Canadian Journal of Forest Research
Revue canadienne de recherche forestière

**Tree squirrel abundance and demography in managed
coniferous forests of British Columbia are within the range
of natural fluctuations of old-growth stands**

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2016-0458.R1
Manuscript Type:	Review
Date Submitted by the Author:	01-Jan-2017
Complete List of Authors:	Sullivan, Thomas; University of BC, Ransome, Douglas; British Columbia Institute of Technology Sullivan, Druscilla; Applied Mammal Research Institute Lindgren, Pontus; Applied Mammal Research Institute Klenner, Walt; British Columbia Ministry of Forests
Keyword:	Coniferous forests, <i>Glaucomys sabrinus</i> , Managed stands, Old-growth forest, <i>Tamiasciurus</i>

SCHOLARONE™
Manuscripts

**Tree squirrel abundance and demography in managed
coniferous forests of British Columbia are within the range of
natural fluctuations of old-growth stands**

**Thomas P. Sullivan, Douglas B. Ransome, Druscilla S. Sullivan, Pontus M.F.
Lindgren, and Walt Klenner**

Received _____. Accepted _____.
Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on _____.

Thomas P. Sullivan.¹ Department of Forest and Conservation Sciences, Faculty of Forestry, University of B.C., 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.
Douglas B. Ransome, Druscilla S. Sullivan, Pontus M.F. Lindgren. Applied Mammal Research Institute, 11010 Mitchell Avenue, Summerland, BC V0H 1Z8, Canada.
Walt Klenner. British Columbia Ministry of Forests, Lands, and Natural Resource Operations, 441 Columbia St., Kamloops BC, V2C 2T3 Canada

¹ Corresponding author. E-mail: tom.sullivan@ubc.ca

Word count: 12,796

Abstract: The American red squirrel (*Tamiasciurus hudsonicus* Exrleben) and northern flying squirrel (*Glaucomys sabrinus* Shaw) are important mammal species in coniferous forests that are widely distributed across temperate and boreal ecological zones. Although apparently preferring late-successional forests, there is not a clear pattern of the responses of *T. hudsonicus* and *G. sabrinus* population dynamics in young second-growth and old-growth conifer forests. We used a compilation of study results that had standardized methodology and sampling effort to compare tree squirrel responses across a range of forest conditions. We tested the hypotheses (H) that abundance, reproduction, recruitment, and survival would be higher in (H₁) old-growth than second-growth stands, (H₂) unthinned than thinned second-growth stands, and (H₃) lightly- than heavily-thinned stands. Tree squirrel populations in old-growth stands were considered the “standard” treatment to which other treatments in second-growth stands (unthinned and variously thinned) were compared. Thinned stands were grouped into low, medium, and high densities of trees. Datasets from seven published studies included 2804 *Tamiasciurus* and 837 *G. sabrinus* individuals, 25 study years, and 158 trapping periods. Mean abundance of *Tamiasciurus* was similar among treatment stands, ranging from 0.62/ha to 1.29/ha. Mean numbers of *G. sabrinus* were highest in old-growth stands at 0.65/ha, followed by the low- and medium-density stands at 0.50/ha, the high-density stands at 0.25/ha, and finally the unthinned second-growth stands at a low of 0.12/ha. In terms of effect size, mean proportional change in abundance, relative to that within old-growth stands, of both squirrel species in the three thinned stands were within the range of natural fluctuations in old-growth stands. Populations of *Tamiasciurus* in the unthinned stands were not within the range of

fluctuations in the old-growth stands. Mean number of successful pregnancies and total recruits were similar among stands for *Tamiasciurus*, with variability in female breeding and winter survival. Mean number of recruits of *G. sabrinus* was highest in old-growth stands with no other differences in demographic attributes among stands. The biological significance of these differences in demographic variables was small in terms of effect sizes. *Tamiasciurus* and *G. sabrinus* seem to persist in a relatively broad range of young managed forest habitats, as well as in old-growth stands.

Key-words: Coniferous forests, *Glaucomys sabrinus*, managed stands, old-growth forest, population dynamics, *Tamiasciurus*.

Introduction

Coniferous forests are widely distributed across temperate and boreal zones of North America and Eurasia. Undisturbed conifer forests were recently widespread but now are among some of the most intensively altered habitats (Norse 1990; Rosencranz and Scott 1992; Lindenmayer and Franklin 2002). For example, in the Pacific Northwest (PNW) of North America only 14% of the original old-growth forest in Washington and Oregon, U.S.A., remains (Strittholt et al. 2006). Unmanaged second-growth forests tend to have rotation ages of less than 100 years and may not necessarily develop attributes of mature conifer forests, such as regular production of cone crops (Burns and Honkala 1990; Benkman 1993; Holiman et al. 1998). Consequently, wildlife species that are apparently dependent on mature and old-growth coniferous forests, such as tree squirrels in the genera *Tamiasciurus* and *Glaucomys*, may decline on both local and global scales.

The American red squirrel (*T. hudsonicus* Exrleben) and northern flying squirrel (*G. sabrinus* Shaw) are an important group because of their close association with forest canopies (Aubry et al. 2003). They occupy a range of forest types, particularly older forests with tall trees, complex stand structure, snags, and large-diameter woody debris (Smith et al. 2003). Both species are common inhabitants of temperate and boreal coniferous forests of North America (Wells-Gosling and Heaney 1984; Steele 1998). They prefer conifer forests, particularly spruce (*Picea* spp.) - fir (*Abies* spp.) and pine (*Pinus* spp.) forests (Brink and Dean 1966; M. Smith 1968; C. Smith 1968), but are also found in conifer-hardwood mixtures and pure hardwood forest (Kemp and Keith 1970; Rusch and Reeder 1978; Holloway and Malcolm 2006). Population fluctuations of

holarctic tree squirrels (*Tamiasciurus* and *Sciurus*) have been related to availability of seed crops of coniferous trees (M. Smith 1968; Kemp and Keith 1970; Gurnell 1987; Andren and Lemnell 1992; Lurz et al. 1995). Recent work in northern Canada has confirmed this important relationship between red squirrels and coniferous seed crops, particularly white spruce (*Picea glauca* (Moench) Voss) (Boonstra et al. 2001; Fletcher et al. 2010; LaMontagne et al. 2013).

Evidence that populations of *T. hudsonicus* are limited by available food resources has been demonstrated by supplemental food experiments (Sullivan 1990; Klenner and Krebs 1991; Sullivan and Klenner 1993; Ransome and Sullivan 1997, 2004). An apparent exception to this pattern was the study by Rusch and Reeder (1978) who reported stable densities of *T. hudsonicus* despite strong fluctuations in the seed-crop. As discussed by Sullivan (1990) and Klenner (1991), these stable densities were probably related to the fragmented nature of the habitat where even good spruce habitat did not provide enough food in a mast year to generate population fluctuations. Mixed conifer-hardwood and hardwood (deciduous) forests have been described as marginal habitats for *T. hudsonicus* (Kemp and Keith 1970, Rusch and Reeder 1978).

Glaucomys sabrinus occurs in forested regions over most of northern North America including coniferous, mixed coniferous-deciduous, and occasionally strictly deciduous forests (Wells-Gosling and Heaney 1984). These sciurids function as indicators of ecological productivity via their foraging on, and dissemination of, coniferous seeds and ectomycorrhizal fungi (Maser and Maser 1988; Carey 2000). They also serve as prey for raptors and mammalian carnivores (Carey and Harrington 2001; Ransome et al. 2004). These processes enhance forest regeneration by forming new

mycorrhizal colonies that enhance growth and health of trees, and this dispersal is especially important for young tree growth in early seral stages (Cazares et al. 1999; Molina et al. 1999). Consequently, tree squirrels might prove to be vital links (“keystone species”) between critical below-ground processes and higher trophic levels, especially in late-seral forests (Carey et al. 1999; Smith et al. 2003).

Tree squirrels are important management indicator species because of their association with forest canopies and their responses to potential impacts from forest management, particularly harvesting (Smith et al. 2005). Stands with high structural diversity and overstory cover, at least of the dominant tree layer, provide decreased predation risk for tree squirrels (Vahle and Patton 1983, Carey 2000). Holloway and Malcolm (2006) reported that these habitat attributes were related to higher numbers of both sciurids in relatively intact coniferous and deciduous forests in Ontario. Compared with old-growth forests, shelterwood harvesting seemed to lower habitat quality for both species in Ontario (Holloway and Malcolm 2006) and for *G. sabrinus* in California (Waters and Zabel 1995). Abundance of *T. hudsonicus* and *G. sabrinus* were 40% and 60% lower, respectively, in partially cut stands with $\geq 50\%$ basal area removed than uncut stands (Herbers and Klenner 2007). Late successional (legacy) features such as large live Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco. var *glauca* (Beissn.) Franco), interior spruce (*Picea engelmannii* x *P. glauca* (Moench) Voss), or other coniferous trees, snags, and abundant coarse woody debris seem to maintain both species in managed stands (Carey 2000; Smith et al. 2003). However, Holloway et al. (2012) concluded that the current minimum retention standard of 15% basal area of

133 green-tree retention (GTR) will not provide suitable habitat for *G. sabrinus* in the PNW
134 of the U.S.A.

135 These conclusions from harvesting studies beg the question: what roles do the
136 matrix habitat and age of harvest around the GTR play through time post-harvest to
137 ameliorate the impact of initial tree removal on tree squirrels? In addition, do
138 management interventions such as pre-commercial thinning (PCT) and commercial
139 thinning (CT) help to develop stand structure attributes in regenerating stands to provide
140 habitat for tree squirrels? Seemingly in many study situations, the matrix stands of
141 second-growth forests are not considered at all, yet they form the future habitat supply
142 for tree squirrels and most other forest-dependent wildlife species.

143 There is not a clear pattern of the comparative responses of *T. hudsonicus* and *G.*
144 *sabrinus* population dynamics in young regenerating and old-growth conifer forests, at
145 both stand and, ultimately, landscape scales. However, Allard-Duchene et al. (2014)
146 showed that the peak of habitat use by red squirrels occurs about 20 years earlier after
147 cutting than after fire. An understanding of this response may be crucial to long-term
148 productivity and persistence of tree squirrels in regenerating stands, at least with
149 respect to natural population levels observed in undisturbed conifer forest. Because of
150 the ongoing conversion of old-growth conifer forests to younger seral stages, and the
151 association of tree squirrels with conifer seed crops, Raphael (1988) and Buchanan et
152 al. (1990) have predicted long-term population declines for tree squirrels and other old
153 forest-dwelling small mammals. It may also be helpful to conservation of the
154 beleaguered Eurasian red squirrel (*Sciurus vulgaris* L.) which, because of competition
155 with the introduced American gray squirrel (*Sciurus carolinensis* L.), now exists primarily

in non-mature conifer forests in the United Kingdom (Lurz et al. 1995) and potentially in Europe as well. Benkman (1993) and Holiman et al. (1998) have made similar predictions for conifer-seed dependent crossbills (*Loxia* spp.).

