Forest Ecology and Management 285 (2012) 187–194

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance

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ARTICLE INFO

Article history:
Received 27 June 2012
Received in revised form 20 August 2012
Accepted 20 August 2012
Available online 15 September 2012

Keywords:
Biodiversity
Douglas-fir (*Pseudotsuga menziesii*) forests
Glaucomys sabrinus
Green-tree retention
Harvest intensity
Landscape context

ABSTRACT

In many regions of the world, forest management has shifted from practices emphasizing timber production to more sustainable harvesting that integrates ecological values, including maintenance of biodiversity, wildlife habitat, and ecological goods and services. To this end, management strategies emphasize retention of stand structures that meet the needs of forest-obligate wildlife species and enhance connectivity across landscapes. However, little is known about the effects on arboreal rodents of varying the amount or spatial distribution of retained structures. We quantified the responses of northern flying squirrels (*Glaucomys sabrinus*) to retention harvests of varying levels (15%, 40%, 75%, and 100% of original basal area) and spatial patterns (trees uniformly dispersed vs. aggregated in 1-ha patches), using six experimental treatments replicated at three locations in southwestern Oregon and Washington. Relative abundance of northern flying squirrels decreased following harvest; minimum number of squirrels known alive (MNKA) in the control (100%) and 75% retention treatment was significantly higher than in the 15% or 40% treatments. In mixed-effects regression models, MNKA increased with treatment-unit basal area and amount of surrounding mature (>80-year-old) forest, suggesting that squirrel abundance was influenced by local structure and landscape-scale variables. However, only basal area contributed to best-fit models of reproductive female abundance. Our results suggest a threshold response of northern flying squirrels to green-tree retention somewhere between 40% and 75% that is likely to be influenced by the spatial pattern of retention and landscape context. This study underscores previous conclusions that northern flying squirrels are sensitive to logging at both local and larger landscape scales, and demonstrates the current minimum retention standard of 15% will not provide suitable habitat for this species.

1. Introduction

In the last two decades, forest management has shifted from practices emphasizing timber production to more sustainable harvesting that integrate ecological values, including the maintenance of biodiversity, wildlife habitat, and ecological goods and services (Gale and Cordray, 1991; Lindenmayer et al., 2000; McComb and Lindenmayer, 1999). New management strategies emphasize the retention of forest structural legacies, and to promote successional processes more likely to produce the complex, multi-layered canopies typical of older forests (Carey, 2000a; Franklin et al., 2002, 1997). This contrasts sharply with traditional harvesting techniques, typically clearcut logging, that result in even-aged stands with a simplified stand structure (lacking residual large trees, snags, and logs), and loss of species diversity (Carnus et al., 2006; Imbeau et al., 2001; White and Mladenoff, 1994).

Green-tree retention is one of the primary strategies being employed in new forest management approaches in western North America, implemented as part of the Northwest Forest Plan (Tuchmann et al., 1996; USDA and USDI, 1994). A goal of green-tree retention is to mitigate the impacts of timber harvest on organisms that are dependent on structures characteristic of older forests by retaining features that enhance the structural complexity of future stands (Franklin et al., 1997; Lindenmayer and Franklin, 2002). On matrix lands available for timber harvest in the Pacific Northwest, federal standards specify that live trees must be retained in at least 15% of each cutting unit. They further recommend that 70% of this retention is in moderate to large-sized ($\geqslant$0.2 ha) aggregates, with the remainder as smaller aggregates or individual dispersed trees

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http://dx.doi.org/10.1016/j.foreco.2012.08.025

(USDA and USDI, 1994). Aggregates are hypothesized to act as refugia for forest-dwelling species and as source populations for adjacent harvested areas (Franklin et al., 1997; Aubry et al., 1999; Lehmkuhl et al., 1999), and to be similar to the "islands" of undisturbed forest left after fires or wind storms (Foster et al., 1997; Franklin et al., 1995). Dispersed trees provide for a uniform distribution of canopy cover, coarse woody debris, and snags, and potentially can moderate impacts to forest-floor and soil-dwelling organisms following disturbance (Aubry et al., 1999).

Although the Northwest Forest Plan established a minimum of 15% retention and recommended use of large aggregates, the benefits to wildlife and trade-offs for other forest values of varying levels or patterns of retention, were untested. To address these gaps in knowledge, several private and public research institutions jointly established the Demonstration of Ecosystem Management Options (DEMO) Experiment in Washington and Oregon, USA (Aubry et al., 2009, 1999). Its primary goal was to assess biological responses to varying levels and patterns of retention and to use this information to guide future management promoting the maintenance and recovery of species characteristic of mature and older forests. Experimental treatments combine one of four levels of retention (100%, 75%, 40% and 15% of original basal area) and, for the two lower levels of retention, one of two spatial patterns (trees uniformly dispersed or in 1-ha aggregates).

The DEMO experiment focused on plant, small mammal, and avian responses. The northern flying squirrel (*Glaucomys sabrinus*) was a species of particular interest because of its strong association with older forests (Holloway and Smith, 2011) and its importance as a primary prey species for the imperiled northern spotted owl (*Strix occidentalis caurina*; Forsman et al., 1984, 2001). The northern flying squirrel is considered a keystone species because of its importance as the primary disperser of mycorrhizal fungi (Maser et al., 1986; North et al., 1997), and its use as an indicator of sustainable forest management in many jurisdictions (Carey, 2000a; McLaren et al., 1998; Smith et al., 2004). Smith (in press) describes the northern flying squirrel as a sentinel of ecological processes because its life history is linked to ecological functions across multiple spatial scales. These include facilitating obligate symbiotic relationships of 'foundation' species, supporting populations of 'umbrella' species, revealing habitat-occupancy thresholds for species with habitat-area requirements, and ensuring connectivity among elements of dynamic, fragmented landscapes (Smith, in press).

The northern flying squirrel depends on old-forest structure for at least two fundamental aspects of its life history (Smith, 2007). It prefers cavities for denning (Carey et al., 1997; Bakker and Hasting, 2002; Hough and Dieter, 2009; Pyare et al., 2010); indeed, females exclusively use cavities as natal dens (Carey et al., 1997; Holloway and Malcolm, 2007) for successful reproduction (Smith, 2007). Both the density of reproductive females (Smith et al., 2004) and overall population density (Carey, 1995; Carey et al., 1999; Smith et al., 2004; Gomez et al., 2005; Holloway and Malcolm, 2006; Lehmkuhl et al., 2006) are directly related to the availability of large trees or snags. Northern flying squirrels also rely on the structure of mature forests to facilitate their specialized locomotion (Scheibe et al., 2007). Essential structural features include high canopies and relatively open under- and mid-story layers that provide high launch points and unobstructed gliding space that allow longer glide distances and increase energetic efficiency (Scheibe et al., 2006). Canopy removal eliminates these habitat features, compelling northern flying squirrels to use external nests for denning, to move greater distances to find cavities (Smith, 2007; Pyare et al., 2010), and to use energetically more expensive quadrupedal locomotion to move across modified landscapes (Flaherty et al., 2010a).

