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Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades

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ABSTRACT

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

1. Introduction

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

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

Considerable evidence exists that northern flying squirrels are relatively more abundant, and correlates of squirrel fitness are optimized, in forests with many large live trees (Smith et al., 2004; Gomez et al., 2005; Holloway and Malcolm, 2006; Lehmkuhl et al., 2006), many large dead trees (Carey, 1995; Smith et al., 2004; Holloway and Malcolm, 2006; Meyer et al., 2007b), well-developed understories (Carey et al., 1999a; Pyare and Longland, 2002), and many large logs on the ground (Carey et al., 1999a; Gomez et al., 2005; Smith et al., 2005). Collectively, these structural elements

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are typical of late-seral (mature and old-growth) forests. Some or all of these elements are largely lacking in most of the young forests now covering extensive areas of the Pacific Northwest (Spies and Cline, 1988; Halpern and Spies, 1995; Franklin et al., 2002).

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

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

A recent meta-analysis of effects of silvicultural practices on northern flying squirrels (Holloway and Smith, 2011) attempted to resolve the inconsistencies of the work done so far, and found that studies asserting a benefit or no effect of harvesting on squirrel populations (Cote and Ferron, 2001; Ransome and Sullivan, 2002; Gomez et al., 2005) lacked statistical power needed to support those assertions. The implication of Holloway and Smith's meta-analysis is that forest management practices that are currently widespread in the Pacific Northwest (thinning and clearcutting) have negative short-term and long-term impacts on northern flying squirrels.

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

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

2. Methods

2.1. Study area description

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

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

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

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

Pre-thinning sampling of the vegetative structure within each stand in 1993 established that stands within each block were similar with respect to tree basal area (overall mean 34.8 m^2/ha; average CV for 4 blocks = 8.7%) and tree density (overall mean density 718 trees per ha; average CV over 4 blocks = 10.1%; (Davis et al., 2007). Before treatment commenced, each stand was assigned randomly to one of the thinning treatments or as an unthinned control. Thinning began in late 1994, and was completed by February 1997. Most harvest activity occurred simultaneously on all blocks between February 1995 and September 1996 and with no particular pattern to order of treatments.

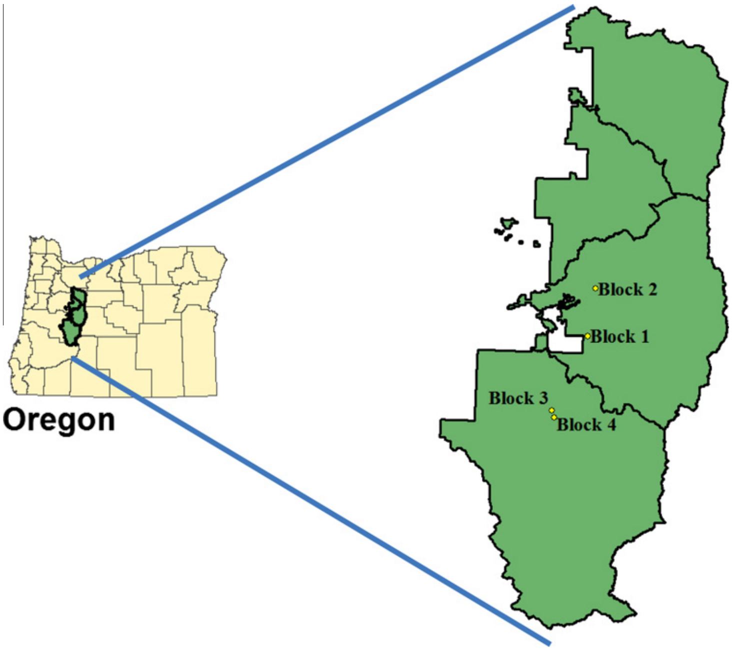

Fig. 1. Location of the Young Stand Thinning & Diversity Study within the Willamette National Forest, Oregon, USA.

Table 1
Treatment level means (and SE) of habitat variables in the Young Stand Thinning and Diversity Study, measured in 2006, 10 years after thinning and just prior to estimation of northern flying squirrel population density in 2007–2008. Superscript letters indicate significant differences at $\alpha = 0.05$, from single-classification ANOVA; tree density and basal area were log-transformed, and % cover variables were arc-sin-square-root transformed before comparison.

