

1           **Thinning of Young Douglas-fir Forests Decreases Density of**  
2           **Northern Flying Squirrels in the Oregon Cascades.**

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15 **Abstract**

16           Large-scale commercial thinning of young forests in the Pacific Northwest is currently  
17 promoted on public lands to accelerate the development of late-seral forest structure for the  
18 benefit of wildlife species such as northern spotted owls (*Strix occidentalis caurina*) and their  
19 prey, including the northern flying squirrel (*Glaucomys sabrinus*). Attempts to measure the  
20 impact of commercial thinning on northern flying squirrels have mostly addressed short-term  
21 effects (2-5 years post-thinning) and the few published studies of longer-term results have been  
22 contradictory. We measured densities of northern flying squirrels 11-13 years after thinning of  
23 young (55-65 years) Douglas-fir forest stands in the Cascade Range of Oregon, as part of the  
24 Young Stand Thinning & Diversity Study. The study includes 4 replicate blocks, each consisting  
25 of an unthinned control stand and 1 stand each of the following thinning treatments: Heavy Thin;  
26 Light Thin; and Light Thin with Gaps. Thinning decreased density of northern flying squirrels,  
27 and squirrel densities were significantly lower in heavily thinned stands than in more lightly  
28 thinned stands. Regression analysis revealed a strong positive relationship of flying squirrel  
29 density with density of large (>30 cm diameter) standing dead trees and a negative relationship  
30 with % cover of low understory shrubs. Maintaining sufficient area and connectivity of dense,  
31 closed canopy forest is recommended as a strategy to assure that long-term goals of promoting  
32 late-seral structure do not conflict with short-term habitat requirements of this important species.

33 **Key words:** northern flying squirrel, *Glaucomys sabrinus*, silvicultural thinning, commercial  
34 thinning

35

## 36 1. Introduction

37 In the Pacific Northwest of North America, forest managers confronted with the legacy of  
38 decades of clearcut harvest and subsequent plantation establishment are increasingly employing  
39 a strategy of multiple commercial thinnings and long rotations to accelerate the development of  
40 late-seral structure and function from young homogeneous forests (Hayes *et al.*, 1997; Tappeiner  
41 *et al.*, 1997; Carey *et al.*, 1999b; Sullivan *et al.*, 2001). Whereas there may be economic and  
42 other objectives in pursuing this strategy (Busing and Garman, 2002), one goal is to provide  
43 more complex habitat for wildlife species with a wide range of needs (Hagar *et al.*, 1996; Hayes  
44 *et al.*, 1997; Humes *et al.*, 1999; Hayes *et al.*, 2003).

45 The northern flying squirrel (*Glaucomys sabrinus*) has been considered a keystone  
46 species (Carey, 2002; Smith, 2007) in Pacific Northwest forests because it serves several  
47 important ecological functions. In much of the region, this squirrel is the primary prey of the  
48 threatened northern spotted owl (*Strix occidentalis caurina*) (Carey *et al.*, 1992; Forsman *et al.*,  
49 2001; Forsman *et al.*, 2004). In addition to this arboreal rodent's importance as prey for owls and  
50 other predators (Reynolds and Meslow, 1984; Wilson and Carey, 1996; Fryxell *et al.*, 1999; Bull,  
51 2000), its consumption of both hypogeous and epigeous fungi and dispersal of fungal spores aids  
52 in maintaining mycorrhizal communities (Maser *et al.*, 1978; Li *et al.*, 1986; Zabel and Waters,  
53 1997; Gomez *et al.*, 2005). Northern flying squirrels also are thought to be an important vector  
54 for dispersal of canopy lichens (Rosentreter *et al.*, 1997; Zabel and Waters, 1997). Because of  
55 these relationships, this squirrel has been used as a forest-health indicator species in diverse  
56 regions of North America (McLaren *et al.*, 1998; Betts and Forbes, 2005; Smith *et al.*, 2005), and  
57 thus is of central concern in planning forest management and maintaining biological diversity in  
58 coniferous forests.

59 Considerable evidence exists that northern flying squirrels are relatively more abundant,  
60 and correlates of squirrel fitness are optimized, in forests with many large live trees (Smith *et al.*,  
61 2004; Gomez *et al.*, 2005; Holloway and Malcolm, 2006; Lehmkuhl *et al.*, 2006), many large  
62 dead trees (Carey, 1995; Smith *et al.*, 2004; Holloway and Malcolm, 2006; Meyer *et al.*, 2007b),  
63 well-developed understories (Carey *et al.*, 1999a; Pyare and Longland, 2002), and many large  
64 logs on the ground (Carey *et al.*, 1999a; Gomez *et al.*, 2005; Smith *et al.*, 2005). Collectively,  
65 these structural elements are typical of late-seral (mature and old-growth) forests. Some or all of

66 these elements are largely lacking in most of the young forests now covering extensive areas of  
67 the Pacific Northwest (Spies and Cline, 1988; Halpern and Spies, 1995; Franklin *et al.*, 2002).

68 As stated above, a goal of some public land managers is to use commercial thinning to  
69 accelerate the development of late-seral features within young forests, to provide high-quality  
70 habitat for late-seral species, including the northern flying squirrel. In the last 2 decades,  
71 experiments and retrospective studies have been attempting to test the effectiveness of this  
72 strategy, with varying results. Most found negative short-term (2-5 years) impacts of thinning  
73 (Carey, 2001; Herbers and Klenner, 2007; Meyer *et al.*, 2007a) or similar partial harvest  
74 techniques (Waters and Zabel, 1995; Bull *et al.*, 2004; Holloway and Malcolm, 2006) on  
75 northern flying squirrel populations, though 2 studies found no short-term effect of thinning  
76 (Ransome and Sullivan, 2002; Gomez *et al.*, 2005).

77 Because thinning is expected to eventually improve habitat conditions for northern flying  
78 squirrels through acceleration of large tree growth rates, increasing mid-story complexity, and  
79 enriching understory diversity, and because these developments are relatively slow and may  
80 change trajectory over decades, studies of wildlife responses over the long term gain value in  
81 proportion to time since thinning. Only 3 studies have been published which describe mid-to-  
82 long-term effects of thinning on northern flying squirrels, and results are contradictory. In a  
83 retrospective study of 55- to 65-yr-old stands in western Washington, Carey (2000) reported  
84 lower abundance of flying squirrels in twice-thinned stands than in unthinned stands with  
85 legacies of large live trees, snags, and logs. Wilson (2010), in a re-sampling of Carey's sites 12  
86 years after half of the stands were treated with variable-density thinning, found that flying  
87 squirrel densities were very low in both thinned and unthinned stands. Ransome *et al.* (2004)  
88 found that pre-commercial thinning of young densely-stocked lodgepole pine (*Pinus contorta*)  
89 forests had a neutral or positive effect on flying squirrel density 12-14 years after treatment.

