LIMITING FACTORS FOR NORTHERN FLYING SQUIRRELS (*GLAUCOMYS SABRINUS*) IN THE PACIFIC NORTHWEST: A SPATIO-TEMPORAL ANALYSIS

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Abstract

Northern flying squirrels may be important indicators of the long-term health and management of Pacific Northwest forests, including development of successful regional strategies for managing northern spotted owl habitat under the Northwest Forest Plan. I used live-trapping, radio-telemetry, and within-stand measures of squirrel habitat to (1) assess mid-term effects of variable-density thinning on squirrel populations in young, managed forest, (2) quantify multi-dimensional space use by individual squirrels, (3) contrast squirrel populations across 33 natural and managed stands that were representative of wide gradients in within-stand structural complexity found in Pacific Northwest forests, and (4) test hypotheses evaluating the relative importance of four primary limiting factors for flying squirrel populations—food, competition, predation, and dens. Squirrel populations remained low 12 years after stands were treated with variable-density thinning. At the same time, high-density populations were found elsewhere across western Washington. Most space use by individual squirrels occurred above the forest floor and there were marked differences in movement patterns and behaviors between the breeding and non-breeding seasons and between forest supporting low- and high-density squirrel populations. Forests that supported high squirrel abundances generally exhibited high amounts of multi-dimensional structure in the midstory and overstory layers, low to moderate amounts of understory, and few canopy gaps. Three variables, variance in overstory tree d.b.h., area intercept at 10-m above ground, and amount of canopy gaps ≥100m^2 could correctly classify 97% of the stands as supporting either high or low squirrel abundances. The structural complexity of a forest and how individual structural components are apportioned within multi-dimensional space may determine the capacity of a forest to support abundant squirrel populations. A predation-structural complexity hypothesis is consistent with results reported from this and several past studies in the region and suggests that predation may be a primary limiting factor for squirrels, with food, dens, and competition playing hierarchically less important roles in most regional forests. Efforts to restore structural complexity across a dynamic forest landscape may need to consider the spatial and temporal permeability of forests for flying squirrels, especially before long-term ecological benefits of management activities like variable-density thinning are realized.

Key Words: northern flying squirrel, northern spotted owl, *Strix occidentalis caurina*, Pacific Northwest, radio telemetry, forest structure, livetrapping, variable-density thinning, structural complexity, landscape permeability, predator-prey ecology.

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CHAPTER ONE—INTRODUCTION

Background

Increasing human populations, finite natural resources, environmental degradation and fragmentation, and concern over loss of species and climate change have led to polarized values over the importance of wild lands, forest-based employment, wood products, clean air and water, and healthy forests (Harris 1984, Kohm and Franklin 1997, WWI 2009). This polarization has been especially pronounced in the Pacific Northwestern U.S. where over-harvesting of old-growth forest has led to greatly restricted timber harvesting across public forest lands, growing controversy over state land management, and increasing regulation and scrutiny of management activity on industrial and other privately-owned forest lands (Arabas and Bowersox 2004, Thomas et al. 1990, Tuchmann et al. 1996). Resolving conflict over the use and management of forests will likely require a combination of scientific, social, cultural, and political solutions (Berkes et al. 2003, Carey 2007, Pimentel et al. 2000).

The basis for scientific solutions includes thorough understanding of how ecosystems function in the face of both natural and anthropogenic change (Lindenmayer and Franklin 2002). However, even after decades of research, our understanding of forest ecosystems is still limited, especially given the myriad species and ecological interactions involved. One approach to effectively managing forests as we continue to advance our understanding of these complex ecosystems is to find key organisms that represent the general health and functioning of each system. This includes indicator species (species that represent a particular ecosystem process or condition, or that can be used as a proxy for forest health), keystone species (species that have roles that appear out of proportion with their abundance and distribution), and functional groups (groups of related species representing trophic hierarchies within a community; Noss 1990, Paine 1969a, 1969b, 1995, Power et al. 1996). However, care must be taken in selecting the organisms used to index change. Rare species can be difficult to study (e.g., Molina et al. 2006). Common species can be generalists—adaptable to a wide range of habitat conditions—and therefore, not necessarily sensitive indicators (e.g., insensitivity of common deer mouse [*Peromyscus maniculatus*; Wilson and Reeder 2005] to corridors; Mech and Hallett 2001). Top-level predators often range widely and respond to landscape-level variables, and thus may not respond to, or be measurable at, finer-scaled management-unit levels (e.g., similarity of black bear [*Ursus americanus*] home ranges across differently-managed landscapes; Koehler and Pierce 2003). At the opposite end of the spectrum, abundant, yet relatively sessile species may respond to fine-scale changes (on the order of meters to tens of meters), but not to coarse management-level scales (10s to 100s of hectares) due to small home ranges or limited mobility (e.g., association between mycorrhizal fungi diversity and distance to nearest tree; Luoma et al. 2006). Thus, relative abundance, ecological scale, and trophic hierarchy are important considerations when choosing appropriate indicator species.

Northern Flying Squirrels

The northern flying squirrel (*Glaucomys sabrinus*) is a small, nocturnal gliding rodent from the Family Sciuridae that is widely distributed and common throughout boreal and northern temperate forests of North America (Wells-Gosling and Heaney 1984). Flying squirrels occupy a central place in complex food webs (Carey 2000a, Ransome and Sullivan 1997, Smith 2007, Waters et al. 2000, Weigl 2007, Weigl et al. 1992). In the Pacific Northwest, this web includes a northern spotted owl (*Strix occidentalis caurina* [A.O.U. 1998])-flying squirrel-fungi-conifer trophic heirarchy (Carey et al. 1992). Flying squirrels are forest obligates and dependent on trees for travel, dispersal, and food (Wells-Gosling and Heaney 1984). They also appear especially sensitive to human-induced disturbances (Carey 2000b, 2001, Herbers and Klenner 2006, Holloway and Malcolm 2006, 2007, Waters and Zabel 1995). Thus, flying squirrels might serve as useful indicators for evaluating the ecological effects of forest management activities (Carey 2000a).

The flying squirrel may also be an important species for evaluating the effectiveness of the Northwest Forest Plan, a series of documents that have guided the direction of forest management practices in the Pacific Northwest for more than 15 years (FEMAT 1993, USDA and USDI 1994a, 1994b). At the heart of this plan is recovery of federally-threatened spotted owl populations that have declined due to extensive harvesting of late-seral (e.g., old-growth) forest (USFWS 1990, 1992). Northern flying squirrels are a primary food for spotted owls, comprising ≤50% of owl diets across much of Oregon and Washington (Forsman 1984, Forsman et al. 1991). Spotted owl home range size has been shown to decrease with increasing squirrel densities (Carey and Peeler 1995, Carey et al. 1992, Zabel et al. 1995) suggesting that understanding habitat needs and potential limiting factors for flying squirrel populations may be critical to recovery of spotted owls and their habitat across the region.

Literature Review

General Habitat

Flying squirrels are primarily found in conifer-dominated forests throughout most of their geographic distribution, including spruce (*Picea spp.* [USDA 2008]) taiga forests at the edge of the Arctic Circle, Douglas-fir (*Pseudotsuga menziesii*) rainforests in the Pacific Northwest, dry pine (*Pinus* spp.) forests in the Rocky Mountains and interior west, and mixed-spruce forests of eastern Canada and the U.S. (Arbogast 2007, Grodzinski 1971, Smith 2007, Weigl 2007, Wells-Gosling and Heaney 1984). Flying squirrels can also be found in deciduous-dominated and mixed deciduous-conifer forest (Holloway and Malcolm 2006, Menzel et al. 2006, Payne et al. 1989, Weigl 1968, 2007), including ecotones between hardwood and conifer forest (Weigl 2007). They are not found in areas devoid of trees (e.g., in clearcuts, meadows, or volcanic blast zones; Anderson and MacMahon 1985, Andersen et al. 1980, Gashwiler 1970, Tevis 1956).

Population studies suggest flying squirrels are most abundant in the Pacific Northwest, with high-density populations (e.g., >2 squirrels per ha) found in every Pacific Northwest state and province from northern California to southeast Alaska (e.g., Carey et al. 1999a, Lehmkuhl et al. 2006, Meyer et al 2007a, Ransome and Sullivan 2003, Ransome et al. 2004, Smith et al. 2004, Waters and Zabel 1995). In general, older forests support more squirrels than younger forests (Carey 1995a, Maser et al. 1985, Payne et al. 1989, Ritchie et al. 2009, Weigl 1978, Witt 1992) with estimates up to 3.2-4.0 squirrels/ha for some coastal old-growth rainforests (e.g., Carey et al. 1992, Smith and Nichols 2003). However, not all old-growth forests support high densities (e.g., Carey 1995a). Some young forests can also support relatively high densities (e.g., 2.2-2.5 squirrels/ha; Lehmkuhl et al. 2006, Rosenberg and Anthony 1992) or densities equal to those found in some older forest (Ransome and Sullivan 2003, Ransome et al. 2004, Waters and Zabel 1995). Squirrel abundances appear to be generally lower in eastern U.S. and Canada forests compared to some Pacific Northwest forests, with many studies reporting presence-absence or relative abundances rather than actual abundance or density estimates (e.g., Bowman et al. 2005, O'Connell et al. 2001, Ritchie et al. 2009, Weigl et al. 2002). Reported densities in the east have been highest in spruce and mixed spruce forest (0.3-0.9 squirrels/ha; Holloway and Malcolm 2006).

Several habitat components within forests have been associated with high-quality flying squirrel habitat. These include understory cover (Carey et al. 1999a, Pyare and Longland 2002), patch-level changes in vegetation composition (Carey et al. 1999a), large snags (Carey 1995a, Holloway and Malcolm 2006, Meyer et al. 2007b, Smith et al. 2004), large trees (Gomez et al. 2005, Holloway and Malcolm 2006, Lehmkuhl et al. 2006, Smith et al. 2004), ericaceous shrubs (Carey 1995a), high canopy cover (Lehmkuhl et al. 2006, Meyer et al. 2007a), nearness to conifer or mixed-conifer forest (Ford et al. 2004, Holloway and Malcolm 2007, Hough and Dieter 2009, Menzel et al. 2006, Payne et al. 1989), nearness to water in xeric forest (Meyer et al. 2007a), abundant coarse woody debris (Carey et al. 1999a, Smith et al. 2005), large coarse woody debris (Gomez et al. 2005), increased litter depth (Meyer et al. 2007a) and availability of fungi (Carey 1991, 1995, Carey et al. 1992, 1999a, Holloway and Malcolm 2007, Lehmkuhl et al. 2004, Pyare and Longland 2002, Rosenberg and Anthony 1992, Smith et al. 2004).

Reproductive Potential

It has been hypothesized that nocturnality and gliding have energetic costs that promote primarily *K*-selected traits for flying squirrels, including a lower basal metabolism than non-gliding arboreal sciurids, a long period of maternal investment, slow growth and maturation, and relatively large mass for neonates (Stapp 1992). However, two different reproductive strategies have been observed in northern flying squirrels in the Pacific Northwest. In high-density populations, reproduction was primarily by older (2+ year-old) females whereas in low-density populations, virtually all females, regardless of age, showed advanced signs of reproduction each year (Villa et al. 1999). This suggests that flying squirrels may have evolutionary adaptations that allow for a *K*-strategy potential, but they also appear capable of using an *r*-strategy in response to unfavorable habitat conditions (MacArthur and Wilson 1967, Pianka 1970).

Northern flying squirrels generally produce 1 litter of 1-4 offspring per year. In contrast, other sciurids can have multiple litters per year, especially when food resources are abundant (e.g., Douglas' squirrels; Smith 1968, Wells-Gosling and Heaney 1984). The breeding season can vary from year to year and by geographic location with most litters born in the spring and summer (Davis 1963, Reynolds et al. 1999, Villa et al. 1999, Weigl et al. 1992), with some evidence of occasional fall births (e.g., Raphael 1984, Vernes 2004). Males are capable of reproducing from early February through August in the Pacific Northwest whereas females generally come into estrus in May and June (Forsman et al. 1994, Villa et al. 1999). Flying squirrels are highly promiscuous—females mate with multiple males and give birth to litters of mixed paternity (Wilson 2000, 2003).

Flying squirrel population fluctuate in abundance both within and across years (Carey 2001, Fryxell et al. 1998, Keith and Cary 1991) with large variations observed in annual survival rates (e.g., 32-68%, Gomez et al. 2005; 0-58%, Villa et al. 1999). In general, young squirrels have higher mortality rates than adults, with reports of few adults living > 7 years (Villa et al. 1999).

Movement Patterns and Behaviors

Flying squirrels use a combination of gliding, climbing, and hopping when moving outside the den. The forearm and patagium musculature of flying squirrels, along with tail-to-body-length ratios that are greater than other Sciurids, allow for relatively high maneuverability while gliding, including the ability to make sharp turns (up to 180°) when needed (Hampson 1965, Hayssen 2008, Thorington and Heaney 1981). Reported average glide angles have varied, likely due to both the height of the launch tree and specific landing targets (e.g., 27 degrees below horizontal, Vernes 2001; 36-44 degrees, Scheibe et al. 2006). Sharp claws and dexterity in both front and hind feet allow for vertical travel on tree boles that vary widely in bark rugosity and diameter as well as horizontal travel across small fine branches between connecting tree canopies. Flying squirrels appear least adapted to moving across the forest floor, and often use a combination of hopping and running to negotiate through understory vegetation (personal observations).

Flying squirrels are nocturnal and focus most activity outside the den between dusk and dawn (Radvanyi 1955). They have several nocturnal adaptations, including rod-dominated retina that promote light-sensitive vision, and the largest vibrissa length-to-head-width ratio of any squirrel species which can aid in detection of objects near the face (Ahl 1987, Carvalho et al. 2006, Walls 1942, Yolton et al. 1974). Onset of activity appears to be triggered by an internal biological pacemaker and degree of light (DeCoursey 1990, Radvanyi 1955, Ferron 1983a). Flying squirrels are reported to have two activity periods, with the primary period beginning shortly after dusk, followed by a second, shorter activity period later in the evening (Weigl and Osgood 1974). A decline in activity on nights around a full moon has been reported in captive squirrels (Radvanyi 1955). During winter, temperature can be a key factor in reducing activity (Ferron 1983a, Cotton and Parker 2000a). Anecdotal observations suggest occasional, but rare, diurnal activity (Wells-Gosling and Heaney 1984).

Most space-use studies of flying squirrels have been based on estimating home ranges using periodic triangulation of radio-collared squirrels (Holloway and Malcolm 2007, Martin and Anthony 1999, Menzel et al. 2006, Mowrey and Zasada 1984, Urban 1988, Weigl and Osgood 1974, Weigl et al. 1992, Wilson et al. 2008, Witt 1992). Reported home range estimates have varied widely (ca. 3-60 ha), with males generally having larger home ranges than females (Holloway and Malcolm 2007, Martin and Anthony 1999, Menzel et al. 2006, Urban 1988, Witt 1992). In the Pacific Northwest, home range size was found similar between two old-growth forests and two second-growth forests in the western Oregon Cascades where population densities were similar (Martin and Anthony 1999). Few studies have continuously monitored northern flying squirrels while they engage in activity outside the den (e.g., Mowrey and Zasada 1984). Other free-ranging flying squirrels have been continuously monitored during nocturnal activity periods (e.g., Siberian flying squirrel *Pteromys volans*; Selonen and Hanski 2006).

Information on space use has also come from calculating the mean maximum distance moved (MMDM) between successive trap stations to measure of home range diameter (Otis et al. 1978, White et al. 1982). MMDMs may reflect the diameter of core foraging areas rather than total home range diameter (Carey 2000b, Holloway and Malcolm 2007, Skalski and Robson 1992, Witt 1992). MMDM was found to be smaller in Oregon Coast Range old forest with high squirrel densities (mean ± SE, 87 ± 2 m) compared to young forest with low densities in the Puget Trough (116 ± 13 m; Carey 1995a, 2000b). In the Oregon Cascades, MMDM values between squirrel populations in young (87 ± 7 m) and old (84 ± 6 m) forest were similar, as were squirrel densities (Rosenberg and Anthony 1992).

Limiting Factors for Flying Squirrels

Several major limiting factors have been proposed for flying squirrels apart from permanent removal of forest or forest fragmentation due to urbanization and agricultural development.

Food

Food is the most commonly cited limiting factor for flying squirrels (Carey 1995a, Lehmkuhl et al. 2004, Maser et al. 1986, Pyare and Longland 2002; Smith et al. 2004, Ransome and Sullivan 1997, 2004, Waters et al. 2000). Flying squirrels consume a wide variety of foods including fungi, nuts, seeds, fruits, buds, bird eggs, cones, insects, and sap (Maser et al. 1985, Carey 1991, 1992, Colgan et al. 1999, Flaherty et al. 2000, Lehmkuhl et al. 2004, Meyer et al. 2005, Pyare and Longland 2001a, Thysell et al. 1997, Weigl 1968, Weigl et al. 1992, Wells-Gosling and Heaney 1984).

Hypogeous (truffles) and epigeous (mushrooms) fungi appear to dominate squirrel diets in the Pacific Northwest (Carey et al. 2002, Colgan et al. 1999, Jacobs and Luoma 2008, Lehmkuhl et al. 2004, Maser and Maser 1988, Maser et al. 1986, Trappe et al. 2009) and several studies have made positive associations between squirrel abundance and fungi (Lehmkuhl et al. 2006, Pyare and Longland 2002, Waters and Zabel 1995). Fungi have been found in diets year-round (Maser et al. 1978, 1985, 1986) and many fungi rely on mycophagists like flying squirrels to help enhance germination and disseminate spores through defecation (Cork and Kenagy 1989, Li et al. 1986). Eating a variety of fungal species may help compensate for any nutritional deficiencies found in any single fungal species (Trappe et al. 2009).

Non-fungal foods may also be important to flying squirrels. In western Washington, several direct observations were made of squirrels eating foods that included Douglas-fir seeds and seedlings, big-leaf maple (*Acer macrophyllum*) samaras, black cottonwood (*Populus trichocarpa*) catkins, and salal (*Gaultheria shallon*) berries (Thysell et al. 1997, this study). Lichens can also be a significant component of winter diets, especially where snow restricts foraging on the ground (Mckeever 1960, Rosentreter et al. 1997). These non-fungal foods may provide a nutritionally-balanced diet across seasons and from year to year, especially as northern flying squirrels are not known to store foods like other squirrels (Weigl 2007). However, unlike fungal spores which pass through the digestive tract intact, most non-fungal foods are highly digestible making them difficult to detect during microhistological analyses (McIntire and Carey 1989).

Free-ranging flying squirrel populations have increased in abundance after short-term food supplementation (Ransome and Sullivan 1997, 2004). Other squirrels are known to fluctuate in response to food availability (e.g., Douglas' squirrels, Smith 1970, Sullivan 1990, Sullivan and Sullivan 1982; eastern gray squirrels, Gurnell 1996). Food can be difficult to sample in the field, especially give the spatial and temporal scale at which ephemeral foods like fungi occur, and it is not unusual to have fungal species showing up in squirrel diets that are not detected during simultaneous field sampling (e.g., Carey et al. 2002, Lehmkuhl et al. 2004, Pyare and Longland 2001b). Many studies have used an indirect approach to evaluating the importance of food by measuring plant species diversity or presence or abundance of taxa that have known mycorrhizal associates (e.g., Carey 1995a, Carey et al. 1999a, Lehmkuhl et al. 2006).

Dens

Squirrels use two general types of dens while resting or sleeping during the day—cavities in both live and dead (e.g., snags) trees, and external nests constructed on suitable platforms (e.g., large limbs, epicormic branching, irregular forking, witch's broom; Bull et al. 2004, Carey et al. 1997, Cotton and Parker 2000b, Mowrey and Zasada 1984). Dens can be lined or constructed from sticks, moss, lichens, bark, and leaves (Hayward and Rosentreter 1994, Patterson et al. 2007, Wells-Gosling and Heaney 1984).

Several studies suggest that cavity dens may be an important limiting factor for flying squirrels. For example, snags were found to be used more frequently than other den structures in southeast Alaska (e.g., Bakker and Hastings 2002). Cavities in both live and dead trees were found important in young and old forest in western Oregon and Washington (Carey et al. 1997). Cavity dens may be especially important for raising young—in forests where external nest use was common, females switched to using small snags, well-decayed residual stumps (<2 m tall), or nestboxes to raise offspring (Carey et al. 1997, Carey 2002). There is also likely competition for cavity dens with more aggressive species including mustelids, owls, and other squirrels (Carey et al. 1997, Holloway and Malcolm 2006, Laudenslayer et al. 2002, Ruggiero et al. 1991, Smith et al. 2004).

Squirrels readily use nestboxes (Carey 2002, Carey et al. 1997, Maser et al. 1981, Ransome and Sullivan 2004, Reynolds et al. 1999). However, adding nestboxes or artificial cavities to forests that lacked cavity dens has not been shown to increase population levels, at least in the short term (Carey 2002, Ransome and Sullivan 2004). Also, some studies show higher use of external nests than cavity dens in some forests, regardless of geographic location or climate (Carey et al. 1997, Cotton and Parker 2000b, Mowrey and Zasada 1984, Hackett and Pagels 2003). The capacity to build and use nests year-round may be an important adaptive trait for exploiting young forests with few cavities (Carey et al. 1997).

Flying squirrels are highly social and typically den in mixed-sex groups comprised of 2-5 individuals, although up to 9 individuals have been reported using a single den (Banfield 1974, Carey et al. 1997, Wells-Gosling and Heaney 1984). These group sizes are relatively small compared to southern flying squirrels which can den in groups of >20 (Muul 1968, Stapp et al. 1991). Group denning in *Glaucomys* may be, at least in part, social behavior that is an evolutionary consequence of energy conservation (Layne and Raymond 1994). Females leave group dens to give birth and initially raise litters in isolation from other adults (Carey et al. 1997). Den mates could be genetically related, but limited investigation into nesting and kinship for northern flying squirrels has been inconclusive (Wilson 2000). Microsatellite DNA analysis suggests that adult southern flying squirrels do not nest in family groups (Winterrowd et al. 2005). Northern flying squirrels switch dens on a frequent basis (on average, 2-4 times per month) but can also remain in the same den for several months at a time (Carey et al. 1997, Cotton and Parker 2000b). No clear association exists between frequency of den switching and type of den or den structure, but in one study, the structures used for the longest periods of time by groups of squirrels were large snags and large live trees supporting cavities (Carey et al. 1997). Both of these structures have been associated with high quality squirrel habitat (Carey 1995a, Gomez et al. 2005, Holloway and Malcolm 2006, Lehmkuhl et al. 2006, Meyer et al. 2007b, Smith et al. 2004). Den switching could be related to predator avoidance, social needs, or a response to a build-up of parasites in the den (Carey et al. 1997).

Competition

Flying squirrels compete with other arboreal rodents for many of the same food, den, and cover resources (Harestad 1991, Smith and Balda 1979, Thysell et al. 1997, unpublished data). Early experimental studies of the threatened subspecies of northern flying squirrel, *G. sabrinus coloratus*, in the Appalachians suggested that competition with the more aggressive southern flying squirrel (*G. Volans*) may have restricted habitat to conifer-dominated mountain tops (Weigl 1978, Weigl et al. 1992). Subsequent research into the habitat preferences between these two species, however, suggests that competition may be limited (Bowman et al. 2005, Weigl 2007).

In some coastal temperate forests of the Pacific Northwest (British Columbia, Washington, and Oregon), flying squirrels can co-exist in high abundance with a suite of other arboreal and semi-arboreal rodents, including Douglas' squirrels (*Tamiasciurus douglasii*), western gray squirrels (*Sciurus griseus*), Townsend's chipmunks (*Tamias townsendii*), woodrats (*Neotoma* spp.), red tree voles (*Arborimus longicaudus*), and deer mice (P*eromyscus* spp.). These forests may allow for niche diversification that reduces competition for resources (Carey et al. 1999a). Other forests in this region are dominated by only one of these species (Carey 1995a, 2000b, 2001, Carey et al. 1999a), with flying squirrel populations reaching high levels when other Sciurids are absent (e.g., some islands in southeast Alaska; Smith and Nichols 2003).

Flying squirrels are not as vocal as other squirrels and are therefore thought not to be strongly territorial (Jackson 1961, Smith 1970, 1978). However, flying squirrels have used cheek rubbing of their scent glands and laid scent trails using droplets of urine when introduced to new surroundings in captivity (Ferron 1983b, Hampson 1965). These behaviors are not only useful for orientation, but also may serve as a passive strategy for addressing intra- or inter-specific competition (Ferron 1983b).

Predation

Complex interactions between predators and mammalian prey may regulate prey population levels (e.g., Hanski et al 1993, Turchin 1993) and predation has been a regularly hypothesized limiting factor for flying squirrels (Carey 2000b, Carey et al. 1992, 1997, 1999a, Rosenberg and Anthony 1992, Smith 2007, Waters and Zabel 1995, Wilson and Carey 1996). However, few studies have provided direct empirical evidence in support of the relative importance of predation in limiting squirrel populations. Radio-telemetry studies in non-urban forests of western Washington showed that predation from weasels and owls accounted for virtually all mortality (Wilson and Carey 1996, this study). Studies of squirrel populations within known spotted owl territories have also suggested high squirrel mortality during owl breeding years in some forests (Carey et al. 1992).

The association between northern spotted owls and flying squirrels has received the most attention in the Pacific Northwest, but numerous other avian and mammalian predators prey on flying squirrels in this region. These include medium to large owls (e.g., screech owls [*Megascops spp*.], barn owls [*Tyto alba*], barred owls [*Strix varia*], spotted owls, boreal owls

[*Aegolius funereus*], great horned owls [*Bubo virginianus*], and great gray owls [*Strix nebulosa*]) and mustelids (long-tailed weasels [*Mustela frenata*], ermine [*Mustela erminea*], marten [*Martes americana*], and fishers [*Martes pennanti*]; Arthur et al. 1989, Bull 2000, Forsman 1976, Forsman et al. 1984, Teeple 1983, Wilson and Carey 1996).

Forest structure (defined here as the collective above-ground, bio-physical structural components of a forest that include tree boles and canopies, shrub and herbaceous plant layers and coarse woody debris) may play an important role in regulating predation. For example, understory vegetation can provide protective cover for squirrels while they are foraging on the ground (Carey 1995a, Holloway and Malcolm 2007, Pyare and Longland 2002, Smith et al. 2005). Likewise, tree canopies may serve as important arboreal protective cover (Carey 1991, Carey et al. 1999a, Meyer et al. 2007a, Pyare and Longland 2002). Positive associations between squirrel density and canopy cover have been made in some (e.g., Lehmkuhl et al. 2006, Waters and Zabel 1995), but not all (e.g., Ransome et al. 2004) forests.

Parasites and Disease

Flying squirrels are host to a wide range of parasites common to small rodents, including fleas, ticks, lice, nematodes, mites, and chiggers (Foley et al. 2007, Weigl 1968, Wetzel and Weigl 1994, Whitaker et al. 1983). Endo-parasites have caused squirrel mortality in the Appalachians (Weigl 1968, 2007). In the Pacific Northwest, regional outbreaks of mange (*Notoedres centrifera*) have caused high western gray squirrel mortality (Cornis et al.

2001). However, there have been no published reports of flying squirrel mortality or outwards signs of stress (e.g., hair loss) due to either parasites or diseases in the Pacific Northwest, in spite of numerous long-term studies in the region. Given the extensive tracts of contiguous forest in this region, disease may only play a localized role in limiting squirrel populations.

Problem Statement

Collectively, the body of knowledge on the biology and ecology of northern flying squirrels has substantially grown over the last several decades. However, there are several issues that still remain unresolved—issues that are critical for determining the usefulness of flying squirrels as an index to forest management.

Problem 1.—Negative Effects of Management Activities

Most studies suggest that tree removal (e.g. thinning) has negative effects on squirrel populations, at least in the short term (Bull et al. 2004, Carey 2000b, 2001, Herbers and Klenner 2007, Meyer et al. 2007a, Holloway and Malcolm 2006, 2007, Ransome et al. 2004, Waters and Zabel 1995, Waters et al. 2000). One reported exception was young (17-yr old), highly-stocked (≤7600 stems/ha) lodgepole pine forest (Ransome et al. 2004). The few studies that have reported no significant effects of thinning still generally show higher capture rates or abundance estimates in unthinned stands compared to thinned stands (e.g., Gomez et al. 2005, Ransome and Sullivan 2002).

Negative effects of thinning could be due to several factors, including: (1) immediate disruption in the form of noise or human presence during activities such as the operating of heavy equipment around squirrel dens that cause squirrels to leave the area; (2) permanent removal of habitat components, including dens and trees that provide protective cover and substrate for locomotion; (3) temporary removal of understory vegetation due to the mechanical effects of logging equipment; and (4) removal of tree-related food sources, including fungi, lichens, catkins, and samaras.

Several large-scale thinning studies have been established to develop and test new silvicultural strategies for meeting long-term Northwest Forest Plan objectives, including providing habitat for spotted owls (Poage and Anderson 2007). One of these, the Forest Ecosystem Study (hereafter, FES) tests the efficacy of using variable-density thinning in young, structurally simple second-growth forests to accelerate important ecological processes that lead to the development of structurally complex forest needed by spotted owls (Carey et al. 1999b; Carey 2003). The variable-density thinning prescription used on the FES focused on two ecologically relevant scales: (1) small (inter-tree) canopy gaps found important in creating structural complexity (defined here as the relative quantity, arrangement and composition of structural components in multi-dimensional forest space) in naturally-occurring mature forest (Spies et al. 1990) and (2) patch-level understory variation at a 40-80m scale found in structurally and biologically complex old forest (Carey et al. 1999a). Short-term (3-5 year post-thinning) population responses to variable-density thinning were positive for most forest-floor small mammals, songbirds, and understory plants (Carey and Wilson 2001, Haveri and Carey 2000, Palazzotto 2005, Thysell and Carey 2001). Flying squirrel populations declined after variable-density thinning was applied, but then recovered (compared to controls) within 3-4 years (Carey 2000b, 2001). However, both pre- and post-treatment flying populations were low (0-1 squirrels/ha) compared to complex forest in the region.

Thus, attempts to actively manage forests by removing trees have generally not favored flying squirrels, at least in the short term, and there is need to better understand how practices like variable-density thinning, a silvicultural tool that is being used widely across the region to promote development of complex forest, influence flying squirrel populations over the long term. This not only includes continued monitoring of squirrel populations in response to variable-density thinning, but also better understanding of why squirrel populations decline after forests are thinned.

Problem 2.— Methodology

Almost every study evaluating flying squirrel habitat has been based on top-down population-level approaches that focus primarily on *where* squirrels are found in horizontal space. These include captures in live traps, nest box surveys, and radio-telemetry studies of home range or den locations. These approaches have added significant insight into our understanding of the biology and ecology of flying squirrels but they may not be sufficient for fully evaluating limiting factors. One primary reason is that population-level studies provide little information about how individual squirrels are using multi-dimensional forest space while active outside their dens. Techniques like live-trapping only capture a small portion of a squirrel's space use—activity on the forest floor that may be, in part, a behavioral response to bait in traps (e.g., trap "happiness" or "shyness"; White et al. 1982). Trapping data also does not provide information about how a squirrel arrived at a trap, how much time a squirrel spent near a trap, or how important that location was relative to locations or time spent elsewhere during its activity period. This is especially problematic for an arboreal species like flying squirrels as important above-ground habitat components could be missed. It could also lead to an overly narrow focus on the importance of forest-floor resources at or near trap stations (e.g., fungi, understory vegetation).

Likewise, most radio-telemetry studies evaluating space use have focused on obtaining home range estimates (e.g., Holloway and Malcolm 2007, Hough and Dieter 2009, Martin and Anthony 1999, Urban 1988, Weigl and Osgood 1974, Weigl et al. 1992, Witt 1992), usually limiting observations to indirect, two-dimensional triangulated points (several locations per night to one location per every several days) to avoid autocorrelation (Swihart and Slade 1985). There are several concerns with such an approach. First, simple Euclidean-based home range estimates (e.g., minimum convex polygons) assume there are no differences in quality of space being used, and can misrepresent habitat relationships when important habitat components are patchily distributed (Mitchell and Powell 2008). Second, home range estimates provide no information on how space is actually being used—they do not take into account, for example, individual behaviors or movement patterns. Third, higher-order organisms like mammals do not move randomly through space—factors like memory and physiological need help determine future behaviors (Adams-Hunt and Jacobs 2007). Therefore, autocorrelation is a fundamental component of most animal movement patterns and behaviors. Fourth, home range estimates only reflect movement within a two-dimensional horizontal plane, yet flying squirrels use all of the multiple dimensions of a forest, from denning in substrates that can be high in the canopy of trees, to gliding between trees from the canopy to the forest floor, to digging truffles on the forest floor.

One alternative to using home range is to describe movement paths and behaviors based on continuous-tracking (e.g., homing) of individuals. Such direct observations of movement are advantageous in that environmental cues that affect movement can be more readily observed, and thus, mechanisms of observed patterns can often be generated more quickly compared to using indirect observations (Turchin 1998). However, evaluating the three-dimensional space used by animals can be costly and challenging (Waser and Wiley 1979, this study). The logistics, training, and technique development to follow nocturnal animals like flying squirrels is especially prohibitive and limited efforts have been made to closely follow squirrels while they are active outside their dens (e.g., Mowrey and Zasada 1984, Witt 1992). One of the few published telemetry studies to continuously-track squirrels occurred in interior Alaska where three females were followed for one night each (Mowrey and Zasada 1984). Tracking was aided by direct visual observation due to long daylight hours at that latitude.

