POPULATION ECOLOGY AND RESOURCE LIMITATION OF NORTHERN FLYING SQUIRRELS AND DOUGLAS SQUIRRELS

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We accept this thesis as conforming to the required standards

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Date Sept. 6, 2001
Habitat preferences and population dynamics of northern flying squirrels (*Glaucomys sabrinus*) and Douglas squirrels (*Tamiasciurus douglasii*) were examined in old-growth and mature second-growth stands in British Columbia, Canada. Using mark-recapture techniques to estimate population dynamics, I tested the hypothesis that old-growth stands provided higher quality habitat than second-growth stands for these species. Populations were monitored in two old-growth and two mature second-growth stands from August 1995 to May 1999. There were no differences in movement, density, recruitment, weight of males, survival, percentage of the population breeding, and the duration that individuals remained on the study plots between stand types for *G. sabrinus*. Similarly, with the exception of recruitment, there were no differences in these parameters between stand types for *T. douglasii*. Recruitment of *T. douglasii* was higher in second-growth than old-growth stands. Old-growth stands were not higher-quality habitat than second-growth stands for either species for the period of enquiry and the parameters I measured.

Population dynamics of *G. sabrinus* and *T. douglasii* were also examined in thinned and unthinned stands. I tested the hypothesis that unthinned stands provided higher-quality habitat than thinned stands for these species. Populations were monitored using mark-recapture techniques on two thinned and two unthinned stand from August 1995 to May 1999. Commercial thinning was initiated 9 and 7 months following the first trap session. There were no differences in movement, density, recruitment, weight of males, survival, percentage of males breeding, and the duration that individuals remained in thinned and unthinned stands for *G. sabrinus* and *T. douglasii*. Unthinned stands were not higher-quality
habitat than commercially-thinned stands for either species for the period of enquiry and the parameters I measured.

Finally, effects of food and den site supplementation on the population dynamics of *G. sabrinus* and *T. douglasii* were examined in mature second-growth stands in British Columbia, Canada. I tested the hypothesis that populations of these squirrels were limited primarily by abundance of food, not den sites. The experimental design included a randomized complete block design with three replicates and four treatments (food supplementation, food and nest box supplementation, nest box supplementation, and control). Populations were sampled intensively from June 1996 to March 1999.

There were no differences in movement, density, recruitment, weight of males, percentage of males breeding, and the duration that individuals remained on the grids among treatments for *G. sabrinus* and *T. douglasii*. However, survival of *G. sabrinus* decreased significantly from pre- to post-treatment periods in stands without food supplementation. When food was added, survival increased significantly or remained unchanged. In addition, occupancy rate of nest boxes in stands supplemented with nest boxes and food was 6- to 12-times higher (1998 – 88.4%, 1999 – 75.0%) than in stands with nest boxes only (1998 – 7.0%, 1999 – 12.2%). *G. sabrinus* occupied the majority of the nest boxes. Nest boxes in stands supplemented with food primarily contained covered nests (76.5%) while beds dominated (68.3%) those in stands supplemented with nest boxes only. I concluded that *G. sabrinus* readily used nest boxes but their populations were not limited by the availability of den sites; availability of food appeared to limit their populations. Populations of *T. douglasii* were not limited by the availability of food or den sites during my study.
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CHAPTER 1: GENERAL INTRODUCTION

*Strix occidentalis* (spotted owl) is a rare resident of British Columbia with only 28 sightings before 1985 (Dunbar and Forsman 1985). Consequently, *S. occidentalis* has been listed as 'endangered' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and is 'red listed' (being considered by the Wildlife Branch for designation as 'endangered' or 'threatened') in British Columbia. Over the last decade *S. occidentalis* has been the focus of numerous studies, debates, and conflicts among forestry-based industries and other interest groups. Many studies have shown that *S. occidentalis* often used old-growth forests in greater proportion than its abundance, which indicates that they prefer old-growth forests (Forsman et al. 1984; Gutierrez et al. 1984; Allen and Brewer 1985; Carey et al. 1990, 1992; Miller et al. 1992; Lehmkuhl and Raphael 1993; Hunter et al. 1995; Meyer et al. 1998; Swindle et al. 1999). The decline of *S. occidentalis* in the Pacific Northwest has been attributed to declines in old-growth forests (Forsman et al. 1977, 1984; Franklin et al. 1990). Consequently, if trends in present timber harvest continue, the abundance of *S. occidentalis* will likely decline in the Pacific Northwest (Franklin et al. 1990; Noon and Biles 1990).

In response to this information, the province of British Columbia initially delineated 21 spotted owl conservation areas (SOCAs). The criterion for delineating the SOCAs was based primarily on the assumption that old-growth forests represent optimal habitat for *S. occidentalis*. By setting aside adequate amounts of old-growth forest it was hoped that all habitat requirements of *S. occidentalis* would be maintained. However, this assumption may not be valid. Short-term measurements of habitat use or availability reveal little about the value of the habitat unless the underlying resource distributions limiting populations are understood (Hobbs and Hanley 1990). Forest age class has become a surrogate feature for old-growth forest characteristics (multilayered and relatively dense canopy, mixed species composition dominated by large trees, numerous large
logs and other woody debris on the ground, numerous large diameter snags). These characteristics are probably more important than the age of the forests (Thomas et al. 1990). For example, recent studies have found that reproductive success among S. occidentalis is not sensitive to relatively large changes in the quantity of old-growth forests within their home ranges (Lehmkuhl and Raphael 1993; Iverson 1996; Meyer et al. 1998). In fact, in three studies, owls with the highest reproductive success had a significantly greater proportion of younger forests in their home range than those site occupied by owls with lower reproductive success (Irwin 1993; Franklin 1997; Thome et al. 1999). Sites repeatedly used for foraging by S. occidentalis were dominated by intermediate-aged forests (40- to 80-years old; Miller et al. 1992; Irwin 1993). The habitat use of S. occidentalis was compared between a second-growth stand regenerated after a wildfire (natural landscape) and managed second-growth stands regenerated after harvesting and slash burning (managed landscape). Owls using the managed landscape foraged more in these stands and had higher reproductive success than those foraging in the natural stands (Miller et al. 1992). Owls that foraged in the natural landscape used a greater proportion of mature and old-growth stands and had lower reproductive success. They suggested that the higher reproductive success might be attributed to easier foraging in managed stands where the densities of trees were less. Other studies also reported a positive relationship between prey abundance and reproductive success of S. occidentalis (White 1996; Thome et al. 1999), home range size and habitat use (Zabel et al. 1995), and their survival during natal dispersal (Miller et al. 1997).

Understanding the relationship between S. occidentalis and the resources they depend upon will be vital in designing effective management programs for them. More importantly, understanding how these vital resources (especially prey) are altered by forest practices are critical. This information is needed to ameliorate the negative influences of past forest management (primary harvest of old-growth stands) on S. occidentalis habitat, as well as using forest management practices as an effective tool to enhance their habitat.
Two prey-based hypotheses have been proposed to explain the general selection of old-growth forests by *S. occidentalis* (Forsman et al. 1982, 1984): 1) prey are more abundant in old-growth forests (prey abundance hypothesis), and 2) prey are more efficiently hunted by owls in old-growth forests because of the more open understory (prey availability hypothesis).

*Glaucomys sabrinus* (northern flying squirrel) is the most important prey item of *S. occidentalis* (Carey et al. 1992; Forsman et al. 1977; 1984) in coastal forests of British Columbia. However, very little information is currently available concerning habitat preference, population dynamics, and resource limitation of *G. sabrinus*. No information is available regarding how forest management practices influence population dynamics of *G. sabrinus*. This is critical since most forest-management practices result in reducing tree densities or modifying the structural characteristics of a stand (e.g., partial cutting, shelterwood, patch cutting, pre-commercial and commercial thinning). As the availability of old-growth stands declines, these forest practices are expected to increase and become standard treatments. Consequently, these practices can have a significant influence on the population dynamics of *G. sabrinus* and, in turn, the foraging habitat for *S. occidentalis* (Carey 1995).

**OBJECTIVES AND ORGANIZATION OF THE THESIS**

The proximate goal of my research is to enhance our understanding of the population ecology and resource limitation of *G. sabrinus*. This information then can be used to manage more effectively for *S. occidentalis* (ultimate goal). To meet my proximate goal, I first address whether prey (*G. sabrinus*) are, in fact, more abundant in old-growth than second-growth forests (prey abundance hypothesis; Chapter 2). Secondly, I examine the response of *G. sabrinus* to stand manipulation (commercial thinning; Chapter 3). If the abundance of *G. sabrinus* is reasonably similar between old-growth and second-growth stands, and their abundance does not decline after reducing tree densities, then the potential exists to increase the availability of *G. sabrinus* to *S. occidentalis* through stand management. Finally, identifying the primary resource
that limits the abundance of *G. sabrinus* (Chapter 4) will provide additional information that can be used to enhance their densities, thus improve foraging habitat for *S. occidentalis*.

*Tamiasciurus douglasii* (Douglas squirrel) is sympatric with *G. sabrinus* throughout their range in the Lower Mainland of British Columbia and the Pacific Northwest. Consequently, an additional objective is to examine the population ecology, resource limitation, and response to stand management by *T. douglasii*. This information is limited or lacking altogether. The general objectives of this research are:

1) To test the prey *abundance* hypothesis by investigating thoroughly the population dynamics of *G. sabrinus* and *T. douglasii* in old-growth and mature second-growth stands (Chapter 2),

2) To examine the population dynamics of *G. sabrinus* and *T. douglasii* in commercially thinned stands and unthinned stands (Chapter 3),

3) To test the hypothesis that population sizes of *G. sabrinus* and *T. douglasii* are primarily limited by the availability of food, not den sites (Chapter 4).

The first two objectives identify if there are differences in population dynamics of *G. sabrinus* and *T. douglasii* among old-growth and mature second-growth stands and commercially thinned and unthinned stands. The third will help identify why any differences may occur (resource limitation).

**Study Animals**

*G. sabrinus* is a small arboreal sciurid found in forested regions over most of North America (Wells-Gosling and Heaney 1984). They are typically found in habitats dominated by conifers or a mixed coniferous-deciduous overstory. Stomach and fecal analyses indicate that *G. sabrinus* primarily consumes hypogeous fungi during snow-free periods and lichens during winter (McKeever 1960; Maser et al. 1978, 1985, 1986; Hall 1991; Colgan 1997). *G. sabrinus* does not
appear to be territorial and individuals are often seen feeding together (Coventry 1932) and denning together (Maser et al. 1981; Mowrey and Zasada 1984; Carey et al. 1997; Cotton and Parker 2000). In addition, *G. sabrinus* use multiple den sites (cavities and constructed nests) on consecutive days (1 – 13 den sites - Carey 1991; Weigl and Osgood 1974; Carey et al. 1997). They inhabit two types of nests: those inside tree cavities and those constructed in the canopy of conifers or witches’ broom (Mowrey and Zasada 1984).

*T. douglasii* is a small arboreal sciurid found in coniferous forests dominated by Pacific silver fir (*Abies amabilis*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudostuga menziesii*), and western hemlock (*Tsuga heterophylla*). Its range extends from San Francisco, California, north through the Coast Ranges in the Sierra Nevada and Cascades of Oregon and Washington to its northern limit along the southwest coast of British Columbia (Ingles 1965; Banfield 1974). Its diet primarily consists of hypogeous and epigeous fungi, and conifer cones (Smith 1970, 1981; Fogel and Trappe 1978). During winter and early spring, its diet consists primarily of conifer cones and fungi stored during the previous late summer and fall. Consequently, *T. douglasii* maintain individual territories year round with a central food cache (Smith 1981). *T. douglasii* has two potential breeding seasons (ca. March and June), but one litter per year is most common (Koford 1982). The number of litters and population size fluctuate in accordance with the periodicity of local cone crops (Smith 1968, 1970; Cowan and Guiguet 1973). *T. douglasii* appears to have a bimodal, diurnal, activity period with the greatest activity occurring in early morning and late evening. The timing of activity coincides with the coolest parts of the day (Smith 1968). *T. douglasii* are active all year, but reduce activity during periods of extreme weather. Nests are often in cavities of trees and are made of fine strands of cedar bark and moss. Outside nests are also constructed in the canopy of conifer trees, and burrows in the ground (Smith 1968; Maser et al. 1981).
CHAPTER 2: POPULATION DYNAMICS OF GLAUCOMYS SABRINUS AND TAMIASCIURUS DOUGLASII IN OLD-GROWTH AND SECOND-GROWTH STANDS OF COASTAL CONIFEROUS FOREST.

INTRODUCTION

Six hypotheses have been proposed to explain the general selection of old-growth stands by *S. occidentalis* (Forsman et al. 1984). Two of these hypotheses are based upon the abundance and availability of prey. *G. sabrinus* is the primary prey of *S. occidentalis* (Forsman et al. 1977, 1982, 1984; Carey 1993; Carey et al. 1992), thus explaining the numerous studies examining relative abundance of *G. sabrinus* in second-growth and old-growth stands. Comparisons of density for *G. sabrinus* in old-growth and second-growth forests have produced variable results. In some studies *G. sabrinus* were more abundant in old-growth forests (Volts 1986; Carey 1989, 1991; Carey et al. 1992, 1999; Witt 1992; Ransome and Sullivan 1997; see Appendix 1) than second-growth forests indicating that these latter forests were sub-optimal habitat (Volts 1986; Carey 1989; Witt 1992). Others have found no difference in abundance of *G. sabrinus* between old-growth and second-growth forests (Anthony et al. 1987; Aubry et al. 1991; Corn and Bury 1991; Gillbert and Allwine 1991; Rosenberg and Anthony 1992; Waters and Zabel 1995). Except for the last two studies, conclusions were based on density alone, which may not necessarily reflect habitat quality (Van Horne 1983). For example, second-growth and mature stands maintained similar densities of *Tamiasciurus hudsonicus* (red squirrel); however, the low proportion of females in breeding condition, low survival, and high recruitment in second-growth stands indicated that these stands were sub-optimal habitat for *T. hudsonicus* (Sullivan and Moses 1986). Ransome and Sullivan (1997) found that the mean weight of adult male *G. sabrinus* was less in old-growth than in second-growth stands, while recruitment, survival rates, and the proportion of females in breeding condition were not significantly different. However, the density of *G. sabrinus* was significantly higher in old-growth than second-growth stands. Other
studies reported similar densities, weight, distances moved, and recapture rates between old-growth and second-growth stands for *G. sabrinus* (Rosenberg and Anthony 1992; Waters and Zabel 1995). In most studies, *G. sabrinus* were trapped for 16 - 21 days in the fall for two years or less.

The occurrence and timing of breeding, and litter sizes of *T. douglasii*, varies in response to changes in production of conifer seeds (Smith 1968). Similarly, the abundance of *T. douglasii* varies among years in response to the abundance of conifer cones (Smith 1970; Buchanan et al. 1990). Since seed production in *P. menziesii* increased with size and age of trees, it has been suggested that old dominant trees and diverse genetic stock in naturally-regenerated late-seral forests provide a more-reliable minimum seed crops than even-aged, genetically uniform, second-growth stands (Sullivan and Sullivan 1982; Buchanan et al. 1990; Carey 1991). However, others have found no difference in abundance of *T. douglasii* among young, mature, and old-growth forests (Anthony et al. 1987; Carey 1989). Buchanan et al. (1990) reported marked variation in winter abundance of *T. douglasii*, but concluded that squirrels were, in general, more abundant in old forests than in young forests.

The primary objective of my study was to test the hypothesis that mature second-growth stands provided sub-optimal habitat for *G. sabrinus* and *T. douglasii*, relative to old-growth stands. My secondary objective was to expand our understanding of their ecology in these stands.

**MATERIALS AND METHODS**

**Study areas**

Study areas were located in the Capilano and Coquitlam watersheds, north of Vancouver and Coquitlam, respectively, in the south-coast of British Columbia, Canada (Figure 1). Elevation of the Coquitlam old-growth and mature second-growth stands (hereafter referred to as
second-growth) ranged from 280 to 540 m and 280 to 400 m, respectively. Elevation of the Capilano old-growth and second-growth stands ranged from 600 to 660 m and 280 to 300 m, respectively. All stands were located in the Coastal Western Hemlock dry maritime (CWHdm) biogeoclimatic subzone (Meidinger and Pojar 1991). Climate is characterized by cool mesothermal climate: cool summers and mild winters. Mean annual temperature is ca. 8°C and ranges from 5.2°C to 10.5°C. The mean temperature for the coldest month is 0.2°C (range: -6.6°C to 4.7°C). Annual precipitation is 2228 mm (range: 1000 to 4400 mm) with less than 15% occurring as snowfall (Meidinger and Pojar 1991).

Dominant coniferous species in old-growth stands were *T. heterophylla* and western red cedar (*Thuja plicata*). Each old-growth stand was surrounded by > 1000 ha of similar-aged trees with a few recent (10- to 20-year-old) cut blocks (10 to 30 ha) throughout. Stands were previously unharvested with ages ranging from 100 to 850 years old resulting from uneven-aged gap recruitment characteristic of old-growth forests (Daniels et al. 1995). Diameters at breast height ranged from 10.0 cm to 165.0 cm with a mean diameter (± SE) of 47.3 ± 3.6 cm and 49.0 ± 2.8 cm for Coquitlam and Capilano old-growth stands, respectively. Density (± SE) of dominant conifers was 265.8 (± 23.5) and 257.9 (± 27) trees/ha in Coquitlam and Capilano old-growth stands, respectively (Table 1). Dominant vegetation included Oregon beaked moss (*Kindbergia oregana*), step moss (*Hylocomium splendens*), cotton moss (*Plagiothecium undulatum*), red huckleberry (*Vaccinium parvifolium*), sword fern (*Polystichum munitum*), and salal (*Gaultheria shallon*).

Dominant coniferous species in second-growth stands were *T. heterophylla* and *T. plicata* with varying amounts of *P. menziesii* and *A. amabilis*. Stands were composed of even-aged trees (60 to 70 years old) that regenerated after clear-cut logging in the period 1920 – 1930, intensively burned and naturally regenerated. Few old-growth legacies (live and dead) remained. Second-
growth stands were surrounded by > 600 ha of similar-aged trees. Diameters at breast height ranged from 10.0 cm to 96.5 cm with a mean diameter (± SE) of 36.1 ± 1.2 cm and 30.7 ± 0.6 cm for Coquitlam and Capilano second-growth stands, respectively. Density (± SE) of dominant conifers was 476 (± 43.5) and 776.3 (± 59.9) trees/ha in Coquitlam and Capilano second-growth stands, respectively. Dominant understory vegetation was similar to the old-growth stands.