90 A recent meta-analysis of effects of silvicultural practices on northern flying squirrels  
91 (Holloway and Smith, 2011) attempted to resolve the inconsistencies of the work done so far,  
92 and found that studies asserting a benefit or no effect of harvesting on squirrel populations (Cote  
93 and Ferron, 2001; Ransome and Sullivan, 2002; Gomez *et al.*, 2005) lacked statistical power  
94 needed to support those assertions. The implication of Holloway and Smith's meta-analysis is

95 that forest management practices that are currently widespread in the Pacific Northwest (thinning  
96 and clearcutting) have negative short-term and long-term impacts on northern flying squirrels.

97 As with most of the studies cited above, the major impetus for the Young Stand Thinning  
98 & Diversity Study (YSTDS) was to investigate the effects of commercial thinning on habitat for  
99 late-seral species and to assess the potential for accelerating the development of late-successional  
100 features such as those associated with high abundance of northern flying squirrels. Similar work  
101 has taken place in British Columbia (Ransome and Sullivan, 2002; Ransome *et al.*, 2004),  
102 Washington State (Carey, 2000; Wilson, 2010), northeastern Oregon (Bull *et al.*, 2004), and the  
103 northern Oregon Coast Range (Gomez *et al.*, 2005), but the YSTDS is the only experiment of  
104 this kind in the Oregon Cascades. The design of the YSTDS facilitates testing of a set of 3  
105 orthogonal hypotheses about differences among treatments, minimizing the Type I error rate  
106 relative to multiple comparisons (Lehmann, 1986). With respect to the northern flying squirrel in  
107 particular, the 3 null hypotheses are: (1) that flying squirrel density does not differ between  
108 thinned and unthinned treatments; (2) that flying squirrel density does not differ among different  
109 thinning intensities; and (3) that flying squirrel density does not differ between lightly thinned  
110 stands with and without small gaps.

111 Garman (2001) described responses of ground-dwelling small mammals and amphibians  
112 2-5 years post-thinning for the YSTDS, but his protocol did not target tree squirrels and  
113 relatively few were captured, so data were insufficient to derive estimates of density.  
114 Nevertheless, Garman (2001) indicated that thinning had negative short-term impacts on flying  
115 squirrel densities, agreeing with most other studies that have more thoroughly investigated short-  
116 term responses of flying squirrels to thinning and similar silvicultural treatments. Here we  
117 describe patterns of density for northern flying squirrels 11-13 years after thinning in young  
118 Douglas-fir forests.

119

## 120 **2. Methods**

### 121 **2.1 Study Area Description**

122 The YSTDS comprises a randomized block design with 16 forest stands located on the  
123 Willamette National Forest on the west slope of the Cascade Range in Oregon (Fig. 1). The  
124 study is composed of 4 replicate blocks, each consisting of an unthinned control stand and 1  
125 stand each of the following thinning treatments: (1) a Heavy Thin treatment leaving 125-137  
126 trees per hectare (tph) and underplanted with native conifer seedlings; (2) a Light Thin treatment,  
127 approximating the timber industry standard, with 250-275 residual tph; and (3) a Light Thin with  
128 Gaps (hereafter simply “Gaps”) treatment, again with 250-275 tph but with an additional 20% of  
129 the stand harvested to create 0.2-ha gaps planted with native conifer seedlings. Thinnings were  
130 conducted by removing trees of relatively small diameter.

131 All stands are located within the western hemlock (*Tsuga heterophylla*) zone of Franklin  
132 and Dyrness (1988) and were established after clearcutting and planting 55-65 years before  
133 thinning was initiated in 1995. Slopes range from 0 to 24%, and elevation ranges from 430-920  
134 meters. Stand areas average 31 ha, ranging from 15 to 53 ha.

135 Stands within 2 blocks (Christy and Sidewalk) are directly contiguous with each other or  
136 separated only by narrow riparian corridors or roads; distances among stands within the other 2  
137 blocks (Cougar and Mill Creek) average 1.6 km and no 2 stands within a block are more than 4  
138 km apart. Thus, landscape context for the stands within each block is similar over the scales at  
139 which northern flying squirrels can travel. Distances between blocks range from 2.5 km to 21  
140 km.

141 Before thinning, Douglas-fir (*Pseudotsuga menziesii*) was the dominant overstory tree  
142 species with varying amounts of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja*  
143 *plicata*), and hardwoods including bigleaf maple (*Acer macrophyllum*), and golden chinquapin  
144 (*Chrysolepis chrysophylla*). The understory consisted primarily of vine maple (*Acer circinatum*),  
145 cascara buckthorn (*Rhamnus purshiana*), bitter cherry (*Prunus emarginata*), Oregon-grape  
146 (*Mahonia nervosa*), salal (*Gaultheria shallon*), and swordfern (*Polystichum munitum*).

147 Pre-thinning sampling of the vegetative structure within each stand in 1993 established  
148 that stands within each block were similar with respect to tree basal area (overall mean 34.8  
149 m<sup>2</sup>/ha; average CV for 4 blocks = 8.7%) and tree density (overall mean density 718 trees per ha;  
150 average CV over 4 blocks = 10.1%; (Davis *et al.*, 2007). Before treatment commenced, each

151 stand was assigned randomly to one of the thinning treatments or as an unthinned control.  
152 Thinning began in late 1994, and was completed by February 1997. Most harvest activity  
153 occurred simultaneously on all blocks between Feb 1995 and Sept 1996 and with no particular  
154 pattern to order of treatments.

155 To increase the density of snags with diameter at breast height (dbh)  $\geq$  30 cm to at least  
156 2.5 snags/ha in all treatment units, a small percentage of trees (ranging from 0.13-1.42%)  
157 distributed through each stand were killed by chainsaw topping to a height no less than 15 m in  
158 late 2001. Half of the topped trees were also inoculated with heart-rot fungus to accelerate decay.  
159 In 2009, these artificial snags were surveyed for cavity formation and use by birds and mammals,  
160 but the snags were still relatively sound and no evidence of use by flying squirrels was found.

161 Measurements of vegetation 5-7 years after treatment revealed that thinning created  
162 substantial differences in overstory cover, tree density, and tree basal area among the treatments  
163 (Davis *et al.*, 2007; Davis and Puettmann, 2009). Percent cover of low shrubs ( $\leq$  2 m high) was  
164 reduced about 40% ( $P < 0.001$ ) by harvest damage in thinned stands; a corresponding reduction  
165 in tall shrubs ( $>$  2 m high) was also significant (55% reduction;  $P = 0.002$ ), but by 2001 both low  
166 and tall shrub cover had recovered to levels indistinguishable from the Controls (Davis and  
167 Puettmann, 2009). In 2006, 10 years after thinning (Table 1), trees per ha, basal area, and  
168 percent overstory cover in all thinned treatments were still lower than in Control stands (all  $P <$   
169  $0.01$ ; A. Ares, unpublished results). Percent cover of low shrubs in 2006 was significantly lower  
170 in Control stands than in thinned stands ( $p = 0.0004$ ). Though high variability among blocks  
171 masked statistical differences, there was weak evidence that percent cover of tall shrubs in 2006  
172 was greater ( $p = 0.0702$ ) in Control stands than in thinned stands. We defined large snags as  $\geq$   
173 30 cm dbh based on the minimum size likely to be used by flying squirrels (Mellen-McLean *et*  
174 *al.*, 2009). Density of large snags was low and variable (mean 8.06 per ha, s.d. = 5.98), and in  
175 2006 treatments and controls could not be distinguished by snag density ( $P = 0.54$ ), though there  
176 was a large difference among blocks ( $P = 0.0193$ ). Volume of coarse woody debris (CWD)  $>$  10  
177 cm diameter ranged from a mean of 107 m<sup>3</sup>/ha in Light Thin stands to a mean of 270 m<sup>3</sup>/ha in  
178 Heavy Thin stands (s.d. = 112.2), and though thinning increased CWD volume, high variability  
179 among replicates severely compromised our ability to detect statistical differences among  
180 treatments (B. McComb, unpublished results).