Consideration of both local (treatment-unit) and landscape scales is critical to management because the ways in which species respond to stand-level characteristics may vary with landscape context (Smith et al., 2005, 2004; Wiens, 1989). For flying squirrels in particular, landscape composition influences occupancy of habitat patches (Ritchie et al., 2009; Shanley et al., 2012; Smith, in press), dispersal abilities, and seasonal movements (Smith et al., 2011). In our analyses of northern flying squirrel responses to experimental retention treatments, we also considered the distribution of forest ages in the surrounding landscape.

Specific objectives of our study were: (1) to quantify northern flying squirrel abundance among treatments representing the gradient of basal area retention (including the 15% minimum retention standard), and one of two spatial patterns; (2) to determine stand- (treatment-unit) and landscape-scale variables that best predict the relative abundance of northern flying squirrels within these treatments; and (3) to determine the stand- and landscape-scale variables that best predict the relative abundance of reproductive females.

2. Materials and methods

2.1. Study areas and experimental design

The full experiment was implemented as a randomized complete block design at six locations (blocks). Based on preliminary data and financial constraints, however, sampling of northern flying squirrels was limited to three blocks: (1) Watson Falls (Umpqua National Forest, Oregon); (2) Butte (Gifford Pinchot National Forest, Washington); and (3) Capitol Forest (Washington Department of Natural Resources). Elevations range from 210 m at Capitol Forest to 1310 m at Watson Falls (Halpern et al., 1999). Douglas-fir (*Pseudotsuga menziesii*) was the dominant overstory species in each block (Maguire et al., 2007). At the time of harvest, stand ages ranged from 65 to 130 years. Due to the limited availability of large, uniform tracts of forest necessary to establish standard flying squirrel trapping grids (Carey et al., 1991), the stands selected for study were not of uniform age. Watson Falls ($\sim$130 years old) was surrounded primarily by older, undisturbed forests. Butte occurred in a matrix of relatively young ($\sim$80-year-old) forest of natural, post-fire origin. Capitol Forest ($\sim$65-year-old stands that had regenerated naturally after clearcut logging) was surrounded by younger (recent clearcut to $\sim$65 year-old), second-growth forests. Experimental units were square (360×360 m) or slightly rectangular (320×400 m) treatment areas encompassing $\sim$13 ha (Maguire et al., 2007). A rectangular sampling grid with 40-m spacing was established on each treatment unit; points on the grid periphery were 40 m from the edge of the treatment unit. Each treatment unit had either 63 or 64 sample points, depending on its shape (7×9 or 8×8 grid). Details on site selection, stand characteristics, and previous management histories are presented elsewhere (Aubry et al., 1999; Halpern and McKenzie, 2001; Halpern et al., 2005; Maguire et al., 2007). The six experimental treatments include the following (Fig. 1; for details see Aubry et al., 1999):

(1) 100% retention – Control (no harvest).
(2) 75% aggregated retention (75%A) – Three circular 1-ha patch cuts (gaps) were made in a triangular array, removing 25% of the basal area in the harvest unit. Inside each gap, all trees >18 cm at diameter breast height (dbh) were removed.
(3) 40% dispersed retention (40%D) – Dominant and co-dominant trees were retained in an even distribution throughout the harvest unit. The total basal area retained varied among blocks, but was equivalent to the basal area (±5%) of the five 1-ha patches of the corresponding aggregated retention treatment.

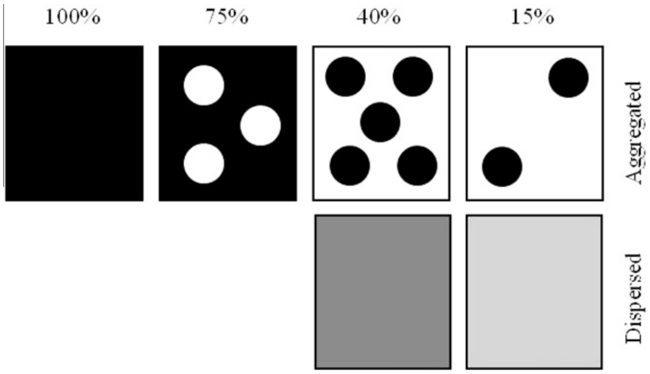

Fig. 1. Schematic representation of the six experimental treatments representing varying levels (proportion of original basal area) and spatial patterns (dispersed or aggregated) of green-tree retention. From Halpern and McKenzie (2001).

(4) 40% aggregated retention (40%A) – Five undisturbed 1-ha circular patches were retained at fixed distances. All remaining trees >18 cm dbh were removed.
(5) 15% dispersed retention (15%D) – Dominant and co-dominant trees were retained in an even distribution throughout the treatment unit. The total basal area retained varied among blocks, but was equivalent to the basal area (±5%) of the two 1-ha patches of the corresponding aggregated retention treatment.
(6) 15% aggregated retention (15%A) – Two undisturbed 1-ha circular patches were retained at fixed distances (opposite diagonal halves of the harvest unit). All remaining trees >18 cm dbh were removed.

Harvests were completed in autumn 1997 in Butte, spring 1998 in Capitol Forest, and autumn 1998 in Watson Falls (Halpern and McKenzie, 2001). Different yarding methods were used in each block: helicopter yarding at Butte, suspension cables at Capitol Forest, and ground-based equipment at Watson Falls (Halpern and McKenzie, 2001). Experimental prescriptions, including yarding methods, coarse woody debris retention, and snag creation were applied uniformly among experimental units within each block to reduce extraneous sources of variation (Aubry et al., 1999).