Better understanding of individual movement and behaviors is also important in that population-level properties emerge from the interaction of individuals, and natural selection operates on the individual, not populations (Grimm and Railsback 2005, Lomnicki 1992). A more holistic understanding of potential limiting factors affecting flying squirrels may therefore require study at both the individual and population levels.

Problem 3.— Forest Classification and Structural Complexity

Although most studies show that older forests generally support more flying squirrels than younger forest, there are still several exceptions that suggest that habitat needs for flying squirrels are not fully understood. Related, there also appears to be no ubiquitous measures capable of separating high-quality squirrel habitat from low-quality habitat. Part of this issue is that it is difficult to synthesize information from past studies given the wide variation in questions being asked, hypotheses tested, sample sizes, study designs, field methodologies, analytical approaches, and magnitudes of squirrel abundances found. For example, diverse rationales have been given to explain the presence and abundance of squirrels in forest other than old forest, including the importance of legacy trees and snags in young forests that may provide old-growth-like conditions (Carey 1995a), concerns over sampling methodology (Carey 1995a, 1995b, Rosenberg et al. 1994), use of appropriate density estimators (Rosenberg et al, 1995, Ransome and Sullivan 2003), and that flying squirrels are forest generalists, with the plasticity to survive under a wide range of ecological conditions (Rosenberg and Anthony 1992, Smith 2007, Smith et al. 2005, Wheatley et al. 2005).

Understanding habitat needs of flying squirrels may also be confounded by the large variation in structural complexity found in Pacific Northwest forests. For example, older forests vary markedly in their complexity across a range of spatial scales, from small patches of trees to entire landscapes (Carey et al. 1999a, Franklin et al. 2002, 2005, Lindenmayer and Franklin 2002, Spies and Franklin 1991) making it difficult to quantify such forests (NCSSF 2008). Likewise, the amount of legacy structural components (retained old trees, snags, and large fallen trees leftover from a previous forest), can vary widely in young forests, depending on harvest prescription or the size and scale of natural stochastic events (Franklin et al. 2005). Thus, if there are limiting factors associated with the structural (and related biological) complexity of a forest, they would not necessarily be captured by grouping and contrasting forests based on age (e.g., young vs. old) or through evaluation of a few forest types—both of these strategies have been commonly used in the past to evaluate squirrel habitat. Visits to many of the flying squirrel study sites used in the Pacific Northwest also suggest that the wide variation in within-stand structural complexity unique to each forest cannot always be appreciated by simply reading published literature (personal observations).

Better quantification of structural complexity may help resolve some of these issues, and could lead to better measures of high-quality squirrel habitat. One option is to classify stands based on ecological stages of forest development (Carey 2003, Carey and Curtis 1996, Franklin et al. 2002) but natural disturbance events (e.g., wind, ice, fire, disease) occur across a wide gradient of scales and make stand-level classification into a specific stage difficult, especially for old forests that have a long history of natural disturbances (e.g., Olympic Peninsula; Henderson et al. 1989, personal observations). Underlying forest development stages, however, are four ecological processes that have been suggested as the primary drivers in shaping forest structural complexity: (1) *canopy stratification*—the process whereby trees differ in age and growth habits and provide multiple forest layers in the midstory and overstory; (2) *decadence*—the process of decay and decomposition of both live and dead wood that provide benefits such as cavities for wildlife, substrates for fungi, and soil nutrients; (3) *crown-class differentiation*—the process of competition among tree cohorts that leads to dominant and subordinate trees; and (4) *understory development*—the process whereby variability in light, temperature, moisture, and growing space provide structurally-diverse growth on the forest floor (Carey 2003). Several of these processes were important analysis-generated predictors of flying squirrel habitat in the Oregon Coast Ranges (Carey et al. 1999a). More importantly, however, is that each structuring process continuously operates at some level within any forest, regardless of forest type or pattern and scale of past disturbance. Additionally, the effects of these processes on forest structure can be readily quantified, suggesting that measures of ecological processes may be more useful in classifying stands for their relative structural complexities than using forest development stages, ages, or otherwise few classification groups.

Problem 4.—Analysis of Limiting Factors

Although there is growing consensus over many aspects of the biology, ecology, and adaptations of flying squirrels (e.g., Carey 2000a, Smith 2007, Weigl 2007) there have been few studies that explicitly evaluate relationships between habitat components and potential underlying limiting factors regulating squirrel populations. A clearer understanding of these relationships is needed because it can provide stronger ecological context and rationale for why specific habitat components are important. It could also help reconcile some of the results from past studies that have found different habitat components to be important across different forests and study sites. For example, one habitat component can be associated with more than one potential limiting factor, such as large live trees providing both den substrates and food resources. Conversely, multiple habitat components can be associated with one limiting factor suggesting the possibility of substitution among habitat components (e.g., both understory cover and large woody debris providing protective cover from predators while squirrels are foraging on the forest floor).

The hierarchical relationships among limiting factors may also be important in evaluating habitat components within and across sites. There are several possible relationships: (1) one factor could dominate other factors due to a habitat component in limited supply (Liebig's law of the minimum; Blackman 1905), or habitat component with the narrow tolerance range (Shelford's law of tolerance; Shelford 1913), (2) two or more factors could dominate due to their strong interactions (e.g., dominant interactions; Paine 1992), or (3) multiple factors could be important, but hierarchical (limiting hierarchies; Berryman et al. 1987). These relationships among factors could hold true across the squirrel's geographic range, or could be site specific and thus, confound the ability to develop ubiquitous measures of high-quality squirrel habitat.

Analyses of relationships among habitat components and limiting factors may also lead to better understanding of how best to manage both flying squirrel and spotted owl habitat. However, such analyses require an approach that can model specific relationships among potential simultaneous influences, a limitation of traditional univariate and multivariate models (Bollen 1989, Grace 2006). Structural equation modeling (SEM) is a statistical framework based on analysis of covariances that combines conventional analytical techniques (e.g., general linear model, factor analysis) into multivariate, systems-based models. SEM originated from path analysis (e.g., Wright 1934), and has been gaining a foothold in natural science disciplines (Grace 2006). Modern SEM has several advantages over traditional univariate and multivariate analyses, including (1) the acceptance of inter-correlated variables; (2) full use of data by estimating unstandardized parameters (traditional regression only analyzes standardized [e.g., correlation] parameters which represents a loss of information); (3) both individual indicators as well as overall model fit can be evaluated; (4) there is allowance for multiple indicators per factor which can help reduce measurement errors; (5) non-normal data, dichotomous outcomes, and relatively small sample sizes can be analyzed through the use of Bayesian estimation techniques;

(6) model building is initiated with a conceptual model based on theory and ecological rationale which can help reduce spurious conclusions due to statistical chance; and (7) SEM software provides a graphical interface that allows for purposeful decision-making when specifying individual relationships among variables during model building and greater visual inspection of ecological assumptions going into each model compared to using equations alone (Grace 2006, Kline 2005).

Study Objectives and Hypotheses

My overall goal for this study was to add to the understanding of the biology and ecology of northern flying squirrels so that their usefulness as an index of forest management activities can be better understood and applied, including managing habitat for spotted owls. To address each of the problems above, I focused my study on four broad objectives.

Objective 1: To evaluate the mid-term responses of squirrel populations to variable-density thinning designed to improve habitat conditions for squirrel and spotted owls.

My first objective was to determine if populations on the Forest Ecosystem Study remained depressed, as previously reported (Carey 2000b, 2001, Carey et al. 1999b), or if conditions had become more favorable for squirrels a decade after variable-density thinning was applied. Because squirrels in treated stands had apparently recovered to control levels within 5 years of treatment (Carey 2001), my working hypothesis was that, if food were important, flying squirrel populations on treated stands should continue to increase and surpass those of control stands, given that the plant diversity on treated stands continued to increase relative to control stands (Aukema and Carey 2008), and would therefore provide greater abundance and diversity of food resources, including associated fungi. Other sciurids could also increase in response to variable-density thinning. I expected this would be the case for chipmunks, as by 1998, chipmunk populations were rapidly increasing in response to increasing understory development (Carey 2001). Douglas' squirrel abundance could also increase due to increased abundance of mast-producing shrubs, but because their populations have been shown to vary over time in response to conifer seed supply (Buchanan et al. 1990, Smith 1970, Sullivan and Sullivan 1982), I expected to see larger annual fluctuations in Douglas' squirrels compared to other sciurids.

An alternate outcome would be that flying squirrel populations remain depressed on treated stands after 1998, but not necessarily on control stands. Niche expansion for chipmunks or Douglas' squirrels could lead to direct competition for resources like food or dens important to flying squirrels (e.g., competitive exclusion; Gause 1934, Hardin 1960). Increased abundance of other prey species that responded favorably to variable-density thinning (mice and voles; Carey and Wilson 2001, unpublished data) could also attract predators and lead to opportunistic predation of flying squirrels (e.g., Holt 1984).

A third outcome would be that flying squirrel populations on both treated and control stands remained depressed. This could be the result of spillover predation (e.g., Oksanen et al. 1992) by predators that were attracted to increased prey on treated stands but also foraged over broader areas that included control stands. It could also be a response to seasonal, annual, or longer-term (e.g., el niño) changes in moisture, temperature, and plant phenology that limited food availability over time and kept populations low across the broader region (Fretwell 1972).

Objective 2: To gain better understanding of how squirrels use forest space.

My second objective was to explore space use of individual flying squirrels to (1) better understand both the spatial and temporal scales at which individual squirrels use multi-dimensional forest space, (2) provide context for interpreting live-trapping data, and (3) strengthen the ecological rationale for building habitat models that could test the relative importance of limiting factors for squirrel populations (see objective #4). I developed and used a continuous-tracking radio-telemetry methodology to follow squirrels through the woods while they were active outside their dens as an alternative approach to home-range study and as a complementary approach to my population-level study of flying squirrels.

Movement patterns and behaviors could be primarily driven by a need for obtaining food. If this were true, I would expect to observe behaviors that suggested squirrels minimized energetic costs associated with obtaining food (e.g., optimal foraging strategy; MacArthur and Pianka 1966), such as (1) a foraging pattern with a bivariate normal distribution centered on dens (e.g., central place foraging; Orians and Pearson 1979), (2) a positive relationship between either the time spent or distance covered to reach foraging sites compared to the time spent at foraging patches (e.g., diet and patch models, Stephens and Krebs 1987; Marginal Value Theorem, Charnov 1976), (3) seasonal shifts in foraging areas to capitalize on seasonally-available foods (Fretwell 1972), and (4) less effort (time or distance travelled) needed to meet energy demands in high-quality habitat compared to low-quality habitat.

However, like other prey species, flying squirrels may need to keep predation risk low while foraging, given the catastrophic consequences (Brown and Kotler 2007). Therefore, if a predation-mediated foraging strategy was being used by squirrels, evidence of risk avoidance should be observable in feeding behavior (Anderson 1986, Jacob and Brown 2000). Such behaviors might include (1) activity centered away from the den to reduce detection of the den where squirrels are vulnerable and spend most of their time, (2) use of multiple, widely-spaced activity sites each night with limited time spent at each site to minimize detection, (3) movement patterns that keep squirrels near protective cover when possible, and (4) less risky movement patterns observed during the winter when squirrel predation is highest (Villa et al. 1999, Wilson and Carey 1996).

Objective 3: To sample flying squirrel populations and habitat components across forests in western Washington that varied widely in structural complexity.

As an expansion of previous research on habitat relationships for flying squirrels in the region (Carey et al. 1999a), my third objective was to sample forests that varied widely along several gradients of structural complexity, much wider than had been attempted in the past, to (1) determine if forest-structuring processes, or the habitat components these processes create, could used as ubiquitous predictors of habitat quality for flying squirrels across the structurally-diverse forests found in the region; (2) help distinguish among stands in their ability to support high- or low-density populations; (3) put results of the FES study within broader regional context; and (4) determine whether some of the results found in past studies may have been constrained by limits in structural complexity sampled or due to some overall persistent environmental limitation (e.g., mild temperatures and high rainfall on the Olympic Peninsula resulting in dominance by shade-tolerant, low-mycorrhizal-diversity conifer species; Carey 1995a).

I hypothesized that forest structuring processes, or the habitat components they help create, could explain squirrel abundances across the region. If this were true, then I would expect to see significant relationships between and among ecological processes or habitat components and squirrel populations across my study sites. Because of the wide gradients in forest conditions sampled, I also hypothesized that some habitat components found important across multiple past studies in the Pacific Northwest (e.g., large live trees and snags) should also show up as being important predictors in my study. Results from Carey et al. (1999a) suggested that study at multiple scales may also be important, so I focused my analysis at both the individual (hereafter, patch) and population (hereafter, stand) level scales.

Objective 4: To evaluate the relationships and relative importance among habitat components and limiting factors influencing squirrel populations.

I used a structural equation modeling approach to examine four limiting factors that appear to have the greatest potential to regulate flying squirrel populations in contiguous Pacific Northwest forests—food, competition, dens, and predation as a way to (1) provide ecological context for why processes and habitat components might be important, (2) strengthen rationale for managing these processes and components for both squirrel and spotted owl habitat, and (3) help resolve questions over why squirrel populations often decline after forests are thinned.

My conceptual hypothesis was that all four factors played important roles in regulating squirrel populations (Figure 1), but that if there was universality in the hierarchy among factors, either food or predation would be the most influential factor, followed by competition, and lastly dens. If food were limiting, squirrel abundances should be positively associated with seasonal and year-round food resources, or surrogates for food resources, including (1) trees and shrub species that support mycorrhizal fungi, (2) tree and shrubs that support alternative food resources like hard mast (e.g., nuts,

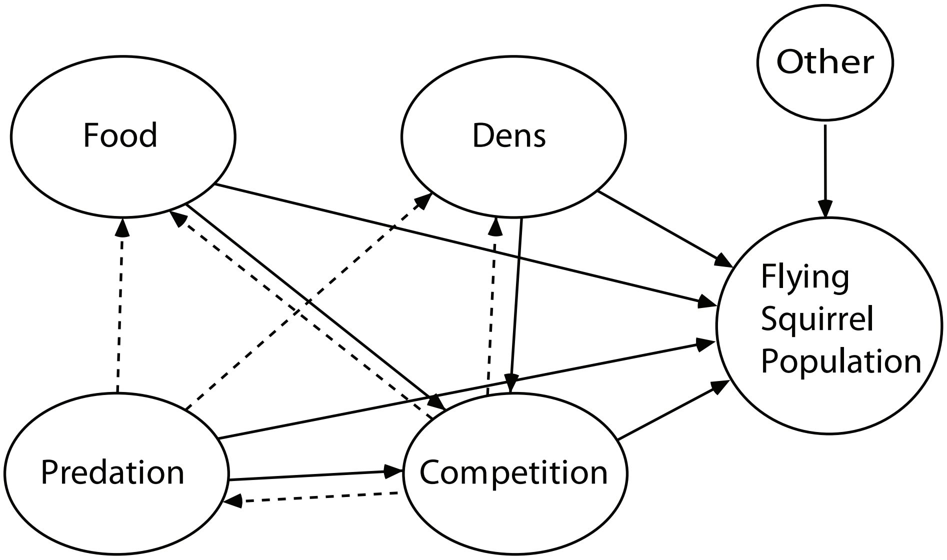

Figure 1. Conceptual model illustrating proposed direct (solid line) and diffuse (dashed line) relationships among potential limiting factors influencing northern flying squirrel (*Glaucomys sabrinus*) populations. Inverse effects (squirrel effects on factors) are not included.

samaras) or berries, (3) older trees that provide more diverse lichen species and supporting greater amounts and diversities of fungi; and (4) large fallen trees. If predation were limiting, I would expect to observe positive associations between squirrel abundances and protective cover where (1) squirrels are the least evolutionarily adapted (e.g., while moving on the ground where their patagium limits their travel speed and quietness while moving through the understory; personal observations); (2) while gliding (e.g., midstory layers) where they lose the speed and maneuverability advantage to aerial predators like owls (Appendix); or (3) where they spend the most time or distance covered based on my telemetry results. If dens were limiting, squirrels should be most abundant in habitat that provides abundant, secure, high-quality dens, including large live trees and large snags (e.g., Carey 1995a, Smith et al. 2004). Finally, if competition were limiting, flying squirrel populations should show negative associations with other Sciurids (Townsend’s chipmunks and Douglas’ squirrels) or habitat elements that have been shown to be strongly associated with them, including understory vegetation and cone-producing overstory trees (Carey 2000b, Harestad 1991, Hayes et al. 1995, Smith 1970).

CHAPTER TWO—STUDY AREA AND METHODS

Study Areas

I delineated thirty-three stands in nineteen tracts of forest for study (Figure 2; Table 1). Stands were distributed across two adjacent physiographic provinces of western Washington state—the Puget Trough and Olympic Peninsula (Franklin and Dyrness 1973).

Puget Trough

Sixteen 32-ha stands in 2 second-growth tracts of Douglas-fir forest (8

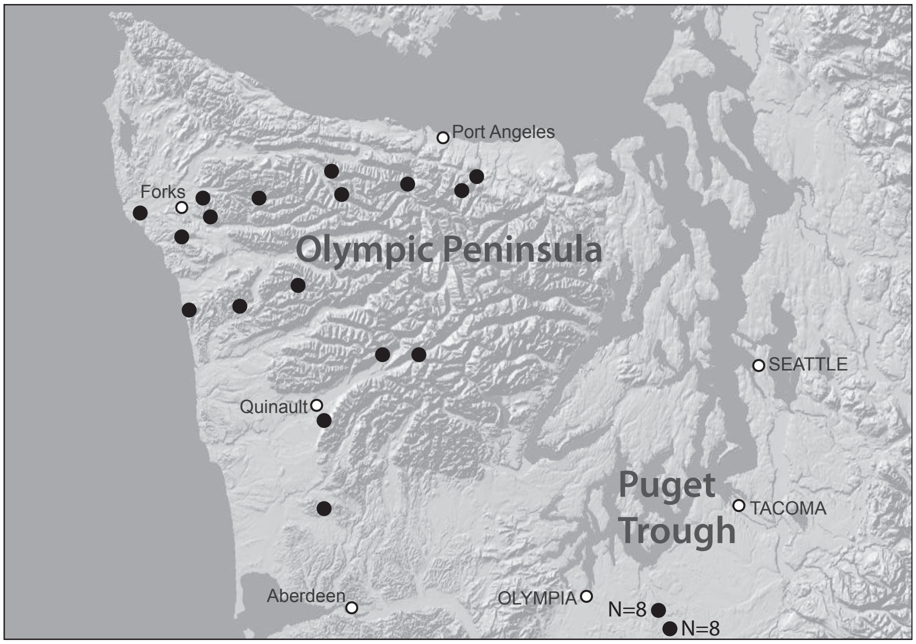

Figure 2. Stand locations for live-trapping, radio-telemetry, and forest structure studies of northern flying squirrel populations and their habitat in the Puget Trough and Olympic Peninsula of Washington State from 1991-2006. One stand was delineated in each of the Olympic Peninsula forests. Eight stands were delineated in each Each Puget Trough forest as part of the Forest Ecosystem Study (Carey et al. 1999b).

Table 1. Study areas for sampling northern flying squirrel (*Glaucomys sabrinus*) populations and forest structure across western Washington 2004-2006. Stands in bold supported high-density (>2.0 squirrels/ha) populations.

					Relative Forest Structuring Process Score[1]					
Forest Tract	**Std#**	**Canopy Age**	**Last Known Catastrophic Event[2]**	**Management History[2]**	**CC**	**UD**	**DE**	**CS**	**Total**	**Dominant Tree Species[3]**
Legacy[a]	101	67+	Clearcut 1937	VDT 1993	2.6	4.7	2.4	0.2	9.9	DF
Legacy[a]	102	67+	Clearcut 1937	None	8.1	5.6	1.9	0.0	15.6	DF
Legacy[a]	103	67+	Clearcut 1937	VDT 1993	6.9	5.5	2.6	0.3	15.3	DF
Legacy[a]	104	67+	Clearcut 1937	None	7.5	3.2	1.9	0.0	12.6	DF
Legacy[a]	201	67+	Clearcut 1937	VDT 1993	5.3	4.6	0.8	0.1	10.8	DF
Legacy[a]	202	67+	Clearcut 1937	VDT 1993	4.9	6.1	0.2	0.2	11.4	DF
Legacy[a]	203	67+	Clearcut 1937	None	6.9	4.1	3.0	0.0	14	DF
Legacy[a]	204	67+	Clearcut 1937	None	7.1	5.5	0.8	0.1	13.5	DF
Timber[a]	301	79	Clearcut 1925	2 Thins 1972-89	5.4	6.2	0.7	0.7	13	DF
Timber[a]	302	79	Clearcut 1925	2 Thins 1972-89,VDT 1993	1.9	7.5	1.2	1.1	11.7	DF
Timber[a]	303	79	Clearcut 1925	2 Thins 1972-89,VDT 1993	3.2	9.2	0	1.7	14.1	DF
Timber[a]	304	79	Clearcut 1925	2 Thins 1972-89	5.7	7.1	4.4	1.3	18.5	DF
Timber[a]	401	79	Clearcut 1925	2 Thins 1972-89,VDT 1993	1.9	8.0	1.5	1.8	13.2	DF
Timber[a]	402	79	Clearcut 1925	2 Thins 1972-89	6.4	7.7	0.6	0.8	15.5	DF
Timber[a]	403	79	Clearcut 1925	2 Thins 1972-89,VDT 1993	3.5	10.0	0.1	0.9	14.5	DF
Timber[a]	404	79	Clearcut 1925	2 Thins 1972-89	4.5	7.0	0.6	0.5	12.6	DF
Rugged Flats[d]	902	83-300+	Wind 1921	None	4.5	6.5	10.0	3.3	24.3	WH
Quinault RNA[d]	903	425+	Wind (unknown)	None	0.0	6.5	4.4	9.2	20.1	SS,WH
Kalaloch	**909**	**83-300+**	**Wind 1921**	**None**	6.6	**6.1**	**7.3**	**5.3**	25.3	**WH,SF**
Stequaleho	**910**	**150-300+**	**Unknown**	**None**	5.4	**4.7**	**7.9**	**4.8**	22.8	**WH,SF**
Goodman Ck.	**912**	**83-500+**	**Wind 1921**	**None**	7.0	**5.5**	**9.5**	**6.4**	28.4	**WR,WH**
La Push	913	83+	Wind 1921	None	4.5	5.5	6.4	2.2	18.6	WH
Bear Ck.[d]	915	83-275+	Wind 1921	None	7.6	5.5	7.4	2.6	23.1	WH,SF
Humptulips[d]	**917**	**375+**	**Unknown**	**None**	5.8	**2.9**	**8.7**	**3.6**	21	**WH**
Eaton Ck.[d]	944	83+	Wind 1921	None	7.5	6.5	5.6	1.0	20.6	WH
N.F. Sol Duc[b]	**963**	**120-175**	**Fire ca. 1887**	**None**	10.0	**0.7**	**2.7**	**0.5**	13.9	**DF,WH**
N.F. Quinault[e]	969	100-400	Fire (unknown)	PISI hi-grade in 1940s	1.9	6.9	5.8	4.8	19.4	WH,DF
Grave's Ck.[e]	**970**	**100-500**	**Fire (unknown)**	**None**	2.0	**7.8**	**8.3**	**10.0**	28.1	**WH,DF**

Table 1. Continued.

					Relative Forest Structuring Process Score[1]					
Forest Tract	**Std#**	**Canopy Age**	**Last Known Catastrophic Event[2]**	**Management History[2]**	**CC**	**UD**	**DE**	**CS**	**Total**	**Dominant Tree Species[3]**
Sol Duc Falls [b]	**971**	**300**	**Fire ca. 1710**	**None**	8.5	**2.1**	**1.5**	**6.1**	18.2	**WH,DF**
Elwha Ranger [b]	974	150-300	Fire ca. 1857	None	5.3	4.1	4.3	7.0	20.7	WH,DF
Cox Valley [b]	**982**	**300**	**Fire ca. 1694**	**None**	9.7	**1.2**	**1.9**	**4.8**	17.6	**DF,WH**
Heart O' Hills [b]	996	100+	Fire ca. 1910	None	6.0	0	3.4	1.4	10.8	WH,WR
Ruby Beach [e]	999	100-500+	Wind (unknown)	None	5.6	0.6	8.8	4.1	19.1	WH,WR

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[1] Scores based on a relative scale of 0-10 with 10 representing the stand with the highest score for that process and 0 representing the stand with the lowest score for that process. See text for details. CC= crown-class differentiation; UD= understory development; DE= decadence; CS= canopy stratification

[2] Stand history sources: (a) Carey et al., 1999a; (b) northern spotted and barred owl nesting data; S. Gremel, Wildlife Biologist, Olympic National Park, Port Angeles, WA; (c) Forest inventory data, S. Horton, Wildlife Biologist, Washington Department of Natural Resources, Forks, WA; (d) Carey and Johnson 1995; (e) No data available--age ranges based on size and species ages from other study areas. Where stand age is reported as a range, more than 1 age cohort dominated the canopy. A plus (+) indicates presence of residual trees that were older than the age values reported here, but were not an important contributor to overall canopy cover. Stands affected by the 1921 windstorm may have had substantial release of understory hemlocks that were older than the minimum 83 yrs reported here. VDT=variable-density thinning; Thins=conventional thinning.

[3] Tree Species: SF= Pacific silver fir (*Abies amabilis*); DF= Douglas-fir (*Pseudotsuga menziesii*); SS= Sitka spruce (*Picea sitchensis*); WH= western hemlock (*Tsuga heterophylla*); WR= western redcedar (*Thuja plicata*).

stands per forest) on the US Army Fort Lewis Military Reservation near Yelm, Washington were studied from 1991-2000, and from 2004-2005 as part of the Forest Ecosystem Study (Carey et al. 1999b): (1) a 67-yr old forest (as of 1991; hereafter, Legacy Forest) that had never been thinned (basal area of ca. 43 m^2/ha with 450-515 trees/ha), with a sparse understory of mosses, a patchy, low-density shrub layer (principally salal, *Gaultheria shallon*) and moderate amounts of residual trees and snags (6.2/ha) left during the previous harvest, and (2) a 79-yr old forest (as of 1991; hereafter, Timber Forest) that had been commercially-thinned twice in the 1970s and 1980s (basal area of ca. 46 m^2/ha with 200-250 trees/ha) with a moderately-developed understory of salal, swordfern (*Polystichum munitum*), and bracken fern (*Pteridium aquilinum*), little (<2%) coarse woody debris, and few old-growth legacies. Both forests originated from wide-scale clearcutting in the region. Variable-density thinning treatments were applied to 4 of the 8 stands in each forest in 1993; the remaining stands were left untreated. Each treated stand was divided into 1600m^2 cells, with cells assigned to one of two different thinning intensities based on a 2:1 ratio of light thinnings to heavy thinnings. In addition, 15% of the cells in each stand existed in either actual root-rot (*Phellinus weirii*) pockets, or were treated to simulate root-rot pockets (leaving ca. 40 trees/ha). Treatments reduced stand-level basal area to 30 m^2/ha (291 stems/ha) in the Legacy Forest and 37 m^2/ha (147 stems/ha) in the Timber Forest, with individual cells ranging from 11-49 m^2/ha basal area (109-457 trees/ha) in the Legacy Forest and 15-60 m^2/ha basal area (59-224 tree/ha) in the Timber Forest (see Carey et al. 1999b for more details).

Olympic Peninsula

Seventeen additional tracts of forest were studied from 2005-2006 (Table 1). One 32-ha stand was delineated within each tract. Each of these natural (non-managed, with fire or wind being the primary disturbances) tracts were chosen to be unique in their structural complexity (Table 1). Collectively, the Olympic Peninsula and Puget Trough stands represented relatively full gradients of habitat conditions influenced by each of the four structuring processes found in conifer-dominated forest west of the Cascade Mountains, except that I did not select forests in early seral stages or forests with sparse canopies (as squirrels are seldom found there), or forests with extremely high tree density (e.g., "doghair" western hemlock [*Tsuga heterophylla*] forests). Stands were managed by the USDA Forest Service, Olympic National Forest (n=5), Washington Department of Natural Resources (n=4), and the Olympic National Park (n=8), and located primarily across the western and northern portions of the Olympic Peninsula, resulting in variation of dominant tree species composition, annual rainfall, and elevation (near sea level to 3200 ft; Table 1).

All 33 stands were embedded in larger tracts of similar forest ranging from eighty to several thousand hectares. Additionally, all tracts were embedded in larger forested landscapes that were permeable to flying squirrels—there were few if any landscape-level barriers to movements (although there were sometimes non-forested edges near one side of a stand). The five Forest Service stands had been previously sampled for squirrel populations in 1987-88 (Carey 1995a). Each of the Olympic Peninsula stands had historic use by spotted owls, but none were detected by field observers during this study. Barred owls were detected on or near several of my study sites in both provinces during this study (personal observations) and in recent years (Scott Gremel, Olympic National Park, personal communication). There is growing concern over the displacement of spotted owls by barred owls (Kelly et al. 2003).

Field Methods

Livetrapping

Livetrapping grids (8 x 8 matrix with 40-m spacing between stations) were established in each stand (Figure 3). Two Tomahawk 201 traps were placed at each station, one on the ground and one 1.5m high in a tree, and baited with peanut butter, oats, and molasses (Carey et al. 1991). Pre-baiting occurred the week prior for any stands trapped for the first time. Captured squirrels were ear-tagged, weighed, sexed, aged, and released following professional guidelines for the use of wild mammals in research (Davis 1963, Carey et al. 1991, Gannon et al. 2007, Villa et al. 1999).

Traps were left open for two 4-night periods separated by three nights for most stands. The effectiveness of these procedures, including high probabilities of captures ($p>0.50$) with no significant differences between initial capture probabilities and subsequent capture probabilities, has been previously documented and discussed (Carey 1995a, 2000b, Carey et al. 1991). However, I found initial captures of flying squirrels to be low during

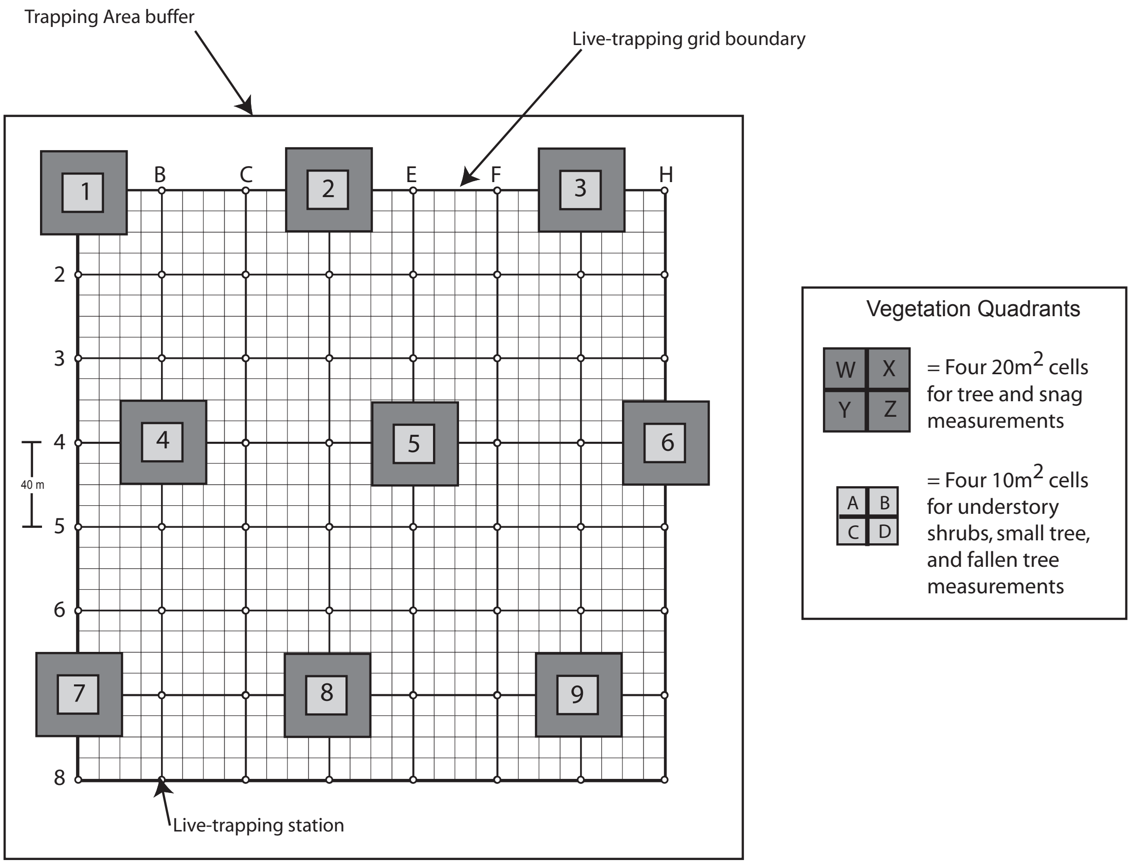


Figure 3. Diagram showing the spatial relationship for sampling northern flying squirrels (*Glaucomys sabrinus*) using a live-trapping grid and measuring forest structure using 9 systematically spaced plots (dark= overstory; light= understory) at each of 33 stands across western Washington. Each plot was further divided into 4 quadrants to facilitate sampling (see inset).

the first week on a few of the Olympic Peninsula stands. Therefore, to ensure that I was not underestimating populations, I trapped for an additional third week on any stand if the number of individual squirrels captured during week 2 was ≥ 2 times as high as the number of individuals captured during week 1. This additional trapping effort also minimized the likelihood of overinflated abundance estimates using my various estimators and helped ameliorate for potential effects of poor weather or other proximate environmental or behavioral factors that might influence trappability.