Figure 1. Location of old-growth (■) and second-growth (●) stands in the Capilano and Coquitlam watersheds.
Table 1. Density (± SE, trees/ha) of four main tree species in the Capilano (Cap) and Coquitlam (Coq) old-growth (OG) and second-growth (SG) stands.

<table>
<thead>
<tr>
<th>Grid</th>
<th>T. heterophylla</th>
<th>T. plicata</th>
<th>P. menziesii</th>
<th>A. amabilis</th>
<th>Total¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cap OG</td>
<td>148 (19.4)</td>
<td>66 (14.1)</td>
<td>0 (0)</td>
<td>47 (14.3)</td>
<td>261 (26.8)</td>
</tr>
<tr>
<td>Coq OG</td>
<td>150 (25.4)</td>
<td>93 (21.8)</td>
<td>15 (6.4)</td>
<td>0</td>
<td>258 (23.9)</td>
</tr>
<tr>
<td>Cap SG</td>
<td>445 (58.7)</td>
<td>185 (39.3)</td>
<td>20 (9.2)</td>
<td>130 (37.4)</td>
<td>780 (59.9)</td>
</tr>
<tr>
<td>Coq SG</td>
<td>130 (21.9)</td>
<td>238 (31.2)</td>
<td>85 (25)</td>
<td>8 (4.1)</td>
<td>461 (44.2)</td>
</tr>
</tbody>
</table>

¹Includes all species encountered in twenty 200-m² plots/grid with plots systematically located (every 50 m) along transects 100 m apart.

Live-trapping and population dynamics

Stands contained a 13-ha live-trapping grid consisting of 80 (8 by 10) stations located at 40-m intervals. Tomahawk live-traps (Model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) equipped with a nest box (1-liter plastic jar with coarse brown cotton) and a trap cover (rolled roofing cut and bent to offer protection from wind and rain on 3 sides) were mounted ca. 1.5 m above ground on a tree trunk at each trap station. Squirrels were live-trapped every 5 to 6 weeks during fall, winter, and spring from August 1995 to March 1999. Trapping was not conducted from fall 1996 to spring 1997 due to excessive snow in the Capilano old-growth stand. Traps were set one hour before dark on day 1 and checked on the morning of day 2 and then closed. Traps were reset before dark on day 2 and checked again on the morning of day 3, and then locked open until the next trap session. From August to December 1995, traps were
set for three nights. However, few additional squirrels were captured on the third night. Consequently, a two-night trap session was adapted for the remainder of the study. Sunflower seeds (*Helianthus annuus*) were placed in the nest box when traps were locked open to function as a prebait for the next session. Traps were baited with a mixture of peanut butter and whole oats when traps were set.

Squirrels were identified with individually numbered ear tags. For each capture, ear tag number, location, weight, gender, and breeding condition were recorded. Breeding condition of females was evaluated by palpation of the mammary glands and classified as 'non-breeding' (small mammary glands) or 'breeding' (large mammary glands). Breeding condition of males was evaluated by palpating the testes and classified as either 'non-breeding' (testes abdominal) or 'breeding' (testes scrotal; Krebs et al. 1969; McCravy and Rose 1992).

Trappability, movement, population size, percentage of squirrels in breeding condition, weight, recruitment, survival, and duration that individuals remained on the grid were estimated. Comparisons of these parameters between old-growth and second-growth stands were used to evaluate habitat quality for *G. sabrinus* and *T. douglasii*. To examine seasonal variation in some parameters, trap sessions were grouped into three periods: winter (September – February), spring (March – May), and summer (June – August). Trappability (Jolly 1965; Jolly and Dickson 1983; Krebs and Boonstra 1984) is the probability that an individual present in the population will be included in that particular sample (Efford 1992). Comparison of trappability among seasons was based on three replicates (Coq. OG, Coq. SG, and Cap. SG) due to poor accessibility of the Cap. OG during winter. Population size was estimated for each trap session using the Jolly-Seber model modified for small sample sizes (Seber 1982). The reliability of Jolly-Seber estimates decreases when few tagged animals are captured (Krebs et al. 1986). Therefore, the minimum number of animals know to be alive (MNA—Krebs 1966) was also calculated as a precautionary measure and to indicate the lower limits of the Jolly-Seber estimates. All statistical tests were
based on Jolly-Seber estimates for the reason indicated by Jolly and Dickson (1983). However, on occasion, the Jolly-Seber estimates appeared biologically unreasonable when the estimated population size doubled from one trap session to the next, then returned to the level of the previous trap session. For these estimates, if the trappability was less than 20%, they were replaced by MNA estimates. MNA estimates were also used for the first and last trap sessions. The Jolly-Seber model does not estimate population size for these sessions. Trapping sessions were grouped into five periods: 1) August 1995 – November 1995, 2) February 1996 – July 1996, 3) September 96 – July 1997, 4) September 97 – April 1998, and 5) September 1998 – April 1999. Movement was calculated as mean distance moved between points of first capture on consecutive trapping sessions. Population densities were calculated as mean estimated population size divided by effective trapping area (trapping grid + \( \frac{1}{2} \) mean distance moved). Recruits were classified as new squirrels captured at least twice. Distinguishing recruits from resident individuals during initial trap sessions is difficult. Therefore, recruitment was not calculated for the fall 1995 trap sessions. Individuals joining the population after this period were classified as recruits.

Jolly survival was calculated for each trap session \( i \) and can be defined as total number of marked animals in the population just before the \( i + 1 \) sample, divided by the total number of marked animals in the population immediately after sample \( i \) (Nichols and Pollock 1983). Weight at sexual maturity, coupled with the lowest weight attained by any known adult was used to determine age categories. \( T. \text{douglasii} \) and \( G. \text{sabrinus} \) weighing \(<165 \pm 5 \) g and \( 100 \pm 5 \) g, respectively, were never sexually mature and were classified as juveniles. No known adults weighed less than these values. Squirrels captured only during the breeding season were included in the calculation of percentage of individuals breeding. Comparisons of weight between stand types were based on mean weight of each resident adult male averaged for each year of the study. Comparisons of mean weight of adults among seasons were based upon an averaged weight for
each individual in each season (years combined). Duration represents the number of weeks that had elapsed from first to last capture for individuals captured at least twice.

Statistical analyses

Differences in population size and breeding between stand types were evaluated by a model I, split-plot (with time as the split) two-way analysis-of-variance (ANOVA, Sokal and Rohlf 1981). Density was averaged for each period (t = 5) while breeding was calculated for each year (t = 4). Differences in duration, weight, recruitment, and survival between stand types were evaluated by a model I, two-way ANOVA (Sokal and Rohlf 1981). Differences in mean trappability and weights of squirrels among seasons were evaluated by a model I, two-way ANOVA (Sokal and Rohlf 1981). A Bonferroni multiple comparison test was used to determine significant differences in parameters among seasons and time periods. Recruitment was square-root transformed, while trappability and survival rates were arcsine transformed before performing ANOVAs to better approximate a normal distribution. Differences were considered significant if $P \leq 0.05$ for all comparisons.

RESULTS

Trappability

Overall trappability of $G. \ sabrinus$ for the two replicates was 78.1 and 72.1% in old-growth stands and 68.3 and 79.2% in second-growth stands. Mean trappability varied significantly among seasons with trappability (± SE) in winter (87.1% ± 2.8) being greater than in spring (70.3% ± 3.7) and summer (63.9% ± 3.4; $F_{(2,4)} = 30.5$, $P = 0.004$). Trappability of $T. \ douglasii$ was 71.2 and 49.2% in old-growth stands, and 62.2 and 53.9% in second-growth stands. Mean trappability (± SE) in winter (77.5% ± 5.7), spring (69.5% ± 6.3), and summer was
significantly different (52.1% ± 4.1; \( F_{(2,4)} = 28.2, P = 0.004 \)) with \( T. \) douglasii being more trappable in winter than summer.

**Movement**

The mean distance moved (± SE) from first-capture points on consecutive trap sessions was not significantly different (\( F_{(1,3)} = 0.39, P = 0.57 \)) between male (99.1 ± 7.1 m) and female (69.2 ± 5.9 m) \( G. \) sabrinus. Mean distance moved (± SE) from first-capture points on consecutive trap sessions for \( G. \) sabrinus in old-growth (85.4 ± 5.9 m) was not significantly different from that in second-growth stands (81.3 ± 7.7 m; \( F_{(1,3)} = 0.001, P = 0.98 \)). A buffer strip of 40 m (½ mean distance moved) was added to trapping grids to estimate effective trapping area for each stand (ca. 15.8 ha). Mean distance moved (± SE) from first-capture points on consecutive trap sessions for female \( T. \) douglasii (65.6 ± 5.0 m) was not significantly different from males (66.5 ± 6.1 m) (\( F_{(1,3)} = 0.48, P = 0.53 \)). The mean distance moved between consecutive trap sessions for \( T. \) douglasii in old-growth stands (79.8 ± 7.2 m) was greater, but not significantly different, from that in second-growth stands (58.4 ± 4.5 m; \( F_{(1,3)} = 0.46, P = 0.54 \)). A buffer strip of 38 m and 29 m was added to old-growth and second-growth grids, respectively, to estimate effective trapping area for each stand (ca. 15.5 & 14.1 ha, respectively).

**Population density**

A total of 261 \( G. \) sabrinus were captured 1311 times. Old-growth and second-growth stands contained 151 and 110 individuals, respectively. The Jolly-Seber estimate for the Coquitlam second-growth stand for July 1996 (44) was replaced by MNA (20). Trappability for this stand at this time was 13%. Density (± SE) of \( G. \) sabrinus in old-growth (1.5 ± 1.8, range: 0.3 – 2.9 squirrels/ha) and second-growth stands (1.0 ± 1.4, range: 0.06 – 1.8 squirrels/ha) were
not significantly different ($F_{(1,1)} = 3.1, P = 0.33$; Figure 2) and there were no time by stand interactions ($F_{(4,7)} = 0.42, P = 0.79$).

A total of 383 $T. douglasii$ were captured 1248 times during the study. Old-growth and second-growth stands contained 141 and 242 $T. douglasii$, respectively. Densities of $T. douglasii$ in old-growth and second-growth stands were not significantly different ($F_{(1,1)} = 22.3, P = 0.13$; Figure 3). Mean density of $T. douglasii$ in second-growth stands (2.4 and 2.2 squirrels/ha) was 2-times larger than that in old-growth stands (1.0 and 1.0 squirrels/ha).

![Figure 2. Estimated population sizes (Jolly-Seber Model) of $G. sabrinus$ in old-growth and second-growth stands.](image)
Recruitment

There was no significant difference in mean recruitment for *G. sabrinus* between old-growth and second-growth stands ($F_{(1,1)} = 1.06, P = 0.49$). Mean (± SE) recruitment for *G. sabrinus* in old-growth and second-growth stands was $1.42 \pm 0.16$ and $1.29 \pm 0.17$ individuals per trap session, respectively. However, there was a significantly greater recruitment rate for *T. douglasii* in second-growth than old-growth stands ($F_{(1,1)} = 1405.9, P = 0.02$). Mean (± SE) recruitment for *T. douglasii* in old-growth and second-growth stands was $1.63 \pm 0.23$ and $2.19 \pm 0.30$ individuals per trap session, respectively.
Weight

Mean weights (± SE) of adult male *G. sabrinus* in old-growth stands (124.2 ± 1.3 g) and second-growth stands were not significantly different (123.5 ± 1.5 g; $F_{(1,1)} = 2.40, P = 0.37$). Individual mean weights (± SE: Figure 4) in winter (120.9 ± 1.1) and summer (118.7 ± 1.7) were significantly lighter than that in spring (129.8 ± 1.3; $F_{(2,3)} = 9.64, P = 0.04$). Mean weights (± SE) of adult male *T. douglasii* in old-growth (195.0 ± 2.18) and second-growth (195.2 ± 1.29 g) stands were not significantly different ($F_{(1,1)} = 0.03, P = 0.89$).

Survival rates

There were no significant differences in mean Jolly survival rates for *G. sabrinus* ($F_{(1,1)} = 1.16, P = 0.48$) or *T. douglasii* ($F_{(1,1)} = 0.71, P = 0.55$) between old-growth and second-growth stands. Mean survival rates (± SE) for *G. sabrinus* in old-growth and second-growth stands were 0.81 ± 0.04 and 0.80 ± 0.03, respectively, while survival rates for *T. douglasii* were 0.82 ± 0.04 and 0.81 ± 0.03, respectively.
Figure 4. Mean weight (± SE) of adult male *G. sabrinus* for three time periods: winter (W, closed circles), spring (SP, opened squares) and summer (S, closed triangles) in old-growth (OG) and second-growth (SG) stands in the Coquitlam (Coq.) and Capilano (Cap.) watersheds.

**Breeding**

The percentage (± SE) of female *G. sabrinus* that bred in old-growth stands (89.0 ± 3.3%) was not significantly different from that in second-growth stands (92.9 ± 7.1%). Females with large nipples were encountered throughout the winter: 13 in September, 24 in October, one in November, three in January and one in March. The percentage of male *G. sabrinus* that bred in old-growth (97.6 ± 1.6%) and second-growth stands (97.2 ± 2.8%) was not significantly different. The percentage of male *T. douglasii* that bred in old-growth stands (95.4 ± 2.4%) was not significantly different from that in second-growth stands (94.6 ± 4.0%).
Duration individuals remained on study grids

Mean duration (± SE) that individuals remained on the study grids for female *G. sabrinus* (51.1 ± 3.0 wk) was not significantly different from males (45.5 ± 2.8 wk; $F_{(1,3)} = 1.86, P = 0.27$). Mean duration (± SE) for *G. sabrinus* in old-growth stands (45.4 ± 3.0 wk) was not significantly different from that in second-growth stands (50.4 ± 2.9 wk; $F_{(1,3)} = 0.95, P = 0.40$). Numbers of *G. sabrinus* captured 100 weeks and 156 weeks after first capture were 26 and 8, respectively. Four individuals were captured 180 (3.5 years) weeks after first capture. Mean duration (± SE) on study grids for female *T. douglasii* (49.9 ± 3.8 wk) was not significantly different from males (47.2 ± 4.2 wk; $F_{(1,3)} = 0.02, P = 0.91$). The mean duration for *T. douglasii* in old-growth stands (43.7 ± 4.3 wk) was not significantly different from that in second-growth stands (51.3 ± 3.7 wk; $F_{(1,3)} = 1.05, P = 0.38$). Numbers of *T. douglasii* captured 100 weeks and 156 weeks after first capture were 28 and 6, respectively. Four individuals were captured 180 weeks after first capture.

**DISCUSSION**

*G. sabrinus*: old-growth versus second-growth stands

Habitat quality should be evaluated in terms of survival and reproduction characteristics, as well as density of the species occupying the habitat (Van Horne 1983). Most studies have only evaluated the quality of second-growth and old-growth forests for *G. sabrinus* using density, in absence of information on survival and reproduction. Furthermore, most studies examined populations of *G. sabrinus* in one or two seasons for two years or less. I examined the population dynamics of *G. sabrinus* in mature second-growth and old-growth stands for 4 years, and I evaluated habitat quality for *G. sabrinus* using survival, reproduction, and density. However, my study sites did not represent a random sample from a larger population of second-growth and old-
growth stands. Consequently, my results were limited to differences between the stand types examined rather than to differences between stand types in general. Furthermore, as I only examined two stands from each stand type, the power to detect significant difference, if present, between stand types was quite low, a common limitation for large-scale studies.

Overall, I failed to detect significant differences in movement, density, recruitment, weight, survival rates, percentage of the population breeding, and the duration that individuals remained on grids between old-growth and second-growth stands. Therefore, the hypothesis that mature second-growth stands provided sub-optimal habitat for *G. sabrinus*, relative to old-growth stands was not supported by my study. This hypothesis is also not supported by other studies. Previous studies have found no difference in densities, body weight, and movement of *G. sabrinus* between old-growth and second-growth stands (Rosenberg and Anthony 1992; Waters and Zabel 1995; Martin and Anthony 1999; Appendix 1). Carey (1995) reported that *G. sabrinus* populations in young forests with old-growth legacies and understory development might equal those in old growth. Second-growth stands lacking old-growth legacies and understory development had fewer squirrels. In addition, he found that the oldest old-growth stand in his study had a very low abundance of *G. sabrinus*, while two younger stands (57 and 100 years old) had the highest habitat rank for *G. sabrinus*. Overall, he reported higher densities in old-growth than second-growth stands (with the 100-year-old stand classified as old growth). Sex ratios, percentage of females breeding, and adult weights were similar between old-growth and second-growth stands. Finally, the abundance and weight of young *G. sabrinus* were lower in old-growth than in second-growth stands (Carey 1995).

In contrast, a number of studies have reported the opposite trend (Volts 1986; Carey et al. 1992, 1999; Witt 1992). Volts (1986) reported higher population sizes of *G. sabrinus* in old-growth (23.7 and 11.7 individuals) than in a second-growth (8.1 individuals) stand. Carey et al. (1992) reported significantly higher densities of *G. sabrinus* in old-growth (1.9 squirrels/ha) than
in second-growth stands (0.9 squirrels/ha) in Oregon; and 0.5 and 0.2 squirrels/ha in old-growth and second-growth stands, respectively, in the Olympic Peninsula. However, the results and methods used by Carey et al. (1992) might not support their conclusions (Rosenberg et al. 1994; see Carey 1994 for a reply). Witt (1992) found a mean density of 0.12 and 0.85 squirrels/ha in second-growth and old-growth stands, respectively. However, population sizes in old-growth stands were estimated by the program CAPTURE, (based upon probabilistic models; Otis et al. 1978). Density estimates for *G. sabrinus* in second-growth stands were based upon number of individuals captured (enumeration). Since enumeration methods count individuals trapped, while probabilistic models estimate both trapped and untrapped segments of the population, enumeration methods are negatively biased and under-estimate true population size (Hilborn et al. 1976; Jolly and Dickson 1983; Nichols and Pollock 1983). Consequently, Witt’s (1992) comparisons between old-growth and second-growth stands are unreliable since different methods to estimate population size were used in different stand types. Finally, Carey et al. (1999) reported that densities in old-growth (2.1 squirrels/ha) and mature stands (2.3 squirrels/ha) were significantly higher than that in young stands (1.4 squirrels/ha). However, the methods they used may be biased, favouring higher density estimates in old-growth than second-growth stands (Appendix 2).