2.2. Northern flying squirrel sampling

We sampled the 18 experimental units (three blocks × six treatments) for 2 years each, pre- and post-harvest. We conducted the pre-harvest sampling during autumn 1995 and 1996, and the post-harvest sampling during autumn 1998 and 1999 (Butte and Capitol Forest) or autumn 1999 and 2000 (Watson Falls). Sampling occurred during autumn because this is the period when all age and sex groups typically are most susceptible to live-trapping (Carey et al., 1991). Each experimental unit was sampled with an 8 × 8 or 9 × 7 array of traps (13-ha) with 40-m spacing between stations (Carey et al., 1991). We placed 2 Tomahawk No. 201 live traps (Tomahawk Live Trap, Tomahawk, WI) at each of the 63 or 64 grid points in each treatment unit; one trap was attached to the bole of the nearest large tree at a height of ~1.5 m, and one live trap was placed on the ground at each grid point (Carey et al., 1991).

In each sampling year, we trapped all grids for 16 days (two consecutive 8-day sessions); the first starting in mid-late September, the second in mid-late October. We fitted traps with insulated nest boxes, baited them with a mixture of peanut butter, rolled oats, and molasses, and checked them daily. We marked captured flying squirrels with ear tags, weighed them to the nearest gram, and assessed reproductive status by observing the condition of mammae or position of testes. For adult females, we noted whether they were currently lactating, or showed evidence of having reproduced the previous summer (post-lactating condition). Animals were handled in accordance with guidelines established by the American Society of Mammalogists (ASM, 1998). We obtained collecting permits from the Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife based on proposed methods approved in advance with the Institutional Animal Care and Use Committees of Oregon State University and the University of Washington.

2.3. Habitat measurements

Stand- (treatment-) scale measurements of forest habitats were taken during concurrent studies of ground conditions, understory vegetation, and forest structure (Halpern and McKenzie, 2001; Halpern et al., 2005; Maguire et al., 2007). In each experimental unit, we established nested permanent plots and transects at a subset of grid points, and sampled each for downed coarse woody debris, snags, and live trees before and after treatment (see Halpern et al., 1999; Maguire et al., 2007 for details). In the controls (100%), we established 32 plots at alternate grid points. In aggregated treatments (75%A, 40%A, and 15%A), we established plots at all five grid points in each gap or aggregate and in a subset of points in the surrounding matrix (forest or harvested area). In total, we sampled 37 plots in 40%A, and 32 plots in 75%A and 15%A. Due to low post-harvest tree densities in the dispersed treatments (40%D and 15%D) we sampled all 63 or 64 grid points. Each plot contained a smaller 0.04-ha circular plot for live trees (dbh $\geqslant$ 5 cm) nested within a larger 0.08-ha circular plot for snags (>50 cm tall, >25 cm dbh). In each plot, we recorded species and dbh for each tree or snag. We sampled coarse woody debris (CWD) using the line-intersect method of Brown (1974), with each plot sampled by four 6-m lines arranged radially, 4–10 m from the plot center. We then computed four habitat descriptors from plot values in each experimental unit for the post-harvest period: (1) total basal area (m^2/ha; BA), (2) total number of snags/ha (Snag); (3) number of snags $\geqslant$60 cm dbh/ha (Snag > 60); and (4) total volume of coarse woody debris $\geqslant$10 cm dbh (m^3/ha; CWD; see Table 1). For the aggregated treatments, we computed values as weighted means of the two environments within each treatment.

We quantified forest ages in the surrounding landscape from spatial land cover layers using ArcGIS 10.0. We used forest resource inventory (FRI) data for the Washington blocks, and land cover data from the Interagency Vegetation Mapping Project (IVMP; based on Landsat Thematic Imagery) for the Oregon block. We determined the operational landscape to be a value of 500 m extending beyond each grid. This distance was chosen for

Table 1
Mean northern flying squirrel (*Glaucomys sabrinus*) relative abundance (±1 SE) and measures of stand structure in the post-harvest time period for each green-tree retention experimental block in western Oregon and Washington. Sample size for each block is six.

Variables	Experimental block		
	Watson falls	Butte	Capitol forest
Total MNKA	6.7 (±2.5)	17.3 (±4.6)	3.2 (±1.3)
No. reproductive females*	0.5 (0.4)	2.5 (0.5)	0 (0.2)
BA (m^2/ha)	24.3 (±5.7)	29.2 (±7.4)	29.5 (±8.5)
Snags (no./ha)	18.3 (±4.2)	31.9 (±5)	24.2 (±5)
Snags > 60 (no./ha)	4.4 (±1.7)	13.5 (±2.4)	5.0 (±1.3)
CWD (m^3/ha)	145.3 (±21.6)	390.5 (±119.9)	166.0 (±11.7)
LAge > 80 (%)	0.470 (±0.021)	0.113 (±0.027)	0.001 (±0.000)

[*] Median (and range) values are reported for this variable.

Table 2

Results of randomized block split-plot ANOVA comparing northern flying squirrel (*Glaucomys sabrinus*) abundance before and after harvest (period) among the six green-tree retention treatments (treatment) in the three experimental blocks in western Oregon and Washington.

ANOVA terms	SS	*df*	MS	F	*P*
Block	24.31	2	12.15	7.17	0.012
Treatment	5.87	5	1.17	0.69	0.641
Block × treatment (whole plot error)	16.95	10	1.69		
Period	35.22	1	35.22	50.60	<0.001
Period × treatment	17.67	5	3.53	5.08	0.001
Residual	8.35	12	0.70		

comparability with other studies (Holloway and Malcolm, 2006), and because it corresponded with the average seasonal movement distances observed for northern flying squirrels in a long-term study in western Washington (Wilson, 2010). We extracted landscape variables as the percentage of total area in each of four age classes: 0–30, >30–80, >80–200, and >200 years (the latter two considered to be "mature" forest). Finally, we corrected all ages derived from FRI and IVMP to the post-harvest period (1998).

2.4. Data analysis

We estimated the relative abundance of flying squirrels in the pre- and post-harvest time periods as the minimum number known alive (MNKA; Krebs, 1966) across all four trapping sessions. MNKA is an index commonly used as a measure of abundance for comparative purposes (Slade and Blair, 2000). We chose MNKA as the most appropriate estimator because the low number of recaptures between grid sessions would bias population density estimators (Rosenberg and Anthony, 1992). Moreover, MNKA estimates are strongly correlated with modeled density estimates (Holloway and Malcolm, 2006; Wilson, 2010). Although recently developed methods can be used to model detectability and density from multi-year studies such as the DEMO experiment (e.g., Converse and Royle, 2012), it is unclear how well these approaches would perform when there is very low capture probabilities and high heterogeneity among individual animals, combined with many dispersing individuals potentially present on individual grids for short periods of time.

