POPULATION ECOLOGY, HOME RANGE SIZE, AND CACHING BEHAVIOUR OF RED SQUIRRELS (TAMIASCIURUS HUDSONICUS) IN TERRA NOVA NATIONAL PARK, NEWFOUNDLAND

JOHN J. REYNOLDS

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POPULATION ECOLOGY, HOME RANGE SIZE, AND CACHING BEHAVIOUR OF RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*) IN TERRA NOVA NATIONAL PARK, NEWFOUNDLAND

by

John J. Reynolds

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ABSTRACT

The population ecology, home range size, and caching behaviour of red squirrels was studied in black spruce habitat in Terra Nova National Park, Newfoundland. Density was almost twice as high during summer 1995 (a year of heavy cone crop) than in 1994, but densities in both years were similar to those reported in other studies. Densities ranged from 0.4 - 1.3 squirrels /ha in 1994 and 1.0 - 2.7 /ha and 0.8 - 3.7 /ha on grids 95-1 and 95-2 respectively in 1995. Transients (animals captured only once) were a minor component of the population in both years. The larger number of spring recruits and higher summer body weight in 1995 indicate that the greater density was due to higher overwinter survival during 1994/1995. Total adult sex ratios (based on all animals captured) were significantly biased in favour of males in 1994 and for the combined adults in 1995.

Summer home range size in 1995 ranged from 0.34 - 4.1 ha (95-1) and 1.8-2.4 ha (95-2) using the minimum convex polygon method and from 0.34 - 4.8 ha (95-1) and 4.3 - 8.0 ha (95-2) using the adaptive kernal method. These values are generally larger than home range and territory sizes reported in other studies. The presence of deciduous food and the breeding season, may have contributed to the larger home range size. Home ranges were not exclusive and all showed signs of overlap.

North American red squirrels exhibit variation in caching behaviour across their range. Larderhoarding dominates in the west and scatterhoarding dominates in the east. One proposed explanation for this variation is predation risk. If safe feeding and caching sites are unavailable, then moving to, and eating at scattered caches may elevate the risk of predation for the caching individual. It was predicted that in areas of low understory shrub cover, predation risk is higher and safe caching sites are rare. Therefore, creating larger caches at one or a few low-risk sites would be the better strategy.

The caching behaviour of red squirrels was documented in 1995 in grids 95-1 (high cover) and 95-2 (low cover). In both grids, both single cone and large caches (11+ cones) occurred more frequently than expected, but cache size frequency distributions did not differ significantly between grids. The mean (± SE) number of cones in large caches (30.9 ± 2.5) was significantly greater in low cover than in high cover (18.3 ± 2.6). Large caches accounted for 65% and 20% of all cones stored in the low and high cover grids respectively. The size of the cache (single or multiple cones) was not dependent on the distance from the nearest tree in low cover, but in high cover, single cone caches were found farther from a tree (mean ± SD: 1.5 m ± 1.3) than multiple cone caches(1.0 m ± 0.67). It appears that the amount of cover may be one component of red squirrel caching behaviour.

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Chapter 1: Introduction

Food hoarding allows an animal to have some control over the availability of food in space and time (Vander Wall, 1990). Two basic patterns are recognized: larderhoarding and scatterhoarding. Larderhoarding involves storing most of the food in one concentration in a small part of the home range, while scatterhoarding involves forming many caches of one or a few food items dispersed throughout the home range (Smith and Reichman, 1984). The type of food hoarding pattern exhibited is associated with the amount of both inter- and intraspecific competition, and has important implications for social behaviour. Larderhoarding is believed to occur in species which experience little interspecific competition for food or when caches can be defended from interspecific competitors. Larderhoarders are often territorial which prevents cache theft by conspecifics (Smith and Reichman, 1984). Scatterhoarding usually occurs when there is extensive inter- and intraspecific competition for the hoarded food. With high levels of competition, large hoards are harder to defend and may be more easily located (Smith and Reichman, 1984). Scattering caches presumably makes it less economical for a competitor to pilfer these small, scattered caches than to forage on its own and since scattered caches are difficult to defend, scatterhoarding is associated with non-territorial species (Stapanian and Smith,1978).

North American red squirrels (*Tamiasciurus hudsonicus*) have been categorized as larderhoarders (Stapanian and Smith 1978; Smith and Reichman,1984; Vander Wall, 1990). Seeds from conifer cones are their primary food source and cones are harvested from throughout their individual territories and stored in a central midden composed of cone scales and cores (Gurnell, 1987). Removing cones from trees and caching them in the damp midden material prevents the cones from opening, providing the animal with a supply of cones necessary for winter survival. These middens may contain thousands of cones and can supply food for one or two winters (M.C. Smith, 1968; Finley, 1969).

Red squirrels are believed to be able to larderhoard conifer cones because they face little interspecific competition for this food source. Larger herbivores would have to eat the whole cone to obtain the seeds, however, the woody tissue in the cone makes it indigestible (Smith and Reichman, 1984; Hurly and Robertson, 1987). Also, the size and hardness of the cones make them difficult to open for smaller herbivores such as mice (Smith, 1981). Therefore, food competition is primarily intraspecific and territoriality reduces this. The spacing and food storing system is unlike most other tree squirrels (*Sciurus* spp.) which scatterhoard the nuts of deciduous trees and are non-territorial (Gurnell,1987).

Much of the information on food use and caching behaviour in red squirrels comes from the western portion of its range (C.C. Smith, 1968; M.C. Smith, 1968; Finley, 1969; Kemp and Keith, 1970; Rusch and Reeder, 1978; Kelly, 1978; Gurnell, 1984). Recently, studies on eastern populations have shown that the caching behaviour of red squirrels is more flexible and that a mix of both larder and scatterhoarding is used (Hurly and Robertson, 1987, 1990; Dempsey and Keppie, 1993).

Although it has not been rigorously tested, red squirrels which scatterhoard are believed to be territorial (Hurly and Robertson, 1987, 1990; Dempsey and Keppie, 1993). Therefore, either the scatterhoards themselves or the area in which they are placed (i.e. the territory) can be defended. This is in contrast with the European red squirrel (*Sciurus vulgaris*) which can also occupy coniferous habitat and eat conifer seeds. Cones are scatterhoarded by this squirrel (Wauters and Dhondt, 1987; Wauters and Casale, 1996) but individual exclusive territories are not defended (Wauters and Dhondt, 1992). If scatterhoarding red squirrels are territorial and are presumably able to defend a larderhoard, then some factor other than defendability of caches must account for the prevalence of scatterhoarding behaviour in this species.

Dempsey and Keppie (1993) suggested that predation may be a factor in hoarding strategy. Many studies have shown that predator avoidance affects foraging behaviour and that predation risk may be greater in areas with low vegetative cover (see Lima and Dill, 1990 for a review). Grey squirrels (*Sciurus carolinensis*) perceive a high risk of predation further from protective cover (Lima et al., 1985) and fox squirrels (*Sciurus niger*) perceive open patches as risky (Brown et al., 1992).

A recent study has shown that cover is also important for red squirrels. Juvenile red squirrels that were eventually preyed on spent more time exposed in trees and on the ground than juveniles which survived their first summer (Stuart-Smith and Boutin, 1995). Also, juveniles during their first summer spent less time in covered places and more time in exposed places than adults (Stuart-Smith and Boutin, 1995) which may explain the lower survival rate of first summer juveniles as compared to adults (Stuart-Smith, 1993). Similarly, Yahner (1987) showed that in marginal habitat, red squirrels used feeding sites which were associated with higher densities of understory trees, indicating that minimizing exposure while feeding is important. Moreover, Sullivan et al. (1994) have shown that feeding damage on young lodgepole pine (*Pinus contorta*) increased with the amount of understory shrub cover available. These authors assumed that the ability of predators to capture squirrels and /or the perceived risk of predation may be increased in open microhabitats.

Consequently, red squirrels should alter their food caching behaviour in response to differing levels of understory shrub cover. Because eating a cone requires more time than locating, cutting, carrying and storing it (C.C. Smith, 1968) and because squirrels eat relatively close to caches (at the midden for larderhoarders - Finley,1969; at a mean distance from caches of ca. 1m for scatterhoarders - Dempsey and Keppie,1993), then squirrels should select safe, protected sites for caching and feeding. Presumably, in low cover, safe caching sites are rare. If caches are scattered, then getting to and eating at caches may elevate the risk of predation for the squirrel, especially when movement can be used by avian predators to locate prey (Kaufman, 1974; Sarno and Gubanich, 1995). Under these conditions, creating larger caches at one or a few low risk sites would be the better strategy. In high cover, where the perceived risk of predation may not be as great and where safe caching and feeding areas may be numerous, it may be easier and more efficient to cache food in the general area in which it is found. Hence, many smaller caches would be expected. I tested these ideas by comparing the size and spatial distribution of red squirrel caches in areas of high and low understory cover in a boreal forest in Newfoundland.

Specifically, I predicted that if the relative amount of understory cover influences the pattern of caching then:

1) red squirrels would make larger caches (i.e., containing more cones) in areas of low understory cover than in high cover areas;

2) since placing caches near trees would provide a squirrel with a source of cover and would allow for a quick escape if a predator is detected, then caches should be placed closer to trees in low cover areas than in high cover sites.

Caching behaviour may be affected by levels of intraspecific competition which may in turn be affected by population density. However, little is known about the population ecology of red squirrels since their introduction to the island approximately 34 years ago (Minty, 1976; Payne, 1976; Goudie, 1978). The introduction of red squirrels has been attributed as the cause of the population decline of the Newfoundland red crossbill (*Loxia curvirostra percna*) whereby it is suggested that squirrels outcompete crossbills for black spruce (*Picea mariana*) cones (Benkman, 1989). Red squirrels are believed to be twice as dense on the island of Newfoundland as they are on the mainland (Benkman, 1989; Pimm, 1990) and Benkman (1992: 41) suggests "that a tenfold difference in density is closer to reality." Therefore, I used mark - recapture techniques to describe red squirrel population demography and radio - telemetry to document space use patterns of individual red squirrels.

Chapter 2: Materials and Methods

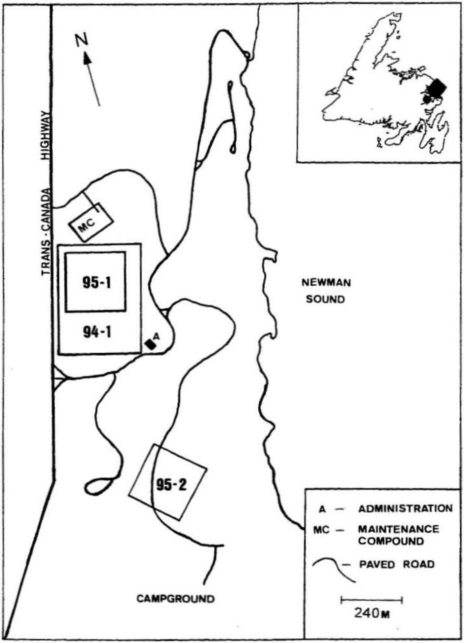
2.1 Study Sites

Red squirrel populations were studied for two summers in Terra Nova National Park (48°33' N, 53°58' W), Newfoundland. Squirrels were first detected in the park around 1977-1978 (Bateman et al., 1983). Potential mammalian predators in this area include lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), and weasel (*Mustela* spp.). Pine marten (*Martes americana*) are present but considered very rare (Bateman et al, 1983). Potential avian predators include northern goshawk (*Accipiter gentilis*), and great horned owl (*Bubo virginianus*; Burrows, 1980).

In 1994, a 15-ha trapping grid with 48 trapping stations located at 60-m intervals in an 8-by 6 pattern was established in the area between the Park Maintenance compound and the Administration Building of the Park Headquarters area near Newman Sound (grid 94-1, Fig. 2.1). This area was composed mainly of black spruce with some balsam fir (*Abies balsamea*). Understory consisted of alder (*Alnus rugosa*) and *Kalmia* shrubs.