To accurately assess habitat quality for *G. sabrinus* one must have information on survival and reproduction, in addition to abundance (Van Horne 1983). If survival rates and percentage of the population breeding are similar between stand types, then quality of habitat can be based upon density. In my study, I failed to detect significant differences between stand types for all population parameters measured, including density. However, the relative abundance of *G. sabrinus* between stand types was not consistent (Figure 2). Abundance of *G. sabrinus* in the Capilano second-growth stand was always lower than that in the old-growth stand. But the abundance of *G. sabrinus* in the Coquitlam second-growth stand was often higher than that in the
Coquitlam old-growth stand. Other studies have reported the same variability in densities of *G. sabrinus* within similar stand types. Ransome and Sullivan (1997) reported that one old-growth stand had an abundance of *G. sabrinus* three-fold larger than the other. Similarly, Volts (1986) captured twice as many *G. sabrinus* in one old-growth stand (22 individuals) than the other (9 individuals), while 8 and 4 individuals were captured in second-growth stands. Carey et al. (1999) reported a three-fold difference in the range of maximum densities for old-growth (1.1 – 3.6/ha), niche diversification (1.0 – 3.7), and competitive exclusion (0.7 – 2.0/ha) stages.

Rosenberg and Anthony (1992) reported similar densities of *G. sabrinus* between second-growth and old-growth stands, but the range of densities was larger in old-growth (1.4 – 3.3 squirrels/ha) than second-growth (1.7 – 2.5 squirrels/ha) stands. Similarly, Waters and Zabel (1995) found that density estimates for *G. sabrinus* were most variable in old-growth stands in northeastern California, but did not differ between old (3.3 squirrels/ha) and young (2.3 squirrels/ha) stands.

Finally, the relative abundance of *G. sabrinus* varied among stands in different years (Rosenberg and Anthony 1992; this study) and within stands in different years (Carey 1995; this study, Figure 2). Given the number of studies that have found no difference in abundance of *G. sabrinus* between old-growth and second-growth forests and the large disparity in their abundance within stand types and within the same stand in different years, it can be concluded that *G. sabrinus* are not consistently more abundant in old-growth than second-growth stands. The primary conclusion that can be drawn is that the quality of habitat provided by old-growth stands, on occasion, is slightly better than that in second-growth stands.

*S. occidentalis* often use old-growth forests in greater proportion than its abundance, which suggests that spotted owls prefer old-growth forests (Allen and Brewer 1985; Carey et al. 1990, 1992; Forsman et al. 1984; Gutierrez et al. 1984; Hunter et al. 1995; Lehmkuhl and Raphael 1993; Miller et al. 1992; Meyer et al. 1998; Swindle et al. 1999). The decline of the spotted owl in the Pacific Northwest has been attributed to declines in old-growth forests
Forsman et al. 1977, 1984; Franklin et al. 1990). Examining the studies conducted to date, the relative abundance of *G. sabrinus* in second-growth and old-growth stands cannot explain the selection of old-growth stands by *S. occidentalis*. Second-growth stands can, and often do, support large populations of *G. sabrinus*. However, this conclusion is based upon relative abundance of *G. sabrinus* between old-growth and second-growth stands (prey abundance hypothesis). In general, densities of trees are higher in second-growth than old-growth stands. Reduced tree densities in older stands may enhance capture rates of *G. sabrinus* by *S. occidentalis*. Consequently, prey may be more available to owls in old-growth than second-growth stands (prey availability hypothesis). Therefore, silvicultural practices that reduce tree densities in second-growth stands may enhance availability of *G. sabrinus* to *S. occidentalis* (Meyer et al. 1998).

**G. sabrinus**: population dynamics

I found that the mean distance moved within old-growth and second-growth stands was not significantly different (85.4 and 81.3 m, respectively). Others have reported similar results: Rosenberg and Anthony (1992; 77.8 and 92.4 m), Waters and Zabel (1995), Ransome and Sullivan (1997; 93.2 m), and Martin and Anthony (1999; 63.5 and 76.1 m). Carey et al. (1991) reported that *G. sabrinus* moved greater distances in second-growth (112 m) than in old-growth stands (93 m), as did Carey (1995): second-growth stands (102 m) and old-growth stands (87 m). *G. sabrinus* routinely change den sites (Mowrey and Zasada 1984; Witt 1992; Carey et al. 1997; Cotton and Parker 2000). On average, squirrels used two dens/month with den sites for males and females being 211 and 108 m apart, respectively (Carey et al. 1997). Mean movement in my study represented distances traveled between points of first captures in consecutive trap sessions (5 to 8 weeks apart). Movement in other studies represented distances traveled between consecutive trap nights. Therefore, I expected the mean distance moved in my study to be much
greater than that reported by others, since my data would also incorporate changes in den sites. However, movement appeared to be quite similar across studies. Consequently, changes in den sites may not be accompanied by changes in foraging sites.

Mean movement, as determined from live-trapping, may only represent distances traveled during foraging on the ground (Witt 1992). The mean distances moved by *G. sabrinus* were less on food-supplemented grids (78.3 m) than in untreated second-growth (93.6 m) and old-growth (92.7 m) stands (Ransome and Sullivan 1997). The similarity in weight between male and female *G. sabrinus* (Witt 1991; Rosenberg and Anthony 1992) suggests that foraging areas of similar sizes are used by each sex. However, mean distance moved by male *G. sabrinus* was 43% greater than that for females in my study (although the difference was not significant). This suggests that movement by *G. sabrinus* estimated from live-trapping studies, although influenced by food availability, does not represent only distances traveled during foraging. Martin and Anthony (1999) found that home ranges for males were 51% larger than those for females; however, mean distances moved were not different. They suggested that parental care by females would generate small home ranges while larger home ranges for males would enhance their breeding opportunities. As I trapped during the male breeding season and female-nursing season, these same factors may explain the slight differences in mean movement I observed between male and female *G. sabrinus*.

Adult male *G. sabrinus* weighed more in spring than summer or winter (Figure 4). The same trend was seen in the interior of British Columbia (pers. obs.). The timing of this increase occurred after a period when food availability and quality was lowest (winter) and cost of thermoregulation highest (Stapp 1992). Witt (1991) found that mean weights in winter were heavier than those in spring and summer. *Glaucomys volans* (southern flying squirrel) were also heavier in winter than summer, but there were no seasonal differences in basal metabolic rate (Stapp 1992). Witt (1991) attributed the higher weight in winter than summer to greater
availability of food in fall and early winter than in summer. However, there was no response in weight to food supplementation (Ransome and Sullivan 1997). Various evolutionary explanations for these observations are discussed by Stapp (1992, 1994) and Holmes and Austad (1994).

The peak breeding season for *G. sabrinus* is March and April (Davis 1963; Cowan and Guiguet 1973). *G. sabrinus* were also observed breeding in late April to early-July, with a peak from late May to early June (Carey 1991). I found that male *G. sabrinus* were scrotal from the end of February to early June, two months earlier than that reported by Carey (1991). Females with large nipples were observed from August through to early October; however, I had few trapping session in the months of June and July. A number of females were observed in November, January, and March with large nipples, indicating winter breeding. Reproductively active females have also been reported in other studies from March to December (Cowan and Guiguet 1973; Raphael 1984; Witt 1991; Forsman et al. 1994). Breeding later in the fall and winter may represent second litters.

*T. douglasii: population dynamics*

Carey et al. (1991) found that recapture rates of *T. douglasii* were low, and hence they recommended alternative sampling methods than those used for *G. sabrinus*. The methods used in my study to capture *T. douglasii* were similar to those recommended for *G. sabrinus* by Carey et al. (1991) but with a few modifications. I set traps one hour before dark on day 1 and checked on the morning of day 2 and then closed them. Traps were reset before dark on day 2 and checked again on the morning of day 3. Most captures of *T. douglasii* occurred on the mornings of day 2 and 3. Consequently, the amount of time spent in the traps by *T. douglasii* was less than when traps are left open for 24 hrs (Carey et al. 1991). A similar method has been used successfully with *T. hudsonicus*, where traps are set in the morning of day 1 and checked and
closed 4 - 6 hours later (Sullivan and Moses 1986; Sullivan 1990; Klenner and Krebs 1991; Sullivan and Klenner 1993). Mean trappability in my study, across stands, was 59%. Only 9 of 383 (2.3%) individuals died during the four-year study. The trapping methodology used in my study was effective for studying *T. douglasii* and is recommended to others. However, individuals should remain in traps for no more than 4 – 5 hours at a time to minimize mortality due to stress.

I failed to detect a significant difference in the abundance of *T. douglasii* between old-growth and second-growth stands, except during a large increase in their abundance in second-growths stands in 1996 and 1997 (Figure 3). Their abundance returned to levels found in old-growth stands in 1998 and 1999. Marked variations in the abundance of *T. douglasii* have been reported, but, in general, young and mature stands appeared to have fewer squirrels than in old-growth stands (Carey 1989, Table 7; Buchanan et al. 1990). However, similar abundance of *T. douglasii* in second-growth and old-growth stands has also been reported by Anthony et al. (1987) and Carey (1989, 1995). Population densities of *T. douglasii* fluctuate dramatically in response to seasonal or annual variations in food supply (Buchanan et al. 1990; Smith 1970; Sullivan and Sullivan 1982). Western hemlock cone production follows a 3- to 4-year cycle with some cones being produced every year (Fowells 1965). Cone production in Douglas-fir trees follows a 2- to 7-year cycle (Allen and Owens 1972). Peak cone production occurred in the winter 1996/1997 in this study (R. Planden, British Columbia Ministry of Forests, pers. comm.). Buchanan et al. (1990) suggested that higher proportions of western hemlock trees, coupled with a greater cone production in old-growth stands than in second-growth stands, resulted in higher abundance of *T. douglasii* in old-growth stands. However, in my study, *T. douglasii* maintained higher numbers in second-growth than old-growth stands in some years. Second-growth stands had higher densities of western hemlock and Douglas fir than that found in old-growth stands (Table 1). *T. douglasii* maintain individual territories year round with a central food cache (Smith 1981). Territorial
behaviour determines spacing of individuals within a population, but densities are determined by food availability (Sullivan and Sullivan 1982). Consequently, peak cone crops in winter 1996/1997 provided an increase in habitable territories in second-growth stands, but only temporarily. After peak productions in cone crop, densities of *T. douglasii* returned to levels observed in old-growth stands. The hypothesis that mature second-growth stands provide sub-optimal habitat for *T. douglasii* was not supported by my study. In contrast, mature second-growth stands, in some years, provided better habitat than that found in old-growth stands.

In summary, the hypothesis that old-growth stands supply higher quality habitat than mature second-growth stands for *G. sabrinus* and *T. douglasii* was not supported by my study. Although, my results are dependent upon a nonrandom sample of stand types and small sample size (two stands of each type). However, the disparity in abundance of *G. sabrinus* within stand types and within the same stand in different years in my study and previous studies, precludes simply concluding that *G. sabrinus* are more abundant in old-growth than second-growth stands. The primary conclusion one can draw is that quality of habitat provided by old-growth stands is occasionally better than second-growth stands. However, second-growth stands can, and often do, support large populations of *G. sabrinus*. Therefore, the relative abundance of *G. sabrinus* in second-growth and old-growth stands, alone, cannot explain the selection of old-growth stands by spotted owls. I noted that changes in den sites by *G. sabrinus* might not be accompanied by changes in foraging sites. Mean distance move by male *G. sabrinus* was greater than that for females. Adult male *G. sabrinus* weighed more in spring than summer or winter. Breeding throughout the winter was observed for *G. sabrinus* and may represent second litters.
CHAPTER 3: POPULATION DYNAMICS OF *GLAUCOMYS SABRINUS* AND *TAMIASCIURUS DOUGLASII* IN COMMERCIAL-THINNED AND UNTHINNED STANDS OF COASTAL CONIFEROUS FOREST.

**INTRODUCTION**

The possibility of deliberately manipulating prey densities in *S. occidentalis* habitat to benefit owls through silvicultural prescription deserves consideration: specifically, can silviculture produce a more diverse prey base, more abundant prey populations, or reduce fluctuations in the abundance of major prey species (Thomas et al. 1990)? For example, thinning through enhanced tree diameters, crown structure, tree growth, understory development, and reduced density of trees (Hayes et al. 1997; Sullivan et al. 2001), can move second-growth stands out of the closed-canopy stage and accelerate the development of conditions found in late seral forests (McComb et al. 1993; Baily 1996; Carey and Curtis 1996; Carey et al. 1999; Carey 2000). Consequently, through silvicultural techniques, old-growth characteristics may be incorporated into young stands, thereby creating habitat for old-growth dependant species like *S. occidentalis* and many others. Furthermore, it has been suggested that reducing tree density (thinning) may improve prey availability to *S. occidentalis* (Carey and Peeler 1995).

Although *G. sabrinus* is the most important prey item of *S. occidentalis* in coastal British Columbia, the influence of reducing tree densities on their populations is unknown. I examined the influence of commercial thinning on populations of *G. sabrinus* and *T. douglasii* and tested the hypothesis that unthinned stands provided higher-quality habitat for these species than thinned stands.
MATERIALS AND METHODS

Study areas

Study areas were located in the Malcolm Knapp Research Forest (MKRF), Maple Ridge, British Columbia and Chehalis Lake, near Harrison Mills, B.C., Canada (Figure 5). Elevation of the Chehalis Lake thinned and unthinned stands ranged from 160 to 240 m and 260 to 360 m, respectively. Elevation of the MKRF thinned and unthinned stands ranged from 265 to 310 m and 400 to 425 m, respectively. All stands were located in the Coastal Western Hemlock dry maritime (CWHdm) biogeoclimatic subzone (Meidinger and Pojar 1991). The climate is characterized by cool mesothermal climate: cool summers and mild winters. Mean annual temperature is ca. 8°C and ranges from 5.2°C to 10.5°C. The mean temperature for the coldest month is 0.2°C (range: -6.6°C to 4.7°C). Annual precipitation is 2228 mm (range: 1000 to 4400 mm) with less than 15% occurring as snowfall (Meidinger and Pojar 1991). The dominant coniferous species were T. heterophylla and T. plicata with varying amounts of P. menziesii and A. amabilis.
The Chehalis Lake stands were composed of even-aged trees (60- to 70- years old) that had regenerated naturally after clear-cut logging in 1920-1930. Few standing old-growth legacies (live and dead) remained. Stands containing the unthinned and thinned sites were greater than 100 and 200 ha, respectively. Diameters at breast height (dbh) for the unthinned stand ranged from 11.3 to 98.2 cm with a mean diameter (± SE) of 35.2 ± 0.9 cm and a mean height of 32 ± 1.5 m. Density (± SE) of dominant conifer species was 647 (± 52) trees/ha. Diameters at breast height for the thinned stand (pre-treatment) ranged from 13.5 to 76.4 cm with a mean diameter (± SE) of 31.9 ± 0.6 cm and height of 37 ± 1.9 m. Pre-treatment density (± SE) of dominant conifer species was 718 (± 61). Diameter and density of the post-treatment stand was 36.8 cm and 352 trees/ha, respectively. Thinning was initiated in April 1996 using a 13.6-m tall swing yarder with a static skyline and a motorized carriage. Intermediate supports were used to minimize damage to
leave trees, organic layer, and existing coarse woody debris. Corridors were spaced approximately 45 to 55 m apart and were approximately 4.5 m wide. Leave trees were disease and pathologically free trees greater than 27-cm dbh and 30% live crown. Thinning was completed in October 1996 for a total thinned area of 53.1 ha. The treatment site suffered extensive blow-down in January 1999 and was salvage logged in the spring of 1999. Dominant vegetation included *K. oregana, H. splendens, P. undulatum, V. parvifolium, P. munitum*, and *G. shallon*.

The MKRF stands were composed of even-aged trees (60- to 70- years old) that regenerated after clear-cut logging in the period 1920-1930 and an intense fire in 1931 that burned greater than 4000 ha. Few old-growth legacies (live, dead, standing, and down) remained. Diameters at breast height for the unthinned stand ranged from 11.2 to 73.8 cm with a mean diameter (± SE) of 31.2 ± 1.0 cm. Density (± SE) of dominant conifer species was 775 ± 49.6 trees/ha. Diameters at breast height for the thinned stand ranged from 12.8 to 88.1 cm with a mean diameter (± SD) of 38.1 ± 1.9 cm. Pre-treatment density (± SE) of dominant conifer species was 670 ± 72.7 trees/ha. Density of the post-treatment stand was 320 ± 32.7 trees/ha. Thinning was initiated in November 1997 and completed by February 1998 with a total area thinned of 19.5 ha. A skidder was used to remove timber from 3.3 ha while 6.5 ha were not thinned as a result of individual-tree blow down in the recent past. The remaining area (9.7 ha) was harvested using a 13.6-m tall swing yarder with a static skyline and a motorized carriage. Intermediate supports were used to minimize damage to the leave trees, organic layer, and existing coarse woody debris. Mean corridor width was 4 m spaced every ca. 60 m. Dominant species of vegetation included *K. oregana, P. undulatum, P. munitum*, large leafy moss (*Rhizomnium glabrescens*), and *G. shallon*. 

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Live-trapping and population dynamics

Chehalis Lake stands contained a 13-ha live-trapping grid consisting of 80 (8 by 10) stations located at 40-m intervals. However, grid dimensions for the MKRF stands incorporated a 9-ha (6 X 16) grid with trap stations every 30 m and traps at every other station (48 traps). The smaller grid was required to accommodate a smaller thinning operation. Squirrels were live-trapped in the Chehalis stands every 5 to 6 weeks during the snow-free period from August 1995 to December 1998. Squirrels were trapped in MKRF from May 1997 to March 1999 with a final 7-day trap session in March 2000 using the procedures outlined in Chapter 2.

Trappability, movement, population size, percentage of squirrels in breeding condition, weight, recruitment, survival, and duration on the grid were estimated as outlined in Chapter 2, with some modifications. Comparisons of these parameters between treatments were used to determine if thinned stands were suboptimal habitat for *G. sabrinus* and *T. douglasii*. MNA estimates were used for the first and last trap sessions in Chehalis and first trap sessions in MKRF. Population sizes for the last trap session in MKRF were estimated using the M(h) (capture probabilities vary by individual) model of CAPTURE (Otis et al. 1978). Trapping sessions were grouped into three periods: pre-treatment (Chehalis: August 1995 – October 1996; MKRF: May 1997 – October 1997), post-treatment 1 (Chehalis: February 1997 – July 1997; MKRF: April 1998 – March 1999) and post-treatment 2 (Chehalis: November 1997 – December 1998; MKRF: March 2000). Movement was calculated as mean distance moved between points of first capture on consecutive trapping sessions for Chehalis. Movement in MKRF also included distance moved between points of capture on consecutive trap nights as few squirrels were captured. Post-treatment 2 for MKRF had only one trap session, thus, all new individuals captured during this session were classified as recruits.
Statistical analyses

The experimental design consisted of a randomized-complete block design with two blocks (replicates): Chehalis and MKRF. Differences in movement, population size, recruitment, weight, and survival between treatments were evaluated by a model I, split-plot (with time as the split; \( t = 3 \)) two-way analysis-of-variance (ANOVA; Sokal and Rohlf 1981). Parameters were grouped into three periods (pre-treatment, post-treatment 1, and post-treatment 2; \( t = 3 \)), except movement and survival, which combined post-treatment years (\( t = 2 \)). Differences in duration that individuals remained on live-trapping grids between treatments were evaluated by a model I, two-way ANOVA (Sokal and Rohlf 1981). Recruitment was square-root transformed, while survival rates were arcsine transformed before performing analysis of variance to better approximate a normal distribution. Differences were considered significant if \( P \leq 0.05 \) for all comparisons.

