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Does Density Reflect Habitat Quality for Red Squirrels During a Spruce Cone Failure?

by

Matthew Thompson Wheatley ©

A thesis submitted to the faculty of Graduate Studies and Research in partial fulfilment of

the requirements for the degree of Master of Science

Department of Biological Sciences

Edmonton, Alberta

Spring, 1999

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Abstract

This study was designed to determine if the relative importance of different habitats changed in terms of population demographics for red squirrels (*Tamiasciurus hudsonicus*) during a spruce cone failure. I quantified density, survival, female reproduction, juvenile production, immigration, and animal condition during two years of a spruce cone failure in white spruce, lodgepole pine and mixed conifer habitats in the foothills of west-central Alberta. Spruce habitats showed relatively unstable squirrel densities, a lower proportion of lactating females, lower survival, lower juvenile production, lower immigration, and little difference in animal condition relative to pine and mixed conifer habitats. Survival and female reproduction were variable between years for all habitats but showed trends for spruce to have the lowest values overall. Adult and juvenile immigration appeared more important in replacing mortality than juvenile production primarily in spruce and mixed conifer, and to a lesser extent in pine habitats. Given the characteristic fluctuations in spruce cone crops, these results question the historical "high quality" rating of white spruce habitat for red squirrels.

Acknowledgements

This research was supported financially through grants to M. Wheatley from the Foothills Model Forest in Hinton Alberta (92% of support), a Boreal Alberta Research Grant from the Canadian Circumpolar Institute at the University of Alberta, and a grant from Weldwood of Canada in Hinton. In-kind support was generously provided by the Foothills Model Forest in Hinton, Weldwood of Canada (Hinton Division), the Environmental Training Center in Hinton (N.A.I.T.), and the Canadian Forest Service.

Big big thanks to the following people who helped me complete this research and achieve my goals: ***Field Assistance:*** Carrie Melanson and Joe Litke. ***Supervision:*** Karl Larsen and Stan Boutin. ***Committee Members:*** Ellen Macdonald and Jan Murie. ***In Hinton:*** Dan Farr. ***Abroad:*** Shawna Pelech, Jim Herbers, Walt Klenner. ***Fellow Proletarians:*** Warren Schaffer, Mark Pioreski, Lisa Takats, Carrie Gotzke, Karen Graham, Ian Hamilton, and Hiroki Currie. ***Academic and Emotional Support:*** Jason Fisher, Crissy Corkum, Hiroki Currie and Ainsley Sykes. ***Sanity 5-oh:*** The Friday-RATT Ecology Think Tank (we had us some stoooopid fun!), Mr. 4-string Ernie and my CD collection. ***Logistical, Financial and Emotional Support:*** Richard Wheatley, Barb Purin and Beryle Wheatley. ***All of the above and then some:*** Maureen Madsen.

Table of Contents

Page

List of Tables:

List of Figures:

Chapter One. Introduction.

The ability to make long-term predictions in wildlife management, and the techniques used to generate these predictions, are complex issues in Alberta. Several million hectares of Alberta's public land have been allocated to private forest companies for harvest and, as a result, increasing pressure has been put on these companies to define a clear rationale as to how management decisions regarding timber and wildlife resources are to be made. The search for methods to make this process easier and more objective has led to the development of quantitative computer-based models as tools to predict the effects of management alternatives on wildlife populations (Bonar 1993). These models have been developed and planned for use in some areas of Alberta (e.g. Beck *et al.* 1996). However, they often rely on assumptions that are difficult, and costly, to address empirically (Verner *et al.* 1986).

Data employed in the development of these models can be collected at two general levels, extensive and intensive (Van Horne 1986). Extensive studies are based on broad correlation of a species' densities with habitat features. Extensive studies produce low-cost predictive models based upon many assumptions regarding habitat features and a species' densities (e.g. high density means high habitat quality). These are by far the most commonly employed data sets in wildlife management (e.g. Habitat Suitability Index Models, Multiple Regression Models) and are commonly justified using assumptions derived from habitat selection theory (e.g. Fretwell and Lucas 1969, Fretwell 1972, Fagen 1988, Nelson and Buech 1996). Conversely, intensive studies investigate the processes that potentially could influence the survival and productivity of a species, contending that if these processes are understood, the effects of habitat alteration can be predicted. Intensive studies are high-cost and try to examine whether or not model assumptions (i.e. suspected wildlife-habitat relationships) are valid or are in need of modification (Schlamberger and O'Niel 1986). An intensive study commonly attempts to relate the demographics of individuals in a population to habitat features and associated resource availabilities in order to identify key demographic parameters influencing observed animal densities (e.g. Van Horne 1982). Both types of studies make different attempts to improve wildlife-habitat models and avoid inaccurate predictions.

Inaccurate wildlife-habitat predictions can arise for many reasons (following list from Laymon and Barrett 1986) such as (1) assumed linear relationship of animal density and habitat parameters (Meents et al. 1983); (2) seasonal changes in habitat use (Patterson 1976); (3) density as a misleading indicator of habitat quality (Van Horne 1983); and (4) the effect of predators on the abundance of their prey (Morin 1981). These potential problems are difficult to address for most terrestrial vertebrates because they require knowledge of population demography and how it is related to the features of a habitat and its animal community. Because the goal of habitat assessment is to determine how differences in our perception of habitat quality translate into differential use by a particular species, model assumptions (e.g. density reflects habitat quality) should be tested with population data, preferably including estimates of density, survival and reproductive success on an intensive level (Cole and Smith 1983, Van Horne 1983, Brooks 1997). Such an assessment is the aim of this thesis.

In 1994, a large scale modeling project was undertaken on a forest management area in the foothills of central Alberta (Beck *et al.* 1996). Several single-species predictive models were developed including one for the North American red squirrel (*Tamiasciurus hudsonicus*), a model that I agreed to evaluate. Because the preliminary model was already developed using the literature (Banks *et al.* 1996), it could have been evaluated either extensively (by relating model output to observed relationships between habitat and relative abundance) or intensively (by evaluating whether density is related to habitat quality in terms of population demographics). I chose to evaluate the model intensively for the following reasons.

Red squirrels are found resident in varying conifer habitats and rely almost exclusively on conifer cones as their main food source (see Obbard 1987 and references therein). In white spruce (*Picea glauca*) habitat this food source availability is characterized by large, periodic fluctuations due to irregular seed production of the white spruce trees. Such fluctuations can show periods from 3-12 years (Hellum 1976) in white spruce habitat and are not seen in other conifer habitats. White Spruce habitat is considered biologically important to red squirrels (Rusch and Reeder 1979). The existing red squirrel model, and the historical literature on red squirrel populations, had rated white spruce habitat as relatively "higher quality" than other coniferous and deciduous habitats. Therefore, given the potential for resource availability (spruce cones) to fluctuate in white spruce habitat unlike other squirrel habitats, I evaluated the model using intensive methods, suspecting that density might be a misleading indicator of habitat quality as reflected in population demographics.

The current study was designed to compare the demographics of squirrel populations in three conifer habitats. My goal was to determine if density reflected habitat quality over two years of spruce cone failure when the potential for a change in the relative importance of habitats would be greatest. Chapter Two consists of a detailed quantification of red squirrel demography in three different conifer habitats over two years of a spruce cone failure. I relate these findings to resource availability, which I quantified in each habitat. I also determine which demographic components are important in determining observed squirrel densities during this time.

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Verner J., M.L. Morrison and C.J. Ralph, eds. 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Chapter Two. Does density reflect habitat quality for red squirrels during a spruce cone failure?