Two major questions are: 1) will tree squirrels occupy and persist in managed second-growth forests at population levels and productivity comparable to mature or old-growth conifer forests? and 2) will stand thinning (PCT or CT), and potentially fertilization, accelerate stand development to provide structural components required by squirrels in young stands?

Comparing results among published studies (e.g., a meta-analysis) is difficult because of differences in methods used to assess squirrel responses and different statistical approaches to analysis. Therefore, we used a compilation of study results from the Sullivan and Ransome research programs that had standardized methodology and sampling effort. This approach has been used by other researchers in a variety of ecological investigations (e.g., Mendoza et al. 2014). Our studies used intensive mark-recapture sampling of *T. hudsonicus*, Douglas squirrel (*T. douglasii* Audubon and Bachman), and *G. sabrinus* with multiple trapping periods in summer and some winter seasons over time periods of 1 to 6 years. In addition to abundance, the demographic attributes of reproduction, recruitment, and survival were included in analyses. These aspects of population dynamics are almost wholly missing from the sciurid literature except for a few programs, such as the Kluane Red Squirrel Project in the Yukon, Canada (<http://redsquirrel.biology.ualberta.ca/>). As noted by van Horne (1983) and Wheatley et al. (2002), abundance or density alone may be a poor and potentially misleading attribute when evaluating habitat quality for a wildlife species.

We tested the hypotheses (H) that for tree squirrels: abundance, reproduction, recruitment, and survival will be higher in (H₁) old-growth than second-growth stands, (H₂) unthinned than thinned second-growth stands, and (H₃) lightly thinned (≥ 1200 trees/ha) than heavily (≤ 500 trees/ha) thinned stands. Second-growth stands in these studies originated primarily from clearcutting, but also from wildfire, and had few if any structural legacies from the original stands.

Methods

Study areas

A total of seven studies were located throughout southern BC (Fig. 1) with the site characteristics listed in Table 1. All areas included second-growth forest in large (> 1000 ha) openings after clearcut harvesting or wildfire, with ages of stands ranging from 17 to 70 years. Old-growth forest stands ranged in age from 80 to 250 years and were, on average, 2-10 km away from second-growth stands. Old-growth stands ranged from a minimum of 3- to 7-times older than corresponding treatment stands within a study. In general, our second-growth stands were located in large (>1000 ha) openings created by contiguous clearcutting or wildfire, with old-growth stands 2-10 km away. Major tree species were lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), Douglas-fir, interior spruce, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the interior study areas; western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata*), and variable amounts of coastal Douglas-fir (*P. menziesii* (Mirb.) Franco) and Pacific silver fir (*A. amabilis* (Dougl.) Forbes) in the coastal study areas.

Tree squirrel populations in old-growth stands were considered the “standard” or “control” (natural control) treatment to which other treatments in second-growth stands (unthinned and variously thinned) were compared. Thinned stands occurred primarily from silvicultural intervention as PCT or CT and also as “naturally” thinned during re-growth of forests after disturbance. Thinned stands were grouped into three densities: low (300-500 trees/ha), medium (501-1200 trees/ha), and high (1201-2300 trees/ha). Tree squirrel populations in the unthinned stand treatment were also considered as another “control” (management control) for comparison with squirrel populations in the three densities of thinned stands.

Squirrel populations

Tree squirrel populations were sampled at 2-, 3-, or 4-week intervals during summer (April-September) periods and at irregular intervals during winter (October-March). Each treatment stand had a 9-ha trapping grid with 100 (10 x 10 or 6 x 16 + 4) stations at 30-m intervals with one Tomahawk live-trap (Model 201, Tomahawk Live trap Company, Tomahawk, Wisconsin) equipped with a nest box (1-L plastic jar with coarse brown cotton) at every other station, resulting in ~5 traps/ha. Traps were baited with sunflower seeds (*Helianthus annuus*) and set in the evening on day 1 and checked in the morning and afternoon of day 2 and morning of day 3. All captured squirrels were ear-tagged with individually numbered tags (Monel no.1, National Band and Tag Co.), breeding condition noted, weighed on Pesola spring balances, and point of capture recorded. Duration of the breeding season was noted by palpation of male testes and the condition of mammarys of females (Krebs et al. 1969). A pregnancy was considered

successful if a pregnant female captured in one month was recaptured lactating in the following month. Squirrels were released on grids immediately after processing. All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

Abundance estimates of animals were derived from the Jolly-Seber stochastic model for open populations with small sample size corrections (Seber 1982; Jolly and Dickson 1983). The Jolly-Seber model assumes marked and unmarked animals have the same capture probability in each sampling session (Krebs 1999). The reliability of this model declines when population sizes are very low and no marked animals are captured (Seber 1982). At those times when the Jolly-Seber estimate was not calculated, the number of individual squirrels captured was used as the population estimate. We calculated the effective trapped area (ETA) for each grid based on mean maximum distance moved (MMDM) by squirrels between trapping periods. A buffer of one-half the value of the MMDM was added to the grid size and used to estimate the total area within which populations were sampled (Wilson and Anderson 1985). Estimates of population size were converted to a density estimate by dividing population estimates for each trapping period by the ETA. We consider this estimate a “density index” (Krebs et al. (2011). Jolly trappability was calculated according to Krebs and Boonstra (1984).

Proportion of adult squirrels breeding was based on the number of unique adults in reproductive condition (males were scrotal or females with large nipples) relative to the total number of adults captured during the breeding and lactation season. Squirrels were classified by age. Body mass was compared between obvious juveniles when first captured to their mass when they were recruited into the population and first showed

signs of sexual maturity: *T. hudsonicus* juvenile < 165 g and < 180 g, adult $\geq$ 165 or $\geq$ 180 g; *T. douglasii* juvenile < 165 g, adult $\geq$ 165 g; *G. sabrinus* juvenile < 100 g, adult $\geq$ 100 g. Juveniles were considered to be young animals recruited during the study. Recruits were defined as new animals that entered the population through reproduction and immigration. Mean survival rates (28-day) for summer and winter periods were estimated from the Jolly-Seber model. Comparison of body mass among stands was based on mean mass of each adult male averaged for each year of a given study.

Data analysis

The various datasets fit a randomized block design that incorporated both spatial and temporal replication, and so a 2-way ANOVA (Zar 1999; Model III with stand treatment as the fixed factor and block as the random factor) (IBM Corp. 2014) was conducted (Sullivan et al. 1996). This analysis assumed no interaction between blocks and levels of treatment and tested for differences in mean abundance of *Tamiasciurus* and *G. sabrinus* in summer and winter periods, and overall. This same analysis was used to evaluate the effects of stand treatment on mean values for Jolly trappability, proportion of males and females breeding, number of successful pregnancies, number of recruits, Jolly-Seber monthly survival in summer and winter periods, and body mass of adult males for each of *Tamiasciurus* and *G. sabrinus*. For these analyses, a single estimate for the given parameter for each year and treatment was derived to use the variability among years and blocks to test for differences among levels of the treatment. These single estimates were the mean values of multiple trapping periods over 4 to 6 months for each year of the study; thus, they represent a reliable estimate for these parameters.

We also calculated overall means $\pm$ 95% confidence intervals (CIs) for abundance, proportion of females breeding, number of successful pregnancies, number of recruits, Jolly-Seber monthly survival in summer and winter periods, and body mass (an index of physical condition) of adult males for each of *Tamiasciurus* and *G. sabrinus* across the five treatment stands.

Proportional data were transformed by arcsin square root (Fowler et al. 1998). Duncan's multiple range test (DMRT), adjusted for multiple contrasts, was used to compare mean values based on ANOVA results (Saville 1990). In all analyses, the level of significance was at least $P = 0.05$.

To determine the biological significance of the magnitude of the observed effects of forest management activities on abundance of the three sciurid species, we calculated the annual proportional change in numbers of red or Douglas squirrels and northern flying squirrels within old-growth stands. This effect size represented the "naturally occurring" variance in these parameters typical of old-growth stands (controls). However, this 'naturally-occurring' effect size includes changes among years in these parameters; thus, they would be the upper limits of the naturally-occurring effect size. To quantify the impacts of forest management on the three squirrel species, the proportional difference in these parameters between old-growth and treatment stands, within each year and study site was calculated for each post-treatment year. This difference was the proportional change in abundance (and related parameters of reproduction, recruitment, and survival) of a given tree squirrel population to the forestry treatment and was the 'effect size' defined by Steidl et al. (1997) and Johnson (1999). Assessing effect size within a replicate (block) and year removes the variations that

occur among years, isolating the effect size to treatment effects. We calculated mean values and 95% CIs for the annual proportional changes in abundance, as well as for the demographic variables of reproduction, recruitment, and survival in the old-growth stands for each population, and for the proportional difference in these variables between old-growth and treatment stands. This same approach was used in a previous population analysis (Sullivan et al. 1998) and analytical review (Sullivan and Sullivan 2003). Evaluation of significant differences using non-overlapping confidence intervals provides a useful way of assessing the strength and biological significance of the actual “effect size” of treatment (Gerard et al. 1998; Johnson 1999). As discussed by Graybill and Iyer (1994) and Steidl et al. (1997), confidence intervals are very likely a better measure for assessing practical importance of results than relying on hypothesis testing alone and retrospective power analyses.

Results

Datasets

There were 17 spatial replicates for *Tamiasciurus* and 12 spatial replicates for *G. sabrinus*. Total numbers of individual squirrels were 2804 *Tamiasciurus* and 837 *G. sabrinus*. Total number of study years was 25 with 158 trapping periods overall (Table 2). Mean Jolly trappability was similar among treatment stands for both *Tamiasciurus* ($F_{4,31} = 0.30$; $P = 0.88$) and *G. sabrinus* ($F_{4,16} = 1.50$; $P = 0.25$), with overall means ranging from 61-68% for *Tamiasciurus* and 51-61% for *G. sabrinus* (Figs. 2a+b).