Because the number of traps was limited, and in order to accommodate the use of two grids in 1995, the trapping grid used in the previous year was shortened to 5.8 ha with 81 trapping stations located at 30-m intervals in a 9-by 9 pattern. The portion of the 1994 grid closest to the maintenance area was used. An additional trapping grid of the same dimensions was established approximately 0.8 km away along the road which leads to the Newman Sound Campground. Although this grid was of the same dimensions, the total effective area was smaller (5.4 ha) due to the road which intersected the grid. The grids near the maintenance area and that near Newman Sound Campground will be referred to as grids 95-1 and 95-2 respectively (Fig. 2.1). Both grids consisted mainly of

Figure 2.1. Location of the study grids in 1994 (94-1) and 1995 (95-1: high cover, 95-2: low cover) in Terra Nova National Park, Newfoundland. Top inset: arrow indicates the approximate position of the study area.


N
TRANS - CANADA HIGHWAY
MC
95-1
94-1
A
95-2
NEWMAN SOUND
CAMPGROUND
A — ADMINISTRATION
MC — MAINTENANCE COMPOUND
— PAVED ROAD
240M

black spruce with smaller amounts of balsam fir. Larch (*Larix laricina*) was present in grid 95-2. Grids 95-1 and 95-2 were chosen to represent areas of high and low understory shrub cover, respectively. For a more detailed account of the vegetation composition and structure of the grids in 1995, see sections 2.4.1 and 3.3.1. Due to the large size of the grids and lack of traps, the study areas were not replicated.

2.2 Population Ecology

2.2.1 *Live Trapping*

In 1994 all stations on each grid were live-trapped on two non-consecutive days per week. On average, sites were trapped every 3 ± 0.5 days. Trapping commenced on May 16 and ended August 17, 1994. In 1995, all stations on each grid were trapped approximately once per week. Occasionally, traps were set twice per week in order to capture individuals selected for radio-collaring. These data were included in estimates of population size. Summer trapping ran from June 2 - August 30 for grid 95-1 and May 29 - September 1 for grid 95-2. All trapping stations on both grids were trapped twice in the autumn between November 11and 18.

One live trap ("Havahart" Small Mammal Trap No. 0745, Wood Stream) was located at each station in 1994 and at alternate stations in 1995. Traps were set at 08:00 h, baited with a mixture of peanut butter and rolled oats, and checked four to six hours later. On initial capture, squirrels were outfitted in each ear with individually numbered metal ear tags (Monel size 1, National Band and Tag Co., Newport, Kentucky) through which were threaded coloured disks (1 cm diameter) in a unique combination of colours for each squirrel. The disks allowed individuals to be visually identified at a distance. At all captures squirrels were weighed to the nearest 5 grams using a Pesola spring scale (Le Naturaliste, Ste-Foy, Quebec), and classified by age (adult or juvenile), sex, and reproductive condition. Juveniles (young-of-the-year) were distinguished from adults on the basis of low body weight (< 150g, Sullivan, 1990) and generally smaller size. Adult females were classified as either pregnant (based on relatively high weight and abdominal palpation), lactating (nipples enlarged), or non - reproductive. Adult males were classified as breeding or non - breeding based on testes position (scrotal or regressed, respectively). The location of each capture was also recorded.

2.2.2 *Demography*

Population size was estimated with the Jolly-Seber model of population estimation (Jolly, 1965; Seber, 1965) using the program JOLLY (Krebs, 1989). The crucial assumption of this model is equal catchability (i.e., every animal in the population has the same probability of being caught) which must be tested before population estimates can be used with confidence. The computer program LESLIE (Krebs, 1989) was used to test this assumption. This program uses the method of Leslie et al. (1953) which tests for equal catchability within the marked portion of the population. This test compares the sum of the estimated number of newly marked animals with the sum of the observed number of newly marked animals.

Trappability (the fraction of the population trapped), population density, survival, recruitment, proportion of reproductive animals, body weight, and sex ratios were monitored for the single large grid in 1994 and both grids in 1995. Jolly trappability (%) was determined as in Krebs and Boonstra (1984) and is defined as the total number of marked individuals divided by the estimated marked population size for each trapping session. Trappability values were then averaged to provide a mean for the entire trapping period.

Population density was calculated as the population size estimate divided by grid area. Although variances for estimates of population size are valid only for large samples (Krebs, 1989), Begon (1983) recommends their use as an indication of the reliability of the estimate. Standard errors are calculated for population size estimates by the JOLLY program. These are omitted from figures for clarity but are available in Appendix A.

Survival was calculated as the average of Jolly-Seber survival estimates (number of marked individuals surviving from one trapping session to the subsequent trapping session) between trapping sessions and is expressed per 3 days in 1994 and per 7 days for both grids in 1995, because these were the typical intervals between trapping sessions. For trappability, population density, and survival two analyses were done: i) using all squirrels captured and ii) omitting transient animals (captured only once). This provided estimates for the overall population and for residents, respectively (Sullivan and Klenner, 1993).

The Jolly-Seber model provides an estimate of recruitment (number joining the population between trapping intervals) but does not provide information on sex or age of the recruits. Therefore, recruits were defined as all squirrels captured for the first time regardless of whether they became transient or resident animals (Sullivan and Moses, 1986) and these were tallied for each month based on sex and age. For ease of comparison, the number of recruits was divided by grid area in order to account for grid size differences. Body weight was averaged over the summer for each individual. These values were then used to obtain mean summer weights for males and females separately. The proportion of reproductive animals was based on summer trapping while sex ratios include fall trapping sessions in 1995. Adult sex ratios on each grid were determined separately for i) the total number of adults captured and ii) residents only (single captures omitted). All means are reported with ± 1 SE.

2.3 Radio-Tracking and Home Range Analysis

For the purpose of this study, home range is considered to be "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943: 351). Territory is the defended part of the home range and may encompass all or only part of it (Burt, 1943). To determine home range size, selected squirrels were fitted with radio-transmitters (L.L. Electronics, Mahomet, Illinois) beginning on July 11 and July 17, 1995 for grids 95-1 and 95-2, respectively. Radio transmitters were approximately 6 g and were attached around the squirrel's neck with a cable tie. Each transmitter emitted a specific frequency signal in the range of 153.200 - 153.425 MHz and had a battery life of six months. Squirrels were selected based on residency status. The consistency of capture between trapping sessions was used as an indicator that the animal was a resident on the grid and for 95-1, all collared animals were repeatedly trapped on the grid in 1994. For both grids, all collared animals were adults (>= 1 year).

Each grid was monitored every other day by locating squirrels with a hand-held antenna and radio receiver (model TR-4, Telonics, Mesa, Arizona). Radio tracking was never conducted on days when traps were opened. Squirrels were tracked between 08:00 - 20:00 h and for each session, an attempt was made to locate all radio-collared individuals at least once. Radio signals were followed until the squirrel could be located visually. The position of the squirrel was then recorded by triangulation with respect to the 30 m interval grid.

Home range size was estimated using the minimum convex polygon method (MCP; Mohr, 1947) and for comparison, with the adaptive kernal estimator (Worton, 1989). The adaptive kernal estimates the utilization distribution: the probability density function that gives the probability of finding an animal at a particular location on a plane

(Worton, 1989). No assumptions are made about the shape of the utilization distribution, and therefore the adaptive kernal estimator is nonparametric. Both estimates of home range size were calculated using the Calhome- California Home Range computer program (Calhome, 1992). All radio-fixes were used in the calculations since the number of fixes per animal was relatively low. If the MCP home range is convex in shape then this estimate should approach an asymptote as the number of radio-fixes increase (Anderson, 1982). Therefore, MCP area was plotted against the number of radio-fixes for each squirrel and asymptotes were estimated visually. Fixes were added randomly to the MCP estimate as suggested by Harris et al. (1990) since squirrel locations were obtained discontinuously.

As an index of the exclusivity of home ranges, the proportion of an individual's home range contained within that of another squirrel (% overlap) was calculated. The MCP estimate was used to determine % overlap since these home ranges were generally smaller and therefore provided a more conservative estimate of overlap.

2.4 Cache Sampling

2.4.1 *Vegetation Analysis*

Cache sampling was conducted from October - November 1995 on grids 95-1 and 95-2 (Fig. 3.1) which differed in the amounts of understory cover. To ensure that any differences in caching behaviour were not due to differences in the food species available to be cached, and to provide a quantitative assessment of understory cover, the vegetation composition and structure were compared between grids. Eighteen 0.01 ha circular plots were randomly located at grid intervals (2 plots per each of 9 lines) on each of grids 95-1 and 95-2 (Sullivan, 1990). The species, number of individuals, and diameter at breast height of all trees in these plots were recorded. An estimate of relative horizontal screening cover (visual obstruction) provided by trees and shrubs was made at each of these circular plots using a vegetation profile board (Nudds, 1977). The board was 2.0 x 0.3 m and marked with 240 5x5 cm squares. It was placed at the selected grid interval, faced in a random direction, and the number of squares not covered by foliage in each 0.5 m interval was counted from 10 m away. This standard distance was chosen since at 15 m the board was usually completely covered by vegetation whereas at 5 m most of the board remained visible.

2.4.2 *Cache Size and Distribution*

My original intention was to describe caches within the home range of individual squirrels. However, I was unable to obtain estimates of fall home ranges (see sections 3.2 and 4.2) and instead, caches were randomly sampled on the grids. Trapping grids were subdivided into 15 m intervals resulting in 288 grid stations (centric-systematic-area sampling method - Krebs,1989). These stations were numbered and a random number generator was used to select stations about which a 7.1 m^2 circular sampling plot was established. There were 65 and 70 selected sample plots on grids 95-1 and 95-2, respectively.

Starting on October 21, sample plots were searched for caches by digging through moss, soil, and litter to a depth of 15 cm with a hand shovel (Hurly and Robertson, 1990). Cones were considered cached if they were buried, pushed into the ground, or piled together in small depressions above ground. Only cones produced during the study year were counted. Cones from previous years were not counted as it could not be determined if these were buried by squirrels or had fallen from the trees and buried over time. New black spruce cones were generally hard and purple-brown in color. Cones from previous years were dark brown-black in color and could easily be broken apart.

In each sample-plot the number of caches, the number of cones per cache, and the distance each cache was located from the nearest tree were recorded. Distance from the nearest tree (DNT) was taken as a straight line from the centre of the cache to the tree trunk.

2.4.3 *Statistical analysis*

Diameter at breast height (DBH) for the various tree species was compared between study grids using two-tailed t-tests at 0.05 level of significance. Since the spruce DBH data were non-normal, a randomization test (Edgington, 1980) was used to determine significance. The MINITAB statistical package was used to carry out randomizations. Results were considered significant when test statistics were associated with a probability of 0.05 or less. Horizontal screening cover was square root transformed before analysis and comparisons between each grid at different height levels were made using one-way analysis of variance. Significance was determined using randomization.

Caches were categorized according to the number of cones/cache. These ranged from 1 - 10 cones. Caches containing more than 10 cones were combined into one category (>= 11 cones). The distribution of cache sizes should conform to a left-truncated Poisson distribution (no zero class - Cohen, 1960) if cache size is randomly determined (Hurly and Robertson, 1990). The frequency distributions for grids 95-1 and 95-2 were each tested against their corresponding expected distribution using the Kolmogorov-Smirnov goodness of fit test and against each other with the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981).

Similarly, to determine whether the spatial distribution of caches was random, the frequency distribution of the number of caches found per sample plot was compared to a corresponding Poisson distribution (zero class included) for each grid. This was done using the Kolmogorov-Smirnov goodness of fit test, while the Kolmogorov-Smirnov two-sample test was used to compare distributions between grids.

A 2x3 contingency table was used to determine if cache size was dependent on distance from the nearest tree (Sokal and Rohlf, 1981). Caches were classified as single-cone or multiple-cone (>1) caches. Distance was arbitrarily classified as near (0 - 2.0 m), medium (>2.0 - 4.0 m) or far (>4.0 - 6.0 m). Randomization tests were used to determine significance. Means ± 1 standard error were used as a measure of central tendency unless otherwise indicated.

