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Biology of Gliding Mammals

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Ecology of Northern Flying Squirrels: Implications for Ecosystem Management in the Pacific Northwest, USA

Abstract

Northern flying squirrels (Glaucomys sabrinus) in the USA Pacific Northwest are keystone species that disseminate the spores of ectomycorrhizal fungi symbiotic with Pinaceae and that are preyed upon by a variety of vertebrate predators. Substantial research has shown that these squirrels tend to be most abundant in naturally regenerated forests >100 years old (old growth and younger mixed-age forest with legacies from old growth), whereas abundance in second-growth forests is highly variable and often quite low. Flying squirrels vary in life history attributes from north to south, including adult body mass, rate of juvenile weight gain, age of sexual maturation for females, proportion of females that are sexually active, survivorship, population age structure, and population density. Some life-history attributes and predation seem density-dependent. There is less variation between managed and old forest within physio-graphic provinces than among physio-graphic provinces. The most common difference between managed and natural forests is population density. Environmental correlates of abundance vary among areas, but seem to include abundance of coarse woody debris in drier regions dominated by Douglas-fir (Pseudotsuga menziesii), abundance of ericaceous shrubs in wetter regions

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dominated by western hemlock (Tsuga heterophylla), abundance of cavity trees, and habitat breadth-variety of vegetation site types that differ in species composition, foliage height diversity, and, possibly, deciduous trees that produce cavities and seeds, nuts, catkins, or other food that augments the squirrel's diet. Flying squirrel ecology provides practical insights for forest ecosystem management and conservation of biodiversity in Pacific Northwest forests.

Keywords

Glaucomys sabrinus, flying squirrel, keystone species, ecosystem management

1. Introduction

Northern flying squirrels (*Glaucomys sabrinus*) have become of increasing interest in North America because of their sensitivity to forest management. Twenty-five subspecies have been recognized in North America [51]. Relictual populations in the eastern United States, *G. s. coloratus* and *G. s. fuscus,* are federally protected as endangered species. In the Pacific Northwest, *G. s. oregonensis* is the most important prey of the threatened Northern spotted owl (*Strix occidentalis caurina*) [10, 12]. Recovery and maintenance of viable populations of the spotted owl may depend upon providing habitat for both the owl and the flying squirrel in second-growth, managed forests.

Flying squirrels and spotted owls are not the only species associated with old-growth forests [1, 42]. Hundreds of species of plants, fungi, and animals have been suggested as associated with old growth. The metaphysics of old growth and world views of interested parties have led to a polarization of forest management paradigms that is becoming engraved upon the land through allocation of land to specific uses: agricultural production of timber versus conservation of biological diversity in systems of reserves. Research on Northern flying squirrels and Northern spotted owls has produced a third alternative: conservation of biodiversity through active, intentional ecosystem management [7].

Wells-Gosling and Heaney [51] provide a review of the entire species. My goal in this paper is to review studies on *G. s. oregonensis* that provide guidance on how to manage coniferous forest ecosystems within the context of general sustainability--production of economic goods and ecological services over the long term in a culturally acceptable manner [7, 8]. First, I describe the area of consideration and methods that I have used to study flying squirrels. Then I summarize the distribution, patterns of abundance, life history, and role of the northern flying squirrel as a keystone species in coniferous forests in the Pacific Northwest. I discuss results of research in eastern Oregon, British Columbia, northern California, and elsewhere when it furthers understanding of *G. s. oregonensis*.

2. Environmental Context

The Pacific Northwest of the United States of America includes the parts of the states of Washington and Oregon south of British Columbia, north of California, and west of the Crest of the Cascade Mountain Range to the Pacific Ocean (Fig. 1), an area 600 km N-S (49 degrees N to 42 degrees N) and 200 km E-W. The Pacific Northwest contains 9 physiographic provinces: Olympic Peninsula, Coast Ranges, Puget Trough, Northern Cascades, and Southern Washington Cascades in Washington and Coast Ranges, Klamath Mountains, Interior Valleys (Willamette, Umpqua, and Rogue Rivers),