Tamiasciurus - abundance

Mean annual or seasonal abundances per ha for *Tamiasciurus* in old-growth, unthinned, and low-, medium-, and high-density stands for all studies are listed in Table 3. Mean abundance of *Tamiasciurus* was similar among treatment stands during summer and winter periods and overall (Table 4). Not surprisingly, mean numbers of *Tamiasciurus* differed among blocks ($P < 0.01$) in summer and overall, but stand x block interactions were not significant (Table 4). However, overall mean abundance of *Tamiasciurus* was significantly higher (non-overlapping CIs) in old-growth, low-density, and high-density stands than in unthinned stands (Fig. 3a). In terms of effect size, mean proportional changes in abundance in the three thinned stands were within the range of natural fluctuations in the old-growth stands (Fig. 3b). Mean proportional change of *Tamiasciurus* populations in the unthinned stands for this measurement was less than 1.0, and hence was not within the natural variability in abundance of the old-growth populations (Fig. 3b).

***Tamiasciurus* – demographic attributes**

Mean proportion of male *Tamiasciurus* breeding was similar among stands ranging from 73% to 87% (Table 5), but there was a significant ($F_{4,28} = 3.07$; $P = 0.03$) difference in mean proportion of females breeding (Table 4; Fig. 4a). Although no differences among means was detected by DMRT, there were 12-13% fewer female squirrels in reproductive condition (range 57% to 70%) in the low-density stands than unthinned or old-growth stands (Fig. 4a). In terms of effect size, mean changes in proportion of breeding female *Tamiasciurus* in the three thinned stands were 65% to 69% of those in the old-growth stands, but still within the range of natural fluctuations in the old-growth

stands (Fig. 4b). Reproduction was further analyzed by mean number of successful pregnancies which was similar among treatment stands, ranging from 3.3 to 6.1 (Table 4, Fig. 5a). Assessment of the effect size indicated that mean proportion of the number of successful pregnancies between old-growth and treatment stands had overlapping 95% CIs for all stands for this measure of reproduction (Fig. 5b). There were no significant differences among treatment stands in the mean number of recruits (Table 4), being consistent at 12-16 new squirrels per sampling unit in a given annual or seasonal period across the five stands (Fig. 6a). In terms of effect size, mean proportional changes in number of recruits of *Tamiasciurus* were again within the naturally fluctuating numbers of new squirrels in the old-growth stands (Fig. 6b).

Mean monthly summer survival of *Tamiasciurus* was similar among stands ranging from 74% to 81% (Fig. 7a), but mean winter survival was significantly ($F_{4,19} = 4.90$; $P < 0.01$) different among stands (Table 4). Mean winter survival of squirrels ranged from 84% to 92% and was lower in the high-density stand than the old-growth, unthinned, and medium-density stands, but similar to that in the low-density stands (Fig. 8a). In both seasons, the effect size of these comparisons for the unthinned and thinned stands had 95% CIs that overlapped with those of the old-growth stands (Figs. 7b and 8b).

Mean male body mass of *Tamiasciurus* ranged from a low of 208 g in the unthinned stands to 225 g in the high-density stands, but the comparison among stands was not formally significant ($F_{4,31} = 2.36$; $P = 0.07$) (Tables 4 and 6). However, overall mean mass was significantly (non-overlapping 95% CIs) higher in the high-density than unthinned stands.

These demographic measurements for *Tamiasciurus* differed among blocks in all categories except for male breeding and summer survival. Only summer survival of *Tamiasciurus* had a significant stand x block interaction (Table 4).

***G. sabrinus* – abundance**

Mean annual or seasonal abundances per ha for *G. sabrinus* in old-growth, unthinned, and low-, medium-, and high-density stands for all studies are listed in Table 3. Mean abundance of *G. sabrinus* was similar among treatment stands during summer and winter periods, but significantly ($F_{4,24} = 3.76$; $P = 0.02$) different overall (Table 7; Fig. 9a). Mean numbers of flying squirrels were highest in the old-growth stands at 0.65/ha, followed by the low- and medium-density stands at 0.50/ha, the high-density stands at 0.25/ha, and finally the unthinned stands at a low of 0.12/ha (Fig. 9a). There were 35 occasions when *G. sabrinus* were trapped simultaneously in old-growth and managed stands within each study (Table 3). For 11 pairings (31%), abundances of *G. sabrinus* were within 10% of each other (including stands with zero squirrels captured). For 12 pairings (34%), abundance of *G. sabrinus* in old-growth stands exceeded that in managed stands by an average factor of 2.0. Similarly, abundance of *G. sabrinus* in managed stands exceeded that in old growth on 12 occasions (34%) and by an average factor of 2.25. Mean numbers of *G. sabrinus* differed among blocks ($P < 0.01$) in summer and overall, with significant stand x block interactions for the three periods (Table 7). In terms of effect size, mean proportional change in abundance in the unthinned and three thinned stands were within the range of natural fluctuations in the old-growth stands, with respect to overlapping 95% CIs (Fig. 9b). However, both the

unthinned and high-density stands had a wide range of variability in effect size (Fig. 9b) that reflected their low densities in these stands (Fig. 9a).

***G. sabrinus* – demographic attributes**

There were no significant differences among treatment stands in mean proportion of males or females breeding (range 55% to 67%) (Table 5, Fig. 10a). In terms of effect size, mean proportional changes in proportion of breeding female *G. sabrinus* in the unthinned and three thinned stands were highly variable compared with those in the old-growth stands, but still within the range of natural fluctuations in the old-growth stands (Fig. 10b). To further analyze reproduction, we assessed mean number of successful pregnancies which were similar among stands (Table 7) ranging from 0.7 to 2.5 (Fig. 11a). Effect size was again variable but in all stands was still within the range of values estimated for the old-growth stands (Fig. 11b). Mean number of recruits was significantly ($F_{4,17} = 3.87$; $P = 0.02$) different among treatment stands (Table 7; Fig. 12a). Although no differences among means were detected by DMRT, there were overall 2.3 to 2.6 times as many recruits appearing in the old-growth than unthinned or medium-density stands. Overall mean numbers of recruits in the low-density stands was 6.7, in the high-density stands was 5.4, compared with 8.0 in the old-growth stands (Fig. 12a). However, effect size for total recruits indicated overlapping 95% CIs for all stands (Fig. 12b).

Mean monthly summer and winter survival measurements of *G. sabrinus* were similar among stands (Table 7, Figs. 13a and 14a). Mean summer survival ranged from 76% to 89% and winter survival ranged from 67% to 76%. Mean proportional changes

in survival indicated that the biological significance of these differences was small when comparing stands. Mean body mass for *G. sabrinus* was similar among stands and ranged from 127 g to 136 g (Tables 6 and 7).

These demographic measurements differed among blocks for proportion of females breeding, recruits, and body mass, but there were no significant stand x block interactions (Table 7).

Discussion

Datasets

Our analysis is the first analytical review of multi-datasets that had a standard methodology investigating demographic responses of tree squirrel populations in natural and managed coniferous forests. As noted, there were 17 spatial replicates for *Tamiasciurus* and 12 for *G. sabrinus* covering five stand types over 25 years of study. We investigated population responses of these tree squirrels in seven different geographic regions of southern BC with consistent “controls” of natural stands: old-growth stands and unthinned second-growth stands. Managed second-growth stands included three relatively broad densities (trees/ha): low (300-500), medium (501-1200), and high (1201-2300), that originated from PCT or CT, or as a natural process, in young regenerating forests after clearcutting or wildfire. This relatively wide range of stand densities (e.g., extremes in silvicultural treatments, Sullivan et al. 2013) was crucial to understanding the responses of tree squirrels to variable levels of stand development through time. They were also designed to influence stand development to co-produce wood products and structural features for wildlife. This range of stand densities and our

many regional replicates of large-scale treatments allowed extrapolation of inferences to managed young stands across a wide geographic area such as the PNW of North America. Old-growth stands likely had little or no influence on the pattern of results in second-growth stands, and hence this pattern should remain robust in landscapes devoid of old-growth forest.

Our quantitative analyses of population size relied on the ETA (a boundary strip method) rather than the spatial estimators of Efford (2009). Both types of estimators have provided similar relationships such that trends in density could be inferred across methods (Krebs et al. 2011). In addition, we measured qualitative attributes of reproduction, recruitment, and survival as well as abundance for all populations with multiple sampling periods in different seasons over several years. Thus, mean values calculated per year or season were based on several sampling periods. Such qualitative measures are often missing in many studies of tree squirrel responses to forest management. However, these data are critical when inferring habitat quality, especially for *Tamiasciurus*. This genus of sciurid is often territorial; thus young of the year may be typically displaced to suboptimal habitats prior to winter (Klenner 1991). Populations in these sink habitats would be characterized by low reproduction, low survival, and low body weights, even though abundance could exceed that in optimal source populations (Wheatley et al. 2002). Assessment of habitat quality must be based upon reproduction and survival, in addition to abundance. Only when there are no significant differences in reproduction and survival among stand types, can an assessment of habitat quality be based upon abundance alone.

In terms of habitat quality, the importance of seed crops of coniferous trees as a driving factor in population dynamics of red squirrels has been reported by several authors (M. Smith 1968; Kemp and Keith 1970; Gurnell 1987; Fletcher et al. 2010). We did not have a measure of variability in cone crops among our treatment stands nor across study areas, and we recognize this limitation. However, we have assumed that the potential influence of the coniferous seed supply was consistent among stands within a given study area, as cone crops tend to be synchronous across large geographic areas (Koenig and Knops 1998).

In addition, our analyses included estimations of effect size, relative to control stands (old-growth). This is the preferred analysis to distinguish between 'no significant differences' and 'inconclusive results', when retrospective power analyses were inappropriate, as discussed by Steidl et al. (1997). Our analyses varied slightly from Steidl et al. (1997), as we did not identify a 'biologically' significant effect size. Setting a specific quantity that distinguished significant differences (biologically) from no significant differences (biologically) would be subjective with little support from the literature. Alternatively, we have included the effect size in graphs which allows the reader to assess biological significance according to their research and experiences.

Tamiasciurus

Mean abundance of *Tamiasciurus* was similar across all stand types, although overall mean ($\pm$ 95% CIs) numbers were less in the unthinned stands. The biological significance of this difference was observed in the three thinned stands that had proportional changes in abundance within the range of natural fluctuations in the old-

growth stands. Populations of *Tamiasciurus* in the unthinned stands did not fit within fluctuations in the old-growth stands. Thus, these results did not support the abundance part of our hypotheses that abundance and demographic attributes would be higher in H_1 : old-growth than second-growth stands, H_2 : unthinned than thinned second-growth stands, or H_3 : lightly thinned than heavily thinned stands. Most demographic attributes for *Tamiasciurus* also followed this pattern of not supporting hypothesis predictions, except for mean proportion of females breeding and mean monthly winter survival. Results of proportion of females breeding seemed to support, in part, both H_1 and H_2 , and possibly H_3 . This reproductive parameter did not relate to the similar number of successful pregnancies and recruitment of new squirrels among stands. Results for winter survival seemed to partly support H_1 and H_2 when comparing *Tamiasciurus* populations in old-growth and unthinned stands to the high-density stands. However, in terms of the biological significance of these demographic effects, the actual “effect sizes” observed in the unthinned and thinned stands were well within the mean values of natural fluctuations of demographic variables.