Habitat selection theory suggests that individuals should settle in areas where fitness and survival are optimized. The result should be that population densities are maintained or adjusted to levels in accordance with resource availability and intraspecific competition (Fretwell and Lucas 1969, Fretwell 1972, Lidicker 1975, Rosenzweig 1981, Pulliam and Caraco 1984, Parker and Sutherland 1986, Fagen 1988). From this it follows that individuals should select and use areas that are best able to satisfy their life requirements and as a result, greater use will occur in higher-quality habitat (Schlamberger and O'Neil 1986, Fagen 1988). Such theory remains unvalidated for most terrestrial vertebrates, but commonly forms the basis of many single-species wildlife-habitat predictive models (Hobbs and Hanley 1990, Van Horne and Weins 1991, Verner *et al.* 1986).

With widespread application of habitat selection theory in wildlife management, Van Horne (1983) outlined how pressure to develop a rapid means of habitat-quality assessment commonly resulted in the abandonment of biological understanding in favour of simple census techniques that related relative abundance directly to habitat quality. She contended that density could be a misleading indicator of habitat quality because of social interactions (i.e. dominance) or ephemeral populations of non-breeding individuals (dispersal sinks). These problems were further emphasized with the development of source-sink theory (Pulliam 1988) which suggests that non-viable populations could be maintained in low-quality habitat by immigration exceeding or equalling mortality and emigration. These ideas, and the potential for resource availability to fluctuate between habitats (e.g. Van Horne 1982), suggest that the relative importance of habitats could change for a species over time resulting in habitat-specific demographic changes of populations, or in the movement of individuals between habitats due to changes in resource availability.

As a result, definitions of habitat quality were broadened to include not only animal density but also survival, reproduction, and movements of individuals between habitats (Cole and Smith 1983, Van Horne 1983, 1986, Verner et al. 1986, Fagen 1988, Hobbs and Hanley 1990, Van Horne and Weins 1991). The latter are often discussed, but rarely measured (e.g. Brennan *et al.* 1986, Nelson and Buech 1996). Where these parameters are measured (Alder 1986, Sullivan 1979, Martell 1983, Ostfeld and Klosterman 1986, Alder and Wilson 1987, Krohne 1988, Halama and Dueser 1994, Seamon and Alder 1996), differences between studies in location, time and data collection methods make generalizations about the effect of habitat on individuals difficult. In general, the role habitat type plays in population demographics is still relatively unknown because we do not fully understand the relationships between individuals in a population, their habitat, and its resource availability (Batzli 1968, Hansson 1977, Mackin-Rogalska 1979, Van Horne 1981, Cockburn and Lidicker 1983, Ostfeld *et al.* 1985, Ostfeld and Klosterman 1986).

This lack of understanding is emphasized in the use of habitat selection theory forming the basis of single-species wildlife-habitat predictive models (e.g. Multiple Regression and Habitat Suitability Index Models using density as an indicator of habitat quality). Problems with application of these models arise because once a habitat type is rated by a model, that rating is not changed over time. However, the success of individuals in that habitat could vary markedly over time. If resource availability can fluctuate in specific habitats, so may the success of individuals in that habitat, resulting in theoretical predictions not being supported. This has not, however, delayed managers from applying the models, even though these potential problems remain unaddressed and the output is potentially misleading (e.g. Beck *et al.* 1996).

In 1994, Weldwood of Canada Hinton Division, the Foothills Model Forest, the University of Alberta Department of Renewable Resources, and Alberta Fish and Wildlife developed 35 single-species habitat models for use on the Weldwood Forest Management Area in west-central Alberta (the 35 species are listed in Beck *et al.* 1996). Among the species selected was the North American red squirrel (*Tamiasciurus hudsonicus*) for which a Habitat Suitability Index Model was developed (Banks *et al.* 1996). This model assumes that certain habitats are consistently of higher quality as indicated by historical measures of relative abundance. The abundance of conifer cones, a primary food source for red squirrels, is known to fluctuate widely in areas of high squirrel densities (a cycle of 3-12 years in white spruce, Hellum 1976) indicating the potential for density to be a misleading indicator of habitat quality. Unlike many species, research methods for red squirrels (see Obbard 1987 for review) allow for accurate quantification of both resource availability and population demographics in a habitat-specific manner. Red squirrels defend individual, non-overlapping, traditional territories (C. Smith 1968) making individuals relatively easy to locate and follow. Furthermore, conifer cones, the primary food source for red squirrels, can be quantified between habitats and related to population demographics, making it possible to explore the effect that habitat and its related resource availability has on resident individuals.

Previous work on North American red squirrels has focussed both on the population (Kemp and Keith 1970, Rusch and Reeder 1979, Sullivan and Moses 1986, Klenner and Krebs 1991, Sullivan *et al.* 1996) and individual level (C. Smith 1968, M. Smith 1968, Gurnell 1984, Boutin and Schweiger 1988, Boutin *et al.* 1993, Larsen and Boutin 1994). Although the proximate factors affecting the behavior of individuals in specific habitats may be somewhat clear, the relative roles that different habitat types play in squirrel demographics are less known. To date, only two studies have compared red squirrel populations in different natural habitats (Kemp and Keith 1970, Rusch and Reeder 1979). These studies were completed in habitats considered to be of lesser importance to red squirrels (e.g. aspen, aspen-black spruce, aspen-balsam poplar). Other population-level research on red squirrels has either manipulated resource levels (Klenner and Krebs 1991, Klenner 1991), or has compared populations among seral stages of forest associated with forest harvesting (Sullivan and Sullivan 1982, Sullivan and Moses 1986, Sullivan *et al.* 1996). Furthermore, in cases where natural habitats were compared, study sites were not replicated (e.g. Kemp and Keith 1970, Rusch and Reeder 1979, but see Sullivan *et al.* 1996 for silviculture treatment replication) or research objectives were not focussed on habitat (e.g. Kemp and Keith 1970).

Earlier studies suggested that white spruce habitats consistently support the highest densities of squirrels, have the heaviest animals, and have the highest survival rates compared to other deciduous and coniferous habitats (Rusch and Reeder 1979). Further, they suggest that the proportion of females breeding and the number of young weaned are higher in spruce habitats due to a relatively higher nutritional value and lower handling time of the spruce cone. None of these studies were conducted in years of white spruce cone failure when the potential for habitat quality to decline is greatest.

The objective of this research was to determine if density reflected habitat quality for red squirrels during a spruce cone failure. I wanted to determine if white spruce habitat was consistently superior than other coniferous habitats during this time and to control for geographic location and sampling period. To do this, I compared the demographics of red squirrel populations in three different coniferous habitats over two years of spruce cone failure. I measured resource availability by quantifying spruce and pine cone abundance (the two primary food resources in all three habitat types) across the study areas for both years. My hypothesis was that white spruce habitat would consistently support higher densities, heavier animals, and a greater number of reproductively active individuals compared to other coniferous habitats (i.e. it is relatively higher quality habitat and resident squirrels are self-replacing). I determine if reported similarities or differences of squirrel populations in different habitats are consistent with my results in which individual red squirrels were measured in different habitats at the same place and time during a spruce cone failure.