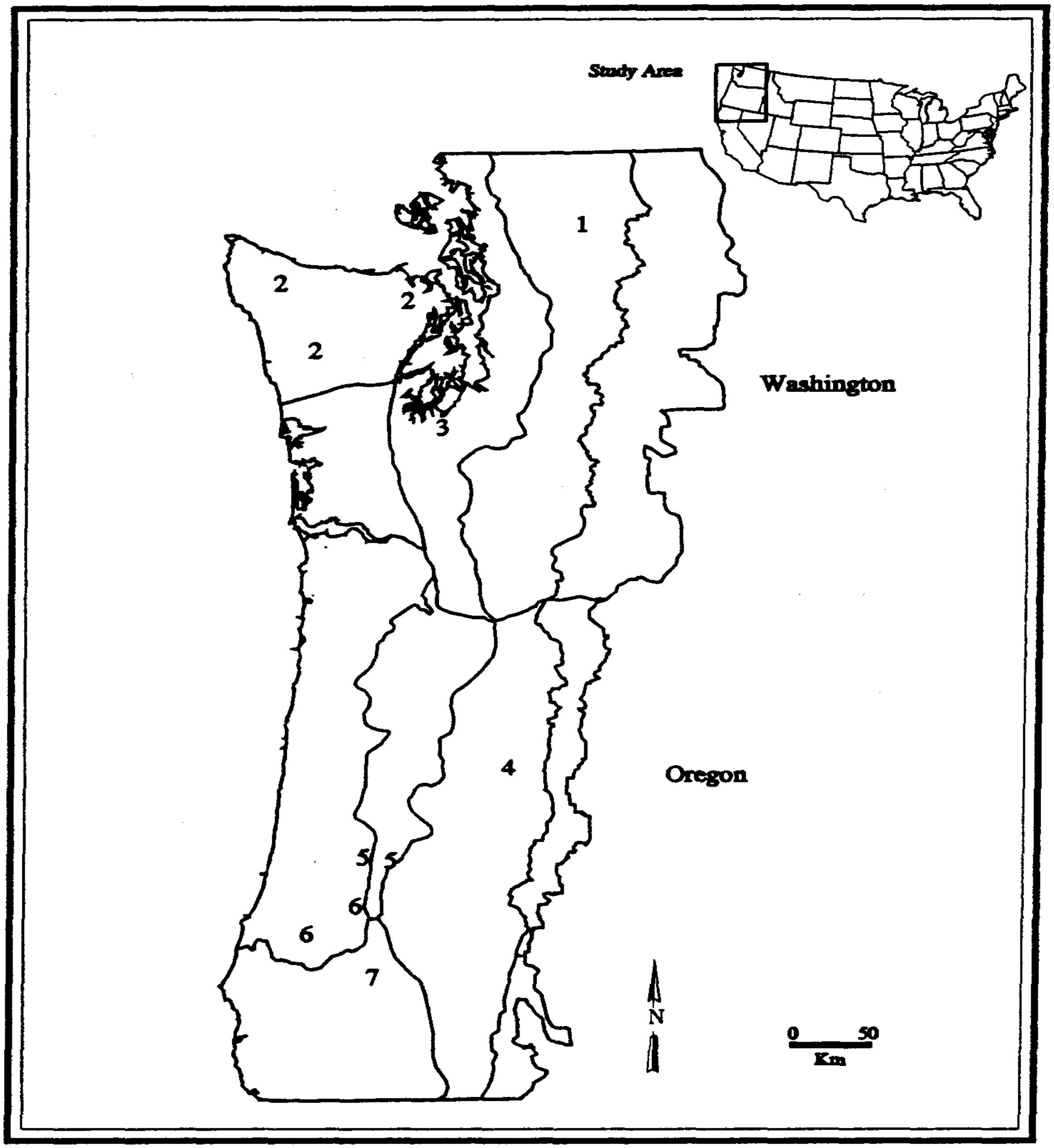

Fig. 1. Locations of major study areas for studies of *Glaucomys sabrinus* in the Pacific Northwest USA: (1) Northern Cascades, Washington, (2) Olympic Peninsula Washington, (3) Puget Trough, Washington, (4) Western Cascades, Oregon, (5) Interior Valleys, Oregon, (6) southern Coast Ranges, Oregon, and (7) Klamath Mountains, Oregon.

Western Cascades, and High Cascades in Oregon. Mountain ranges run N-S. The Pacific Coast abuts the Olympic Mountains, Coast Ranges, and Klamath Mountains which are followed easterly by the Puget Sound, Puget Trough, and Interior Valleys which abut the Cascade Ranges. In summary, the area is topographically diverse (sea level to > 2,000 m, > 4,000 m on a few volcanic peaks). The Crest of the Cascade Range forms a zoogeographic barrier for arboreal species (*G. s. fulginosus* is the subspecies east of the crest). The Columbia River separates Washington and Oregon and is a zoogeographic barrier. Interior valley grasslands, rivers, farmlands, and urban developments help to isolate metapopulations of different physiographic provinces.