181

## 182 **2.2 Mammal Sampling**

183           In 2007-08 (11-13 years after thinning), all stands were sampled to estimate abundance of  
184 small mammals, especially northern flying squirrels. Trapping occurred for 4 consecutive nights  
185 in each stand from late September to late November. Two stands in each block were sampled  
186 simultaneously and the other 2 stands in the same block were sampled in the following week.  
187 The order for sampling stands within blocks was randomized, and blocks were sampled  
188 sequentially. Considerations for the order of sampling among blocks included elevation,  
189 seasonal road closures due to snow or hunting, and proximity to other blocks.

190           We used variable-length transects, varying in number from 4 to 11 depending on stand  
191 shape, but each stand included a total of 100 trapping stations. This meant that most trapping  
192 arrays did not form rectangles but rather had more complex shapes (Fig. 2); nevertheless,  
193 distance between transects and between traps on each transect was 30 m, such that the trapping  
194 stations formed a grid network from which we were able to compute the total area of the trapping  
195 array, as well as distances moved by each flying squirrel between captures.

196           One trap was placed at each station. In each stand, Sherman traps (Model LFATDG)  
197 alternated with Tomahawk traps (Model 201) along each transect, so that 50 Sherman traps and  
198 50 Tomahawk traps were distributed evenly throughout the 100 stations in each stand. Half (25)  
199 of the Tomahawk traps were attached to the boles of trees (approx. 1.5 m high), and the other 25  
200 were placed on the ground; tree and ground placements of Tomahawk traps alternated along  
201 transects. Thus, effective spacing among Tomahawk traps was 60 m. Sherman traps were used to  
202 capture terrestrial rodents and insectivores, and so were placed on the ground; we include  
203 Sherman traps in this analysis because a substantial number of flying squirrels were captured in  
204 them. To increase capture rates, all traps were locked open and pre-baited once 10 days before  
205 the trap session began. During the trapping session, traps were checked twice daily to minimize  
206 mortality of trap-prone diurnal species, particularly chipmunks. Traps were set in the afternoon  
207 on the 1st day of each trap session, checked twice each day for 3 days, then checked and closed  
208 on the morning of the 5<sup>th</sup> day; thus, each trap session included 4 nights. In both years, traps were  
209 baited with a mixture of peanut butter, oats, and sunflower seeds. Upholstery cotton was placed



210 in each trap for insulation, and traps were placed within weather-resistant covers. Captured  
211 mammals were identified to species, weighed, sexed, marked with individually-numbered  
212 eartags, and immediately released at the point of capture. Trap mortalities were frozen for later  
213 necropsy to confirm species and sex. All procedures were conducted under protocols approved  
214 by the Institutional Animal Care and Use Committee at Oregon State University.

### 215 **2.3 Analytical procedures**

216 We calculated trap-nights (TN) as total Tomahawk and Sherman traps deployed  
217 multiplied by the number of nights deployed. We computed corrected trap-nights by subtracting  
218 1 TN for each trap found to be inoperable and 0.5 TN for each trap found closed but empty.

219 We computed estimates of flying squirrel abundance using program MARK (White and  
220 Burnham, 1999). Within MARK, we used the Huggins full closed captures model with  
221 heterogeneity to derive estimates of population size within each stand for each year separately.  
222 The Huggins model assumes population closure and allows for capture probabilities to vary by  
223 individual, by behavioral response to trapping, and through time, and is thus relatively robust to  
224 the low and heterogeneous capture probabilities typical of northern flying squirrels. We assumed  
225 that our populations were demographically closed for the brief period of our trapping regime (4  
226 days), and employed tests for closure (Stanley and Burnham, 1999) to confirm that any  
227 violations of this assumption were negligible.

228 Because we trapped for fewer nights (4) than many previous studies, and because  
229 population estimators are sensitive to low capture probabilities, we employed an additional check  
230 on our results by also computing densities based on total number of individuals captured without  
231 estimating additional uncaptured animals.

232 We computed the effective area trapped in each stand (Table 2) by adding a buffer  
233 around the perimeter of each trapping array. Buffer width was one-half of the mean maximum  
234 distance moved (MMDM) by flying squirrels in that stand. Because we could detect no statistical  
235 difference in MMDM between years or sexes (ANOVA,  $P = 0.70$  and  $0.46$ , respectively), we  
236 used the average MMDM for the 2 years for each stand without regard to sex. Because northern  
237 flying squirrels are known to have larger home ranges in low density populations (Carey, 1995,  
238 2000), we used different computations for MMDM depending on estimated abundance of each

239 particular stand: for each stand with estimated abundance  $\geq 10$  for either year, MMDM was  
240 computed from data specific to that stand; for stands with estimated abundance  $< 10$  animals, and  
241 thus having few data to compute MMDM, we used mean MMDM for all animals in all low-  
242 abundance stands to compute the array buffer. Mean MMDM for 6 high-density stands was 75.2  
243 m, ranging from 59 to 102 m, and MMDM for all low-density stands was 101 m. Effective area  
244 trapped was computed as MMDM multiplied by array perimeter, added to the area of the  
245 trapping array. We then computed density of flying squirrels in each stand as the number of  
246 animals estimated with MARK, divided by the effective area of trapping (Table 2).

247 We compared the effects of thinning on northern flying squirrel density, MMDM, sex  
248 ratio, and sex-specific body mass using a randomized block one-way ANOVA design with  
249 repeated measures. Treatment and year were fixed effects; block and the block by treatment  
250 factors were random effects. Density estimates and sex-specific body mass were square-root-  
251 transformed to correct for unequal variances, and sex ratios were logit transformed. We used a  
252 set of orthogonal contrasts to minimize Type I error rate (Lehmann, 1986). The set consisted of 3  
253 comparisons: Control stands vs. all thinning treatments; Heavy Thin vs. Light Thin and Gaps;  
254 and Light Thin vs. Gaps. These comparisons test 3 corresponding hypotheses: (1) that flying  
255 squirrel density, MMDM, sex ratio, and body mass did not differ between thinned and unthinned  
256 treatments; (2) did not differ between heavy and light thinning intensities; and (3) did not differ  
257 between lightly thinned stands with and without small gaps. Our comparison-wise criterion for  
258 statistical significance was  $\alpha < 0.05$ .