METHODS

Study Area Locations

My study areas were located within 30 km of the townsite of Hinton (53° N, 117° W), Alberta (Figure 2-1). The study region consists of foothills running northwest to southeast along the front range of the Rocky Mountains. The topography is moderate to steep, with elevation ranging from 1200 to 1600 m. Major rivers in the area include the Athabasca, McLeod and the Gregg River. Mature (80-120 year) coniferous forest (*Pinus contorta, Picea glauca, Picea mariana, Abies spp.*) covers over 80% of the area, with

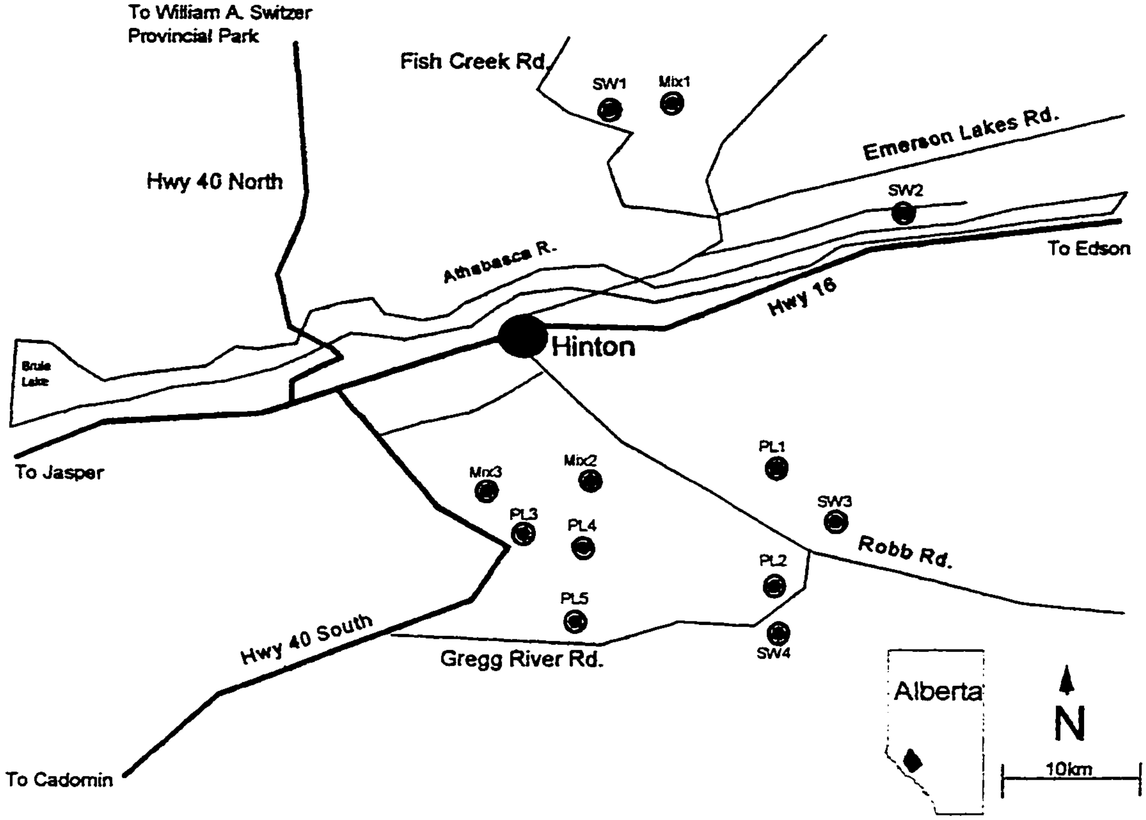

Figure 2-1. Locations of study sites near Hinton, Alberta. PL = Lodgepole Pine, SW = White Spruce, Mix = Mixed Conifer Habitat (White Spruce and Lodgepole Pine).

smaller proportions of both younger (fire and logging origin) and older stands dispersed throughout. Aspen (*Populus tremuloides)* forests are more common at lower elevations than in those of the study areas.

I chose three habitat types for study in the area based on their abundance in the landscape and suggested biological importance to red squirrels: lodgepole pine, white spruce and areas of a mix between lodgepole pine and white spruce (referred to as mixed conifer, see Corns and Annas 1986 for general habitat descriptions of the area). In April 1995, I established twelve live-trapping grids with coordinates flagged at 30 m intervals within each grid. These consisted of 5 replicates in lodgepole pine (dropped to 4 replicates in year 2), 4 replicates in white spruce and 3 replicates in mixed conifer habitat in areas of mature forest (80 to 100+ years old) that previously had not been logged. All grids were at least 5 km apart. I selected these sites based on tree species composition (i.e. habitat type), stand age, the size of continuous habitat patches (5-20 ha, Table 2-1), and access. My study grids were all located within the same natural subregion (the upper foothills; Beckingham *et al.* 1996) with the exception of one white spruce grid located in the lower foothills subregion near the Athabasca river.

Grid size varied (15-30 ha) based on the size of continuous habitat patches and/or the number of resident squirrels initially captured. Initial goals were set at 15-25 animals per grid (based on logistics) and grids were chosen so that all animals on each grid were within continuous forest of the same habitat type.

Study Area Habitat Descriptions

Five 100-m random transects per grid were established to sample tree species composition. At 5-m intervals along each transect, I recorded the species of the closest tree with a diameter at breast height >15 cm (100 trees per grid in total). Dominant understory species were noted on either side of each transect (not quantified). This sampling indicated the following: lodgepole pine (*Pinus contorta)* areas consisted of at least 80% pine (total canopy tree composition mean = 89% pine, range = 80-95%, n = 5 grids), with an understory consisting of alder (*Alnus crispa*), wild rye (*Elymus spp.*),

Table 2-1. Size (in hectares) of study grids.

Grid #	**Size (ha)**
Spruce 1	13 ha
Spruce 2	12 ha
Spruce 3	5 ha
Spruce 4	5 ha
Mix 1	11 ha
Mix 2	17 ha
Mix 3	9 ha
Pine 1	21 ha
Pine 2	8 ha
Pine 3	16 ha
Pine 4	15 ha

Labrador tea (*Ledum spp.*) and mosses (*Ptilium spp., Sphagnum spp.*). White spruce (*Picea glauca*) and fir (*Abies spp.*) were present in these areas at low densities, but were immature and occupied an understorey position. Lodgepole pine study sites faced southwest on moderate to steep slopes (i.e. 10-50%).

White spruce areas consisted of at least 86% spruce (total canopy tree composition mean = 94% white spruce, range = 86-99%, n = 4 grids), with an understorey of feather moss (*Hylocomium spp.*), common horsetail (*Equisetum spp.*) and birch shrub (*Betula spp.*). Spruce study areas were flat with little variation in topography.

Mixed conifer areas consisted of a roughly equal mix of white spruce and lodgepole pine (spruce:pine ratios of the three mixed conifer grids were 49:51, 59:41 and 58:42) with some deciduous species interspersed at low densities. Understorey vegetation varied somewhat within each mixed site but was dominated by alder in all cases. Mixed areas had undulating to steep terrain in all directions with lodgepole pine dominating the higher dry areas and white spruce dominating the lower ravine areas.

Resource Availability

In late summer of each year, an index of white spruce and lodgepole pine cone production was recorded throughout the study sites. These counts were done in all habitat types for white spruce and lodgepole pine trees. Counted trees were selected systematically. These trees were the closest ones to each grid stake that had a diameter at breast height >15 cm. Observers counted all new cones visible in the top 3 m of the east side of each tree. Observations were taken with the aid of binoculars.

Population Enumeration

Population size was determined by complete enumeration through live trapping and direct observation of marked individuals. Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) were placed on middens and runways so that trap density was at least 5 traps per hectare. Traps were baited with peanut butter. Captured animals were ear tagged with metal (Monel Metal Eartag #1) and colored eartags (wires and plastic discs) allowing me to identify individuals using binoculars and focus trap effort on untagged animals. Squirrels were enumerated in all areas from 20 April - 30 May, and again from 20 August to 10 September for both 1995 and 1996. A separate trapping session was done on 5-15 October, 1995 to ensure enumeration of late immigrants. Trapping sessions (3-4 grids over 3-4 days) were always scheduled such that a grid from each habitat type was included in each trapping session to eliminate temporal trapping biases between habitats.

For each squirrel captured, I recorded the grid location, sex, weight (in grams), and reproductive condition (see *Female Reproductive Activity* below). Territorial behavior upon release (i.e. a rattle call indicating territory ownership, see Lair 1990) also was noted. Only residents (individuals displaying territorial behavior or those caught consistently over 2 weeks in the same area) were included in density calculations.

Weight was recorded using a Pesola® spring scale. For each season, weight was calculated for each animal by using the initial capture weight for individuals caught only once and the lowest weight value recorded for individuals caught multiple times in a trapping session. Pregnant females (noted via pre-partum weights) and young of the year were excluded when determining average adult weight for each habitat.