Our analysis clearly demonstrated that populations of *Tamiasciurus* occurred at comparable abundance levels in old-growth and thinned second-growth stands. Except for the noted demographic variables, measurements of population quality were also generally similar among these stands. Body mass appeared to be a good indicator of body condition for our *Tamiasciurus*, as noted in other studies by Cote and Ferron (2001) for *T. hudsonicus* and by Wauters and Dhondt (1989) for *S. vulgaris*. In particular, *S. vulgaris* inhabiting good habitats had significantly higher mean body weights than those from poor habitats (Wauters and Dhondt 1989). Presumably all five

stand types in our analysis provided good habitat conditions for *Tamiasciurus*. We do not have specific measurements on cone production, but all stands in these studies had trees with some cones. In addition, various species of nuts, berries, and fungi are readily eaten by red squirrels (Steele 1998), and many of these foods are available in young to mid-successional stands such as our second-growth stands that ranged in age from 17 to 70 years (Allard-Duchene et al. 2014). Based on our regression analyses, *Tamiasciurus* occupied a wide range of stand densities and ages.

Thus, we conclude that *Tamiasciurus* is a habitat generalist that will occupy a wide variety of coniferous forests as also reported for *T. hudsonicus* by Bayne and Hobson (2000), Cote and Ferron (2001), and Swihart et al. (2007). Exceptions include young (< 25 years of age) heavily thinned (500 trees/ha) stands (Sullivan et al. 1996) and the variety of unthinned stands in this analysis. However, they do disappear for at least the first decade after clearcutting of mature and old-growth forests and removal of cone-bearing trees (Wolff and Zasada 1975; Thompson et al. 1989; Cote and Ferron 2001; Herbers and Klenner 2007). *Tamiasciurus* re-appear in sapling and pole-size stands (> 10 years old) where some authors have reported that these habitats may act initially as “dispersal sinks” (Sullivan and Moses 1986; Buchanan et al. 1990; Fisher and Wilkinson 2005). Conversely, other reports have concluded that red squirrels reach their highest densities in older undisturbed forests with few squirrels appearing in younger stands (Kemp and Keith 1970; Rusch and Reeder 1978; Fisher and Wilkinson 2005; Fisher and Bradbury 2006; Holloway and Malcolm 2006). These latter reports did not include population data from young managed coniferous stands of a variety of densities that likely would have resident *Tamiasciurus*, as reflected in our analytical review.

G. sabrinus

Although mean abundance of *G. sabrinus* was similar among treatment stands during summer and winter periods, the overall analysis did detect differences with flying squirrel numbers being less in the unthinned stands than all other stands. Similarly, the lower numbers in the high-density stands than old-growth stands also followed this pattern. The stand x block interaction may negate this analysis, but overall mean abundance $\pm$ 95% CIs produced a similar result. In terms of the magnitude (biological significance) of these differences in mean abundance of flying squirrels, the actual “effect sizes” in the unthinned and thinned stands were well within the mean proportional values of natural fluctuations of this tree squirrel in old-growth stands. Low-density (≤ 500 trees/ha) stands were the least similar managed stands in this comparison, with mean proportional change < 1.0 . Thus, these results supported, in part, the abundance and recruitment aspects of H_1 : that abundance and demographic attributes would be higher in old-growth than second-growth stands, but not H_2 : unthinned than thinned second-growth stands, or H_3 : lightly thinned than heavily thinned stands. The similarity of all other demographic attributes for *G. sabrinus* among treatment stands did not support hypothesis predictions.

The number of occurrences that abundance of *G. sabrinus* in old-growth stands exceeded, was similar to, or fell below that in managed stands was evenly distributed across 35 pair-wise comparisons. When abundance of *G. sabrinus* in old-growth stands exceeded or fell below managed stands, they did so by a factor of 2 or 2.5 (respectively). These findings strongly support the conclusions of Ransome and Sullivan

(2003) that old-growth stands only occasionally provide better habitat (based upon abundance *and* reproduction and survival) than managed second-growth stands for *G. sabrinus*. Clearly, managed second-growth stands (especially medium- and high-density stands) often maintain healthy populations (based on abundance, reproduction, and survival) of *G. sabrinus* relative to old-growth stands. Furthermore, there is equal probability that health of *G. sabrinus* populations in managed second-growth stands may exceed that in old-growth stands as the antithesis.

Consistently low numbers of *G. sabrinus* were recorded in low-density second-growth stands in interior (Ransome et al. 2004; Sullivan et al. 2013), but not coastal areas (Ransome and Sullivan 2002, 2003; Gomez et al. 2005). Manning et al. (2012) reported that heavy thinning decreased density of *G. sabrinus* in coastal forest, but was a particularly weak study with a 4-night trapping regime and paucity of squirrel data. Mean abundance of *G. sabrinus* did not differ between lodgepole pine stands ranging from 1,942 to 2,303 trees/ha and old-growth forest at 28-30 years after PCT (Sullivan et al. 2010). Presumably the increase in tree diameters and heights, as well as understory coniferous structural diversity, in thinned stands at these densities may have provided sufficient canopy closure and concomitant food and cover (Sullivan et al. 2010). Lehmkuhl et al. (2006) found that a threshold of 55% canopy cover separated stands with low- and high-density populations of *G. sabrinus*.

We had no direct measures of food sources such as hypogeous fungi (truffles) in these stands. Colgan et al. (1999) reported that biomass of hypogeous fungi decreased following medium and heavy variable-density thinning in Washington. However, these authors found a shift in species dominance that resulted in a greater abundance of the

more nutritious hypogeous fungi in thinned than control stands. In a longer-term study, total relative frequency and biomass of hypogeous fungi was similar among heavily- and moderately-thinned stands, as well as unthinned stands 10 and 17 years after CT in California (Waters et al. 1994). Although we did not evaluate response of hypogeous fungi to PCT, higher abundance of *G. sabrinus* in high-density stands might reflect a positive response of hypogeous fungi to thinning. Gomez et al. (2005) and Lehmkuhl et al. (2006) both concluded that the presence of hypogeous sporocarps may be more important for flying squirrels than forest structure. Rosenberg and Anthony (1992) suggested that food availability, predation, and competition with other species (e.g., *Tamiasciurus*, Smith 2012) may limit abundance of *G. sabrinus* more than structural components of forests. In terms of absolute abundance, Gomez et al. (2005) reported densities of flying squirrels $\geq 1.5/\text{ha}$ in structurally simple Douglas-fir forests that were comparable to those recorded for this sciurid in late-successional forests (Carey et al. 1992, 1999; Smith et al. 2003). Our patterns of overall mean abundance of *G. sabrinus* reached this level in various stand conditions. Smith (2007), Trudeau et al. (2012), and Priol et al. (2014) suggested that *G. sabrinus* may be more of a generalist species occupying a broader array of forest habitats than earlier postulated.

Conclusions

Based on our comprehensive analysis of datasets derived from identical methodologies over a matrix of second- and old-growth forests, we conclude that *Tamiasciurus* and *G. sabrinus* seem to persist in a relatively broad range of young managed forest habitats, as well as in old-growth stands. Their negative population

responses to various harvesting regimes of mature and old-growth forests suggests strongly that forest and wildlife managers need to focus on diversified management of second-growth forests as future habitat supply for these tree squirrels. The attention given to partial harvesting regimes to maintain some “old-forest” components is admirable, but clearcutting will continue to be the major harvesting method in temperate and boreal forests well into the foreseeable future. Many of these “matrix” habitats will be managed to sustain a flow of wood products, and it is these habitats that will be required to support viable populations of tree squirrels and other old-growth dependent wildlife species.

What, then, is our message to managers who may be exposed to a host of contradictory results based on incomplete meta-analyses or studies with “snapshots” of data in space and time? In the absence of analytical reviews like ours, managers should look for comprehensive studies (covering at least three years) with multiple sampling periods of mark-recapture data for tree squirrel populations representing different seasons and quantitative (abundance) as well as demographic (reproduction, recruitment, and survival) measurements.

Acknowledgements

We thank the British Columbia (BC) Ministry of Forests, Lands, and Natural Resource Operations for financial support to prepare this document. Many of our studies over the past 28 years helped to formulate this review and we thank the Silviculture, Forest Practices, Research Branches, and several Forest Districts, BC Ministry of Forests, Forest Resource Development Agreements, Forest Renewal BC,

Gorman Bros. Lumber Ltd., Northwood Pulp and Timber Ltd., Weyerhaeuser Company Limited, Canadian Forest Products Limited (Grande Prairie, Alberta), L & M Lumber Ltd., and the Sustainable Forest Management Network, University of Alberta for support. L. Imbeau and an anonymous reviewer provided very helpful comments on an earlier version of the manuscript.