Chapter 3: Results

3.1 Population Data

3.1.1 *Equal Catchability Test and Trappability Estimates*

Results of the Leslie, Chitty, and Chitty test for equal catchability (Leslie et al., 1953) indicate unequal catchability within the marked population for grids 94-1 and 95-2. The assumption of equal catchability holds only for grid 95-1 and only these data can be used as population estimates (see appendix B for detailed results of these tests). The 94-1 and 95-2 data will be used as indices of population size and therefore must be interpreted with caution. Enumeration methods of population estimation such as minimum number alive (MNA- Krebs, 1966) were not used, because this method is more negatively biased than the Jolly-Seber estimator even when the assumption of equal catchability is not met (Jolly and Dickson, 1983). See Nichols and Pollack (1983) and Jolly and Dickson (1983) for discussions of the advantages of the Jolly-Seber model over the MNA even under conditions of unequal catchability.

Summer trappability was highest in grid 94-1 and lowest on grid 95-2 and was always higher among the resident populations (Table 3.1). Since the assumption of equal catchability does not hold for the 94-1 and 95-2 data, these trappability values are positively biased (Krebs and Boonstra, 1984) and therefore overestimated. Low trappabilities in this study (< 70%) also provide further justification for not using the MNA enumeration technique since the accuracy of this method declines when trappability falls below 80% (Hilborn et al., 1976).

Table 3.1. Estimates of Jolly trappability (fraction of the population trapped) for red squirrels during the summers of 1994 and 1995. Values are calculated as in Krebs and Boonstra (1984) and are estimated for i) all animals captured and for ii) resident animals only (animals trapped more than once). Estimates for 94-1 and 95-2 are overestimates (see text).

		Animals used in estimate	
Year	Grid	All captures	Residents only
1994	94-1	66 %	67 %
1995	95-1	56 %	56 %
	95-2	51 %	53 %

3.1.2 *Population Density*

Figure 3.1 shows population density of red squirrels from mid-May to mid-August 1994. Density remained steady throughout the summer except for a slight peak in mid-July. Mean (± SE) density was 1.0 ± 0.05 squirrels / ha (range 0.5-1.6). Removal of single captures (transients) from the analysis did not have much effect. The trend for residents was similar and mean density was 0.96 ± 0.04 squirrels / ha (range 0.4-1.3).

On both grids 95-1 (high cover) and 95-2 (low cover), the density of resident squirrels was approximately 2/ha until mid-July when density declined on grid 95-2 to approximately 1/ha (Fig. 3.2). Mean summer resident density for grid 95-1 (2.0 ± 0.13, range 1.0-2.7) was higher than that for grid 95-2 (1.7 ± 0.13, range 0.8-2.6). This difference in resident density between both grids remained throughout the fall when density was 1.9 times greater on 95-1 (2.3 squirrels /ha) than on 95-2 (1.2 / ha).

Transient animals were a minor component of the total population (Fig. 3.2) on both grids with one exception. In mid-August, several transients were captured on 95-2. This coincided with the midsummer decline in resident animals on the same grid. Mean summer density was slightly higher for grid 95-2 (2.1 ± 0.21, range 0.8-3.7) than for 95-1 (2.0 ± 0.14, range 1.0-2.7).

Although density estimates for grid 95-2 may not be accurate due to violations of the equal catchability assumption, the trends in density are similar between both grids throughout the study period. This is more apparent for the resident populations. Generally, both populations in 1995 increased from June to mid-July and then declined. Another peak occurred on August 9, but was again followed by a decline until the end of the month. Both fall density estimates were above the final summer estimates.

When comparing both years, the most noticeable observation is that density in 1995 was double that of 1994. The trend, however, in the 1994 data was similar to that

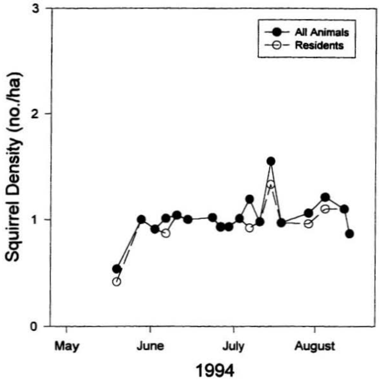
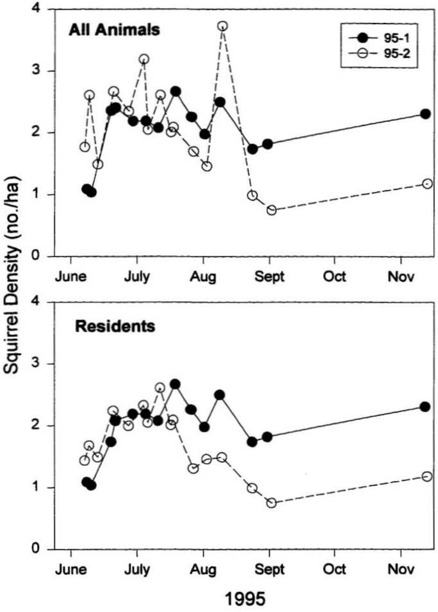


Figure 3.1. Jolly-Seber estimates of red squirrel population density on grid 94-1 from May - August 1994. Estimates are based on i) all animals captured and ii) residents only (animals captured more than once).

Figure 3.2. Jolly-Seber estimates of red squirrel population density for grids 95-1 and 95-2. Estimates are based on i) all animals captured and ii) residents only (animals captured more than once).


All Animals
95-1
95-2
Residents
Squirrel Density (no./ha)
0
1
2
3
4
June
July
Aug
Sept
Oct
Nov
1995

of 1995 with respect to the density peak around mid-July and the tendency to decrease toward the end of August. The 1994 estimates were less variable over time than the 1995 data.

3.1.3 *Survival and Recruitment*

Survival was high in both years, for all animals and for residents (Table 3.2). Grid 95- 2 had the lowest survival.

Spring recruitment for both males and females was much higher in 1995 than in 1994 (Fig. 3.3). There were more adult male than adult female recruits, and no adult females entered the population in July 1994 or 1995. It is interesting to note that in 1994, juveniles appeared in early July, but in 1995 none were detected in the trapping record until the end of August when two females were caught on grid 95-1. No juveniles were caught on 95-2 until trapping resumed in November.

3.1.4 *Reproduction*

More adults were in reproductive condition in 1995 than in 1994 (Table 3.3). This difference was particularly noticeable for males. Whereas over 80% of the males were in breeding condition in 1995, only 58% were found to be so in 1994. However, these proportions are based on total numbers caught throughout the summer and the time at which an individual is caught may affect how it is classified. Therefore, the proportion of trapped animals that were in reproductive condition is shown for each month (Fig. 3.4). Males did not show signs of being reproductive after June in 1994, whereas 25% of males trapped on grid 95-1 were still in breeding condition in August 1995. Females in reproductive condition were caught in all summer months. Grid 95-2 had the highest proportion of reproductive females and this occurred in July and August.

Table 3.2. Mean ± SE Jolly-Seber estimates of probability of survival between summer trapping sessions for red squirrels on all grids. Survival estimates were calculated for i) all animals captured and for ii) residents only (animals captured more than once). The average interval between trapping sessions was 3 and 7 days in 1994 and 1995 respectively.

		Animals used in estimate	
Year	Grid	All animals	Residents only
1994	94-1	0.91 ± 0.03	0.94 ± 0.02
1995	95-1	0.90 ± 0.05	0.91 ± 0.05
	95-2	0.79 ± 0.05	0.85 ± 0.05

Figure 3.3. Number of recruits (individuals captured for the first time) per hectare on the study grids for 1994 (May - August) and 1995 (June - August, and November). Numbers above bars indicate the number of trapping sessions in each month.

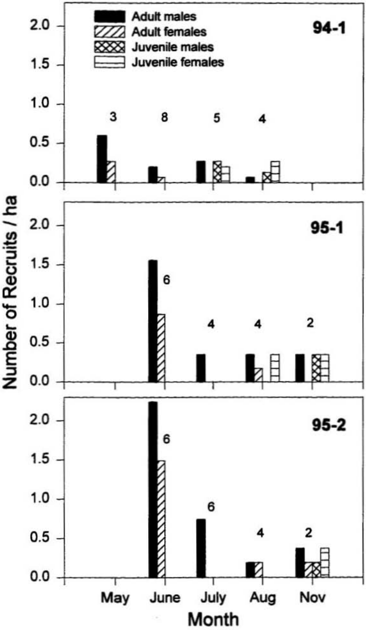
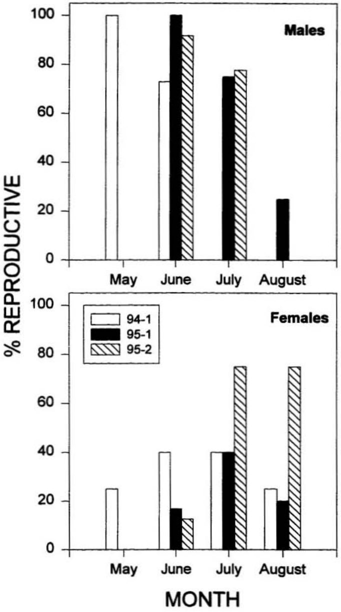

Adult males
Adult females
Juvenile males
Juvenile females
94-1
95-1
95-2
Number of Recruits / ha
0.0
0.5
1.0
1.5
2.0
3
8
5
4
6
4
4
2
6
6
4
2
May
June
July
Aug
Nov
Month

Table 3.3. The proportion of live-trapped male and female red squirrels that were in reproductive condition during the summers of 1994 (May 16 - August 17) and 1995 (June 2 - August 31). Numbers in brackets refer to the total number of individuals trapped.

		% Reproductive	
Year	Grid	Males	Females
1994	94-1	58 (17)	40 (5)
1995	95-1	85 (13)	43 (7)
	95-2	82 (17)	67 (9)

Figure 3.4. The percentage of adult male and female red squirrels in reproductive condition for each month during the summers of 1994 (May - August) and 1995 (June - August).


Males
Females
94-1
95-1
95-2
% REPRODUCTIVE
100
80
60
40
20
0
May
June
July
August
MONTH

The higher proportion of reproductive animals in late summer 1995 and the lack of juveniles in the trapping record until the end of August suggest that the breeding season was later in 1995 than in 1994 (Fig. 3.4). However, it is possible that early litters did not survive because juveniles were forced to emigrate or were killed due to high density of adult animals. Trapping was not initiated before May and June in 1994 and 1995, respectively, so the total length of each breeding season is not known.

3.1.5 *Body Weight*

Mean summer body weights for male and female red squirrels are shown in Table 3.4. Females were grouped into reproductive and non-reproductive animals since pregnancy and lactation affect normal body weight (C.C. Smith, 1968; Lair, 1985; Humphries and Boutin, 1996). Mean weight for both grids in 1995 tended to be higher than that of the previous year both for males and the two categories of females. Lack of independence between grids 94-1 and 95-1 and small sample sizes preclude statistical comparisons between years for each category. However, 6 adult males trapped in 1994 were recaptured on grid 95-1. A paired t-test of the mean weights between years showed that these individuals were heavier in 1995 than in 1994 (paired $t = 2.27$, $df = 5$, $P < 0.05$). Adult males tended to be heavier on 95-2 than on 95-1 but this was not significant (t-test assuming unequal variances $t = 1.44$, $df = 24$, $P = 0.16$). Again, small sample sizes prevent statistical comparisons for the female categories. In both years, reproductive females were heavier than either non-reproductive females or males.

3.1.6 *Sex Ratio*

The total adult sex ratio deviated significantly from a 1:1 ratio in 1994 when there were 3 times as many males as females (Table 3.5). Resident adults were male-biased

Table 3.4. Mean ± SE summer body weights (g) of adult male and female red squirrels live-trapped in 1994 and 1995. Mean weights are shown separately for non-reproductive and reproductive females. Number in brackets refers to the number of individuals trapped.

Year	Grid	Males	Females	
			non-reproductive	reproductive
1994	94-1	174.2 ± 2.5 (17)	173.8 ± 2.8 (3)	188.1 ± 0.6 (2)
1995	95-1	186.1 ± 2.0 (13)	190.6 ± 3.6 (4)	198.8 ± 2.6 (3)
	95-2	192.0 ± 3.6 (17)	189.2 ± 4.6 (3)	196.8 ± 6.5 (6)

Table 3.5. Number of male and female red squirrels trapped on the study grids in 1994 and 1995, the corresponding sex ratios, and the binomial probability (*P*) of observing this or a greater deviation from a 1:1 sex ratio. Adult categories are based on i) the total number of adults captured and ii) residents only (animals captured more than once). The 1995 data includes both November trapping sessions.