259 We explored relationships between stand-level flying squirrel densities and habitat  
260 characteristics by developing *a priori* a set of mixed-effect linear regression models with block  
261 held as a random effect. Habitat variables available to us were tree density, tree basal area,  
262 density of large snags, tree diameter, overstory canopy cover, herbaceous plant cover, low shrub  
263 cover, and tall shrub cover (A. Ares, unpublished data). One year before sampling of flying  
264 squirrels commenced, these habitat components were measured on permanent 0.1-ha circular  
265 plots, placed systematically throughout each stand, and covering approximately 7.5% of the area  
266 of each stand. To ensure adequate sampling effort of gap interiors and gap edges in Gaps stands,  
267 plots were placed in the center of 10 randomly-chosen 0.2-ha gaps, and 10 more plots on the  
268 edges of 10 other randomly-chosen gaps; in addition, 10 plots were placed randomly in the

269 matrix surrounding the gaps. Percent overstory cover was measured at the center of each circular  
270 plot and at 4 points 10.25 m distant from center in each cardinal direction. Overstory cover  
271 included live foliage and tree boles, limbs, and snags. Diameter at breast height (dbh) was also  
272 measured for of all trees > 5 cm dbh in each plot. All understory species present in the plot were  
273 recorded. Within each plot, 8 subplots (each 0.1 m<sup>2</sup>) were evenly spaced along each of 2 parallel  
274 14.5-m transects, providing a total of 16 subplots per plot. In each subplot, percent cover of all  
275 understory plant species was visually estimated, as was percent cover of ground surface features  
276 including exposed mineral soil, coarse litter, and fine litter. Graminoids and bryophytes were not  
277 identified below family level. Along each 14.5-m transect, line intercept methods were employed  
278 to estimate understory tall shrub cover and cover of trees with dbh < 5 cm. Low shrubs were  
279 distinguished from tall shrubs by potential stature of plant at maturity of less or more than 1 m,  
280 respectively. More details about this measurement protocol may be found in Davis *et al.* (2007)  
281 and Davis and Puettman (2009).

282 Our explorations of northern flying squirrel habitat associations were primarily driven by  
283 *a priori* hypotheses about effects of thinning on squirrel densities. Specifically, we reasoned that  
284 variables representing the overstory (percent overstory cover, tree density, basal area) would be  
285 profoundly reduced by thinning, would be reduced more in Heavy Thin stands than in Light Thin  
286 stands, and would have important implications for flying squirrel locomotion and avoidance of  
287 predators (Wilson, 2010). All 3 of those variables were still significantly higher in Control  
288 stands than in thinned stands in 2006 (A. Ares, unpublished data), so we reasoned that one or  
289 more was likely related to flying squirrel densities; because all were highly collinear with each  
290 other, we chose one variable (tree basal area) which had the highest correlation with our  
291 measured flying squirrel densities for inclusion in our models. Large snags are generally  
292 considered an important habitat component for flying squirrels (Carey, 1995; Carey *et al.*, 1999a;  
293 Smith *et al.*, 2004; Holloway and Malcolm, 2006), so we included density of snags with dbh  $\geq$ 30  
294 cm in our modeling. In 2006, percent cover of low shrubs (species whose maximum height  
295 generally does not exceed 1 m) was the only understory variable that was significantly different  
296 between control stands and thinned stands; while there seemed little compelling reason to expect  
297 *a priori* that this stratum would influence flying squirrel abundance, the pattern seemed  
298 compelling enough to include in exploratory analyses. A set of 8 models were fitted, residuals  
299 were examined for departures from normality and/or homoscedasticity, and variables were

300 transformed where necessary to meet statistical assumptions. All ANOVA and regression  
301 analyses were performed in SAS version 9.2 (SAS, 2003). Regression models were ranked  
302 based on Akaike's Information Criterion, corrected for small sample size (AICc).

### 303 **3. Results**

304 In 2007-08, a total of 11,873 corrected trap-nights were deployed, approximately equally  
305 distributed between the 2 years. A total of 103 individual flying squirrels were captured 134  
306 times in 2007; 144 individuals were captured 213 times in 2008 (Table 2). Approximately 12%  
307 of all flying squirrel captures were in Sherman traps. All other flying squirrel captures were in  
308 Tomahawk traps; approximately 59% of those were in traps set on tree boles, and the rest were in  
309 traps set on the ground. Capture probability ( $p$ ) within stands ranged from 0.18 to 1.00, and  
310 averaged 0.48.

311 Flying squirrel density (Table 3 and Figure 3) was significantly greater ( $P < 0.0001$ ) in  
312 unthinned Control stands (mean 2.02 squirrels/ha, SE = 0.78) than in thinned stands (0.39/ha, SE  
313 = 0.31), and significantly greater ( $P = 0.0034$ ) in the Light Thin and Gaps treatments (0.50/ha,  
314 SE = 0.35) than in Heavy Thin (0.17/ha, SE = 0.10). Differences between Light Thin (0.44/ha,  
315 SE = 0.38) and Gaps (0.55/ha, SE = 0.31) treatments were not significant ( $P = 0.36$ ). Differences  
316 in densities between years also did not reach the level of statistical significance ( $P = 0.11$ ), but  
317 were higher in 2008 than in 2007 in all thinned treatments and correspondingly lower in Control  
318 stands (Fig. 3).

319 Using the more conservative approach of simple enumeration of individuals (i.e.,  
320 computing densities without estimation of additional uncaptured animals) resulted in lower  
321 densities overall, of course, and more so for Controls than for thinned stands, but did not change  
322 significance of differences appreciably, nor our overall conclusions. Flying squirrel density  
323 using this approach was significantly greater ( $P < 0.0001$ ) in unthinned Control stands (mean  
324 1.43 squirrels/ha, SE = 0.54) than in thinned stands (0.33/ha, SE = 0.22), and greater ( $P =$   
325 0.0298) in the Light Thin and Gaps treatments (0.40/ha, SE = 0.25) than in the Heavy Thin  
326 treatment (0.18/ha, SE = 0.09). Light Thin (0.46/ha, SE = 0.32) and Gaps (0.35/ha, SE = 0.17)  
327 treatments were not significantly different ( $P = 0.51$ ). Density differences between years were  
328 more pronounced using this enumeration approach ( $P = 0.05$ ). Carrying out this alternative test

329 increased our confidence that our population estimates are reliable, but doing so also ignores the  
330 certainty that naïve counts of individuals captured are inherently negatively biased. For this  
331 reason, we refer hereafter to our results using statistically estimated population densities only.

332 Thinning treatments did not affect maximum distance moved by individual flying  
333 squirrels (Table 3,  $P = 0.73$ ) and distances moved were similar for males and females ( $P = 0.17$ ).  
334 Neither sex ratio ( $P = 0.94$ ) nor sex-specific body mass ( $P = 0.68$  for females and  $0.23$  for males)  
335 differed among treatments.

336 The mixed-effects linear regression model best supported by our data included snag  
337 density and percent cover of low shrubs (Table 4). Flying squirrel density was positively related  
338 with snag density, and negatively related with low shrub cover. Each of these 2 relationships was  
339 highly statistically significant ( $P < 0.001$ ).