References

- Allard-Duchene, A., D. Pothier, A. Dupuch, and D. Fortin. 2014. Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession. *For. Ecol. Manage.* **313**: 7-25.
- Andren, H. and Lemnell, P. 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. *Ecography* **15**: 303-307.
- Aubry, K.B., Hayes, J.P., Biswell, L.B., Marcot, B.G. 2003. The ecological role of tree-dwelling mammals in western coniferous forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press. Pp. 405-443.
- Bayne, E.M., and Hobson, K.A. 2000. Relative use of contiguous and fragmented boreal forest by red squirrels (*Tamiasciurus hudsonicus*). *Can. J. Zool.* **78**: 359-365.
- Benkman, C.W. 1993. Logging, conifers, and the conservation of crossbills. *Cons. Biol.* **7**: 473-479.
- Boonstra, R., S. Boutin, A. Byrom, T. Karels, A. Hubbs, K. Stuart-Smith, M. Blower, and S. Antpoehler. 2001. The role of red squirrels and arctic ground

- 636 squirrels. *In* Ecosystem Dynamics of the Boreal Forest: The Kluane Project. C. J.
637 Krebs, S. Boutin, and R. Boonstra, eds. Oxford University Press, New York.
- 638 Brink, C.H. and Dean, F.C. 1966. Spruce seeds as a food of red squirrels and flying
639 squirrels in interior Alaska. *J. Wildl. Manage.* **30**: 503-512.
- 640 Buchanan, J.B, Lundquist, R.W, and Aubry, K.B. 1990. Winter populations of Douglas'
641 squirrels in different-aged Douglas-fir forests. *J. Wildl. Manage.* **54**: 577-581.
- 642 Burns, R.M. and Honkala, B.H. 1990. *Silvics of North American Conifers*. Vol. 1.
643 Handbook 654. USDA Forest Service. Washington, DC.
- 644 Carey, A.B. and Harrington, A.H. 2001. Small mammals in young forests: implications
645 for management for sustainability. *For. Ecol. Manage.* **154**: 289-309.
- 646 Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations.
647 *Ecol. Applic.* **10**: 248-257.
- 648 Carey, A.B., Horton, S.P., and Biswell, B.L. 1992. Northern spotted owls: influence of
649 prey base and landscape character. *Ecol. Monogr.* **62**: 223-250.
- 650 Carey, A.B., Kershner, J., Biswell, B., DeToledo, L.D., 1999. Ecological scale and forest
651 development: squirrels, dietary fungi, and vascular plants in managed and
652 unmanaged forests. *Wildl. Monogr.* **142**.
- 653 Cazares, E., Luoma, D.L., Amaranthus, M.P., Chambers, C.L. and Lehmkuhl, J.F. 1999.
654 Interaction of fungal sporocarp production with small mammal abundance and diet
655 in Douglas-fir stands of the southern Cascade range. *Northwest Sci.* **73**: 64-76.
- 656 Colgan, W., III., Carey, A.B., Trappe, J.M., Molina, R., and Thysell, D., 1999. Diversity
657 and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir
658 forest. *Can. J. For. Res.* **29**: 1259-1268.

- 659 Cote, M. and Ferron, J. 2001. Short-term use of different residual forest structures by
660 three sciurid species in a clear-cut boreal landscape. *Can. J. For. Res.* **31**: 1805-
661 1815.
- 662 Efford, M.G., D.L. Borchers, and A.E. Byrom. 2009. Density estimation by spatially
663 explicit capture-recapture: likelihood-based methods. Pages 255-269 in *Modeling*
664 *demographic processes in marked populations* (E.G. Cooch, D.L. Thomson, and
665 M.J. Conroy, eds.). Springer, New York.
- 666 Fisher, J.T. and Wilkinson, L. 2005. The response of mammals to forest fire and timber
667 harvest in the North American boreal forest. *Mammal Rev.* **35**: 51-81.
- 668 Fisher, J.T. and S.M. Bradbury. 2006. Understorey protection harvest expedites
669 recolonisation of boreal forest stands by North American red squirrels. *Forest Ecol.*
670 *Manage.* 234: 40-47.
- 671 Fletcher, Q. E., S. Boutin, J. E. Lane, J. M. LaMontagne, A. G. McAdam, J. R.
672 Speakman, C. J. Krebs, and M. M. Humphries. 2010. The functional response of a
673 hoarding seed predator to mast seeding. *Ecology* **91**: 2673-2683.
- 674 Fowler, J., Cohen, L., and Jarvis, P., 1998. *Practical Statistics for Field Biology*. Second
675 Edition. John Wiley and Sons. 259 pp.
- 676 Gerard, P.D., Smith, D.R., and Weerakkody, G. 1998. Limits of retrospective power
677 analysis. *J. Wildl. Manage.* **62**: 801-807.
- 678 Gomez, D.M., Anthony, R.G., and Hayes, J.P., 2005. Influence of thinning of Douglas-fir
679 forests on population parameters and diet of northern flying squirrels. *J. Wildl.*
680 *Manage.* 69: 1670-1682.

- 681 Graybill, F.A. and Iyer, H.K., 1994. Regression analysis: concepts and applications.
682 Duxbury Press, Belmont, California. 701 pp.
- 683 Gurnell, J. 1987. The Natural History of Squirrels. Christopher Helm. London. 201 p.
- 684 Herbers, J. and Klenner, W. 2007. Effects of logging pattern and intensity on squirrel
685 demography. J. Wildl. Manage. **71**: 2655-2663.
- 686 Holiman, W.C., Benkman, C.W. and Willson, M.F. 1998. The importance of mature
687 conifers to red crossbills in southeast Alaska. For. Ecol. Manage. **102**: 167-172.
- 688 Holloway, G.L. and Malcolm, J.R. 2006. Sciurid habitat relationships in forests
689 managed under selection and shelterwood silviculture in Ontario. J. Wildl. Manage.
690 **70**: 1735-1745.
- 691 Holloway, G.L. and Smith, W.P. 2011. A meta-analysis of forest age and structure
692 effects on northern flying squirrel densities. J. Wildl. Manage. **75**: 668-674.
- 693 Holloway, G.L., Smith, W.P., Halpern, C.B., Gitzen, R.A., Maguire, C.C., and West, S.D.
694 2012. Influence of forest structure and experimental green-tree retention on
695 northern flying squirrel (*Glaucomys sabrinus*) abundance. For. Ecol. Manage. **285**:
696 187-194.
- 697 IBM Corp. 2014. IBM SPSS Statistics for Windows, Version 22.0. IBM Corp, Armonk,
698 NY.
- 699 Johnson, D.H. 1999. The insignificance of statistical significance testing. J. Wildl.
700 Manage. **63**: 763-772.
- 701 Jolly, G. M., and Dickson, J. M. 1983. The problem of unequal catchability in mark-
702 recapture estimation of small mammal populations. Can. J. Zool. **61**: 922-927.

- 703 Kemp, G.A., and Keith, L.B., 1970. Dynamics and regulation of red squirrel
704 (*Tamiasciurus hudsonicus*) populations. *Ecology* **51**: 763-779.
- 705 Klenner, W., 1991. Red squirrel population dynamics. II. Settlement patterns and the
706 response to removal. *J. Anim. Ecol.* **60**: 979-993.
- 707 Klenner, W., and Krebs, C.J., 1991. Red squirrel population dynamics. I. The effect of
708 supplemental food on demography. *J. Anim. Ecol.* **60**: 961-978.
- 709 Koenig, W.D., and J.M.H. Knops. 1998. Scale of mast-seeding and tree-ring growth.
710 *Nature* **396**: 225-226.
- 711 Krebs, C. J. 1999. *Ecological Methodology*. Addison Wesley Longman, Inc. 624 p.
- 712 Krebs, C.J., and Boonstra, R. 1984. Trappability estimates for mark-recapture data. *Can.*
713 *J. Zool.* **62**: 2440-2444.
- 714 Krebs, C.J., Boonstra, R., Gilbert, S., Reid, D., Kenney, A.J., and Hofer, E. J. 2011.
715 Density estimation for small mammals from livetrapping grids: rodents in northern
716 Canada. *J. Mammal.* **92**: 974-981.
- 717 Krebs, C.J., Keller, B.L., and Tamarin, R.H., 1969. *Microtus* population biology:
718 demographic changes in fluctuating populations of *Microtus ochrogaster* and *M.*
719 *pennsylvanicus* in southern Indiana. *Ecology* **50**: 587-607.
- 720 LaMontagne J.M., C.T. Williams, J.L. Donald, M.M. Humphries, A.G. McAdam, and S.
721 Boutin. 2013. Linking intraspecific variation in territory size, cone supply, and
722 survival of North American red squirrels. *J. Mammal.* **94**: 1048-1058.
- 723 Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., and Boulanger, J. 2006. Demography of
724 northern flying squirrels informs ecosystem management of western interior forests.
725 *Ecol. Applic.* **16**: 584-600.

- 726 Lindenmayer, D.B., and Franklin, J.F. 2002. Conserving forest biodiversity: a
727 comprehensive multiscaled approach. Island Press, Washington, DC.
- 728 Lurz, P.W., Garson, P.J., and Rushton, S.P. 1995. The ecology of squirrels in spruce
729 dominated plantations: Implications for forest management. *For. Ecol. Manage.* **79**:
730 79-90.
- 731 Manning, T., Hagar, J.C., and McComb, B.C., 2012. Thinning of young Douglas-fir
732 forests decreases density of northern flying squirrels in the Oregon Cascades. *For.*
733 *Ecol. Manage.* **264**: 115-124.
- 734 Maser, C. and Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and
735 coniferous forests in Oregon. *Great Basin Nat.* **48**: 358-369.
- 736 Meidinger, D., and Pojar, J., 1991. Ecosystems of British Columbia. Research Branch
737 Ministry of Forests, Victoria, B.C. Special Report Series No. 6. 330 p.
- 738 Mendoza, S.V., Harvey, C.A., Saenz, J.C. et al. 2014. Consistency in bird use of tree
739 cover across tropical agricultural landscapes. *Ecol. Applic.* **24**: 158-168.
- 740 Molina, R., O'Dell, T., Dunham, S. and Pilz, D. 1999. Biological diversity and
741 ecosystem functions of forest soil fungi: management implications. In: Meurisse,
742 R., Ypsilantis, W.G. & Seybold, C. (eds.). *Proceedings: Pacific Northwest Forest &*
743 *Rangeland Soil Organism Symposium*, March 17-19, 1998, USDA, Forest Service,
744 Pacific Northwest Research Station, Portland Oregon, General Technical Report
745 PNW-GTR-461.
- 746 Norse, E.A. 1990. *Ancient forests of the Pacific Northwest*. Island Press, Washington.
- 747 Priol, P., M.J. Mazerolle, L. Imbeau, P. Drapeau, C. Trudeau, and R. Ramiere. 2014.
748 Using dynamic N-mixture models to test cavity limitation on northern flying squirrel

- 749 demographic parameters using experimental nest box supplementation. *Ecol. Evol.*
750 **4**: 2165-2177.
- 751 Ransome, D.B., Lindgren, P.M.F., Sullivan, D.S., and Sullivan, T.P. 2004. Long-term
752 responses of ecosystem components to stand thinning in young lodgepole pine
753 forest: I. Population dynamics of northern flying squirrels and red squirrels. *For.*
754 *Ecol. Manage.* **202**: 355-367.
- 755 Ransome, D.B., and Sullivan, T.P., 1997. Food limitation and habitat preference of *G.*
756 *sabrinus* and *T. hudsonicus*. *J. Mammal.* **78**: 538-549.
- 757 Ransome, D.B., and Sullivan, T.P. 2002. Short-term population dynamics of *Glaucomys*
758 *sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands
759 of coastal coniferous. *Can. J. For. Res.* **32**: 2043-2050.
- 760 Ransome, D.B., and Sullivan, T.P. 2003. Population dynamics of *Glaucomys sabrinus*
761 and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal
762 coniferous forest. *Can. J. For. Res.* **33**: 587-596.
- 763 Ransome, D.B., and Sullivan, T.P. 2004. Effects of food and den-site supplementation
764 on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *J. Mammal.* **85**:
765 206-215.
- 766 Raphael, M.G., 1988. Habitat associations of small mammals in a subalpine forest,
767 southeastern Wyoming. In: Szaro, R.C., Severson, K.E., Patton, D.R. (Tech. Eds.),
768 Management of amphibians, reptiles, and small mammals in North America. USDA
769 For. Serv. Gen. Tech. Rep. RM-166, pp. 359-367.