RESULTS

Trappability

Mean trappability (gender and years combined) of *G. sabrinus* was similar between the Chehalis thinned and unthinned stands during pre-treatment trapping (63.9% and 62.1%, respectively; Table 2). Trappability was slightly less (7 - 10%) in the thinned than unthinned stand during post-treatment trapping. Trappability of *G. sabrinus* was 40 to 50% lower in the MKRF thinned than unthinned stand during pretreatment and post-treatment trapping. Trappability of *T. douglasii* was similar in the Chehalis thinned and unthinned stands during pre-treatment trapping (38.7% and 41.1%, respectively). Their trappability was similar in the thinned (74.6%) and unthinned (71.0%) stands in the first post-treatment year, but less in the thinned stand (62.9% and 78.1%, respectively) in the second post-treatment year. Trappability of *T.*
douglasii was much lower on the MKRF thinned site than unthinned site during pre-treatment and post-treatment trapping (Table 2).

Table 2. Mean trappability for *G. sabrinus* and *T. douglasii* in thinned and unthinned stands for Chehalis and the Malcolm Knapp Research Forest (MKRF).

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Chehalis</th>
<th></th>
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<th>MKRF</th>
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<tbody>
<tr>
<td></td>
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<td>Thinned</td>
<td>Unthinned</td>
<td>Thinned</td>
<td>Unthinned</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>63.9%</td>
<td>62.1%</td>
<td>33.3%</td>
<td>68.1%</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Post-treatment 1</td>
<td>39.2%</td>
<td>49.3%</td>
<td>50.0%</td>
<td>93.8%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>72.5%</td>
<td>79.6%</td>
<td>-‡</td>
<td>17.9%†</td>
<td></td>
<td></td>
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<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>38.7%</td>
<td>41.1%</td>
<td>33.3%</td>
<td>52.7%</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>74.6%</td>
<td>71.0%</td>
<td>39.4%</td>
<td>75.8%</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Post-treatment 2</td>
<td>62.9%</td>
<td>78.1%</td>
<td>22.5%†</td>
<td>25.0%†</td>
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</tbody>
</table>

† Probability of capture estimated from CAPTURE
‡ Too few animals captured to estimate probability of capture

**Movement**

There were no significant differences in movement (Table 3) between thinned and unthinned sites (*F* (1,4) = 7.6, *P* = 0.22), nor was there a time by treatment interaction (*F* (1,2) = 4.2, *P* = 0.18) for *G. sabrinus* or *T. douglasii* (*F* (1,4) = 0.80, *P* = 0.54) and (*F* (1,2) = 1.62, *P* = 0.33), respectively. A buffer strip of one half the mean distance moved (Chehalis: 52 m, MKRF: 36 m) was added to live-trapping grids to estimate effective trapping area (Chehalis: 17.8 ha, MKRF: 11.6 ha) for *G. sabrinus*. Similarly, a buffer strip of half the mean distance moved (Chehalis: 40 m, MKRF: 37 m) was added to live-trapping grids to estimate effective trapping area (Chehalis: 15.8 ha, MKRF: 11.7 ha) for *T. douglasii*. 
Table 3. Mean distance moved (± SE) between first capture points on consecutive trapping periods for *G. sabrinus* and *T. douglasii* in thinned and unthinned stands for Chehalis and the Malcolm Knapp Research Forest (MKRF).

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Chehalis</th>
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<th>MKRF</th>
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<td></td>
<td>Thinned</td>
<td>Unthinned</td>
<td>Thinned</td>
<td>Unthinned</td>
<td></td>
</tr>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>96.9 (± 13.4)</td>
<td>116.9 (± 19.2)</td>
<td>49.3 (± 19.7)</td>
<td>91.1 (± 18.8)</td>
<td></td>
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<tr>
<td></td>
<td>Post-treatment</td>
<td>82.9 (± 27.7)</td>
<td>97.6 (± 29.5)</td>
<td>42.4 (1)†</td>
<td>74.8 (± 17.9)</td>
<td></td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>67.0 (± 17.5)</td>
<td>60.0 (2)†</td>
<td>63.5 (± 13.6)</td>
<td>63.7 (± 6.6)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>60.0 (± 7.4)</td>
<td>112.1 (± 19.8)</td>
<td>81.6 (± 9.8)</td>
<td>78.9 (± 7.0)</td>
<td></td>
</tr>
</tbody>
</table>

† Sample size

Population density

A total of 129 *G. sabrinus* were captured 530 times. Seventy-seven *G. sabrinus* were captured in unthinned stands while 52 were captured in thinned stands. There were no significant differences in the overall population size between thinned and unthinned sites ($F_{(1, U)} = 33.6, P = 0.11$) nor was there a time by treatment interaction ($F_{(1, U)} = 0.01, P = 0.99$). Mean (± SE; Figure 6) population size for *G. sabrinus* during pre-treatment trapping in thinned and unthinned stands was $8.1 (± 1.9)$ and $12.4 (± 1.7)$, respectively. Mean population size in thinned and unthinned stands during the first post-treatment year was $7.8 ± 2.7$ and $12.9 ± 3.8$, respectively, and for the second post-treatment year, it was $8.6 ± 2.1$ and $12.5 ± 2.2$, respectively. Mean density on the Chehalis thinned and unthinned stands were 0.65 and 0.89 individuals/ha, respectively, while MKRF had 0.09 and 0.51 individuals/ha, respectively.

A total of 250 *T. douglasii* were captured 793 times during the study. There were no significant differences in population size between thinned and unthinned sites ($F_{(1, U)} = 11.0, P = ...
0.19) nor was there a time by treatment interaction ($F_{(2,9)} = 0.02$, $P = 0.98$). Mean (± SE; Figure 7) population size for *T. douglasii* during pre-treatment trapping in thinned and unthinned stands was 12.8 (± 3.0) and 7.5 (± 2.0), respectively. Mean population size in thinned and unthinned stands during the first post-treatment year was 22.5 ± 4.8 and 19.7 ± 4.5, respectively, and in the second post-treatment year, it was 16.3 ± 3.4 and 16.6 ± 2.8, respectively. Mean density in the Chehalis thinned and unthinned stands were 1.18 and 0.87 individuals/ha, respectively, while MKRF had 1.08 and 1.00 individuals/ha, respectively. A large but temporary increase in abundance of *G. sabrinus* and *T. douglasii* occurred after thinning was initiated on the Chehalis treatment site. Similarly, a large increase in the abundance of *T. douglasii* occurred in March 1997 in both the Chehalis thinned and unthinned stands.

![Figure 6](image.png)

Figure 6. Estimated population sizes of *G. sabrinus* in thinned and unthinned stands for Chehalis and Malcolm Knapp Research Forest (RF). Shaded bars represent timing of thinning.
Figure 7. Estimated population sizes of *T. douglasii* in thinned and unthinned stands for Chehalis and Malcolm Knapp Research Forest (RF). Shaded bars represent timing of thinning.

**Recruitment**

There was no significant difference in recruitment for *G. sabrinus* between thinned and unthinned stands (*F*<sub>1,6</sub> = 22.2, *P* = 0.13) nor was there a time by treatment interaction (*F*<sub>1,6</sub> = 0.08, *P* = 0.92). Mean (± SE) recruitment for *G. sabrinus* in thinned and unthinned stands was 0.61 (± 0.23; Table 4) and 1.2 (± 0.45) individuals/trap session, respectively. There was no significant difference in recruitment for *T. douglasii* between thinned and unthinned stands (*F*<sub>1,6</sub> = 1.05, *P* = 0.49) nor was there a time by treatment interaction (*F*<sub>1,6</sub> = 0.09, *P* = 0.91). Mean (± SE) recruitment for *T. douglasii* in thinned and unthinned stands was 3.1 ± 0.95 and 2.9 ± 0.81 individuals per trap session, respectively.
Table 4. Mean recruitment (individuals/trap session, ± SE) for *G. sabrinus* and *T. douglasii* on thinned and unthinned stands for Chehalis and the Malcolm Knapp Research Forest (MKRF).

<table>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Thinned</td>
<td>Unthinned</td>
</tr>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>0.2 (± 0.2)</td>
<td>0.7 (± 0.3)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>1.2 (± 0.6)</td>
<td>2.4 (± 1.5)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>0 (4)†</td>
<td>0.3 (± 0.3)</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>2.0 (± 1.0)</td>
<td>2.3 (± 0.9)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>5.2 (± 2.1)</td>
<td>5.6 (± 2.5)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>1.8 (± 0.85)</td>
<td>1.5 (± 0.5)</td>
</tr>
</tbody>
</table>

† sample size
‡ Number of new individuals captured.

**Weight**

Mean weight (± SE) of adult male *G. sabrinus* in thinned stands (126.7 ± 2.1 g; Table 5) was not significantly different from that in unthinned stands (128.5 ± 1.5 g; *F*<sub>1, 6</sub> = 6.20, *P* = 0.24) with no time by treatment interaction (*F*<sub>1, 4</sub> = 0.36, *P* = 0.72). Mean weight of adult male *T. douglasii* in thinned (199.1 ± 1.9) and unthinned stands (198.0 ± 1.6 g) stands was not significantly different (*F*<sub>1, 4</sub> = 0.002, *P* = 0.97), nor was there a time by treatment interaction (*F*<sub>1, 4</sub> = 0.32, *P* = 0.74).
Table 5. Mean weight (g; ± SE) of adult male G. sabrinus and T. douglasii in thinned and unthinned stands at Chehalis and the Malcolm Knapp Research Forest (MKRF).

<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Thinned</td>
<td>Unthinned</td>
</tr>
<tr>
<td>G. sabrinus</td>
<td>Pre-treatment</td>
<td>127.3 (± 2.7)</td>
<td>123.9 (± 2.0)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>118.6 (± 4.7)</td>
<td>126.4 (± 2.8)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>129.5 (± 4.0)</td>
<td>129.1 (± 3.5)</td>
</tr>
<tr>
<td>T. douglasii</td>
<td>Pre-treatment</td>
<td>199.5 (± 5.2)</td>
<td>209.7 (± 4.6)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>186.9 (± 2.1)</td>
<td>191.2 (± 2.8)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>198.8 (± 4.7)</td>
<td>197.6 (± 3.5)</td>
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</tbody>
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† Sample size

Survival rates

There were no significant differences in survival rates for G. sabrinus ($F_{(1,1)} = 11.7, P = 0.18$, Table 6) or T. douglasii ($F_{(1,1)} = 12.4, P = 0.18$) between thinned and unthinned stands, nor was there a time by treatment interaction ($F_{(1,2)} = 0.05, P = 0.84; F_{(1,2)} = 0.06, P = 0.82$, respectively). Mean survival rate (± SE) for G. sabrinus in thinned and unthinned stands was 0.75 ± 0.05 and 0.81 ± 0.05, respectively, while survival rates for T. douglasii were 0.76 ± 0.04 and 0.82 ± 0.04, respectively.
Table 6. Mean Jolly survival (± SE) of *G. sabrinus* and *T. douglasii* in thinned and unthinned stands at Chehalis and the Malcolm Knapp Research Forest (MKRF).

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<th>MKRF</th>
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<td></td>
<td>Thinned</td>
<td>Unthinned</td>
</tr>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>0.74 (± 0.07)</td>
<td>0.85 (± 0.05)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>0.81 (± 0.07)</td>
<td>0.77 (± 0.09)</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>0.84 (± 0.07)</td>
<td>0.89 (± 0.06)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>0.71 (± 0.08)</td>
<td>0.76 (± 0.06)</td>
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</table>

**Breeding**

In general, there were no differences in the percentage of male *G. sabrinus* and *T. douglasii* that bred in thinned and unthinned stands. In most years 100% of the males were in breeding condition (Table 7).

**Duration individuals remained on study grids**

Mean duration (weeks, ± SE) that individuals remained on trapping grids for *G. sabrinus* in thinned stands (46.8 ± 7.0 wk) was not significantly different from that in unthinned stands (48.4 ± 5.8 wk; $F_{(1, U)} = 0.60, P = 0.58$). Mean duration for *T. douglasii* in thinned stands (36.5 ± 3.6 wk) was similar to that in unthinned stands (46.2 ± 5.3 wk; $F_{(1, U)} = 15.9, P = 0.16$).
Table 7. Mean percentage (%) of adult male *G. sabrinus* and *T. douglasii* breeding in thinned and unthinned stands at Chehalis and Malcolm Knapp Research Forest (MKRF). Sample sizes in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
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<th>Chehalis Thinned</th>
<th>Chehalis Unthinned</th>
<th>MKRF Thinned</th>
<th>MKRF Unthinned</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>100% (11)</td>
<td>100% (12)</td>
<td>-</td>
<td>50% (6)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>100% (13)</td>
<td>100% (17)</td>
<td>-</td>
<td>100% (5)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>67% (3)</td>
<td>86% (7)</td>
<td>-</td>
<td>100% (3)</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>100% (12)</td>
<td>100% (8)</td>
<td>-</td>
<td>100% (2)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>100% (25)</td>
<td>100% (30)</td>
<td>100% (3)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>100% (5)</td>
<td>90% (10)</td>
<td>-</td>
<td>-</td>
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</tbody>
</table>

**DISCUSSION**

This is the second study to examine the influence of commercial thinning on *G. sabrinus* and *T. douglasii*. Carey (2000) conducted a retrospective analysis comparing post-treatment populations of *G. sabrinus* and *T. douglasii* between thinned and unthinned stands. My study was the first to examine the influence of commercial thinning coupled with intensive pre- and post-treatment live trapping using mark-recapture of *G. sabrinus* and *T. douglasii*. Consequently, the scope of this study is limited as the number of post-treatment years examined is few relative to the number of years the treatment stands will continue to change in response to thinning. However, the scope of this study allows me to examine the influence of reducing tree densities on *G. sabrinus* and *T. douglasii* in absence of large changes in stand structure, understory development, and microclimate. In addition, my study sites were not selected randomly. Treatment sites were
the only sites available and control sites were selected to minimize heterogeneity between treatment and control sites. Consequently, inferences from my study can only be made for the stand examined. Furthermore, I only examined the influence of thinning 60- to 70-year-old western hemlock stands on population dynamics of *G. sabrinus* and *T. douglasii*. Results might vary in stands of different ages, species composition, climate, or stand histories. Reliable inferences regarding the influence of thinning on population dynamics of *G. sabrinus* and *T. douglasii* can only be made after similar results have been obtained over a variety of stand conditions in different geographical areas.

Overall, I failed to detect significant differences in movement, density, recruitment, weight, survival rates, percentage of males breeding, and duration that individuals remained on the grids between thinned and unthinned stands for *G. sabrinus* and *T. douglasii*. In addition, there were no time by treatment effects. For *G. sabrinus*, abundance was slightly lower on thinned than unthinned sites prior to thinning, but the magnitude of this difference did not change after thinning. If thinning had a significant negative impact on population sizes of *G. sabrinus* and *T. douglasii*, a marked divergence in their abundance on thinned sites relative to unthinned sites after thinning would have been seen. However, their abundance on thinned sites, although slightly less, paralleled that on unthinned sites. Consequently, the lower overall abundance on thinned sites than unthinned sites may be best explained by initial site differences. In addition, survival and percentage of adult males breeding were not significantly different between thinned and unthinned stands. Therefore, the hypothesis that unthinned stands supplied higher quality habitat than thinned stands for *G. sabrinus* and *T. douglasii* was not supported by my study.

In contrast, Carey (2000) found that 70-year-old stands (unthinned) with live, dead, standing, and fallen legacies had a greater abundance of *G. sabrinus* (0.8 and 1.2 individuals captured/100 trap nights) than similar-aged stands lacking legacies and commercially thinned twice prior to their study (0.7 and 0.5 individuals captured/100 trap nights). Similarly, Waters
and Zabel (1995) reported the lowest density of *G. sabrinus* occurred in shelterwood stands (> 200 years old; 0.4 squirrels/ha), while those in old growth (3.3 squirrels/ha) and young (75 to 95 years old; 2.3 squirrel/ha) stands were similar. However, in their study, density of trees in shelterwood stands (60 trees/ha) was 17% the density of the thinned stands in my study (320 and 352 trees/ha). Density of trees on thinned sites in Carey (2000) was 60% that in my study. Consequently, retaining a greater density of trees following thinning in my study may have had a smaller impact on the abundance of *G. sabrinus* than that seen in these other studies.

Alternatively, unthinned sites in Carey (2000) varied significantly from thinned sites in legacy retention, shrub cover, and coarse woody debris. Unthinned sites had numerous residual large snags (3.5 trees/ha) and large live trees (2.7 trees/ha) while snags were removed from thinned sites and large legacy trees were few (< 1 tree/ha). Unthinned sites had 34% understory cover and 7.5% cover of fallen trees while thinned sites had 88% and 2.5%, respectively. Carey (2000) discussed other differences between sites with legacy retention and thinned sites and their potential influence on *G. sabrinus*. However, given the large difference in forest structure (legacies, snags, understory, and down wood) between legacy retention and thinned sites, it is difficult to determine whether the lower abundance of *G. sabrinus* on thinned sites in Carey (2000) can be attributed to differences in forest structure or stand density.

To determine the impact of habitat manipulation on the abundance of *G. sabrinus* we must first examine the link between habitat features and their population dynamics. Populations of *G. sabrinus* appear to be limited by food abundance (Waters and Zabel 1995; Ransome and Sullivan 1997; Chapter 4) but not by nest site availability (Waters and Zabel 1995; Colgan 1997, Chapter 4). Stomach and fecal analyses indicate that *G. sabrinus* primarily consumes hypogeous fungi during the snow-free period and lichens during the winter (McKeever 1960; Maser et al. 1978, 1985, 1986; Hall 1991; Colgan 1997). Consequently, the abundance of hypogeous fungi may be the limiting resource for *G. sabrinus* in areas where this food source dominates their diet. North
et al. (1997) found that in young managed stands, hypogeous fungi may be limiting as a food source for species that rely on them, especially in winter. Carey et al. (1999) reviewed the link between abundance and diversity of hypogeous fungi with coarse woody debris (CWD). Overall, they reported a strong connection between sporacarp abundance and CWD in Oregon. In addition, of all the habitat elements they measured, CWD proved to be the best predictor of the realized habitat space, activity, and carrying capacity of *G. sabrinus*. Consequently, the difference in the abundance of *G. sabrinus* between thinned and unthinned sites in Carey (2000) may be attributed to greater amounts of CWD on unthinned than thinned sites, as suggested by Carey (2000), and not a direct consequence of reduced densities of trees. The lack of a significant difference in abundance of *G. sabrinus* following thinning in my study may reflect the minimal changes to forest structure (CWD, soil disturbance, and understory vegetation) other than reduced densities of trees.

