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

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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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(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 (~130 years old) was surrounded primarily by older, undisturbed forests. Butte occurred in a matrix of relatively young (~80-year-old) forest of natural, post-fire origin. Capitol Forest (~65-year-old stands that had regenerated naturally after clearcut logging) was surrounded by younger (recent clearcut to ~65 year-old), second-growth forests. Experimental units were square (360 × 360 m) or slightly rectangular (320 × 400 m) treatment areas encompassing ~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.