#### 340 **4. Discussion**

341 Most previous studies of northern flying squirrel response to thinning and similar  
342 silvicultural treatments have been short-term, and most have indicated negative effects on  
343 squirrel densities (Waters and Zabel, 1995; Carey, 2001; Bull *et al.*, 2004; Holloway and  
344 Malcolm, 2006; Herbers and Klenner, 2007; Meyer *et al.*, 2007a; Holloway and Smith, 2011).  
345 However, some of these short-term studies were unable to detect differences in northern flying  
346 squirrel densities between thinned stands and control stands (Ransome and Sullivan, 2002;  
347 Gomez *et al.*, 2005), most likely due to lack of statistical power (Holloway and Smith 2011).  
348 Our longer-term study provides evidence that the negative impacts of commercial thinning on  
349 northern flying squirrel can persist even after 11-13 years. This finding of persistent negative  
350 impacts of commercial thinning on flying squirrel density is supported by a large negative effect  
351 size (Hedges'  $d = -1.53$  for Control vs. all thinned treatments), the result of large differences  
352 between means and relatively low variability among replicates.

353 In addition, we found that intensity of thinning (Heavy vs. Light Thin) also significantly  
354 affected northern flying squirrel densities. Densities on average were twice as high in Light Thin  
355 and Gaps stands as in Heavy Thin stands, and this difference was consistent for the 2 years of  
356 our study. The only habitat variable we measured which exhibits the same pattern is percent  
357 cover of overstory canopy, which is clearly higher in Light Thin and Gaps stands (overall mean

358 64%, SE 5%) than in Heavy Thin stands (mean 47%, SE 7%). Other variables representing forest  
359 density (trees/ha, basal area) were generally higher in Light Thin and Gaps stands than in Heavy  
360 Thin stands, but differences may be obscured by high variability (Table 1). Only 2 other studies  
361 have investigated the effects of thinning intensity on northern flying squirrels. Gomez *et al.*  
362 (2005), working in forests thinned to 2 levels very similar to ours, found no effect of thinning on  
363 flying squirrel densities regardless of intensity. Herbers and Klenner (2007) found that thinning  
364 decreased densities of northern flying squirrels in south central British Columbia from 0.64 to  
365 0.26 squirrels/ha, but that the decrease did not vary over 3 levels of thinning intensity, nor with  
366 harvest pattern (uniform vs. patch cuts).

367         It is interesting to note that, in both years of this study, squirrel densities in Gaps stands  
368 were slightly higher than in Light Thin stands. Variability among replicates is so high in relation  
369 to the small differences between Light Thin stands and Gaps stands that the significance of such  
370 a difference is highly doubtful. Although Gaps stands were designed to have 20% fewer trees  
371 and less dense canopies than Light Thin stands, by 2006 differences in trees/ha, basal area, and  
372 percent overstory cover were not significant between these 2 treatments (Table 1), so there seems  
373 little reason to think that any apparent difference in squirrel density relates directly to thinning,  
374 even if the differences had been large enough to qualify as statistically significant, which they  
375 were not. Such a conclusion would certainly be contrary to previous findings (ours and others')  
376 that thinning decreases flying squirrel densities, and would be unique in implying that forest  
377 openings were in some way beneficial to the squirrels. Longer and more frequent monitoring of  
378 flying squirrel abundance in the YSTDS treatment stands should resolve this apparent anomaly.

379         More time and monitoring are also needed to estimate when impacted flying squirrel  
380 populations might recover to levels comparable with those in unthinned stands, and to compare  
381 the influence of various habitat features on that recovery. Future sampling efforts should  
382 include measurements specifically designed to test hypotheses regarding the influence of  
383 particular habitat features (e.g., mid-story occlusion as protection from predators; see Wilson  
384 2010) on northern flying squirrel population ecology, rather than relying opportunistically on  
385 data collected for analysis of vegetative responses to thinning.

386         The densities of flying squirrels we report here (0 to 3.54 squirrels per ha, mean = 0.79;  
387 Table 2) are consistent with the range (0 to 4 squirrels per ha) reported by other authors and

388 reviewed by Smith (2007). Mean density for our Control stands (2.02/ha) was quite high  
389 compared to 9 previous studies (mean 1.06/ha) of northern flying squirrels in young forests  
390 (Carey *et al.*, 1992; Rosenberg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel,  
391 1995; Ransome and Sullivan, 2002; Ransome and Sullivan, 2003; Gomez *et al.*, 2005; Lehmkuhl  
392 *et al.*, 2006), and is higher or comparable to the high densities (mean 1.44/ha) reported by several  
393 authors for mature and old-growth forests in the Pacific Northwest (Carey *et al.*, 1992;  
394 Rosenberg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995; Ransome and  
395 Sullivan, 2003; Lehmkuhl *et al.*, 2006; Herbers and Klenner, 2007). While the high densities we  
396 measured may suggest that these young stands represent unusually good habitat for flying  
397 squirrels, we do not have the measures of reproductive fitness or survival necessary to refute the  
398 possibility that these areas could be operating as demographic sinks, occupied by subdominant  
399 animals from areas of higher quality habitat (Van Horne, 1983; Wheatley *et al.*, 2002). Other  
400 authors (Smith and Nichols, 2003; Lehmkuhl *et al.*, 2006) have reported dense populations of  
401 flying squirrels that exhibited negative growth rates, suggesting they might be operating as  
402 demographic sinks. We recommend that future work on the Young Stand Thinning & Diversity  
403 Study sample flying squirrel populations for at least 3 consecutive years, and make more effort to  
404 quantify reproductive success, so that reproductive fitness and rates of survival and population  
405 growth can be compared among treatments. Until then, inferences about the negative effects of  
406 thinning on flying squirrels are incomplete.

407         We know of only 2 other experimental studies that have measured northern flying  
408 squirrel densities more than 5 years after thinning. Wilson (2010) found that flying squirrel  
409 densities were low (<0.2 squirrels/ha) 12 years after variable-density thinning on the Forest  
410 Ecosystem Study (FES) in the Puget Trough of western Washington. Wilson's conclusion was  
411 that variable-density thinning had not yet promoted the development of high-quality habitat for  
412 flying squirrels in that time frame, primarily due to lack of sufficient midstory development (e.g.,  
413 recruitment and growth of shade-tolerant trees under the existing canopy) and loss of overstory  
414 trees from various causes (wind, suppression mortality, and laminated root rot) unrelated to the  
415 thinning treatments, resulting in limited development of greater complexity in forest structure.  
416 Wilson's work, like ours reported here, found no support for the hypothesis that thinning for  
417 increased forest complexity results in habitat that supports high densities of northern flying  
418 squirrels, at least in short- or mid-term time frames. Forest structural processes (accelerated tree

419 growth, development of mid-story occlusion, recruitment and decay of snags) that are  
420 presumably critical to high densities of northern flying squirrels will apparently take longer than  
421 12 years to develop after thinning of young forests. Thus, it will be important to continue to  
422 monitor critical habitat components and flying squirrel densities over the long term in  
423 manipulative stand-level studies designed to accelerate late-seral forest conditions.