Colgan et al. (1999) examined the abundance of hypogeous fungi in thinned and unthinned stands. They noted that although the biomass of hypogeous fungi in thinned stands declined significantly compared to unthinned stands, diversity appeared to increase in their lightly thinned stands. They suggested that a greater abundance of truffles may have been available in thinned stands than unthinned stands during winter, a period of lowest overall abundance and when food is most limiting for species that rely on them (North et al. 1997). Furthermore, some of the most nutritious truffles were most abundant in thinned stands (Colgan et al. 1999). Waters et al. (1994) found no evidence that commercial thinning resulted in decreased total hypogeous fungi production 10 years and 17 years post-thinning. They found no difference in total relative frequency or total biomass in 70-year-old stands with 3 levels of thinning: heavy, moderate, and unthinned. Therefore, moderate reduction in tree densities may not result in significantly lower abundance of *G. sabrinus* if the original stand attributes are maintained. Furthermore, if these stand attributes are enhanced through stand management, as recommended by Carey (2000) and...
Carey et al. (1999), then abundance of *G. sabrinus* may be enhanced in second-growth stands, in the long term, with stand management.

Reducing densities of trees has the potential to enhance prey availability for avian predators. For example, bats preferred young, thinned stands, possibly because lower density of trees resulted in less cluttered flight paths (Humes 1996). Similarly, difficulties with negotiating densely-stocked young stands while in flight probably caused spotted owls to avoid locations containing relatively large amounts of young forest (Meyer et al. 1998). Finally, prey availability was more important than prey abundance in habitat selection by a forest raptor, goshawk (*Accipiter gentilis*; Beier and Drennan 1997). Although abundance is a component of availability, if prey were above a rather low threshold, goshawks selected foraging sites where structural characteristics favoured their foraging strategies. In my study, thinning appeared to have had minimal impact on abundance and dynamics of *G. sabrinus* in the short term, so their availability to *S. occidentalis* may be enhanced through reduced tree densities. However, my results represent the short-term influence of commercial thinning on populations of *G. sabrinus*. In addition, the low power associated with the small sample size (n=2) used in my study would make it difficult to detect significant differences between thinned and unthinned sites if differences existed. Ideally, conclusions should be based upon longer-termed studies with more replication than that presented here.

However, in a current study, we have examined the abundance of small mammals, including *G. sabrinus*, in 30-year-old lodgepole pine stands thinned to 3 densities (500, 1000, 2000 stems/ha), control (unthinned) and an old-growth stand (see Sullivan et al. 2001 for stand and treatment description). Thinning was conducted 12 years ago. In a randomized complete block design with three replicates (Prince George, Kamloops, and Penticton, British Columbia, Canada) mean (n = 3) densities of *G. sabrinus* (MNA/9 ha) in 500, 1000, 2000 stems/ha, unthinned, and old-growth stands were 0.22, 1.33, 2.33, 1.94, 1.50 individuals, respectively.
The abundance of *G. sabrinus* was higher in 30-year-old stands thinned to 2000 stems/ha than in unthinned and old-growth stands. Consequently, the results seen in my study may not change dramatically in the long term.

Overall, I failed to detect significant differences in movement, density, recruitment, weight, survival rates, percentage of males breeding, and duration that individuals remained on the grids between thinned and unthinned stands for *T. douglasii*. Unthinned sites with legacies and thinned sites without legacies maintained similar densities of *T. douglasii* (Carey 2000). Abundance of *T. douglasii* fluctuates in accordance with the abundance of food (Sullivan and Sullivan 1982; Buchanan 1990) and territorial behaviour may space individuals to density levels determined by the available food supply (Sullivan and Sullivan 1982). Trees removed during thinning were primarily suppressed and intermediate component of the stands. Consequently, removal of the suppressed and intermediate trees may not have significantly influenced the abundance of cones available to *T. douglasii*. Support for this conclusion is evident in winter 1996/1997 when populations of *T. douglasii* responded similarly to a peak in cone production in the Chehalis stands (Figure 7). Population sizes of *T. douglasii* in the Chehalis stands increased from 15 individuals to over 50 in both the thinned and unthinned stand six months after thinning was completed. Since territorial behaviour spaces individuals to density levels determined by the available food supply (Sullivan and Sullivan 1982), the abundance of food must have been similar between the thinned and unthinned stands.

These results may persist over the long term, as seen in Carey (2000), since thinning enhances diameter, branch size, and live-crown ratios of leave trees (Hayes et al. 1997; Sullivan et al. 2001). Open-grown Douglas-fir trees receiving sunlight from all directions produced 10-fold more seeds than trees in closed stands (Fowells 1965). Consequently, thinning may enhance stand structure of second-growth stands, promote cone production, and maintain large populations of *T. douglasii*. In fact, after a seven-night trap session, the estimated population size was three-
fold larger in the thinned stand (26 individuals) than unthinned (8 individuals) stand two years post-treatment in the MKRF. However, the Chehalis thinned stand suffered extensive blow-down in January 1999 and was salvage logged in the spring of 1999. Consequently, I could not determine whether this difference was a treatment effect or site effect.

Both *G. sabrinus* and *T. douglasii* showed a large, but temporary, increase on the Chehalis thinned stand after thinning was initiated. Thinning started on the north edge of the stand and progressed south to include the trapping grid (1-2 months later). I feel this increase was the result of individuals moving onto the grid, displaced by the disturbance north of the grid. However, once thinning was completed, population levels returned to pre-treatment levels. I did not trap during the commercial thinning operations in MKRF, consequently, a similar pattern was not documented in MKRF.

In summary, the hypothesis that unthinned stands supply higher quality habitat than thinned stands for *G. sabrinus* and *T. douglasii* was not supported by my study. The possibilities of deliberately manipulating prey densities in *S. occidentalis* habitat to benefit owls through silvicultural prescription deserves consideration (Thomas et al. 1990). As post-thinning densities of *G. sabrinus* and *T. douglasii* did not change significantly from pre-treatment densities, then reducing the density of trees may have enhanced their availability to avian predators like *S. occidentalis*. Although, caution must be emphasized in interpreting these results. My study is limited in scope as few post-treatment years were examined and the power to detect differences had they been present was low, a common situation with large-scale studies. However, my results indicate that commercial thinning deserves further evaluation and consideration as a potential silvicultural technique to manipulate prey densities.
CHAPTER 4: EFFECTS OF FOOD AND DEN-SITE SUPPLEMENTATION ON POPULATIONS OF GLAUCOMYS SABRINUS AND TAMIASCIURUS DOUGLASII

INTRODUCTION

Previous studies have suggested that *G. sabrinus* is limited by the availability of den sites (Volts 1986; Carey 1991, 1995; Carey et al. 1992, 1997). They also reported that the abundance of *G. sabrinus* is correlated with abundance of large snags (Volts 1986; Carey 1995), and abundance of large trees with decay and understory vegetation (Carey 1995). In contrast, other studies found no correlation between abundance of *G. sabrinus* and snags (Rosenberg and Anthony 1992; Waters and Zabel 1995), cavities (Waters and Zabel 1995), and other understory characteristics (Rosenberg and Anthony 1992; Waters and Zabel 1995). However, as the abundance of food increased, the abundance of *G. sabrinus* increased (Waters and Zabel 1995; North et al. 1997; Ransome and Sullivan 1997). It was often believed that *G. sabrinus* was an old-growth dependent species based on its requirement for cavities. However, until recently (Waters and Zabel 1995; Ransome and Sullivan 1997), no studies actually compared abundance of *G. sabrinus* with abundance of cavities or food. In addition, most studies were based upon correlation and not causation. Inferences about the relative importance of food and cavities as limiting factors for *G. sabrinus* should be based upon experimental testing where the abundance of food and den sites are manipulated (Carey 1995).

A number of studies have experimentally manipulated the availability of food in populations of small mammals and arboreal sciurids. In a review of food supplementation experiments with terrestrial vertebrates, Boutin (1990) generalized that on food-supplemented grids, home ranges were smaller, weights were heavier, litter size increased, population density increased 2- to 3-fold, growth rates were higher, and more energy was spent on territorial defense. Arboreal sciurids (*T. hudsonicus*, *T. douglasi*, and *G. sabrinus*) have responded positively to food supplementation experiments using sunflower seeds (Sullivan and Sullivan 1982; Sullivan 1990;
Klenner and Krebs 1991; Sullivan and Klenner 1993; Ransome and Sullivan 1997). Increased densities of 50 to 600% over unfed populations have been reported (Sullivan and Sullivan 1982; Sullivan 1990; Klenner and Krebs 1991; Sullivan and Klenner 1993; Ransome and Sullivan 1997), as well as longer breeding seasons, second litters, and smaller home ranges (Sullivan and Sullivan 1982; Klenner and Krebs 1991). These results are consistent with some of Boutin's (1990) conclusions, indicating that these species may be limited by food availability. However, supplemental feeding had little effect on survival and weight of adults (Klenner and Krebs 1991; Sullivan and Klenner 1993; Ransome and Sullivan 1997), survival and growth rates of juveniles (Sullivan and Sullivan 1982; Sullivan 1990; Klenner and Krebs 1991), or breeding (Sullivan 1990; Klenner and Krebs 1991; Sullivan and Klenner 1993; Ransome and Sullivan 1997). Food has often been supplemented during summer months. Since most arboreal sciurids consume a variety of food items during summer months, this may not represent the period when food is most limiting. North et al. (1997) concluded that hypogeous sporocarps may be limiting to mycophagists in managed stands, especially in winter. Supplying food during winter may be a more appropriate period to test food limitation in these species (Ransome and Sullivan 1997). No studies, to date, have simultaneously manipulated abundance of food and den sites for arboreal sciurids. Consequently, the relative importance of these resources in limiting their population size has not been evaluated.

To address resource limitation in *G. sabrinus* and *T. douglasii* experimentally, the abundances of food and den sites were manipulated. Comparison of population dynamics among manipulated sites was used to evaluate the relative importance of food and den sites in limiting population sizes of *G. sabrinus* and *T. douglasii*. I tested the hypothesis that populations of *G. sabrinus* and *T. douglasii* are primarily limited by abundance of food, not den sites.
MATERIALS AND METHODS

Study areas

Additional study areas were located in the Capilano watershed and Seymour Demonstration Forest (SDF; Figure 8), north of Vancouver, British Columbia, and the Malcolm Knapp Research Forest (MKRF), near Maple Ridge, British Columbia, Canada. Elevation of Capilano stands ranged from 280 to 450 m. Stands were composed of even-aged trees (60- to 70-years old) that regenerated after clear-cut logging in the period 1920 – 1930, intensively burned, and naturally regenerated. Few old-growth legacies (live and dead) remained. Stands were surrounded by > 1000 ha of similar-aged trees and separated by a minimum distance of one km.

Elevation of the SDF stands ranged from 200 to 300 m. Stands were composed of even-aged trees (60- to 70-years old) that regenerated after clear-cut logging in the period 1920 – 1930, burned, and naturally regenerated. Two intense bush fires occurred in 1910 and 1921 (Kahrer 1989). Few old-growth legacies (live and dead) remained. Stands were surrounded by > 1000 ha of similar aged trees and separated by a minimum distance of 800 m.

Elevation of the MKRF stands ranged from 265 to 400 m. Stands were composed of even-aged trees (60- to 70-years old) that regenerated after clear-cut logging in the period 1920 – 1930 and an intense fire in 1931 that burned > 4000 ha. Few old-growth legacies (live, dead, standing, and down) remained. A minimum distance of 800 m separated stands.
Figure 8. Location of controls (■) and grids supplemented with food (●), food and nest boxes (○), and nest boxes (♦) in three replicate study blocks: Capilano watershed, Seymour Demonstration Forest and Malcolm Knapp Research Forest.
All stands were located in the Coastal Western Hemlock dry maritime (CWHdm) biogeoclimatic subzone (Meidinger and Pojar 1991). Dominant coniferous species in all stands were *T. heterophylla* and *T. plicata* with varying amounts of *P. menziesii* and *A. amabilis*. Dominant vegetation included *K. oregana, H. splendens, P. undulatum, P. munitum*, and *G. shallon*.

**Live-trapping and population dynamics**

Stands contained a 13-ha live-trapping grid consisting of 80 (8 by 10) stations located at 40-m intervals. Squirrels were live-trapped every 5 to 6 weeks during the snow-free period from June 1996 to March 1999 using the procedures outlined in Chapter 2. However, trapping was not conducted during the summer 1998 due to disturbance by black bears (*Ursus americanus*).

Trappability, movement, population size, percentage of squirrels in breeding condition, weight, recruitment, survival, and duration that individuals remained on the grids were estimated as outlined in Chapter 2 with some modifications. Trapping sessions were grouped into three periods: pretreatment (May 1996 – May 1997), post-treatment 1 (June 1997 – March 1998) and post-treatment 2 (April 1998 – April 1999). All recruits were classified as new squirrels captured at least twice. Distinguishing recruits from resident individuals during initial trap sessions is difficult. Therefore, recruitment was not calculated for the fall 1996 trap sessions. Individuals joining the population after November 1996 were classified as recruits. However, post-treatment 2 for Capilano watershed had only one trap session due to inaccessibility of study sites from excessive snow, thus, new individuals captured during this period were classified as recruits. Percentage of females breeding was not calculated as too few post-treatment trap sessions occurred during their breeding season.
(spring) and trappability is lowest at this time (Chapter 2), especially on food-supplemented grids (Ransome and Sullivan 1997).

**Food and cavity supplementation**

Treatment areas were 30 ha and centered on live-trapping grids. Den-site supplementation consisted of 30 (5 by 6) stations located at 100-m intervals (1 nest box/ha). Nest box design follows that of Flyger (Figure 9a, from Carey and Gill 1983) with a few modifications. The entrance was placed adjacent to the tree trunk (Figure 9b) to reduce exposure of squirrels to predators while entering and exiting the nest box. Asphalt roofing was placed on top to enhance waterproofing.

![Figure 9](https://via.placeholder.com/150)

**Figure 9.** Diagram (A; from Carey and Gill 1983) and picture (B) of nest boxes used to enhance den-site availability for *G. sabrinus* and *T. douglasii*.

Since research sites were dominated by *T. heterophylla*, nest boxes were constructed from rough-cut *T. heterophylla* harvested from local stands. *G. sabrinus* constructed more nests in higher nest boxes (4.5 m above ground) than lower nest boxes (1.7 m) with no preference to aspect (Harestad 1990). Consequently, nest boxes were mounted ca. 5.5 m
above ground on the south side of a dominant conifer tree nearest the station in February and March 1997. Nest boxes were examined twice for evidence of occupancy (fall 1998, winter 1999). Nests were classified as covered nests (bed in a covered nest chamber; Figure 10) or beds (beds without a covering of nest materials) as described by Harestad (1990). However, nest boxes were not examined in the Capilano watershed in 1999 due to extensive snow. Nest boxes were examined a year later to determine nest type, occupant, and construction material only.

All nests found in 1999 were removed and examined for hair to determine the species that occupied the nest box. Hair samples were collected from three locations (entrance, edge of baffle, and center of nest) to ensure consistency in determination of occupant. Features used to distinguish *G. sabrinus* and *T. douglasii* hairs were thickness and colour (Figure 11).

Figure 10. Covered nests (A) and beds (B) found within nest boxes (photos by D. Blevins).
Figure 11. Photos showing distinguishing features of hair from (a) abdomen, (b) tail, and (c) back of *G. sabrinus* and *T. douglasii* (photos by D. Blevins).
Food supplementation consisted of 90 (9 by 10) stations per stand at 60-m intervals (3 feeders/ha). Feeders were constructed out of wood, lined and covered with plastic for waterproofing, and suspended ca. 7.5 m high between two trees ca. 5 – 10 m apart during the first 12 months of food supplementation. Feeders were suspended between trees to reduce disturbance by *U. americanus*. Feeders were also covered with wire mesh to improve accessibility for squirrels when suspended. Feeders were placed on the ground for the final 8 months of the study as food supplementation was only conducted during the winter while bears were in hibernation. Each feeder was filled with sunflower seeds (*Helianthus annuus*; ca. 7 kg) on a 5- to 6-week schedule, or when seed was depleted, from April 1997 to May 1998 (8 supplementations), and September 1998 to April 1999 (3 supplementations). Seed persisted in feeders longer during the latter half of the study, thus they required less seed. Overall, greater than 19,000 kg of sunflower seed was distributed during the study with an average of 315 kg/grid/supplementation. However, feeders in the Capilano Watershed were filled only once in post-treatment year two (November 1998) as sites were inaccessible due to snow.

**Statistical analyses**

The experimental design consisted of a randomized-complete block design with three replicates (with four treatments): Capilano watershed, SDF and MKRF. Differences in mean movement, population size, recruitment, weight, breeding, and survival between treatments were evaluated by a model I, split-plot (with time as the split) two-way analysis-of-variance (ANOVA; Sokal and Rohlf 1981). Movement, weight, and survival were grouped into two time periods: pre-treatment and post-treatment. Density and recruitment were grouped into three time periods: pre-treatment, post-treatment 1, and post-treatment 2.
Breeding was grouped into four time periods: 2 pretreatment and 2 post-treatment.

Differences in duration that individuals remained on the grids between stand types were evaluated by a model I, two-way ANOVA (Sokal and Rohlf 1981). Significant differences between group means were identified with a Bonferroni multiple comparisons test (Sokal and Rohlf 1981). When time by treatment interactions were significant, the analysis was broken down into time effects within treatments. A two-sample \( t \)-test (two-tailed; Sokal and Rohlf 1981) was used to identify significant difference between time periods within treatments. Recruitment was square-root transformed, while breeding and survival rates were arcsine transformed before performing ANOVAs to better approximate a normal distribution. Differences were considered significant if \( P \leq 0.05 \) for all comparisons unless otherwise stated.