	Control	Heavy	Light	Gaps
Density of trees ($\geqslant$8 cm dbh) per ha	686 (33)^{A}	233 (39)^{B}	307 (50)^{B}	273 (41)^{B}
Basal area (m^2/ha) of trees	52.7 (4.3)^{A}	21.4 (1.6)^{C}	31.0 (2.6)^{B}	25.6 (2.3)^{BC}
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%)^{A}	47% (7%)^{C}	67% (5%)^{B}	60% (4%)^{B}
% Cover herbs	23% (4%)	25% (1%)	29% (4%)	28% (4%)
% Cover low shrubs	19% (3%)^{A}	44% (6%)^{B}	41% (3%)^{B}	43% (5%)^{B}
% Cover tall shrubs	46% (5%)	37% (9%)	27% (5%)	28% (6%)

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

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

2.2. Mammal sampling

In 2007–2008 (11–13 years after thinning), all stands were sampled to estimate abundance of small mammals, especially northern flying squirrels. Trapping occurred for four consecutive nights in each stand from late September to late November. Two stands in each block were sampled simultaneously and the other two stands in the same block were sampled in the following week. The order for sampling stands within blocks was randomized, and blocks were sampled sequentially. Considerations for the order of

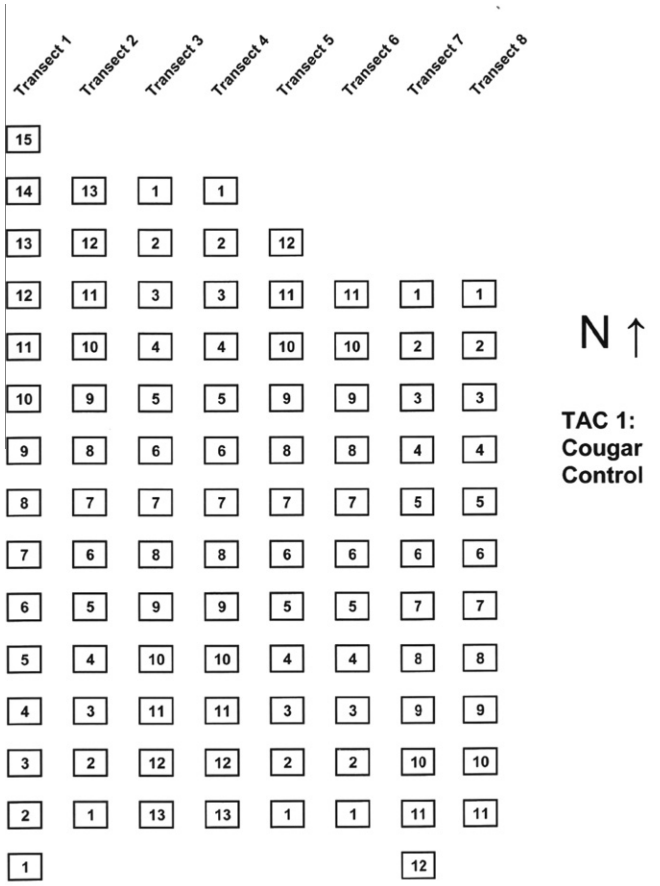

Fig. 2. Example of one of the trapping arrays based on variable-length transects. Numbered boxes indicate positions of trapping stations along transects. Inter-trap distance equals 30 m in both dimensions.

sampling among blocks included elevation, seasonal road closures due to snow or hunting, and proximity to other blocks.