Squirrel populations were sampled each spring and fall from fall 1991 to 1997, each fall from 1998-2000 and fall 2004, spring 2005, and fall 2005 in the Puget Trough. Results from 1991-1998 have been previously reported (Carey 2000b, 2001). On the Olympic Peninsula, squirrel populations were sampled 1-3 times each during fall 2005, spring 2006, and fall 2006—additional sampling effort (sessions) occurred on stands that had few captures or where disruption of traps by black bears (*Ursus americanus*) required that traps be closed before a session was completed. Periodically, additional trapping (2-4 nights) was conducted throughout the year to replace radio-collars of flying squirrels that were captured during fall or spring trapping sessions (see below)—results from these additional sessions were not systematic, and are not reported here. Given the resources available for this study, I chose to sample as many Olympic Peninsula stands as possible during a short time period (1-3 seasons) to capture a wide gradient of structural complexity in lieu of sampling fewer stands more intensively to measure more precise changes in populations over time or to average populations over time. Sampling Olympic Peninsula stand relatively concurrent to the FES sampling period also allowed me to evaluate any regional effects (e.g., el niño weather patterns) that might have confounded FES results.

Radio-Telemetry

Low-density squirrel populations from four stands each in the Legacy Forest (Stands 201, 202, 203, 204) and Timber Forest (Stands 301, 302, 303, 304) were chosen for radio-telemetry study from November 1993 to January

1996. Squirrels from all eight stands in the Legacy Forest (Stands 101, 102, 103, 104, 201, 202, 203, 204) and two stands with high squirrel densities on the Olympic Peninsula (stands 909, 912) were studied from December 2005-March 2006.

Because my objective was to evaluate space use, my sampling strategy was to attach radio collars to as many of the individuals in each population as practical, and then randomly select individuals to follow on any given night. Trapping was presumed to produce an unbiased and comprehensive sample of squirrels from each forest. In general, attempts were made to radio-collar ≥10 individuals ≥120g (primarily adults) in each forest during each live-trapping session. Squirrels were anesthetized with methoxyflurane or isoflurane and fitted with 6-month, 4.0g replaceable collar-style radio transmitters (Holohil Ltd., Carp, Ontario, Canada). The actual number of squirrels monitored relative to the total individuals captured in each forest varied due to numbers of captures, mortality, and transmitter lifespan: Fall 1993 (Legacy Forest—8 of 32; Timber Forest—8 of 10), Spring 1994 (Legacy Forest—12 of 31; Timber Forest—13 of 16), Fall 1994 (Legacy Forest—11 of 19; Timber Forest—10 of 13), Spring 1995 (Legacy Forest—10 of 10; Timber Forest—0 of 3), Fall 2005 (Legacy—8 of 8; Stand 909—3 of 24; and Stand 912—9 of 29). Overall, 13-100% of the total population of squirrels was sampled in each forest during any given session with ≥75% of the population sampled during half of the sampling periods.

Movement patterns were collected from each squirrel with as equal intensity as possible. Squirrels were arranged randomly in a pool and then followed systematically for each session. Each technician randomly selected one squirrel to monitor each sampling night. This procedure was followed until a squirrel died, its radio-transmitter failed, or five nights of activity were collected during a given 4-6 week session. Data for analysis was grouped into breeding (May-August) and non-breeding (November-April) periods.

Tracking protocols were developed and pilot studies were conducted over an 18-month period from 1992-1993 on the Puget Trough study sites. The final protocol used for data collection maximized data accuracy given radio signal bounce and terrain, minimized disturbance to squirrels that were being followed, and ensured the safety of personnel that were monitoring the movements and activities of squirrels at night (Appendix). Technicians began each track at dusk by monitoring radio signals from near (10-20 m) the den using a hand-held receiver and an H-antenna. If a squirrel left its den, the technician would follow behind, monitoring squirrel position and direction of travel by continuously homing in on the squirrel while attempting to keep a distance of 10-20m from the squirrel at all times. When squirrels were travelling to an activity site, they usually did so in a relatively straight horizontal line, and technicians could follow directly behind. When a squirrel stopped, technicians would circle around the squirrel to determine its location, while continuing homing to keep a 10-20 m distance from the squirrel. This tracking method did not appear to unduly affect squirrel behaviors as they were measured here (Appendix). Other flying squirrels have exhibited similar lack of response to observers while being continuously monitored (e.g., Selonen and Hanski 2006).

Squirrels were usually observed during their first activity periods. Beginning at dusk, squirrels were monitored at their dens for ≥3 hours, or until they left their dens. If a squirrel left its den, it was monitored until either (1) it returned to the same den and stayed for 20 min, (2) stopped at a different den and remained motionless for 40 minutes, or (3) if not returning to a den, then for a minimum of 3 hours of activity. Tracks were categorized as being "complete" if the squirrel was monitored from a starting den to a stopping den, "180+" if the technician stopped tracking after 3 hours, "incomplete" if the technician started monitoring the squirrel after it left the den (rare) or stopped tracking the squirrel before 3 hours (more common). During protocol development, it was noted that most activity occurred during the first several hours after dark, as has been previously reported (Weigl and Osgood 1974). To confirm this, squirrels were monitored continuously from dusk until dawn over nine nights (February 21-22, 27-28, 1995; June 26-27, 1995; February 12-14, 1996). These tracks were grouped with complete tracks for analysis, except where noted.

A tape or digital hand-held recorder was used to record tracking information. Transcriptions of recorded information were usually made the next morning, and observers used this information, along with flagging in the field, to recreate the paths used by squirrels the previous night.

Coordinates were obtained for three types of stopping locations—diurnal dens, travel points, and activity sites—and entered into a database for analysis. Dens were determined prior to squirrels moving each night, and as part of a separate study of den use (Carey et. al. 1997). Travel points represented locations where squirrels changed direction of travel or where squirrels stopped traveling but stayed in one general location for <5 minutes. Activity sites were defined as locations where squirrels stopped traveling and engaged in localized activity for ≥5 minutes. Straight lines were drawn between point types as they accrued during the track (ie. discrete representations of the track). Subjective estimates of path error widths were from 0 m to 10 m. Because most rapid movement away from a site was by gliding, glides were relatively linear in horizontal direction, and squirrels needed to climb a tree prior to gliding again, an experienced technician usually had opportunity to catch up with the squirrel and determine its location before it glided again. Therefore, these discrete paths were considered realistic of the actual horizontal paths used by the squirrel to travel between activity sites. Because the tracking protocol kept technicians ≥10m from squirrels and much of the squirrel activity took place in the canopy, direct observations of squirrels were rare and specific behaviors at activity sites (e.g., foraging vs. social) could not always be determined.

Habitat and Forest Structure

I measured squirrel habitat at both the patch- (i.e., individual) and stand- (i.e., population) level scales. I defined a patch as the area that individual squirrels spent most of their time based on radio-telemetry results (ca. 80-120m in diameter; see below). I used 40x40m (1600m^2; overstory) and 20m x 20m (400m^2; understory and large fallen trees, except line-transects were used to collect fallen tree data on the FES; see below) plots to represent habitat at each patch (Figure 3). Plot sizes appeared adequate to capture most of the within-stand structural complexity found in older forest within the region (Bradshaw and Spies 1992, Carey et al. 1999a, Cohen et al. 1990) as well as the variation in tree density for variable-density thinned stands (Carey et al. 1999b). Plots were systematically spaced approximately 80m apart across each of the 33 stands and measured from 2006-2007 (Figure 3). This spacing allowed for most (>95%) squirrels to be associated (e.g., nearest trap station[s]) with only 1 patch. Thus, I assumed my sampling plots were adequately-spaced across the stand and represented independent samples of individual squirrel habitat. Each plot was centered on a live-trapping station point and then divided into four horizontal quadrants to facilitate data collection. Quadrants were delineated using hypsometers, along with trap-line flagging and survey stakes placed at trap stations. Occasionally, individual plots were shifted up to 40m (one trap station) if they fell on non-vegetative surfaces such as creeks or small landslides.

I measured habitat variables that could be associated with at least one of the four potential limiting factors for squirrels being explored during this study (food, predation, dens, or competition). To capture the multi-dimensional characteristics of forest structure at each plot, I also took measures that could be used to recreate individual tree components (e.g., individual tree boles and canopies) and used both volume and cover layers when possible for understory measures. This allowed me to evaluate the composition and distribution of structural components in both vertical and horizontal space during analyses.

My second-level of habitat evaluation was at the stand scale to capture any larger or multiplicative effects of structure that may have influenced stand-level populations or that were not adequately captured at the patch level. To do so, I either averaged data across plots, or in the case of canopy gaps (see below), sampled 100% of the stand.

Overstory.—Overstory data included tallies of all live and dead trees ≥10cm d.b.h. by species and d.b.h. class (10-cm increments), and tallies of live conifer trees ≥1.5m tall and <10 cm d.b.h. In addition, 1-9 representative live trees for each species-d.b.h. class present in each stand were measured for total height, height to live crown, and crown radius. A database record was created for each tallied tree, and assigned the bole and canopy characteristics of representative trees. Canopies of smaller trees (<75 cm d.b.h.) were modeled as cones, and canopies of larger trees and tree boles were modeled as elliptic paraboloids to obtain crown and bole volumes (both absolute and relative to total forest space at 90% total tree height), and area intercepts (horizontal slices of boles and crowns) at various heights above the ground. Simple geometric shapes are fairly robust for comparing relative crown sizes and estimating volumes for many conifer species and age classes in the region (Van Pelt and North 1996, Van Pelt and Sillett 2008, Van Pelt et al. 2004). Parabolic stem models are applicable to most conifers, though more precise measures are generally favored for estimating tree bole volumes for commercial purposes as the top third of conifer boles can sometimes be conical (Plank and Cahill 1984, Williams et al. 2003, Whittaker et al. 1974). However, boles contributed little to overall tree volume compared to live crowns so I chose not to use more complex formulae for modeling trees during this study.

If a representative tree was measured on a plot, information from that tree was applied to all trees of similar size class and species for that plot. Otherwise, a randomly-selected representative tree from the remaining plots was chosen. The total number of representative trees measured per stand was based on the relative frequency of each species-DBH class: a total count of 1-5 trees, 6-10 trees, and >10 trees across the 9 plots were represented by 1, 2, and 3 trees respectively. In addition, a tree was measured within any single plot if >10 trees for a species-dbh class were present in that plot. When 2 or more trees were chosen to represent a species-DBH class, they were randomly chosen from plots distributed across the stand to account for any patch-level variation present due to disturbances (fire, wind events) or geologic features (slopes, riparian areas) that might have caused variation in the canopy architecture of individual trees within a given species-d.b.h. class.

Canopy Gaps.—I defined canopy gap (hereafter, gap) as a horizontal area of space not occupied by trees and delineated by the maximum radial edges of the crowns of adjacent trees ≥10cm d.b.h. (usually the lowest third of most tree crowns for conifer species). I used a 100m^2 gap that was ≥10m wide by ≥10m long as the minimum gap size because it was large enough that a squirrel had to either glide across or travel around it to reach the other side. Gaps were mapped by observers walking through each stand along trap lines, using live-trapping station points and associated flagging as reference points to divide stands into 10m x 10m cells, and transcribing each gap onto a map divided into similar units (figure 3). These maps were then converted into a database by categorizing each $100m^2$ cell as either being a gap or non-gap cell. I also distinguished gaps associated with perennial creeks and lined with trees that had ground-to-crown canopies (hereafter, creek gaps) from other gaps to evaluate whether their structural difference was important in explaining squirrel abundances. Use of non-creek gaps during analyses reduced total canopy gap percentage for 6 stands (#902, 4.3%; #909, 2.5%; #910, 5.1%; #915, 6.3%, #917, 4.5%, and #970, 8.8%).

Understory.—Percent cover estimates (0-1%, 2-5%, 6-10%, 11-25%, 26-50%, 51-75%, 76-100%) were collected by life form and height layer (0.1-0.5m, 0.6-1.0m, 1.1-1.5m, 1.6-2.0m, 2.1-3.0m, 3.1-4.0m, 4.1-5.0m, >5.0m) and converted to volume estimates for mosses, forbs, low shrubs, medium shrubs, tall shrubs, understory conifers <1.5m tall and mid-story deciduous trees <10cm d.b.h. There was high correlation between percent cover and volume (e.g., low shrubs, r^2=.93; forbs, r^2=.99, ferns, r^2=0.84). Life-form categories were chosen to represent similar ecological functions for flying squirrels: moss (forest floor space not occupied by herbaceous or woody vegetation—a measure of forest-floor protective cover, and an indirect measure of forest-floor patchiness), forbs (herbaceous plants important as food sources for competitors; limited protective cover), low shrubs (dense, woody, trailing, bushy undergrowth species like salal and Oregon grape that provide year-round dense forest-floor cover as well as seasonal fruit), medium shrubs (erect plants including huckleberry [*Vaccinium* spp.], currant, and wild rose that provide little to moderate protective cover, but potentially important seasonal food resources), tall shrubs (e.g., Indian plum, California hazelnut, red elderberry, and vine maple that typically can grow >2m tall, providing both berries and hard mast like nuts, as well as important cover above the forest-floor vegetation layer), mid-story deciduous trees <10 cm d.b.h. (e.g., red alder, bigleaf maple, and black cottonwood that provide a variety of food resources as well as future mature trees that can provide both food and protective cover), and understory conifers (protective cover while traveling on the forest floor).

Large Fallen Trees.—Percent cover of large (≥50cm diameter at the large end) fallen trees on Olympic Peninsula stands was sampled by measuring the length and average diameter of the portion of every fallen tree that fell within each 10m^2 quadrant in each plot. To be consistent with previous protocols for long-term study of decadence on the FES, percent cover of large fallen trees was calculated for FES stands by using 1200m of line- intercept along the 6 center trapping lines within each stand for every fallen tree ≥50cm d.b.h. (or ≥50cm at the large-diameter end of the tree if the base was missing). Intercept values were assigned to plots based on the nearest 40-m segment and converted to volumes. Only well-defined (e.g., class I-IV; Maser et al. 1979) fallen trees were measured. I focused on large fallen trees because management for large fallen trees is being emphasized in the region due to their relative scarcity, particularly in young, managed forests (e.g., Rose et al. 2001), quantity of large fallen trees was higher in the Legacy Forest which supported higher abundances of flying squirrels compared to the Timber Forest (Carey et al. 1999b, Carey 2000b), and volume of large fallen trees has been associated with flying squirrel abundance in young stands elsewhere (e.g., Gomez et al. 2005). It also allowed me to evaluate wide gradients in amounts of high-quality coarse woody debris (compared to smaller woody debris that is often not limiting in young forest) that serve both food and protective cover functions.

<u>Activity Sites</u>.—Additional vegetation measures were collected at all activity sites for radio-collared squirrels, usually within 2 weeks after use by squirrels from 1993-1996 on the FES. Measures were taken on 5.6 m radius plots and included percent cover using an octave scale (0-2%, 2.1-4%, 4.1-8%, 8.1-16%, 16.1-32%, 32.1-64%, >64%) at 4 height layers (0.0-0.5 m, 0.6-2.0m, >2.0m for forbs, non-overstory shrubs and small trees, and overstory trees). A similar set of measures were simultaneously taken at randomly selected long-term permanent plot locations within each stand (Carey et al. 1999b).

Ecological Process Scores

I quantified the influence of forest structuring processes on each stand using similar measures to Carey et al. 1999a (which were interpreted from exploratory factor analysis), but with modifications based on examining forest structural complexity in the field and further advancements in the conceptual construct for these processes (Carey 2003; see below). Given the number of stands sampled, I also chose measures that could be readily obtained from the ground in a reasonable time period.

For crown-class differentiation, I used the proportion of each stand that did not contain canopy gaps $\geq 100\text{m}^2$. Although this was not a direct measure of competition between individual trees of the same cohort, stands with few or no canopy gaps were more likely to have inter-tree competition than stands with large gaps.

For decadence, I used proportion of the volume of standing dead (≥10-cm d.b.h.) and large (≥50-cm d.b.h.) fallen trees to the total volume of wood in each stand (the boles of live, dead, and fallen trees). This metric did not capture the full spectrum of decadence (e.g., it did not capture decadence in live trees), but it captured most of the intermediate process of decadence between death of live trees and incorporation of large woody debris into the forest-floor. It also captured the majority of dead wood volume found in these stands.

For understory development, I created an understory diversity index (UDI) based on the Berger-Parker index (e.g., Magurran 1988) that accounts for evenness, but adjusted to account for horizontal variation across 5 life form categories in the understory (forbs, ferns, and low, medium, and tall shrubs):

$\text{UDI} = (5 - (C_{max} \div C_{ave})) * S$, with

C_{ave}=average percent cover across life forms,

C_{max}= percent cover of the life form with the highest percent cover, and S=proportion of area not dominated by moss (e.g., dominated by one or more of the 5 life forms measured)

A value of zero indicated either a completely absent understory (e.g., an understory dominated by moss, rock, or soil) or complete dominance by one life form, and a score of 5 indicated complete co-dominance of all 5 life forms across the plot.

For canopy stratification, I used stand-averaged variance in diameter for live trees ≥10-cm d.b.h. This did not necessarily capture all growth habits for each tree species, but it did capture most of the variation in tree sizes and ages characteristics of both a highly simplified, uniform young forest at one end, and a highly-stratified multi-layered complex old forest at the other end (Spies and Franklin 1991).

Scores were re-indexed on a scale of 0-10 for each process, with 10 representing the stand with the highest value for that process and 0 being the lowest (Table 1).

Movement Patterns

I examined several temporal metrics for movements including rates of travel, time spent in travel and at activity sites, and amounts of time spent on the ground compared to in the canopy. Spatial metrics included maximum distances moved from the den, distance between dens, activity sites and travel points, circuit and travel distances, and spatial extent covered among dens and activity sites across nights and seasons.

I used the Mann-Whitney U-test (evaluating central tendency), the two-sample Kolmogorov-Smirnov test (evaluating central tendency and shape using cumulative distribution functions), and the Wald-Wolfowitz Runs test (evaluating central tendency and shape by ranking data; SPSS 2007) to evaluate differences in vegetation between activity sites and control plots. Differences were considered significant if $p \leq 0.05$ across all three tests. There was no contra-indication for grouping sex and years. Therefore, I pooled most data but evaluated forests separately. Activity sites were classified as ground-only (squirrels spent virtually all of their time on the ground), ground-dominated (squirrels spent time on both the ground and in the canopy but more time was one the ground), canopy-only (all time at the activity site was spent in the canopy), and canopy-dominated (most time was spent in the canopy, but there was also some time spent on the ground).

Population Estimation

Population abundance for flying squirrels was estimated in several ways: (1) minimum number known alive (MNKA); (2) individuals captured per unit effort, corrected for sprung traps and total captures (ICPUE; Nelson and Clark 1973); (3) Chapman modification of the Lincoln-Peterson index (CLP; Chapman 1951); (4) and four estimators from program CAPTURE as implemented in program MARK that account for variation in time (Darroch M_t, Chao M_t), individual heterogeneity (Jackknife M_h), or both (Chao M_{th}; White et al. 1982, White and Burnham 1999). Mean maximum distance moved (MMDM) between subsequent captures was also calculated for each stand where ≥2 individuals were captured at more than one trap station, and used as a index of area sampled (adding ½ MMDM around the boundary of the trapping grid; Otis et al. 1978). For stands that were trapped for 3 weeks, I removed the first week of trapping data from analysis as few (<5) individuals were captured in week 1 and all were captured at least once during week 2 or week 3.

I used three metrics to represent squirrel populations during analyses. First, all abundance estimates, except CPUE, were highly correlated (adjusted r^2=0.93-0.97) as has been shown in previous studies (e.g., Carey 2000b, Holloway and Malcolm 2006, Lehmkuhl et al. 2006). I therefore chose maximum MNKA as my abundance measure for most regression-based analyses given that MNKA was the least derived estimate, it may better represent potential carrying capacity of a forest than averaging abundances across time periods (Carey et al. 1999a), and I was interested in comparing relative differences in abundance across study sites rather than refining small differences among population sizes that can be confounded by sampling effort, season (e.g., fall trapping samples adults and juvenile recruitment whereas spring trapping samples the previous fall population after winter mortality), short-term stochastic events, or individual behaviors that can result in heterogeneous captures (Rosenberg et al. 1995, White et al. 1982). I report results from other estimators to allow comparison with previously reported studies in the region. I also used cumulative MNKA over the 14-year sampling period on the FES for contrasting long-term capacity of FES stands to support squirrel populations with maximum canopy gap sizes (gaps were known to enlarge due to continued windthrow and tree disease during this period, whereas other variables measured in 2005-2006 could have either increased or decreased since 1991).

Second, I replaced MNKA with a dichotomous variable for stands supporting either high or low abundances for some analyses. I chose this conservative approach for several reasons. First, flying squirrel populations vary in abundance across seasons and years (e.g., Carey 2000b, 2001, Carey et al. 1999a, Fryxell et al. 1998, Lehmkuhl et al. 2006, Ransome et al. 2004, Smith and Nichols 2003). Therefore, squirrel populations shift on a much more frequent timescale than do habitat components (with the exception of a stand-level catastrophic event such as a windstorm) and dividing populations into two groups allowed me to test the robustness of my findings based on MNKA. Second, it helped ameliorate for the fact that maximum MNKA for 9 of the 33 stands was based on one sampling period. Third, separating populations into low and high densities is consistent with the observation that two life history strategies are used by flying squirrels (e.g., *r*- or *K*-selection; MacArthur and Wilson 1967, Villa et al. 1999) and likely represented by a sigmoidal population growth curve having *r*-selected populations in the lag phase where growth is slow due to few individuals, and most K-selection populations in the deceleration phase where population growth again slows in the face of ecological resistance such as delayed reproduction in younger females (Villa et al. 1999), with few populations in between. Related, high density populations (>2/ha) would take years if not decades to develop from a population of few individuals, given average reproduction and mortality rates. Therefore, high-density populations represent a set of forest conditions that have allowed populations to build over a substantial time period (suggesting a relatively stable, high-quality environment), whereas low-density populations suggest habitat conditions that have not allowed populations to build, or the occurrence of a recent event that greatly depleted populations (suggesting an unstable or limiting environment). There were no contra-indications to the assumption that population levels reflected habitat quality (Van Horne 1983; see discussion). Separating populations into high and low abundance groups could also produce metrics useful for distinguishing high-quality squirrel habitat for management purposes.

My third abundance metric was biomass (weight) obtained from first captures of each individual within a trapping session. I used biomass when contrasting flying squirrel abundance with other sciurids given there can be a four-fold difference in body size among them. Stand-level biomass and MNKA were highly correlated (r^2=.98) for flying squirrels. For individuals killed and partially consumed by predators (primarily weasels) or for animals that escaped before they could be weighed, I assigned average biomass based on forest, season, sex, and age class.

Descriptive Statistics and Univariate Analyses

Descriptive statistics were calculated for most data sets and displayed as sample sizes, means, standard errors, and boxplots. Relationships between squirrel abundance and nominal forest age, ecological process scores, and potential habitat predictors were assessed using linear regression (comparing squirrel MNKA) and 95% confidence intervals (comparing HIGH and LOW stands). Data were screened for missing values, evaluated for linearity using scatter plots, and assessed for normality by examining normal probability plots of residuals, skewness, and kurtosis. I included all outliers in my analyses as I assumed that the variables being examined were representative of the natural variation found in the region, and not an anomaly due to sampling error or other extrinsic factor not otherwise being considered. Non-normal variables were sufficiently transformed using logarithmic (L_n) or, in a few cases, odd-root ($X^{1/3}$) transformations. I report untransformed values here to aid in interpretation. Four Olympic Peninsula stands were excluded from biomass-related analyses because trapping sessions only occurred late November-early December when chipmunks normally go into winter torpor. Therefore, a lack of captures did not necessarily reflect low chipmunk abundances for those stands. All analyses were conducted using AMOS (2009) or SPSS (2007).

Multivariate Analyses

Steps for Structural Equation Modeling (SEM)

I used a multi-step process to build and analyze SEM models. First, I built conceptual models for assumed ecological relationships based on the results from this study, previous studies, and ecological theory. I followed standard SEM convention using exogenous (independent) variables, endogenous (dependent) variables, and error variables (indicating both random measurement error and unspecified causal influences; note—error variables are omitted in final figures reported here). Observed (directly measured) variables were represented as boxes. For some models, I also used circles to indicate composite variables (unobserved variables that represented a heterogeneous collection of causes that create a concept) rather than latent variables (unmeasured cause influencing its indicators) given that for each factor, I assumed a high degree of individual effects of each indicator on the factor, little interchangeability among indicators, and low covariance between most indicator variables (Grace 2006). Relationships between variables included direct pathways (represented as single arrows pointing from exogenous to endogenous variables), indirect pathways (single arrow between endogenous variables) and covariances (double-headed arrows between two variables or their error terms representing an unmeasured relationship that was not explicit to the model).

I ran most models using both maximum likelihood estimation and Bayesian estimation as implemented in AMOS (2009). Bayesian estimation is superior to maximum likelihood when assumptions of multivariate normality are not fully met and for small sample sizes (Grace 2006). For classifying stands into HIGH-LOW groups, I used mixture modeling as a model-based Bayesian alternative to discriminant analysis (Fraley and Raftery 2002). This procedure uses a probit model formulation (similar to a logistic model) that allowed my dichotomous endogenous variable (HIGH or LOW) to be modeled as a continuous probability function and approximate a normal distribution. I allowed AMOS to use all data to help build algorithms for mixture-modeling classification.

Individual model fit was assessed using Chi-square (considering models as adequate if Chi-square P values were >0.05 suggesting no difference between model and the data) and RMSEA (root mean square error of approximation; with values <.05 indicating close fit, values <0.08 indicating a reasonable fit, and values >0.1 indicating poor fit; Browne and Cudeck 1993). For making comparisons among models, I used absolute values of AIC (Akaike Information Criterion, Akaike 1987), BCC (Browne-Cudeck criterion; Browne and Cudeck 1989), and DIC (Bayesian Deviance Information Criterion) with smaller values suggesting better models (Lee 2007, Schreiber et al. 2006).

My final step was to evaluate whether models could be improved, by making adjustments based on critical ratios (similar to t-tests; removing paths not significant at α= 0.05), modification indices (considering the addition of paths for indices >4.0), and inspecting standardized residuals (considering models as mis-specified if residuals between any two indicators were near or >2.0), and equivalent models (e.g., changing arrow direction or replacing single paths with covariances), but only if there was ecological rationale to do so (Grace 2006). For models with similar fit indices, I chose the most parsimonious model as my best model, but also discuss implications of similar models.

Model Assumptions

Ecological Processes.— I assumed that all four ecological processes had significant influence on squirrel abundances. I also assumed that the amount of forest without canopy gaps (e.g., crown-class differentiation) had a direct influence of on understory development, with some degree of correlation among other variables, given that effects from multiple processes could be observed, in some cases, with similar habitat components (Table 2).

Temporal Relationships of Sciurid Biomass.— I used fall-only post-treatment (variable-density thinning) livetrapping data from 1993 to 2005 to assess relationships among flying squirrels, competitors (Douglas' squirrel and chipmunks), forest, and variable-density thinning treatment on the FES over time. I assumed there were direct effects of forest, treatment, and biomass of competitors on flying squirrel biomass over time, and for each species, there were correlations or covariances between consecutive-year flying squirrel biomass.

Movement Patterns.—I was interested in explaining spatio-temporal relationships of squirrel movement patterns as a way to potentially distinguish between food-driven and predator-mediated movement strategies. I built separate models for the breeding and non-breeding seasons and assumed that both forest (HIGH or LOW in the non-breeding

Table 2. Variables used in structural equation modeling examining relationships among habitat elements for northern flying squirrels (*Glaucomys sabrinus*) and *a priori* assumptions of major relationships with forest structuring processes and factors potentially limiting squirrel populations in western Washington. "X"s denote direct influences (processes) or relationships (factors) assumed during analyses.

	Forest Structuring Process				Limiting Factor			
Habitat Variables	**Decadence**	**Canopy Stratifi-cation**	**Crown-class Differentiation**	**Understory Development**	**Food**	**Dens**	**Competition**	**Predation**
Overstory								
Snags ≥20cm (count/basal area/volume)	X		X				X	
Snags >50cm (count/basal area)	X				X	X	X	
Live Trees ≥75cm (count)	X	X	X		X	X	X	X
Live Trees ≥10cm (basal area)		X	X		X			X
Live deciduous ≥10cm (basal area, presence/absence)		X		X	X			
Live and Dead Trees (basal area)	X	X	X	X	X		X	
Live and dead conifers (basal area)	X	X	X		X		X	
Height to live crown/crown ratio		X	X					X
Crown volume		X	X			X	X	X
Stand-level canopy gaps	X		X	X	X		X	X
Plot-level canopy gaps	X		X	X	X		X	X
Area intercept at 5m, 20m		X	X	X				X

Table 2. Continued

Habitat Variables	Forest Structuring Process Decadence	Canopy Stratification	Crown-class Differentiation	Understory Development	Limiting Factor Food	Dens	Competition	Predation
Area intercept at 10m, 15m		X						X
Total volume crowns and boles, live and dead	X	X	X		X	X	X	X
Bole volume (live, dead, total)	X	X	X		X	X	X	X
Variance in live tree d.b.h.		X			X	X	X	X
Tree species diversity (count)		X			X	X	X	
Understory								
Moss cover		X	X	X	X		X	X
Forb cover/volume				X			X	
Fern cover/volume				X			X	X
Low shrub cover/volume				X	X		X	X
Med. shrub cover/volume				X	X		X	X
Tall shrub cover/volume				X	X		X	X
Live midstory (4-10cm) deciduous (volume)				X	X		X	X
Fallen trees ≥50cm (volume, percent, presence/absence)	X				X			
Understory diversity index				X	X		X	
Understory conifers (volume)		X		X				X
Total understory volume		X		X	X		X	X

season; Legacy or Timber Forest during the breeding season) and sex would influence spatio-temporal metrics in all models. For each season, I compared two alternative scenarios for the relationships among variables:

1. The number of activity sites is a function of quality (time spent and activity location) and this relationship determines the distance covered, proportion of the night spent in travel, and travel rates. This scenario assumes that site quality is the primary driver of movement patterns and that resource locations are relatively known to the squirrel. I hypothesized that this scenario would hold true for squirrels in the non-breeding season.

2. The number of activity sites and quality of activity sites (time spent or site location) is driven by travel time and distance covered in search of resources. This scenario would support the hypothesis that resource locations are not well known, and the squirrel must spent more effort in finding resources compared to the previous scenario. I hypothesized that this scenario would hold true for the breeding season when squirrels are driven by the need to search for mates in addition to finding food.

Evidence in support of a food driven foraging strategy would include (1) the number of activity sites should decrease as the mean distance between activity sites and dens increases (e.g., central-place foraging); (2) there should be fewer activity sites and less distance moved between activity sites in HIGH forest compared to LOW forest if food quality is higher or food abundance is greater and well distributed; (3) there should be a positive relationship between time spent at activity sites and both travel rates and distances covered between activity sites (e.g., Marginal Value Theorem); and (4) as the amount of time spent at activity site increases, squirrels should use fewer numbers of activity sites.

Evidence in support of a predation-mediated strategy would include (1) as either the number of activity sites increase or the average time spent in activity increases, the average distance between subsequent activity sites should also increase (to reduce the potential that a predator could home in on a new location based on the previous location); (2) as the number of activity sites increase, the relative proportion of canopy-dominated activity sites should increase (more time spent under safe conditions); (3) as the distance between activity sites increases, squirrels should travel at faster rates; and (4) rates of travel should increase as the mean distance between activity sites and dens decreases (to minimize den detection by predators).

Limiting Factors.— I assumed that all four limiting factors (food, predation, dens, and competition) could play a significant role in regulating squirrel populations. However, I predicted that the final model would show strong influences of food and predation, with weaker, but still significant influences of dens and competition given the prevalence of food-limitation hypotheses in the literature and evidence of predation-mediated behaviors found during my radio-telemetry study. Therefore I built a series of 15 single- and multi-factor models that collectively evaluated all combinations of relationships among the four factors. I first built and tested single limiting-factor models

(Models #1 through #4). I then merged final models #1-4 into multi-limiting-factor models. I ran each model twice, once using patch (plot)-level data to predict patch-level MNKA, and again using stand-level data averaged across plots (except for gaps) to predict stand-level MNKA.

For predation, I chose variables that provide structural occlusion (i.e., habitat components that could restrict the ability of a predator to detect squirrels either visually, aurally, or by scent) or could help ward off a direct attack (Table 2). These included stem density of trees (live and dead; horizontal occlusion from the ground to bottom of crowns); crown volume (three-dimensional cover above bare boles); height to crown (vertical influence of crown depth); canopy gaps (horizontal absence of cover); horizontal intercepts at 10 m, 15 m and 20 m above the ground (vertical measures of occlusion at mid-story levels); variance in live tree d.b.h. (vertical cover provided by multi-layered trees); large live trees (full, deep canopies); and percent moss cover (stealth on the forest floor). For food, I chose variables that indirectly measured relative amounts of food resources known to be used by squirrels, including fungi, berry and seed-producing plants, and lichens (Maser et al. 1985, Thysell et al. 1997). These included counts of live conifer trees (associations with mycorrhizal fungi), crown volume (e.g., lichens), counts of large trees (lichens), tree species diversity, large fallen trees; low, medium, and tall shrubs, and deciduous midstory trees. For dens, I chose habitat components indicative of high quality dens, including large snags (≥50 cm d.b.h.), large live trees (≥75 cm d.b.h.), variance in live trees ≥10 cm d.b.h., crown volume, and overstory species diversity.