To compare northern flying squirrel responses to harvest treatments, we used a randomized block split-plot analysis of variance (ANOVA), with harvest treatment as the whole-plot (fixed effect) and harvest period (pre- and post-) as the split plot (random effect); experimental block was also included as a random effect. We square-root transformed total MNKA to normalize the variance. Following the ANOVA, we conducted four *a priori* orthogonal contrasts of post-harvest abundance to test the following hypotheses:

1. Abundance (MNKA) will be significantly greater in control (100%) and 75% retention treatments than at lower levels of retention (100% + 75%A > 40%A + 40%D + 15%A + 15%D).
2. Abundance (MNKA) will differ in aggregated and dispersed treatments (40%A + 15%A ≠ 40%D + 15%D).
3. In aggregated treatments, abundance (MNKA) will be greater at 40% than at 15% retention (40%A > 15%A).
4. In dispersed treatments, abundance (MNKA) will be greater at 40% than at 15% retention (40%D > 15%D).

The first hypothesis tested whether northern flying squirrels responded to significant reduction and fragmentation of local habitat. The second addressed the overall response to spatial pattern of retention. The last two tested whether minimum retention standards (15%) were less effective than 40% retention in providing suitable habitat and whether this depended on the spatial pattern in which trees were retained.

We used mixed-model regression analysis to investigate the influence of stand structural and landscape predictors on two measures of response: (1) flying squirrel relative abundance (MNKA) and (2) number of reproductive females. The analysis of reproductive females included all individuals which showed any evidence of reproductive activity. Experimental block was included as a random effect in both analyses. We used mixed-effect linear regression to analyze total abundance (MNKA) and mixed-effect generalized-linear Poisson regression to analyze the number of reproductive females. We considered an *a priori* set of candidate models for each response variable based on expert opinion and published relationships (see Tables 3 and 4). Predictors included basal area, snag density, CWD volume, and percentage of surrounding landscape in forest >80 years old (LAge > 80; see Table 1 for summary values by block). The first three variables are strongly correlated with northern flying squirrel abundance (Carey et al., 1999; Smith et al., 2004; Holloway and Malcolm, 2006; Wilson, 2010) and the fourth is known to be important in influencing both local-scale abundance (Shanley et al., 2012) and dispersal success (Smith et al., 2011). The combinations of variables in the candidate set is based on known interdependencies among variables; for example, in younger stands with lower basal area, greater density of large snags can significantly increase northern flying squirrel density (Rosenberg and Anthony, 1992). We used an information theoretic approach (Burnham and Anderson, 1998) to identify the best predictors of total abundance and the number of reproductive females. Models with the lowest Akaike Information Criterion corrected for small sample sizes (AIC_c) and highest Akaike weight (w_i)

Table 3

Candidate model set and results for relative abundance of northern flying squirrels (*Glaucomys sabrinus*) among the six green-tree retention treatments in the three experimental blocks in western Oregon and Washington.

Candidate model set	*K*	AIC_c	ΔAIC_c	w_i
Null	2	70.77	2.15	0.13
Snags	3	75.84	7.22	0.01
Snags > 60	3	76.44	7.82	0.01
CWD	3	84.54	15.92	0
BA	3	70.11	1.49	0.18
BA + Snags	4	78.8	10.18	0
BA + Snags > 60	4	72.96	4.34	0.04
BA + CWD	4	83.04	14.42	0
LAge > 80	3	69.62	1	0.23
BA + LAge > 80	4	68.62	0	0.37
Snags > 60 + LAge > 80	4	76.43	7.81	0.01
BA + Snags > 60 + LAge > 80	5	73.92	5.3	0.03

Table 4

Candidate model set and results for relative abundance of northern flying squirrel (*Glaucomys sabrinus*) reproductive females among six green-tree retention treatments in the three experimental blocks in western Oregon and Washington.

Candidate model set	*K*	AIC_c	ΔAIC_c	w_i
Null	2	17.73	0.92	0.11
Snags	3	18.15	1.34	0.09
Snags > 60	3	18.73	1.92	0.07
CWD	3	19.39	2.58	0.05
BA	3	17.20	0.39	0.15
BA + Snags	4	18.85	2.04	0.06
BA + Snags > 60	4	16.81	0.00	0.18
BA + CWD	4	16.84	0.03	0.17
LAge > 80	3	20.36	3.55	0.03
BA + LAge > 80	4	19.79	2.98	0.04
Snags > 60 + LAge > 80	4	21.89	5.08	0.01
BA + Snags > 60 + LAge > 80	5	20.03	3.22	0.04

were determined to have the best fit among the candidate model set. We used quasi AIC_c ($QAIC_c$) for the analysis of reproductive females to account for over-dispersion. The AIC_c/$QAIC_c$ values (difference between each given model and the minimum AIC_c/$QAIC_c$) and the Akaike weight (w_i) were calculated for both response variables. We conducted the ANOVA analysis in STATA version 11.2 (STATA Corp LP, College Station, TX, USA), whereas we conducted all regression analyses in R ver. 2.10 (R Development Core Team) with the 'lme4' package (Bates et al., 2012).

3. Results

3.1. Influence of green-tree retention harvest on northern flying squirrels

Overall, we captured 405 and 163 individual northern flying squirrels before and after harvest, respectively. Abundance varied significantly among blocks ($P = 0.012$; Table 2). As we predicted, relative abundance declined strongly after harvest in the 40% and 15% retention treatments ($P < 0.001$; Fig. 2, Table 2). Effects of treatment also were significant (significant period × treatment interaction; $P = 0.001$, Table 2). Variation in post-harvest abundance supported hypothesis 1: relative abundance in 100% and 75%A was significantly greater than at lower retention (40%A, 40%D, 15%A, and 15%D; $P = 0.01$). Hypothesis 4 also was supported: in dispersed treatments, relative abundance was significantly greater at higher retention (40%D > 15%D; $P = 0.05$). However, results did not support Hypothesis 2 (overall response to pattern; $P = 0.32$) or Hypothesis 3 (response to level of retention in aggregated treatments; $P = 0.45$; Table 2).

3.2. Influence of local- and landscape-scale factors on northern flying squirrels

Northern flying squirrel abundance was correlated with both local (treatment-unit) forest structure and forest age in the surrounding landscape (Table 3). Among candidate models, the best-ranked model included local basal area and amount of mature forest (>80 yr) in the surrounding landscape (both positive relationships; Fig. 3, Table 3). The next two best ranked models included either basal area or percent of mature forest. Overall, the combined AIC_c weight of the top 3 models was 0.78 demonstrating basal area and the amount of mature forest are strongly correlated with north flying squirrels relative abundance.