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

One trap was placed at each station. In each stand, Sherman traps (Model LFATDG) alternated with Tomahawk traps (Model 201) along each transect, so that 50 Sherman traps and 50 Tomahawk traps were distributed evenly throughout the 100 stations in each stand. Half (25) of the Tomahawk traps were attached to the boles of trees (approx. 1.5 m high), and the other 25 were placed on the ground; tree and ground placements of Tomahawk traps alternated along transects. Thus, effective spacing among Tomahawk traps was 60 m. Sherman traps were used to capture terrestrial rodents and insectivores, and so were placed on the ground; we include Sherman traps in this analysis because a substantial number of flying squirrels were captured in them. To increase capture rates, all traps were locked open and pre-baited once 10 days before the trap session began. During the trapping session, traps were checked twice daily to minimize mortality of trap-prone diurnal species, particularly chipmunks. Traps were set in the afternoon on the 1st day of each trap session, checked twice each day for 3 days, then checked and closed on the morning of the 5th day; thus, each trap session included four nights. In both years, traps were baited with a mixture of peanut butter, oats, and sunflower seeds. Upholstery cotton was placed in each trap for insulation, and traps were placed within weather-resistant covers. Captured mammals were identified to species, weighed, sexed, marked with individually-numbered eartags, and immediately released at the point of capture. Trap mortalities were frozen for later necropsy to confirm species and sex. All procedures were conducted under protocols approved by the Institutional Animal Care and Use Committee at Oregon State University.

2.3. Analytical procedures

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

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

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

We computed the effective area trapped in each stand (Table 2) by adding a buffer around the perimeter of each trapping array. Buffer width was one-half of the mean maximum distance moved (MMDM) by flying squirrels in that stand. Because we could detect no statistical difference in MMDM between years or sexes (ANOVA, $P = 0.70$ and 0.46, respectively), we used the average MMDM for the 2 years for each stand without regard to sex. Because northern flying squirrels are known to have larger home ranges in low density populations (Carey, 1995, 2000), we used different computations for MMDM depending on estimated abundance of each particular stand: for each stand with estimated abundance $\geqslant 10$ for either year, MMDM was computed from data specific to that stand; for stands with estimated abundance <10 animals, and thus having few data to compute MMDM, we used mean MMDM for all animals in all low-abundance stands to compute the array buffer. Mean MMDM for six high-density stands was 75.2 m, ranging from 59 to 102 m, and MMDM for all low-density stands was 101 m. Effective area trapped was computed as 0.5 MMDM multiplied by array perimeter, added to the area of the trapping array. We then computed density of flying squirrels in each stand as the number of animals estimated with MARK, divided by the effective area of trapping (Table 2).

We compared the effects of thinning on northern flying squirrel density, MMDM, sex ratio, and sex-specific body mass using a randomized block one-way ANOVA design with repeated measures. Treatment and year were fixed effects; block and the block by treatment factors were random effects. Density estimates and sex-specific body mass were square-root-transformed to correct for unequal variances, and sex ratios were logit transformed. We

Table 2
Effective trapping areas, total individuals captured, estimated abundances[a], and densities[b] of northern flying squirrels (*Glaucomys sabrinus*) on the Young Stand Thinning & Diversity Study, September–November of 2007 and 2008.

			Total individual flying squirrels captured		Flying squirrel abundance[a] (individuals)		Flying squirrel density[b] (individuals/ha)	
Treatment	Block	Effective trapped area (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

[a] Abundance estimated with Program MARK closed population estimators.
[b] Density estimates based on abundance estimated with Program MARK.

used a set of orthogonal contrasts to minimize Type I error rate (Lehmann, 1986). The set consisted of three comparisons: Control stands vs. all thinning treatments; Heavy Thin vs. Light Thin and Gaps; and Light Thin vs. Gaps. These comparisons test three corresponding hypotheses: (1) that flying squirrel density, MMDM, sex ratio, and body mass did not differ between thinned and unthinned treatments; (2) did not differ between heavy and light thinning intensities; and (3) did not differ between lightly thinned stands with and without small gaps. Our comparison-wise criterion for statistical significance was $\alpha < 0.05$.