424 Ransome *et al.* (2004), working 12-14 years after pre-commercial thinning of young  
425 lodgepole pine forests in British Columbia, found densities of 0.14, 0.37, and 0.51 northern  
426 flying squirrels/ha in stands thinned to low, medium, and high tree densities, respectively, and  
427 0.20 flying squirrels/ha in unthinned control stands. Medium- and high-density thinning  
428 treatments had significantly higher flying squirrel densities than control stands ( $P = 0.05$ ).  
429 Remarkably, high-density thinned stands had 70% higher flying squirrel densities than in old-  
430 growth stands (0.31 squirrels/ha). This is an unexpected finding, and the authors point out that  
431 the observed density differences do not necessarily reflect differences in habitat quality, which  
432 should be assessed on the basis of relative reproductive fitness of the squirrels. Unfortunately, as  
433 in our own study, Ransome *et al.* (2004) lacked direct information concerning reproductive  
434 fitness of flying squirrels, but they found no effects of thinning on recruitment, movement, or  
435 survival of flying squirrels. Adult male body mass, an indirect indicator of fitness, was  
436 significantly greater for animals in old-growth stands than in high-density thinned stands,  
437 indicating that the thinned stands may not have provided habitat quality comparable to that in  
438 old-growth. Additionally, the densities reported by Ransome *et al.* (2004) were relatively low,  
439 and squirrel densities were not measured before thinning, so conclusions that pre-commercial  
440 thinning can produce high-quality habitat for northern flying squirrels are not well supported.

441 Northern flying squirrels are primarily mycophagous, feeding largely on the fruiting  
442 bodies of hypogeous fungi (truffles), and several authors have stressed the importance of truffle  
443 abundance (Waters and Zabel, 1995; Gomez *et al.*, 2005; Lehmkuhl *et al.*, 2006) and habitat  
444 features that have been correlated with abundance of truffles, such as coarse woody debris,  
445 particularly large logs (Carey *et al.*, 1999a; Smith *et al.*, 2004). Attempting to explain their  
446 unique finding that squirrel densities were higher in thinned stands than in old-growth, Ransome  
447 *et al.* (2004) speculated that post-thinning increases in squirrel densities might be the result of  
448 concomitant increases in food resources, particularly hypogeous fungi, epigeous fungi, and



449 understory vegetation. Unfortunately, understory vegetation was not measured before thinning,  
450 and fungal biota were not measured at any stage, so it was not possible to test these speculations.  
451 Our study also lacks data to directly address the relationship between squirrel density and  
452 abundance of food resources, though response to thinning by one genus of epigeous mushroom  
453 (*Cantharellus* sp.) was measured on our sites (Pilz *et al.*, 2006). Thinning had strong short-term  
454 negative impacts on abundance and mass of *Cantharellus* sporocarps, but those impacts had  
455 almost entirely disappeared by 6 years after thinning. *Cantharellus* are not generally considered  
456 to be forage species for northern flying squirrels, and we cannot say whether fungal taxa more  
457 important to flying squirrels (i.e., truffles) showed similar patterns of changes in abundance.

458         In our work, the strong negative effect of thinning on northern flying squirrel densities  
459 was associated with decreased live tree basal area, and to differences in density of large snags.  
460 This association with canopy variables (live trees and snags) supports the conclusion of others  
461 that forest canopy structure, particularly abundance of large live trees (Smith *et al.*, 2004; Gomez  
462 *et al.*, 2005; Smith *et al.*, 2005; Lehmkuhl *et al.*, 2006) and large snags (Carey, 1995; Carey *et*  
463 *al.*, 1999a; Smith *et al.*, 2004; Holloway and Malcolm, 2006), is the most important determinant  
464 of habitat quality for northern flying squirrels. Smith *et al.* (2005) stressed that response of  
465 northern flying squirrels to any particular habitat feature might depend on the relative abundance  
466 of such features within a local landscape, so that features in low abundance may be limiting. This  
467 may be the case for our sites, where trees were relatively small (mean dbh = 27.2 cm), and large  
468 snags were scarce and variable (Table 1). Holloway and Smith (2011) recently presented meta-  
469 regression results that indicate studies showing the greatest negative effects of harvest practices  
470 on northern flying squirrels tended to have the lowest rates of retention of large snags (> 40 cm  
471 dbh), most having fewer than 8 snags/ha. The importance of large snags as nesting sites for  
472 northern flying squirrels has been extensively documented (Carey *et al.*, 1997; Cotton and  
473 Parker, 2000; Bakker and Hastings, 2002; Menzel *et al.*, 2004; Meyer *et al.*, 2005; Meyer *et al.*,  
474 2007b; Wilson *et al.*, 2008).

475         Wilson (2010) argued that flying squirrels in the Pacific Northwest are largely limited by  
476 the amount of protective cover from predators, primarily owls and weasels, and that 4 factors  
477 could be used collectively to measure protective cover and predict squirrel abundance (large live  
478 trees, area of canopy and bole intercept at 10 m above ground, and percent area of stand without

479 gaps > 100 m<sup>2</sup>) or distinguish between stands supporting high or low abundances (variance in  
480 live tree dbh, area of canopy and bole intercept at 10 m above ground, and percent of stand  
481 without gaps > 100 m<sup>2</sup>). Our data roughly agree with Wilson's findings, though there are some  
482 important differences. Overstory cover in our Light Thin stands had recovered in the first 5  
483 years after thinning and was no longer statistically distinguishable from Control stands (Davis *et al.*  
484 *et al.*, 2007), yet densities of flying squirrels 12 years after thinning were still much lower in Light  
485 Thin stands; thus, overstory cover alone does not appear to provide the habitat quality needed for  
486 flying squirrels to occupy stands in high densities. Vertical structural complexity on our YSTDS  
487 stands was estimated from 3-yr post-thinning data with 2 metrics (live crown ratio and foliage  
488 height diversity; Davis *et al.* 2007), and no differences were found among the treatments, but it is  
489 not clear that these structural metrics are appropriate for measuring the sort of occlusion that  
490 Wilson (2010) hypothesized was vital for flying squirrels to avoid predators, nor that conditions  
491 have remained unchanged in the intervening 9 years. We have not mapped or measured the  
492 canopy gaps in the YSTDS stands, but it seems likely that the large gaps (ca. 2000 m<sup>2</sup>) created in  
493 our Gaps treatment stands would be formidable barriers to the gliding locomotion of flying  
494 squirrels, and certainly our finding of much lower densities of flying squirrels in Gaps stands  
495 than in Controls does not contradict those of Wilson (2010).