Female Reproductive Activity

The reproductive condition (nipple condition; Layne 1954, Becker 1992) of every female was assessed and scored as one of five categories; (1) long and pink (engorged and lactating), (2) long and dark (beginning to wean but still lactating), (3) medium length and dark (weaning), (4) small and dark (completely weaned or not lactating) or (5) small and pink (never before reproductive). Young red squirrels leave the nest at 37-39 days and begin to gather their own food by 45 days (Layne 1954, Nice *et al.* 1956, Ferron, 1980, 1981). Therefore, for this study a female was scored as being reproductively successful if she lactated longer than 45 days, enough time for her young to emerge and begin gathering their own food. I captured lactating females at least twice a week in order to determine which ones were reproductively successful (had nipples medium length and dark for at least 45 days). Females lactating for shorter periods were considered to have lost their litter before emergence (e.g. unable to sustain lactation, predation, etc).

Juvenile Production and Adult Immigration

By the second week of June when juvenile emergence was expected, middens of lactating females were visited at least every other day. When juveniles were observed outside of the nest, three to five traps were set on the midden and peanut butter was spread on the base of the trees to attract juveniles to the traps (2-5 days of trapping). In most cases, the number of juveniles was obvious through direct observation but trapping was continued for approximately four days after the number of observed juveniles were captured to ensure that none were missed. If no young were observed on a lactating female's midden, traps were still set for juveniles until the resident female was no longer reproductive. Using this method, all juveniles were known on each study area and a per hectare measure of juvenile production was calculated for each habitat. Because all adults and all juveniles were identified, new untagged animals caught in spring and fall represented immigration into the area.

Survival

I scored the loss of resident squirrels from the study areas as mortality and considered the proportion remaining on the study areas as survival. Red squirrel middens are traditional (Obbard 1987) and ownership of a midden appears critical for long-term survival of individuals (Larsen and Boutin 1994). Further, it is apparent through removal experiments that resident squirrels fail to relocate to "higher quality" territories even when given the opportunity (Larsen and Boutin 1995). Given this, it is generally accepted that the disappearance of adult residents from the study grids represents mortality rather than emigration.

Survival estimates were based on observed loss from a marked cohort between 20 April to 10 September, 1995 (summer 1995 mortality), from the end of the trapping season on 20 October, 1995 to 20 May, 1996 (winter mortality), and from 1 May to 10 September, 1996 (summer 1996 mortality). These cohorts included only resident adults that were present on the study areas.

RESULTS

Resource Availability

Spruce cone abundance was low, a virtual failure, in both years (Table 2-2). Pine cone abundance was more consistent between years and the number of cones in pine was four to twenty-nine times higher (for 1995 and 1996 respectively) than in spruce for both years. I counted cones on fewer trees in 1996 because of the lower variation in the data compared to 1995.

Table 2-2. Descriptive statistics for cone counts done in spruce, mixed conifer, and pine habitats over two years near Hinton, Alberta.

Descriptive Statistics	Spruce 1995	Spruce 1996	Pine 1995*	Pine 1996*
N (# trees counted)	448	124	320	136
Mean # cones/tree	14.0	1.0	55.0	30.0
SD	32.64	3.7	56.66	30.1
SE	1.54	0.33	3.16	2.6
Median	1	0	41	20
Range	0-300	0-30	0-300	20-160

*Only new cones of the year counted

Squirrel Densities

A total of 320 individual red squirrels were trapped over the summers of 1995 and 1996. In 1995, average densities of squirrels holding territories in spruce were two to three times higher than those in pine and mixed conifer habitats for both spring and fall (Figure 2-2). This difference decreased by fall 1996. In the fall of 1996, little difference in squirrel density was observed between habitats. Over the two years of study, both pine and mixed conifer habitats showed relatively stable densities with little or no change. Mixed conifer densities varied little from roughly 1.5 animals per hectare. Densities in spruce had the most pronounced change from 1995 to 1996, dropping by half in 1996 when other habitats had no change. Significant differences in density were found between habitats in spring 1995 (one-way Anova, $F_{2,9} = 31.86$, $p < 0.001$) but not in fall 1996 (one-way Anova, $F_{2,8} = 3.14$, $p = 0.10$).

Animal Condition

I found no differences between grids within habitat type (using one-way Anovas

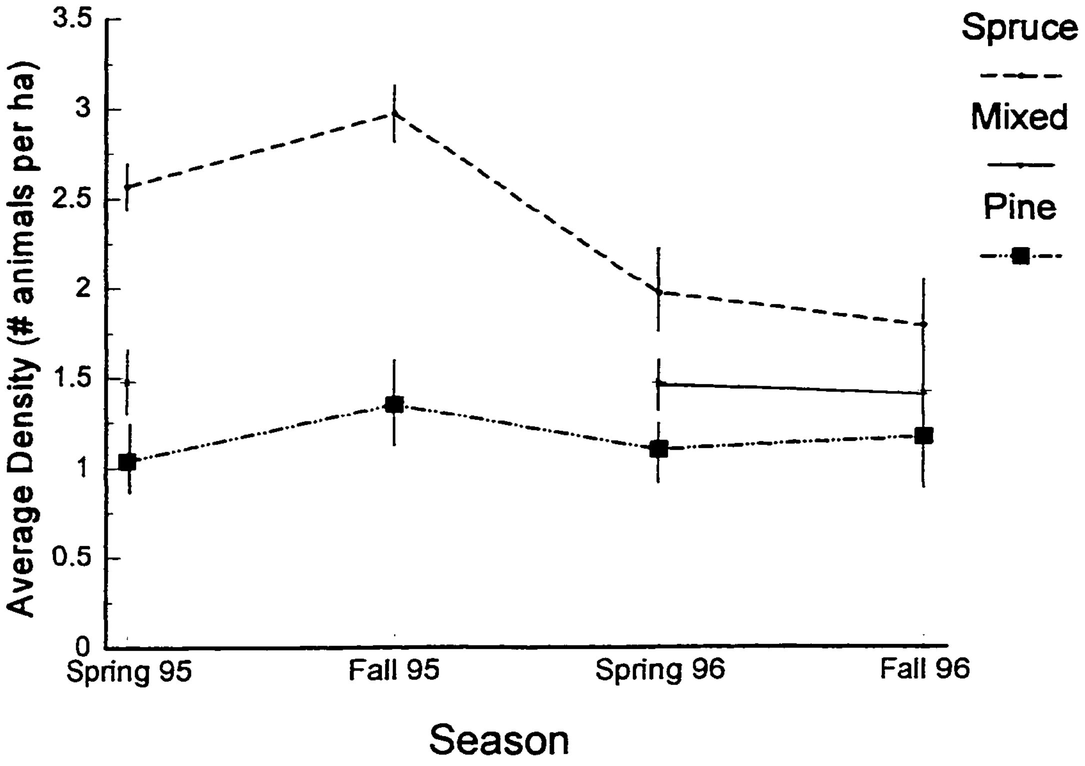

Figure 2-2. Average densities of red squirrel populations in three conifer habitats over two years near Hinton, Alberta. Sample sizes (# trapping grids) for Spruce, Mixed and Pine are 4, 3, 4 respectively, except Spring 1995 n = 4, 3, 5, and Fall 1995 n = 3, 0, 3. Error bars indicate standard error of the mean.

comparing average weights per grid within habitats, all p-values >0.05 for tests comparing grids with >6 squirrels measured per grid). Therefore, I pooled all animals within sex and habitat type.

Female weights differed little between habitats in the spring of 1995 (Figure 2-3) but were lower in spruce than in pine and mixed habitats in the fall of 1995. Similar differences were found in the spring of 1996. Almost no difference between habitats was found for female squirrel weights in the fall of 1996. Weights of female squirrels tended to decrease over time in all habitats from spring 1995 to fall 1996. The most pronounced decreases were in spruce and mixed conifer habitat. Female weights in pine decreased less overall and decreased more gradually over time compared to other habitats.