We explored relationships between stand-level flying squirrel densities and habitat characteristics by developing *a priori* a set of mixed-effect linear regression models with block held as a random effect. Habitat variables available to us were tree density, tree basal area, density of large snags, tree diameter, overstory canopy cover, herbaceous plant cover, low shrub cover, and tall shrub cover (A. Ares, unpublished data). One year before sampling of flying squirrels commenced, these habitat components were measured on permanent 0.1-ha circular plots, placed systematically throughout each stand, and covering approximately 7.5% of the area of each stand. To ensure adequate sampling effort of gap interiors and gap edges in Gaps stands, plots were placed in the center of 10 randomly-chosen 0.2-ha gaps, and 10 more plots on the edges of 10 other randomly-chosen gaps; in addition, 10 plots were placed randomly in the matrix surrounding the gaps. Percent overstory cover was measured at the center of each circular plot and at four points 10.25 m distant from center in each cardinal direction. Overstory cover included live foliage and tree boles, limbs, and snags. Diameter at breast height (dbh) was also measured for all trees >5 cm dbh in each plot. All understory species present in the plot were recorded. Within each plot, eight subplots (each 0.1 m^2) were evenly spaced along each of two parallel 14.5-m transects, providing a total of 16 subplots per plot. In each subplot, percent cover of all understory plant species was visually estimated, as was percent cover of ground surface features including exposed mineral soil, coarse litter, and fine litter. Graminoids and bryophytes were not identified below family level. Along each 14.5-m transect, line intercept methods were employed to estimate understory tall shrub cover and cover of trees with dbh <5 cm. Low shrubs were distinguished from tall shrubs by potential stature of plant at maturity of less or more than 1 m, respectively. More details about this measurement protocol may be found in Davis et al. (2007) and Davis and Puettmann (2009).

Our explorations of northern flying squirrel habitat associations were primarily driven by *a priori* hypotheses about effects of thinning on squirrel densities. Specifically, we reasoned that variables representing the overstory (percent overstory cover, tree density, basal area) would be profoundly reduced by thinning, would be reduced more in Heavy Thin stands than in Light Thin stands, and would have important implications for flying squirrel locomotion and avoidance of predators (Wilson, 2010). All three of those variables were still significantly higher in Control stands than in thinned stands in 2006 (A. Ares, unpublished data), so we reasoned that one or more was likely related to flying squirrel densities; because all were highly collinear with each other, we chose one variable (tree basal area) which had the highest correlation with our measured flying squirrel densities for inclusion in our models. Large snags are generally considered an important habitat component for flying squirrels (Carey, 1995; Carey et al., 1999a; Smith et al., 2004; Holloway and Malcolm, 2006), so we included density of snags with dbh $\geqslant$30 cm in our modeling. In 2006, percent cover of low shrubs (species whose maximum height generally does not exceed 1 m) was the only understory variable that was significantly different between control stands and thinned stands; while there seemed little compelling reason to expect *a priori* that this stratum would influence flying squirrel abundance, the pattern seemed compelling enough to include in exploratory analyses. A set of eight models were fitted, residuals were examined for departures from normality and/or homoscedasticity, and variables were transformed where necessary to meet statistical assumptions. All ANOVA and regression analyses were performed in SAS version 9.2 (SAS, 2003). Regression models were ranked based on Akaike's Information Criterion, corrected for small sample size (AICc).

3. Results

In 2007–2008, a total of 11,873 corrected trap-nights were deployed, approximately equally distributed between the 2 years. A total of 103 individual flying squirrels were captured 134 times in 2007; 144 individuals were captured 213 times in 2008 (Table 2). Approximately 12% of all flying squirrel captures were in Sherman traps. All other flying squirrel captures were in Tomahawk traps; approximately 59% of those were in traps set on tree boles, and the rest were in traps set on the ground. Capture

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

Dependent variable	Factor	*df*	*F*	*P*
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

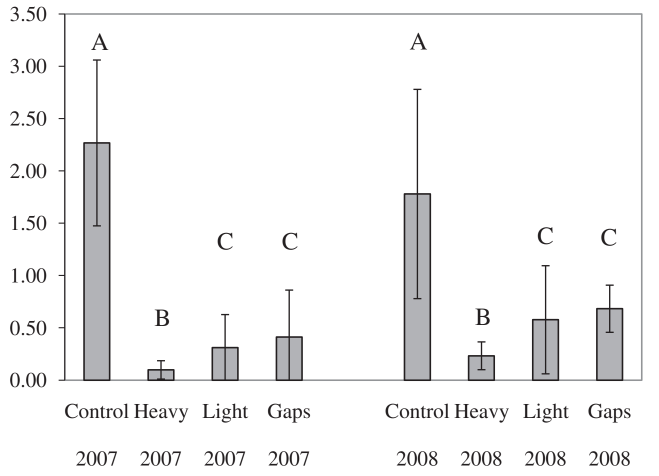

Fig. 3. Mean density (individuals per ha) of northern flying squirrels (*Glaucomys sabrinus*) in treatment stands of the Young Stand Thinning and Diversity Study, 2007 and 2008. Each treatment was replicated four times. Error bars represent ±1 SE.

probability (*P*) within stands ranged from 0.18 to 1.00, and averaged 0.48.