**RESULTS**

**Trappability**

Mean (± SE; gender and years combined) trappability of *G. sabrinus*, averaged across blocks (n = 3), was significantly higher on controls (78.3% ± 3.7) than stands supplemented with food (60.5% ± 4.6), food and nest boxes (56.4% ± 3.6), and nest boxes (69.2% ± 2.8; \( F_{(3,6)} = 4.91, P = 0.047 \); Table 8). There was no time by treatment effect for trappability of *G. sabrinus* (\( F_{(3,6)} = 0.60, P = 0.63 \)). Overall trappability of *T. douglasii* was not significantly different among control sites (57.0% ± 4.2) and sites supplemented with food (52.8% ± 4.1), food and nest boxes (56.7% ± 3.1), and nest boxes (58.2% ± 4.2; \( F_{(3,6)} = 0.07, P = 0.97 \)) with no time by treatment effect (\( F_{(3,6)} = 0.44, P = 0.73 \)).
Table 8. Mean (% ± SE) trappability for *G. sabrinus* and *T. douglasii* on controls and in stands supplemented with food, food and nest boxes, and nest boxes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest boxes</th>
<th>Nest boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>74.1 ± 4.6%</td>
<td>58.2 ± 4.6%</td>
<td>69.0 ± 4.3%</td>
<td>81.4 ± 6.6%</td>
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<tr>
<td></td>
<td>Post-treatment</td>
<td>46.2 ± 6.6%</td>
<td>54.5 ± 5.7%</td>
<td>69.5 ± 3.7%</td>
<td>75.4 ± 3.8%</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>58.7 ± 5.3%</td>
<td>62.4 ± 5.2%</td>
<td>54.5 ± 6.4%</td>
<td>58.6 ± 7.2%</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>49.2 ± 5.4%</td>
<td>53.8 ± 3.3%</td>
<td>62.0 ± 2.5%</td>
<td>57.5 ± 4.5%</td>
</tr>
</tbody>
</table>

**Movement**

Mean distance moved from first-capture points (Table 9) on consecutive trap sessions were not significantly different among treatments for *G. sabrinus* ($F_{(3,6)} = 0.32, P = 0.81$) or between pre- and post-treatment periods ($F_{(1,6)} = 0.06, P = 0.81$), nor was there a time by treatment interaction ($F_{(3,6)} = 1.06, P = 0.43$). Mean distance moved for *T. douglasii* were not significantly different among treatments ($F_{(3,6)} = 1.11, P = 0.42$) or between pre- and post-treatment periods ($F_{(1,6)} = 0.21, P = 0.66$), nor was there a time by treatment interaction ($F_{(3,4)} = 1.09, P = 0.41$). A buffer strip of half the mean distance moved by *G. sabrinus* (45 m) and *T. douglasii* (30 m) was added to live-trapping grids to estimate effective trapping area; 16.7 and 14.3 ha, respectively.
Table 9. Mean (m ± SE) distance moved from first capture points on consecutive trapping periods for *G. sabrinus* and *T. douglasii* on controls and in stands supplemented with food, food and nest boxes, and nest boxes. Sample sizes in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest Boxes</th>
<th>Nest Boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>88.0 ± 10.1</td>
<td>103.3 ± 14.8</td>
<td>69.4 ± 7.3</td>
<td>84.5 ± 8.0</td>
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<td></td>
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<td></td>
<td>(38)</td>
<td>(23)</td>
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<td></td>
<td>Post-treatment</td>
<td>92.2 ± 15.7</td>
<td>114.0 ± 45.1</td>
<td>89.1 ± 8.5</td>
<td>86.2 ± 9.1</td>
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<td>(13)</td>
<td>(6)</td>
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<tr>
<td></td>
<td>Mean</td>
<td>89.1 ± 8.4</td>
<td>105.5 ± 14.6</td>
<td>82.1 ± 6.1</td>
<td>85.3 ± 6.0</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>66.2 ± 6.8</td>
<td>55.9 ± 6.0</td>
<td>50.4 ± 5.7</td>
<td>48.4 ± 6.9</td>
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<td>(40)</td>
<td>(73)</td>
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<td></td>
<td>Post-treatment</td>
<td>63.6 ± 7.0</td>
<td>59.8 ± 6.9</td>
<td>60.0 ± 5.2</td>
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<td>(33)</td>
<td>(28)</td>
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<tr>
<td></td>
<td>Mean</td>
<td>65.0 ± 4.9</td>
<td>57.0 ± 4.7</td>
<td>55.9 ± 3.9</td>
<td>54.9 ± 4.9</td>
</tr>
</tbody>
</table>

**Population density**

A total of 489 *G. sabrinus* were captured 2084 times during the study. Stands supplemented with food, food and nest boxes, nest boxes, and controls contained 140, 111, 115, and 123 *G. sabrinus*, respectively (Figure 12). Jolly-Seber estimates for the MKRF food-supplemented grid for June 1997 (44) and January 1998 (33) were replaced by MNA estimates for those trap sessions, 12 and 9, respectively. Trappability for these periods were 2% and 6%, respectively.
Figure 12. Estimated population size for *G. sabrinus* on controls and in stands supplemented with food, food + nest boxes, and nest boxes in three research blocks (A. Seymour Demonstration Forest; B. Malcolm Knapp Research Forest; C. Capilano Watershed). Arrows and shaded bars indicate time of nest box and food supplementation, respectively.
B. Malcolm Knapp Research Forest

C. Capilano Watershed
There were no significant difference in estimated population sizes for *G. sabrinus* among treatments ($F_{(16)} = 0.36, P = 0.78$). However, the mean population size ($\pm SE$) across all treatments in the second post-treatment year ($9.2 \pm 0.78$) was significantly lower than pre-treatment ($14.1 \pm 0.90$) and the first post-treatment year ($16.5 \pm 0.85; F_{(2,16)} = 10.9, P = 0.001$; Table 10). There was no time by treatment interaction ($F_{(2,16)} = 0.19, P = 0.98$).

Table 10. Mean ($\pm SE$) estimated population size for *G. sabrinus* and *T. douglasii* on controls and in stands supplemented with food, food and nest boxes, and nest boxes. Density per ha is in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest boxes</th>
<th>Nest boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>16.5 ± 1.6</td>
<td>13.3 ± 1.2</td>
<td>13.7 ± 2.0</td>
<td>12.3 ± 2.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.99)</td>
<td>(0.83)</td>
<td>(0.82)</td>
<td>(0.74)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>16.5 ± 1.8</td>
<td>15.8 ± 1.2</td>
<td>18.3 ± 1.6</td>
<td>15.6 ± 2.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.22)</td>
<td>(0.95)</td>
<td>(1.10)</td>
<td>(0.93)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>11.8 ± 2.1</td>
<td>9.0 ± 1.0</td>
<td>9.8 ± 1.3</td>
<td>7.7 ± 1.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.71)</td>
<td>(0.49)</td>
<td>(0.59)</td>
<td>(0.46)</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment</td>
<td>22.2 ± 3.4</td>
<td>27.5 ± 2.9</td>
<td>17.1 ± 2.8</td>
<td>12.5 ± 2.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.55)</td>
<td>(1.92)</td>
<td>(1.20)</td>
<td>(0.87)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>36.4 ± 7.1</td>
<td>35.3 ± 4.1</td>
<td>26.7 ± 2.4</td>
<td>31.4 ± 4.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2.55)</td>
<td>(2.47)</td>
<td>(1.87)</td>
<td>(2.20)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>14.2 ± 3.1</td>
<td>15.4 ± 3.4</td>
<td>15.1 ± 4.6</td>
<td>20.1 ± 3.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.99)</td>
<td>(1.08)</td>
<td>(1.06)</td>
<td>(1.41)</td>
</tr>
</tbody>
</table>
A total of 969 *T. douglasii* were captured 2982 times during the study. Stands supplemented with food, food and nest boxes, nest boxes, and controls, contained 234, 300, 214, and 221 *T. douglasii*, respectively (Figure 13). There were no significant differences in estimated population sizes for *T. douglasii* among treatments ($F_{(3,6)} = 0.48, P = 0.71$). However, there were significantly more *T. douglasii* in the first post-treatment year (32.6 ± 2.5) than pre-treatment (19.8 ± 1.6) and post-treatment year 2 (16.5 ± 1.6; $F_{(2,16)} = 6.5, P = 0.01$; Table 10). There was no time by treatment interaction ($F_{(2,16)} = 0.54, P = 0.77$).

Figure 13. Estimated population size for *T. douglasii* on controls and in stands supplemented with food, food + nest boxes, and nest boxes in three research blocks (A. Seymour Demonstration Forest; B. Malcolm Knapp Research Forest; C. Capilano Watershed). Arrows and shaded bars indicate time of nest box and food supplementation, respectively.
B. Malcolm Knapp Research Forest

C. Capilano Watershed
Recruitment

There were no significant differences in mean recruitment for *G. sabrinus* among treatments ($F_{(3,6)} = 0.21, P = 0.89$) nor was there a time by treatment interaction ($F_{(6,16)} = 0.70, P = 0.66$). Mean (± SE) recruitment on controls and stands supplemented with food, food and nest boxes and nest boxes, was 2.8 ± 0.46, 2.3 ± 0.33, 1.9 ± 0.41, and 2.6 ± 0.37 individuals/trap session, respectively. However mean recruitment (± SE) decreased significantly from pre-treatment (2.3 ± 0.3) to post-treatment year 1 (1.1 ± 0.2) and post-treatment year 2 (0.43 ± 0.1; $F_{(11,16)} = 10.3, P = 0.01$). There were no significant differences in mean recruitment for *T. douglasii* among treatments ($F_{(1,6)} = 1.54, P = 0.30$), nor was there a time by treatment interaction ($F_{(6,16)} = 1.15, P = 0.38$). Controls and stands supplemented with food, food and nest boxes and nest boxes, had a mean recruitment of 3.3 ± 0.6, 2.3 ± 0.4, 1.4 ± 0.3, and 2.7 ± 0.5 individuals/trap session, respectively. However mean recruitment (± SE) decreased significantly from pre-treatment (4.3 ± 0.5) to post-treatment year 1 (1.7 ± 0.3) and to post-treatment year 2 (1.32 ± 0.3; $F_{(11,16)} = 7.27, P = 0.06$).

Body weight

Mean weight (± SE) of adult male *G. sabrinus* among controls and sites supplemented with food, food and nest boxes, and nest boxes were not significantly different ($F_{(3,6)} = 1.37, P = 0.33$; Table 11). However, *G. sabrinus* weighed (± SE) more during post-treatment (130.3 ± 1.2) than pre-treatment trapping (119.0 ± 0.9; $F_{(1,8)} = 24.3, P = 0.001$). Mean weight (± SE) of adult male *T. douglasii* among controls and sites supplemented with food, food and nest boxes, and nest boxes were not significantly different ($F_{(3,6)} = 0.86, P =$
Table 11. Mean (g ± SE) weight for *G. sabrinus* and *T. douglasii* on controls and in stands supplemented with food, food + nest boxes, and nest boxes. Sample sizes in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest boxes</th>
<th>Nest boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>118.2 ± 1.59</td>
<td>118.3 ± 1.92</td>
<td>119.9 ± 1.90</td>
<td>120.2 ± 1.8</td>
</tr>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment</td>
<td>(60)</td>
<td>(45)</td>
<td>(39)</td>
<td>(43)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>130.7 ± 3.3</td>
<td>128.3 ± 1.8</td>
<td>133.7 ± 1.96</td>
<td>127.9 ± 2.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(38)</td>
<td>(45)</td>
<td>(48)</td>
<td>(35)</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>123.0 ± 1.71</td>
<td>123.3 ± 1.41</td>
<td>127.5 ± 1.56</td>
<td>123.6 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>Pre-treatment</td>
<td>193.1 ± 2.2</td>
<td>195.6 ± 2.2</td>
<td>190.7 ± 1.7</td>
<td>191.3 ± 1.4</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td></td>
<td>(93)</td>
<td>(85)</td>
<td>(75)</td>
<td>(71)</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>200.4 ± 1.6</td>
<td>200.4 ± 2.0</td>
<td>198.4 ± 2.0</td>
<td>207.2 ± 2.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(81)</td>
<td>(68)</td>
<td>(59)</td>
<td>(68)</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>196.5 ± 1.4</td>
<td>197.7 ± 1.5</td>
<td>194.1 ± 1.4</td>
<td>199.1 ± 1.5</td>
</tr>
</tbody>
</table>

Survival rates

There were no significant differences in mean Jolly survival rates (all years) among treatments for *G. sabrinus* ($F_{(3,6)} = 1.19$, $P = 0.39$) and *T. douglasii* ($F_{(3,6)} = 3.4$, $P = 0.09$). However, there was a time by treatment effect ($F_{(3,8)} = 6.55$, $P = 0.02$; Table 12) for *G. sabrinus*. Mean survival significantly ($\alpha = 0.10$) increased by 9% ($t_{(23)} = 10.31$, $P = 0.09$) and
remained unchanged \((t_{(2)} = 0.61, P = 0.52)\) from pre-treatment to post-treatment trapping on grids supplemented with food, and food + nest boxes, respectively. However, controls and grids supplemented with nest boxes had a significant decrease in survival by 12\% \((t_{(2)} = 22.2, P = 0.04)\) and 13\% \((t_{(2)} = 14.40, P = 0.06)\), respectively, from pre-treatment to post treatment trapping. There were no time by treatment interactions for \(T. douglasii\) \((F_{(3,8)} = 0.30, P = 0.83)\).

Table 12. Mean (± SE) survival for \(G. sabrinus\) and \(T. douglasii\) on controls and in stands supplemented with food, food + nest boxes, and nest boxes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest boxes</th>
<th>Nest boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>(G. sabrinus)</td>
<td>Pre-treatment</td>
<td>0.84 ± 0.03</td>
<td>0.89 ± 0.03</td>
<td>0.92 ± 0.03</td>
<td>0.92 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>0.93 ± 0.04</td>
<td>0.84 ± 0.03</td>
<td>0.80 ± 0.04</td>
<td>0.79 ± 0.04</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>0.88 ± 0.02</td>
<td>0.87 ± 0.02</td>
<td>0.87 ± 0.02</td>
<td>0.85 ± 0.03</td>
</tr>
<tr>
<td>(T. douglasii)</td>
<td>Pre-treatment</td>
<td>0.79 ± 0.05</td>
<td>0.77 ± 0.03</td>
<td>0.85 ± 0.03</td>
<td>0.86 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Post-treatment</td>
<td>0.72 ± 0.05</td>
<td>0.73 ± 0.05</td>
<td>0.77 ± 0.05</td>
<td>0.80 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>0.76 ± 0.04</td>
<td>0.75 ± 0.03</td>
<td>0.82 ± 0.03</td>
<td>0.83 ± 0.03</td>
</tr>
</tbody>
</table>

**Breeding**

Mean percentage (across years) of male \(G. sabrinus\) breeding were not significantly different among control sites (87.1\%), and sites supplemented with food (89.8\%), food + nest boxes (97.0\%), and nest boxes (87.0\%; \(F_{(3,6)} = 0.74, P = 0.57\); Table 13). However, a trend worth noting was that a higher percentage (mean of post-treatment 1 and 2) of males bred on grids supplemented with food (79.8\%) and food and nest boxes (93.4\%) than those on controls (71.1\%) and sites supplemented with nest boxes (71.6\%) during treatment. \(G.\)
*sabrinus* with large nipples were observed throughout the winter on all sites: 12 in
November, 13 in December/January, and 17 in February/March. Mean percentage (± SE) of
male *T. douglasii* in breeding condition was similar among control sites (95.6%), and sites
supplemented with food (89.0%), food + nest boxes (91.1%), and nest boxes (89.7%; \( F_{3,6} =
1.23, P = 0.38 \)). A few female *T. douglasii* with large nipples were observed throughout the
winter on all sites: two in November, one in December/January, and nine in February/March.

**Duration individuals remained on study grids**

Mean duration (± SE) on the study grids for female (56.2 ± 3.2 wk) and male (49.7 ± 2.8 wk) *G. sabrinus* was not significantly different (\( F_{1,4} = 3.0, P = 0.10 \)). Mean duration (±
SE) for *G. sabrinus* were not significantly different among control sites (53.9 ± 4.8 wk), and
sites supplemented with food (49.3 ± 3.7 wk), food + nest boxes (55.1 ± 4.4 wk), and nest
boxes (53.2 ± 4.1 wk; \( F_{3,14} = 0.73, P = 0.55 \)). Forty-seven *G. sabrinus* were captured 100
weeks after first capture while 10 were captured 130 weeks (2.5 years) after first capture.
Mean duration (± SE) on study grids for female *T. douglasii* (45.3 ± 2.3 wk) was not
significantly different from males (43.3 ± 2.3 wk; \( F_{1,14} = 0.14, P = 0.71 \)). Mean duration (±
SE) for *T. douglasii* were not significantly different among control sites (42.5 ± 3.0 wk), and
sites supplemented with food (45.5 ± 3.3 wk), food + nest boxes (44.3 ± 3.0 wk), and nest
boxes (50.0 ± 3.5 wk; \( F_{3,14} = 0.23, P = 0.87 \)). Fifty-two and 10 *T. douglasii* were still being
captured 100 weeks and 130 weeks (2.5 years), respectively, after first capture.
Table 13. Mean (n = 3) percentage (%) of adult male *G. sabrinus* and *T. douglasii* breeding on controls and in stands supplemented with food, food + nest boxes, and nest boxes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Period</th>
<th>Food</th>
<th>Food + Nest boxes</th>
<th>Nest boxes</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. sabrinus</em></td>
<td>Pre-treatment 1</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Pre-treatment 2</td>
<td>93.3</td>
<td>97.3</td>
<td>97.7</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>96.7</td>
<td>98.7</td>
<td>98.9</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>89.0</td>
<td>100.0</td>
<td>77.7</td>
<td>86.7</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>70.5</td>
<td>87.5</td>
<td>65.5</td>
<td>55.5</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>79.8</td>
<td>93.4</td>
<td>71.6</td>
<td>71.1</td>
</tr>
<tr>
<td><em>T. douglasii</em></td>
<td>Pre-treatment 1</td>
<td>88.0</td>
<td>91.7</td>
<td>93.0</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Pre-treatment 2</td>
<td>93.7</td>
<td>94.0</td>
<td>94.3</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>90.9</td>
<td>92.9</td>
<td>93.7</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 1</td>
<td>96.0</td>
<td>91.3</td>
<td>97.0</td>
<td>96.3</td>
</tr>
<tr>
<td></td>
<td>Post-treatment 2</td>
<td>73.0</td>
<td>85.5</td>
<td>68.5</td>
<td>83.5</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>84.5</td>
<td>88.4</td>
<td>82.8</td>
<td>89.9</td>
</tr>
</tbody>
</table>

**Occupancy of nest boxes**

Nest boxes were examined twice (fall 1998 and winter 1999) to determine occupancy rate of nest boxes (Table 14). Mean occupancy rates of nest boxes in stands supplemented with food and nest boxes in 1998 and 1999 (88.4 % and 75.0%, respectively) were 6- to 12-times higher than those in stands without food (7.0 % and 12.2%, respectively). *G. sabrinus* constructed 68.1% and 83.3% of the nests in stands supplemented with food and nest boxes.
and those with nest boxes only, respectively. Covered nests dominated (76.5%) nest boxes in stands supplemented with food while beds were found in most (68.3%) nest boxes in stands supplemented with nest boxes only. A few boxes were occupied at the time of checking by either *G. sabrinus* or *T. douglasii*.