In spring 1995, male squirrels in both spruce and mixed conifer habitats were heavier than those in pine. No other differences were found for male weights between habitats for any other season. Male squirrel weight in spruce and mixed conifer habitats tended to decrease more over time relative to males in pine.

Female Reproductive Activity

In 1995, the highest proportion of post-estrous females that lactated at least 45 days was found in pine habitat followed by spruce and mixed conifer respectively (Figure 2-4). In 1996, pine and spruce areas showed similar proportions (36% and 32% respectively) with mixed areas showing the lowest. All areas showed a reduction of at least half in the proportion of females lactating for 1996 relative to 1995. The pattern of differences between habitats also changed between years but pine areas did not show proportions lower than those of spruce and mixed conifer areas for both years. For 1995, sample sizes differed from the actual number of grids because of low trapability in some areas.

In many cases the same individual females were measured in the same areas for both 1995 and 1996 creating a lack of independence for female reproduction measurements between years. Therefore, I chose to do single separate Anovas for each year comparing the proportion of lactating females between habitats. This revealed a

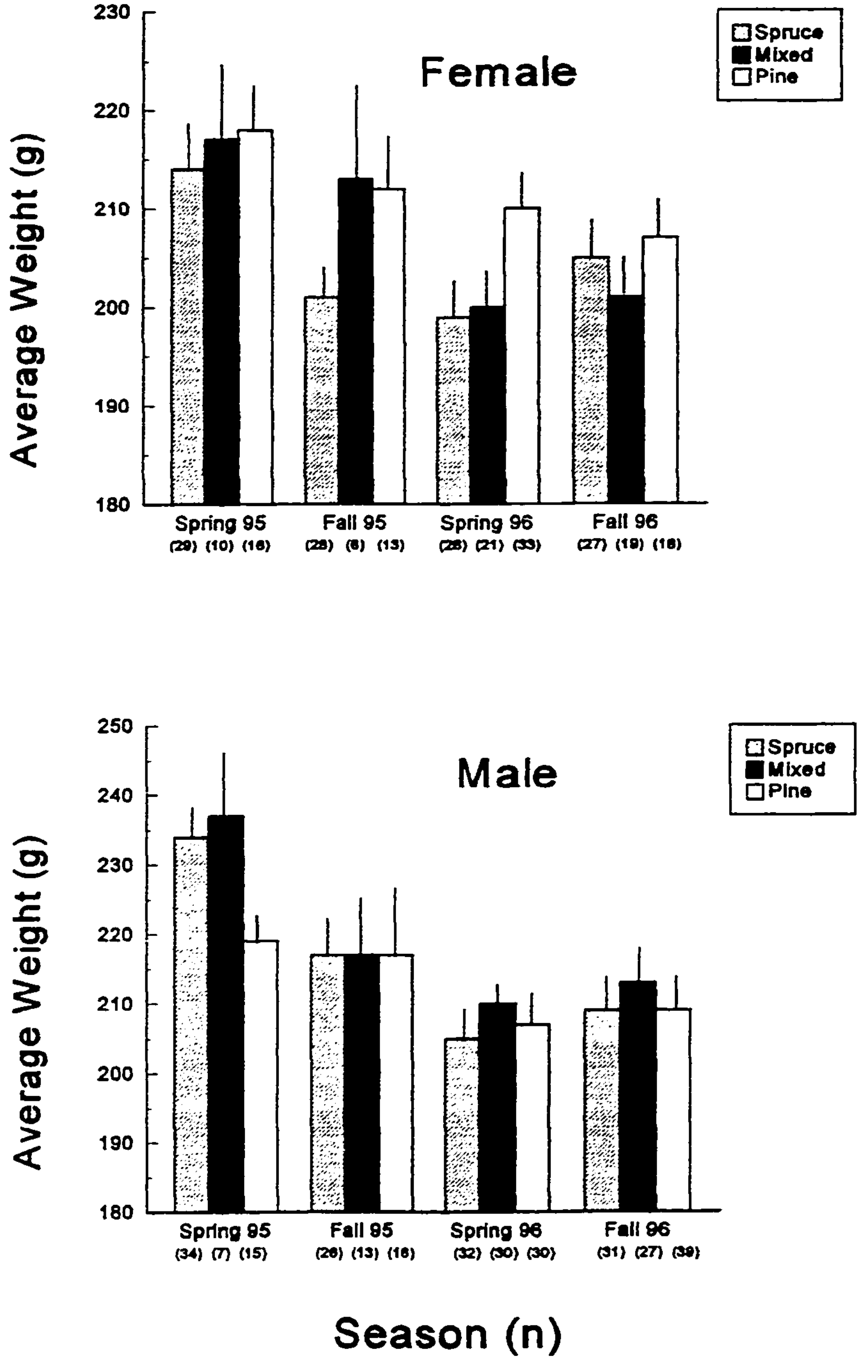

Figure 2-3. Average weights of male and female red squirrels over two years in three conifer habitats. Sample size (# of individual squirrels) is shown in brackets underneath each corresponding bar. Note y-axis does not start at zero. Error bars indicate standard error of the mean.

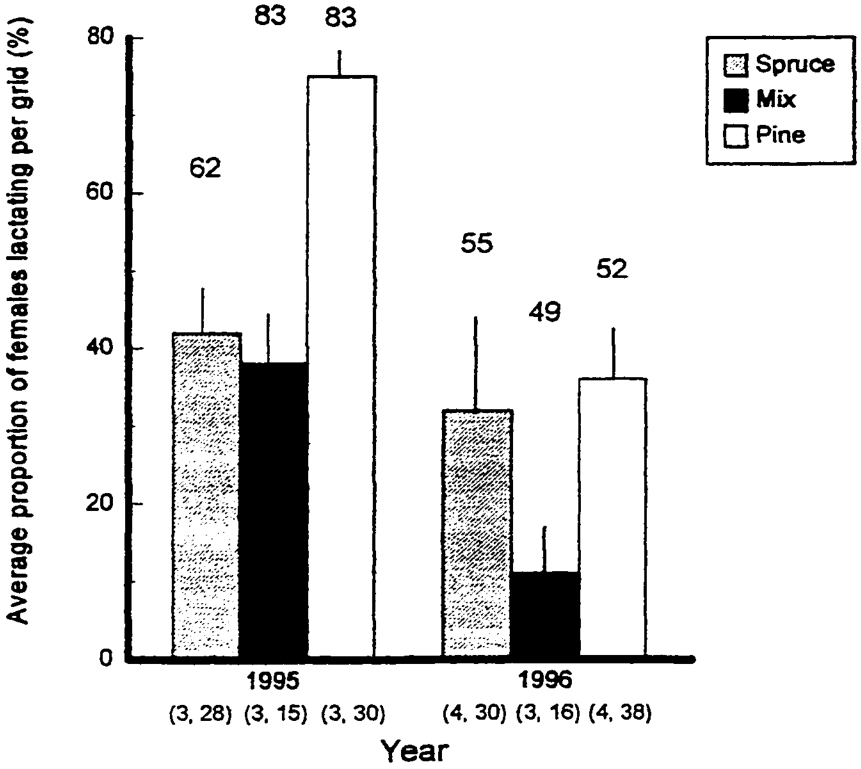

Figure 2-4. Average proportion of post-estrous female red squirrels that lactated a minimum of 45 days (i.e. weaned a litter and considered to complete lactation) in the three conifer habitats. The average proportion of squirrels beginning lactation for each habitat is shown above each corresponding bar. The number of trapping grids followed by the number of individual squirrels from each habitat are shown in brackets under each corresponding bar. The number of individual used per grid to determine average proportions are shown in Appendix 1. Error bars indicate standard error of the mean.

significant difference between habitats for 1995 ($F_{2,6} = 10.49$, $p = 0.011$) but not for 1996 ($F_{2,9} = 2.0$, $p = 0.19$).