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

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

Model	AICc	ΔAIC	AIC (wt)
Null model	47.6	35.8	0.000
Log(GLSA) = log (basal area)	18.9	7.1	0.015
Log(GLSA) = log (snag density)	40.4	28.6	0.000
Log(GLSA) = arcsin-sqrt (% cover low shrubs)	21.9	10.1	0.003
Log(GLSA) = log (basal area) log (snag density)	17.2	5.4	0.034
Log(GLSA) = log (basal area) arcsin-sqrt (% cover low shrubs)	16.9	5.1	0.040
Log(GLSA) = log (snag density) arcsin-sqrt (% cover low shrubs)	11.8	0	0.510
Full model (all three regressors)	12.3	0.5	0.398

Using the more conservative approach of simple enumeration of individuals (i.e., computing densities without estimation of additional uncaptured animals) resulted in lower densities overall, of course, and more so for Controls than for thinned stands, but did not change significance of differences appreciably, nor our overall conclusions. Flying squirrel density using this approach was significantly greater ($P < 0.0001$) in unthinned Control stands (mean 1.43 squirrels/ha, SE = 0.54) than in thinned stands (0.33/ha, SE = 0.22), and greater ($P = 0.0298$) in the Light Thin and Gaps treatments (0.40/ha, SE = 0.25) than in the Heavy Thin treatment (0.18/ha, SE = 0.09). Light Thin (0.46/ha, SE = 0.32) and Gaps (0.35/ha, SE = 0.17) treatments were not significantly different ($P = 0.51$). Density differences between years were more pronounced using this enumeration approach ($P = 0.05$). Carrying out this alternative test increased our confidence that our population estimates are reliable, but doing so also ignores the certainty that naïve counts of individuals captured are inherently negatively biased. For this reason, we refer hereafter to our results using statistically estimated population densities only.

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

The mixed-effects linear regression model best supported by our data included snag density and percent cover of low shrubs (Table 4). Flying squirrel density was positively related with snag density, and negatively related with low shrub cover. Each of these two relationships was highly statistically significant ($P < 0.001$). The full model including all three regressors was included for completeness. The fit of the full model (AIC wt = 0.398) was slightly poorer than that of the best model (AIC wt = 0.510). Thus, the two models are nearly equivalent in explaining densities of northern flying squirrels in these young stands.

4. Discussion

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

In addition, we found that intensity of thinning (Heavy vs. Light Thin) also significantly affected northern flying squirrel densities. Densities on average were twice as high in Light Thin and Gaps stands as in Heavy Thin stands, and this difference was consistent for the 2 years of our study. The only habitat variable we measured which exhibits the same pattern is percent cover of overstory canopy, which is clearly higher in Light Thin and Gaps stands (overall mean 64%, SE 5%) than in Heavy Thin stands (mean 47%, SE 7%). Other variables representing forest density (trees/ha, basal area) were generally higher in Light Thin and Gaps stands than in Heavy Thin stands, but differences may be obscured by high variability (Table 1). Only two other studies have investigated the effects of thinning intensity on northern flying squirrels. Gomez et al. (2005), working in forests thinned to two levels very similar to ours, found no effect of thinning on flying squirrel densities regardless of intensity. Herbers and Klenner (2007) found that thinning decreased densities of northern flying squirrels in south central British Columbia from 0.64 to 0.26 squirrels/ha, but that the decrease did not vary over three levels of thinning intensity, nor with harvest pattern (uniform vs. patch cuts).