For competition, I chose biomass of Townsend’s chipmunks and Douglas’ squirrels, along with habitat components associated with either species including forbs, ferns, shrubs (low, medium, and tall), and mid-story and overstory deciduous trees (Smith 1970, Harestad 1991).

Stand-level High-Low Classification.—For my final multivariate analysis, I used mixture modeling to build and test sets of habitat and ecological process predictors that could be used to distinguish between stands supporting HIGH and LOW populations. I chose stand-averaged variables based on the results from linear regression and limiting factor models. I assumed that the best model was the one that could correctly classify the most stands into HIGH or LOW groups with highest probabilities.

CHAPTER THREE—RESULTS

Squirrel Populations

I captured 4,047 individually-marked sciurids 10,776 times during ca. 336,000 trap nights from 1991-2006. This included 1,957 captures of 1,012 flying squirrels, 1,008 captures of 556 Douglas' squirrels, and 7,753 captures of 2,469 Townsend's chipmunks.

In the Puget Trough, flying squirrel populations continued to remain low. By 2004, squirrel abundances were at their lowest levels since these populations crashed in 1995 (0-7 squirrels per stand; mode= 0; Table 3, Figure 4a and 4b). Legacy stands continued to have slightly more individuals than Timber stands, but this was primarily driven by one stand (#101) that supported 7 squirrels in 2005 (Table 3). Douglas' squirrel populations continued to be low and variable throughout the study (Figure 4a). Chipmunk populations, however, continued to increase after 1998 across all stands and were highest in Timber stands treated with variable-density thinning, followed by Timber control stands, and Legacy treated stands (Figure 4b). Increase in chipmunk abundance drove increases in total sciurid biomass after 1998 across all Timber stands and treated Legacy stands (figure 4a and 4b).

Sciurid abundances varied widely across Olympic Peninsula stands; 0-49

Table 3. Northern flying squirrel (*Glaucomys sabrinus*) capture summaries and abundance estimates for 33 stands in 19 forests across Western Washington, 2004-2006. Values reported here are for the trapping session with the highest minimum number known alive (MNKA). ICPUE= unique individuals captured per 100 trap nights; CPUE= captures per 100 trap nights. Both ICPUE and CPUE were corrected for sprung and unavailable traps (Nelson and Clark 1973). *= no recaptures; VDT=variable-density thin stands; C=control stands.

Forest	Stand #	Number of Sessions	Max. MNKA	MMDM	ICPUE	CPUE	Lincoln-Peterson (Chapman)	Darroch (M_t)	Chao (M_t)	Jackknife (M_h)	Chao (M_{th})
Legacy (VDT)	101	3	7	97	0.78	1.55	7	7	13	22	13
Legacy (C)	102	3	7	124	0.76	1.09	12	10	12	12	17
Legacy (VDT)	103	3	1	n/a	0.10	0.10	1	1*	1	1	1
Legacy (C)	104	3	3	97	0.33	0.55	3	3	4	6	7
Legacy (VDT)	201	3	0	n/a	0	0	0	0	0	0	0
Legacy (VDT)	202	3	3	120	0.32	1.07	3	3	3	4	4
Legacy (C)	203	3	2	101	0.21	0.53	2	2	2	2	2
Legacy (C)	204	3	3	n/a	0.31	0.31	3	3*	3	3	3
Timber (C)	301	3	3	121	0.32	0.54	3	3	3	4	3
Timber (VDT)	302	3	3	144	0.34	0.46	3	4	4	5	5
Timber (VDT)	303	3	1	80	0.11	0.22	1	1	1	1	1
Timber (C)	304	3	1	n/a	0.11	0.11	1	1*	1	1	1
Timber (VDT)	401	3	1	n/a	0.12	0.12	1	1*	1	1	1
Timber (C)	402	3	2	n/a	0.23	0.23	2	2*	2	4	2
Timber (VDT)	403	3	1	n/a	0.12	0.12	1	1*	1	1	1
Timber (C)	404	3	2	80	0.23	0.23	2	2*	3	4	2
Rugged Flats	902	2	3	n/a	0.30	0.30	3	3*	5	3	3
Quinault RNA	903	2	2	n/a	0.20	0.20	2	2*	3	4	2
Kalaloch	909	2	24	108	2.56	5.34	26	26	28	30	32
Stequaleho	910	3	28	94	2.94	6.10	32	31	42	49	51
Goodman Ck.	912	1	29	81	3.22	6.32	35	32	33	37	38

Table 3. Continued.

Forest	Stand #	Number of Sessions	Max. MNKA	MMDM	ICPUE	CPUE	Lincoln-Peterson (Chapman)	Darroch (M_t)	Chao (M_t)	Jackknife (M_h)	Chao (M_{th})
La Push	913	1	11	63	1.16	2.75	11	11	12	12	14
Bear Ck.	915	2	6	57	0.61	1.52	6	6	6	7	6
Humptulips	917	2	33	104	3.85	10.86	34	34	37	39	38
Eaton Ck.	944	2	7	135	0.73	1.88	7	7	8	9	8
N.F. Sol Duc	963	1	25	56	2.82	4.41	32	39	38	42	41
N.F. Quinault	969	1	0	n/a	0	0	0	0	0	0	0
Grave’s Ck.	970	1	30	118	3.42	5.36	43	47	49	54	59
Sol Duc Falls	971	1	33	74	3.64	5.52	39	48	50	56	52
Elwha Ranger	974	1	0	n/a	0	0	0	0	0	0	0
Cox Valley	982	1	49	41	5.55	7.92	74	89	80	93	91
Heart O’ Hills	996	1	13	67	1.34	3.60	13	13	13	15	13
Ruby Beach	999	2	12	125	1.39	3.02	12	11	12	12	14

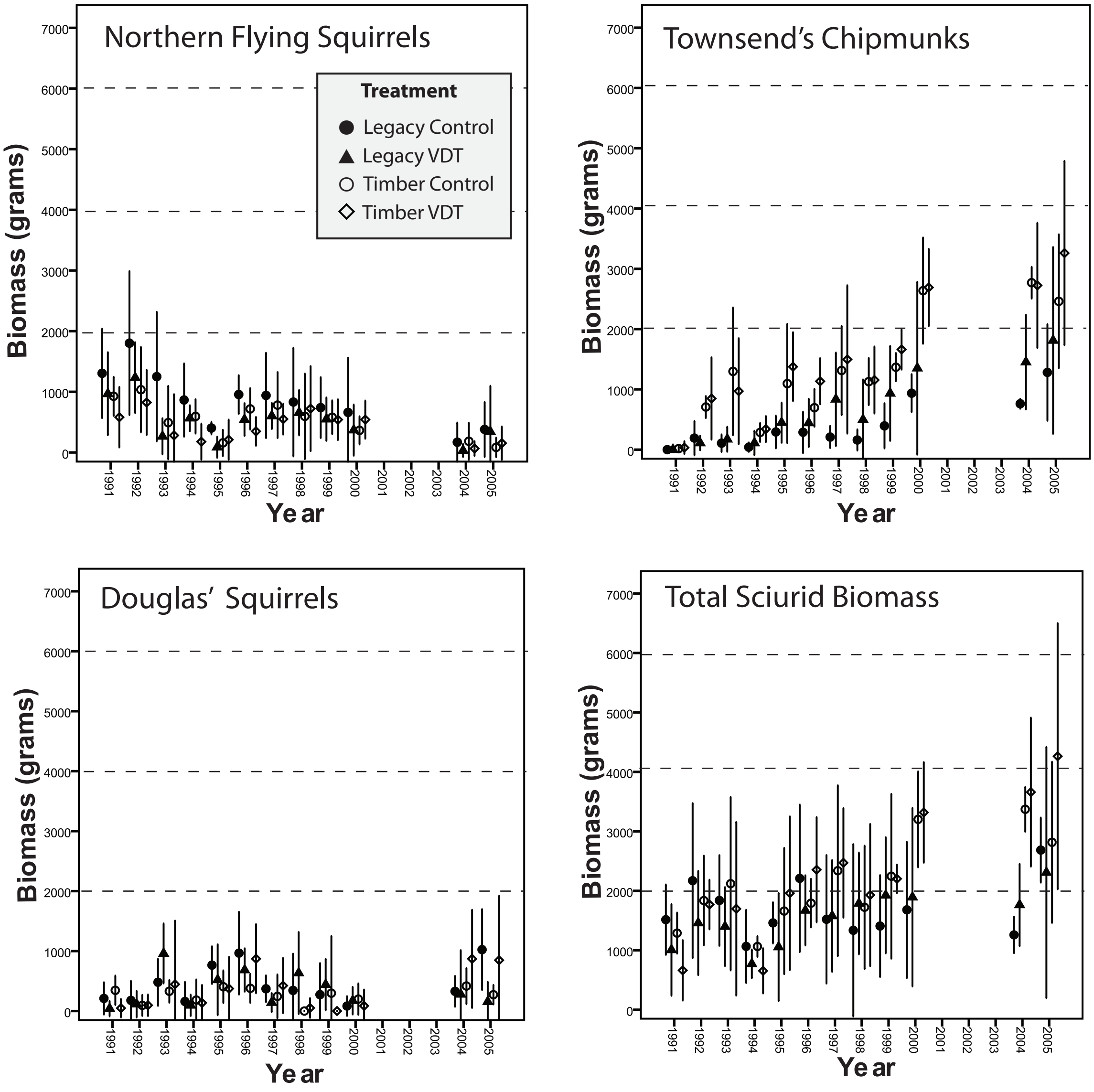


Figure 4a. Biomass of Sciurids across four treatments over 12 fall live-trapping sessions on the Forest Ecosystem Study, western Washington, from 1991-2005. Error bars represent 95% confidence intervals. Data were not collected from 2001-2003. Sample size included 546 northern flying squirrels, 258 Douglas' squirrels, and 1,468 Townsend's chipmunks.

flying squirrels were captured per trapping session per stand (Table 3). Six Olympic Peninsula stands had fewer than 7 individuals captured, including several that were >200 yrs old (Table 3).

Cluster analysis divided all 33 stands into two groups—those that supported

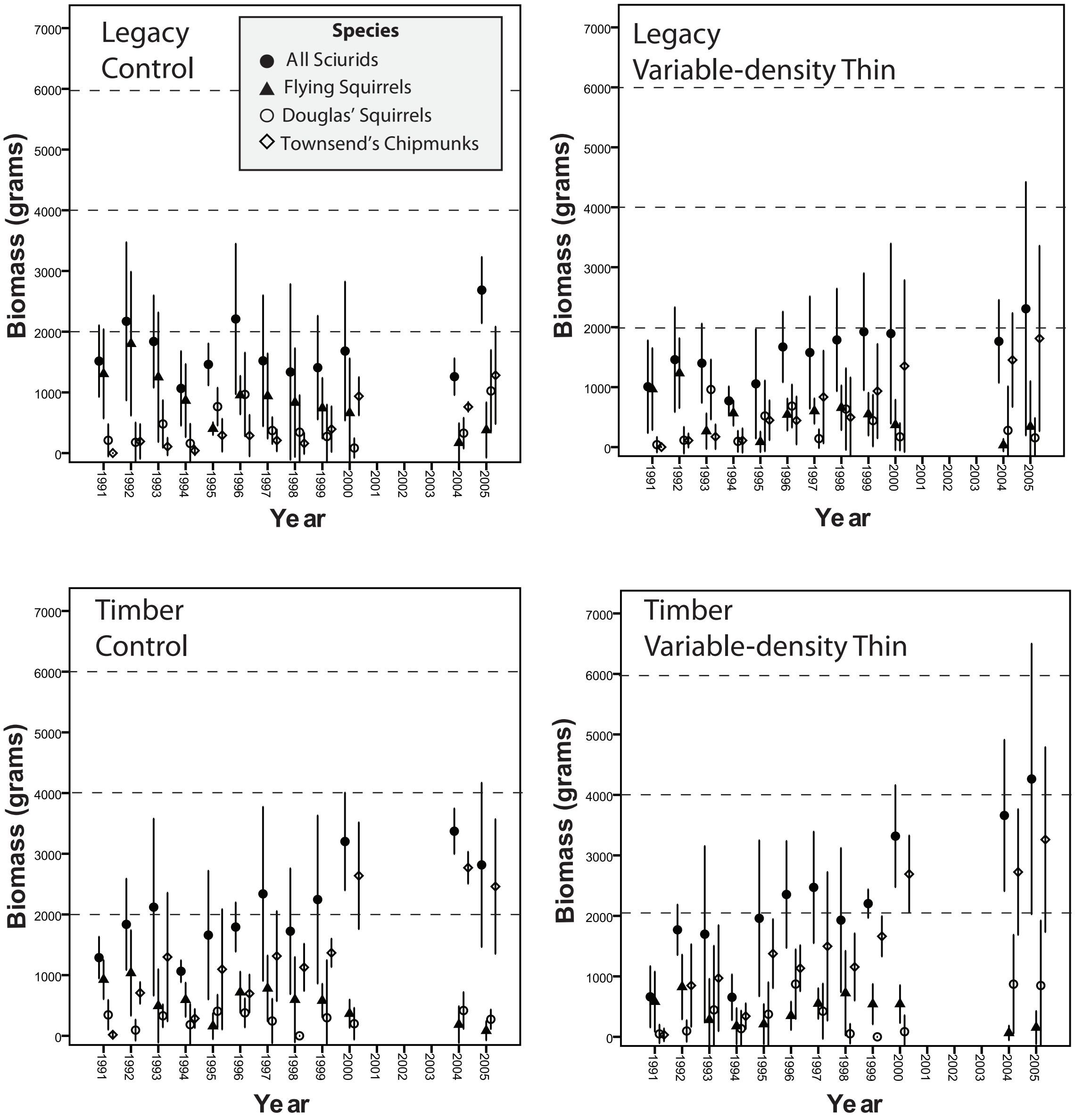


Figure 4b. Biomass of Sciurids across four treatments over 12 fall live-trapping sessions on the Forest Ecosystem Study, western Washington, from 1991-2005. Error bars represent 95% confidence intervals. Data were not collected from 2001-2003. Sample size included 546 northern flying squirrels, 258 Douglas' squirrels, and 1,468 Townsend's chipmunks.

0-15 squirrels/stand (MNKA; ca. <1.1/ha; hereafter, LOW stands) and those that supported 25-49 squirrels/stand (MNKA; ca. >2.0/ha; hereafter, HIGH stands). Eight Olympic Peninsula stands were grouped as HIGH stands, and all other stands were grouped as LOW stands. Classification based on the jackknife estimator put the stand with the highest squirrel abundance (Stand 982) into a separate third group but I considered this estimate to be grossly overinflated, and used only two groups for further HIGH-LOW analyses. Averaging across trapping periods for stands trapped in more than one season would not have changed the composition of stands categorized as either HIGH or LOW groups.

MMDM was highly variable, ranging from 41-118m in HIGH stands and 57-144m in LOW stands (Table 3). MMDM was not available for all stands, as several stands had few or no captures. In addition, several of the MMDMs were based on relatively few individuals ($n<5$) captured at more than one location.

There was a negative, but relatively poor linear fit between flying squirrel biomass and both chipmunk ($r^2=0.07$) and Douglas' squirrel ($r^2=0.03$) biomass across the study sites (Figure 5). Chipmunk biomass varied widely when flying squirrel biomass was low (in part due to positive response of chipmunks to understory development on FES stands) and was generally low or moderate as flying squirrel biomass increased. Douglas' squirrel biomass was relatively low overall, but two stands (#970 and #999; Figure 5), both with high decadence process scores and well-developed shrub layers, supported relatively high biomass. Only one of these (#970) also supported high flying squirrel biomass.

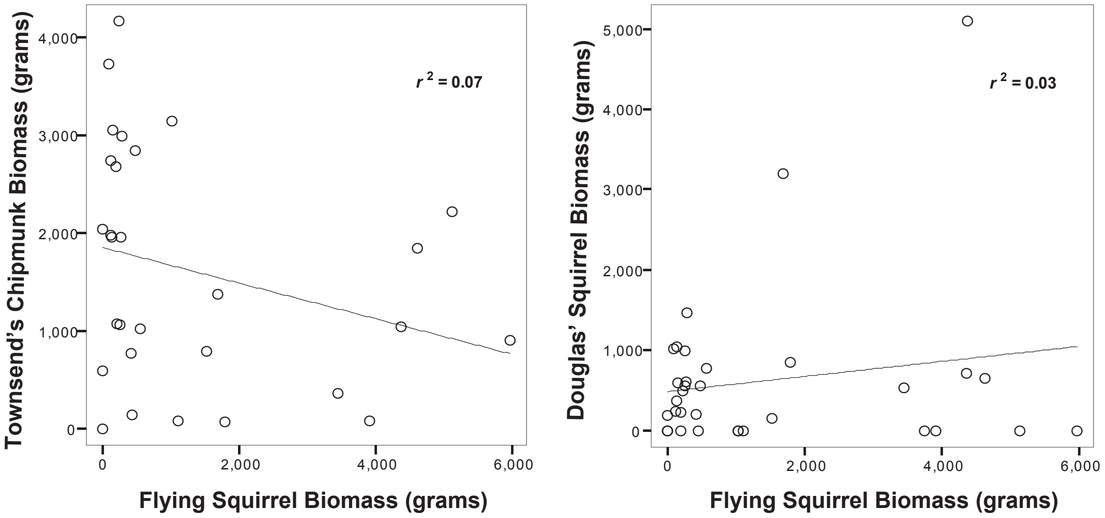


Figure 5. Scatterplots with linear regression lines contrasting northern flying squirrel (*Glaucomys sabrinus*) biomass with biomass of other arboreal rodents for 29-33 stands in western Washington sampled from 2004-2006. Sample size was 348 flying squirrels, 113 Douglas' squirrels, and 617 Townsend's chipmunks.

Movement Patterns and Behaviors

Seventy-one squirrels (35 females, 36 males) were monitored for 480 track-nights (one squirrel per observer per night= 1 track night). Sample size varied by forest and season (Tables 4 and 5). Each individual was monitored from 1-26 times, and tracked outside their den from 1-22 times (mean=5.4; median= 4). Variation in sample size per individual was influenced by mortality, persistence of a few individuals across multiple seasons and years, population size, and transmitter lifespan. For example, squirrel mortality was relatively high in 1994-95 due to predation by both long-tailed weasels and great horned owls, and many radio-collared squirrels were killed in the Legacy and Timber populations before 5 tracks could be obtained within a given session (Wilson and Carey 1996). At the same time, two female

Table 4. Temporal metrics (means ± standard error with sample size in parentheses) for northern flying squirrel (*Glaucomys sabrinus*) movement patterns in western Washington, 1993-2006. Numbers in parentheses below each column heading represent the number of individual squirrels.

	Non-breeding Season (Winter)						**Breeding Season (Summer)**				
	Females			**Males**			**Females**		**Males**		
	Timber Forest (6)	**Legacy Forest (13)**	**High-Density Forests (7)**	**Timber Forest (9)**	**Legacy Forest (11)**	**High-Density Forests (5)**	**Timber Forest 1994 (6)**	**Legacy Forest (10)**	**Timber Forest 1994 (7)**	**Legacy Forest 1994 (4)**	**Legacy Forest 1995 (5)**
Circuit Rate (km/hr) [1]	0.35±0.04 (n=36)	0.27±0.01 (n=72)	0.26±0.03 (n=18)	0.30±0.01 (n=51)	0.30±0.02 (n=58)	0.30±0.03 (n=19)	0.26±0.02 (n=21)	0.25±0.01 (n=52)	0.24±0.03 (n=13)	0.27±0.03 (n=11)	0.51±0.04 (n=33)
Travel Rate (km/hr) [1]	0.55±0.04 (n=36)	0.50±0.03 (n=72)	0.65±0.09 (n=18)	0.49±0.03 (n=51)	0.55±0.04 (n=58)	0.53±0.04 (n=19)	0.42±0.03 (n=21)	0.44±0.02 (n=52)	0.36±0.03 (n=13)	0.42±0.04 (n=11)	0.74±0.04 (n=33)
Sunset to First Movement (minutes) [3]	98.2±7.8 (n=35)	94.1±4.3 (n=72)	110.9±13.4 (n=18)	97.9±13.2 (n=48)	112.4±8.9 (n=58)	92.7±8.4 (n=19)	67.1±7.7 (n=20)	104.8±7.8 (n=52)	85.3±6.4 (n=13)	66.8±6.6 (n=11)	83.3±4.0 (n=33)
Total Track time (minutes)[2]	121.1±10.6 (n=30)	155.2±12.3 (n=63)	102.2±8.0 (n=14)	139.1±9.9 (n=48)	133.9±7.8 (n=45)	112.1±11.4 (n=13)	178.9±14.6 (n=16)	142.9±9.6 (n=42)	165.83±22.4 (n=6)	205.7±5.9 (n=10)	210.4±14.6 (n=27)
Total Travel Time (minutes)[2]	76.7±7.8 (n=30)	97.7±8.1 (n=63)	45.0±4.7 (n=14)	91.2±7.7 (n=48)	86.2±6.7 (n=45)	62.9±6.6 (n=13)	119.8±12.3 (n=16)	82.0±5.6 (n=42)	112.3±20.4 (n=6)	127.2±6.3 (n=10)	139.7±11.1 (n=27)
Segments per hour[1]	6.03±1.56 (n=36)	4.24±0.18 (n=72)	4.38±0.37 (n=18)	5.02±0.38 (n=51)	4.41±0.20 (n=58)	5.08±0.37 (n=19)	3.64±0.44 (n=21)	4.32±0.23 (n=52)	3.12±0.22 (n=13)	3.56±0.30 (n=11)	5.11±0.21 (n=33)
Segments per km[1]	21.13±5.73 (n=36)	16.07±0.62 (n=72)	18.79±1.52 (n=18)	18.02±1.77 (n=51)	16.23±0.88 (n=58)	18.39±1.28 (n=19)	14.55±1.32 (n=21)	17.75±0.88 (n=52)	14.41±1.05 (n=13)	13.69±1.01 (n=11)	12.65±1.18 (n=33)
Activity sites per hour[1]	1.60±0.15 (n=36)	1.58±0.09 (n=72)	2.54±0.18 (n=18)	1.44±0.10 (n=51)	1.77±0.12 (n=58)	2.22±0.21 (n=19)	1.66±0.16 (n=21)	1.91±0.12 (n=52)	1.30±0.20 (n=13)	1.49±0.14 (n=11)	1.86±0.15 (n=33)
Percent of total track time spend in travel[1]	63.3±3.1 (n=36)	62.2±2.3 (n=72)	44.4±4.2 (n=18)	65.4±2.5 (n=51)	58.0±2.4 (n=58)	59.1±4.1 (n=19)	65.1±3.7 (n=21)	59.7±2.4 (n=52)	66.7±5.7 (n=13)	63.4±3.0 (n=11)	67.3±3.1 (n=33)
Percent of total track time on the ground[1]	14.1±2.6 (n=36)	13.0±1.8 (n=72)	13.2±3.0 (n=18)	7.9±1.3 (n=51)	8.9±1.3 (n=58)	11.7±3.2 (n=19)	16.5±2.5 (n=21)	12.9±1.7 (n=52)	16.0±2.8 (n=13)	10.9±3.1 (n=11)	9.6±1.8 (n=33)
Percent of total track time at canopy activity sites[1]	22.6±3.2 (n=36)	24.7±2.5 (n=72)	42.3±4.4 (n=18)	26.7±2.7 (n=51)	33.0±2.9 (n=58)	29.2±4.3 (n=19)	18.5±3.2 (n=21)	27.4±2.6 (n=52)	17.3±5.5 (n=13)	25.7±3.4 (n=11)	23.1±3.2 (n=33)
Percent of total activity time spent at ground-dominated sites[1]	36.6±5.9 (n=36)	40.8±4.6 (n=72)	23.9±5.2 (n=18)	28.0±4.7 (n=51)	28.5±4.4 (n=58)	28.1±7.3 (n=19)	46.8±6.0 (n=21)	33.4±4.4 (n=52)	54.9±10.5 (n=13)	30.7±9.0 (n=11)	32.1±5.8 (n=33)

[1]Based on all tracks; [2]Based on all-night, complete, and 180+ tracks; [3]Based on track originating from den for 1st activity period

Table 5. Spatial metrics (means ± standard error with sample size in parentheses) for northern flying squirrel (*Glaucomys sabrinus*) movement patterns in western Washington, 1993-2006. Numbers in parentheses below each column heading represent the number of individual squirrels being monitored.

	Non-breeding Season (Winter)						Breeding Season (Summer)				
	Females			Males			Females		Males		
	Timber Forest (6)	Legacy Forest (13)	HIGH Forests (7)	Timber Forest (9)	Legacy Forest (11)	HIGH Forests (5)	Timber Forest (6)	Legacy Forest (10)	Timber Forest (7)	Legacy Forest 1994 (4)	Legacy Forest 1995 (5)
Maximum distance moved from the den[1]	230.4±24.7 (n=36)	195.3±9.6 (n=72)	125.7±13.8 (n=18)	246.8±20.1 (n=51)	239.3±19.0 (n=58)	183.1±22.1 (n=19)	236.7±25.9 (n=21)	193.3±11.9 (n=52)	273.9±43.8 (n=13)	324.7±40.3 (n=11)	661.7±69.5 (n=33)
Mean distance between den and all activity sites[1]	184.7±12.9 (n=102)	149.2±4.7 (n=269)	87.2±7.3 (n=77)	207.8±10.8 (n=155)	191.1±9.8 (n=212)	129.7±8.4 (n=78)	159.3±10.1 (n=97)	146.6±5.1 (n=238)	185.9±17.7 (n=44)	192.6±14.8 (n=54)	392.4±23.8 (n=201)
Mean distance between den and first activity site[3]	162.4±23.3 (n=33)	136.2±9.3 (n=69)	87.5±16.9 (n=18)	187.9±19.4 (n=45)	158.7±16.1 (n=56)	108.5±23.4 (n=19)	125.2±14.7 (n=19)	101.2±8.2 (n=48)	123.6±20.0 (n=12)	116.5±21.6 (n=11)	266.8±46.8 (n=33)
Mean travel distance between den and first activity site[3]	255.9±36.6 (n=33)	196.5±18.3 (n=69)	114.9±17.3 (n=18)	229.3±24.3 (n=45)	209.5±23.2 (n=56)	127.5±26.6 (n=19)	175.6±23.9 (n=19)	118.8±9.3 (n=48)	185.7±34.5 (n=12)	155.4±40.2 (n=11)	340.3±60.6 (n=33)
Mean travel distance between subsequent activity sites/night[4]	185.7±23.0 (n=34)	149.0±13.3 (n=72)	77.0±7.8 (n=18)	155.5±11.8 (n=48)	156.0±12.6 (n=58)	114.4±24.5 (n=19)	146.4±18.1 (n=20)	99.9±5.3 (n=49)	152.1±28.2 (n=12)	176.1±35.0 (n=11)	306.6±44.0 (n=33)
Maximum travel distance between subsequent activity sites/night[4]	310.4±32.7 (n=34)	243.0±16.8 (n=72)	141.6±15.7 (n=18)	278.0±21.9 (n=48)	265.7±22.5 (n=58)	197.0±26.8 (n=19)	254.4±28.8 (n=20)	188.9±13.8 (n=49)	275.1±47.3 (n=12)	380.0±68.7 (n=11)	627.5±70.4 (n=33)
Mean distance between all activity sites per season[1]	168.3±23.3 (n=6)	108.6±11.2 (n=16)	66.8±12.1 (n=7)	143.7±13.6 (n=11)	194.9±24.2 (n=11)	115.5±25.9 (n=5)	144.8±14.5 (n=6)	138.2±12.4 (n=12)	112.3±10.4 (n=8)	154.4±21.5 (n=4)	533.2±128.7 (n=4)
Maximum distance between all activity sites per season[1]	435.6±62.7 (n=6)	240.1±29.4 (n=16)	142.4±35.6 (n=7)	330.3±52.4 (n=11)	499.1±59.2 (n=11)	250.0±72.8 (n=5)	329.1±31.0 (n=6)	299.2±37.5 (n=12)	252.4±30.7 (n=8)	411.0±100.2 (n=4)	1688.0±393.5 (n=4)
Total Circuit Distance[2]	643.4±70.2 (n=30)	691.2±54.2 (n=63)	430.7±42.1 (n=14)	670.1±50.7 (n=48)	713,1±58.0 (n=45)	574.6±73.3 (n=13)	775.1±79.7 (n=16)	591.5±42.6 (n=42)	642.8±149.4 (n=6)	913.1±102.0 (n=10)	1771.0±196.7 (n=27)

[1] Based on all tracks; [2] Based on all-night, complete, and 180+ tracks; [3] Based on tracks originating from den. [4] based on all tracks with activity sites.

squirrels on the Legacy Forest persisted through these predation events, one of which lived to be ≥7 years old, and both were monitored over three seasons. Likewise, in January 2006, a pair of nesting barred owls was detected within the core activity areas of the Legacy Forest population, and all but one squirrel was preyed upon within a 4-week period, presumably by these two owls (Appendix).

Of the 480 track nights of monitoring, squirrels left their den and engaged in activity on 384 occasions, and were tracked for 921 hours over a total distance of 277 km. Of the tracks where activity was recorded, 240 were complete (including 31 tracks during all night monitoring), 88 were recorded as 180+, and 56 were incomplete. A total of 254 tracks were recorded during the non-breeding season and 130 tracks during the breeding season. Over two-thirds of the 180+ tracks (57 of 88) occurred during the breeding season. Squirrels remained in their dens (e.g., no movement outside the den) on 96 track-nights. Most no-movement nights (92 of 96) occurred during the winter non-breeding season.

Temporal Metrics

Squirrels usually left their dens between 1-2 hrs after sunset during both the breeding and non-breeding season (Table 4). There were no apparent differences in leave time between sexes or among forests. Average leave time was slightly earlier during the breeding season (88.26 ± 3.8 minutes) than during the non-breeding season (100.3 ± 3.8 minutes). Leave time ranged from 18 minutes after sunset to almost 11 hours after sunset—both extremes occurred during the non-breeding season.

During all-night tracks (n=26), 22 squirrels had 1 activity period, 3 squirrels had 2 activity periods, and 1 squirrel had 3 activity periods. All squirrels left their dens during all-night tracks and stayed active an average of 248.5 (± 41.6 SE) minutes during the breeding season and 179.0 (± 31.6 SE) during the non-breeding season.

Overall, squirrel activity periods outside the den ranged from as little as 2 minutes during the non-breeding season, to as long as 593 minutes during the breeding season (Table 4, Figure 6). Mean activity duration was 116.6 (± 4.0 SE) minutes during the non-breeding season and 166.1 (± 5.5 SE) during the breeding season, with both sexes spending considerably more time out of the den during the breeding season. Of the eighty-six 180+ tracks (where observers stopped tracking after 3 hours), fifty-seven were during the breeding season (44% of the total breeding season tracks) and 29 were during the non-breeding season (11% of the total non-breeding tracks). Thus, the average amount of time spent out of the den during the breeding season was likely much higher than reported here (Figure 6). However, the tracking protocol appeared to capture most of the primary activity period during the non-breeding season (Figure 6).