**DISCUSSION**

My study is the first to simultaneously manipulate the abundance of food and den sites, coupled with intensive pre- and post-treatment live trapping using mark-recapture of *G. sabrinus* and *T. douglasii*. To determine whether populations of *G. sabrinus* and *T. douglasii* were limited by availability of food or den sites, I manipulated these resources for two years following a ten-month pretreatment period. Furthermore, I evaluated the influence of these manipulations on survival and reproduction, in addition to density, a minimum requirement to assess habitat quality (Van Horne 1983).

Overall, for *G. sabrinus*, there were no differences in movement, density, recruitment, weight of males, and duration that individuals remained on the grids among controls and in stands supplemented with food, food and nest boxes, and nest boxes. Survival of *G. sabrinus* decreased significantly from the pre- to post-treatment period in stands without food.
<table>
<thead>
<tr>
<th>Research Site</th>
<th>Treatment</th>
<th>% Occupied</th>
<th>Occupant</th>
<th>Nest Type</th>
<th>Construction Material</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1998</td>
<td>1999</td>
<td>G. sabrinus</td>
<td>T. douglasii</td>
</tr>
<tr>
<td>UBC Research Forest 2</td>
<td>Food + Nest Boxes</td>
<td>96.5%</td>
<td>92.8%</td>
<td>65.2%</td>
<td>30.4%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(29)</td>
<td>(29)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>UBC Research Forest 4</td>
<td>Nest Boxes</td>
<td>6.9%</td>
<td>13.3%</td>
<td>75.0%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(28)</td>
<td>(30)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SDF 1</td>
<td>Food + Nest Boxes</td>
<td>82.7%</td>
<td>57.1%</td>
<td>62.5%</td>
<td>37.5%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(29)</td>
<td>(14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>'SDF 4</td>
<td>Nest Boxes</td>
<td>6.6%</td>
<td>11.1%</td>
<td>75.0%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30)</td>
<td>(27)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capilano Watershed 1</td>
<td>Food + Nest Boxes</td>
<td>85.7%</td>
<td>89.5%</td>
<td>76.5%</td>
<td>17.6%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(28)</td>
<td>(19)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capilano Watershed 3</td>
<td>Nest Boxes</td>
<td>7.1%</td>
<td>38.4%</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(28)</td>
<td>(26)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>Food + Nest Boxes</td>
<td>88.4%</td>
<td>75.0%†</td>
<td>68.1%</td>
<td>28.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nest Boxes</td>
<td>7.0%</td>
<td>12.2%†</td>
<td>83.3%</td>
<td>0%</td>
</tr>
</tbody>
</table>

† Occupant, nest types, and construction material was estimated from 1999 data only. ‡ Mean from SDF and UBC Research Forest only. Values for Capilano Watershed provided for determining occupant and nest type. * Values are less than 30 as some nest boxes were disturbed by *U. americanus.*
However, survival increased significantly or remained unchanged in stands with food during the same period. Therefore, the hypothesis that populations of *G. sabrinus* are limited by availability of food was not supported by my live-trapping results. However, it was supported by the results obtained from examining the nests boxes.

The results from three independent blocks indicated that food supplementation had a significant effect on *G. sabrinus*. In 1998 and 1999, 88.4% and 75.0%, respectively, of nest boxes were occupied by squirrels in stands supplemented with food and nest boxes, while 7.0% and 12.2%, respectively, were occupied in stands supplemented with only nest boxes. In addition, most nest boxes on food supplemented grids contained covered nests, while those in stands without food supplementation contained beds. These results indicate that, overall, *G. sabrinus* readily used nest boxes but the availability of den sites did not limit their population size. The addition of nest boxes had no influence on populations of *G. sabrinus* in Washington (Colgan 1997) nor *G. volans* (Brady et al. 2000). *G. volans* readily used nest boxes but a 65% increase in den sites, during a nest-box supplementation study, failed to enhance their densities (Brady et al. 2000). *G. volans*, however, is more dependant upon cavities as den sites than *G. sabrinus* (Weigl 1978).

The lack of a response by *G. sabrinus* to nest-box supplementation was expected. For a resource to limit population size there must be a density-dependent relationship. For a density-dependent relationship to exist, as cavity availability declines, the rate of mortality must increase or rate of reproduction must decrease. Consequently, intraspecific competition exists among individuals for a finite abundance of den sites and the use by one individual restricts the use, thus, fitness of others.
However, *G. sabrinus* routinely den together (Maser et al. 1981; Mowrey and Zasada 1984; Carey et al. 1997; Feen 1997; Cotton and Parker 2000) and use multiple den sites (cavities and constructed nests) and on consecutive days (1 – 13 den sites - Carey 1991; Weigl and Osgood 1974; Carey et al. 1997; Feen 1997). Switching den sites on consecutive days implies unoccupied den sites are available; thus, use does not exceed availability. Harestad (1990) found that the availability of den sites exceeded use for *G. sabrinus* and *T. douglasii*. He reported that only 46 of 80 nest boxes were used after 4.5 years, 22 by *G. sabrinus* and 5 by *T. douglasii* (19 unknown). His study was conducted in the MKRF, one of the blocks used in my study. Consequently, the use of alternative nesting structures, coupled with communal denning and switching den sites on consecutive days, precludes the necessary requirement that the use of a cavity by one individual restricts its use by others. Finally, population sizes of *G. sabrinus* fluctuate significantly from one year to the next in the same stand (Carey 1995; Chapter 2). A resource that limits the abundance of *G. sabrinus* must also fluctuate in a similar manner. It is unlikely that cavity availability fluctuates significantly from one year to the next. Overall, the availability of den sites did not limit population sizes of *G. sabrinus* or *T. douglasii*.

My results indicate that *G. sabrinus* was limited by food abundance during my study. Grids with food supplementation had a significantly greater percentage of nest boxes used and survival increased or remained unchanged from the pre- to post-treatment period. However, survival of *G. sabrinus* decreased significantly from the pre- to post-treatment period on grids without food. The poor response of density to food supplementation was unexpected. Other studies with arboreal sciurids reported significant increases in population size in response to food supplementation: 5- to 10-fold increase for *T. douglasii* (Sullivan...
and Sullivan 1982); 2- to 4-fold increase for *T. hudsonicus* (Sullivan 1990; Klenner and Krebs 1991); and a 2-fold increase for *G. sabrinus* (Ransome and Sullivan 1997). The typical response to food supplementation for terrestrial vertebrates was a 3- to 4-fold increase in density (Boutin 1990). However, the high use of nest boxes on food-supplemented grids, relative to that in stands without food, indicated that *G. sabrinus* was positively influenced by food supplementation. I propose three explanations for this result.

Female *G. sabrinus* often seek cavities to raise young (Carey et al. 1995, 1997). Consequently, the greater use of nest boxes in stands supplemented with food, relative to nest-box supplemented sites, may indicate that a greater number of reproductive females occurred in stands supplemented with food than those without food. However, *G. sabrinus* are least trappable in spring (Chapter 2), especially on food-supplemented grids (Ransome and Sullivan 1997). Consequently, we could not estimate the percentage of females breeding. However, a significant increase in female reproduction on food-supplemented grids, over that in stands without food, would support the hypothesis that populations of *G. sabrinus* are limited by food abundance. Although the percentage of male *G. sabrinus* breeding was not significantly different among treatments, the slightly higher percentage of reproductive males on grids with food supplementation over those without, might be biologically important and may further indicate that *G. sabrinus* is limited by food abundance.

Alternatively, *G. sabrinus* used, on average, two dens/month with den sites for males and females being 211 and 108 m apart, respectively (Carey et al. 1997). Potentially, the greater use of nest boxes in stands supplemented with food, over sites supplemented with nest boxes, may have represented an increase in den-site use per individual, rather than an
increase in reproduction or density. As nest boxes were 100 m apart, an increase in the number of nest boxes used per individual would have been reflected in mean distance moved by individuals. However, as there was no difference in movement by *G. sabrinus* among treatments or between pre- and post-treatment periods, it is unlikely that this possibility can explain the greater use of nest boxes when coupled with food supplementation.

Finally, food supplementation may have resulted in increased densities of *G. sabrinus* and *T. douglasii*, but the intensity of live trapping was not sufficient to capture the change. The primary incentive for squirrels to enter traps is access to food. I found that *G. sabrinus* entered traps readily, once trapping has begun, on the first night of trapping following an extended period (2-3 months) of not trapping (personal observations). *G. sabrinus* may forage by regularly visiting and evaluating the status of fungal-rich food patches that have been used in previous years (Pyare and Longland 2001). Therefore, I suggest that traps, as a source of food, were included into the regular foraging routes of individuals, prior to treatments and during treatments. Individuals joining the population on food-supplemented grids during treatment had no incentive to visit traps due to an excess of food, thus, did not include traps into their foraging routes. Consequently, the untrappable population may have been much larger in stands supplemented with food than those without food. Although we found no significant difference in trappability associated with the treatments, post-treatment trappability of individuals was lower on grids supplemented with food than those without food. This difference was also reflected in the sample sizes obtained for movement (Table 9). The number of occasions individuals were captured on consecutive trapping periods was high for all treatments during pre-treatment trapping (23 to 56). However on 13 and 6 occasions individuals were captured on consecutive trapping periods during food
supplementation, while 53 and 42 occasions occurred in stands without food. I feel the reduced trappability associated with food supplementation is biologically significant and may, in part, explain my inability to document an increase in density associated with food supplementation.

A lack of a response in movement and weight of males in response to food supplementation was expected. Three years of food supplementation on *G. sabrinus* had no influence on these parameters (Ransome and Sullivan 1997). Other studies with arboreal sciurids also found that supplemental food had little effect on survival and weight of adults (Klenner and Krebs 1991; Sullivan and Klenner 1993) and percentage of adults breeding (Sullivan 1990; Klenner and Krebs 1991; Sullivan and Klenner, 1993). The poor response of these parameters to food supplementation might be due to timing of food supplementation (Ransome and Sullivan 1997). Food has often been supplemented during summer months. Since most arboreal sciurids consume a variety of food items during summer months, this may not represent the period when food is most limiting (North et al. 1997; Ransome and Sullivan 1997). It has been suggested that winter is a more-appropriate period to test for food limitation in these species (Ransome and Sullivan 1997). I found that survival of *G. sabrinus* was higher in stands supplemented with food than those without food. These results further support the conclusion that populations of *G. sabrinus* were limited by abundance of food during my study.

However, I suggest that food alone cannot limit the abundance of *G. sabrinus*. This species exhibits a biphasic nocturnal activity pattern. They are active shortly after sundown for a few hours and just before sunrise for a shorter period of time (Weigl and Osgood 1974; Cotton and Parker 2000). If food abundance alone limits their population, then natural
selection would favour those individuals that forage throughout the night. These individuals would acquire a greater proportion of the limited resource than those that maintain the dusk-and dawn-activity pattern. Thus, the biphasic activity pattern would be selected against when food is limited.

I suggest that the population size of *G. sabrinus* is determined by an interaction between predation and food supply, possibly integrated through predator-sensitive foraging (PSF). The PSF hypothesis (McNamara and Houston 1987; but see Sinclair and Arcese 1995; Krebs 1996) assumes that predators affects prey populations when prey forage in riskier habitats as a response to declining food abundance in safe foraging habitats. An extension of the PSF hypothesis would incorporate the time spent foraging. Predators would affect prey populations when prey forage for longer periods of time as a response to declining food abundance. Thus, the biphasic activity pattern of *G. sabrinus* might be the consequence of individuals minimizing the joint risk of predation and starvation. Since *G. sabrinus* is nocturnal and active throughout the winter they are an important prey species for owls. For example, *G. sabrinus* is an important prey species for *S. occidentalis* in some parts of its range (Forsman et al., 1977; 1984; Cutler and Hays 1991; Carey et al. 1992; Zabel et al. 1995). In British Columbia *G. sabrinus* comprised up to 47% of the diet of *S. occidentalis* (Thomas et al. 1990; Dunbar and Blackburn 1994). A pair of *S. occidentalis* can consume up to 500 squirrels annually (Heinrichs 1983). Other avian predators include barn owls (*Tyto alba*), barred owls (*Strix varia*), great horned owls (*Bubo virginianus*), goshawks, and red-tailed hawks (*Buteo jamaicensis*; Wells-Gosling and Heaney 1984). Consequently, the risk of predation on *G. sabrinus* by avian predators might be substantial and may interact with food abundance to limit their population size.
Similar to previous studies, percentage of males breeding and survival of *T. douglasii* were unaffected by food supplementation. However, during periods of high food abundance, factors other than food availability limited populations of *T. hudsonicus* (Klenner and Krebs 1991). Peak cone production occurred in the winter of 1996/1997 in my study (R. Planden, Ministry of Forests, pers. comm.), just prior to food supplementation. Consequently, other factors, such as spacing behaviour, may have limited the abundance of *T. douglasii* below that permitted by food abundance.

Finally, food supplementation also influenced the style of nests used. Covered nests dominated sites with food supplementation while beds dominated sites supplemented only with nest boxes. Bark was the primary material used for nests with varying amounts of moss.

In summary, the hypothesis that populations of *G. sabrinus* are primarily limited by abundance of food, not den sites, was supported by my study. *G. sabrinus* readily used nest boxes, but only in stands supplemented with food. Consequently, increasing the abundance of den sites would have a limited impact on populations of *G. sabrinus* in the stand types I examined. Improving the amount of food available to *G. sabrinus*, especially in winter, would have a greater impact on their populations than den-site availability. This information may be most useful when management goals include enhancing current populations of *G. sabrinus*. For example, the U.S. Fish and Wildlife Service currently list two subspecies of *G. sabrinus* as endangered: *G. sabrinus fuscus* and *G. sabrinus coloratus*, which inhabit the central and southern Appalachians, respectively. Recovery plans for these subspecies may be most effective if they incorporated practices that would enhance their food abundance. In addition, recent studies have found a positive relationship between prey abundance and reproductive success of *S. occidentalis* (White 1996; Thome et al. 1999), home range size.
and habitat use (Zabel et al. 1995), and their survival during natal dispersal (Miller et al. 1997). Consequently, forestry practices that enhance the abundance of food for *G. sabrinus* may, in turn, enhance the prey abundance for *S. occidentalis*. 
CHAPTER 5: GENERAL CONCLUSIONS

The proximate goal of my research was to improve our current understanding of the population ecology and resource limitation of *G. sabrinus* and *T. douglasii*. The ultimate goal was to use this information to manage more effectively for *S. occidentalis*.

To meet my proximate goal I examined whether *G. sabrinus* and *T. douglasii* were, in fact, more abundant in old-growth than mature second-growth forests (Chapter 2). Secondly, I examined the response of *G. sabrinus* and *T. douglasii* to stand manipulations (commercial thinning; Chapter 3). Finally, I explore the primary resource that limits the abundance of *G. sabrinus* (Chapter 4). Each of these investigations improves our current knowledge of *G. sabrinus* and *T. douglasii*.

OLD-GROWTH VERSUS SECOND-GROWTH STANDS

The objective of Chapter 2 was to test the prey abundance hypothesis by thoroughly investigating the population dynamics of *G. sabrinus* and *T. douglasii* in old-growth and mature second-growth stands. Most studies have evaluated the quality of second-growth and old-growth forests for *G. sabrinus* and *T. douglasii* by measuring density, in the absence of information on survival and breeding. Furthermore, most studies have examined populations of *G. sabrinus* and *T. douglasii* in one or two seasons for two years or less. Consequently, results from these studies have been variable. I examined the population dynamics of these species for four years and collected information on movement, population size, recruitment, weight, survival, breeding, and duration that individuals remained on the grids. Consequently, this is the most thorough investigation to date addressing the habitat preference of these species. However, my study sites did not represent a random sample from a larger population of second-growth and old-growth stands. Thus, my results were
limited to differences between the stand types examined rather than to differences between stand types in general. Furthermore, as I only examined two stands from each stand type, the power to detect significant differences between stand types, if present, is quite low, a common limitation for large-scale studies.

I failed to detect differences in movement, density, recruitment, weight of males, survival, percentage of the population breeding, and the duration that individuals remained on the grids between stand types for *G. sabrinus*. Similarly, with the exception of recruitment, I failed to detect differences in these parameters between stand types for *T. douglasii*. Recruitment of *T. douglasii* was higher in second-growth than in old-growth stands. Therefore, in this study, old-growth stands did not appear to supply higher-quality habitat than mature second-growth stands for *G. sabrinus* and *T. douglasii*. Given the number of studies that have found no difference in abundance of *G. sabrinus* between old-growth and second-growth forests, coupled with the large disparity in their abundance within stand types and within the same stand in different years, *G. sabrinus* are clearly not consistently more abundant in old-growth than second-growth stands. The primary conclusion that can be drawn is that the quality of habitat provided by old-growth stands, on occasion, is slightly better than that in second-growth stands. Finally, more *T. douglasii* were captured in mature second-growth than old-growth stands during a period of high cone availability. Thus the hypothesis that mature coastal second-growth stands in British Columbia provided sub-optimal habitat, relative to old-growth stands, for *G. sabrinus* and *T. douglasii* was not supported by my results.

I also presented evidence of late fall – early winter breeding for *G. sabrinus*, as well as seasonal fluctuations in weight and trappability, larger movement by males than females,
and the age of some squirrels exceeding 3.5 years. Most of these observations have not been well documented in the past.

**COMMERCIAL VERSUS THINNED STANDS**

The objective of Chapter 3 was to test the hypothesis that unthinned stands provided higher-quality habitat than thinned stands for *G. sabrinus* and *T. douglasii*. My study is the first to examine, experimentally, the influence of commercial thinning on populations of *G. sabrinus* and *T. douglasii* using intensive pre- and post-treatment live trapping and mark-recapture. I examined the population dynamics of these species for three years and collected information on movement, population size, recruitment, weight, survival, breeding, and duration that individuals remained on the study grids.