			Sex		Ratio	
Year	Grid	Category	Male	Female	(M:F)	*P*
1994	94-1	Adults				
		Total	17	5	3.20:1	<0.009
		Residents	11	5	2.20:1	<0.11
		Juveniles	6	7	0.86:1	0.50
1995	95-1	Adults				
		Total	15	7	2.14:1	>0.067
		Residents	12	6	2.00:1	<0.12
		Juveniles	2	4	0.50:1	0.34
	95-2	Adults				
		Total	19	10	1.90:1	>0.068
		Residents	8	7	1.14:1	0.50
		Juveniles	1	2	0.50:1	0.50
	95-1/2*	Adults				
		Total	34	17	2.00:1	<0.012
		Residents	20	13	1.54:1	>0.15

* Combined adult data from grids 95-1 and 95-2.

but this was not significant. The juvenile sex ratio was nearly 1:1. On grid 95-1, neither the total adult, resident adult, nor juvenile sex ratios were significantly different from expected. Similar results were obtained for grid 95-2. Total and resident adult sex ratios compared between grids 95-1 and 95-2 did not differ significantly from each other (G-test for heterogeneity - Sokal and Rohlf, 1981; Total: $G = 0.0402$, $df = 1$, $P > 0.05$; Residents: $G = 0.693$, $df = 1$, $P > 0.05$). When combined, the 1995 adult data revealed a significant male bias for total adults but not for residents.

It is interesting to note that in both years, adult males outnumbered adult females, but juvenile ratios tended to be in favour of females. Conclusions for juveniles are tenuous since the number of individuals caught was low.

3.2 Home Range Data

Although attempts were made to locate each squirrel during each day of tracking, this was not always possible. Often, the signal for specific frequencies could not be picked up every tracking day even though the grid and surrounding area were thoroughly searched. Failure to detect a signal was most notable on grid 95-2. Equipment failure may have been a possible cause but due to the intermittent nature of signal detection, squirrels were probably moving out of range of the receiver. As well, an effort was made to locate squirrels during all hours of the tracking day but again, due to the variation in signal detection, this was not possible.

Table 3.6 shows the dates of the first and last radio fix and total number of fixes for each collared squirrel on both grids. All squirrels were monitored for approximately the same time period but the number of fixes per squirrel varied. Originally, I selected four males and three females from grid 95-1, and two individuals of each sex from grid 95-2 for the home range study. Data could not be obtained for two of the females on grid

Table 3.6. Length of tracking period, total number of fixes, and home range size for each radio-collared squirrel on both study grids, 1995. Home ranges were determined using both the minimum convex polygon (MCP) and the adaptive kernal method.

Grid	Tag no.	Sex	Length of Tracking Period		Total No. of fixes	Home Range Size (ha)	
			First fix	Last fix		MCP	Adaptive Kernal
95-1	109-111	Male	July 13	Aug. 25	9	4.1	4.8
	114-115	Male	July 24	Aug. 28	11	1.3	2.4
	137-209	Male	July 14	Aug. 25	13	0.34	0.34
	142-138	Male	July 13	Aug. 22	14	2.5	5.7
	234-210	Female	Aug. 3	Aug. 28	6	0.67	0.89
95-2	236-237	Male	July 19	Aug. 25	20	2.4	7.1
	238-271	Female	July 19	Aug. 25	17	1.8	4.3
	243-258	Female	July 19	Aug. 25	9	2.2	8.0

95-1. After the first failed attempt, one of the squirrels was no longer trapped. The second squirrel was collared but the transmitter failed. A subsequent attempt was also unsuccessful. It should be noted that squirrel 109-111 (male) from grid 95-1 lost its collar after July 13 and was re-collared on August 1. On grid 95-2, one of the males lost its collar but a second attempt at re-collaring this individual was not made.

Home range sizes for both methods are also shown in Table 3.6. The adaptive kernal estimates were always larger than MCP estimates except for squirrel 137-209, where both methods produced identical values. Plots of MCP home range area against the number of radio fixes produced asymptotes for three squirrels on 95-1 (Fig.3.5). Home range size still appears to be increasing for the male 114-115 and the female 234-210 when the final locations are added. On grid 95-2, only one plot (238-271) reaches an asymptote (Fig.3.6). An asymptote indicates that the area used is convex and is an indication of the accuracy of the estimate (Anderson, 1982).

On grid 95-1, home range overlap was greatest for 137-209 where 100% of its home range was located inside that of 109-111 (Table 3.7 and Fig. 3.7). Squirrel 142-138 also had a large amount of overlap with 109-111; 64% of its home range was contained within 109-111's boundaries. This is not surprising since these two squirrels had the largest home ranges. The female's (234-210) home range was relatively exclusive of the other radio-collared squirrels, overlapping with only one other individual (Fig. 3.7). On grid 95-2, the largest amount of overlap was between the female 238-271 and the male 236-237 with 45% of the female's home range being located in that of the male (Table 3.8 and Fig. 3.8). Both female ranges overlapped but this appears to be due to an excursion by 243-258.

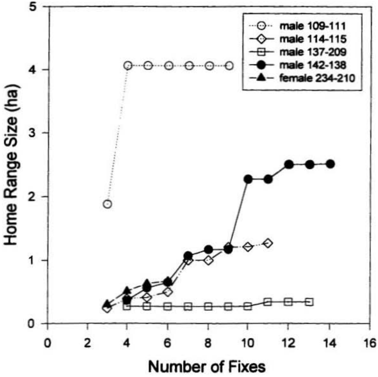


Figure 3.5. Home range area (using the minimum convex polygon method) as a function of the number of radio-fixes for each of the radio-collared squirrels on grid 95-1. Radio-fixes were added randomly to each successive estimate. The home range estimate should approach an asymptote as the number of fixes increases. An asymptote indicates that the area used by the animal is convex in shape.

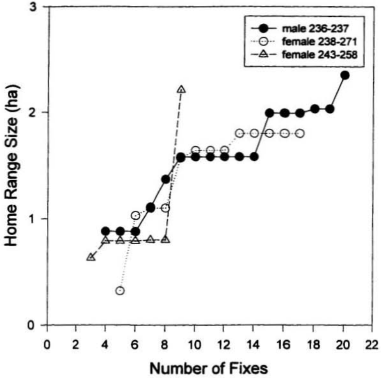


Figure 3.6. Home range area (using the minimum convex polygon method) as a function of the number of radio-fixes for each of the radio-collared squirrels on grid 95-2. Radio-fixes were added randomly to each successive estimate. The home range estimate should approach an asymptote as the number of fixes increases. An asymptote indicates that the area used by the animal is convex in shape.

Table 3.7. Home range overlap matrix for the radio-collared squirrels on grid 95-1. Values are the percentage of a squirrel's home range located inside the home range of the corresponding individuals and were calculated using the MCP estimate of home range size.

	Percentage of squirrel's home range found inside that of:			
Squirrel	109-111	114-115	137-209	142-138
109-111 (male)	X	4	8	39
114-115 (male)	11	X	2	39
137-209 (male)	100	8	X	35
142-138 (male)	64	20	5	X
234-210 (female)	0	2	0	0

Figure 3.7. Minimum convex polygons of the radio-collared squirrels on grid 95-1 using 100% of the fixes for each squirrel. The square demarcates the outer boundaries of the trapping grid which was extended 30m on all sides (9 ha) for the tracking study.

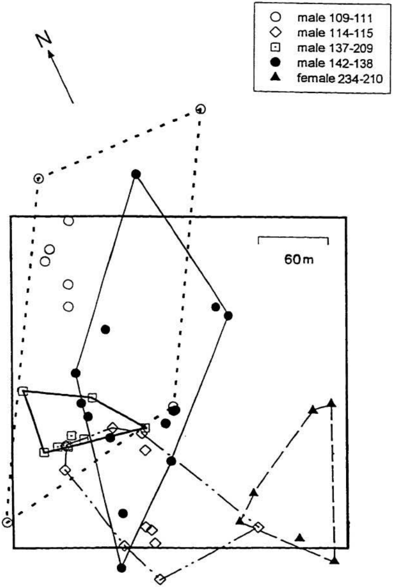
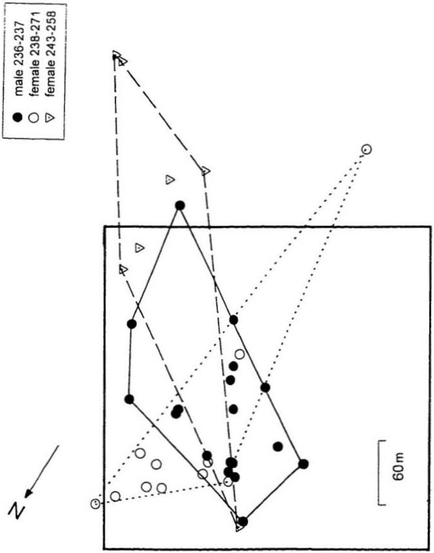

○ male 109-111
◇ male 114-115
⊡ male 137-209
● male 142-138
▲ female 234-210
N
60m

Table 3.8. Home range overlap matrix for radio-collared squirrels on grid 95-2. Values are the percentage of a squirrel's home range located inside that of the corresponding individual and were calculated using the MCP estimate of home range size.

	Percentage of squirrel's home range found inside that of:		
Squirrel	236-237	238-271	243-258
236-237 (male)	X	34	33
238-271 (female)	45	X	20
243-258 (female)	35	16	X

Figure 3.8. Minimum convex polygons of the radio-collared squirrels on grid 95-2 using 100% of the fixes for each squirrel. The square demarcates the outer boundaries of the trapping grid which was extended 30 m on all sides (9 ha) for the tracking study.


● male 236-237
○ female 238-271
▷ female 243-258
60m
N

3.3 Caching Data

3.3.1 *Vegetative Structure and Composition of Study Grids*

Both grids were similar in species composition with black spruce being the dominant tree type (Table 3.9). Grid 95-2 differed in that it contained larch. Although a few individuals of this species were present on grid 95-1, they were not located in any of the sample plots. The DBH of spruce and fir trees was greater on grid 95-1 than grid 95-2 (spruce: $t = 2.23$, $P = 0.031$, $df = 498$; fir: $t = 3.42$, $P = 0.001$, $df = 79$). White birch (*Betula papyrifera*) DBH did not differ between grids ($t = 1.39$, $P = 0.18$, $df = 25$). Small sample sizes for red maple (*Acer rubrum*) precluded statistical analysis. Tree density was also similar between grids 95-1 and 95-2 (Table 3.9) except for the apparent absence of larch on grid 95-1. However, density of understory alder (*Alnus rugosa*) was much greater on grid 95-1 (Table 3.9).

Understory growth (horizontal screening cover) was almost twice as great on grid 95-1 (mean no. of squares uncovered = 59.33 , 95% C.I. (0.13 - 182.40)) as on 95-2 (mean = 105.22, 95% C. I.(13.01 - 240.06)) ($t = -2.13$, $P = 0.041$, $df = 34$). This was apparent at all height levels but significant only for the 1.0-1.5 m range (Table 3.10). In summary, grids 95-1 and 95-2 varied little in the composition and size of overstory tree species but understory vegetation provided almost twice as much cover on grid 95-1 than on grid 95-2. Grids 95-1 and 95-2 will be referred to as high and low cover respectively.

3.3.2 *Cache Size and Distribution*

A total of 131 and 76 caches were found on the high and low cover grids respectively. Red squirrels exhibit non-random variation in the size of caches that they construct (Fig. 3.9). The observed distribution of cache sizes did not conform to the

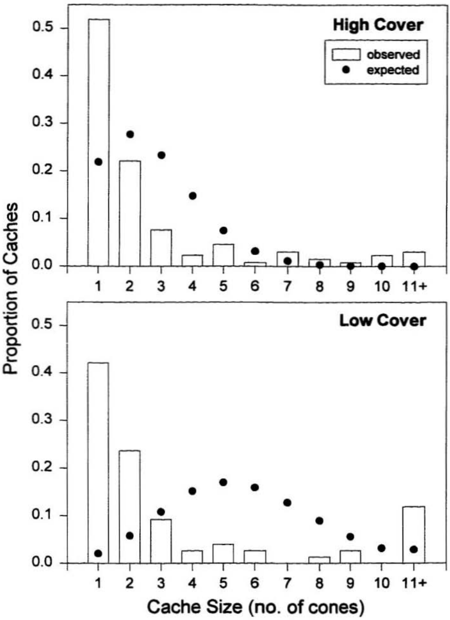
Table 3.9. Characteristics of the vegetation composition of both study grids in 1995. Relative abundance is the proportion of trees accounted for by each particular species. Diameter at breast height is given as mean ± standard error. Density for each species is the number of trees counted divided by the total area sampled (0.18 ha).