Squirrels spent most of their time in the canopy, with 40% of their time in canopy-associated travel, 43% of their time at canopy-dominated activity sites, and only 17% of their total time out of the den spent at ground-

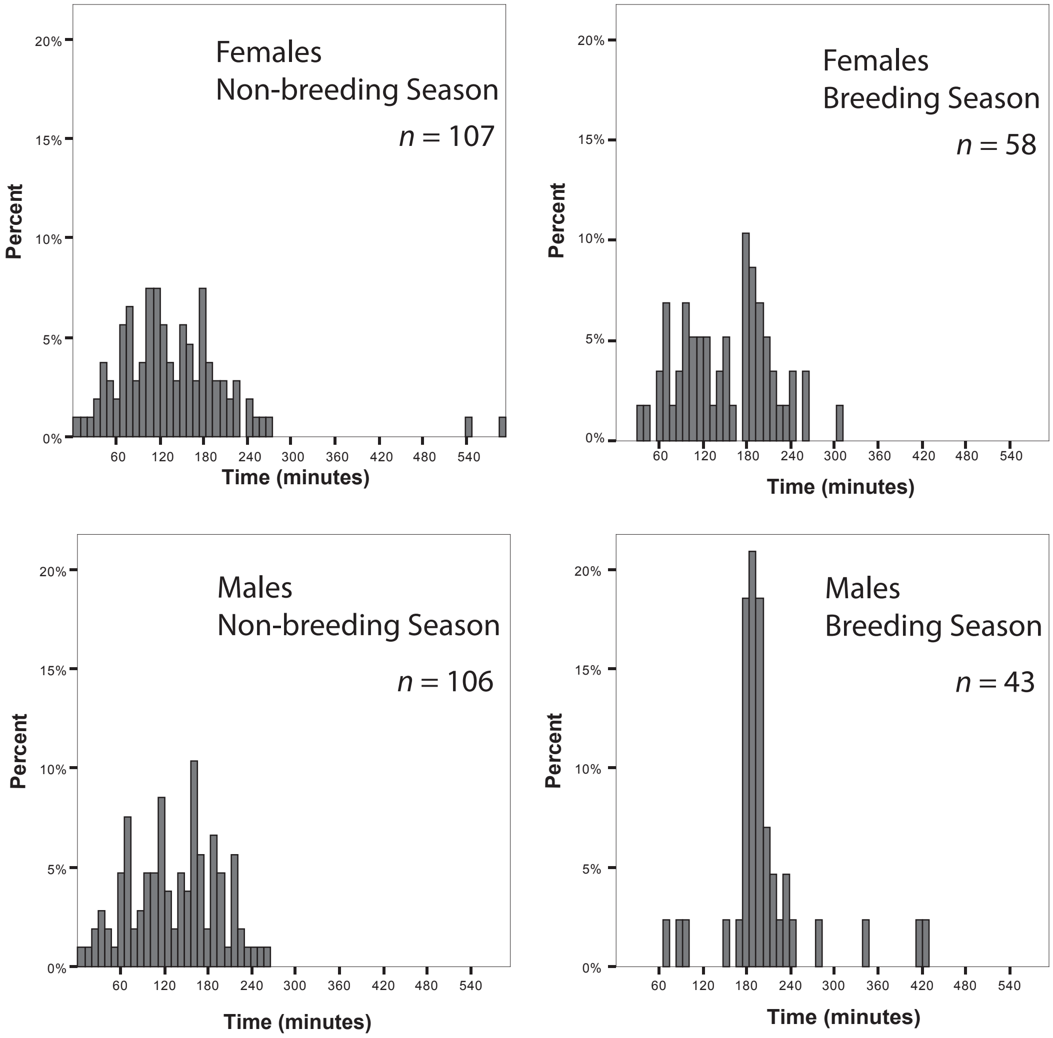


Figure 6. Histogram of the total time spent out of the den during the first activity period at night for radio-collared northern flying squirrels (*Glaucomys sabrinus*) in western Washington from 1993-2006. Spikes near 180 minutes were an artifact of the monitoring protocol which limited tracking to 3 hours on several occasions. Sample size is total number of tracks and includes complete tracks, 180+ tracks, and first activity periods for all-night tracks.

dominated activity sites. Lowest travel rates were observed in the HIGH Forests (Table 4). Travel rates were generally higher during the non-breeding season, except for high travel rates by Legacy Forest males in 1995 during the breeding season compared to both the prior breeding season in 1994 and during the non-breeding season. Legacy and Timber Forest males travelled at similar rates during the breeding season in 1994. The least amount of time spent on the ground was observed for breeding males in the Legacy Forest in 1995 and the most by breeding males and females in the Timber Forest in 1994 (Table 4). Squirrels spent an average of 13.7±0.3 minutes at each activity site with more time spent at sites where canopy activity was the primary activity (Legacy Forest, 15.2±0.6 minutes; Timber Forest 17.9±1.0 and HIGH Forests, 13.6±1.1 minutes) than at sites where ground activity was the primary activity (Legacy Forest, 10.6±0.3 minutes; Timber Forest, 10.5±0.4 minutes; HIGH Forests, 9.9±0.7 minutes). There were no significant differences between sexes or between the breeding and non-breeding season.

Spatial Metrics

Squirrels traveled in circuits ranging from 15m to 5,339m during the study (Table 5). Mean maximum distance moved from the den during the non-breeding season averaged 195-239m in the Legacy Forest, 230-247m in the Timber Forest and 126-183m in the HIGH Forests (Table 5). Centers of activity outside the den were distinctly separate from den locations and averaged 149-191m from the den in the Legacy Forest and 185-208m in the Timber Forest, but only 87-130m in the HIGH forests during the non-breeding season (Table 5). As a result, squirrels spent up to 43% more movement time in travel relative to total time out of the den in the Legacy and Timber Forests compared to the HIGH forests, and this was reflected in increased circuit distances, distances moved between subsequent activity sites for a given night, and distances between all activity sites during a season (Table 5). Distances moved within forests during the non-breeding season appeared similar for both sexes on a nightly-basis, but males generally covered larger distances when mean and maximum distances between all activity sites for each individual were averaged over a season (Table 5; Figure 6).

During the breeding season, females exhibited similar spatial patterns to those exhibited during the non-breeding season (Table 5; Figure 7). In contrast, males would use similar activity sites to those used during the non-breeding season, but would also make wide forays outside their typical activity site areas, travelling circuit distances up to >5 km (Table 5; Figure 7). This behavior and spatial pattern change appeared to be searches for breeding females as sharp intermittent deviations from an otherwise elliptical circuit often brought males to radio-collared females. Male breeding behavior changed from 1994 to 1995, with circuit distance and mean maximum distance from the den almost twice as high in 1995 as it was in 1994 for the Legacy Forest (Table 5). This suggested that the peak of the breeding season varied from year to year. Males would always initiate a breeding circuit first, and then travel back to their core activity areas before returning to their den, suggesting that breeding behavior took priority over foraging behavior during this season.

Circuit path overlap between two or more squirrels being monitored simultaneously on the same evening occurred on only 29 of 384 occasions (7.6% of total tracks). Of these, 17 overlaps occurred during the breeding

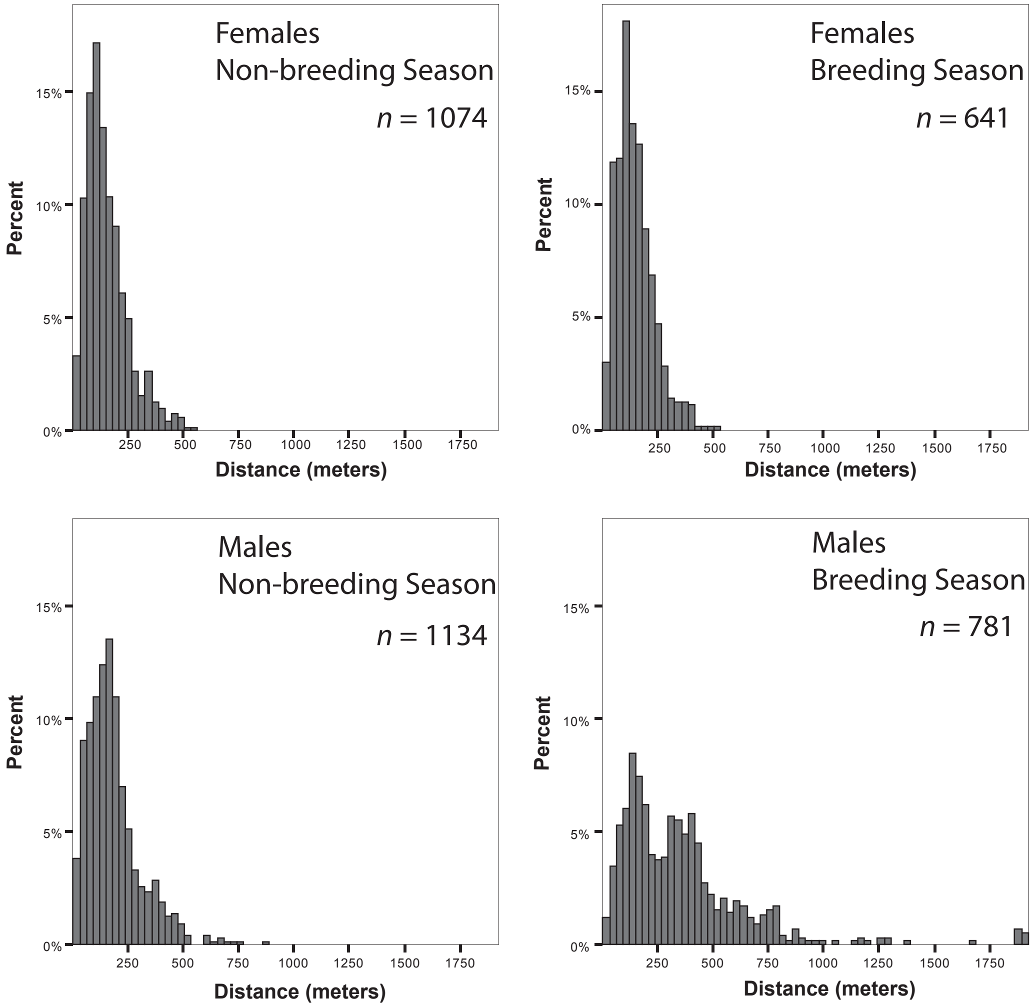


Figure 7. Histogram of distance to den for all activity sites and travel points measured during radio-telemetry studies of northern flying squirrels (*Glaucomys sabrinus*) in western Washington from 1993-2006. Sample size is total number of activity sites and travel points collected during 384 track-nights where squirrels engaged in activity outside of the den.

season and 12 during the non-breeding season. All non-breeding overlap occurred among den mates (either sex). Breeding season overlaps included den mates (either sex) and males residing in different dens. Numbers of nightly overlaps are likely much higher than reported here because only a small subset of squirrels was being monitored in each forest on a given night. However, technicians occasionally had time to passively monitor radio frequencies of non-target squirrels while tracking a squirrel, and often noted that other radio-collared squirrels were in proximity to the squirrel being monitored, especially during the breeding season on the FES and during the non-breeding season in the HIGH forest (unpublished data; Appendix).

Squirrels appeared relatively consistent in their use of the same general foraging areas over time. On 27 occasions where individual squirrels were monitored during more than one non-breeding session, the average shift in distance between the center of core foraging areas for subsequent sessions was 79.0m±10.8 SE for 12 females and 67.5±12.8m for 8 males, both well within the maximum distance moved among activity sites within a night (Table 5; Appendix).

Activity Sites

A total of 1,490 activity sites were recorded during the study, including 954 sites on the Legacy Forest, 385 on the Timber Forest, and 151 on the two HIGH forests. Of these, some level of ground activity occurred on 50% of the sites (46% during the non-breeding season and 55% during the breeding season), and 66% of sites had some level of canopy activity (71% during the non-breeding season and 60% during the breeding season). Of sites where some level of ground activity occurred, ground activity was the predominant activity 77% of the time (74% during the non-breeding season and 80% during the breeding season). For activity sites where some level of canopy activity occurred, canopy activity was predominant 93% of the time, and consistent in both seasons.

Vegetation was measured on the Legacy and Timber forests at 1019 activity sites and 280 control plots (Legacy=160; Timber Forest=120) based on the total area in each forest where squirrel activity took place.   On the Legacy Forest during the non-breeding season, squirrels used sites with less cover in the 0-0.5m strata than was found on control sites (Table 6). In addition, they also used sites with more cover in the 0.5-2.0m strata for activity sites where squirrels spent some or all of their time on the ground compared to control sites. On the Timber Forest during the non-breeding season, there were no differences between control sites and activity sites where squirrels spent activity on the ground. However, there was less cover in the 0-0.5m strata and more cover in the overstory canopy compared to control sites for sites where squirrels spent some or all of their time in the canopy (Table 6).

During the breeding season, squirrels used activity sites with significantly higher cover in the understory and midstory layer above 2.0m and in overstory layer in both forests, regardless of whether activity took place on the ground or in the canopy (Table 6).   There were no significant relationships between activity sites and both the 0-0.5m strata and 0.5-2.0m strata.

Table 6. Mean percent cover of vascular plant layers (±S.E.) by stratum for the Legacy and Timber forest activity sites and control plots, 1993-1996 for northern flying squirrel (*Glaucomys sabrinus*) activity sites. Bold numerals indicate significant (*P* <0.05) differences between controls and activity sites within forests for a given life form strata based on three non-parametric tests for two independent samples.

	Legacy Forest[a]		**Timber Forest**[b]	
	Ground-Dominated Activity	**Canopy-Dominated Activity**	**Ground-Dominated Activity**	**Canopy-Dominated Activity**
Non-breeding Season	(*n*=132)	(*n*=170)	(*n*=76)	(*n*=128)
0-0.5m Understory Strata	**7.4±1.1**	**8.0±1.1**	26.8±2.7	**19.5±1.8**
0.5-2.0m Understory Strata	**22.7±1.7**	20.8±1.4	33.9±2.8	37.5±2.1
>2.0m Understory/ Midstory Strata	**2.1±0.6**	1.6±0.3	7.9±1.7	4.6±0.6
Overstory Canopy	56.6±1.3	60.4±0.8	37.1±2.5	**52.3±1.5**
Breeding Season	(*n*=159)	(*n*=234)	(*n*=74)	(*n*=40)
0-0.5m Understory Strata	13.8±1.2	13.4±0.9	25.9±2.7	27.5±3.6
0.5-2.0m Understory Strata	21.3±1.4	18.9±1.0	38.8±2.8	32.3±4.0
>2.0m Understory/ Midstory Strata	**5.1±0.7**	**3.8±0.4**	**12.51±1.5**	**12.6±2.8**
Overstory Canopy	**61.0±0.9**	**63.2±0.3**	**52.9±2.1**	**56.5±2.5**

[a] Percent cover of Legacy Forest control plots (n=160): ground cover (14.5±1.2), low understory (16.4±1.0), midstory (1.4±0.2), overstory (54.6±1.4).

[b] Percent cover of Timber Forest control plots (n=120): ground cover (27.6±1.8), low understory (29.4±1.8), midstory (4.4±1.0), overstory (43.2±2.1)

Univariate Habitat Predictors

Ecological Processes

There was a relatively strong linear relationship between nominal stand ages and total structural processes scores ($r^2 = 0.73$). Contributions to this fit were primarily driven by canopy stratification ($r^2 = 0.88$) and, to a lesser extent, decadence ($r^2 = 0.52$). There was virtually no linear fit for crown-class differentiation ($r^2 = .02$) or understory development ($r^2 < 0.01$).

Linear relationships between ecological process scores and squirrel abundance were positive but moderate, with crown-class differentiation and canopy stratification showing the strongest positive relationship ($r^2 = 0.24$), followed by decadence ($r^2 = 0.15$; Figure 8). There was a negative relationship between abundance and understory development ($r^2 = 0.25$; Figure 8). HIGH stands generally had moderately-high scores for crown-class differentiation (7.4±0.8 SE) and decadence (6.0±1.2 SE), median scores for canopy stratification (5.2±0.9 SE) and lower scores for understory development (3.9±0.9 SE; Table 1). In contrast, LOW stands had moderately-high scores for understory development (5.8±0.5 SE), median scores for crown-class differentiation (5.0±0.4 SE) and low scores for decadence (3.2±0.6 SE) and canopy stratification (1.8±0.5 SE).

Overstory and Canopy Gaps

Highest stand-level univariate predictors of MNKA included positive

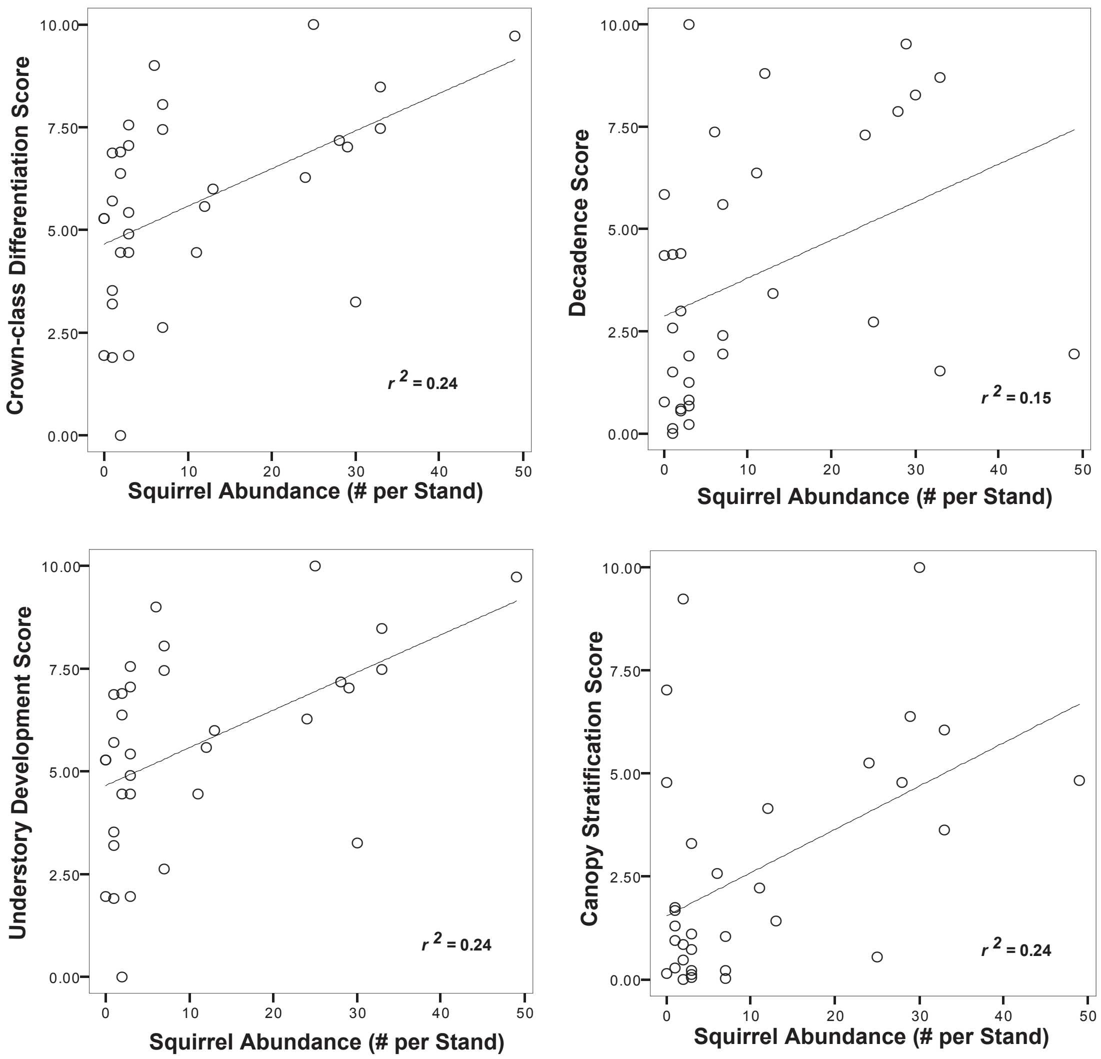


Figure 8. Scatterplots with linear regression lines contrasting northern flying squirrel (*Glaucomys sabrinus*) abundance (mean number known alive) with measures of ecological process scores for 33 stands in western Washington in 2005-2006.

associations with basal area of live trees (r^2 = 0.50; HIGH=78.7±6.8 m^2/ha; LOW= 47.4±3.3 m^2/ha), counts of large live trees (r^2 = 0.46; HIGH= 55.5± 10.3 per ha; LOW= 21.4±3.8 per ha), volume of live tree boles (r^2=0.37; HIGH= 1,558±150 m^3/ha; LOW=934±85 m^3/ha), density of large snags (r^2 = 0.38; HIGH=25.0±3.5/ ha; LOW= 9.0±1.8/ha), basal area of large snags (r^2 =0.29; HIGH=14.4±2.5 m^2/ha; LOW= 5.2±1.1 m^2/ha), crown volume (r^2 = 0.37; HIGH= 69,605±5,354 m^3/ha; LOW=36,516±3,989

Table 7. Rank order of 8 stands with high abundances of flying squirrels (*Glaucomys sabrinus*) relative to 33 stands sampled in western Washington for select habitat components in the overstory and midstory forest layers. See text for definitions of specific habitat components.

Stand	**MNKA**	**Large Live Trees (density)**	**Large Snags (density)**	**Trees≥10 cm d.b.h. (Basal Area)**	**Variance in Live Tree d.b.h.**	**Lack of 100m^2 Canopy Gaps**	**Crown Volume**	**Crown Ratio**	**10-m area intercept**	**15-m area interecept**	**20-m area intercept**
982	49	1	5	1	8	2	5	13	11	14	14
917	33	11	4	13	11	7	3	5	1	1	7
971	33	3	16	7	6	4	6	7	6	8	12
970	30	13	6	9	1	27	2	1	7	2	4
912	5	5	2	2	5	11	12	12	8	11	3
910	6	2	1	6	9	9	4	8	3	3	6
963	7	20	15	14	24	1	15	19	25	10	11
909	8	7	9	8	7	15	7	3	2	4	2

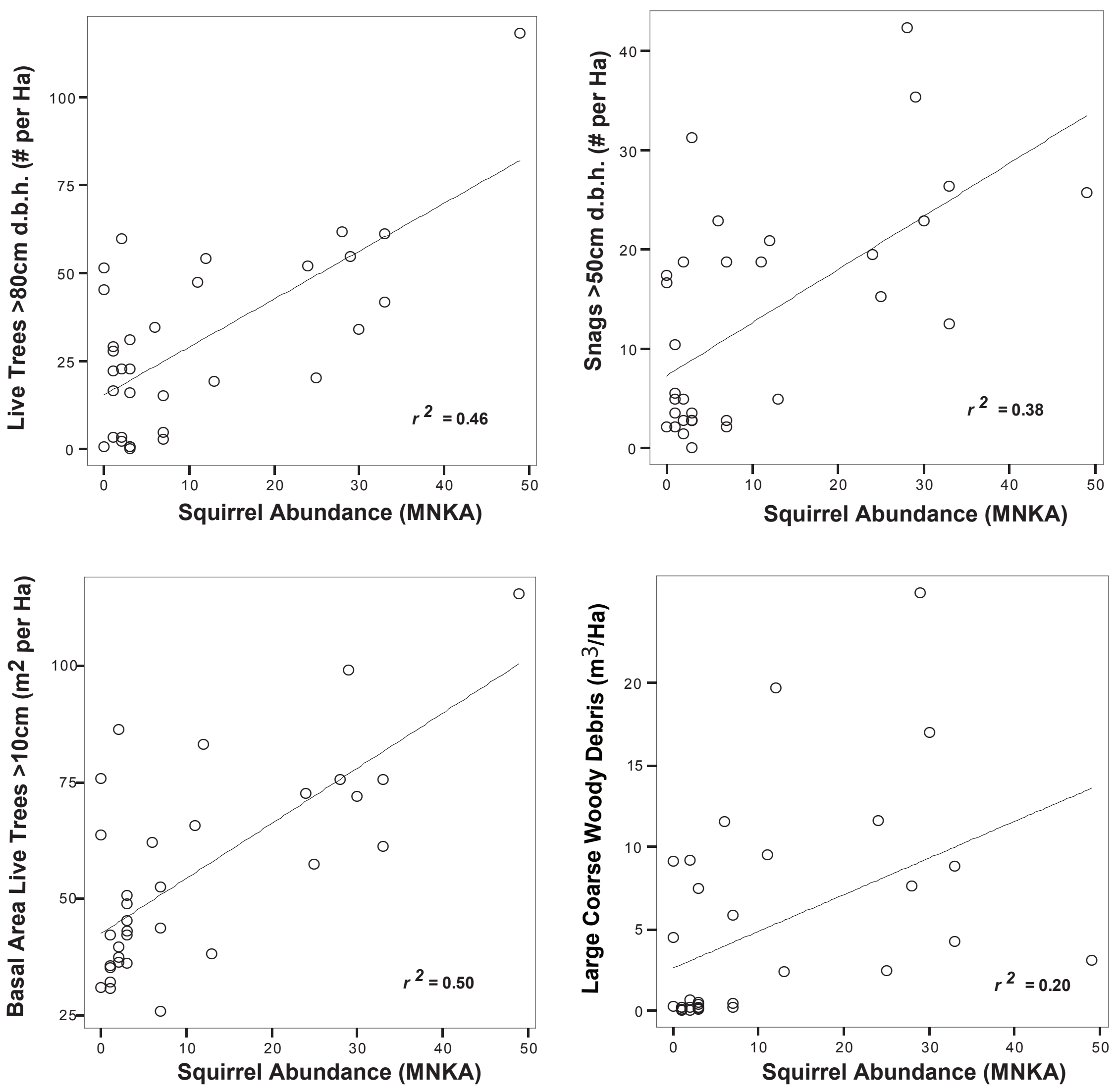


Figure 9a. Scatterplots with linear regression lines contrasting northern flying squirrel (*Glaucomys sabrinus*) abundance (mean number known alive) with measures of select habitat components for 33 stands in western Washington in 2005-2006.

m^3/ha), and overstory species diversity (r^2 =0.23; Table 7; Figure 9a, 9b). A negative relationships was found with height to live crown (r^2 = 0.33; HIGH=14.1±0.8m; LOW= 20.9±1.0m). Poor relationships were found with counts of all snags >10cm d.b.h. (r^2 = 0.04; HIGH=46.8±1.1 per ha; LOW= 40.1±3.2 per ha) and basal area of deciduous trees (r^2 = 0.06; HIGH= 78.7±6.8 m^2/ha; LOW=47.4±3.3 m^2/ha).

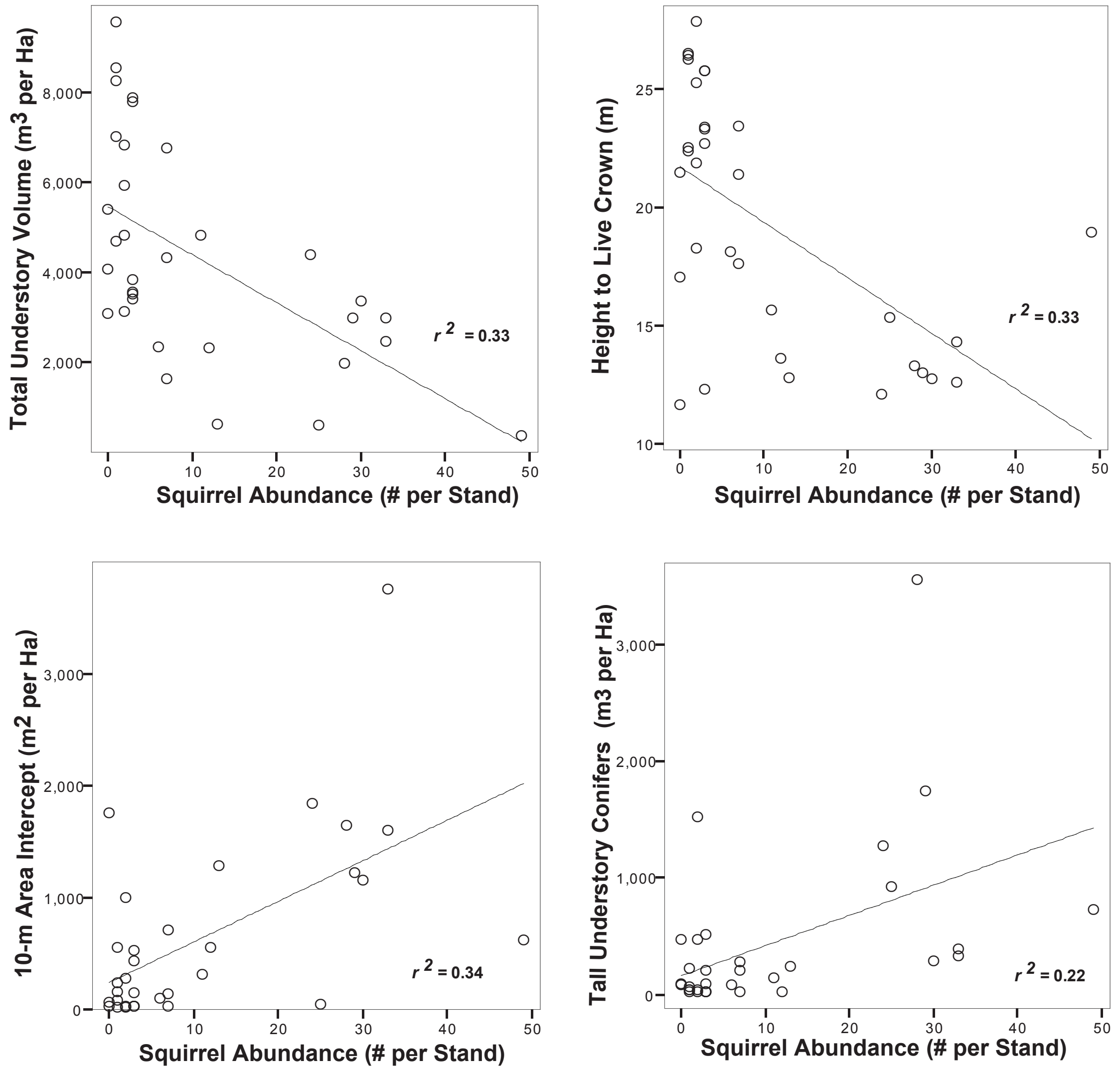


Figure 9b. Scatterplots with linear regression lines contrasting northern flying squirrel (*Glaucomys sabrinus*) abundance (mean number known alive) with measures of select habitat components for 33 stands in western Washington in 2005-2006.

An S-curve regression line was the best fit for the association between cumulative MNKA and both percent gaps ≥100m^2 across the stand and percent gaps ≥400m^2 for Puget Trough stands (Figure 10). There was a sharp drop in cumulative abundance when stand-level gaps ≥100m^2 reached 15% and when gaps ≥400m^2 reached 5% suggesting possible maximum

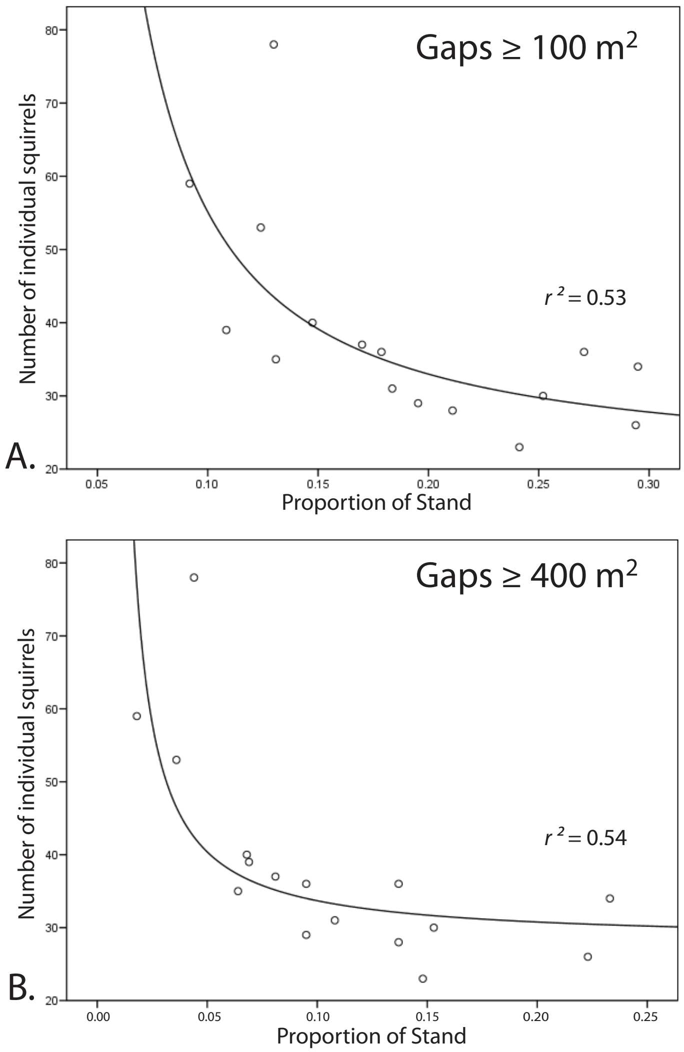


Figure 10.--Scatter plots with S-curve regression lines contrasting cumulative MNKA (mean number known alive) for northern flying squirrels (*Glaucomys sabrinus*) against the total proportion of stand-level canopy gaps (A) ≥100m² and (B) ≥400m² for16 stands in the Puget Trough, Washington from 1993-2005.

gap thresholds for the ability of these stands to support markedly different squirrel abundances over a 14-year period (Figure 10).