Overall, I failed to detect differences in movement, density, recruitment, weight, survival rates, percentage of males breeding, and duration that individuals remained on the grids between thinned and unthinned stands for *G. sabrinus* and *T. douglasii*. In addition, there were no time by treatment effects. Because post-thinning densities of *G. sabrinus* and *T. douglasii* did not change significantly from pre-treatment densities, reducing the density of trees may have the potential to enhance their availability to avian predators like *S. occidentalis*. An important underlying assumption is that *S. occidentalis* will use the modified second-growth stands.

However, caution must be emphasized in interpreting these results. My study is limited in scope as few post-treatment years were examined and the power to detect differences, had they been present, was quite low due to low replication. In addition, my study sites were not selected randomly. Treatment sites were the only sites available and control sites were selected to minimize heterogeneity between treatment and control sites.
Consequently, inferences from my study can only be made for the stand examined. Furthermore, I only examined the influence of thinning 60- to 70-year-old western hemlock stands on population dynamics of *G. sabrinus* and *T. douglasii*. Results might vary in stands of different ages, species composition, climate, or stand histories. Reliable inferences regarding the influence of thinning on population dynamics of *G. sabrinus* and *T. douglasii* can only be made after similar results have been obtained over a variety of stand conditions in different geographical areas. However, my results indicate that commercial thinning deserves further evaluation and consideration as a potential silvicultural prescription to deliberately manipulate prey availability.

**RESOURCE LIMITATION**

The objective of Chapter 4 was to test the hypothesis that population sizes of *G. sabrinus* and *T. douglasii* are primarily limited by the availability of food, not den sites. My study is the first to simultaneously manipulate the abundance of food and den sites, coupled with intensive pre- and post-treatment live trapping using mark-recapture of *G. sabrinus* and *T. douglasii*. To determine whether populations of *G. sabrinus* and *T. douglasii* were limited by availability of food or den sites, I manipulated these resources for two years following a ten-month pre-treatment period. I also evaluated the influence of these manipulations on survival and reproduction, in addition to density.

For *G. sabrinus*, I failed to detect differences in movement, density, recruitment, weight of males, and duration that individuals remained on the grids among controls and stands supplemented with food, food and nest boxes, and nest boxes. Survival of *G. sabrinus* decreased significantly from the pre- to post-treatment period in stands without food. Survival increased significantly or remained unchanged in stands with food during the same
period. In addition, greater than 75% of the nest boxes were occupied in stands supplemented with food and nest boxes, while less than 12% were occupied in stands supplemented with only nest boxes. Most nest boxes on food supplemented grids contained covered nests, while those in stands without food supplementation contained beds. The majority of the nests were constructed by G. sabrinus. These results clearly indicate that G. sabrinus readily used nest boxes, but only on sites supplemented with food. Food supplementation had a strong influence on G. sabrinus while the availability of den sites did not.

**Management Implications**

Two prey-based hypotheses have been proposed to explain the general selection of old-growth forests by S. occidentalis (Forsman et al. 1982, 1984): 1) prey are more abundant in old-growth forests (prey abundance hypothesis), and 2) prey are more efficiently hunted by owls in old-growth forests because of the more open understory (prey availability hypothesis). The possibility of deliberately manipulating prey densities in S. occidentalis habitat to benefit owls through silvicultural prescription deserves consideration: specifically, can silviculture produce more diverse prey bases, more abundant prey populations, or reduce fluctuations in the abundance of major prey species (Thomas et al. 1990)? For this to be a possibility one must first determine if S. occidentalis select foraging habitat based on prey abundance or availability. Prey abundance can be addressed directly as I have done in Chapter 2. In Chapter 2, I failed to detect a difference in population dynamics of G. sabrinus and T. douglasii between second-growth and old-growth stands. My results, coupled with the results from other studies (Appendix 1) indicate that second-growth stands often maintain large populations of G. sabrinus. Consequently, the preference for old-growth stands by S.
occidentalis cannot be explained by prey abundance alone. It is difficult to address the prey availability hypothesis directly. Therefore, it is often assumed that for areas with similar populations of G. sabrinus, those with fewer trees might have higher prey availability to avian predators. If this is true, because old-growth stands generally have fewer larger trees than second-growth stands, selection of old-growth stands by S. occidentalis may be better explained by prey availability than abundance.

Since I failed to detect a difference in population size between pre- and post-treatment periods for G. sabrinus and T douglasii, commercial thinning may be an effective tool to enhance the availability of G. sabrinus in second-growth stands to avian predators such as S. occidentalis. Although S. occidentalis may select different habitats for different reasons (e.g., old growth for thermal regulation, nesting, predator avoidance), thinning second-growth stands adjacent to old-growth stands may provide foraging habitat adjacent to stands used for other purposes. Alternatively, enhancing prey availability between S. occidentalis activity centers may improve survival during dispersal. Miller et al. (1997) found that mortality of dispersing juvenile owls decreased with increasing use of open sapling stands in California. They suggested that the reduced mortality associated with open sapling stands might be related to the increased availability of prey (dusky-footed woodrats, Neotoma fuscipes) in those stands. In fact, they suggested that dispersal is limited by prey availability because the majority of deaths during dispersal were from starvation. Therefore, commercially thinning stands along travel routes between spotted owl conservation areas (SOCAs) may enhance the availability of G. sabrinus to dispersing juveniles, thus improving their survival.
The net benefit of manipulations of forest structure to enhance prey for *S. occidentalis* must be evaluated carefully. Habitat manipulations designed to improve foraging habitat for *S. occidentalis* may potentially provide habitat for predators or species thought to be competitors of spotted owls. This, in turn, might have deleterious effects on *S. occidentalis*. It has been hypothesized that competition from *S. varia* and predation on *S. occidentalis* by *B. virginianus*, may increase with increasing amounts of forest edge associated with harvest of mature and old-growth forests (Thomas et al. 1990).

Since its recent expansion into British Columbia, *S. varia* has become sympatric with *S. occidentalis* and might be a competitor. However, the influence of *S. varia* on *S. occidentalis* is unclear (Dunbar and Blackburn 1994). *S. varia* are thought to prefer younger forests, possibly due to greater prey abundance and availability than that in old-growth forests (Hamer et al. 1989). *S. varia* are thought to primarily consume terrestrial prey items (Microtines). Hamer et al. (1989) speculated that *S. varia* selected younger second-growth forests because of the high canopy closure and poorly developed understory. These characteristics may improve the availability of terrestrial prey to *S. varia*. In contrast, old-growth stands often have open canopies and well-developed understory and ground vegetation, which may reduce accessibility of terrestrial prey to *S. varia*. Commercial thinning may improve visibility and accessibility of terrestrial prey for *S. varia* in the short term. However, it is predicted that as young forests develop old-growth characteristics, the habitat will become less acceptable to *S. varia*, and more acceptable to *S. occidentalis* (D. Johnson, pers. comm.; D. Hayes, pers. comm. as cited in Dunbar and Blackburn 1994).

Thinning, through enhanced tree diameters, crown structure, tree growth, understory development, and reduced density of trees (Hayes et al. 1997; Sullivan et al. 2001), can move
second-growth stands out of the closed-canopy stage and accelerate the development of conditions found in late seral forests (McComb et al. 1993; Baily 1996; Carey and Curtis 1996; Carey et al. 1999; Carey 2000). Consequently, accelerating the development of old-growth characteristics in second-growth stands may reduce the abundance of *S. varia* in the long term. In contrast, Blackburn (1991) reported similar rates of detection of *S. varia* in second-growth and old-growth forests. Consequently, accelerating the development of old-growth characteristics in second-growth stands may not reduce the potential competition between *S. varia* and *S. occidentalis*.

*B. virginianus* are the most common documented predator of *S. occidentalis* (Miller 1989; Dunbar and Blackburn 1994; Johnson 1993). *B. virginianus* is thought to be common in habitats containing a greater edge to area ratio, greater abundance of early seral stages, and less interior habitat (Johnson 1993). Thus, habitat fragmentation and increased edge associated with harvesting mature and old-growth forests may favour *B. virginianus*, although this has not been substantiated (Thomas et al. 1990). The contrast between a clear-cut/forest ecotone would be greater than a thinned/unthinned ecotone. Similarly, commercially-thinned stands might result in less fragmentation and reduction in interior habitat than clear-cuts. Therefore, commercial thinning might provide an alternative to clear cutting for stands adjacent to spotted owl activity centers. However, thinning stands that would otherwise be unharvested might increase the risk of predation of *S. occidentalis* by *B. virginianus*. The influence of commercial thinning on *B. virginianus* is poorly understood and must be assessed. Habitat manipulations aimed at improving prey abundance for *S. occidentalis* must be accompanied by simultaneous monitoring of reproductive success and
survival rates of *S. varia*, *S. occidentalis*, and their primary predators. Only then can the full influence of the habitat manipulations on *S. occidentalis* be assessed.

The primary goal of habitat manipulation should be the development of superior habitat in forests that are currently sub-optimal for *S. occidentalis*. Developing superior habitat involves developing stand characteristics that mimic as closely as possible current old-growth conditions (Thomas et al. 1990). These conditions include a multi-layered and relatively closed canopy, a mixed species composition dominated by large trees, numerous large snags, and considerable amounts of large logs and other woody debris on the ground (LaHaye 1988; Forsman et al. 1984; Gutierrez et al. 1984). Large trees with broken tops, secondary crowns, large limbs, hollow boles, and clusters of limbs infected by dwarf mistletoe should be created or maintained, either in clumps or as scattered individuals within the stand (Thomas et al. 1990). The focus of habitat manipulations needs to be the development of superior habitat for *S. occidentalis*, rather than providing minimal habitat requirements while maximizing revenue. Consequently, any habitat manipulations conducted with the aim to create superior habitat for *S. occidentalis* must be accompanied by intensive monitoring to determine the effects of the habitat manipulation on *S. occidentalis* and their competitors and predators.

Finally, I concluded that populations of *G. sabrinus* are strongly influenced by availability of food not den sites. Potentially, silvicultural practices that enhance their primary food source would enhance their abundance. Stomach and fecal analyses indicate that *G. sabrinus* primarily consumes hypogeous fungi during snow-free periods and lichens during winter (McKeever 1960; Maser et al. 1978, 1985, 1986; Hall 1991; Colgan 1997). The total dry weight of hypogeous fungi in coarse woody debris exceeded that in soil by
more than 10 fold in mature forests (Amaranthus et al. 1994). Therefore, forest practices that emphasize the retention of mature trees and coarse woody debris may promote abundance and diversity of hypogeous fungi (Amaranthus et al. 1994). This, in turn, may enhance populations of *G. sabrinus*. 


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### APPENDIX 1. A REVIEW OF STUDIES ON *G. Sabrinus*

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Stand types</th>
<th>Density (animals/ha ± 1 SE)</th>
<th>Other</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Second Growth</td>
<td>Old Growth</td>
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<td>PSME</td>
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<td>0.032/trap night</td>
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<td>0.029/trap night</td>
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<td>PSME</td>
<td>0.014/trap night</td>
<td>0.027/trap night</td>
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<td>TSHE</td>
<td>0.2 (± 0.1)</td>
<td></td>
</tr>
<tr>
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<td>Washington: Olympic Peninsula</td>
<td>TSHE:</td>
<td>0.2 (± 0.1)</td>
<td>0.5 (± 0.2)</td>
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<tr>
<td>Carey 2000</td>
<td>Western Washington</td>
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<td></td>
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<td></td>
<td></td>
<td>PSME/Thinning</td>
<td>2 reps.</td>
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</tr>
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<td>Carey et al. 1992</td>
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<td>0.9 (± 0.2)</td>
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<td></td>
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<td>1.9 (± 0.1)</td>
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<td>Carey et al. 1999</td>
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<td>1.4 (0.7 – 2.0)</td>
<td>2.1 (1.1 – 3.6)</td>
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<td>Martin and Anthony 1999</td>
<td>Central Oregon: Cascade Mnts</td>
<td>PSME/TSHE/THPL</td>
<td>Movement between old- and second-growth</td>
<td></td>
</tr>
<tr>
<td>Ransome and Sullivan 1997</td>
<td>Vernon, British Columbia</td>
<td>PICO</td>
<td>0.66 (± 0.02)</td>
<td>1.03</td>
</tr>
<tr>
<td>Rosenberg and Anthony 1992</td>
<td>Western Oregon</td>
<td>PSME</td>
<td>1.9 (± 0.2)</td>
<td>2.3 (± 0.3)</td>
</tr>
<tr>
<td>Volts 1986</td>
<td>Oregon: Western slope Cascades</td>
<td>PSME/TSHE</td>
<td>8.1/4 (/grid)</td>
<td>23.7/11.7 (/grid)</td>
</tr>
<tr>
<td>Waters and Zabel 1995</td>
<td>Northeastern California</td>
<td>ABCO/ABMA</td>
<td>2.3 (± 0.2)</td>
<td>3.3 (± 0.6)</td>
</tr>
<tr>
<td>Witt 1992</td>
<td>Western Oregon: Coast Range</td>
<td>PSME</td>
<td>0.0 – 0.24</td>
<td>0.52 – 1.28</td>
</tr>
</tbody>
</table>

PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, ABCO = *Abies concolor*, ABMA = *Abies magnifica*  
PICO = *Pinus contorta*

Carey et al. (1999) examined vegetation and abundance of squirrels at > 2000 points in 19 stands in three seral stages. They described diets of squirrels in stands and identified key processes contributing to biodiversity and scale at which emergent properties appeared. However, the methodology used by Carey et al. (1999) to determine and compare abundance of *G. sabrinus* among stands may, inadvertently, favor higher density estimates for old-growth stands. Carey et al. (1999) sampled 8 old growth, 3 mature (niche diversification stage) and 5 young stands (competitive exclusion stage). Most sites had 100 grid points ranging from 10 by 10 to 7 by 15 with 40-m spacing. Trapping was conducted from 1985 to 1989 in either the spring, fall, or both, but was highly variable (Table 15).

Table 15. Variability of trap-nights among stand types, seasons, and years (modified from Carey et al. 1999, Table 3).

<table>
<thead>
<tr>
<th></th>
<th>OG†</th>
<th>ND</th>
<th>CE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of stand</td>
<td>&gt; 210 years</td>
<td>100 - 120 years</td>
<td>40 - 60 years</td>
</tr>
<tr>
<td>Number of grids</td>
<td>8</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Number of trap-nights</td>
<td>68,648</td>
<td>15,520</td>
<td>28,781</td>
</tr>
<tr>
<td>Number of trap-nights occurring in the fall (% of total trap nights)</td>
<td>(51.9%)</td>
<td>(15.2%)</td>
<td>(32.7%)</td>
</tr>
<tr>
<td>Number of trap nights occurring from fall 1987 to fall 1989</td>
<td>(52.8%)</td>
<td>(52.6%)</td>
<td>(28.5%)</td>
</tr>
<tr>
<td>Number of trap nights occurring only in the fall in 1987, 1988, and 1989</td>
<td>(30.0%)</td>
<td>(0%)</td>
<td>(0%)</td>
</tr>
</tbody>
</table>

†OG = old-growth stands, ND = niche diversification stage, CE = competitive exclusion stage.
Firstly, relative abundance of *G. sabrinus* varied among stands in different years (Rosenberg and Anthony 1992; my study) and within stands in different years (my study, Figure 2). Carey (1995) reported that over-all catch-per-unit-effort varied three-fold among years. Consequently, varying trapping effort among stand types in different years could produce biased estimates. In Carey et al. (1999), 52% of the sampling in old-growth stands occurred from fall 1987 to fall 1989. During this same period 28% of the sampling in competitive exclusion stands occurred. If abundance of *G. sabrinus* varies between 1985/1986 and 1987/1988/1989, then reliable comparison between stand types cannot be made. In fact, Carey et al. (1992) sampled populations of *G. sabrinus* in the same area and time period as Carey et al. (1999). Figures 6c and 7c, and to a lesser extent 6a and 7b, in Carey et al. (1992) showed a general trend for higher densities (two-fold increase) of *G. sabrinus* in 1988 and 1989 than that in previous years. If the same trend existed in Carey et al. (1999), then the methods used to determine abundance would have a positive bias for old-growth stands. Secondly, Carey et al. (1999) sampled many of the old-growth stands in the fall of 1987, 1988, and 1989 (30% of total sampling effort in these stands) without sampling the niche diversification or competitive exclusions stands. Similarly, 52% of total trapping effort in old-growth stands occurred in the fall while 15% and 33% in the niche diversification (ND) and competitive exclusion (CE) stage, respectively, occurred in the fall. Fall populations are composed of resident adults and young of the year during a time of high food abundance. Spring populations represent those individuals surviving the period of lowest food abundance and are, in general, the lowest population of the year (Sullivan and Sullivan 1982). Carey (2000) reported population sizes of *G. sabrinus* in the spring were 51-60% of fall populations. Consequently, trapping methodologies that sample different stand
types in different seasons may produce biased population estimates favoring those stands sampled disproportional more in the fall. Furthermore, we found that the trappability of flying squirrels was significantly higher in the fall/winter (87.1%) than spring (70.3%). This disparity may be enhanced further in Carey et al. (1999) as traps were baited twice a year (spring and fall) in old-growth stands and only once a year (spring) in second-growth stands in 1987, 1988, and 1989. A more-recent association between traps and food in old-growth stands than that in second-growth stands may have enhanced spring captures in old-growth stands relative to that in second-growth stands. It was not clear whether Carey et al. (1999) prebailed the grids prior to trapping, which would have eliminated this influence. Finally, density estimates are a product of estimated population sizes and estimated effective-trapping areas, the later based upon mean movement. Recent studies have found that average movement within study sites changes significantly among years (Rosenberg and Anthony 1992; Waters and Zabel 1995; Martin and Anthony 1999). Consequently, unequal sampling effort among years for different stand types could yield biased estimates of movement, and concomitantly, biased density estimates. This bias would be exaggerated further when comparison among stand types uses maximum-recorded densities as in Carey et al. (1999). Similarly, use of total-captures-per-unit-effort (includes repeated captures for the same individual) to compare stand types is inappropriate given the unequal trap effort among stand types, seasons, and years. A more appropriate approach would be to compare stand types with data collected from fall 1985 to spring 1987, when trapping effort is similar among stand types, seasons, and years. Carey et al. (1999) appears to have sufficient data collected during this period to address this objective without introducing the potential biases associated with unequal sampling effort among stand types, years, and seasons intrinsic to the later half
of the their study. Although Carey et al. (1999) stated that “maximum densities were well
distributed among years (4-6 yr) and between seasons (12 of 19 in spring), with no indication
of confounding effects due to year or season,” this evaluation does not provide enough
information to adequately determine whether the above concerns had an influence on the
results of their study.