The average proportion of females beginning lactation was lower in 1996 relative to 1995 (Figure 2-4). This implies that post-estrous litter loss was similar between years and fewer females bred overall in 1996 for all habitat types.

Juvenile Production

In 1996 animals in pine habitat had an average juvenile production that was two to three times higher than other habitats (Table 2-3). Mixed conifer habitat produced the lowest number of juveniles. However, these differences were not statistically significant (one-way Anova, $F_{2,8} = 1.6$, $p = 0.26$). Low trap success prevented complete juvenile enumeration in 1995.

Table 2-3. Juvenile emergence from nests of red squirrel populations in three different conifer habitats for summer-fall 1996.

Conifer Habitat (n)*	# juveniles emerged per hectare of habitat. mean (range)
Spruce (4)	0.18 (0-0.40)
Mixed (3)	0.04 (0-0.11)
Pine (4)	0.34 (0.06-0.71)

*Sample size refers to the number of trapping grids

Immigration

The greatest average number of new residents per hectare in the fall of 1996 was found in pine habitat and the least was found in mixed conifer habitat (Table 2-4; juvenile and adult immigration is decoupled in Table 2-5). However, these differences were not statistically significant (one-way Anova, $F_{2,8} = 0.93$, $p = 0.43$). Low trap success prevented complete immigrant enumeration in 1995.

Table 2-4. Immigration (adult and juvenile) for red squirrel populations in three different conifer habitats for winter-fall 1996.

Conifer Habitat (n)*	# of new resident animals per hectare after juvenile dispersal. mean (range)
Spruce (4)	0.10 (0-0.42)
Mixed (3)	0.14 (0-0.24)
Pine (4)	0.42 (0.18-1.1)

*Sample size refers to the number of trapping grids

Survival

Average adult survival for each habitat was partitioned into three time periods: summer 1995 (April - September 1995), winter 1996 (October 1995 - May 1996) and summer 1996 (May - September 1996). Survival was variable over time for all three habitats (Figure 2-5). Pine and spruce habitats had the highest squirrel survival in the summer of 1995, and mixed conifer had the lowest for this time period. Winter 1996 survival rates were highest in the pine habitat followed by mixed conifer and spruce. Summer 1996 survival was highest in the mixed habitat followed by pine and spruce. These data showed a trend for pine to have higher survival rates relative to the other habitats but no significant differences were detected (three one-way Anovas, all p >

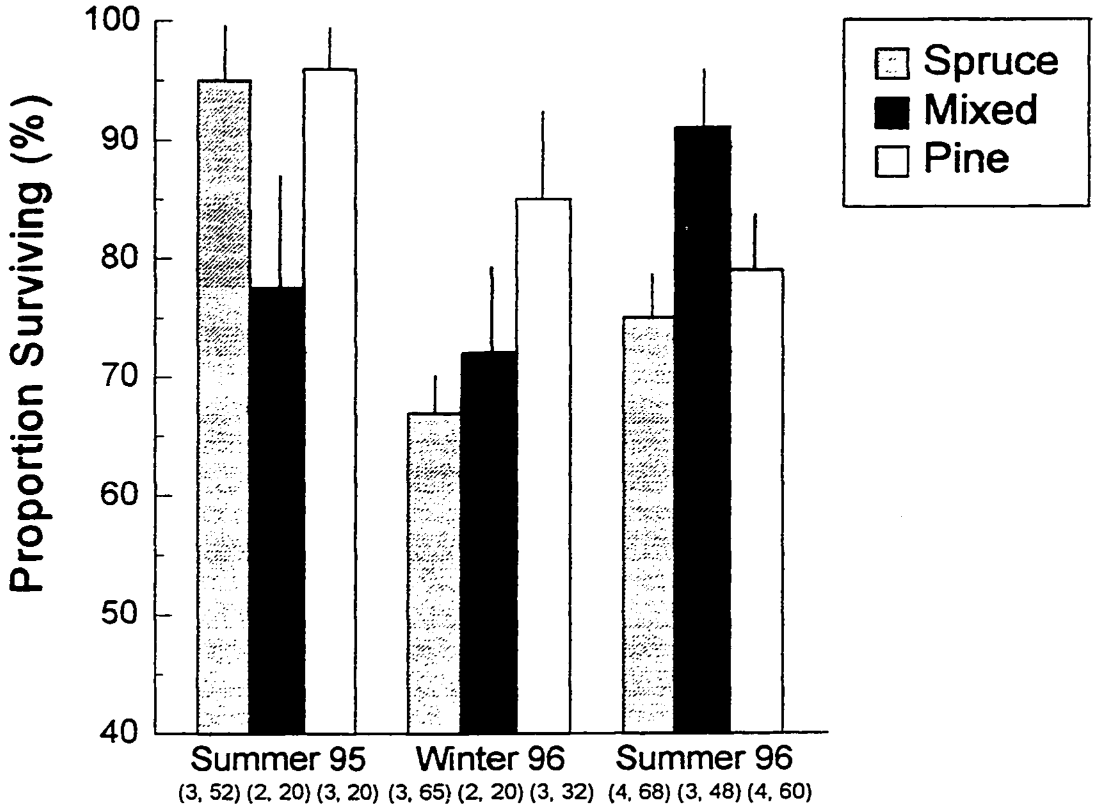

Figure 2-5. Average summer 1995 (April-September 1995), winter (fall 1995 - spring 1996), and summer 1996 (May-September 1996) survival of adult resident red squirrel populations in three conifer habitats. The number of trapping grids followed by the number of individual squirrels from each habitat are shown in brackets underneath each corresponding bar. The number of individuals used per grid to determine average proportions are shown in Appendix 1. Note y-axis does not start at zero. Error bars indicate standard error of the mean.

0.05). Survival data were calculated using the maximum number of grids that had at least 10 marked adult residents at the beginning of each period (i.e. sample size differs between periods).

Population Replacement

Population changes for each grid having sufficient data (summer 1995 and winter 1996 survival could not be determined for every grid) were calculated from the number of residents in fall 1995, their survival and each grid's juvenile production, juvenile immigration and adult immigration (Table 2-5).

Mortality rates were not compensated by juvenile production within the spruce grids. Spruce immigration consisted mostly of adults coming into the areas in winter and summer 1996. However, this immigration did not compensate for mortality, resulting in a negative net change for all three spruce areas.

Mixed conifer areas also had mortality rates that were not compensated by juvenile production. Only adult squirrels immigrated into the areas in winter and summer 1996. This immigration compensated mortality for one of the two mixed conifer grids measured but not the other.

Squirrels in pine habitats compensated for mortality by within-grid juvenile production on only one of the three pine grids. Two of the three pine grids did not and this resulted in a negative net change before immigration for these two grids. After juvenile and adult immigration, which were roughly equal in all cases, all pine grids showed either no net change or a positive net change in the number of individuals. One pine grid (PL1 in Table 2-5) produced up to four times the number of juveniles in the summer of 1996 relative to the other pine grids. Replacement equal to or above mortality on the other two pine grids (PL2 and PL3) was a result of immigration not juvenile production.

Table 2-5. Changes in red squirrel numbers for study grids with sufficient data (survival could not be determined for all grids, therefore, numbers of individuals may not coincide with sample sizes of other demographic measurements). Numbers are expressed as number of individual squirrels. d_x = disappearance or apparent mortality.