Across all 33 stands, there was a moderate negative relationship between percent of stand-level gaps and MNKA (r^2= 0.18; HIGH= 13.0±3.0%; LOW= 19.3±1.4%). This relationship improved when using only non-creek gaps

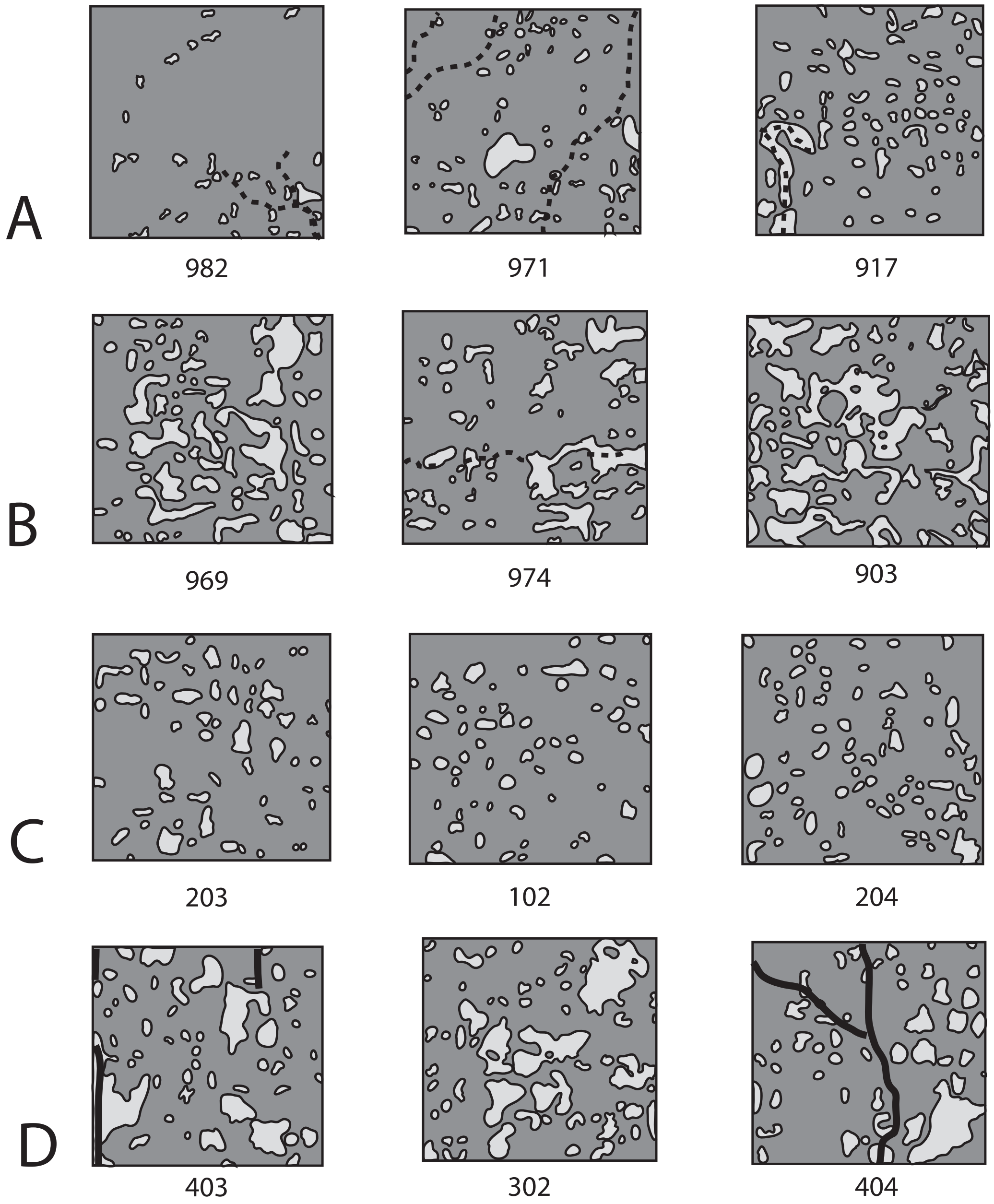


Figure 11. Stand-level maps showing canopy gaps ≥100m^2 for the three stands with (A) highest and (B) lowest squirrel abundances for natural stands on the Olympic Peninsula (gaps resulting primarily from wind and various diseases), and (C) highest and (D) lowest squirrel abundances on managed stands in the Puget Trough (gaps resulting primarily from root rot and root-rot treatments). Canopy gaps are represented by white areas, solid lines represent small streams, and dashed lines represent secondary (dirt) roads. Abundances based on the highest MNKA (mean number known alive) for Olympic Peninsula stands 2005-2006 and cumulative MNKA for Puget Trough stands 1993-2006. Each square represents 10.24 ha (320m each side). Maximum gap size= 7,500m^2.

($r^2 = 0.27$; HIGH= 10.4±2.0%; LOW= 18.8±1.5%) and I therefore used non-creek gaps for all further analyses, except as a measure of crown-class differentiation. In general, HIGH stands had either few gaps, few large gaps (>400m^2), or small gaps whereas LOW stands contained large gaps or a higher percent area in gaps (Figure 11).

Understory and Midstory

Positive relationships with abundance was observed for moss cover ($r^2 = 0.33$; HIGH= 41.0±8.9%; LOW= 14.0±3.2%), and volume of large fallen trees ($r^2 = 0.23$; HIGH=10.0±2.8 m^3/ha; LOW= 3.3±1.0 m^3/ha), with a weaker relationship for smaller understory conifers ($r^2 = 0.13$; HIGH=119±25 m^3/ha; LOW= 83±25 m^3/ha; Figure 9a, 9b). In contrast, squirrel abundance declined with increase in total understory volume ($r^2 = 0.33$; HIGH= 2,400 ± 483 m^3/ha; LOW= 4,968 ± 470 m^3/ha), cover of ferns ($r^2 = 0.17$;HIGH= 15.3 ± 4.6%; LOW= 26.3 ± 3.7%), low shrub cover ($r^2 = 0.23$; HIGH= 23.2 ± 7.2%; LOW= 56.4 ± 5.9%) and tall shrub volume ($r^2 = 0.26$; HIGH= 145±81 m^3/ha; LOW= 561±119 m^3/ha). There were poor linear relationships with both cover and volume of forbs and medium shrubs ($r^2 = 0.01$).

There was a positive relationships between squirrel abundance and volume of tall understory conifer trees (e.g., 4-10cm d.b.h.; $r^2 = 0.35$; HIGH=1,156±386 m^2/ha; LOW=202±63 m^2/ha) and 10-m ($r^2 = 0.36$; HIGH=1,487±386 m^2/ha; LOW=342±89 m^2/ha), 15-m ($r^2 = 0.34$; HIGH=2,775±448 m^2/ha; LOW=705±201 m^2/ha), and 20-m ($r^2 = 0.27$;

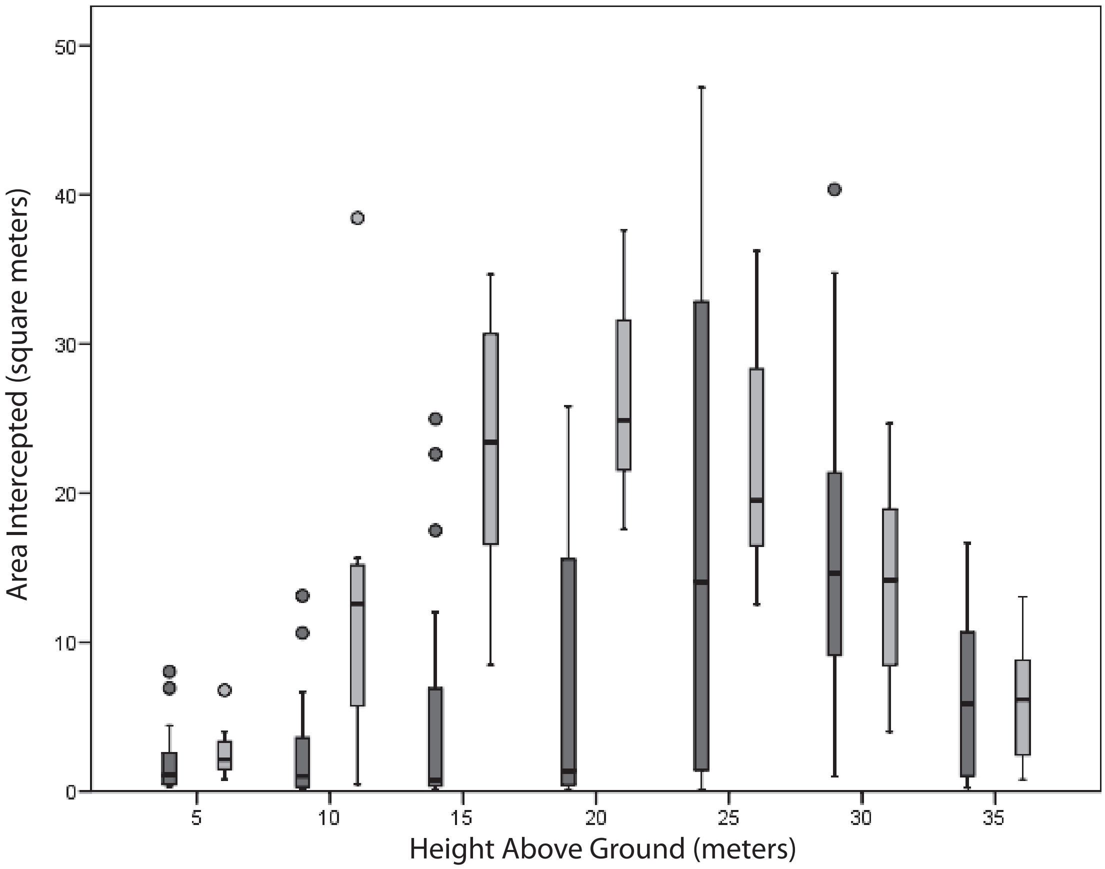


Figure 12. Amount of forest structure (live and dead tree boles and live-tree canopies) intercepted by horizontal planes at various heights above the forest floor for forests supporting low (dark) and high (light) quality habitat for northern flying squirrels (*Glaucomys sabrinus*) across western Washington.

HIGH=3,217±336 m^2/ha; LOW=1,158±365 m^2/ha) intercepts (Figure 9b; Figure 12). Structural components intercepted at these height layers for HIGH stands included deep crowns of overstory trees, smaller crowns of midstory and tall understory shade-tolerant trees, and tree boles. Most LOW stands had only boles intercepted at these height layers. There were no significant differences at 5 meters above ground, where small mid-story conifers and tall deciduous shrubs were present, nor at 25 meters or above, where the intercept of canopies of dominant trees in younger forests or patches of young trees in older forest began.

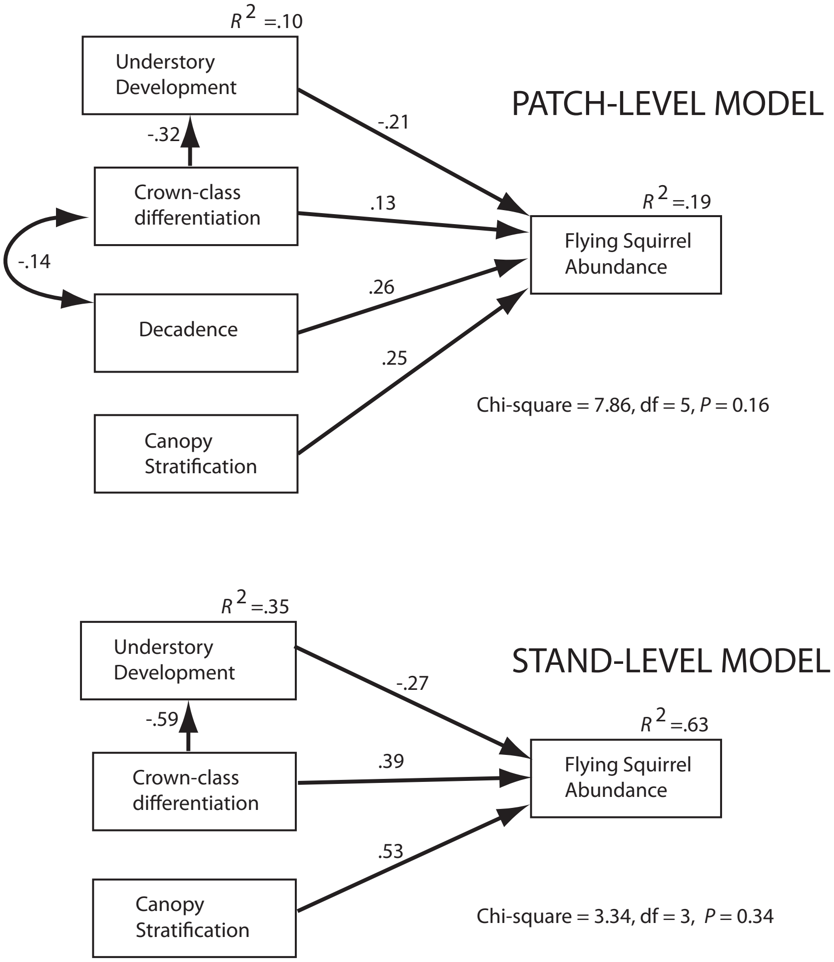


Figure 13. Final SEM models showing significant pathways among forest structuring process scores and stand-level flying squirrel (*Glaucomys sabrinus*) abundance (minimum number known alive) using both patch (*n*=297) and stand (*n*=33) level data for 33 stands in western Washington sampled for squirrel populations from 2004-2006. Values represent standardized estimates.

Multivariate SEM Relationships

Ecological Processes

All four ecological processes showed significant relationships with squirrel MNKA when using patch-level data to predict patch-level MNKA, but only three (understory development, crown-class differentiation, and canopy stratification) were important when averaging across patches to predict

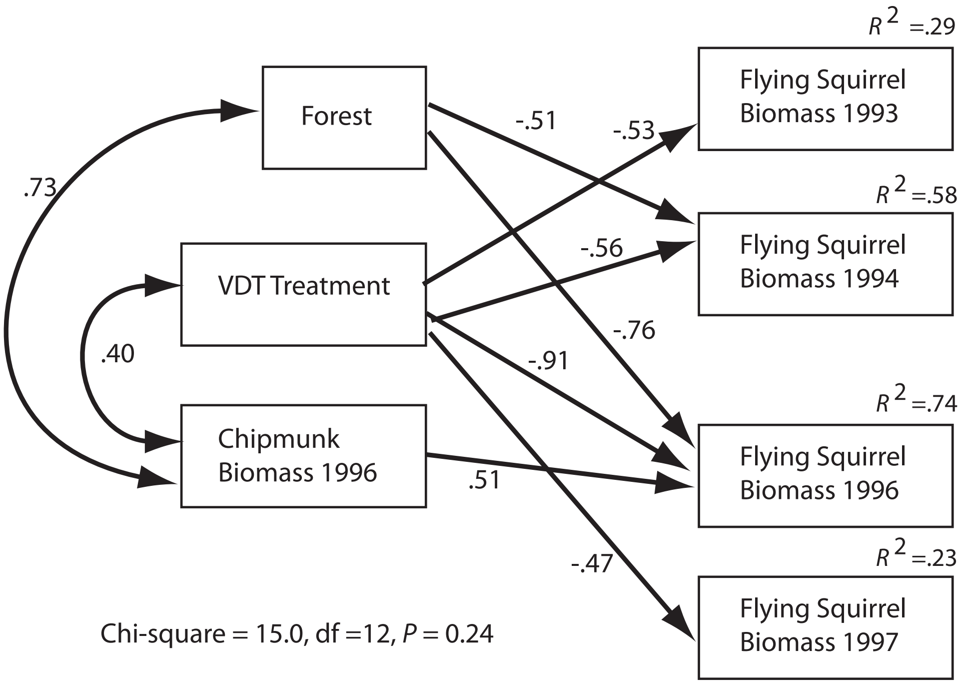


Figure 14. Final structural equation model showing significant pathways among flying squirrel biomass, competitor biomass, forest, and variable-density thinning (VDT) treatment for the Forest Ecosystem Study from 1993-2005. Values represent standardized estimates.

stand-level MNKA (Figure 13). Both models suggested adequate fit with my data (patch model, *P* =0.16; stand model, *P* =0.34) but using stand-averaged data was much better at explaining variance in MNKA than using patch-level data. Strongest predictors in both models included a positive relationship with canopy stratification scores and a negative relationship with understory development scores. As predicted, there was also a significant negative pathway from crown-class differentiation to understory development (γ = -0.27) as fewer and smaller canopy gaps decreased the amount of understory development.

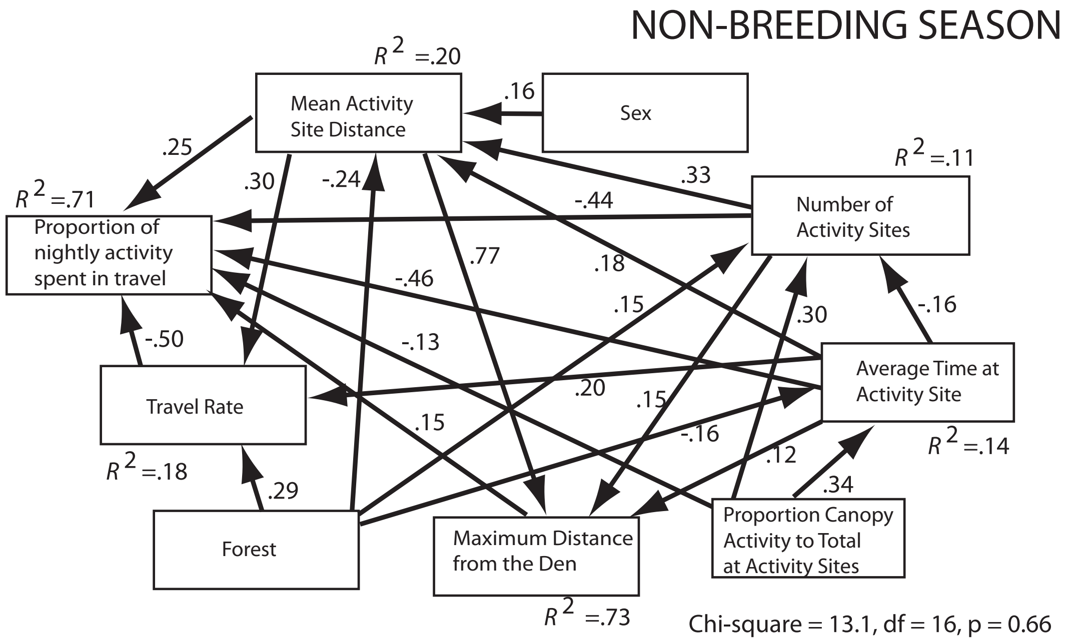
Time Series Model on the FES

My final model suggested that neither Douglas' squirrel nor Townsend's chipmunk biomass had significant negative influence on flying squirrel biomass (Figure 14). The only path found significant for either species was a positive one ($\gamma = 0.51$) for chipmunk biomass on flying squirrel biomass in 1996. Variable-density thinning had a negative effect on flying squirrel populations during four out of the first five years following treatment, but not significantly so after that period. Likewise, there was an additional significant forest interaction with thinning during 1994 and 1996, but not beyond that point. This supported the conclusion that squirrels recovered from the short-term effects of thinning within 3-4 years post-thinning as reported by Carey (2001). It also suggested no subsequent relationships between flying squirrel abundances and competitors, forest or treatment occurred after 1996. There were also no significant relationships (modeled as either direct paths or covariances) between consecutive years for flying squirrel biomass. Modification indices suggested improvements to the model could be made by covarying flying squirrel biomass between some non-consecutive years, but I found no ecological rationale for making such multi-year connections as squirrels on these sites were reproducing every year (Villa et al. 1999). The ability of the model to use forest and treatment to predict squirrel biomass was relatively strong for 1994 and 1996 ($R^2 = 0.58$ and 0.74, respectively) and moderate for 1993 ($R^2 = 0.29$), driven by combined effects of forest and treatment. In summary, my final model suggested that something other than forest, variable-density thinning, or competition from other sciurids influenced squirrel populations once populations recovered from the short-term effects of variable-density thinning.

Movement Pattern and Behavior Models

During the non-breeding season, Scenario #1 (travel and distance being influenced by activity site location and quality) appeared to be a better model than Scenario #2 (activity resulting from travel time and distance covered; Chi-square = 25.5, df=18, P=0.112; AIC=97.5; BCC=101.1; DIC=97.2). As the number of activity sites increased, percent of time spent in the canopy increased, the proportion of time spent in travel decreased, the mean distance between activity sites increased, and the distance between the den and activity sites increased (Figure 15). Also, as the average time spent in activity increased, the total number of activity sites decreased, the distance between activity sites increased, distances between activity sites and the den increased, the relative proportion of time spent in travel decreased, and travel rates increased. Rates of travel also increased as the distance between activity sites increased. Squirrels in HIGH forest had increased travel rates and numbers of activity sites with less time spent at activity sites and less distance travelled to reach activity sites compared to LOW forest. Across all forests, males travelled farther between activity sites, but not significantly farther away from the den.

Scenario #1 and #2 were similar in comparative scores for breeding season movement (Scenario #1, AIC=86.7, BCC=94.0, DIC=87.0; Scenario #2, AIC=87.3, BCC-95.1, DIC=87.2). Both also fit the data relatively well (Scenario #1, Chi-square=20.7, df=21, *P*=0.480; Scenario #2, Chi-



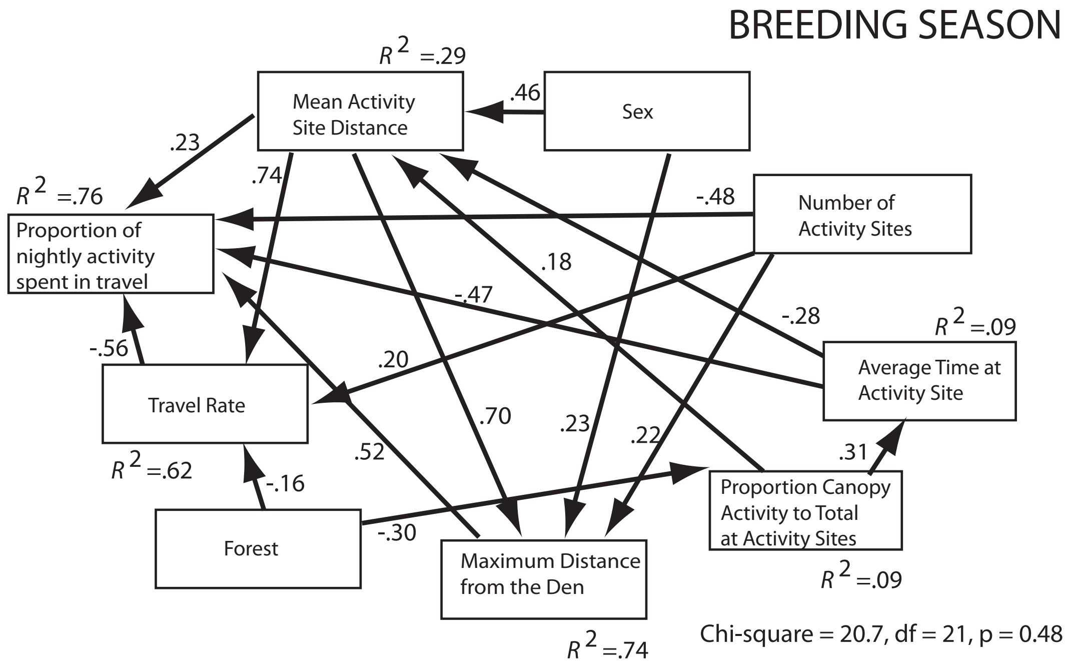


Figure 15. Final SEM models showing significant pathways among spatial-temporal metrics for flying squirrel (*Glaucomys sabrinus*) activity outside their dens during radio-telemetry studies from 1993-2006. Breeding season model (*n*=101) based on data from two low-density forests (Legacy and Timber Forests). Non-breeding season (*n*=213) model based on data from both low-density forests (LOW) and from two forests with high densities (HIGH).

square=17.3, df=19, *P*=0.569). Scenario #1 was the more parsimonious of the two models with two fewer paths. I therefore chose this as my final model, but could not rule out the possibility that travel (which in this case included breeding forays) was having an influence on the location and quality of activity sites. As with the non-breeding season, increased numbers of activity sites led to increased percent of time spent in the canopy and decreased the proportion of time spent in travel (Figure 15). Likewise, as average time at activity sites increased, the proportion of time spent in travel decreased. In contrast to the non-breeding season, increased numbers of activity sites led to increased travel rates. Also, as average time spent at activity sites increased, the distance between activity sites decreased rather than increased, and there was no significant effect of average time at activity on the distance between activity sites and dens.

Limiting Factor Models

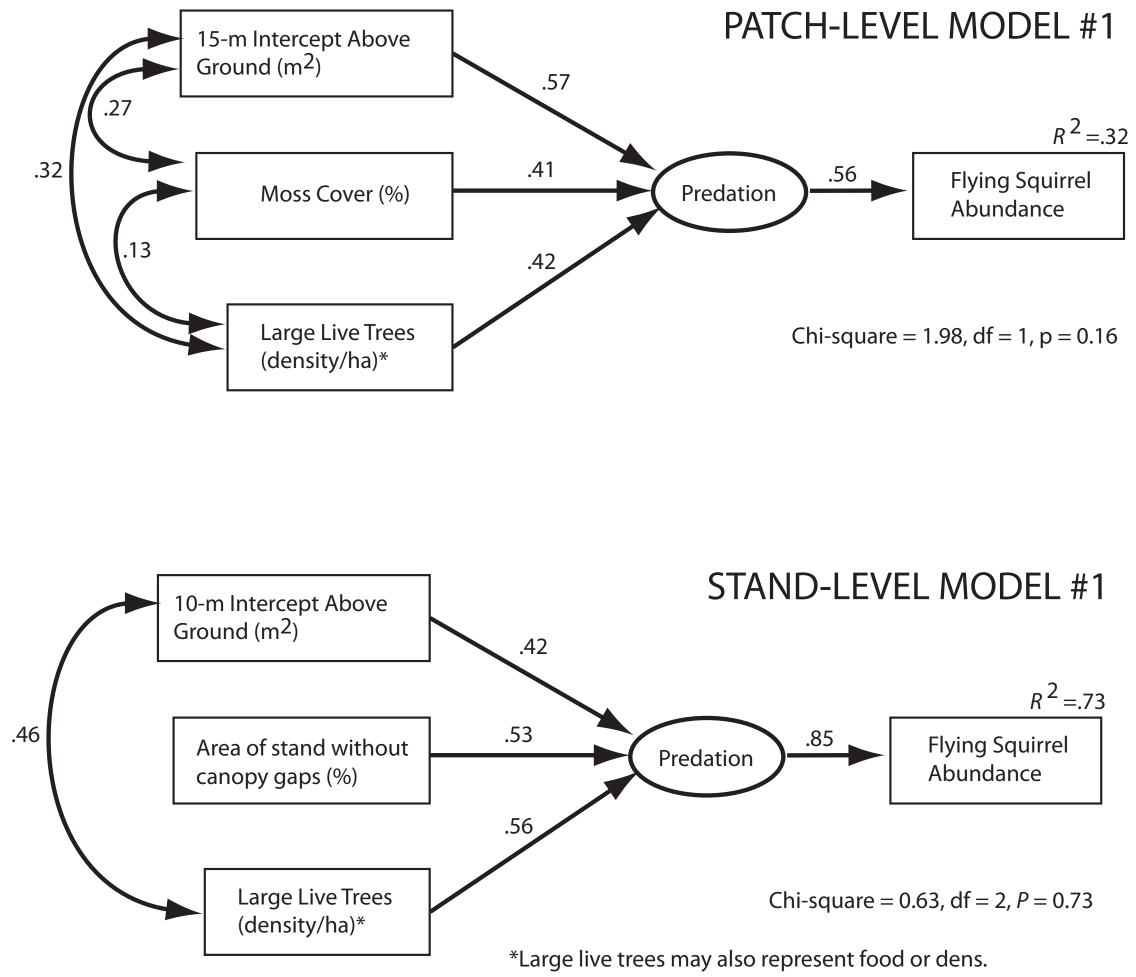
Model evaluation greatly reduced the complexity of all 15 of my models compared to their original constructions (Table 8, 9; Figure 16). At the patch level, this included single-limiting-factor models being reduced to 3 or 4 explanatory variables, and 5 multi-limiting-factor variables being reduced to single-factor models. Models #1 (predation-only), #2 (food only), #3 (den only), and #8 (food and dens) fit the data relatively well and had similar model comparison scores. However, Model #1 (large live trees, moss cover, and 15-m area intercept) was superior in explaining variance in patch-level MNKA (R^2= 0.32) compared to the other three models (R^2 = 0.18-0.20). Therefore, I assumed that Model #1 was the best model of those examined.

Table 8. Patch-level model fit measures for 15 limiting-factor structural equation models that evaluate relationships among predation, food, dens, and competition for predicting flying squirrel (*Glaucomys sabrinus*) populations in 33 stands across western Washington. Patch-level data was used to predict patch-level abundance (n=297).

Model	Factors Evaluated	Final Variables Used	Chi-square	DF	*P*	*N*	RMSEA	AIC	BCC	DIC	R^2
1	Predation	Large trees, moss cover, 15-m intercept	1.975	1	0.160	297	0.057	27.98	28.42	28.26	0.32
2	Food	Large trees, Tree species diversity Large fallen trees	0.063	1	0.802	297	0.000	26.06	26.51	25.97	0.18
3	Dens	Large trees, large snags, tree species diversity	0.366	1	0.545	297	0.000	26.37	26.81	26.31	0.20
4	Competition	Tall shrubs, low shrubs, forbs, ferns	5.082	3	0.166	297	0.048	39.08	39.79	39.06	0.15
5	Predation Food	Large trees, moss cover, 15-m intercept, large fallen trees	1.306	1	0.253	297	0.032	39.31	40.09	39.04	0.32
6	Predation Dens	Large trees, 15-m intercept, moss cover, large snags	7.186	3	0.066	297	0.069	41.19	41.89	35.82	0.30
7	Predation Competition	Reduced to Model #1									
8	Food Dens	Large snags, overstory species diversity, large fallen trees	0.619	1	0.431	297	0.000	26.62	27.07	26.35	0.19
9	Food Competition	Reduced to Model #2									
10	Dens Competition	Large snags, tree species diversity, tall shrubs	1.075	2	0.584	297	0.000	25.08	25.49	24.25	0.23
11	Predation Food Dens		7.186	3	0.066	297	0.069	41.19	41.89	40.84	0.30
12	Predation Food Competition	Reduces to Model #5									
13	Predation Competition Dens	Reduced to Model #6									
14	Food Competition Dens	Reduced to Model #8									
15	Predation Food Competition Dens	Reduced to model #6									

Table 9. Stand-level model fit measures for 15 limiting-factor structural equation models that evaluate relationships among predation, food, dens, and competition for predicting flying squirrel (*Glaucomys sabrinus*) populations in 33 stands across western Washington. Stand-averaged data was used to predict stand-level abundance (*n*=33).

Model	**Factors Evaluated**	**Final Variables Used**	**Chi-square**	**DF**	***P***	***N***	**RMSEA**	**AIC**	**BCC**	**DIC**	***R*²**
1	Predation	Large trees, canopy gaps, 10-m intercept	0.629	2	0.730	33	0.000	24.63	29.07	25.18	0.73
2	Food	Reduced to large trees									0.46
3	Dens	Reduced to large trees									
4	Competition	Low shrubs, forbs, mid-story deciduous	5.717	2	0.057	33	0.241	29.72	34.16	30.97	0.30
5	Predation Food	Reduced to Model #1									
6	Predation Dens	Reduced to Model #1									
7	Predation Competition	Reduced to Model #1									
8	Food Dens	Reduced to large trees									
9	Food Competition	Reduced to large trees									
10	Dens Competition	Reduced to large trees									
11	Predation Food Dens	Reduced to Model #1									
12	Predation Food Competition	Reduced to Model #1									
13	Predation Competition Dens	Reduced to Model #1									
14	Food Competition Dens	Reduced to large trees									
15	Predation Food Competition Dens	Reduced to Model #1									



*Large live trees may also represent food or dens.

Figure 16. Final limiting factor models showing significant relationships among habitat predictors and flying squirrel abundance (minimum number known alive) for 33 stands sampled for flying squirrel (*Glaucomys sabrinus*) populations in western Washington 2004-2006.

Model #6 had similar predictability (R^2= 0.30) but slightly poorer model fit. This model included large snags in addition to the three variables used in Model #1.

Stand-level models were also reduced from their original constructs, with only 2 of the 4 single-limiting factor models having more than 1 exogenous variable, and 13 of the 15 models being reduced to either Model #1 (predation-only, represented by large live trees, canopy gaps, and 10-m area intercept) or to one explanatory variable, large live trees (Table 9). Of the two models with more than one variable, Model #1 had the lowest model fit scores, the lowest model comparison scores, and the highest ability to predict stand-level MNKA (R^2 =0.73) suggesting it was the superior model of the ones examined. Additionally, 7 of the more complex models, including Model#15 that included all 4 limiting factors, reduced to Model #1 rather than to Model #4 (competition). As was the case for my patch-level models, single-factor models for food and dens included large live trees as a variable, so I could not rule out their importance during this analysis.

Stand-level HIGH-LOW Classification

Three components (10-m intercept, canopy gaps, and variance in live tree d.b.h.) could correctly classify 32 of the 33 stands (97%) into HIGH and LOW groups during mixture modeling analysis, with 30 of 33 stands showing high probability ($P > 0.70$) of being classified into the correct group. One HIGH stand (#963; MNKA=25) was misclassified (P =0.82 for being in the LOW group). This stand had a high density of live, small-diameter, relatively short-crowned trees, and few gaps. One additional stand (#970) was marginally classified into the correct HIGH group (P =0.55) using all canopy gaps, but probability of being in the correct group improved (P =0.66) when using only non-creek gaps, and removing creek-associated gaps did not substantially change the probabilities of group membership for other stands. This stand was comprised of approximately equal patches of old, complex forest with tall, deep-canopy trees, a creek lined with crown-to-ground conifer trees, and a sloped patch with a mix of dominant tree size classes. It also had almost twice as much of the stand area in canopy gaps (29.0 %, but only 20.2% when excluding creek-associated gaps) as the HIGH stand with the second largest percent of stand-level gaps (#909, %15).

Adding additional components to my final 3-component model did not improve the model. Other combinations of habitat components examined could correctly classify 30 of 33 stands. This included predictors that appeared important in patch-level and stand-level limiting factor models (e.g., large live trees, large snags, tree species diversity, and moss cover). In each case, however, there were also two or more stands whose probability of group memberships were only marginally correct (e.g., P =0.51-0.60). Therefore, I assumed that the 3-variable model using 10-m intercept, canopy gaps, and variance in live tree d.b.h. was the best one examined.