- 770 Rosenberg, D.K., and Anthony, R., 1992. Characteristics of northern flying squirrel
771 populations in young second- and old-growth forests of western Oregon. Canadian
772 Journal of Zoology **70**: 161-166.
- 773 Rosencranz, A. and Scott, A. 1992. Siberia's threatened forests. Nature **355**: 293-294.
- 774 Rusch, D.A., and Reeder, W.G., 1978. Population ecology of Alberta red squirrels.
775 Ecology **59**: 400-420.
- 776 Saville, D.J. 1990. Multiple comparison procedures: the practical solution. Amer. Stat.
777 **44**: 174-180.
- 778 Seber, G.A.F., 1982. The estimation of animal abundance and related parameters. 2nd
779 edn. Charles Griffin, Co., London, UK.
- 780 Smith, C.C., 1968. The adaptive nature of social organization in the genus of tree
781 squirrels *Tamiasciurus*. Ecol. Monogr. **38**: 31-63.
- 782 Smith, M. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J.
783 Wildl. Manage. **32**: 305-317.
- 784 Selonen V. and Hanski, I.K. 2003. Movements of the flying squirrel *Pteromys volans* in
785 corridors and in matrix habitat. Ecography **26**: 641-651.
- 786 Smith, W.P. 2007. Ecology of *Glaucomys sabrinus*: Habitat, demography, and
787 community relations. J. Mammal. **88**, 862-881.
- 788 Smith, W.P. 2012. Flying squirrel demography varies between island communities with
789 and without red squirrels. Northwest Sci. **86**: 27- 38.
- 790 Smith, W.P., Anthony, R.G., Waters, J.R., Dodd, N.L. and Zabel, C.J. 2003. Ecology
791 and conservation of arboreal rodents of western coniferous forests. In: Zabel, C.J.
792 & Anthony, R.G. (eds.). Mammal community dynamics. Management and

- 793 conservation in forests of western North America. Cambridge University Press,
794 Cambridge, UK. p. 157-206.
- 795 Smith, W.P., Gende, S.M. and Nichols, J.V. 2005. The northern flying squirrel as an
796 indicator species of temperate rain forest: test of an hypothesis. *Ecol. Applic.* **15**:
797 689-700.
- 798 Steele, M.A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species No. 586, 9 p.
- 799 Steidl, R.J., Hayes, J.P., and Schaubert, E. 1997. Statistical power analysis in wildlife
800 research. *J. Wildl. Manage.* **61**: 270-279.
- 801 Strittholt, J.R., Dellasala, D.A., and Jiang, H. 2006. Status of mature and old-growth
802 forests in the Pacific Northwest. *Cons. Biol.* **20**: 363-374.
- 803 Sullivan, T.P. 1987. Red squirrel population dynamics and feeding damage in juvenile
804 stands of lodgepole pine. Forest Resource Development Agreement. Canadian
805 Forestry Service, British Columbia Ministry of Forests. FRDA Report 019.
- 806 Sullivan, T.P., 1990. Responses of red squirrel (*Tamiasciurus hudsonicus*) populations
807 to supplemental food. *J. Mammal.* **71**: 579-590.
- 808 Sullivan, T.P. and Klenner, W. 1993. Influence of diversionary food on red squirrel
809 populations and damage to crop trees in young lodgepole pine forest. *Ecol. Applic.*
810 **3**: 708-718.
- 811 Sullivan, T.P. and R.A. Moses. 1986. Comparison of red squirrel populations in natural
812 and managed stands of lodgepole pine. *J. Wildl. Manage.* **50**: 595-601.
- 813 Sullivan, T.P., and Sullivan, D.S. 2003. Vegetation management and ecosystem
814 disturbance: Impact of glyphosate herbicide on plant and animal diversity in
815 terrestrial systems. *Environ. Rev.* **11**:37-59.

- 816 Sullivan, T.P., Klenner, W., and Diggle, P.K. 1996. Response of red squirrels and
817 feeding damage to variable stand density in young lodgepole pine forest. *Ecol.*
818 *Appl.* **6**: 1124-1134.
- 819 Sullivan, T.P., Nowotny, C., Lautenschlager, R.A., and Wagner, R.G. 1998. Silvicultural
820 use of herbicide in sub-boreal spruce forest: Implications for small mammal
821 population dynamics. *J. Wildl. Manage.* **62**: 1196-1206.
- 822 Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Ransome, D.B. 2010. Green-tree
823 retention and life after the beetle: Stand structure and small mammals 30 years after
824 salvage harvesting. *Silva Fenn.* **44**: 749-774.
- 825 Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., and Ransome, D.B. 2013. Stand
826 structure and small mammals in intensively managed forests: Scale, time, and
827 testing extremes. *For. Ecol. Manage.* **310**: 1071-1087.
- 828 Swihart, R.K., Goheen, J.R., Schnelker, S.A., and Rizkalla, C.E. 2007. Testing the
829 generality of patch and landscape-level predictors of tree squirrel occurrence at a
830 regional scale. *J. Mammal.* **88**: 564-572.
- 831 Thompson, I.D., Davidson, I.J., O'Donnell, S., and Brazeau, F. 1989. Use of track
832 transects to measure the relative occurrence of some boreal mammals in uncut
833 forest and regeneration stands. *Can. J. Zool.* **67**: 1816-1823.
- 834 Trudeau, C., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2012. Winter site occupancy
835 patterns of the northern flying squirrel in boreal mixed-wood forests. *Mamm. Biol.* **77**:
836 258-263.
- 837 Vahle, J.R. and Patton, D.R. 1983. Red squirrel cover requirements in Arizona mixed
838 conifer forests. *J. For.* **81**: 14-15, 22.

- 839 Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl.
840 Manage. **47**: 893-901.
- 841 Waters, J.R., McKelvey, K.S., and Zabel, C.J. 1994. The effect of thinning and
842 broadcast burning on sporocarp production of hypogeous fungi. Can. J. For. Res.
843 **24**: 1516-1522.
- 844 Waters, J.R. and Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of
845 northeastern California. J. Wildl. Manage. **59**: 858-866.
- 846 Wauters, L.A., and Dhondt, A.A. 1989. Variation in length and body weight of red
847 squirrel (*Sciurus vulgaris*) in two different habitats. J. Zool. **217**: 93-106.
- 848 Wells-Gosling, N. and Heaney, L.R. 1984. *Glaucomys sabrinus*. Mammalian Species
849 No. 229. 8 p.
- 850 Wheatley, M., Larsen, K.W., and Boutin, S., 2002. Does density reflect habitat quality
851 for North American red squirrels during a spruce-cone failure? J. Mammal. **83**:
852 716-727.
- 853 Wilson, K. R., and Anderson, D. R. 1985. Evaluation of two density estimators of small
854 mammal population size. J. Mammal. **66**:13-21.
- 855 Wolff, J.O. and Zasada, J.C. 1975. Red squirrel response to clearcut and shelterwood
856 systems in interior Alaska. USDA For. Ser. Res. Note PNW-255.
- 857 Zar, J. H. (1999). *Biostatistical analysis*. 4th edn. Prentice-Hall, Inc., Englewood Cliffs,
858 New Jersey, USA.

Table 1. Characteristics of coniferous forest stands for the study areas and treatment sites, southern British Columbia, Canada from 1981 to 2008. Sw =- white spruce; PI = lodgepole pine; Ab = subalpine fir; Hw = western hemlock; Cw = western red cedar; Df = Douglas-fir. Ecological zones sourced from Meidinger and Pojar (1991).

Reference and years of study	Study area and stand	Density (stems/ha)			Attributes of dominant tree layer (mean ± SE)			Area (ha)	Ecological zone + year of treatment
		Overstory (>3 m height)		Understory (<3 m height)					
		Crop trees ¹	All conifers		DBH (cm)	Height (m)	Age (yr)		
Sullivan and Moses (1986)	Cariboo								SBPS _{dc}
Sullivan (1987)	Unthinned	-	34,778	-	PI 5.0 ± 0.1	4.5 ± 0.1	20	100+	-
(1981-1986) (1)	Old-growth	-	1295	3795	Sw 23.9 ± 1.9 PI 21.9 ± 0.4	19.5-28.4	140-250	100+	-
	Prince George								SBS _{dw}
	Unthinned	-	20,000	-	PI 5.7 ± 0.1	5.7 ± 0.1	20	1000+	-
	Old-growth	-	555	2395	Sw 30.5 ± 1.2 PI 36.0 ± 1.1	Sw 15.2-26.8 PI 24.2	100-120	100+	-
Sullivan et al. (1996)	Penticton								IDF _{dk} PCT 1988

(1989-1991)	Low density	480	480	-	8.0 ± 0.2	5.1 ± 0.1	17	20.0
(2)	Med density	1078	1078	-	8.4 ± 0.1	5.8 ± 0.1	17	20.0
	High density	1928	1928	-	8.5 ± 0.1	5.6 ± 0.1	17	20.0
	Unthinned	-	4755	-	-	-	17	100+
	Old-growth	-	2170	-	Sw 27.9 ± 1.6	19.5-28.4	160-250	100+
					PI 19.8 ± 0.5			
					Ab 20.6 ± 0.8			

MS_{dm}

Kamloops

PCT 1989

Low density	500	500	-	11.6 ± 0.2	8.2 ± 0.1	24	22.0
Med density	900	900	-	11.6 ± 0.2	8.6 ± 0.1	23	15.0
High density	1614	1614	-	8.6 ± 0.1	8.4 ± 0.2	27	19.0
Unthinned	-	7665	-	-	-	27	100+
Old-growth	-	1860	-	Sw 27.4 ± 2.1	19.5-28.4	160-250	100+
				PI 26.1 ± 0.5			
				Ab 22.2 ± 0.6			

SBS_{dw}

Prince George

PCT 1988

Low density	460	460	-	11.1 ± 0.2	8.8 ± 0.2	20	39.0
Med density	944	944	-	11.0 ± 0.3	8.5 ± 0.2	19	32.0
High density	1900	1900	-	8.8 ± 0.3	7.0 ± 0.2	15-20	30.0
Unthinned	-	4300	-	-	-	20	41
Old-growth	-	1980	-	Sw 23.9 ± 1.2	19.5-28.4	160-250	100+
				PI 24.1 ± 0.8			