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

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

The densities of flying squirrels we report here (0–3.54 squirrels per ha, mean = 0.79; Table 2) are consistent with the range (0–4 squirrels per ha) reported by other authors and reviewed by Smith (2007). Mean density for our Control stands (2.02/ha) was quite high compared to nine previous studies (mean 1.06/ha) of northern flying squirrels in young forests (Carey et al., 1992; Rosenberg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995; Ransome and Sullivan, 2002, 2003; Gomez et al., 2005; Lehmkuhl et al., 2006), and is higher or comparable to the high densities (mean 1.44/ha) reported by several authors for mature and old-growth forests in the Pacific Northwest (Carey et al., 1992; Rosenberg and Anthony, 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995; Ransome and Sullivan, 2003; Lehmkuhl et al., 2006; Herbers and Klenner, 2007). While the high densities we measured may suggest that these young stands represent unusually good habitat for flying squirrels, we do not have the measures of reproductive fitness or survival necessary to refute the possibility that these areas could be operating as demographic sinks, occupied by subdominant animals from areas of higher quality habitat (Van Horne, 1983; Wheatley et al., 2002). Other authors (Smith and Nichols, 2003; Lehmkuhl et al., 2006) have reported dense populations of flying squirrels that exhibited negative growth rates, suggesting they might be operating as demographic sinks. We recommend that future work on the Young Stand Thinning & Diversity Study sample flying squirrel populations for at least three consecutive years, and make more effort to quantify reproductive success, so that reproductive fitness and rates of survival and population growth can be compared among treatments. Until then, inferences about the negative effects of thinning on flying squirrels are incomplete.

We know of only two other experimental studies that have measured northern flying squirrel densities more than 5 years after thinning. Wilson (2010) found that flying squirrel densities were low (<0.2 squirrels/ha) 12 years after variable-density thinning on the Forest Ecosystem Study (FES) in the Puget Trough of western Washington. Wilson's conclusion was that variable-density thinning had not yet promoted the development of high-quality habitat for flying squirrels in that time frame, primarily due to lack of sufficient midstory development (e.g., recruitment and growth of shade-tolerant trees under the existing canopy) and loss of overstory trees from various causes (wind, suppression mortality, and laminated root rot) unrelated to the thinning treatments, resulting in limited development of greater complexity in forest structure. Wilson's work, like ours reported here, found no support for the hypothesis that thinning for increased forest complexity results in habitat that supports high densities of northern flying squirrels, at least in short- or mid-term time frames. Forest structural processes (accelerated tree growth, development of mid-story occlusion, recruitment and decay of snags) that are presumably critical to high densities of northern flying squirrels will apparently take longer than 12 years to develop after thinning of young forests. Thus, it will be important to continue to monitor critical habitat components and flying squirrel densities over the long term in manipulative stand-level studies designed to accelerate late-seral forest conditions.

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

Northern flying squirrels are primarily mycophagous, feeding largely on the fruiting bodies of hypogeous fungi (truffles), and several authors have stressed the importance of truffle abundance (Waters and Zabel, 1995; Gomez et al., 2005; Lehmkuhl et al., 2006) and habitat features that have been correlated with abundance of truffles, such as coarse woody debris, particularly large logs (Carey et al., 1999a; Smith et al., 2004). Attempting to explain their unique finding that squirrel densities were higher in thinned stands than in old-growth, Ransome et al. (2004) speculated that post-thinning increases in squirrel densities might be the result of concomitant increases in food resources, particularly hypogeous fungi, epigeous fungi, and understory vegetation. Unfortunately, understory vegetation was not measured before thinning, and fungal biota were not measured at any stage, so it was not possible to test these speculations. Our study also lacks data to directly address the relationship between squirrel density and abundance of food resources, though response to thinning by one genus of epigeous mushroom (*Cantharellus* sp.) was measured on our sites (Pilz et al., 2006). Thinning had strong short-term negative impacts on abundance and mass of *Cantharellus* sporocarps, but those impacts had almost entirely disappeared by 6 years after thinning. *Cantharellus* are not generally considered to be forage species for northern flying squirrels, and we cannot say whether fungal taxa more important to flying squirrels (i.e., truffles) showed similar patterns of changes in abundance.

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

Our modeling of northern flying squirrel habitat relationships also indicates a negative association with the percent cover of low shrubs. We see this as an indirect effect of the decrease in tree basal area (and consequently percent overstory cover). We cannot explain why the model including cover of low shrubs fits the squirrel density data slightly better than the full model which includes basal area, but we point out that the difference in ΔAIC is 0.5, indicating that the models are nearly equivalent.