496         The question of whether flying squirrels are more limited by availability of large trees  
497 and snags or by mid-story structural complexity may ultimately be answered by continued long-  
498 term monitoring of the YSTDS stands. Simulation studies by Garman *et al.* (2003), for which  
499 initial pre-treatment conditions and thinning prescriptions on the YSTDS stands were projected  
500 through harvest and many years of subsequent recovery, predict that the Heavy Thin treatment  
501 will develop large live trees and large snags most quickly. This prescription allows for maximal  
502 growth of large trees in minimal time, and while diameter growth of trees in Heavy Thin stands  
503 has already increased significantly over other thinning treatments and controls (Davis *et al.*,  
504 2007), several decades seem likely to pass before this growth benefits northern flying squirrel  
505 densities. Development of large snags and large volumes of coarse woody debris in these Heavy  
506 Thin stands will require either intentional killing of large trees or restraint from subsequent  
507 thinning to enable large tree mortality through competition. Simulations by Garman *et al.* (2003)  
508 also predict that the YSTDS treatment likely to develop overstory and mid-story complexity  
509 most slowly will be the Light Thin stands. Therefore, dense stands like the YSTDS Control

510 treatment are likely to provide the most mid-story cover from predation in mid-successional  
511 conifer stands. This is supported by our data, where 12 years after thinning, flying squirrel  
512 density was greater in the Control than the thinned stands. However, cover provided by conifer  
513 stems is expected to diminish as suppression mortality reduces stand density in the Control  
514 stands. Development of shade-tolerant tree species such as hemlock and cedar would likely then  
515 lag behind that in thinned stands, where such development started soon after thinning, with the  
516 possible result that the Control stands could become less suitable than thinned stands as habitat  
517 for flying squirrels some decades later. Thus, management of these young forests represents a  
518 tradeoff between providing short-term, ephemeral habitat in dense unthinned stands and thinning  
519 to promote the development of more complex habitat in the longer term.

## 520 **5. Conclusions**

521 Currently, forest managers of public lands in the Pacific Northwest are treating many  
522 thousands of hectares of young forests by thinning and other partial cutting methods, with major  
523 objectives being to accelerate the development of larger trees and promote the sort of structural  
524 complexity more typical of late-seral forests. Regardless of the motivations for this strategy, our  
525 research makes it clear that densities of northern flying squirrels are particularly sensitive to  
526 thinning in young Douglas-fir forests, for at least 12 years after treatment. Whether observed  
527 decreases in density also mean decreases in population viability has not been adequately  
528 addressed, and will require comparison of flying squirrel reproductive fitness and survival rates  
529 between thinned and unthinned young stands. Until this question of fitness is answered, a  
530 conservative strategy would strive to maintain adequate area and connectivity of dense, closed-  
531 canopy forests within managed landscapes to maintain northern flying squirrel populations, by  
532 leaving areas of young forest unthinned.

533 The question of how much closed-canopy forest is “adequate” calls for a landscape-level  
534 assessment of northern flying squirrel habitat associations in the Pacific Northwest, something  
535 not yet accomplished in the region. Northern flying squirrels in New Brunswick (Ritchie *et al.*,  
536 2009) responded more to the total amount of habitat available on a landscape scale than they did  
537 to its configuration within the landscape, and thus manipulation of landscape configuration (i.e.,  
538 connectivity) is unlikely to be useful in maintaining metapopulation viability in the face of  
539 habitat loss. This would seem to argue for caution in carrying out commercial thinning across

540 large portions of the Pacific Northwest landscape, especially if one eventual goal is to sustain the  
541 primary prey of the northern spotted owl. Continued monitoring of northern flying squirrels and  
542 habitat features in the Young Stand Thinning & Diversity Study should eventually tell us when  
543 flying squirrel populations begin to recover in thinned stands, in which treatment levels this  
544 recovery occurs most quickly, and which habitat features are most important in that recovery.

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741

742 Table 1: Treatment level means (and SE) of habitat variables in the Young Stand Thinning and  
 743 Diversity Study, measured in 2006, 10 years after thinning and just prior to estimation of  
 744 northern flying squirrel population density in 2007-08. Superscript letters indicate significant  
 745 differences at  $\alpha=0.05$ , from single-classification ANOVA; tree density and basal area were log-  
 746 transformed, and % cover variables were arc-sin-square-root transformed before comparison.

747

	<b>Control</b>	<b>Heavy</b>	<b>Light</b>	<b>Gaps</b>
Density of trees ( $\geq 8$ cm dbh) per ha	686 (33) <sup>A</sup>	233 (39) <sup>B</sup>	307 (50) <sup>B</sup>	273 (41) <sup>B</sup>
Basal area (m <sup>2</sup> /ha) of trees	52.7 (4.3) <sup>A</sup>	21.4 (1.6) <sup>C</sup>	31.0 (2.6) <sup>B</sup>	25.6 (2.3) <sup>BC</sup>
Large (>30 cm dbh) snags per ha	10.4 (3.8)	5.8 (3.4)	8.5 (3.0)	7.5 (2.5)
Mean tree diameter (cm dbh)	28.8 (1.4)	31.7 (3.7)	34.4 (2.3)	31.8 (2.9)
% cover overstory canopy	81% (2%) <sup>A</sup>	47% (7%) <sup>C</sup>	67% (5%) <sup>B</sup>	60% (4%) <sup>B</sup>
% cover herbs	23% (4%)	25% (1%)	29% (4%)	28% (4%)
% cover low shrubs	19% (3%) <sup>A</sup>	44% (6%) <sup>B</sup>	41% (3%) <sup>B</sup>	43% (5%) <sup>B</sup>
% cover tall shrubs	46% (5%)	37% (9%)	27% (5%)	28% (6%)

748

749 Table 2: Effective trapping areas, total individuals captured, estimated abundances<sup>a</sup>, and  
 750 densities<sup>b</sup> of northern flying squirrels (*Glaucomys sabrinus*) on the Young Stand Thinning &  
 751 Diversity Study, Sept-Nov of 2007 and 2008.

Treatment	Block	Effective Trapped Area (ha)	Total Individual Flying Squirrels Captured		Flying Squirrel Abundance <sup>a</sup> (individuals)		Flying Squirrel Density <sup>b</sup> (individuals/ha)	
			2007	2008	2007	2008	2007	2008
Control	Cougar	12.16	23	17	43	18	3.54	1.48
Control	Mill Creek	12.32	15	34	28	36	2.27	2.92
Control	Christy	11.54	18	27	33	30	2.86	2.60
Control	Sidewalk	17.48	4	2	7	2	0.40	0.11
Heavy Thin	Cougar	15.80	4	6	4	7	0.25	0.44
Heavy Thin	Mill Creek	14.63	1	1	1	1	0.07	0.07
Heavy Thin	Christy	16.24	0	0	0	0	0.00	0.00
Heavy Thin	Sidewalk	14.32	1	5	1	6	0.07	0.42
Light Thin	Cougar	13.39	14	21	12	21	0.90	1.57
Light Thin	Mill Creek	17.88	5	8	5	8	0.28	0.45
Light Thin	Christy	13.19	0	3	0	3	0.00	0.23
Light Thin	Sidewalk	15.59	1	1	1	1	0.06	0.06
Gaps	Cougar	15.46	5	7	6	14	0.39	0.91
Gaps	Mill Creek	11.72	11	6	14	12	1.19	1.02
Gaps	Christy	14.51	0	3	0	6	0.00	0.41
Gaps	Sidewalk	15.54	1	3	1	6	0.06	0.39

752

753 <sup>a</sup> Abundance estimated with Program MARK closed population estimators.