<div> Ransome and Sullivan (1997) (1992-1993) (3) </div>	Vernon-1								MS _{dm}
	Med density	775-1200	775-1200	-	PI 13.8 ± 0.2		28	18	PCT 1977-1983
	Old-growth	-	-	-	-		>120	16	FERT 1987
	Vernon-2								
	Med density	775-1200	775-1200	-	PI 16.8 ± 0.3		20	38	
	Old-growth	-	-	-	-		>120	45	
<div> Ransome and Sullivan (2002) (1997-2000) (4) </div>	Chehalis								CWH _{dm} CT 1996
	Low density	352	352	-	31.9 ± 0.6	-	60-70	53	
	Med density	647	647	-	35.2 ± 0.9	-	60-70	>100	
	MK Forest								CT 1997-98
	Low density	320	320	-	38.1 ± 1.9	-	60-70	19.5	
	Med density	775	775	-	31.2 ± 1.0	-	60-70	>1000	
					Hw, Cw	Hw, Cw			
<div> Ransome and Sullivan (2003) (1995-1998) </div>	Coquitlam								CWH _{dm}
	Low density	476	476	-	36.1 ± 1.2	-	60-70		

(5)	Old-growth	266	266	-	47.3 ± 3.6	19.5-28.4	>250	
	Capilano							
	Low density	776	776	-	30.7 ± 0.6	-	60-70	
	Old-growth	258	258	-	49.0 ± 2.8	19.5-28.4	>250	
					Hw, Cw	Hw, Cw		
Ransome et al. (2004)	Penticton							IDF _{dk} PCT 1988
(2000-2002)	Low density	495	700	1415	17.4 ± 0.3	10.5 ± 0.1	32	20.0
(6)	Med density	1065	1350	2000	15.6 ± 0.2	11.7 ± 0.1	32	20.0
	High density	1555	1580	1915	14.1 ± 0.2	11.4 ± 0.1	32	20.0
	Unthinned	-	5850	7200	8.7 ± 0.5	7.8 ± 0.2	32	100+
	Old-growth	-	1640	6720	Sw 25.7 ± 1.6 PI 20.5 ± 0.5 Ab 27.2 ± 1.5	Sw 22.2 ± 0.7 PI 22.3 ± 0.3 Ab 21.1 ± 1.2	160-250	100+
	Kamloops							MS _{dm} PCT 1989
	Low density	465	730	1710	19.3 ± 0.2	14.3 ± 0.4	39	22.0
	Med density	835	845	485	16.9 ± 0.2	14.0 ± 0.2	38	15.0
	High density	1575	1605	385	14.0 ± 0.2	12.5 ± 0.1	42	19.0
	Unthinned	-	6630	130	10.3 ± 0.3	12.7 ± 0.2	42	100+
	Old-growth	-	1370	18360	Sw 27.0 ± 3.1 PI 28.0 ± 1.1	Sw 22.9 ± 1.2 PI 21.5 ± 0.9	160-250	100+

					Ab 22.0 ± 0.8	Ab 18.5 ± 0.6			
Prince George					SBS _{dw} PCT 1988				
	Low density	440	460	555	20.9 ± 0.3	14.1 ± 0.2	35	39.0	
	Med density	850	944	1035	18.4 ± 0.3	14.8 ± 0.2	34	32.0	
	High density	1615	1900	235	15.4 ± 0.3	13.2 ± 0.2	30-35	30.0	
	Unthinned	-	4095	240	11.6 ± 0.4	13.4 ± 0.2	35	41	
	Old-growth	-	1870	1410	Sw 23.6 ± 3.5 PI 27.8 ± 0.8	Sw 17.7 ± 0.8 PI 23.6 ± 0.4	160-250	100+	
Sullivan et al. (2010) (2006-2008) (7)	Summerland-1								MS _{dm}
	High density	1580	1580	1240	14.2	8.0	29	23	PCT 1985
	Old-growth	-	1110	700	PI 23.2 Fd 38.8	PI 20.7 Fd 23.2	80-143	10	
	Summerland-2								
	High density	2295	2295	510	14.5	10.1	29	17	PCT 1985
	Old-growth	-	975	430	PI 21.5 Fd 33.5	PI 17.7 Fd 15.4	80-143	100+	
	Summerland-3								
	High density	2020	2020	390	15.0	9.4	29	17	PCT 1985
	Old-growth	-	2120	940	PI 16.8 Fd 36.8	PI 16.0 Fd 19.7	80-143	100+	

¹ Crop trees were those trees selected to be retained during the PCT or CT treatment; or naturally occurred at low to medium density. FERT = fertilization; PCT = pre-commercial thinning; CT = commercial thinning..

Table 2. Summary of live-trapping regimes in terms of years, sampling periods, number of individual animals for *Tamiasciurus* and *G. sabrinus* for the study areas, southern British Columbia, Canada from 1981 to 2008.

Reference	Total number of years	Total number of trapping periods	<i>Tamiasciurus</i>	<i>G. sabrinus</i>
			Total number of individuals	Total number of individuals
Sullivan (1987) (<i>n</i> =2)	6	56	373	-
Sullivan et al. (1996) (<i>n</i> =3)	3	25	390	-
Ransome and Sullivan (1997) (<i>n</i> =2)	2	16	253	98
Ransome and Sullivan (2002) (<i>n</i> =2)	4	20	250	129
Ransome and Sullivan (2003) (<i>n</i> =2)	4	17	383	261
Ransome et al. (2004) (<i>n</i> =3)	3	15	587	187
Sullivan et al. (2010) (<i>n</i> =3)	3	9	568	162
Totals	25	158	2804	837
			Total number of spatial replicates = 17	Total number of spatial replicates = 12

Table 3. Mean annual or seasonal abundance per ha of red squirrels (*T. hudsonicus*), Douglas squirrels (*T. douglasii*), and northern flying squirrels (*G. sabrinus*) in old-growth, unthinned, and thinned (by PCT, CT, or naturally) coniferous stands in southern British Columbia, Canada from 1981 to 2008. *n* = number of replicates. Old-Gr = old-growth or mature stand; Unthin = unthinned stand; Low = 300-500 trees/ha; Medium = 501-1200 trees/ha; High = 1201-2300 trees/ha; - = no data.

Reference	<i>n</i>	Site and season	Red or Douglas squirrels					Northern flying squirrels				
			Stand density					Stand density				
			Old-Gr	Unthin	Low	Medium	High	Old-Gr	Unthin	Low	Medium	High
Sullivan (1987) (<i>n</i> =2)	1	Cariboo										
			Summer 1981	0.23	0.59	-	-	-	-	-	-	-
			1982	0.66	0.65	-	-	-	-	-	-	-
			1983	1.00	0.75	-	-	-	-	-	-	-
			1984	0.75	0.95	-	-	-	-	-	-	-
			1985	0.70	0.65	-	-	-	-	-	-	-
			1986	0.85	0.42	-	-	-	-	-	-	-
			Winter 1981-82	0.35	0.56	-	-	-	-	-	-	-
			1982-83	1.25	0.81	-	-	-	-	-	-	-
			1983-84	0.90	0.81	-	-	-	-	-	-	-
			1984-85	0.89	0.95	-	-	-	-	-	-	-
			1985-86	0.51	0.46	-	-	-	-	-	-	-
		1 Prince George										
			Summer 1981	1.20	0.76	-	-	-	-	-	-	-
			1982	0.60	0.90	-	-	-	-	-	-	-

		1983	0.86	0.47	-	-	-	-	-	-	-	-
		1984	1.58	0.29	-	-	-	-	-	-	-	-
		1985	1.10	0.76	-	-	-	-	-	-	-	-
		1986	0.99	0.62	-	-	-	-	-	-	-	-
	Winter	1981-82	0.79	0.83	-	-	-	-	-	-	-	-
		1982-83	0.48	0.63	-	-	-	-	-	-	-	-
		1983-84	1.16	0.34	-	-	-	-	-	-	-	-
		1984-85	1.25	0.69	-	-	-	-	-	-	-	-
		1985-86	1.28	1.05	-	-	-	-	-	-	-	-
Sullivan et al.	1	Penticton										
		Summer	1989	-	-	0.11	0.41	0.73				
(1996)			1990	0.09	0.09	0.19	0.74	0.85	-	-	-	-
(n=3)			1991	0.21	0.05	0.04	0.74	0.40	-	-	-	-
	1	Kamloops										
		Summer	1990	0.35	0.04	0.02	0.14	0.41	-	-	-	-
			1991	0.55	0.19	0.02	0.04	0.45	-	-	-	-
	1	Prince George										
		Summer	1989	-	-	0.41	1.44	1.41				
			1990	1.54	0.61	0.69	1.55	1.79	-	-	-	-
			1991	1.46	0.44	0.51	0.97	1.46	-	-	-	-
Ransome and	1	Vernon-1										
Sullivan (1997)		Summer	1992	1.63	-	-	1.80	-	0.29	-	-	0.98
(n=2)			1993	0.70	-	-	1.40	-	0.26	-	-	0.57
	1	Vernon-2										
		Summer	1992	2.02	-	-	2.01	-	1.30	-	-	0.58
			1993	1.35	-	-	1.53	-	0.89	-	-	0.67

Ransome and Sullivan (2002) (n=2)	1 Chehalis	Summer 1997	-	-	1.90	2.19	-	-	-	1.26	0.84	-
		Winter 1997-98	-	-	1.19	0.88	-	-	-	0.71	0.58	-
	1 MF Forest	Summer 1998	-	-	1.12	1.02	-	-	-	0.34	0.07	-
		Winter 1998-99	-	-	0.59	0.81	-	-	-	0.26	0.04	-
		Winter 1999-00	-	-	0.68	2.22	-	-	-	1.03	0.17	-
	1 Coquitlam	Summer 1995	0.10		0.52			2.16		1.51		
		1996	0.66		2.76			1.83		1.84		
		1997	1.65		3.90			1.24		1.53		
		Winter 1998-99	1.80		2.78			0.86		0.79		
		1999-00	1.60		1.57			0.84		0.72		
	1 Capilano	Summer 1995	0.03		0.23			1.33		0.70		
		1996	0.54		1.52			1.63		1.07		
		1997	2.31		4.74			1.47		0.91		
		Winter 1998-99	2.93		2.75			1.56		0.55		
		1999-00	1.63		1.56			1.33		0.25		
Ransome et al. (2004) (n=3)	1 Penticton	Summer 2000	1.00	0.00	0.38	0.29	0.10	0.14	0.13	0.02	0.08	0.16
		2001	0.58	0.09	0.15	0.23	0.11	0.28	0.15	0.07	0.37	0.40
		2002	0.42	0.05	0.40	0.21	0.09	0.42	0.07	0.00	0.48	0.43
	1 Kamloops											