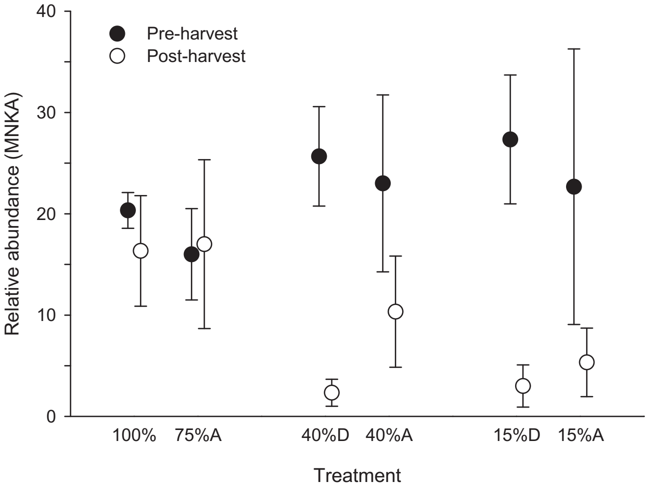

Fig. 2. Pre- and post-harvest relative abundance (mean MNKA ± 1 SE) of northern flying squirrels (*Glaucomys sabrinus*) among the six experimental green-tree harvest treatments in western Oregon and Washington. Treatment codes are: 100% = control, 75%A = 75% aggregated retention, 40%D = 40% dispersed retention, 40%A = 40% aggregated retention, 15%D = 15% dispersed retention, 15%A = 15% aggregated retention.

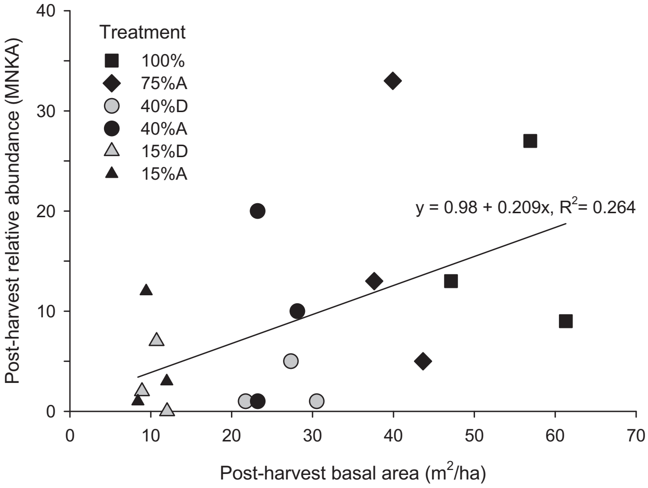

Fig. 3. Relationship between post-harvest northern flying squirrel (*Glaucomys sabrinus*) abundance (MNKA) and basal area (with effect of experimental block partialled out) among the six green-tree retention treatments in each block ($n = 3$ blocks) in western Oregon and Washington. Treatment codes are: 100% = control, 75%A = 75% aggregated retention, 40%D = 40% dispersed retention, 40%A = 40% aggregated retention, 15%D = 15% dispersed retention, 15%A = 15% aggregated retention.

In contrast, only stand structural variables were selected in the best-ranked models for abundance of reproductive females, with the top three models similarly ranked (Table 4). Each of these models included basal area. Two contained either density of snags $\geqslant$60 cm dbh or volume of CWD (both positive relationships). In all three of the top models, all predictors were significant at $P < 0.005$. However, there was little support for the importance of these additional factors; basal area had the strongest influence on abundance of reproductive females with an AIC importance weight for BA = 0.64, compared with AIC importance weights of 0.30 and 0.22 for Snags > 60 and CWD, respectively.

4. Discussion

4.1. Influence of timber harvest

This study was part of a broader experiment designed to assess ecological responses to green-tree retention in mature coniferous forests of the Pacific Northwest (Aubry et al., 1999, 2009). The prediction that northern flying squirrel abundance would decline following significant reduction and fragmentation of forest cover was supported (Hypothesis 1). Abundance was significantly higher in untreated (100%) and mostly intact forests (75%A) than at lower levels of retention (40% and 15%). This clearly indicates that retention levels $\leqslant$40% result in stand conditions with poorer quality habitat for northern flying squirrels. In the Pacific Northwest, northern flying squirrel abundance is greatest in old-growth forests characterized by greater numbers of larger trees and the presence of multi-layered forest canopies (Carey et al., 1999, 1992; Smith, 2007; Smith et al., 2004; Wilson, 2010). Dense, complex canopies are thought to be critical for predator avoidance because they provide protective cover in both the horizontal and vertical planes (Carey, 2000b; Wilson, 2010). This is an important consideration for management given that avian predators (particularly owls) are a primary threat to northern flying squirrels (Carey et al., 1992; Smith, 2007). In this study, all lower retention treatments opened the canopy and reduced the density of dominant canopy trees (Maguire et al., 2007), which likely increased the probability of detection by predators and reduced the potential for movement through stands (Smith, 2007; Smith et al., 2011).

We were unable to detect a significant effect of retention pattern (aggregated vs. dispersed) on northern flying squirrel abundance (Hypothesis 2). However, our ability to do so may have been hindered by a low sample size ($n = 3$) and by variation in landscape context among experimental blocks (Table 1). Despite the absence of a significant effect of retention pattern, mean abundance values in dispersed treatments were consistently low, suggesting that these are particularly unsuitable habitats for northern flying squirrels. Indeed, in this study the 40% dispersed treatments produced stand structures (particularly tree density and canopy cover) similar to those of shelterwood harvest, which are unsuitable for northern flying squirrels in other forest types (Waters and Zabel, 1995; Holloway and Malcolm, 2006). Moreover, reducing basal area to 15% retention further decreases the habitat quality relative to 40% dispersed treatment, demonstrating the 15% minimum retention standard will not sustain northern flying squirrel populations in harvested stands.