754 <sup>b</sup> Density estimates based on abundance estimated with Program MARK.

755 Table 3: ANOVA table for repeated-measures orthogonal comparisons of northern flying  
 756 squirrel (*Glaucomys sabrinus*) densities, mean maximum distance moved (MMDM), sex ratios,  
 757 and sex-specific body mass among thinning treatments of the Young Stand Thinning & Diversity  
 758 Study, 2007-2008.

759

<b>Dependent Variable</b>	<b>Factor</b>	<b>df</b>	<b>F</b>	<b>P</b>
Density (Individual squirrels/ha)	Treatment	3	45.14	< 0.0001
	Block	3	21.05	< 0.0001
	Block*Treatment	9	7.88	0.0003
	Year	1	2.88	0.1106
Mean Maximum Distance Moved (MMDM)	Treatment	3	0.43	0.7347
	Sex	1	1.93	0.1705
	Block	3	0.74	0.5334
	Block*Treatment	4	1.12	0.3570
	Block*Sex	3	1.18	0.3270
	Year	1	0.25	0.6178
Sex Ratio (Male Individuals:Female Individuals)	Treatment	3	0.14	0.9360
	Block	3	3.78	0.0336
	Block*Treatment	9	2.12	0.0954
	Year	1	7.16	0.0173
Female Body Mass	Treatment	3	0.51	0.6756
	Block	3	2.73	0.0473
	Block*Treatment	9	0.50	0.8513
	Year	1	1.23	0.2703
Male Body Mass	Treatment	3	1.46	0.2299
	Block	3	1.50	0.2192
	Block*Treatment	9	0.95	0.4828
	Year	1	1.26	0.2638

760

761 Table 4: Results of mixed-effects regression modeling of northern flying squirrel (*Glaucomys*  
 762 *sabrinus*) habitat relationships on the Young Stand Thinning & Diversity Study, 2007-2008.  
 763 Post-thinning basal area was log-transformed. Flying squirrel density and snag density were  
 764 log+1-transformed because there were values of zero. Percent cover of low shrubs was arc-sin-  
 765 square-root transformed. AICc is Akaike's Information Criterion, corrected for small sample  
 766 size.

767

<b>Model</b>	<b>AICc</b>
Null model	47.6
Log(GLSA) = log(basal area)	18.9
Log(GLSA) = log(snag density)	40.4
Log(GLSA) = arcsin-sqrt(% cover low shrubs)	21.9
Log(GLSA) = log(basal area) log(snag density)	17.2
Log(GLSA) = log(basal area) arcsin-sqrt(% cover low shrubs)	16.9
Log(GLSA) = log(snag density) arcsin-sqrt(% cover low shrubs)	11.8
Full model (all 3 regressors)	12.3

768



769 Fig 1: Location of the Young Stand Thinning & Diversity Study within the Willamette National  
770 Forest, Oregon, USA.

771

772 Fig 2: Example of one of the trapping arrays based on variable-length transects. Numbered  
773 boxes indicate positions of trapping stations along transects. Inter-trap distance equals 30 m in  
774 both dimensions.

775

776 Fig. 3: Mean density (individuals per ha) of northern flying squirrels (*Glaucomys sabrinus*) in  
777 treatment stands of the Young Stand Thinning and Diversity Study, 2007 and 2008. Each  
778 treatment was replicated 4 times. Error bars represent  $\pm 1$  SE.

779

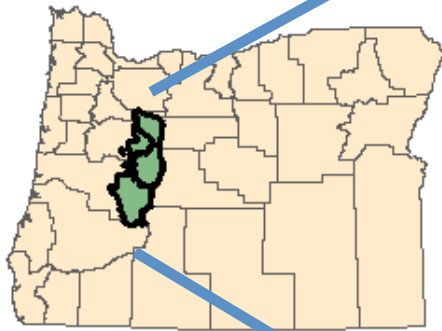
780 **Editors: If possible, please place Figure 2 near second paragraph of “3. Results”.**

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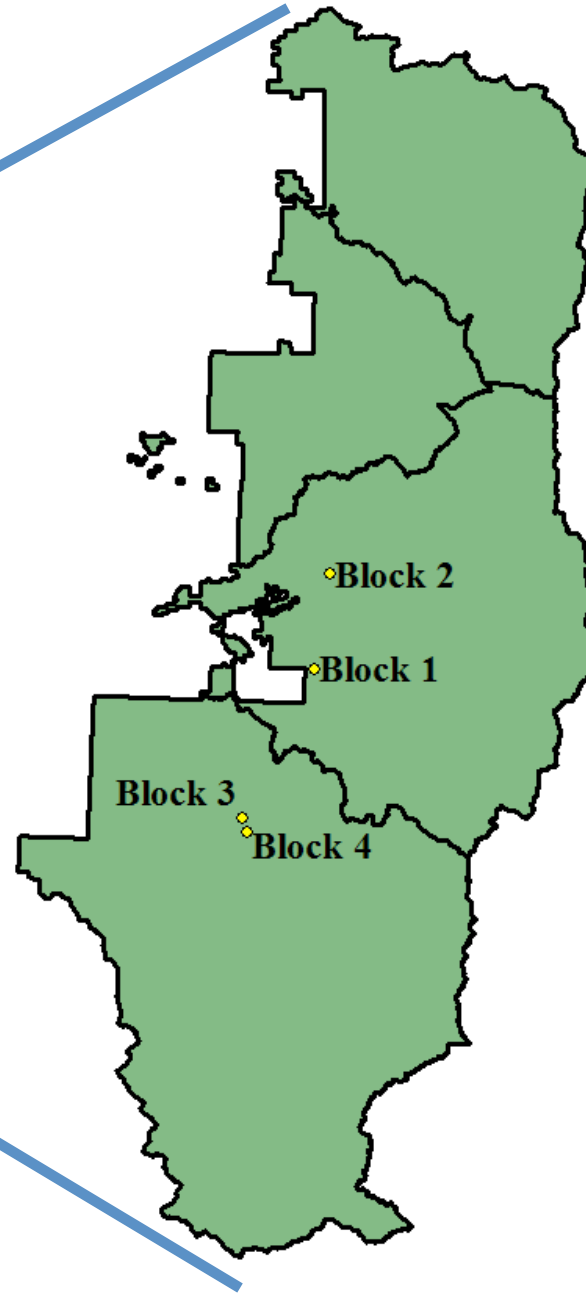
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**Oregon**



Transect 1    Transect 2    Transect 3    Transect 4    Transect 5    Transect 6    Transect 7    Transect 8

15							
14	13	1	1				
13	12	2	2	12			
12	11	3	3	11	11	1	1
11	10	4	4	10	10	2	2
10	9	5	5	9	9	3	3
9	8	6	6	8	8	4	4
8	7	7	7	7	7	5	5
7	6	8	8	6	6	6	6
6	5	9	9	5	5	7	7
5	4	10	10	4	4	8	8
4	3	11	11	3	3	9	9
3	2	12	12	2	2	10	10
2	1	13	13	1	1	11	11
1						12	

N ↑

**TAC 1:  
Cougar  
Control**