Grid	Species	Sample Size (no. of trees counted)	Relative Abundance (%)	Diameter at Breast Height (cm)	Density (stems/ha)
95-1					
	Black spruce	249	82.72	10.77 ± 0.42	1383
	Balsam fir	38	12.62	19.30 ± 1.19	211
	White birch	11	3.65	17.15 ± 2.03	61
	Red maple	3	1.00	17.70 ± 2.85	17
		301			
	Alder				761
95-2					
	Black spruce	251	76.29	9.51 ± 0.38	1394
	Balsam fir	43	13.07	14.48 ± 0.81	239
	White birch	16	4.86	14.02 ± 1.25	89
	Red maple	2	0.61	13.23 ± 1.92	11
	Larch	17	5.17	9.77 ± 1.29	94
		329			
	Alder				100

Table 3.10. Relative amount of understory cover (horizontal screening cover) at 0.5 meter intervals above ground measured as the number of squares uncovered on the cover board for grids 95-1 and 95-2. Lower values indicate greater horizontal cover.

	Mean (95% C.I.)		
Height (m)	95-1	95-2	*P*
0.0-0.5	10.44 (0.37 - 42.71)	11.56 (0.89 - 48.65)	0.883
0.5-1.0	15.11 (-0.38 - 47.76)	24.00 (-0.40 - 84.05)	0.478
1.0-1.5	16.17 (1.58 - 67.93)	36.06 (0.064 - 109.33)	0.0147
1.5- 2.0	18.11 (-0.47 - 62.64)	34.11 (-0.46 - 110.93)	0.0713

Figure 3.9. Observed and expected frequency distributions of cache size in high (95-1) and low (95-2) cover black spruce habitats, Fall 1995. Expected distributions are based on the left - truncated Poisson distribution. Number of caches = 131 and 76 in the high and low cover grids respectively.


High Cover
observed
expected
Low Cover
Proportion of Caches
0.0
0.1
0.2
0.3
0.4
0.5
1
2
3
4
5
6
7
8
9
10
11+
Cache Size (no. of cones)

expected distribution (Kolmogorov-Smirnov test, $P < 0.01$ for both grids). Single cone and large caches were over-represented in both plots. In the low cover grid, caches containing two cones were also more numerous than expected. The distribution of cache sizes did not differ between grids (Kolmogorov-Smirnov two sample test, $P > 0.05$).

In high cover, 52% of caches were composed of only one cone and these accounted for 19% of all cones cached. Only 3% of caches were large (>=11 cones) but these accounted for 20% of cached cones (mean no. of cones in large caches ± SE: 18.3 ± 2.6; range 13-24; n = 4). Single cone caches comprised 42% of caches in low cover , accounting for only 8% of all cones stored. Large caches had 12% of the sampled caches and accounted for 65% of all cones stored (mean no. of cones in large caches: 30.9 ± 2.5; range 22 - 43; n = 9). Large caches in low cover contained more cones ($t = -3.03$, $P = 0.012$, df = 11) than those found in high cover.

Figure 3.10 shows the cumulative proportion of cones for the high and low cover grids according to cache size. Both grids appear similar in the proportion of single cone caches but it is apparent that large hoards accounted for most of the stored cones on the low cover grid.

Since black spruce was the predominant tree in both grids, most caches consisted of these cones. However, 15 caches (12%) in the high cover grid and 6 caches (8%) in the low cover grid were composed entirely of balsam fir cones. Most fir caches consisted of single cones (80% in high cover; 100% in low cover) with the largest fir cache having 10 cones. Only 1 mixed species cache was found. This consisted of 5 spruce cones and 1 fir cone found together in the low cover grid. Also, larch cones were never found in any caches although squirrels were observed feeding on them in August.

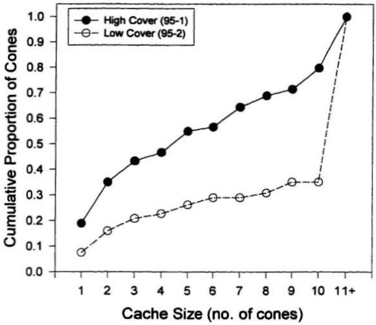


Figure 3.10. Cumulative proportion of all cones stored by cache size in the high (95-1) and low (95-2) cover grids.

Caches were not evenly dispersed throughout both study grids (Fig. 3.11). Both distributions were significantly different from the expected Poisson distributions (Kolmogorov-Smirnov test, $P < 0.01$ for both grids). Coefficients of dispersion (CD) for the distributions on each grid were greater than 1 (high cover: CD = 12.7; low cover: CD = 11.5) indicating that caches were spatially clumped (Sokal and Rohlf, 1981). In high cover, a total of 65 sample plots were searched. Of these, 24 (37%) contained at least 1 cache. In low cover, only 10 out of 70 (14%) contained at least 1 cache. The distributions were not significantly different between grids (Kolmogorov-Smirnov two-sample test, $P > 0.05$).

Figure 3.12 shows cache sizes in relation to distance from the nearest tree. Caches were placed at a median distance of 0.92 m (range 0.02 - 5.93 m) and 1.24 m (range 0.08 - 2.86 m) from the nearest tree in the high and low cover grids respectively. This difference was significant (Mann-Whitney, W = 1226.5, $P = 0.016$). There was a trend for cache size to be dependent on distance in the high cover grid ($X^2 = 5.88$, $P = 0.042$). Single cone caches were placed 1.46 ± 1.34 m (mean ± SD) from a tree, whereas multiple cone caches were found 0.99 ± 0.67 m from the nearest tree. Distance had no effect on cache size in the low cover grid ($X^2 = 0.92$, $P = 0.298$). Single and multiple cone caches were found at similar distances from the nearest tree (single cone caches: mean ± SD = 1.43 ± 0.65 m; multiple cone caches: 1.36 ± 0.90 m).

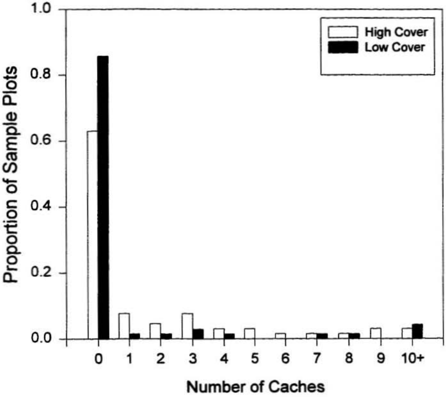
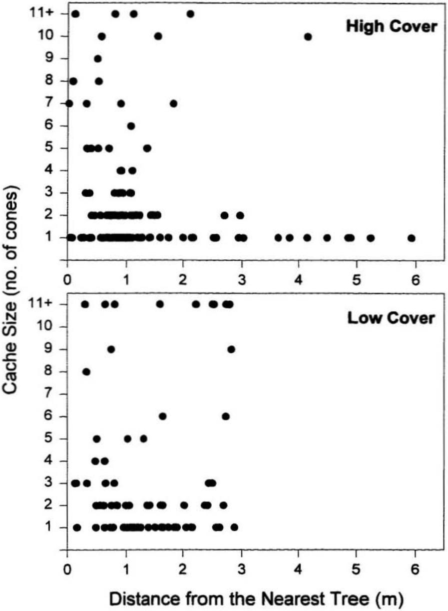


Figure 3.11. Frequency distribution of the number of caches found in each sample plot in the high (95-1) and low (95-2) cover grids. There were 65 and 70 sample plots searched in high and low cover, respectively

Figure 3.12. A plot of cache size relative to the distance from the nearest tree at which the cache was found for all caches in the high (95-1) and low (95-2) cover grids.


High Cover
Low Cover
Cache Size (no. of cones)
11+
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
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Distance from the Nearest Tree (m)

Chapter 4: Discussion

4.1 Red Squirrel Population Ecology

Population density for both years was similar to those reported approximately four years after four male and two female red squirrels were introduced on Camel Island, Notre Dame Bay, Newfoundland (Payne, 1976). Densities in balsam fir/black spruce habitat there ranged from 1.14 - 2.37/ha (Payne, 1976). Values from the present study (1994: 0.5 - 1.6; 1995: 0.8 - 3.7) are generally lower than the minimum density reported for black spruce sites in central Newfoundland (2.0 - 5.8/ha; West, 1989) but are comparable to densities reported for other coniferous habitats in general (Table 4.1). Close agreement of the total population density with that of resident density within each study grid, and the high survival between trapping sessions suggests that squirrels were staying on the study grids for the duration of the summer and fall. This may be indicative of the suitability of the habitat on each grid.

Density in both years showed a tendency to decline at the end of the summer, although this was not as pronounced in 1994. Sullivan and Klenner (1993) showed that population densities declined from mid-summer to the end of August in both food supplemented and control study plots in British Columbia. Rusch and Reeder (1978) also noted a decline from summer to fall and reported that emigration, especially of juveniles occurred from August through October in Alberta. This was related to the need for finding a territory which is necessary for overwinter survival (Kemp and Keith, 1970; Rusch and Reeder, 1978; Larsen and Boutin, 1993). Juvenile dispersal could account for the apparent decrease in 1994, but in 1995 juveniles had only started to appear in traps at the end of August. Therefore, explanations for the decline must lie in the adult population.

Table 4.1. A summary of red squirrel densities reported in various types of coniferous habitat.

Habitat	Density[1] (no./ha)	Location	Source
Western hemlock (*Tsuga heterophylla*)	2.0	British Columbia, Canada	C.C. Smith, 1968
Lodgepole pine (*Pinus contorta*)	1.3	Colorado, U.S.A.	Gurnell, 1984
Unthinned juvenile lodgepole pine	1.1 - 1.2	British Columbia	Sullivan and Moses, 1986
Mature lodgepole pine	0.3 - 2.0		
Scots pine (*Pinus sylvestris*)	0.75 - 2.2	Ontario, Canada	Hurly and Robertson, 1990
Jack pine (*Pinus banksiana*)	0.86 - 2.6	Alberta, Canada	Rusch and Reeder, 1978
White spruce (*Picea glauca*)	0.2 - 0.8	Alaska, U.S.A.	M.C. Smith, 1968
White spruce	1.7 - 2.7	Yukon, Canada	Price, 1994
Black spruce (*Picea mariana*)	2.0 - 5.8	Newfoundland, Canada	West, 1989
Black spruce / balsam fir (*Abies balsamea*)	1.14 - 2.37	Newfoundland, Canada	Payne, 1976
Black spruce / balsam fir	0.5-3.7	Newfoundland, Canada	This Study

Table 4.1. (continued)

Habitat	Density[1] (no./ha)	Location	Source
Mixed black and white spruce	1.6 - 6.8	Alberta, Canada	Rusch and Reeder, 1978
Aspen (*Populus* spp.) / black and white spruce	0.3 - 0.5	Alberta, Canada	Kemp and Keith, 1970
Aspen / black spruce / jack pine	0.5 - 0.6		

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[1] Methods used to calculate density varied between studies

The decline may be due to adult squirrels dispersing from the grids. Adults of both sexes may leave an area if the food supply is low. M.C. Smith (1968) reported emigration of territorial adult squirrels into black spruce habitat when the white spruce cone crop on the study area failed. This explanation is unsatisfactory since both spruce and fir cone crops were reported to be heavy for 1995 (C. Harrison, Forest Geneticist, *pers. comm.*), and therefore food was not expected to be a limiting factor.

Female squirrels may bequeath their territories to their young and disperse in search of a new one (Price et al., 1986; Price and Boutin, 1993). This is most notable in females with late-born juveniles, as these young may be at a disadvantage when competing for territories (Price and Boutin, 1993). However, evidence from the trapping record is not consistent with this explanation since most breeding females that were repeatedly trapped on both grids in 1995 remained for almost the entire summer.