Although not tested explicitly, abundance values at high levels of retention (75%) appeared to indicate no short-term effect on northern flying squirrel abundance relative to controls. Although the resulting gaps (112 m in diameter) are large enough to prevent movement across them (Flaherty et al., 2010a, 2008), individuals are able to glide along edges (Scheibe et al., 2006; Vernes, 2001). However, as retention decreased to 40% in aggregated treatments, the larger non-forested clearings are likely to have prevented gliding and increased the energetic cost of movement (Flaherty et al., 2010a; Scheibe et al., 2006). Northern flying squirrels respond negatively to number and size of large canopy gaps (Patterson and Malcolm, 2010; Shanley et al., 2012; Wilson, 2010), which suggests that the 40%A treatment will provide poor northern flying squirrel habitat in the long term. The probability of northern flying squirrels persisting in the small 1-ha "islands" which are retained in this treatment is low (Smith and Person, 2007) due to expected low immigration rates (Smith et al., 2011). That said, this study focused on immediate responses to green-tree retention, and the longer-term consequences for northern flying populations of varying levels and spatial patterns of retention will require further investigation.

4.2. Influence of stand structure on northern flying squirrels

The results of regression analyses were consistent with interpretations of treatment effects. At the scale of harvest units, residual basal area was the best predictor of total abundance and the number of reproductive females. High basal area is characteristic of older coniferous forests that support a greater density of larger trees (Committee on Environmental Issues in Pacific Northwest Forest Management, 2000; Spies and Franklin, 1991). Our results are consistent with a large body of research in natural and managed forests of the Pacific Northwest indicating that northern flying squirrel abundance is higher in older forests with more complex canopy structures (Carey et al., 1992, 1999; Carey, 1995, 2000b; Waters and Zabel, 1995; Herbers and Klenner, 2007; Wilson, 2010).

Northern flying squirrel use of older forests is related to several aspects of their ecology, including greater availability of food and diurnal nests (Carey et al., 1997; North et al., 1997; Pyare et al., 2010; Smith, 2007). Hypogeous fungal productivity (truffle abundance) is associated with old-forest features, including a well-developed organic soil layers, abundant coarse woody debris, and the presence of large, old trees (North et al., 1997; Waters and Zabel, 1995). Northern flying squirrel survival and recruitment (Lehmkuhl et al., 2006) and population density (Gomez et al., 2005) also are related to truffle biomass. In a study of seasonal patterns of ectomycorrhizal sporocarp (including truffle) production in a subset of the DEMO blocks, Luoma et al. (2004) observed significant but highly variable reductions in sporocarp biomass in all treatments, with virtual elimination of production at low levels of aggregated retention (15%A). Finally, northern flying squirrels use larger live trees and snags preferentially for denning, and maternal dens are nearly always in cavities (Carey et al., 1997; Smith, 2007).

Beyond the positive relationship with basal area, additional measures of forest structure in our study explained little variation in the abundance of reproductive females. A simple explanation for the weak correlation of large snags and CWD in the current study is that these habitat features were not limiting. In high quality old-growth habitat, large trees, snags or decayed down wood were not significant predictors of microhabitat use (Smith et al., 2004). However, in their study these features explained 65% and 77% of the variation, respectively, in northern flying squirrel population density across habitats types. In habitats where large trees and snags were much less available (order of magnitude lower density), the odds of capturing northern flying squirrels increased 17-fold with every unit increase (10 stems/ha) in large tree or snag density. Given the low weights of even the best-fit models, the effects of retention harvest on reproductive female abundance clearly require further study, especially as they relate to the roles of large trees, snags, and CWD in reproductive success and how population density influences those relationships.

4.3. Landscape-scale influences on northern flying squirrels

Landscape context is critical to understanding northern flying squirrel response to local habitat conditions (Smith et al. 2004, Smith and Person, 2007) and especially to recent disturbance (Ritchie et al., 2009; Pyare et al., 2010). In the current study, northern flying squirrel abundance was positively correlated with the amount of mature (>80-year-old) forest in the surrounding landscape. Northern flying squirrels require an interconnected matrix of high-quality habitats to allow both breeding individuals and dispersing juveniles to move freely through the matrix and support self-sustaining populations (Smith et al., 2011). In managed landscapes, residual patches of high-quality habitat can mitigate some of the negative short-term effects of habitat loss and fragmentation (Pyare et al., 2010; Shanley et al., 2012), in addition to increasing the likelihood that viable populations can persist in the long term (Smith et al., 2011). In contrast, large clearcuts may act as barriers to dispersal and movement (Flaherty et al., 2008, 2010b) and can isolate or fragment high-quality habitats (Smith et al., 2011). Because northern flying squirrels are unlikely to occupy (Shanley et al., 2012) or persist for extended periods (>25 years) in relatively small (<50 ha) habitat fragments (Smith and Person, 2007), sustaining viable populations in intensively managed landscapes requires that landscapes are permeable and subpopulations are functionally connected (Smith et al., 2011).

We acknowledge that the relationship with age of surrounding forests is correlative and the variation in northern flying squirrel abundance we observed among blocks could have been a result of several other factors (Smith, 2007; Wilson, 2010). In the Pacific Northwest (PNW) region, northern flying squirrel abundance varies directly with multivariate factors such as "decadence", which is positively correlated with density of large snags and cover of downed wood, or "crown class diversification", which is correlated with density of large conifers (>50 cm dbh), herbaceous and midstory cover, and foliage-height diversity (Carey et al., 1999). Across the range of the northern flying squirrel, numerous studies have established direct relationships between population density and similar stand structural or compositional features, including large diameter trees (Ford et al., 2004; Menzel et al., 2004; Smith et al., 2004; Gomez et al., 2005; Lehmkuhl et al., 2006), large snags (Carey, 1995; Carey et al., 1999; Smith et al., 2004; Holloway and Malcolm, 2006), CWD (Carey et al., 1999; Smith et al., 2004), truffle abundance (Waters and Zabel, 1995; Gomez et al., 2005; Lehmkuhl et al., 2006), and the composition of ecological mammal communities (Smith, 2012). The landscapes sampled in this study represent a broad range of forest types, structures, and ages that influence the composition and dynamics of forest communities in western Oregon and Washington (Spies and Franklin, 1991). It is unlikely that age of forest stands in the surrounding landscape alone is responsible for variation in northern flying squirrel abundance.

4.4. Conclusions

Northern flying squirrels are obligate forest species that appear resilient to small changes in forest structure. Clearly, the current minimum retention standard of 15% will not provide suitable habitat for this species. Instead, responses to the experimental treatments in this study suggest a tolerance threshold in west-side forests of somewhere between 40% and 75%. Refining this threshold would require additional experimentation at intermediate levels of retention. Due to limited replication we are unable to determine whether aggregated retention can mitigate the impacts of harvesting on northern flying squirrels. However, our results and those of previous studies suggest that the reduced canopy cover found in dispersed treatments, even at levels >40%, is unlikely to provide conditions suitable for northern flying squirrels.