Habitat Grid	Fall 1995	Winter d_x	Summer 1996 d_x	Juveniles Produced Summer 1996	Net Change Before Immig.	Adult Immig. Winter-Summer 1996	Juvenile Immig. Fall 1996	Net Change After Immig.
SW 1	25	-8	-2	0	-10	1	1	-8
SW 2	27	-8	-4	5	-7	3	0	-4
SW 3	13	-5	-2	4	-3	0	0	-3
Mix 1	14	-5	-1	0	-6	2	0	-4
Mix 2	15	-3	-1	1	-3	4	0	+1
PL 1	16	0	-4	16	+12	4	4	+20
PL 2	17	-5	-1	4	-2	5	4	+7
PL 3	14	-2	-2	1	-3	1	2	0

DISCUSSION

Several findings emerge from this study. First, white spruce habitat did not consistently support squirrel densities that were significantly higher than other conifer habitats; squirrel densities in white spruce varied between years (a drop in density by up to one animal per hectare over 2 years), most likely as a result of cone availability. Second, the proportion of lactating females and the proportion of resident adults surviving was variable between years in all habitats, but showed trends for spruce to have the lowest levels during years of poor spruce cone crops. Third, spruce did not support heavier squirrels relative to other coniferous habitats. Finally, immigration and juvenile production were lowest in spruce and mixed conifer habitats during a spruce cone failure. In addition, these parameters were, on average, greater in pine but were variable between pine grids. White spruce forest, and areas consisting of roughly 50% white spruce, were of no greater quality, and in some cases of lower quality, than pine forests. Based on information in the literature, my general hypothesis was that white spruce habitat would consistently support higher densities, have heavier animals, show increased survival, and have more reproductively active females relative to other coniferous and deciduous habitats (see Rusch and Reeder 1979: 416, Obbard 1987 and references therein). That is not what I found.

The published literature (summarized in Table 2-6) suggests that spruce forests generally support the highest densities of squirrels, with pine habitats supporting densities roughly half those in spruce, and mixed conifer habitats supporting densities similar to either spruce or pine. Densities found in this study for mixed conifer and pine habitats fell generally within the ranges of reported squirrel densities. However, squirrel densities in spruce were not stable and decreased in 1996 resulting in some of the lowest reported spruce densities (values that were not different from other habitats in this study). It has been suggested that red squirrel territory size, which determines maximum density, is pre-set to be sufficiently large enough to meet the energy requirements for the resident in years of cone failure (C. Smith 1968, Rusch and Reeder 1979). If this were true, I should not have observed a drop in densities in spruce habitats. Territory size in spruce may be set at a size that is optimally defended by an individual in average or good cone years, but not of sufficient size to meet energy demands in poor cone years. In terms of density reflecting habitat quality, my data suggest that the relative qualities of habitats can change over time for the red squirrel.

Table 2-6. Densities of adult red squirrels in various habitat types (modified from Obbard 1987). Present study densities included by range not average.

Habitat	Region	Density (#/ha)	Source
Spruce Forests	New Brunswick	2.5	Klugh (1927)
	New York	5.0	Hatt (1929)
	Massachusetts	2.5	Hatt (1929)
	Alaska	2.0	Brink (1964)
	Saskatchewan	2.5	Davis (1969)
	Central Alberta	2.9- 4*	Rusch and Reeder (1979)
	West-central Alberta	*1.2- 3**	*Present Study*
Mixed Conifer Forests	British Columbia	2.0	C. Smith (1968)
	British Columbia	0.5	Fancy (1981)
	West-central Alberta	*1.0-1.8**	*Present Study*
Pine Forests	Ontario	0.83	Seton (1910)
	Massachusetts	0.83	Hatt (1929)
	British Columbia	1.11	C. Smith (1968)
	Central Alberta	1.0	Rusch and Reeder (1979)
	Colorado	1.3	Gurnell (1984)
	West-central Alberta	*0.7-1.8**	*Present Study*

*Value depends on season

Heavier body weights in female red squirrels have been shown to increase the probability of estrous in nulliparous females (Becker 1992), and increase the probability of successful completion of lactation (Wauters *et al.* 1990) and weaning of young to dispersal age (Rusch and Reeder 1979). Habitat related differences in squirrel body weights have been noted both in European red squirrels (*Sciurus vulgaris*; Wauters and Dhondt 1989) and North American red squirrels (Rusch and Reeder 1979, Boutin and Larsen 1993). Rusch and Reeder (1979) and Wauters and Dhondt (1989) attributed these differences in body mass to habitat resource quality. Differences in squirrel body weights can also be noted between habitats from studies that had geographically separated study sites (e.g. British Columbia, Alberta and Yukon; C. Smith 1968, Boutin and Larsen 1993). However, given the lack of weight differences in this study, weight differences noted between habitats through geographically separated study sites may reflect differences in latitude (i.e. Bergman's rule) rather than habitat type.

Rusch and Reeder (1979) also suggested that weight differences between habitats were partly a result of an increased number of juvenile dispersers into deciduous habitat (aspen) that had relatively poorer resource quality and availability. In the present study, with pine areas showing greater resource availability and juvenile production, such an explanation may apply to the lighter weights of females in spruce (lower resource availability) in the fall of 1995 and the spring of 1996. However, I did not note an abundance of nulliparous females in any habitat and immigration was relatively low in spruce compared to pine habitat. If fall 1995 female weights were due to younger female squirrels in spruce, these may have been juvenile nulliparous but post-estrous females differing only by their lighter weight from older multiparous females. A longer term trapping assessment noting birth dates of individuals would be necessary to determine this.

In this study, the proportion of females lactating at least 45 days for each habitat varied between years, and this annual variation has been observed elsewhere (C. Smith 1968, Kemp and Keith 1970). If a depleting cone cache was limiting squirrels in spruce habitat for at least one year prior to the summer of 1995, a lower proportion breeding in 1995 and a further decline in 1996 would be expected based on the lack of available energy needed to support lactation. However, a concurrent reduction was seen in pine and mixed conifer habitats. This drop was not expected given the apparent availability of pine cones in those areas. Pre-emergence loss of litters for pine females in 1996 did not account for the substantial difference between years. Rather, pre-emergence losses were similar for both years and fewer females gave birth overall in 1996 suggesting a more regional rather than a habitat-related explanation. The higher pre-emergence losses in spruce and mixed habitat may have been related to lack of food resources. Losses could also have been related to higher nest predation contingent on habitat, but habitat-specific predation rates were beyond the scope of this study and are not reported as such in the literature for red squirrels.

For both seasons in both years, survival was above 60% (62-100%) for all habitats. Similar survival levels have been observed for red squirrels, although rarely by habitat type, not recorded seasonally and never replicated to produce a measure of within year variation. C. Smith (1968) recorded 33% overwinter survival of red squirrels between 1964 and 1965 in British Columbia (noted as a drop in numbers by 67% and not related to habitat), while Kemp and Keith (1970) recorded 55% overwinter survival in a mixed spruce forest in Alberta (recorded as 45% mortality). Rusch and Reeder (1979) presented the only habitat-related comparison of squirrel survival rates showing spruce habitats having higher survival (73%) with pine (63%) and aspen (0%) areas at lower levels over three years. I found the opposite for conifer habitats. I also found survival to be variable between seasons. This may have been a result of differential seasonal predation or low sample size. Seasonal and annual variation in survival has previously been noted for red squirrels (Rusch and Reeder 1979). Conclusions regarding survival must be tentative because, other than resource availability, I did not measure other factors such as predation or winter weather that could have affected survival rates.

The failure of juvenile production to replace mortality on most of the grids suggests that immigration of both adults and juveniles are important in replacing mortality. This phenomenon appears to apply to all habitats. In particular, adult and juvenile immigration (not juvenile production) replaced mortality on two of three pine grids, implying that there may be site-related factors involved in determining juvenile production. Some pine areas may have higher juvenile production or survival than others. Given the positive net change after juvenile production and immigration, it is interesting that densities in pine did not increase. Higher immigration in pine habitats did not result in density changes in pine or other conifer habitats. Animals produced in source pine areas may have been filling up sink pine areas that had potentially vacant territories rather than moving to other habitat types. With the relative consistency of the pine cone resource (Lotan 1975), this may be a consistent phenomenon across years.