CHAPTER FOUR—DISCUSSION

Caveats

This study synthesizes some of the largest data sets ever collected on the ecology of free-ranging northern flying squirrels. Some of the results and discussion presented here, however, should be viewed within the limitations of retrospective studies. For example, I made adjustments to all initial SEM models based on post-hoc evaluation of modification indices, standardized residuals, and critical ratios. Although each decision to add or remove paths in these models was made with ecological justification, I could not use SEM as a strictly confirmatory process. My results, however, provide an empirical foundation that can be used to further develop and test limiting factor hypotheses, within both experimental and confirmatory frameworks.

This study was also limited to evaluation of squirrel populations across two adjacent physiographic provinces. There may be confounding regional effects due to variation in plant and wildlife species composition, anthropogenic disturbance histories, and their interactions that could limit the applicability of the results to areas outside these provinces or forest types examined. For example, in other areas within the range of the northern spotted owl, woodrats (*Neotoma* spp.) play important roles as arboreal rodents and as prey for owls, but I found woodrats (*N. fuscipes*) on only one stand during my study (#970; unpublished data). However, the forests evaluated here were representative of lowland and mid-elevation forests west of the Cascade Mountains and contained structural components ubiquitous to conifer-dominated forests elsewhere. The wide gradient of structural complexity sampled, from uniform second-growth single-species forests to multi-aged, mult-species old-growth forests, also represented some of the widest gradients of structural conditions possible in conifer-dominated forests across the distribution range of the northern flying squirrel.

Caution is warranted when assuming abundance reflects habitat quality (e.g., Van Horne 1983). However, I found no evidence to suggest that this assumption was violated: (1) long-term demography studies of juveniles on the FES showed that juveniles caught in live traps or ear-tagged in nestboxes either continued to be captured near where they were first captured, or disappeared entirely—none ever showed up on adjacent stands beyond that which would be expected for normal non-breeding movement distances (the 8 stands within each FES forest sampled across a ca. 1.2km diameter area; Villa et al. 1999, unpublished data). Long-distance dispersal (e.g., several kilometers) by juveniles was possible, but adult immigration into study sites (adults being captured in live-traps that were not previously eartagged) was rare. Rather it appeared that these populations had high site philopatry and genetic diversity across these forests was being maintained through long-distance breeding behavior of adult males rather than emigration or immigration by either juveniles or adults (Wilson 2000, 2003); (2) radio-collared squirrels followed over several seasons continued to use the same general foraging and denning areas until they died, including several juveniles that were monitored (Carey et al. 1997, this study); (3) none of my HIGH stands were comprised of disproportionate numbers of juveniles or breeding yearling females that would be suggestive of habitat sinks. A source-sink effect may be more pronounced at the interface between complex older forest supporting high densities and young forest supporting low densities. However, the boundary of such an interface is not necessarily distinct. For example, three radio-collared squirrels monitored in my primary HIGH forest (Stand 912) used foraging areas that included both young (<40 yr old) and old (>500 yr old) forest that were separated by a secondary gravel road (Appendix). Further understanding of juvenile dispersal in northern flying squirrels is warranted as dispersal is certainly needed to occupy newly-available habitat, and would have had to account for squirrels in second-growth forest today that regenerated from landscape-level clearcutting across low- and mid-elevation Pacific Northwest forests, including both the Legacy and Timber Forests.

Flying Squirrel Populations in Western Washington

Variable-density thinning did not promote habitat conditions for flying squirrels 12 years after treatment. Stands on the FES continued to support few flying squirrels after 1998, with extremely low abundances similar to those resulting from the negative short-term effects that variable-density thinning had during the first few years after implementation. However, multivariate analysis suggests that neither forest nor variable-density thinning were having significant influence on squirrel populations after 1997 while control stands also supported few squirrels. This suggests that a lack of squirrels after 1997 was not due specifically to variable-density thinning, but rather to extrinsic factors that were influencing all 16 stands.

The structural composition of each of the FES stands continued to change during this study. The number of overstory trees was already reduced due to commercial thinnings in the Timber Forest prior to the study. Then, variable-density thinning (including root-rot treatments) reduced the basal area of overstory trees on treated stands in both forests up to 50%. Subsequently, small-scale natural disturbances resulting from suppression mortality (Legacy Forest), loss of trees due to root-rot expansion (both forests), and wind events continued to remove trees over time across all 16 stands. During this interval, insufficient time had passed for development of a substantive midstory layer of trees, either in response to variable-density thinning or to natural events. Thus, the only increases in overstory structural complexity since the onset of the FES was a moderate increase in canopy height of the existing dominant trees and a relatively insignificant contribution to the mid-story through increased bole growth. At the same time, structural complexity in the understory increased, providing favorable habitat for chipmunks and by the end of this study, chipmunk populations on some stands had surpassed the abundance found in complex forest elsewhere in the region (e.g., Carey 1995a, Hayes et al. 1995, Rosenberg and Anthony 1993). However, both univariate and multivariate analyses showed a negative relationship between understory growth and flying squirrel abundance.

At the same time, I found forests supporting both HIGH and LOW flying squirrel abundances on the Olympic Peninsula. This suggests that there were no regional effects confounding FES results. Finding HIGH stands, including one of the highest abundances ever reported (MNKA=49 for an 8x8 trapping grid) was also in marked contrast with previous results that reported generally low populations for this physiographic province (Carey 1995a). I suggest that previous results were limited by the range of forest conditions sampled, especially as the 5 stands sampled by Carey (1995) and this study showed similar population levels. During the 1980s, there was a general lack of forest inventories to help in study site selection, management goals and research questions were focused on Douglas-fir dominated forest, and many desirable stands were scheduled to be harvested with a few years of study, all of which influenced site selection at that time (Carey 1995a, A. Carey personal communication).

Habitat Predictors for Squirrel Populations

Stands that supported high abundances of flying squirrels were comprised of two general forest conditions: (1) a “ground-to-crown” multi-species forest with a multi-layered canopy, variable midstory and patchy understory and (2) dense, closed-canopy forest with high bole density and little or no understory or mid-story. These two forest conditions varied markedly in their structural complexity and arrangement due to both the structural components involved, and how those components were apportioned across the vertical and horizontal layers of these forests (Table 7). HIGH crown-to-ground forest (stands #909, #910, #912, #917, and #970) had relatively high canopy stratification and decadence scores and exhibited classic multi-layered conditions often associated with old temperate rainforest in the region. They also contained low to moderate amounts of stand-level canopy gaps. In contrast, LOW stands could also have high canopy stratification or decadence scores but lacked structure in one or more other dimensions. For example, stand #903 had the second highest canopy stratification score of any of the stands examined, but also had the greatest amount of stand-level canopy gaps of any of the stands examined, and supported few squirrels. This suggests that canopy complexity alone is insufficient to meet squirrel habitat needs. Likewise, stand #902 had the highest decadence score and a relatively low canopy stratification score, and also supported few squirrels, suggesting that measures of decadence that included snags and large fallen trees are also insufficient indicators of high-quality habitat without structural components created by other ecological processes.

HIGH closed-canopy forest (stands #963, #971, and #982) had high crown-class differentiation scores and relatively low decadence scores. Structural occlusion was high in the midstory due to high bole density and high in the canopy due to closely-spaced trees, high crown volume, and few canopy gaps. Such conditions limited the amount of sunlight reaching the forest floor and resulted in relatively little understory development. In contrast, stand #915 (LOW) had a high crown-class differentiation score, but supported few squirrels. In this case, although it also had few and small canopy gaps, the spacing between individual trees was higher and crown volumes were lower than in high-quality stands, resulting in 10-m area intercept values and understory development scores similar to many Legacy and Timber Forest stands, all of which also supported few squirrels.

Overall, three structural components, variance in live-tree d.b.h. for trees >10cm, stand-level canopy gaps, and 10-m area intercept could correctly classify all but one of the 33 stands examined during this study into HIGH and LOW groups. Although variance in live-tree d.b.h. appeared superior in distinguishing HIGH-LOW groups, SEM models also suggested that density of large live trees was better at predicting a gradient of squirrel abundances. There was a moderate linear relationship between these two variables (r^2=0.52) suggesting that there may be some interchangeability between them in classifying forest structure for squirrel habitat. Final analysis of patch-level predictors also suggested that large trees were important, but several of the best models also included large snags, 15-m area intercept, and tree species diversity. However, stand-level models were much better at explaining respective squirrel abundances than patch-level models, and none of these included large snags in final models.

Limiting Factors

I suggest that limiting factors for flying squirrel are hierarchical, with the following order of importance for most forests: (1) predation is the primary limiting factor with forest structure providing essential protective cover for squirrels that allows populations to build and remain relatively high over time; (2) food is secondary in importance, but may become more important as squirrel populations reach high densities; (3) den are not an especially strong limiting factor, but may influence pre-weanling mortality rates in some forests that lack sufficient cavity dens; and (4) competition has diffuse effects on all three other factors, but overall plays a relatively minor limiting-factor role.

Forest Structure and Predation

Collectively, the results from this study suggest the combined effects of individual habitat elements and their apportionment in multi-dimensional space may be important in providing year-round protective cover that allows squirrel populations to build to and persist at high levels over time, adding support to the hypothesis that predation is a primary limiting factor for flying squirrels. Evidence for this support includes: (1) all important predictors used in final multivariate models could be associated with protective cover. In contrast, only one potentially important variable in some final models, large live trees, could be associated with two other limiting factors—food and dens and there was weak additional support for either of these two factors otherwise; (2) when there was some degree of interchangeability among variables during model evaluation (prior to the final models), virtually all predictors could be associated with protective cover (with a notable exception being large snags); (3) many of the highest univariate predictors of abundance also were associated with protective cover; and (4) squirrel behaviors and space use outside the den appeared to be consistent with a predation-mediated foraging strategy, including activity centered away from the den, use of multiple, widely-spaced activity sites during a night, spending most time and space-use in the canopy, and engaging in less risky movement patterns during the winter when predation was highest.

Forest structure provides the interface for interactions between flying squirrels and predators on several levels. First, predators use sight, sound, and smell to different degrees to detect prey. Mustelids use all three modes of detection whereas owls rely primarily on hearing and vision (King 1989, Lynch 2007). High quantities of structure, found in both complex forest and forest with high bole density, provide occlusion that can reduce visual detection. Structure also dampens and deflects acoustical signals, limiting aural detection (Reethof et al. 1977, Linskens et al 1976). This likely affects some predators more than others. For example, owls with assymetrical ears (e.g., spotted and barred owls) can pinpoint sounds both vertically and horizontally and may have less trouble detecting squirrels in structurally complex habitat compared to owls that have symmetrical ears (e.g., great horned owls; Norberg 1977, Volman and Konishi 1989). Structure can also be important in dispersing scent. By limiting time and distance covered on the ground and using gliding as a mechanism for travel, squirrels can minimize their scent trails. However, complex canopies disperse scent more effectively than simplified canopies due to wind turbulence brought on by variation of tree heights and gaps (Conover 2007, Miller et al. 1991, Stacey et al. 1994). Thus, quantity and complexity of forest structure can help limit the ability of predators to detect squirrels by sight, sound, or smell.

Another important interface between structure and predation is protection of squirrels during an attack. Tree crowns may provide sufficient cover to give squirrels the advantage when escaping a predator (Appendix). In contrast, bare boles limit escape options to either going to the backside of the tree or attempting a short glide to an adjacent tree. Both strategies were commonly used by squirrels to avoid humans upon release from traps (personal observations), but they may not be as effective as tree canopies in thwarting attacks by owls.

Finally, an indirect but important link between forest structure and predation is the inverse relationship between overstory structure and understory development. On the FES, not only did increased understory development result from decreases in overstory structural complexity (due to increased spacing between trees from thinning as well as canopy gaps formed by root rot treatment and natural root rot expansion), but it also resulted in increases in abundances of many forest-floor dwelling prey species like mice, voles, and chipmunks (Carey 2001, Wilson and Carey 2000, Palazzotto and Wilson, *in litt.*). This in turn may have increased the attractiveness of these sites to both avian and mammalian predators which could opportunistically prey on flying squirrels that became more exposed to predation risk. It could also result in spillover predation into adjacent, non-thinned stands. This may, in part, explain why control stands on the FES, even though generally remaining higher than treated stands, followed similar population declines relative to treated stands after thinning. Some evidence for this was suggested by a pair of barred owls that were observed using both control and treated stands in the Legacy Forest in 2005 during telemetry studies (Appendix).

In contrast, young forests with little understory development are often depauperate in overall prey biomass other than flying squirrels and may not attract intensive, regular predation. However, episodic predation may be just as catastrophic to flying squirrel populations in these forests once a predator like a weasel begins to cue into squirrels that have little or no understory protective cover, especially given the long lag time needed for repopulation (Wilson and Carey 1996). In addition to the continued reduction of overstory trees due to natural disturbances, this could help explain the lack of recovery of populations on Legacy Forest controls—there was simply insufficient time for populations to rebuild during years between predation events.

My ability to exclusively rule out habitat variables associated with other limiting factors (e.g., large live trees) may have been limited, in part, due to both simplification of my structure measures and merging measures of habitat components that did not fully account for the multi-dimensional properties of structural occlusion. For example, I modeled tree canopies as solid objects, yet the spacing and branching patterns of individual trees can be highly variable, especially for older conifers that have been subjected to multiple small-scale disturbances that affect branch form (e.g., sprouting of epicormic branching in response to increased sunlight or irregular branching due to mistletoe infection). Likewise, individual tree spacing would likely affect the ability of a predator to visually track a gliding flying squirrel through space, but I used measures like variance in tree d.b.h. and counts of trees that averaged individual structures across space. Direct measures of occlusion or inclusion of spatially-explicit information on tree spacing in my data sets may have resulted in greater likelihood of correctly classifying the one stand that was misclassified in my final HIGH-LOW mixed model. Field observations as well as photographs suggest that, like all other HIGH stands, mid-story visibility was generally limited to <20 meters as viewed from the ground in this stand, but this fine-scale composition of structural elements in space was not adequately captured by my measures.

Multi-dimensional Structural Complexity and Predation

All HIGH stands were high in overall amounts of above-ground structure but the apportionment of that structure across multiple dimensions was important and further supported a predation-forest structure hypothesis. Each forest layer contributes to different predator-prey interfaces.

The upper layer (e.g., tree canopies) provides protective cover for flying squirrels in several ways. First, high canopy cover and connectivity allow squirrels to move through the forest using cross-canopy travel across interlocking branches between tree canopies. This behavior is more likely in competitive exclusion forest where there is substantial canopy overlap. In complex forest, horizontal connectivity is less uniform and broken up by vertical layering of trees of various ages and heights, but cross-canopy travel is still likely important while foraging in small clumps of closely-spaced trees.

Second, a deeper canopy means less exposed tree boles, and therefore potentially less risk while climbing up trees. In forests where there is a large distance between the ground and the bottom of a canopy (e.g., both the Legacy and Timber forests), squirrels have a considerable vertical distance to travel that directly exposes them to predators, both in terms of being spotted by predators and in direct attacks, until they can reach the canopy. This may be especially problematic in even-aged second-growth conifer forest where the canopy depth can be <20% of the total tree height.

Third, gaps (e.g., the absence of canopy) reduce horizontal occlusion and squirrels are forced to either glide across gaps or travel around them. Gliding across gaps may increase their vulnerability to predation by exposing them to aerial predators. Spotted owls have been observed killing flying squirrels in mid-glide (Appendix). None of the HIGH stands had more than 20% of their total area in non-creek canopy gaps >100m^2 (29% if including creek-associated gaps) and few had many individual gaps >400m^2. Likewise, there appeared to be maximum threshold values in the percent of gaps in a stand (15% for gaps ≥100m^2 and 5% for gaps >400m^2) and their ability to support higher or lower numbers of squirrels over a 13-yr period on the FES. During analyses, I found up to a 10% difference in total percent of stand-level gaps between using plot-averaged values vs. 100% surveys. This suggests that both the spatial patterning of gaps and their effects on squirrel populations may occur at scales larger than a patch level but smaller than a stand level, and emphasizes the importance of evaluating squirrel habitat at multiple scales (Carey et al. 1999a). Removing canopy gaps lined with crown-to-ground trees increased the ability of models to use gaps to predict squirrel abundance but it did not change the relative importance of gaps compared to other predictor variables. Such gaps may have positive effects for squirrels by providing vertical layers of occlusion not found in terrestrial gaps that do not develop similar conditions.

Flying squirrel populations were also highest where there were substantial amounts of structural components in the mid-story layer (e.g., 10-20 m above ground), either in the form of a midstory canopy, high bole density, or both. A developed midstory reduces both visual and aural detection by predators, especially while squirrels are gliding in the air and landing on tree boles. This occlusion also provides important cover from attack while squirrels are climbing up boles to reach the dominant canopy layer. The mid-story also provides visual occlusion from sit-and-wait predators like spotted owls that specialize in perching in the mid-story while looking for prey (Forsman 1976).   Without midstory canopies, tree boles become the sole source of occlusion at this vertical layer. In competitive exclusion forest, high densities of relatively small boles (from both live and dead trees) can be sufficiently high to provide substantial occlusion, often limiting visibility to less than 20m in HIGH forests (personal observations).

Understory had a negative relationship with squirrel populations in both univariate and SEM models and was generally not found in substantive amounts on any HIGH stand. Rather, most HIGH stands had either patchy or minimal understory as has been found elsewhere (e.g., Oregon Coast Range, Carey et al. 1999a; eastern Cascades, Lehmkuhl et al. 2006), including the almost completely moss-dominated forest floor of the stand with the highest squirrel abundance (Stand #982). Thick vegetation can provide overhead protective cover while squirrels are foraging on the ground. However the patagium of flying squirrels makes ground travel awkward compared to other squirrels, and there is likely a trade-off between amount of understory and increased noise while traveling on the ground which may attract predators. During this study, technicians could often hear squirrels move through thick woody understory. A patchy understory, resulting from complex midstory and overstory layers may provide the best balance among protective cover, food resources, and a squirrel's ability to move undetected on the forest floor.

Coarse woody debris plays numerous important ecological roles in Pacific Northwest forests (Harmon et al. 1986) and has been associated with squirrel abundance (e.g., Carey 1995a, Carey et al. 1999a, Gomez et al. 2005, Smith et al. 2004). However, I found no strong correlation between squirrel abundance and large fallen trees. I suggest that high levels of large fallen trees found in some HIGH stands was a reflection of the ecological processes that led to structural complexity above the forest floor rather than a specific habitat need by squirrels for coarse woody debris as 3 of the 8 HIGH stands had relatively few large fallen trees, including the stand with the highest squirrel abundance (#982; Table 1). A similar argument has been made for snags (Carey et al. 1997). In contrast, several LOW stands (e.g., #902, #903) had substantial amounts of large fallen trees, but the tree death that resulted in those fallen trees also created large canopy gaps that reduced structural occlusion in the midstory and overstory. Several HIGH stands also had high amounts of large fallen trees, but in each case, structural occlusion remained high and the deposition of coarse woody debris appeared to result from falling of widely-scattered individual or small-clumps of trees rather than large patches of trees that created large canopy gaps. Thus, although large fallen trees could enhance squirrel habitat (e.g., by serving as hosts for fungi and protective cover or travel pathways on the forest floor), it might only do so in forests that maintain high structural occlusion and not if it comes at the expense of greatly opening up the canopy.

Squirrel Behavior and Predation

There are several squirrel behaviors observed that further supported a predator-structure hypothesis. First, flying squirrels kept most travel above the forest floor, either through gliding or traveling through the forest canopy across interlocking branches of tree canopies. Gliding is a way to rapidly escape mammalian predators. However, it is likely a less successful means of escape from owls which are more maneuverable in the air compared to flying squirrels. Cross-canopy travel is also a way to stay close to protective cover at all times and protects squirrels from both owls and mustelids. In addition to canopy-focused travel, squirrels spent little overall time on the ground (7-17% of total time during an activity bout; approximately 10-30 minutes) and often consumed food obtained from the ground in a nearby tree. When food was consumed on the ground, squirrels did so quietly and with little motion that might be detectable from aerial perches (Appendix).

Second, foraging areas were distinctly separate from dens, with the closest foraging area, on average, ≥40 m from the den, and the average distance between the den and activity sites ranging from 87 to 208m. This behavior was hypothesized in the Oregon Coast Range and has been documented in the east (Holloway and Malcolm 2007, Witt 1992). Keeping the den distinctly separate from foraging areas reduces the amount of scent around the den where squirrels spend most of their time. It also helps reduce the likelihood that predators would focus their attention at or near dens where multiple squirrels would be at risk of predation.

Third, squirrels used multiple activity sites within a night and the more time spent at a given site, the farther distance squirrels traveled to a subsequent site. Partitioning activity into discrete, widely-spaced locations in a night can help reduce the effects that scent or noise made at one site could have on a subsequent site in attracting predators to an area.

Is a Structural Complexity Hypothesis Universal?

Structural complexity could help explain the distribution and abundances of flying squirrels across their geographic range. On a continental scale, the distribution of squirrels generally follows that of conifer-dominated forest (Wells-Gosling and Heaney 1984). Conifer trees provide year-round protective cover, compared to deciduous forests that lose much of their protective cover in winter when predation on flying squirrels can be the highest (Villa et al. 1999). Populations reach their highest levels in Pacific Northwest coastal forests, where the amount of woody biomass of conifer forest is greater than anywhere else within the squirrel's distribution range (Blackard et al. 2008, Smith 2007). As conifer forests become dryer, overall biomass decreases, tree spacing increases, and structural complexity is eventually reduced to the point where forests support few, if any, squirrels.

The actual capacity of a given forest to support abundant squirrel populations may depend on site-specific structural complexity that results from different combinations of structural components. This could help explain the results from several past studies, including why low squirrel densities can be found in both young and old forest (Carey 1995a, this study), why similar densities can exist in high-stem density young forest and complex old forest (Rosenberg and Anthony 1992), why older forest that contains patches of open water (e.g., large canopy gaps) supports fewer squirrels compared to upland old forest (Smith and Nichols 2003, personal observations), why high canopy cover (e.g., less area in canopy gaps) can be an important predictor of squirrel abundance (Lehmkuhl et al. 2006, Meyer et al. 2007a), why higher than expected squirrel abundances are found in some forests where shade-tolerant species like grand fir (*Abies grandis*) help keep vertical occlusion relatively high in the mid-story (Lehmkuhl et al. 2006, personal observations), and why structural components (e.g., coarse woody debris, large snags, large trees) that are indicative of ecological processes important for creating structural complexity are sometimes, but not always, found to be important predictors (numerous studies). A structural-complexity predation hypothesis may also help inform debates in regions outside the Pacific Northwest where squirrel populations can be scarce and highly fragmented

(Weigl 2007, USFWS 2008a). The importance of structural complexity for high-quality flying squirrel habitat has been questioned in the past (e.g., Gomez et al. 2005, Rosenberg and Anthony 1992), but usually within the context of contrasting young and old forest, not the within-stand quantity, arrangement, and composition of multi-dimensional forest structure that I explored here. Therefore, discussions of squirrel habitat should also include well-defined terminology to avoid any confusion, especially as terms like structure, structural complexity and canopy gaps can mean markedly different things to different practitioners.

The evolution of gliding in mammals may have originated as a way to exploit forests with open, non-connected canopies (Emmons and Gentry 1983). However, such a benefit appears to come at the expense of increased risk of predation for flying squirrels. Northern and southern flying squirrels may have evolved different strategies to help compensate for this risk. Northern flying squirrels exploit conifer-dominated forests where year-round protective cover is high, canopy connectivity can be high, but environmental conditions can be harsh and highly variable by (1) having the capacity to switch from K- to r-selected reproductive strategies in poor habitats (Villa et al. 1999), (2) having generally one reproductive season per year to limit overpopulating areas when resources become scarce (Villa et al. 1999, Wells-Gosling and Heaney 1984); (3) having relatively large biomass and sufficient thermoregulatory capacity to den in small groups, and (4) maintaining genetic diversity across the landscape through breeding behaviors, including wide-ranging males and promiscuous breeding by both sexes (Wilson 2000, this study). In contrast, southern flying squirrels evolved strategies that allow them to exploit more open, deciduous-dominated forest where risk of predator detection is high, but resources like high-quality, storable food can be exploited, including (1) breeding multiple times per year (Muul 1969, Stapp and Mautz 1991); (2) relying on large group denning rather than individual biomass to meet thermoregulatory needs (Muul 1968, Stapp et al. 1991), (3) caching seasonally available high-quality mast foods like acorns that can provide a year-round food source when other resources are scarce (Harlow and Doyle 1990), and (4) being aggressive in defending secure cavity dens (Weigl 1978, 2007). Such strategies may explain why populations of southern flying squirrels do not necessarily decrease after thinnings whereas northern flying squirrel do (e.g., Holloway and Malcolm 2007). Strategies used by both species are flexible enough to allow some capacity to persist at low levels in alternate habitats (e.g., northern flying squirrels in deciduous-dominated forest and southern flying squirrels in conifer-dominated forest) but there may be limits in the ability of either species to greatly expand their distribution range without changes in habitat towards conditions for which they have evolved. Climate change towards warmer, drier conditions, for example, would likely favor southern flying squirrel expansion (Bowman et al. 2005, Smith 2007, Weigl 2007).

Food

As with most previous studies, I did not directly measure food resources. However, I found little support for food being a major limiting factor—I did not find any important habitat components that indirectly supported food (e.g., life forms in the understory or trees with mycorrhizal associates), food-based SEM models were inferior to predation models, and although large live trees were found to be important in some analyses, they were also associated with predation and dens, and were inadequate as a single predictor for explaining squirrel abundances or classify stands into HIGH—LOW groups. There was also little indication that behaviors exhibited in search of food or while moving outside the den were being done solely to maximize energy efficiency. Further, many of the understory life forms (e.g., low shrubs, mid-story deciduous trees) associated with potential food resources had negative associations with squirrel abundance. I did not measure seasonal food abundance or track squirrels continuously throughout the year, so there may have been missed shifts in food resource availability over seasons that I was unable to detect with my sampling strategy. It is also possible that my sampling strategy of using life-form groups combined individual plant species that had both positive and negative effects on squirrel abundance. However, some life form groups were dominated by the same plant species. For example, ericaceous shrubs (primarily salal) dominated the low shrub life form for most stands.

Northern flying squirrels are found in extremely diverse habitats, including forests at high latitudes and elevations (Wells-Gosling and Heaney 1984). Squirrels can persist almost solely on lichens in areas with winter snowpack suggesting they have the ability to switch to low-nutrition diets if needed (Rosentreter et al. 1997). Other flying squirrels are also adapted to harsh conditions and nutritionally-limited diets year-round (e.g. giant woolly flying squirrels [*Eupetaurus cinereus*] live in caves high in the Himalayan Mountains and feed almost exclusively on pine needles from one tree species; Zahler and Khan 2003). This ability to survive under harsh environmental conditions may help explain why food does not appear important when making comparisons among multiple limiting factors and potential habitat components for flying squirrels.

Food availability, however, may play an important limiting factor role once squirrel populations are near or at carrying capacity and therefore might be the ultimate factor in determining the carrying capacity of a stand. Behavioral changes observed in high-density populations such as reduced reproduction by yearling females (Villa et al. 1999) may be triggered by such limits in food. This hypothesis warrants further investigation. One option would be to measure variation in body-fat-to-mass ratios between high and low-density populations. Body mass alone would be insufficient evidence of food availability, as squirrels have the capacity to gorge on food, with up to one third of a squirrel's mass comprised of stomach and food contents (Villa et al. 1999). Another option would be to follow squirrel populations over long periods of time in response to food supplementation. Studies have shown short-term population increases in response to addition of food (Ransome and Sullivan 1997, 2004), but no long-term studies have been reported that would allow simultaneous evaluation of other limiting factors to be observed, such as a time-lag in predator response to increased prey abundance (e.g., Hanski et al. 1991).

Dens

The relative position of dens within a limiting-factor hierarchy was less clear than for other potential limiting factors. Large, live trees were an important predictor in some of the best SEM models, but as with food, there was no clear additional evidence suggesting that the importance of large live trees was due primarily to their ability to support dens rather than providing protective cover. If dens were important, I would have expected to see large snags also being an important predictor in final models, but they only appeared important at the patch level for Model #6 which also included all three predictor variables for predation, and this group of variables could only moderately account for squirrel abundance (e.g., R^2=0.30). At the stand level, there was also no strong evidence in support of dens, as snags were not important in any of the 15 models, and variance in live tree d.b.h. replaced large live trees as a better predictor in classifying HIGH-LOW groups. Given that flying squirrels can build and use external nests where cavity dens are absent or lacking (Carey et al. 1997, Cotton and Parker 2000b, Bull et al. 2004), even under harsh environmental conditions (e.g., interior Alaska; Mowrey and Zasada 1984), and that nestboxes and artificial cavities have not been shown to significantly raise squirrel populations (Carey 2002, Ransome and Sullivan 2004), dens may play a relatively minor limiting-factor role for most forests. However, dens could be limiting for females rearing young in forests that lack secure cavities, as the selection of large well-decayed tree stumps low to the ground could put them at risk for higher predation by terrestrial predators (Carey et al. 1997).

Competition

Virtually all habitat components I examined could have had some relationship with competition. However, direct measures of competition (e.g., biomass of other sciurids) could not significantly contribute to explaining flying squirrel abundance over time on the FES. Additionally, the indirect variables representing competition were poor predictor of abundance for univariate models and both single- and multiple-limiting factor multivariate models at the patch and stand levels, and none were useful in distinguishing between HIGH and LOW stands. In my time-series analysis, chipmunk biomass did show a positive relationship with flying squirrel biomass during one year, but there are several alternative explanations that could account for such a relationship, including increases in mutual food resources or reduced predation for both species during that year, or simply statistical chance. Thus, I suggest that competition may play a relatively low role overall in regulating flying squirrel populations.

On the FES, understory development in response to variable-density thinning and natural small-scale disturbance led to increasingly favorable habitat for chipmunks over time but also reduced mid-story and overstory cover favorable to flying squirrels. In addition, there was a significant, but negative relationship between squirrel abundance and understory development across all of my study sites that was even stronger than the negative relationship found between flying squirrel and chipmunk biomass. This suggests that development of favorable niche space for one species can come at the loss of niche space for another species and result in low abundances for the latter species, rather than low abundances resulting from competition *per se*. Given that chipmunks spend much of their time on the forest floor, there may be greater likelihood that Douglas' squirrels would compete with flying squirrels for arboreal resources. However, there were no discernable temporal patterns suggesting that flying squirrel and Douglas' squirrel populations were influencing each other. The fact that both species remained low and variable over time suggests lack of protective cover may also be important to Douglas' squirrels. Observations of direct competition between these two species were rare. On two occasions, Douglas' squirrels were observed using dens that were previously occupied by radio-collared flying squirrels a few days earlier (unpublished data). In both cases, however, flying squirrels were found in other, apparently suitable dens.

Carey et al. (1999a) found high abundances of flying squirrels, Douglas' squirrels, and Townsend's chipmunks co-existing in older forests in the Oregon Coast Range. They suggested that niche hyperspace (e.g., Hutchinson 1957) was expanded in structurally complex forests, with multi-dimensional forest resources distributed in a way that allowed for these otherwise competing species to co-exist. Niche overlap among species within such hyperspace need not lead to competition (Alley 1982), but if inter-specific competition does play a limiting factor role, it may be highest in complex forest, as increased competition often causes shifts in life-history strategies towards *K*-selected, high-density populations (MacArthur and Wilson 1967, McNaughton 1975, Pianka 1970). For example, if behaviors like reduced reproduction in younger female flying squirrels were density-dependent and driven, in part, by changes in food resource availability, mutual exploitation of food resources by other species could intensify those behaviors.

Spatio-temporal Movement Patterns

Movement patterns outside the den appear to be driven by a search for food that is mediated by predator-avoidance, social interactions with other squirrels, and the need to reproduce during the breeding season. These movement drivers result in highly individualistic, yet relatively spatially-consistent, patterns over time as flying squirrels meet their basic needs outside of the den.

Activity patterns of males and females were similar during the non-breeding season—both were characterized by reduced activity (compared to the breeding season), and simplified, small circuits of short duration. During the middle of winter, and especially during cold (≤ 32° F) weather, squirrels would sometimes not leave the den at all during the first 3-4 hours following dusk. During pilot studies, we monitored squirrels that did not leave the den from dusk until dawn, so no-movement tracks during my formal study likely reflected some of this behavior. Other studies have shown that squirrels can delay onset of movement markedly during winter, but still leave their dens, even when temperatures are low (Cotton and Parker 2000a).

During the breeding season, females stayed within their core areas of use, but their duration of activity increased compared to the nonbreeding season. In contrast, males also stayed out of the den much longer, but also engaged in large roaming circuits in search of females. It appears that this latter behavior by males is relatively short lived and associated with the season when females are in estrus (April-June in these study areas; Villa et al. 1999), and that the peak of this behavior can vary from year to year. Such behaviors appear to put them at increased risk of predation but these risks are compensated to some extent by using increased cover while at activity sites, and travelling at higher rates of speed between sites compared to the non-breeding season. Given that both sexes are promiscuous (Wilson 2000), the overall breeding strategy for flying squirrels, at least in low-density populations, appears to be one where males disperse genes across the landscape whereas females focus on survival by remaining in familiar territory, increasing their likelihood of surviving and successfully bearing and rearing young.

