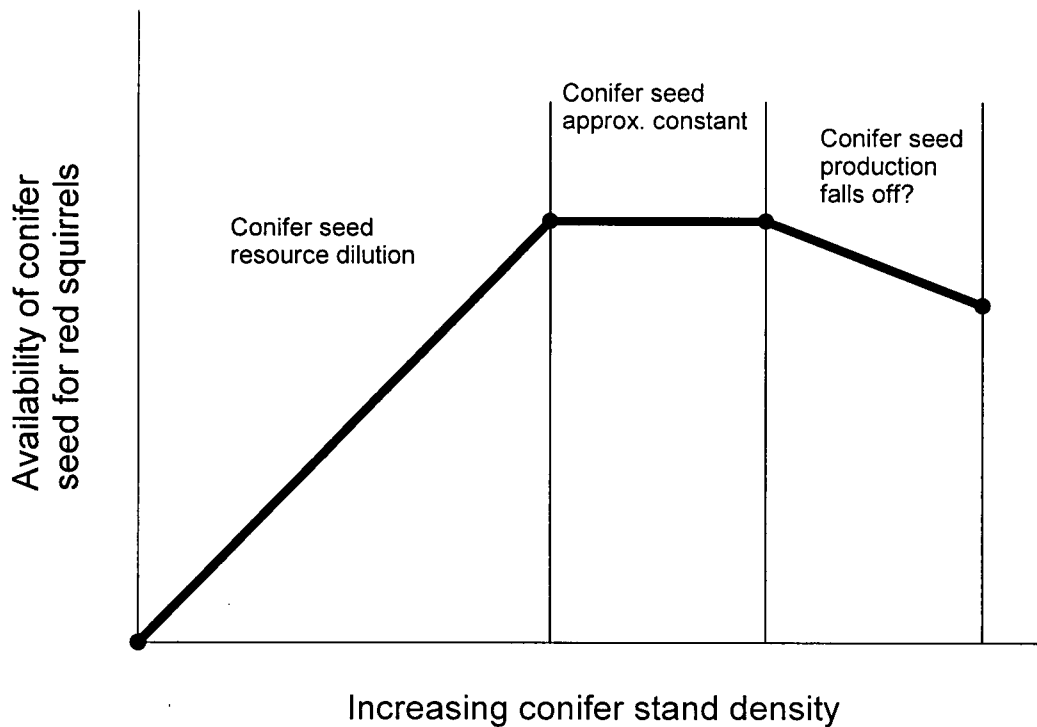
Conifer seed
approx. constant

Conifer seed
production
falls off?

Conifer seed
resource dilution

Availability of conifer
seed for red squirrels

Increasing conifer stand density

Figure 3.8. Possible relationship between availability of conifer seed for red squirrels and conifer stand density. Initially, the availability of conifer seed increases in direct proportion with increasing stand density. Seed production levels off as the total crown surface area of the stand that is exposed to direct sunlight remains constant. During this leveling phase, increasing stand density reduces the seed cone production of individual trees. Finally, at high stand densities seed production begins to decline as the amount of viable seed produced per cone declines.

Chapter 4-

General Conclusions

Previous research suggests that red squirrels will be absent from a forest for less than 20 years after complete canopy removal (*e.g.*, clear-cuts, Sullivan and Moses 1986, Ransome and Sullivan 1997). Logging practices that leave some of the forest canopy intact (*e.g.*, uniform partial cuts) have consistently resulted in reduced squirrel abundance (Wolff and Zasada 1975, Patton *et al.* 1985). However, no studies have examined the effect of incomplete canopy removal on red squirrel demography or behaviour. The purpose of my research was to measure the effect of logging on red squirrels by examining population density and demography and individual territory size, habitat use, and behaviour.

In Chapter 2, I found that red squirrel abundance showed a negative 1:1 relationship with the volume of conifer tree removal from two to four years after logging. In addition, I found no effect of logging on red squirrel recruitment, survival, body weight, or reproduction. In Chapter 3, I found that red squirrels selected for conifer trees greater than 15 cm DBH and that they showed the highest selection for 30-44 cm DBH conifer trees. Red squirrel activity budgets did not change despite large differences in the availability of conifer trees; however, time spent foraging on conifer cones appears to increase when squirrel territories contain dense conifer habitat. I suggested that conifer seed production at three scales explains these patterns. Finally, I found that red squirrels strongly avoided canopy openings created by logging, but that their avoidance of openings did not affect the use of forest-patch cut edge when compared to interior forest habitat.

It is clear that red squirrel abundance declines after logging. Otherwise, logging did not appear to have a biologically meaningful affect on red squirrels across the range of tree removal and during the years that I sampled. There is, however, evidence that uniform partial cuts may become poor habitat for red squirrels during years when little or no conifer seed is produced or when logging dilutes conifer trees further than those sampled in this study. Red squirrels living in conifer-diffuse habitat during years of seed crop failure may have fewer stored resources for overwinter survival when compared to squirrels living in high-density conifer habitat. M. Smith (1968) working in white spruce

forests of Alaska reports that red squirrels regularly fed on cached conifer cones following one year of seed crop failure, but that by the second year cone reserves appeared to be exhausted as no evidence of feeding on cones was observed. He thought that most squirrels either died or relocated to an alternate forest type after two winters without new seed stocks. I suggest that low-density conifer habitat (approximately <50 stems per ha of trees ≥30 cm DBH or <200 stems per ha of trees ≥15 cm DBH in my study) will become unsuitable for red squirrels following only a single year of poor conifer seed production.

Forest Management

To a large degree, managing for red squirrel habitat means managing for conifer seed production. All single tree selection (uniform partial cuts) methods of timber removal will result in fewer conifer seeds being available for at least two, but likely 3 to 5 years after logging. When conifer trees become released from competition for sunlight after logging, it takes a minimum of two years before seed production will reflect the change in stand conditions. However, given the fluctuating pattern of seed crop production in Douglas-fir forests, an increase in individual tree seed production will likely not occur until three to five years after logging. After approximately five years, uniform partial cut methods of logging that retain a substantial number of trees (≥50, 30 cm DBH stems per ha in my study) may show little difference in stand-level seed production when compared to unharvested habitat. Below this stand density threshold, stand level seed production will likely decline with decreasing stand density. Red squirrels living in low conifer stand densities will likely experience critical food shortages during the winter after a seed crop failure.

The effect of complete canopy removal (patch cut or clear cut methods of logging) on red squirrels is obvious. The duration that clear cut forests remain unsuitable habitat for red squirrels is not known but is likely less than 20 years. However, Douglas-fir stands can begin producing seed crops as early as 10 years of age and under some conditions can produce large crops at 15-20 years of age (Allen 1942). Young conifer trees that are widely spaced will likely begin producing conifer seed at an earlier age than

trees growing in high-density stands. The importance of younger forest stands as habitat for red squirrels and the species that feed on red squirrels appears often ignored.

Future Research

Future research on red squirrels in managed forests should include a study design that quantifies stand level conifer seed production and relates it to squirrel demography. Assessing how red squirrel demography relates to stand level seed production will be particularly important during the winter months that follow a seed crop failure. In addition, future studies that involve wildlife species that feed on conifer seed should focus less on the proximate response of logging and include field research greater than 5 years post-harvest. Finally, there is almost no literature describing when clear cuts are reoccupied after logging. Young conifer stands may be high quality habitat for red squirrels under some conditions, while some old conifer stand may be poor quality habitat.

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