The decline in density may be the result of a general increase in territorial behaviour. Territories are established or reaffirmed in the fall as juveniles disperse and the caching of cones takes place (Kemp and Keith, 1970; Rusch and Reeder, 1978; Gurnell, 1987). An increase in agonistic behaviour may force other squirrels to disperse. This is consistent with the high numbers of transient animals in August on grid 95-2. In addition, death of individuals is also a possibility. Price et al. (1990) indicated that when territorial disputes occur, vigilance may be decreased resulting in an increased susceptibility to predation. Two of three Goshawk (*Accipiter* spp.) predation attempts witnessed on their study area occurred during territorial chases.

Despite these explanations, Gurnell (1983) states that the possibility of declining trappability due to the abundance of natural food cannot be dismissed. Good crops of spruce and fir were maturing at this time and squirrels may have been less attracted to the bait. However, data from fall trapping lends support to dispersal/lower survival explanations. Both grids experienced the loss and ingress of individuals. This was more extreme for grid 95-2 where an almost complete turnover was observed in November. Of seven individuals captured on that grid in November, only one (14%) was a recapture from summer trapping. On grid 95-1, eight of 14 (57%) individuals trapped in November were also trapped during the summer. Unfortunately, the data cannot identify whether death or dispersal has the greater effect. An intensive radio-tracking study could determine the fates of missing individuals.

Density was higher in 1995 than in the previous year. Since several studies have shown that *Tamiasciurus* populations are food limited (Sullivan and Sullivan, 1982; Sullivan, 1990; Klenner and Krebs, 1991), a difference in density may be attributed to a difference in cone abundance. Cone crops were classified as light in 1993 and 1994 and as heavy in 1995 for both black spruce and balsam fir (C. Harrison, *pers. comm.*). Although conifer seed-eating Eurasian red squirrels *(Sciurus vulgaris)*, as well as other *Sciurus* species, show a time lag of about one year between a rich food source and a high density (Pullianen, 1984; Gurnell, 1987; Andrén and Lemnell, 1992), this is not believed to be the case for North American red squirrels (Kemp and Keith,1970).

Kemp and Keith (1970), based on an hypothesis proposed by Svärdson (1957), suggest that red squirrels may be able to anticipate the size of cone crops and their reproductive rate can be adjusted accordingly. This stems from the fact that flower buds in conifers differentiate in the year before they flush (Eis, 1967) and are nutritionally superior to vegetative buds (Minty, 1976; Kramer and Kozlowski, 1979). Squirrels will utilize conifer buds as food (C.C. Smith, 1968; Ferron et al., 1986), especially in winters when cone supplies are scarce (M.C. Smith, 1968). Kemp and Keith (1970) suggest that taking advantage of this high quality food source during a winter before a large cone crop will subsequently stimulate red squirrel reproduction. Hence, density would increase without a time lag. Therefore, the availability of an abundant and highly nutritious food source during late winter/early spring 1995, as compared to previous years, should result in more offspring being produced, thereby increasing the density on the grids for summer 1995.

Trapping data from the present study are not fully supportive of this hypothesis. When the difference in grid size is taken into account, the number of juveniles trapped on the study grids was similar between years (Fig. 3.3). Also, juveniles appeared later in 1995 than in 1994, eliminating increased reproduction in spring 1995 as the cause of the increased density. It is possible that females had two litters in 1995 but this is unlikely. Single litters appear to be the rule for red squirrels (Kemp and Keith, 1970; Dolbeer, 1973; Ferron and Prescott, 1977; Rusch and Reeder, 1978). Second litters, however, have been reported in years of mild temperature (Millar, 1970), when the first litter is lost early enough to allow a second successful mating (Larsen and Boutin, 1994), and in areas of mixed or deciduous forests (Lair, 1985). All recruits to the population in early summer were adults and no captures or sightings of juveniles occurred.

The increased density of 1995 is the result of higher overwinter survival during the winter of 1994/1995 than during winter 1993/1994, since the number of adult recruits was greater during late spring in 1995 than in 1994. Winter temperature and food supply have been positively correlated with survival in red squirrels (Rusch and Reeder, 1978) and also with density fluctuations for *S. vulgaris* (Wauters and Dhondt, 1990). The median daily temperature (at Gander; ca. 80 km N of the park; Atmospheric Environment Service, 1993, 1994, 1995) for winter 1993/1994 (December - March; -7.1°C, range: -23.1 - 6.0, $n = 121$) was not significantly different from that of winter 1994/1995 (-6.0°C, range: -16.9 - 3.1, $n = 121$; Mann-Whitney rank sum test, $T = 14450$, $P = 0.645$). Median daily snowfall for winter 1993/1994 (1.0 cm) was not significantly different from that of winter 1994/1995 (0.8 cm; Mann-Whitney rank sum test, T = 14253, $P = 0.410$). Despite the lack of statistically significant differences for temperature and snowfall, the added factor of a light cone crop for 1993 (C. Harrison, *pers. comm.*) may have contributed to lower overwinter survival. Feeding on abundant and nutritionally superior flower buds during late winter may have sustained squirrels until spring, but this needs to be investigated.

Andrén and Lemnell (1992) indicate that the important contribution of a rich food supply is that it increases overwinter survival and subsequent reproduction. Therefore, due to the heavy cone crop of 1995, it is reasonable to predict that overwinter survival may be enhanced for winter 1995/1996 and density should be as high or higher in spring/summer 1996 than in 1995.

Although food may have been more abundant in winter 1995, juveniles were trapped earlier in 1994, suggesting that either the timing of reproduction was earlier or early litters did not survive in 1995. However, red squirrel females are asynchronous breeders and a 1-2 month difference in the onset of estrus can occur among females from the same population (Rusch and Reeder, 1978; Becker, 1993). Moreover, the start of the breeding season may also vary between years (Rusch and Reeder, 1978). Becker (1993) has shown that the maintenance of a positive energy balance is one factor which helps to cue estrus in female red squirrels. Wild squirrels that had access to a supplemental food source (sunflower seed) came into estrus earlier than those without excess food. Similarly, Klenner and Krebs (1991) found that females reached breeding condition one month earlier after a large cone crop. Therefore, it would be reasonable to assume that juveniles would have been trapped or observed earlier in 1995, since the relative amount of food may have been greater. However, Becker (1993) suggested that food abundance in the fall is not as important as cold weather in late winter or early spring. Despite the assumed increase in winter food, colder temperatures may have been a factor delaying reproduction in 1995 as compared to 1994.

The age composition and reproductive experience of the female cohort can also affect the timing of reproduction. Rusch and Reeder (1978) found that breeding was initiated earlier when there was a high proportion of reproductive female yearlings in the breeding population. In contrast, Becker (1993) found that juvenile and primiparous females (those giving birth to a litter for the first time) had their estrus cycle later in the season. However, female red squirrels do not normally breed as yearlings (Millar, 1970; Rusch and Reeder, 1978). Larsen and Boutin (1994) reported that most females in their study were > 2 years of age before having their first litters. Limited data from the present study is supportive of this. Both females that were trapped in 1994 as juveniles did not show any signs of reproduction when recaptured in 1995.

Adult sex ratios were biased towards males in both years, although this was only significantly different from a 1:1 sex ratio for total adults in 1994 and combined total adults in 1995. Davis and Sealander (1971) at their Emma Lake study site and Rusch and Reeder (1978) found a significant preponderance of males in adult sex ratios. Hurly (1987) also found a male bias for adults. In contrast, Kemp and Keith (1970) showed that there was no difference from a 1:1 sex ratio in trapped and shot samples from June - September in Alberta. There have been several explanations for the significant male bias. Males tend to wander away from their territories in search of females during the breeding season and are more likely to be caught (Kemp and Keith, 1970; Rusch and Reeder, 1978). Davis and Sealander (1971) suggested that pregnant squirrels may be less active than males and therefore more difficult to trap or observe.

However, Hurly (1987) concluded that the male bias in his populations was not due to sampling methods and suggested that differential mortality acting on females was responsible. Rusch and Reeder (1978) found that adult females experienced higher annual mortality rates than adult males and Halvorson and Engeman (1983) showed that median adult female longevity was lower than that of males but this was not quite significant. The reduction in female survival has been associated with the higher energetic demands and stress of reproduction. A higher female mortality may have contributed to the higher number of males especially in 1994; a year following a light cone crop. However, since significant male biases were only found when transient animals were included, increased male movement is the more likely explanation.

Juvenile sex ratios were not significantly different from a 1:1 ratio in both years but were always in favour of females. Although sample sizes are small, these results are consistent with the even ratio reported for other studies (Davis and Sealander, 1971; Ferron and Prescott, 1977; Rusch and Reeder, 1978; Lair, 1985; Hurly, 1987; Larsen and Boutin, 1994).

In conclusion, red squirrel density in black spruce habitat in Newfoundland is similar to densities reported in other coniferous habitats throughout their range. Red squirrel numbers appear to fluctuate with food abundance but the lack of long term data precludes strong conclusions. Also, population density needs to be monitored in white spruce and balsam fir habitats. White spruce appears to be preferred by red squirrels (Brink and Dean, 1966) and therefore higher densities may be supported. As well, black spruce cone crops are more dependable than white spruce or balsam fir (Minty, 1976) and viable seed may remain in cones for up to 30 years (Farrar, 1995). Consequently, population fluctuations may be steeper in white spruce and balsam fir forest types than in black spruce.

4.2 Red Squirrel Home Ranges and Territoriality

Rusch and Reeder (1978) state that virtually all investigators of red squirrel populations (e.g. C.C. Smith, 1968; M.C. Smith, 1968; Kemp and Keith, 1970; Zirul and Fuller, 1971) agree that home range and territory are equivalent. Gurnell (1984), however, found that for three squirrels in which territory boundaries were detected, one had its territory approximately equal to its home range, one excluded a portion of its home range adjacent to an unoccupied area, and one defended an area of about 60% of its home range size. Although no attempt was made to delineate territory boundaries, observation of behaviours when squirrels were located were in general agreement with those used by other investigators when mapping territories (territorial calling, chasing, eating, tree climbing, washing, remaining stationary for more than one minute - Price et al., 1986). Home range sizes as determined in this study are generally larger than home ranges and territories reported for other studies (Table 4.2). Several explanations may account for this.

First, the timing of the study may affect home range size. Squirrel locations were obtained from mid-late summer and the flowers and fruit of birch and maple trees were available at this time. Squirrels are able to take advantage of this food source (Ferron et al., 1986; Benhamou, 1996; personal observation) and since these trees were relatively rare on both grids, movements may have been directed out of the normal ranges to reach them. Secondly, the trapping data indicates that male squirrels were in breeding condition during most of the summer. Males will travel outside of their territories in search of estrus females during the breeding season (C.C. Smith, 1968; Rusch and Reeder, 1978). Koford (1982) found that for Douglas squirrels (*Tamiasciurus douglasii*), a larger proportion of locations was found in the central areas (75% polygons) of other individuals during the breeding season than in the post-breeding season. Finally,

Table 4.2. A summary of some home range and territory sizes of red squirrels in various types of coniferous habitat.

Home Range/ Territory	Size (ha)	Habitat	Location	Source
Home range	0.29 - 0.80	Lodgepole pine (*Pinus contorta*)	Colorado, U.S.A.	Gurnell, 1984
Home range	0.3 - 0.4	Balsam fir (*Abies balsamea*)-White cedar (*Thuja occidentalis*) and pine (*Pinus* spp.)	Wisconsin, U.S.A.	Reige, 1991
Home range	0.08 - 1.58	Jack pine (*Pinus banksiana*)-White spruce (*Picea glauca*)	Northwest Territories, Canada	Zirul and Fuller, 1970
Home range	0.34 - 4.1	Black spruce (*Picea mariana*)	Newfoundland, Canada	This Study
Territory	1.6 - 4.8	White spruce	Alaska, U.S.A.	M.C. Smith, 1968
Territory	0.4 - 0.8	White and Black spruce	Alberta, Canada	Kemp and Keith, 1970
Territory	0.24 0.35 0.66	White spruce White and Black spruce Jack pine	Alberta, Canada	Rusch and Reeder, 1978
Territory	0.28	White spruce	Yukon, Canada	Price et al., 1986

Table 4.2. (continued)

Home Range/ Territory	Size (ha)	Habitat	Location	Source
Territory	0.64 - 0.70	Douglas fir (*Pseudotsuga menziesii*)	British Columbia, Canada	Klenner, 1991
Territory	0.65	Jack pine	Alberta, Canada	Larsen and Boutin, 1994

territorial squirrels do not restrict their movements entirely to their territories and occasional exploratory movements do occur (Gurnell, 1984; Price et al., 1986; Benhamou, 1996). Occasional excursions may be omitted when drawing MCPs by using fewer than 100% of the locations (White and Garrott, 1990; Klenner, 1991). Due to the relatively low sample sizes in the present study, this was not feasible. All of these explanations may account for the inability to detect radio signals at various times.