Density-dependent social interactions, rather than food quality or risk of predation, may have driven some of the behavioral differences observed between LOW and HIGH forests. Squirrels in HIGH forests exhibited shorter distances to core activity areas, reduced distances between activity sites, and increased numbers of sites per hour. However, they stayed out of the den similar lengths of time as squirrels in LOW stands. They also used more activity sites, but moved shorter distances, and spent less amounts of time at each site compared to squirrels in LOW forest. If predation risk was reduced in HIGH sites, there would be less need to move as frequently and if food quality was high and abundantly distributed in space, I would have expected squirrels to use fewer sites compared to LOW forests. However, this was not the case. Observers were not always able to distinguish between foraging and social behaviors at activity sites (Appendix) and therefore I could not rule out the possibility that increased numbers of activity sites on HIGH stands were due to increased social interactions that were a consequence of high densities.

Another limitation of my radio-telemetry study was that I was not able to directly assess energy requirements for my radio-collared squirrels, and relatedly, variations in food quality consumed at activity sites. Not only would this information be useful in better understanding food as a limiting factor, it would have likely improved the predictability for some of the endogenous variables in my movement pattern models with low R^2 scores (e.g., number of activity sites used and average time spent at activity sites), and therefore led to a more complete model explaining squirrel movement patterns outside the den.

Implications for Live-Trapping Studies

Live-trapping can be used effectively to estimate population abundance and density in many forests but this study suggests that both behavioral and habitat-related factors can influence trapping success in various ways. First, squirrels do not move randomly through the woods, and therefore violate the statistical assumption that captures (or telemetry fixes) are not autocorrelated in space and time. Rather, squirrels move through the woods in response to complex interactions that include obtaining food in relatively familiar locations, avoiding predators, and meeting social needs, all of which require a combination of memory (where food was found previously or where the movement boundary of another squirrel is located) and evaluation of proximate cues once a squirrel reaches its core foraging areas (e.g., scent of a new food source or presence of another squirrel or a predator). This autocorrelation can be observed from analysis of trapping data (D. McClure and E. D. Ford, University of Washington, *in litt*) and from direct observations of foraging (Pyare and Longland 2001b, this study).

Second, social behavior and interactions with other squirrels was common during each nightly bout of activity, especially at the onset of activity during the breeding season. Therefore, if food is not a driving force when a squirrel is in proximity to a trap, their interest in traps may be reduced.

Third, activity at or near the forest floor represented a relatively small percent of activity time and distance covered while squirrels were active outside their dens. Limited time on the ground means limited opportunity for encountering a trap compared to Townsend’s chipmunks which use the forest floor extensively and have much higher capture and recapture rates (e.g., Carey et al. 1999a).

Fourth, the likelihood that squirrels encounter traps on the ground may be reduced in complex forest compared to forest with simplified structure, especially given the greater amount of physical surfaces and social interactions taking place in the canopy. This phenomenon may explain in part, why an additional week of trapping was needed in several of my structurally complex forests that were being trapped for the first time, even after pre-baiting during the week prior to trapping. Markedly low first-season capture rates have been observed in complex forest elsewhere (e.g., Lehmkuhl et al. 2006, Ransome and Sullivan 2003, Rosenberg and Anthony 1992, Smith and Nichols 2003). Additionally, because scent plumes are more dispersed in complex forest compared to simple closed-canopy forest (Conover 2007), it may be more difficult for squirrels to cue in to baited traps, and therefore squirrels may be less likely to encounter traps on any given night, depending on trap spacing. The direction and strength of scent plumes may also explain why there can be seasonal differences in capture rates (with summer having lower rates than wetter seasons where moisture can help carry scent) and why captures can be higher near bodies of water in drier forests (e.g., Meyer et al. 2007a).

Fifth, squirrels either reduced their duration and extent of activity, or did not leave the den during winter. Reduced activity during this season may reduce the likelihood of squirrels encountering traps. In contrast, increased activity and movement during the breeding season could also influence trapping results by increasing the likelihood that non-resident males are trapped and could explain male-biased sex ratios shown during the spring in some studies (e.g., Witt 1992). Although this behavior did not result in mis-categorizing populations into HIGH or LOW stands for this study, it may be of concern where more precise abundance estimates are desired. For these reasons, fall may be the best single season for sampling flying squirrel population as it appears to better sample resident squirrels at a time when they are active outside the den, and it also provides an indication of the reproductive success for that year.

Finally, mean maximum distances moved between trap stations (e.g., MMDM) is often used to evaluate home range size and effective trapping area. As has been previously suggested in the Pacific Northwest (e.g., Witt 1992) and shown elsewhere (Holloway and Malcolm 2007), this study supports the idea that MMDM represent distances between activity sites rather than overall home range size, but may still be a useful index for making relative comparisons among forests that vary in squirrel densities.

Overall, both movement behaviors and habitat factors may help explain why daily captures of flying squirrels in traps can be heterogeneous and low for some populations (Rosenberg et al. 1995) and emphasizes why live-trapping data should be interpreted within the ecological context in which trapping takes place.

CHAPTER FIVE—MANAGEMENT IMPLICATIONS

Variable-Density Thinning

Some caution appears warranted in the short-term when using thinning to reach long-term forest management goals, including those under the Northwest Forest Plan. Variable-density thinning can have rapid, positive effects for many forest-floor prey species (e.g., mice, voles, chipmunks, neotropical and resident songbirds), especially due to increased understory development (e.g., Carey 2001, Carey and Wilson 2001, Haveri and Carey 2000). However, like most other thinnings, variable-density thinning appeared to keep squirrel populations suppressed and may do so for several decades until long-term ecological processes provides sufficient structural complexity in the midstory and overstory favorable to squirrels.

An important key to the success of variable-density thinning in accelerating squirrel habitat may be focusing early on stimulating mid-story development throughout the stand. In forests that lack a mid-story source (either in the seed bank or as seedlings or saplings on the forest floor) at time of thinning, underplanting with shade-tolerant species may help encourage faster midstory development than relying on natural recruitment of trees. In forests with abundant shade-tolerant regeneration, thinning of saplings may be needed to prevent competitive exclusion that would otherwise slow their growth. In some cases, management of understory vegetation may also be needed to allow new trees to quickly grow above the understory layer so they can outcompete any existing shrubs for sunlight, space, and nutrients.

Flying Squirrel and Spotted Owl Habitat

Understanding important components of high-quality flying squirrel habitat is a critical part of managing for spotted owl habitat and meeting long-term objectives under the Northwest Forest Plan (USFWS 2008b). Two structural conditions appear to be good for flying squirrels—(1) forest with a relatively even-aged dominant layer of trees (especially larger, older trees) and little understory where structural occlusion is high due to a closed canopy and high bole density, and (2) complex, multi-aged forest that provides crown-to-ground cover both vertically and horizontally through forested space. However, only the latter condition provides high-quality spotted owl habitat (Thomas et al. 1990). Thus, focus on developing and managing for structurally-complex forest across a dynamic landscape may be the best long-term strategy for managing habitat for both spotted owls and flying squirrels.

There are no indications that flying squirrels populations as a whole are threatened in the Pacific Northwest (although certain sub-species in the eastern U.S. continue to be threatened due to forest fragmentation and landscape modifications by humans; Weigl 2007). Their plasticity in being able to use a wide range of forested habitats (Smith 2007, Weigl 2007), mobility of males during the breeding season (this study), and promiscuity by both sexes (Wilson 2000) suggests that flying squirrels have sufficient adaptations that will allow them to persist in the region for the foreseeable future. However, squirrel abundance may be much more critical than squirrel presence in a given forest in terms of their ability as a species to fulfill important ecological roles, including serving as abundant prey for spotted owls and other predators, and for promoting fungal diversity. The landscape-level spatial variation in habitat quality that affects squirrel abundances remains markedly different today compared to the past. Prior to the 1900s, there were relatively high amounts of high-quality habitat for squirrels distributed across the landscape, and large patches of unsuitable habitat was limited to catastrophic disturbance events and natural variation in non-forested habitat. Twenty years ago (prior to the Northwest Forest Plan), clearcutting and short-term-rotation forestry over several decades resulted in highly-fragmented landscapes with much less high-quality habitat. Today, a forested landscape exists on federal and some state lands that is more permeable to flying squirrels compared to 20 years ago due to restrictions in large-scale clearcutting, but there continues to be less high-quality habitat on a regional scale than existed a century ago.

Some thought, therefore, could be given to landscape-level strategies that can help transition forests from highly-permeable low-quality habitat to highly-permeable high-quality habitat for flying squirrels over the next several decades. Such strategies might include: (1) keeping some high-stem-density young forests on the landscape to provide moderate to high squirrel populations in the short term, while recognizing that they can be highly ephemeral due to natural processes (e.g., competitive exclusion may open up these stands over only a few decades and reduce their ability to support high squirrel abundances after that point, e.g., Legacy Forest control stands); (2) limiting the likelihood of catastrophic disturbance to existing high-quality habitat such as creating defensible buffers around high-fire-risk squirrel habitat; (3) continue the use of variable-density thinning to promote long-term habitat benefits for squirrels but consider landscape context (stand age, rotation, and juxtaposition) to help facilitate rapid recolonization of thinned stands once stands develop conditions favorable to squirrels (Wilson 2003); and (4) provide additional protection of existing habitat in the region across a wide range of land ownerships through land-use designation and strategic partnerships (e.g., Wilson et al. 2009). Included in all these strategies should also be recognition that a wide range of forest conditions may be needed at certain scales to promote and sustain overall biodiversity that goes beyond the specific needs of flying squirrels.

It is also possible that silvicultural prescriptions could ameliorate some of the negative short-term effects of thinning by focusing on strategies that keep visual occlusion high while still promoting the structural processes that lead to complex forest or that reduce likelihood of catastrophic fire or insect outbreaks. This study provides empirical data upon which such prescriptions might be designed and tested. High-quality squirrel habitat that supported moderate to high densities of flying squirrels exhibited: (1) presence of mid-story trees, deep crowns and high stem density that provide high structural occlusion 10-20m above the ground, (2) <20% non-creek canopy gaps (as defined by this study—note that percent canopy cover could be less than what is implied here) for multi-layered forest and <15% canopy gaps for high-stem density forest without a mid-story, and (3) few canopy gaps ≥400m^2. A silvicultural prescription might include: (1) leaving patches of forest intact (skips) to provide continued horizontal occlusion after treatment (sufficient to limit visibility within the skips and between gaps); (2) keeping gap sizes small (100-400m^2), (3) retaining a range of tree size classes rather than thinning from below to promote only the largest trees, and (4) promoting development of shade-tolerant species throughout the stand. Such a prescription might provide sufficient structure to limit predation in the short term, while still helping to accelerate the development of long-term structural complexity in the stand over the long term. A skip-small gap strategy may be most successful in young stands with high stem density, in stands where dead branches of existing trees persist well below the live crown of the overstory, and in mixed-conifer stands where shade-tolerant conifers are already present at layers below the dominant tree crowns. In each of these cases, there is potential to keep occlusion in the mid-story layers relatively high after thinning. It may also be easier to achieve desired future structural conditions for flying squirrel faster in young stands where the vertical distance between the bottom of the overstory canopy and the understory is relatively small, allowing a midstory layer of trees to more quickly bridge the vertical gap between these layers. Creation of an occasional larger horizontal gap might be appropriate, but in many areas, larger gaps will develop naturally over time due to a range of stochastic events (windstorms, disease pockets, etc). Thus, imposing large gaps too early in stand development may have a multiplicative negative effect with natural gap-creating events.

A skip-small gap prescription may also be useful in xeric forest where thinning and prescribed fires are being used to reduce heavy fuel loads that have resulted from more than a century of fire suppression (Hessburg and Agee 2003). Lehmkuhl et al. (2006) suggested that patchy harvesting of trees to reduce fuel loads might help keep flying squirrels on the landscape after such treatments. My study supports their hypothesis, but also suggests that the scale of patchiness would be important as would be the retention of structural occlusion in the patches that are not harvested. Leaving patches of high-occlusion forest is consistent with the structurally diverse conditions that can result under some naturally-occurring fire regimes that keep fire fuel loads low (Agee 1993, Harrod et al. 1999, White 1985) but is markedly different than commonly used fuel-reduction strategies that focus instead on wide-scale removal of surface, ladder, and crown fuels (e.g., Peterson et al. 2005) that reduce overall structural occlusion throughout a stand.

This study suggests a few additional considerations when managing habitat for flying squirrels. For example, providing travel corridors for squirrels by leaving narrow strips of residual trees across gaps that would otherwise be too large for squirrels to glide across could create predator traps, leaving squirrels more vulnerable than if they travelled around the gap in more closed-canopy conditions. Likewise, thinnings that result in widely-spaced trees that will become future super-canopy dominants may also be detrimental to squirrels in the long term if the vertical distance between these trees and next layer of trees is so great that it would result in long, exposed glides—flying squirrels often use the tallest trees in the area to launch glides (Weigl et al. 1992, personal observations). This "supercanopy" effect may explain, in part, the lack of squirrels captured in my old-growth stand with the highest tree species diversity (Stand 969).

Although predation may play the strongest role in regulating squirrel populations, managing for structural complexity that provides protective cover can in large part be a surrogate for managing for food resources, as it is difficult to build forest structure without relying on the diversity of trees and shrubs that are needed for complex structure. Retaining and promoting diverse understory plants, trees, and shrubs would not only help ensure a more reliable food source for flying squirrels that could be important in maintaining high-density populations once they have sufficient protection from predators, it can also promote broader biodiversity goals such as supporting diverse and abundant plant and wildlife communities, and thus, help meet the overall objectives of the Northwest Forest Plan. Likewise, retention of large, decadent trees and snags can provide den substrates for a wide range of cavity-using species, and therefore contribute to the broader ecological functioning of a forest, even if their role as a limiting factor for flying squirrels may be low relative to other factors.

Future Direction

This study could be furthered in several ways. First, the ubiquity of measures found important in distinguishing HIGH and LOW stands and gradients in squirrel abundances could be further tested through evaluation of a broader range of conditions found within the distribution of the northern spotted owl, especially xeric, hardwood-dominated, and high elevation (e.g., sub-alpine) forests, as well as forests where northern spotted owl diets transition from being primarily flying-squirrel dominated to being dominated by woodrats (*Neotoma* spp.). These metrics could also be explored outside the region, especially in the eastern U.S. where the structural complexity of many forests has been reduced for many centuries.

The data reported here could also be used for designing experimental studies that test threshold values for the variables I found important—thresholds that could be used for both evaluating the effects of current management activities on squirrels and designing new silvicultural prescriptions that might minimize the negative effects of thinning, canopy gap creation, or fire fuels reduction on flying squirrel populations. For example, my evaluation of canopy gaps was limited to naturally-created gaps and gaps created within a matrix of variable-density-thinned forest. Experimentally inducing gaps within an otherwise unthinned forest could improve understanding of the trade-offs among gap size, spacing, and frequency of gaps for flying squirrels.

Further refinement of indices for measuring structural complexity are also needed that can take into account more detailed multi-dimensional aspects of forest structure in the field, as well as measures that can be used for more rapid, landscape-level evaluation of squirrel habitat. Fine-scale occlusion could be measured using laser rangefinders or ground-based LIDAR (light detection and ranging) equipment. At the landscape level, there is also need to bridge the gap between fine-scale structural complexity that appears important for squirrel habitat and coarse-scale analyses (e.g., satellite imagery data). This is especially important given the regional scale at which forest management will need to occur to successfully meet long-term objectives under the Northwest Forest Plan.

I found that my measures of ecological processes were useful in selecting study sites that represented wide gradients in structural complexity, suggesting that such metrics may be a better indicator of forest conditions than assigning forests to a stage or age based on presence of a few habitat components (e.g., large, old trees for "old-growth"). Similar measures that account for the full range of structural complexity gradients found in regional forests could be developed that might serve as a better platform for describing and quantifying forests in the region, especially given that site-specific processes and disturbance histories make each forest unique in their structural composition. Use of structural process indices might also keep focus on managing for important ecological processes, rather than managing for a specific forest stage that might never be reached if process trajectories are continually altered due to anthropogenic or natural influences. These include subtle shifts in structure over time due to small-scale stochastic events like repeated windstorms or small pockets of slowly spreading disease that might not be noticed without regular monitoring efforts. Although none of the process scores that I used were strongly associated with flying squirrel abundance, three in combination (crown-class differentiation, canopy stratification, and understory development) could moderately predict stand-level squirrel abundance. Development of species-specific indices that weigh for the ability of each process to promote specific habitat elements might allow for better quantification of habitats and potential future habitats for a wide range of forest-dwelling species, including flying squirrels.

Finally, further evaluation of the relationships among potential limiting factors and the structural complexity-predation hypothesis is warranted. This is important not only for evaluating the merits and ubiquity of limiting-factor hypotheses that I have proposed, but also for refining our understanding of how best to manage squirrel habitat, including where emphases should be placed in space and time when doing restoration activities that promote habitat for spotted owls and squirrels, especially given the potential economic costs of such activities. More empirical data is also needed on predator-squirrel interactions and behaviors, including the relative importance of vision, scent, and hearing for predators like owls and mustelids to detect and successfully capture squirrels, effects of fine-scale structural occlusion on squirrel detection by predators, and how forest structure and landscape context plays a role in predator-prey dynamics.

In summary, northern flying squirrels appear to be useful indicators of both the health and management of Pacific Northwest forests. They are sensitive to the gradients in structural complexity found across managed and natural forests, their ecology and habitat needs can be met in forests that support biological complexity desired in regional forests, and their populations respond to changes in structure at typical management scales of consideration. Their habitat needs can also be used to develop stand and landscape-level strategies for recovery of the northern spotted owl. Although forest structure can be directly measured, the use of flying squirrels as the lens through which to evaluate forest structure provides important ecological context for why, and at what scale, structure is ecologically relevant. Until we have fuller understanding of the implications that natural processes and management activities have across the full range of forest ecosystems present across the region, a suite of biological indicators will continue to be needed to provide such lenses. Flying squirrels may be one of the best of such indicators at the patch and stand-level scales.

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APPENDIX—ANECDOTAL OBSERVATIONS

There were several ancillary observations of squirrel behaviors made during formal data collection during this study. Some of these observations occurred during telemetry protocol development, where observers were allowed to get as close to squirrels as possible to test the spatial limits for squirrel tolerance of human observers. Others were made during regular night telemetry tracking bouts (visual observations of squirrels were made at 9% of activity sites). Behavioral observations of squirrels also occurred while releasing squirrels during live-trapping studies. Such information is seldom allowed in journals, given space limitations, but I am including a few key observations here to provide context for why some of the data was collected in the manner that it was. Some of the following information could also be useful in design future studies that continue to inform our understanding of flying squirrel ecology.

Squirrel Response to Humans and Noise

Observer bias that changes the behavior of the study animals is always a potential concern in wildlife studies. I found that northern flying squirrels, with some exceptions, could be studied at fairly close range (e.g., 10-20m) with some practice and precautions, as has been observed for other flying squirrels (e.g., Siberian flying squirrels, *Pteromys volans*; Selonen and Hanski 2006). Unlike diurnal sciurids on my study sites which often gave out alarm calls or rapidly sought hiding cover in response to human presence, flying squirrels seemed to tolerate and even ignore humans during most human-squirrel interactions. For example, it was common to observe squirrels foraging immediately upon release from traps during the day, sometimes at (or even on) the feet of technicians, as long as technicians were quiet and did not noticeably move while releasing squirrels. This never occurred with Douglas' squirrels, eastern gray squirrels (*Sciurus carolinensis*; Bayrakci et al. 1999), or Townsend's chipmunks. Technicians could sometimes also follow flying squirrels after trap release during the day to within <1 meter of the squirrel as they continued to forage on the ground (though several attempts over the years to grab food items from their mouths were always unsuccessful), as long as the technicians did not break any sticks or make any other sudden sharp noises. Human voices also did not have any observable effects on squirrel behavior (e.g., changes in body position, movement away from sounds, freezing, or turning of the head towards the noise). However, response to sharp, sudden noises appeared to be deeply-ingrained, as even heavily-sedated squirrels (e.g., during radio collar attachment) would jerk suddenly in response to a sharp noise (e.g., a pencil dropped on a clipboard), whereas they gave little or no responses to most other sounds. Likewise, if squirrels were startled while on the ground by a sharp noise (both during daytime trap releases and while being tracked at night), they would usually find the nearest tree and go to the backside, pause briefly, and then resume activity on the ground or in the canopy. This response to sharp sounds may be an evolutionary adaptation for responding to predator attacks and would be especially useful in tree canopies where owls may inadvertently strike a branch on their way into the canopy to attack a squirrel.

Notes about Continuous-tracking Protocol Development

Consistent and accurate interpretation of telemetry signals for radio-collared squirrels moving in a multi-dimensional forested environment was important for this study. Numerous factors influenced radio-telemetry signal patterns including distance between observer and squirrel, terrain, canopy cover, weather condition (especially rain), individual transmitter and battery condition, antenna condition, spatial position of the transmitter antenna in forested space (canopy, ground, bole), as well as changes in signal that resulted from squirrels engaging in temporally-diverse activities such as gliding, traveling across canopies, and resting.

Protocol development for tracking squirrels occurred over an 18-month timespan in 1992-93 prior to the onset of data collection for this study. During this period, several approaches to monitoring squirrels were tried. Because an extensive secondary road network existed on the Legacy and Timber Forests, I first used vehicles and omni-directional roof-mount antennas to determine general activity periods. I and technicians also tried taking remote (30-250m) single- and triangulated (two observers at the same time) bearings on squirrels using H-antennas and hand-held receivers. Although the terrain on the FES had relatively low relief, we quickly determined that even small changes in topography had large influences in radio-signal direction and strength when measured from a distance and therefore the accuracy of triangulations from a distance was low. This led to strategies that could more accurately measure how squirrels were moving through the woods over space and time in real time. Eventually, we found that the best approach was to follow squirrels by continuously homing on their location, but keeping a distance of 10-20m between the observer and the squirrel. This limited our ability to directly observe squirrel behaviors, but because of the stop-and-go approach that squirrels took when moving through the woods, this trade-off allowed us to delineate discrete horizontal travel paths and localized activity (activity sites) while minimizing behavioral influences due to our presence.

Extensive training of technicians was undertaken before any data was kept for the radio-telemetry study. Inexperienced technicians were usually put under the direct supervision of myself or another experienced technician for up to 4 weeks until they could consistently describe and map a full activity bout while maintaining a discrete distance from squirrels. In addition to this training period, skill in interpreting telemetry error, signal bounce, and radio signal strength was constantly practiced by all observers through homing of squirrels while they were in their diurnal dens by multiple technicians (up to 60 squirrels at a time were being monitored for den use during these periods; Carey et al. 1997). Although technicians could not always keep a minimum 10m distance from squirrels (e.g., squirrels would at times move towards the technician), several observations supported the idea that our protocol had minimal effects on the overall activities of squirrels. For example, after a few nights of following an individual squirrel, technicians could usually predict the general locations where squirrels were likely to go on subsequent evenings (though specific activity spots would constantly change). Sometimes we would wait quietly at a likely foraging area on a subsequent night, rather than following the squirrel as it left the den, to see if squirrels would continue to use the same general foraging areas. Indeed this was repeatedly the case and suggested that our monitoring did not unduly influence squirrels to travel to general locations that they would otherwise not go. Also, as with daytime trap releases when observers made little movement or noise while releasing squirrels, squirrels would sometimes forage at the feet of telemetry observers, after travelling across the ground towards the observer. On rare occasions, squirrels appeared to investigate an observer and would glide down from the canopy and land on a tree in front of (and on 2 occasions, even on) an observer. This happened during both protocol development and during the formal study.

If technicians approached too close to squirrels, any sharp noises made (especially breaking of small branches and twigs) would cause squirrels to bolt suddenly to the nearest tree bole or travel to the back side of the bole they were already on. However, typical foraging activity usually resumed within 1-2 minutes of this disturbance. To help minimize noise, we established an extensive network of light trails throughout all study areas that allowed us to quickly and quietly follow squirrels. These trails generally followed trapping lines (spaced 40m apart) and were especially useful in the Timber Forest where heavy brush made travel fairly noisy otherwise. It also allowed us to work around hazards that would otherwise be difficult to see at night (e.g., concertina wire and foxholes present as a result of military training activities). Trails were also useful in the HIGH forests where complex structural conditions and topography limited our mobility relative to squirrels. We could not, however, track breeding males in either of the HIGH forests where we followed squirrels, given the high travel rates and distances covered by males during the breeding season.

Flashlight beams directed at a squirrel's eyes while they were in trees would sometimes cause them to turn away or go to the backside of a tree, but did not otherwise cause a change in activity. We briefly experimented with night vision goggles and infrared flashlights, but found their use to be limited—squirrels traveled too fast between activity sites, activity high in tree canopies was difficult to see, and we could not keep up with squirrels while wearing goggles. Instead, if a squirrel's eye shine was detected, we would quickly turn the flashight beam away. We also began gluing reflective tape onto radio-transmitters to aid in locating squirrels. This allowed us to make a quick sweep of the canopy with a flashlight beam to pinpoint the squirrel's location, without relying on prolonged contact with the flashlight beam.

Witnessed Predation Events

On two occasions prior to the onset of this study, once in the Oregon Coast Range and once in the Northern Cascades of Washington, I witnessed squirrels being unintentionally released from traps in the presence of a northern spotted owl. In both cases, the owl waited for the squirrels to climb up a tree and glide and then the owls struck the squirrels in mid-air, swooped down, retrieved them from the ground, and carried them off. The extent to which this technique is used to kill flying squirrels is unknown, but it does suggest that squirrels are vulnerable while they are gliding, and experienced spotted owls can capitalize on this vulnerability.

In 1993, I tracked an adult radio-collared male flying squirrel when it was attacked by a great horned owl. The encounter lasted 2 minutes with the owl repeatedly trying to attack the squirrel, and the squirrel giving out shrill calls while moving through the canopy of the same tree. The owl eventually ceased attacking, and the squirrel then remained in the canopy, relatively motionless, for 45 minutes before resuming activity. Likewise, in 1995, a screech owl attacked a trap-released squirrel while it was climbing up a tree bole. The squirrel quickly reached the live canopy (out of sight of the observer) and remained there while the owl continued to attack. The squirrel survived, and was captured in a live trap the following week. Both incidents suggest that canopies can offer sufficient cover to ward off a direct attack by owls.

During the night telemetry session in winter 2005-2006 on the FES, seven squirrels were being monitored that denned less than 600m apart. In early January 2005, a pair of breeding barred owls began calling each night within 80m of one of the squirrel dens. Thereafter, the owls were regularly heard during each tracking night. Within 4 weeks, all but one of the radio-collared squirrels had been preyed upon, and evidence from collar and squirrel remains was consistent with owl predation (Wilson and Carey 1996), forcing us to stop monitoring squirrels in this forest. Given the proximity of the barred owls, and the fact that it was the breeding season when tolerance for other large owls capable of killing squirrels (e.g., great-horned owl for the FES study) was likely low, I assumed that this pair of barred owls caused the rapid squirrel mortality I observed. Barred owls were also detected during telemetry studies on the primary HIGH stand studied (Stand #912) during 2006. However, no rapid depredation was observed, and the limited predation of radio-collared squirrels that did occur (n=4) was consistent with both owl and mustelid predation (in one case, a spotted skunk sprayed me as I dug into the ground to retrieve the collar). One night, a barred owl, apparently attracted to the sounds emitted from the telemetry receiver, flew onto a branch about 15 feet above myself and one other observer and watched us for several minutes before flying off. This attraction to receiver signals was a relatively common occurrence for saw-whet owls on the FES (the cadence and tone of sounds made by telemetry receivers were similar to those made by saw-whet owls during the breeding season).

Social Behavior

Interactions between individual squirrels were noted throughout the study but few were directly observed. Vocalization was also rare during the formal telemetry study (n=13 occasions), and usually involved two or more squirrels in the canopy of the same tree. All vocalizations sounded agonistic in tone and were most common during the breeding season.

I observed two encounters between a juvenile male and adult male during the study (these were the only two known juveniles radio-collared during the study). During the 2005-2006 telemetry session on the Legacy Forest, the juvenile male would travel approximately 400m south immediately upon leaving its den for several consecutive nights to the edge of a core area used by an adult male residing in a different den. The two males would meet up in the same patch of trees for several minutes. The adult male would then move off and continue foraging. If the adult male did not show up, the juvenile would stay in the same patch of trees for 20 minutes or longer, before eventually returning to its den. This behavior continued for 3 weeks in January and February before both were consumed by owls. A similar juvenile male- adult male encounter was also observed in the HIGH forest. In this case, the juvenile male abruptly changed its regular foraging pattern one night (which sometimes included travel with its presumed mother) and travelled to the edge of a core area used by an adult male residing several hundred meters away. The two males met up briefly, and the juvenile then immediately and rapidly travelled back to his regular foraging patches where he met up with his mother. These two cases may have been observations of juveniles exploring their surroundings (both forests), a social need to discover other squirrels in a population of few individuals (Legacy Forest), or may have been pre-breeding behavior as males became scrotal as early as January in these forests (Villa et al. 1999).

Site Fidelity and Territoriality

There were no major shifts in foraging areas within seasons or across years for adult squirrels suggesting that once a foraging area is established for an individual, it may be relatively fixed for life. There were a few exceptions noted, including one male and one female squirrel moving their core activity area 160m and 270m respectively between a 1-year period. Mortality of their respective denmates also occurred during this interim so shifts in their foraging areas used might have been driven by a need to den with other squirrels. Whether core areas were defended was unclear during this study, as aggressive encounters between individual squirrels was rarely observed. However, the relative lack of overlap observed among circuit paths and activity centers, especially in the Legacy and Timber forests suggests that space use by adult squirrels was relatively independent. On the HIGH Forests, there was substantially more crossover of travel paths and shared use of the same activity sites compared to the Legacy and Timber Forest sites than was captured during this study due to my methodology (random sampling of squirrels each night). We routinely monitored the radio signals of other squirrels likely to be in the vicinity of each squirrel being followed, and transcriptions from nightly tracks suggested that overlap in circuit paths occurred routinely among denmates in the HIGH forests. For example, for one denmate group (an adult male, adult female, and the juvenile male described above), crossover and shared use occurred regularly by the adult female and a juvenile male, presumably her offspring, but not the adult male. For a second group (1 adult male, 2 adult females), all three squirrels regularly crossed over each others' paths each night, and interacted directly on several occasions. On one occasion, one of these females was feeding for 20 minutes on fungi growing on a snag until the other female arrived, chased her away, and began feeding on the same snag. There was, however, no overlap observed among squirrels that were not den mates on the HIGH Forests and we rarely made any such observations in the Legacy or Timber Forests. As with the differences observed in general foraging patterns between HIGH and LOW forests, this could suggest that social pressures influence movement patterns and space use in HIGH forest more than they do in LOW forest. If denmates were related in HIGH forests, but not in LOW forests, it might also suggest that squirrels in HIGH forests (where potential denmates are not limiting) put more social emphasis on sharing space use outside the den with related individuals whereas squirrels LOW forests (where food or space is not limiting) put more social emphasis in meeting thermoregulatory needs provided by group denning, regardless of individual relationships.

Foraging Observations

Squirrels exhibited little motion while consuming foods, especially truffles. Both daytime (trap release) and night time (telemetry) observations suggested squirrels consumed truffles in a consistent manner. They would first pull the truffle close to their body and hover over it, then rotate the truffle over and over until most of it was consumed (similar to humans eating corn-on-the-cob). Even when observers were relatively close (<2-3m away), it was difficult to detect much movement. Given the posture, such feeding behavior may help minimize detection by overhead predators.

During daytime follow-up of night telemetry activity sites during the fall, observers frequently observed epigeous fungi cached at the intersection of the main tree bole and low dead branch stubs (1-2m above ground). It was unclear whether these fungi were being cached by flying squirrels or Douglas' squirrels. During bi-annual nestbox inspections on the FES, however, we never found cached food. Thus, there was little evidence to suggest that northern flying squirrels on my study sites relied on caching as strategy for meeting energy needs, especially during winter. The FES sites were seldom covered with snow during winter, but the ground could be frozen for several weeks at a time. However, this did not stop squirrels from making visits to the ground in search of food and on at least two occasions, we observed squirrels digging through frozen ground to forage on truffles during the middle of winter.

Response to Roads

Roads are often cited as a potential hazard for forest-floor small mammals (e.g., Kozel and Fleharty 1979, Swihart and Slade 1984, Clark et al. 2001) but their effect on arboreal rodents has received little attention, with the exception that wide, exposed roads are a clear barrier to movement (Weigl 2007). Several secondary one-lane dirt, gravel, and paved roads bisected the FES study sites (4-10m wide, with associated canopy gaps of similar width). However, trees were tall enough and the distance between trees on opposite sides of the road was short enough that flying squirrels could easily glide across these roads and squirrels regularly crossed them. The same was true for 3 squirrels in my primary radio-telemetry HIGH stand that used large old-growth trees as launching platforms to glide over a secondary gravel road into younger forest on several occasions. In general, squirrels chose gliding over ground travel to cross roads in virtually every case. Most of the time, squirrels crossed roads without hesitation, but on 2 occasions, I observed squirrels hesitate for several minutes before crossing the road. I speculate that they may not have been familiar with the area as both were male squirrels travelling far from their normal core activity areas in search of females during the breeding season. I did not observe any apparent relationship between distance to road (or other canopy gaps) and mortality sites of radio-collared squirrels (Wilson and Carey 1996, this study). This would be difficult to detect, however, as both owls and weasels were capable of carrying and consuming squirrels at locations distant from kill sites.