Wilson (2010) argued that flying squirrels in the Pacific Northwest are largely limited by the amount of protective cover from predators, primarily owls and weasels, and that four factors could be used collectively to measure protective cover and predict squirrel abundance (large live trees, area of canopy and bole intercept at 10 m above ground, and percent area of stand without gaps >100 m^2) or distinguish between stands supporting high or low abundances (variance in live tree dbh, area of canopy and bole intercept at 10 m above ground, and percent of stand without gaps >100 m^2). Our data roughly agree with Wilson's findings, though there are some important differences. Overstory cover in our Light Thin stands had recovered in the first 5 years after thinning and was no longer statistically distinguishable from Control stands (Davis et al., 2007), yet densities of flying squirrels 12 years after thinning were still much lower in Light Thin stands; thus, overstory cover alone does not appear to provide the habitat quality needed for flying squirrels to occupy stands in high densities. Vertical structural complexity on our YSTDS stands was estimated from 3-year post-thinning data with two metrics (live crown ratio and foliage height diversity; Davis et al., 2007), and no differences were found among the treatments, but it is not clear that these structural metrics are appropriate for measuring the sort of occlusion that Wilson (2010) hypothesized was vital for flying squirrels to avoid predators, nor that conditions have remained unchanged in the intervening 9 years. We have not mapped or measured the canopy gaps in the YSTDS stands, but it seems likely that the large gaps (ca. 2000 m^2) created in our Gaps treatment stands would be formidable barriers to the gliding locomotion of flying squirrels, and certainly our finding of much lower densities of flying squirrels in Gaps stands than in Controls does not contradict those of Wilson (2010).

The question of whether flying squirrels are more limited by availability of large trees and snags or by mid-story structural complexity may ultimately be answered by continued long-term monitoring of the YSTDS stands. Simulation studies by Garman et al. (2003), for which initial pre-treatment conditions and thinning prescriptions on the YSTDS stands were projected through harvest and many years of subsequent recovery, predict that the Heavy Thin treatment will develop large live trees and large snags most quickly. This prescription allows for maximal growth of large trees in minimal time, and while diameter growth of trees in Heavy Thin stands has already increased significantly over other thinning treatments and controls (Davis et al., 2007), several decades seem likely to pass before this growth benefits northern flying squirrel densities. Development of large snags and large volumes of coarse woody debris in these Heavy Thin stands will require either intentional killing of large trees or restraint from subsequent thinning to enable large tree mortality through competition. Simulations by Garman et al. (2003) also predict that the YSTDS treatment likely to develop overstory and mid-story complexity most slowly will be the Light Thin stands. Therefore, dense stands like the YSTDS Control treatment are likely to provide the most mid-story cover from predation in mid-successional conifer stands. This is supported by our data, where 12 years after thinning, flying squirrel density was greater in the Control than the thinned stands. However, cover provided by conifer stems is expected to diminish as suppression mortality reduces stand density in the Control stands. Development of shade-tolerant tree species such as hemlock and cedar would likely then lag behind that in thinned stands, where such development started soon after thinning, with the possible result that the Control stands could become less suitable than thinned stands as habitat for flying squirrels some decades later. Thus, management of these young forests represents a tradeoff between providing short-term, ephemeral habitat in dense unthinned stands and thinning to promote the development of more complex habitat in the longer term.

5. Conclusions

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

The question of how much closed-canopy forest is "adequate" calls for a landscape-level assessment of northern flying squirrel habitat associations in the Pacific Northwest, something not yet accomplished in the region. Northern flying squirrels in New Brunswick (Ritchie et al., 2009) responded more to the total amount of habitat available on a landscape scale than they did to its configuration within the landscape, and thus manipulation of landscape configuration (i.e., connectivity) is unlikely to be useful in maintaining metapopulation viability in the face of habitat loss. This would seem to argue for caution in carrying out commercial thinning across large portions of the Pacific Northwest landscape, especially if one eventual goal is to sustain the primary prey of the northern spotted owl. Continued monitoring of northern flying squirrels and habitat features in the Young Stand Thinning & Diversity Study should eventually tell us when flying squirrel populations begin to recover in thinned stands, in which treatment levels this recovery occurs most quickly, and which habitat features are most important in that recovery.

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