Rusch and Reeder (1979) discuss a "spring shuffle" of resident squirrels after winter mortality. Such a shuffle could have accounted for the higher adult immigration compared to juvenile immigration found in this study. Findings of the present study lend support to the spring shuffle idea and may imply that red squirrels do not show as much long-term fidelity to a territory as once thought. In contrast, Larsen and Boutin (1995) provided red squirrels with opportunities to relocate to "higher quality" territories through removal experiments in late August. They found that they failed to relocate and concluded that territory fidelity was very high or that they failed to accurately assess territory quality in their removals. Results may have shown less territory fidelity if these removals had been done in the early spring. Defending and holding a territory may be far more important for survival in the fall with the onset of winter than in the spring when other food resources become far more abundant. For example, individuals may relocate in the early spring, if given opportunity via experimental removals or through natural winter mortalities, either for mating purposes or to a territory with a less depleted food cache. With the apparent repeated result of Rusch and Reeder's spring shuffle in this study, it may be that territory fidelity, or the decision of an individual squirrel to relocate, is both seasonal and opportunistic. Nonetheless, both juvenile and adult immigration appear important in maintaining stable squirrel densities in lodgepole pine and mixed conifer habitat.

Overall, I found that density did not reflect habitat quality for red squirrels during a spruce cone failure. I did not find populations in white spruce to be self-replacing, nor did I find demographic parameters of these populations to be greater or different than those of pine or mixed conifer populations. Given the variability of white spruce cone mast years (a cycle from 3-12 years, Hellum 1976) the potential for intervals greater than two years is high. The data presented in this study suggest that the relative importance of habitats for maintaining sustainable populations of red squirrels can change during periods of resource fluctuations. This has implications regarding the relative roles, and historical quality ratings, of different habitats in maintaining squirrel populations over time. White spruce habitat may be higher quality over short time periods (e.g. 3-4 years) but show average quality, more comparable to other conifer habitats, over longer time periods (e.g. 12-20 years).

Whether or not pine habitat densities are set at levels that preclude resource shortages and those relatively lower densities are reflected in spruce habitats during spruce cone failures is possible but speculative. Although not directly observed in this study, changes in spruce cone abundance could result in either the movement of individuals between habitats (i.e. from spruce to pine), or higher mortality in spruce areas causing negative replacement and population decline. Over long time periods (e.g. 50-100 years) frequent short-term fluctuations in spruce cone abundance would certainly affect habitat quality and the relative importance of habitats over time. This would make population or habitat quality predictions difficult if such fluctuations were not considered.

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Chapter Three. Conclusion.

In this study, I explored the importance of habitat quality for red squirrel populations in three conifer habitats. I designed the study to compare the demographics of squirrels in three conifer habitats that are thought to be of different qualities based on squirrel densities. My primary goal was to determine if the relative quality of habitats changed with fluctuations in conifer cone availability characteristic of one of the three habitats (white spruce). Because of these extreme fluctuations in resource availability in a habitat considered to be of high quality for red squirrels, I suspected that population predictions over time could be inaccurate if such fluctuations were not considered. In years of high or average cone availability white spruce may support highly productive squirrel populations, however, average productivity over time may be lowered by years of low spruce cone abundance. This average production may not differ from populations in other conifer habitats with more stable cone abundance over time.

Squirrel Biology

The observed changes in squirrel densities in spruce habitats from 1995 to 1996 suggests that the cached cones (thought to last up to a year into a cone failure, C. Smith 1968) of squirrels in spruce were depleting causing either mortality or emigration. Survival, juvenile production, adult and juvenile immigration and the proportion of lactating females were comparatively equal or lower in spruce relative to the other habitats. The data presented in Chapter Two suggest that density does not reflect habitat quality during years of spruce cone failure.

Perhaps squirrels in white spruce do very well in good cone years, and poorly during years of cone failure, resulting in success comparable to squirrels in a more resource-stable lodgepole pine habitat over an individual's lifetime. This could have interesting implications in terms of an individual's lifetime reproductive success depending on what habitat and during what phase of a spruce cone cycle an animal is born into. An individual born into spruce habitat during several years of average to high spruce cone abundance may show higher lifetime reproductive success than one born at the beginning of a spruce cone failure. In mixed wood areas where other habitats and their related resources are available, the degree of philopatry seen in a habitat for a given year could be highly dependent on habitat-specific resource fluctuations. Movements between habitats (juvenile and adult), where possible, could be very dynamic depending on the resource availability in each year.

The historical "high quality" rating of white spruce should be interpreted with caution given the somewhat unpredictable and extreme nature of the white spruce cone crop. Until now there have been no studies looking at red squirrel population productivity in different conifer habitats during a spruce cone failure. Density can be a misleading indicator of habitat quality for this animal, and this has implications for trying to predict red squirrel population abundance or productivity across a heterogenous landscape.

Predicting Squirrel Populations

This study was partly motivated by the planned use of a red squirrel predictive model that rated white spruce as "higher quality" habitat than pine and mixed conifer habitats. Generally, wildlife-habitat predictive models are used to generate either abundance measures or habitat availability measures for a species over time periods of up to 100 years (see Morrison *et al.* 1992 for a review). This generally corresponds to a two or three pass system in forest harvesting depending on the tree species harvested (Hunter 1990).

One of the biggest potential problems with single-species predictive models is the lack of change in habitat quality being incorporated over time into the model. When models are constructed, commonly they are based on habitat relationships between features of a habitat and the corresponding relative abundance of that species in that habitat (see Verner *et al.* 1986 for examples). These relationships are derived from simple census techniques that relate a species' relative abundance to easily measured habitat features (canopy height, coarse wood volume, etc.) recorded over relatively short time periods (1-2 years). Once these relationships are derived, the model uses them to generate predictions for a species' abundance or habitat availability over time periods up to 100 years and under different management scenarios.

A predictive model for the red squirrel rating white spruce as higher quality habitat could fall short of accuracy given the fluctuations in cone availability in white spruce. Both regression models and Habitat Suitability Index Models (U.S. Fish and Wildlife Service 1981), that generate predicted squirrel numbers or predicted squirrel habitat availability respectively, would be inaccurate based on our current understanding of habitat-related squirrel demography. For example, over a 100 year simulation, if spruce cone crops fluctuated with periods of 3-12 years (Hellum 1976), up to half of the simulation could have poor spruce cone resources. Therefore, red squirrel habitat predictive models should incorporate a cone crop variable, making the model less deterministic and more analytical (run over several simulations to create average outputs; Morrison *et al.* 1992) to aid in decision making processes. Finally, juxtapositions of habitat types on a managed landscape could be incorporated into a spatial model to predict population abundance in terms of habitat type and its position on the landscape. Such a model would not only require information on habitat-specific resource availability and animal demographics, but also a measure of the movement of individuals between habitats over time (including dispersal capabilities). This would enable managers to predict population abundance over time given various compositions and landscape positions of different habitat types. Such is one of the ultimate goals of wildlife management.

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Appendix 1. Number of individual animals used per grid for reproduction and survival proportion calculations.

Grid	Number of Animals Used in Survival Proportions			Number of Females Used in Reproduction Proportions	
	Summer 95	Winter 95/96	Summer 96	Summer 95	Summer 96
Spruce 1	21	25	17	13	9
Spruce 2	19	27	28	10	14
Spruce 3	-	-	12	-	4
Spruce 4	12	13	11	5	3
Mixed 1	10	10	11	7	6
Mixed 2	-	-	21	4	4
Mixed 3	10	10	16	4	6
Pine 1	-	11	22	-	6
Pine 2	8	12	14	7	24
Pine 3	5	9	11	13	5
Pine 4	7	-	13	10	3

- dashes represent areas of poor trapability where proportions could not be calculated due to low or no samples.