Our results also underscore that northern flying squirrel responses to local changes in structure (harvesting treatments) can be influenced by landscape context, which should be considered explicitly in future management and research. Because the ages and structures of managed forests can vary significantly in this region, we caution against developing generic prescriptions for green-tree retention without further evaluation, perhaps through adaptive management of local conditions that can influence biotic responses. For northern flying squirrels, green-tree retention may not be effective in landscapes dominated by recent harvests. A conservative approach would limit implementation (especially lower levels of retention) in landscapes dominated by early-seral vegetation. Because patch size and forest age within patches has a strong positive influence on the occurrence or persistence of flying squirrels (Smith and Person, 2007; Ritchie et al., 2009; Patterson and Malcolm, 2010; Shanley et al., 2012), we suggest that green-tree retention strategies will be most effective in landscapes matrices with a diverse mix of recent harvests and functionally connected old forest patches.

Acknowledgments

This is a product of the Demonstration of Ecosystem Management Options (DEMO) Study, a joint effort of the USDA Forest Service Region 6 and Pacific Northwest Research Station. Research partners include the University of Washington, Oregon State University, University of Oregon, Gifford Pinchot and Umpqua National Forests, and the Washington State Department of Natural Resources (http://www.fs.fed.us/pnw/rmp/demo/).We acknowledge the many people involved in design and implementation of the DEMO experiment, especially those involved with live-trapping northern flying squirrels and measuring forest habitat attributes. This study could not have been completed without the help of T. Manning who was heavily involved in data collection and management. D. Mills, D. Duron, and C. Heimburg provided vital information regarding the composition of the landscapes surrounding the experimental blocks. K.B. Aubry, J.F. Lehmkuhl, and T. Wilson reviewed an early draft of this manuscript and provided comments that ultimately improved its quality.

References

ASM Animal Care and Use Committee, 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. J. Mammal. 79, 1416–1431.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A., Horton, A.J., 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Sci. 73 (Special Issue), 12–26.

Aubry, K.B., Halpern, C.B., Petersen, C.E., 2009. Variable-retention harvests in the Pacific Northwest: a review of short-term findings from the DEMO study. For. Ecol. Manage. 258, 398–408.

Bakker, V.J., Hasting, K., 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. Can. J. Zool. 80, 1623–1633.

Bates, D., Maechler, M., Bolker, B., 2012. Package "lme4". <http://cran.r-project.org/web/packages/lme4/lme4.pdf>.

Brown, J.K., 1974. Handbook for inventorying downed woody material. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-16. Intermountain Forest and Range Experiment Station, Ogden, UT, p. 24.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Carey, A.B., 1995. Sciurids in Pacific Northwest managed and old growth forests. Ecol. Appl. 5, 648–661.

Carey, A.B., 2000a. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. In: Goldingay, R.L., Scheibe, J.S. (Eds.), Biology of Gliding Mammals. Filander Verlag, Fürth, pp. 45–66.

Carey, A.B., 2000b. Effects of new forest management strategies on squirrel populations. Ecol. Appl. 10, 248–257.

Carey, A.B., Biswell, B.L., Witt, J.W., 1991. Methods for Measuring Populations of Arboreal Rodents. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR-273, Portland, Oregon, USA.

Carey, A.B., Horton, S.P., Biswell, B.L., 1992. Northern spotted owls: influence of prey base and landscape character. Ecol. Monogr. 62, 223–250.

Carey, A.B., Wilson, T.M., Maguire, C.C., Biswell, B.L., 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. 61, 684–699.

Carey, A.B., Kershner, J., Biswell, B.L., Dominguez de Toledo, L., 1999. Ecological scale and forest development: squirrels, dietary fungi and vascular plants in managed and unmanaged forests. Wildl. Monog. 142, 1–71.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. J. Forestry 104, 65–77.

Committee on Environmental Issues in Pacific Northwest Forest Management, 2000. Old-growth forests. In: Environmental Issues in Pacific Northwest Forest Management. National Academy Press, Washington, pp. 44–72.

Converse, S.J., Royle, J.A., 2012. Dealing with incomplete and variable detectability in multi-year, multi-site monitoring of ecological populations. In: Gitzen, R.A., Millspaugh, J.J., Cooper, A.B., Licht, D.S. (Eds.), Design and Analysis of Long-term Ecological Monitoring Studies. Cambridge University Press, Cambridge, UK, pp. 426–442.

Flaherty, E.A., Smith, W.P., Pyare, S., Ben-David, M., 2008. Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. Can. J. Zool. 86, 1050–1058.

Flaherty, E.A., Ben-David, M., Smith, W.P., 2010a. Quadrupedal locomotor performance in two species of arboreal squirrels: predicting energy savings of gliding. J. Compar. Physiol. B 180, 1067–1078.

Flaherty, E.A., Ben-David, M., Smith, W.P., 2010b. Diet and food availability of the endemic Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) in Southeast Alaska: implications for dispersal across managed landscapes. J. Mammal. 91, 79–91.

Ford, W.M., Stephenson, S.L., Menzel, J.M., Black, D.R., Edwards, J.W., 2004. Habitat characteristics of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. Am. Midland Nat. 152, 430–438.

Forsman, E.D., Meslow, E.C., Wight, H.M., 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87, 1–64.

Forsman, E.D., Otto, I.O., Sovern, S.G., Taylor, M., Hays, D.W., Allen, H., Roberts, S.L., Seaman, D.E., 2001. Spatial and temporal variation in diets of spotted owls in Washington. J. Raptor Res. 35, 141–150.

Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., Bazzaz, F.A., 1997. Temperate forest response to natural catastrophic disturbance and chronic anthropogenic stress. BioScience 47, 437–445.

Franklin, J.F., Frenzen, P.M., Swanson, F.J., 1995. Re-creation of ecosystems at Mount St. Helens: contrasts in artificial and natural approaches. In: Cairns, J., Jr. (Ed.), Rehabilitating Damaged Ecosystems, second ed. CRC Press, Boca Raton, pp. 287–333.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry in the 21st Century: The Science of Ecosystem Management. Island Press, Washington, D.C., pp. 111–139.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.

Gale, R.P., Cordray, S.M., 1991. What should forests sustain? Eight answers. J. Forestry 83, 31–36.

Gomez, D.M., Anthony, R.G., Hayes, J.P., 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. J. Wildl. Manage. 69, 1670–1682.

Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E., Halaj, M.G., 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Sci. 73, 27–44 (Special issue).

Halpern, C.B., McKenzie, D., 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. For. Ecol. Manage. 154, 215–225.