Home ranges overlapped on both grids. This indicates that if individual territories do exist, then home range is larger than territory size, at least during the summer. Gurnell (1984) found a difference between home range and territory size as previously stated. This differs from other studies which have shown that territories are mainly contiguous, non-overlapping, and defended year-round (C.C. Smith,1968; Kemp and Keith,1970; Rusch and Reeder, 1978; Price et al., 1986; Larsen and Boutin, 1994). However, territoriality may be relaxed when there is a lack of a defendable food cache. Studies have shown the lack of, or reduction in territoriality in the absence of large cone caches (Layne, 1954; Yahner, 1980; Reige, 1991) but this usually occurs in deciduous forests. Koford (1982) found a seasonal relaxation in territorial behaviour in *T. douglasii* and related this to a difference in the importance of the cone cache. He reasoned that since cone caches were usually exhausted by summer, the benefits of territoriality were decreased especially for females during the breeding season. With many males encroaching on a female's home range, territoriality becomes uneconomical. Dempsey and Keppie (1993) report that only 14% of scatterhoarded caches remained in spring and Benhamou (1996) stated that all known caches were empty in mid-June in a deciduous coniferous forest. Although the present study areas were not searched for caches during the summer, it is likely that any cached food was depleted during the tracking period. Hence, a decrease in territoriality could account for home range overlap.

Due to the disappearance of some of the radio-collared squirrels, I was unable to compare summer and fall home ranges. Territorial behaviour is more noticeable in the fall when cone harvesting and caching reaches its peak (Gurnell, 1987). Therefore, fall home ranges may show less overlap and would be less affected by other factors as previously discussed.

4.3 Caching Behaviour of Red Squirrels

4.3.1 *Cache Size and Distribution*

After an extensive visual search of the study areas in late fall, I am confident that no middens as described in western populations (i.e., Finley, 1969; Kelly, 1978; Gurnell, 1984, 1987) were present on either grid. Therefore, my results indicate that these study populations of Newfoundland red squirrels are scatterhoarders and do not concentrate hundreds or thousands of cones in a central midden as is typically reported for this species (M.C. Smith, 1968; Finley, 1969; Kelly, 1978; Gurnell, 1984). At least for black spruce cones, Newfoundland squirrels show variation in the size of caches that they make, with both single cone and large caches being a deliberate part of the hoarding strategy.

These results are similar to those of Hurly and Robertson (1990) and Dempsey and Keppie (1993) who studied red squirrel food hoarding in Scots pine (*Pinus sylvestris*) and jack pine (*Pinus banksiana*) plantations respectively. In both of these studies, the variation in cache size was not random with single cone and large caches being over-represented.

The large caches found in this study were not as large as those reported for other scatterhoarding red squirrels. Large caches ranged from 13 - 24 cones for the high cover grid while in low cover 22 - 43 cones were found. Hurly and Robertson (1990) found that large caches ranged in size from 11 - 314 cones, while Dempsey and Keppie (1993) reported a maximum cache size of 156 jack pine cones. Clearly, these large caches do not reach the size of middens which contain thousands of cones as reported in western North American populations.

Black spruce was the predominant cone cached since this was the most abundant tree on each grid. The rarity of balsam fir caches is probably due to the lower density of trees as Reige (1991) observed these cones to be readily cached in middens in Wisconsin. Balsam fir's importance on the present study grids may be as a summer food source since cone maturation and seed dissemination begins in late August to early September (Vidakovic, 1991).

Larch cones were not found in caches although squirrels were observed feeding on them in August. Larch cones mature and begin to open in mid-August (Vidakovic, 1991; Farrar,1995) providing an earlier source of seed than black spruce which matures in September. Therefore, squirrels would probably have to cache larch cones early in the season to prevent them from opening and losing their seed. However, competition for these cones may preclude their caching. Crossbills (*Loxia* spp.) were frequently observed feeding on these cones and on a few occasions two or more squirrels were observed feeding together in larch trees. C.C. Smith (1968) observed intraspecific tolerance among red squirrels feeding on seasonally abundant Douglas fir (*Pseudotsuga menziesii*) pollen, a food which cannot be stored or defended. Observations in this study suggest that larch cones are used as an immediate food source and are not cached for subsequent use.

Ground caches of cones do not provide the entire winter food supply of red squirrels. Many cones that appeared to be cut by squirrels were left lying on the forest floor and were not cached. It is not known whether squirrels use these during the winter. Similarly, Ferron et al. (1986) reported that white cedar cones are cut from trees and are left on the ground or snow and not cached, but are eaten much later. Feeding from cones in trees and from cones cached in trees also occurs (Dempsey and Keppie, 1993). This may be possible in the present study due to the semi-serotinous nature of black spruce cones; seeds are shed gradually throughout the winter and viable seed may remain in cones for up to 30 years (Farrar, 1995). Scatterhoards in the ground may possibly be used in "emergency" situations such as during periods of low temperature and inclement weather when foraging in the trees is not possible. Information on when caches are used during the winter and on other foods eaten during this time period is required to determine the overall importance of scatterhoards to the winter diet.

Caches may also be more numerous or larger in forests where the cones must be stored in order to have a winter food supply. White spruce and balsam fir lose most of their seeds during the first autumn (Farrar, 1995), and in the case of fir, the cone no longer remains intact. Also, once cones open the seeds become more readily available to birds such as crossbills, chickadees (*Parus* spp.), pine siskins (*Carduelis pinus*), pine (*Pinicola enucleator*) and evening (*Hesperiphona vespertina*) grosbeaks, and gray jays (*Perisoreus canadensis*) (Smith and Balda, 1979). Therefore, more cones would have to be cached. Also, energetic factors such as the quality and number of seeds /cone, and handling time for the different species can affect the number of cones cached (Gurnell, 1987). An evaluation of caching behaviour in monospecific stands is needed to determine the effect of the type of food species on caching pattern.

4.3.2 *The Effect of Cover on Caching*

Although the distribution of cache sizes did not differ significantly between the two grids, most of the cones (65%) cached in the low cover grid were found in large caches (Fig. 3.10). This was higher than the 20% of cones accounted for by large caches in high cover. Dempsey and Keppie (1993) found that in autumn 1990, large caches accounted for 40% of the total number of cones while Hurly and Robertson (1990) found that 50% of cones were in large caches. Mean number of cones in large caches was also greater in low cover than in high cover. This indicates that in low cover, squirrels rely more on large caches for hoarded food.

The proportion of hoarded food accounted for by the different cache sizes may be the more important aspect of red squirrel food hoarding since the distribution of cache sizes is similar across their range. Michalko (1991) showed that even in the western part of their range where larders are frequent and very large, red squirrels also scatterhoard cones. In her study, she found that the distribution of cache sizes did not correspond to a random distribution and single-cone and large (10+ cones) caches occurred more frequently than expected. However, the scatterhoards did not account for a large proportion (10%) of the total number of cones stored.

Having larger caches in low cover may be due to a lack of safe feeding sites. If these are rare then squirrels may concentrate cones in areas that are safe at which to feed. In low cover, this was expected to be close to trees. However, the median distance from the nearest tree for all caches was greater in low cover than in high cover. Other attributes of the cache sites (such as proximity to shrubs, stumps or rocks) may have made them safer from predators but these characteristics were not described.

Squirrels may have also placed caches in a manner that trades off predation risk and cache theft. If the nearest tree can be considered the source tree, then placing caches away from the source may prevent theft. This is possible since even in midden/territorial systems, red squirrels occasionally enter the territories of others and caches may be discovered (Gurnell, 1984). When presented with two species of pine cones in the centre of their territories, scatterhoarding red squirrels carried these items away from the source, presumably to decrease the probability of losing the cache to competitors (Hurly and Robertson, 1987).

Snow cover and frost penetration into the ground could affect cache placement. Studies have shown that a tree's canopy affects the distribution of snow around a tree with snow depth increasing with distance from the tree trunk (Hardy and Albert, 1995). A lower snow depth is associated with lower snow-ground interface temperatures as well as deeper frost penetration into the ground (Pruitt, 1957; Hardy and Albert, 1995). Red squirrels retrieve caches during the winter and cones may be eaten above or below the snow surface (Dempsey and Keppie, 1993). Because temperature affects the energetic cost of activity (Pauls, 1978), it may be less costly and easier to retrieve caches in areas of relatively higher temperature and less frost penetration.

These previous factors may also account for the spatial clumping of caches and the lack of difference in the distributions on both grids. However, since fall home ranges for individual squirrels were not determined, it is possible that some sample plots were located in areas not utilized by any squirrels, thereby contributing to the large number of sample plots without caches.

There was no relationship between cache size and the distance from the nearest tree (DNT) for the low cover grid. However, in high cover there was a tendency for single cone caches to be found further from a tree than multiple cone caches. Hurly and Robertson (1987) showed that red squirrels cached more valuable items farther from their source than less valuable items. In low cover, predation-risk may be too great to warrant moving single items a greater distance. Further study on the relative food value of the different size caches is warranted.

Alternatively, single-cone caches that have a relatively high DNT may be the result of the distribution of fallen cones on the ground. Squirrels collect cones by cutting individual cones or branchlets with clusters of cones from the tree and allowing them to fall to the ground (Vander Wall, 1990; pers. observ.). Higher DNT single-cone caches may be the result of single cones falling greater distances from the base of the tree. In low cover, this distance may be too far away from cover to cache them where they fall and so squirrels may actively move these cache items closer to trees. However, these explanations are purely speculative. Information is needed on how squirrels place caches about a single source.

4.3.3 *Alternative explanations*

Squirrel population densities were 1.8 and 0.8 squirrels/ ha at the end of summer and 2.3 and 1.2 /ha in November for the high (95-1) and low (95-2) cover grids, respectively. If a higher density results in more intraspecific competition, then my results are consistent with those of Clarke and Kramer (1994a). These authors showed that eastern chipmunks (*Tamias striatus*) that were chased by conspecifics at a food patch were significantly more likely to scatterhoard than unharrassed individuals which tended to larderhoard in their burrows. This is interesting because these results are contrary to prevailing ideas about social organization and caching behaviour. Individual territories for red squirrels are possible because they rely on an easily defended food resource. Interspecific competition for intact conifer cones is low. Intraspecific competition is high however, and larderhoarding is presumed to be the most efficient way to defend food from conspecifics (Smith and Reichman, 1984). Therefore, it is logical to assume that an increase in intraspecific competition should be followed by an increase in the amount of larderhoarding. This was not the case in the present study.

Also, as previously noted, there is evidence to suggest that the extent to which red squirrels scatterhoard has been underestimated. In western populations where the dominant food hoarding strategy was traditionally described as larderhoarding, scatterhoarding is prevalent (Michalko, 1991). Therefore, the assumption that larderhoarding and territoriality evolved in response to strong intraspecific competition may not be completely valid. Presumably, scatterhoarding and larderhoarding evolved under those conditions. A more rigorous evaluation of territorial behaviour and information on cache loss is required for both larderhoarding and scatterhoarding red squirrels.

I was unable to assess the effect of sex and age on cache characteristics. Clarke and Kramer (1994 a,b) have shown that the prevalence and placement of scatterhoards in eastern chipmunks is affected by age and for females, the presence of young in the burrow. However, neither Hurly and Robertson (1990) nor Dempsey and Keppie (1993) found any difference in cache size distribution between individuals, although they did not test for the effect of sex or age on cache configuration.