	Summer 2000	1.03	1.21	1.04	0.53	0.95	0.04	0.14	0.06	0.05	0.14
	2001	1.00	1.24	1.09	0.79	1.74	0.07	0.11	0.07	0.14	0.27
	2002	0.88	1.01	1.25	0.88	1.68	0.03	0.11	0.03	0.05	0.27
1	Prince George										
	Summer 2000	1.24	1.22	1.57	1.49	1.06	0.24	0.19	0.00	0.20	0.25
	2001	1.21	1.23	2.21	1.22	1.37	0.26	0.07	0.09	0.40	0.60
	2002	0.52	0.62	1.65	0.88	0.50	0.34	0.07	0.20	0.34	0.35
Sullivan et al.	1 Summerland-1										
(2010)	Winter 2006-07	1.70				1.67	0.16				0.00
(n=3)	Summer 2007	1.40				1.44	0.04				0.00
	Winter 2007-08	1.54				1.66	0.00				0.09
	Summer 2008	1.69				1.34	0.00				0.07
	1 Summerland-2										
	Winter 2006-07	0.93				1.78	0.13				0.32
	Summer 2007	1.40				1.70	0.12				0.17
	Winter 2007-08	1.63				1.09	0.08				0.18
	Summer 2008	1.25				0.80	0.00				0.39
	1 Summerland-3										
	Winter 2006-07	1.23				2.57	1.11				0.31
	Summer 2007	1.70				2.17	0.94				0.20
	Winter 2007-08	1.93				2.32	0.80				0.35
	Summer 2008	2.08				0.53	0.46				0.33

Table 4. Results of randomized block analysis of variance for comparing mean abundance during summer and winter periods and overall, and demographic attributes for *Tamiasciurus* among five treatment stands.

Attribute and season	Stand	Block	Stand x block
Abundance			
Summer	$F_{4,29} = 0.93; P = 0.46$	$F_{16,29} = 4.26; P < 0.01$	$F_{29,91} = 1.34; P = 0.15$
Winter	$F_{4,5} = 0.78; P = 0.59$	$F_{8,5} = 3.63; P = 0.08$	$F_{4,29} = 1.13; P = 0.37$
Overall	$F_{4,38} = 1.50; P = 0.22$	$F_{25,38} = 4.67; P < 0.01$	$F_{38,119} = 1.25; P = 0.19$
Demography			
Male breeding	$F_{4,29} = 0.87; P = 0.49$	$F_{16,29} = 1.41; P = 0.20$	$F_{29,70} = 0.92; P = 0.60$
Female breeding	$F_{4,28} = 3.07; P = 0.03$	$F_{15,28} = 7.46; P < 0.01$	$F_{28,77} = 0.89; P = 0.63$
Pregnancies	$F_{4,29} = 1.33; P = 0.28$	$F_{14,29} = 5.43; P < 0.01$	$F_{29,89} = 0.59; P = 0.95$
Recruits	$F_{4,31} = 0.45; P = 0.77$	$F_{16,31} = 5.45; P < 0.01$	$F_{31,111} = 0.69; P = 0.89$
Summer survival	$F_{4,31} = 0.37; P = 0.83$	$F_{16,31} = 0.69; P = 0.78$	$F_{31,86} = 1.81; P = 0.02$
Winter survival	$F_{4,19} = 4.90; P < 0.01$	$F_{13,19} = 6.75; P < 0.01$	$F_{19,24} = 0.90; P = 0.59$
Body mass	$F_{4,31} = 2.36; P = 0.07$	$F_{16,31} = 13.00; P < 0.01$	$F_{31,101} = 1.09; P = 0.37$

Table 5. Mean ($\pm$ 95% CIs) proportion of male squirrels in breeding condition in old-growth, unthinned, low-, medium-, and high-density stands. N = sample size (number of annual values).

Species and parameters	Stand density				
	Old-growth	Unthinned	Low	Medium	High
<u><i>Tamiasciurus</i></u>					
Mean	0.79	0.82	0.86	0.87	0.73
95% CI	0.72-0.87	0.71-0.92	0.75-0.96	0.76-0.99	0.60-0.87
n	36	22	23	21	18
<u><i>G. sabrinus</i></u>					
Mean	0.83	0.67	0.94	0.86	1.00
95% CI	0.66-0.99	-0.77-2.10	0.85-1.03	0.67-1.04	1.00-1.00
n	10	3	9	6	2

Table 6. Mean ($\pm$ 95% CIs) body mass (g) of adult male squirrels, as an index of physical condition, in old-growth, unthinned, low-, medium-, and high-density stands. *N* = sample size (number of annual values).

Species & parameters	Stand density				
	Old-growth	Unthinned	Low	Medium	High
<u><i>Tamiasciurus</i></u>					
Mean	215.95	208.11	211.88	216.42	224.56
95% CI	210.25-221.65	202.03-214.19	203.93-219.82	210.12-222.72	218.30-230.81
<i>n</i>	47	25	28	24	29
<u><i>G. sabrinus</i></u>					
Mean	135.66	128.29	126.77	132.69	134.39
95% CI	131.41-139.92	120.56-136.02	123.53-130.00	127.57-137.82	126.52-142.26
<i>n</i>	30	8	14	16	18

Table 7. Results of randomized block analysis of variance for comparing mean abundance during summer and winter periods and overall, and demographic attributes for *G. sabrinus* among five treatment stands.

Attribute and season	Stand	Block	Stand x block
Abundance			
Summer	$F_{4,17} = 2.59; P = 0.07$	$F_{11,17} = 24.13; P < 0.01$	$F_{17,48} = 2.50; P < 0.01$
Winter	$F_{3,6} = 1.46; P = 0.35$	$F_{6,5} = 1.94; P = 0.27$	$F_{6,4} = 5.48; P = 0.01$
Overall	$F_{4,24} = 3.76; P = 0.02$	$F_{18,24} = 12.06; P < 0.01$	$F_{24,60} = 3.22; P < 0.01$
Demography			
Male breeding	$F_{4,5} = 1.41; P = 0.34$	$F_{9,5} = 1.98; P = 0.22$	$F_{5,11} = 1.95; P = 0.17$
Female breeding	$F_{4,16} = 2.10; P = 0.11$	$F_{10,16} = 2.60; P = 0.04$	$F_{16,35} = 0.59; P = 0.87$
Pregnancies	$F_{4,15} = 1.01; P = 0.43$	$F_{9,15} = 2.45; P = 0.05$	$F_{15,48} = 0.88; P = 0.59$
Recruits	$F_{4,17} = 3.87; P = 0.02$	$F_{11,17} = 13.82; P < 0.01$	$F_{17,64} = 0.20; P = 1.00$
Summer survival	$F_{4,16} = 1.00; P = 0.44$	$F_{11,16} = 1.90; P = 0.10$	$F_{16,48} = 1.01; P = 0.47$
Winter survival	$F_{2,4} = 1.71; P = 0.23$	-	$F_{4,10} = 0.05; P = 1.00$
Body mass	$F_{4,16} = 0.74; P = 0.58$	$F_{11,16} = 3.59; P = 0.01$	$F_{16,54} = 0.83; P = 0.65$

List of figures

Figure 1. Map showing locations of study areas in British Columbia, Canada. Numbers of locations correspond with studies listed in Table 1.

Figure 2. Mean ($\pm$ 95% CIs) Jolly trappability for (a) *Tamiasciurus* and (b) *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands. Sample size (number of annual and seasonal values) above upper interval.

Figure 3. (a) Overall mean abundance ($\pm$ 95% CIs) for *Tamiasciurus* populations per ha in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in abundance for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual and seasonal values) above upper interval.

Figure 4. (a) Mean ($\pm$ 95% CIs) proportion of females breeding for *Tamiasciurus* in old-growth, unthinned, low-, medium-, and high-density stands, and b) mean proportional change in proportion of females breeding for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval. Mean values followed by the same superscript letter are similar by Duncan's Multiple Range Test.

Figure 5. (a) Mean ($\pm$ 95% CIs) number of successful pregnancies for *Tamiasciurus* in old-growth, unthinned, low-, medium-, and high-density stands, and b) mean proportional change in number of successful pregnancies for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment

(unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval.

Figure 6. (a) Mean ($\pm$ 95% CIs) number of total recruits for *Tamiasciurus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in number of recruits for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval.

Figure 7. (a) Mean ($\pm$ 95% CIs) Jolly-Seber monthly summer survival for *Tamiasciurus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in summer survival for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval.

Figure 8. (a) Mean ($\pm$ 95% CIs) Jolly-Seber monthly winter survival for *Tamiasciurus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in winter survival for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval. Mean values followed by different superscript letters are significantly different by Duncan's Multiple Range Test.

Figure 9. (a) Overall mean abundance ($\pm$ 95% CIs) for *Glaucomys sabrinus* populations per ha in old-growth, unthinned, low-, medium-, and high-density stands, and (b)

mean proportional change in abundance for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual and seasonal values) above upper interval.

Figure 10. (a) Mean ($\pm$ 95% CIs) proportion of females breeding for *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands, and b) mean proportional change in proportion of females breeding for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval. Mean values followed by the same superscript letter are similar by Duncan's Multiple Range Test.

Figure 11. (a) Mean ($\pm$ 95% CIs) number of successful pregnancies for *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands, and b) mean proportional change in number of successful pregnancies for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval.

Figure 12. (a) Mean ($\pm$ 95% CIs) number of total recruits for *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in number of recruits for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values)

above upper interval. Mean values followed by the same superscript letter are similar by Duncan's Multiple Range Test.

Figure 13. (a) Mean ($\pm$ 95% CIs) Jolly-Seber monthly summer survival for *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in summer survival for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval.

Figure 14. (a) Mean ($\pm$ 95% CIs) Jolly-Seber monthly winter survival for *Glaucomys sabrinus* in old-growth, unthinned, low-, medium-, and high-density stands, and (b) mean proportional change in winter survival for annual fluctuations in old-growth stands compared with the difference (effect size) between the treatment (unthinned, low-, medium-, and high-density) stands and old-growth stands. Sample size (number of annual values) above upper interval. Mean values followed by different superscript letters are significantly different by Duncan's Multiple Range Test.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

Figure 9.

Figure 10. (a) *Glaucomys sabrinus*

Figure 11. (a) *Glaucomys sabrinus*

Figure 12. (a) *Glaucomys sabrinus*

Figure 13.

Figure 14.