Halpern, C.B., McKenzie, D., Evans, S., Maguire, D.A., 2005. Early responses of forest understories to timber harvest with varying levels and patterns of green-tree retention. Ecol. Appl. 15, 175–195.

Herbers, J., Klenner, W., 2007. Effects of logging pattern and intensity on squirrel demography. Wildl. Manage. 71, 2655–2663.

Holloway, G.L., Malcolm, J.R., 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. J. Wildl. Manage. 70, 1735–1745.

Holloway, G.L., Malcolm, J.R., 2007. Nest tree use by northern and southern flying squirrels in central Ontario. J. Mammal. 88, 226–233.

Holloway, G.L., Smith, W.P., 2011. Forest age, stand structure, and northern flying squirrel densities: a meta-analysis. J. Wildl. Manage. 75, 668–674.

Hough, M.J., Dieter, C.D., 2009. Summer nest tree use by northern flying squirrels in the Black Hills, South Dakota. Am. Midl. Nat. 162, 98–111.

Imbeau, L., Mönkkönen, M., Desrochers, A., 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conserv. Biol. 15, 1151–1162.

Krebs, C.J., 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36, 239–273.

Lehmkuhl, J.F., West, S.D., Chambers, C.L., McComb, W.C., Manuwal, D.A., Aubry, K.B., Erickson, J.L., Gitzen, R.A., Leu, M., 1999. An experiment for assessing vertebrate response to varying levels and patterns of green-tree retention. Northwest Sci. 73 (Special Issue), 45–63.

Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., Boulanger, J., 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecol. Appl. 16, 584–600.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, DC.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14, 941–950.

Luoma, D.L., Eberhart, J.L., Molina, R., Amaranthus, M.P., 2004. Response of ectomoycorrhizal fungus sporocarp production to varying levels and patterns of green-tree retention. For. Ecol. Manage. 202, 337–354.

Maguire, D.A., Halpern, C.B., Phillips, D.L., 2007. Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests. For. Ecol. Manage. 242, 708–726.

Maser, C., Maser, Z., Witt, J.W., 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Can. J. Zool. 64, 2086–2089.

McComb, W., Lindenmayer, D., 1999. Dying, dead, and down trees. In: Hunter, M.L. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University, Cambridge, pp. 335–375.

McLaren, M.A., Thompson, I.D., Baker, J.A., 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. Forest. Chron. 74, 241–248.

Menzel, J.M., Ford, W.M., Edwards, J.W., Menzel, M.A., 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. Am. Midland Nat. 151, 355–368.

North, M., Trappe, J., Franklin, J., 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78, 1543–1554.

Patterson, J.H., Malcolm, J.R., 2010. Landscape structure and local habitat characteristics as correlates of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus* occurrence. J. Mammal. 91, 642–653.

Pyare, S., Smith, W.P., Shanley, C.S., 2010. Den use and selection by northern flying squirrels in fragmented landscapes. J. Mammal. 91, 886–896.

Rosenberg, D.K., Anthony, R.G., 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Can. J. Zool. 70, 161–166.

Ritchie, L.E., Betts, M.G., Forbes, G., Vernes, K., 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. For. Ecol. Manage. 257, 1920–1929.

Scheibe, J.S., Smith, W.P., Basham, J., Magness, D., 2006. Cost of transport in the northern flying squirrel, *Glaucomys sabrinus*. Acta Theriol. 51, 169–178.

Scheibe, J.S., Paskins, K.E., Ferdous, S., Birdsill, D., 2007. Kinematics and functional morphology of leaping, landing, and branch use in *Glaucomys sabrinus*. J. Mammal. 88, 850–861.

Shanley, C.S., Pyare, S., Smith, W.P., 2012. Landscape requirements of an ecological indicator: implications for functional units of temperate rainforest ecosystems. Ecol. Indicators. http://dx.doi.org/10.1016/j.ecolind.2012.05.027 (2013, 24:68-74).

Slade, N.A., Blair, S.M., 2000. An empirical test of using counts of individuals captured as indices of population size. J. Mammal. 81, 1035–1045.

Smith, W.P., 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. J. Mammal. 88, 862–881.

Smith, W.P., 2012. Flying squirrel demography varies between island communities with and without red squirrels. Northwest Sci. 86, 27–38.

Smith, W.P., in press. Sentinels of ecological processes: the case of the northern flying squirrel. BioScience.

Smith, W.P., Gende, S.M., Nichols, J.V., 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rain forest of southeastern Alaska. J. Mammal. 85, 663–674.

Smith, W.P., Gende, S.M., Nichols, J.V., 2005. The northern flying squirrel as a management indicator species of north temperate rainforest: test of a hypothesis. Ecol. Appl. 15, 689–700.

Smith, W.P., Person, D.K., 2007. Estimated persistence of northern flying squirrel populations in old-growth rain forest fragments. Biol. Conserv. 137, 626–636.

Smith, W.P., Person, D.K., Pyare, S., 2011. Source-sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska. In: Liu, J., Hull, V., Morzillo, A.T., Wiens, J. (Eds.), Sources, Sinks, and Sustainability across Landscapes. Cambridge University Press, Cambridge, pp. 399–422.

Spies, T.A., Franklin, J.F., 1991. The structure of natural young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. General Technical Report PNW-GTR-285. USDA Forest Service, Pacific Northwest Research Station, Portland, pp. 111–121.

Tuchmann, E.T., Connaughton, K.P., Freedman, L.E., Moriwaki, C.B., 1996. The Northwest Forest Plan: a report to the President and Congress. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

U.S. Department of Agriculture and U.S. Department of Interior (USDA and USDI), l994. Record of Decision for Amendments to Forest Service and Bureau of Land Management Planning Documents within the Range of the Northern Spotted Owl. USDA Forest Service, Portland. Oregon.

Vernes, K., 2001. Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forests of eastern Canada. J. Mammal. 82, 1026–1033.

Waters, J.R., Zabel, C.J., 1995. Northern flying squirrel densities in fir forests of northeastern California. J. Wildl. Manage. 59, 858–866.

White, M.A., Mladenoff, D.J., 1994. Old-growth forest landscape transitions from pre-European settlement to present. Landsc. Ecol. 9, 191–205.

Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397.

Wilson, T.M., 2010. Limiting Factors for Northern Flying Squirrels (*Glaucomys sabrinus*) in the Pacific Northwest: A Spatio-temporal Analysis. PhD Dissertation, Union Inst. Univ., Cincinnati, 207 pp.