Lactating squirrels have higher energetic demands than males (C.C. Smith, 1968) and therefore, females would require more food. However, there is some evidence from other studies that suggests that the sex of the caching individual is unimportant. Time budgets during the breeding season were not significantly different for male and female red squirrels in Quebec, although the reproductive conditions of the observed females could not be confirmed (Ferron et al., 1986). Although the caching patterns of males and previously reproductive females have not been specifically compared, no differences were found in the larderhoarding behaviour between breeding and non-breeding female red squirrels in Alberta (Zimmerling, 1990). Consequently, male and female caching patterns would not be expected to differ. From November trapping sessions sex ratios (male: female = 4:3) and adult: juvenile ratios (4:3) were identical in high and low cover.

Therefore, if sampled caches are representative of all caching squirrels on each grid, then sex and /or age structure would not account for differences between grids.

The quality of the available food resource may affect caching behaviour. Vander Wall (1995) found that caches made by yellow pine chipmunks (*Tamias amoenus*) with a low quality food source had significantly more seeds than caches made with higher quality seed. Red squirrels can also assess the quality of items to be cached and will cache higher quality items further from their source (Hurly and Robertson, 1987) but it is not known how the quality affects the size of the cache. Setterington (1993) found that in jack pine forests, red squirrels do not make various cache sizes based on the cone quality indices of % seed, total seed weight /cone, or number of seeds /cone. Because almost all caches consisted of black spruce cones, then quality is probably not a factor affecting cache sizes in this study (assuming variation in cone quality is not great between grids).

The quantity of food available to be cached may also be a factor affecting the food hoarding strategy. Since the relative abundance and density of black spruce was similar between the high and low cover grids (Table 3.9) and cone production was high for 1995 (C. Harrison, *pers. comm.*), then the availability of food should not have differed between grids. West (1989) showed however, that squirrels took proportionally fewer black spruce cones in a year with a large cone crop than in years with small crops. This could affect the number and size of caches, but the response of squirrels to taking cones should be the same between study grids.

Finally, the dispersion of food is a possible element of food hoarding. In a high density food patch, making large caches may be more efficient. If food is widely dispersed then caching cones near their point of harvest minimizes costs due to caching and recovery (Hurly and Robertson, 1990). Large caches could be due to a high density of cones available in trees. Therefore, it is possible that cones may have had a clumped distribution in the low cover grid. However, cones were abundant on both grids and almost all trees produced good crops (pers. observ.). Consequently, dispersion of food is an unlikely explanation for variation between grids.

4.3.4 *Conclusion*

The difference in cover and assumed difference in predation risk between grids did affect red squirrel caching in terms of proportion of cones accounted for by large caches. Manipulating predation risk directly by increasing the density of predators for example, should also affect the caching pattern in red squirrels. Perhaps a more apparent difference in cache size distributions may have been observed if cover had been manipulated (i.e., pruning of trees and removal of understory shrubs to decrease cover). Hurly and Robertson (1990) showed that the availability of middens affects red squirrel caching behaviour but at sites where middens were provided, cover was also altered by the investigators by pruning branches from trees. This reduction in cover may have been a factor contributing to the use of these simulated middens. It would be interesting to test if squirrels would use these structures in unpruned areas.

Many factors have the potential for affecting the caching strategy of squirrels and these factors may vary in importance spatially and temporally. For example, the amount of cover may not be important in years with a lower food abundance when the risk of starvation may be greater than that of predation. At these times, intraspecific competition may be expected to play a greater role in determining the caching pattern since the need for cache defense may override sensitivity to predation risk. This should in turn affect territorial behaviour. If intraspecific competition is high, territorial behaviour can be costly (Stuart-Smith and Boutin, 1994).

Also, the lack of protective cover may be compensated for by an increase in vigilance while caching and feeding. This is the case for eastern chipmunks which take longer to forage in open patches, as compared to covered areas, due to an increase in vigilance (Otter, 1994). Further research on the behavioural aspects of caching and cache recovery in red squirrels would be beneficial.

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Appendix A

Estimates of red squirrel population size and corresponding standard errors calculated using the Jolly-Seber model of population estimation. The program JOLLY (Krebs, 1989) was used to obtain the estimates. Estimates are based on i) all animals captured and ii) residents only (animals capture more than once) for each grid.

Table A.1. Jolly-Seber estimates of red squirrel population size and corresponding standard errors for i) all animals captured and ii) residents only (animals captured more than once) in grid 94-1. Estimates cannot be calculated for the first and last trapping sessions.

Trapping session			Population size (no. of squirrels) ± SE	
			All animals	Residents only
1	May	17	-	-
2		19	8.1 ± 2.0	6.3 ± 1.0
3		28	15.0 ± 4.3	15.0 ± 4.2
4	June	2	13.7 ± 1.6	13.7 ± 1.4
5		6	15.1 ± 1.7	13.0 ± 0.0
6		10	15.6 ± 1.7	15.6 ± 1.2
7		14	15.0 ± 1.3	15.0 ± 0.0
8		23	15.3 ± 1.3	15.3 ± 0.3
9		26	14.0 ± 1.5	14.0 ± 1.0
10		29	14.0 ± 1.5	14.0 ± 1.0
11	July	3	15.2 ± 2.3	15.2 ± 1.9
12		7	17.8 ± 3.4	13.8 ± 2.0
13		11	14.7 ± 2.7	14.7 ± 2.3
14		15	23.2 ± 5.6	20.0 ± 3.9
15		19	14.5 ± 2.6	14.5 ± 2.2
16		29	15.9 ± 2.9	14.4 ± 2.4
17	Aug.	4	18.2 ± 3.0	16.5 ± 2.4
18		11	16.5 ± 2.7	16.5 ± 2.3
19		13	13.0 ± 2.7	13.1 ± 2.6
20		17	-	-

Table A.2. Jolly-Seber estimates of red squirrel population size and corresponding standard errors for i) all animals captured and ii) residents only (animals caught more than once) in grid 95-1. Estimates cannot be calculated for the first and last trapping sessions.

Trapping session			Population size (no. of squirrels) ± SE	
			All animals	Residents only
1	June	2	–	–
2		8	6.3 ± 1.1	6.3 ± 1.1
3		10	6.0 ± 1.0	6.0 ± 1.0
4		19	13.6 ± 6.1	10.0 ± 3.6
5		21	13.9 ± 2.9	12.0 ± 2.0
6		29	12.6 ± 1.9	12.6 ± 1.3
7	July	5	12.6 ± 2.2	12.6 ± 1.7
8		11	12.0 ± 1.8	12.0 ± 1.3
9		19	15.4 ± 3.4	15.4 ± 3.1
10		26	13.0 ± 2.5	13.0 ± 2.2
11	Aug.	1	11.4 ± 2.2	11.4 ± 1.8
12		8	14.4 ± 4.8	14.4 ± 4.6
13		23	10.0 ± 6.2	10.0 ± 6.2
14		30	10.5 ± 3.0	10.5 ± 2.9
15	Nov.	11	13.3 ± 4.0	13.3 ± 4.0
16		18	–	–

Table A.3. Jolly-Seber estimates of red squirrel population size and corresponding standard errors for i) all animals captured and ii) residents only (animals caught more than once) in grid 95-2. Estimates cannot be calculated for the first and last trapping sessions.

Trapping session			Population size (no. of squirrels) ± SE	
			All animals	Residents only
1	May	29	–	–
2	June	7	9.5 ± 2.7	7.7 ± 1.2
3		9	14.0 ± 5.2	9.0 ± 2.2
4		13	8.0 ± 2.0	8.0 ± 0.9
5		20	14.3 ± 4.3	12.0 ± 2.7
6		27	12.6 ± 3.2	10.7 ± 2.1
7	July	4	17.1 ± 6.3	12.5 ± 3.1
8		6	11.0 ± 2.4	11.0 ± 1.5
9		12	14.0 ± 4.7	14.0 ± 4.1
10		17	10.8 ± 2.9	10.8 ± 2.4
11		18	11.2 ± 3.0	11.2 ± 2.5
12		27	9.1 ± 2.9	7.0 ± 1.9
13	Aug.	2	7.8 ± 2.7	7.8 ± 2.5
14		9	20.0 ± 18.7	8.0 ± 5.3
15		23	5.3 ± 2.4	5.3 ± 2.0
16	Sept.	1	4.0 ± 2.0	4.0 ± 1.7
17	Nov.	12	6.3 ± 11.1	6.3 ± 11.1
18		18	–	–

Appendix B

Results of the Leslie, Chitty, and Chitty Test (Leslie et al., 1953) for equal catchability within the marked population. Estimates were calculated using program LESLIE (Krebs, 1989). The relative value of the percent error between the observed and expected number of newly marked animals is used to assess the assumption of equal catchability.

Table B.1. Results of the Leslie, Chitty, and Chitty test for equal catchability within the marked segment of the population for grid 94-1. Estimated number of new animals marked for the first time is calculated as in Leslie et al. (1953). Estimates cannot be obtained for the first two and last trapping sessions. Similarity of the sums of the observed and expected newly marked animals indicates equal catchability.

Trapping session			Estimated no. of new animals marked for the first time	Observed no. of new animals marked for the first time
1	May	17	-	-
2		19	-	-
3		28	2.8	6
4	June	2	3.3	1
5		6	1.8	1
6		10	0.4	2
7		14	-0.2	0
8		23	0.0	0
9		26	0.0	0
10		29	0.0	0
11	July	3	0.0	-1
12		7	1.9	3
13		11	4.8	2
14		15	-1.9	2
15		19	-0.1	1
16		29	1.1	3
17	Aug.	4	4.3	3
18		11	-0.5	0
19		13	0.0	0
20		17	-	-
			17.7	23

$$\% \text{ error} = \frac{\text{obs.} - \text{exp.}}{\text{obs.}} \times 100\% = \frac{23 - 17.7}{23} \times 100\% = 23.0\% \text{ underestimate}$$

Suggests unequal catchability within the marked population.

Table B.2. Results of the Leslie, Chitty, and Chitty test for equal catchability within the marked segment of the population for grid 95-1. Estimated number of new animals marked for the first time is calculated as in Leslie et al. (1953). Estimates cannot be obtained for the first two and last trapping sessions. Similarity of the sums of the observed and expected newly marked animals indicates equal catchability.

Trapping session			Estimated no. of new animals marked for the first time	Observed no. of new animals marked for the first time
1	June	2	-	-
2		8	-	-
3		10	0.7	1
4		19	2.0	3
5		21	4.8	4
6		29	0.7	1
7	July	5	2.4	1
8		11	-0.9	0
9		19	0.0	1
10		26	1.5	0
11	Aug.	1	-0.3	0
12		8	0.0	1
13		23	2.7	2
14		30	5.5	2
15	Nov.	11	-0.4	3
16		18	-	-
			18.7	19

$$\% \text{ error} = \frac{\text{obs.} - \text{exp.}}{\text{obs}} \times 100\% = \frac{19 - 18.7}{19} \times 100\% = 1.6\% \text{ underestimate}$$

Suggests equal catchability within the marked population.

Table B.3. Results of the Leslie, Chitty, and Chitty test for equal catchability within the marked segment of the population for grid 95-2. Estimated number of new animals marked for the first time is calculated as in Leslie et al. (1953). Estimates cannot be obtained for the first two and last trapping sessions. Similarity of the sums of the observed and expected newly marked animals indicates equal catchability.

Trapping session			Estimated no. of new animals marked for the first time	Observed no. of new animals marked for the first time
1	May	29	-	-
2	June	7	-	-
3		9	2.0	4
4		13	2.5	0
5		20	0.6	3
6		27	2.0	3
7	July	4	0.8	2
8		6	3.3	0
9		12	-3.3	0
10		17	2.7	1
11		18	-1.1	-1
12		27	0.0	1
13	Aug.	2	0.0	0
14		9	0.0	2
15		23	0.0	0
16	Sept.	1	0.0	0
17	Nov.	12	1.5	4
18		18	-	-
			11	19

$$\% \text{ error} = \frac{\text{obs.} - \text{exp.}}{\text{obs.}} \times 100\% = \frac{19 - 11}{19} \times 100\% = 42\% \text{ underestimate}$$

Suggests unequal catchability within the marked segment of the population.