Summers are warm and dry; fall, winter, and spring are cool and wet. This climate has resulted in fast-growing, productive coniferous forests of tall, long-lived trees of high timber value. Most of the Pacific Northwest is in the Western Hemlock Zone, a zone of wet to mesic forests dominated by Western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and Western redcedar (*Thuja plicata*). Sitka spruce (*Picea sitchensis*) *is* found along the coast, Pacific silver fir (*Abies amabilis*) as elevation increases, and subalpine forests and alpine environments at high elevations. There is a pronounced NS moisture-temperature gradient, with northern forests cool, moist, and dominated by western hemlock and silver fir. Return intervals for catastrophic fires are 350-550 years or longer; destructive windstorms occur about every 25 years. Southern forests are drier and warmer than northern forests and are dominated by Douglas-fir, other conifers, and evergreen hardwood species. Return intervals for catastrophic fires are 250-350 years; intermediate-scale fires occur at 10-25-year intervals. Temperature and moisture also vary with soil type, slope position, and aspect in accord with exposure to the sun in the afternoon. The complex moisture-temperature gradient results in: (1) markedly different natural disturbance regimes and seral-stage distributions of natural forests, (2) markedly different species composition and vegetation structure of natural forests, and (3) differences in ecological processes among forests in different provinces [42]. Timber harvesting and forest management generally have tended to simplify and homogenize these forests [4, 8, 10, 12, 15].

3. Study Areas

Prior to 1985, little research on northern flying squirrels had been conducted in the Pacific Northwest [31, 32, 33, 53, 54]. I chose 3 areas (Fig. 1) in which to replicate studies of flying squirrels in old-growth and second-growth forests: Olympic Peninsula (14 stands in 3 locations, 1987-89), central Western Cascades (10 stands in 1 location, 1987-89), and southwestern Oregon (19 stands scattered over 1,500 km^2, primarily in the Coast Ranges, but including stands in the Interior Valleys and Klamath Mountains, 1985-1991). I led field studies in southwestern Oregon and Olympic Peninsula [4, 10] and R. G. Anthony [29, 39, 40] led replicate and subsequent studies in the central Western Cascades. I expanded geographic coverage by initiating a large-scale manipulative study in 16 stands in 2 second-growth Douglas-fir forests [14, 15], 1 bigleaf maple (*Acer macrophyllum*)-conifer stand, and 1 old-growth conifer stand in the Puget Trough (1991-1997) and a small-scale comparison of 3 old-growth and 2 second-growth stands in the Northern Cascades in 1991-92 and 1996 [4]. In all, intensive study areas were distributed over >550 km N-S. Subsequently, others studied *G. s. flaviventris* in northeastern California [49] and *G. s. columbiensis* in eastern British Columbia [37].

4. Field Methods

Trapping aimed at flying squirrels in the Pacific Northwest has generally followed standard procedures [6]: wire box traps were set in grids with 40 m between each of 100 trap stations, 2 traps/station (1 1.5-m high in a tree and 1 on the ground) baited with peanut butter, molasses, and oats, and opened for 6-8 nights in fall after onset of fall rain or in spring before onset of summer drought. Traps were: (1) set with firm placement to preclude shaking during investigation by squirrels, (2) covered with waxed-paper cartons and woody debris to provide a sheltered environment with a familiar surface, (3) adjusted as needed to ensure crisp release with mild pressure and complete closure. Squirrels were handled gently using handling cones—0.5-cm wire-mesh cylinders (just large enough to contain squirrels) attached to cloth funnels that fit snugly over trap entrances. These cones markedly reduce chances of bruising and other injuries to flying squirrels often caused by manual handling. The standard procedures produced probabilities of capture and recapture of 0.50 [6]. Departures from these procedures often resulted in inadequate sample sizes and use of extended sampling periods to compensate for low captures, even with relatively high population densities [3, 4, 39, 40, 49]. In Puget Trough, squirrels also were captured by blocking entrances to nest boxes and cavities [14, 15] and in box traps set for small mammals in the summer.

Captured flying squirrels were described in terms of mass, reproductive condition, and age [47]. Reproductive categories were: never reproductive, testes scrotal, testes regressed, estrus, pregnant, lactating, post-lactating, and regressed. Genitalia and mammaries were described in narratives. Age was based on mass, reproductive condition, pelage color, facial features, and, during data analysis, capture history. Flying squirrels dying in traps were necropsied to determine reproductive condition, numbers of placental scars, embryos, and fetuses, and age based on epiphyseal closure. In 2 stands in southwestern Oregon, all squirrels caught were killed and necropsied to compare age and reproductive condition based on field examination to descriptions based on necropsy. Age (A) is reported by year (Jan-Dec): I = year of birth, II = year following the birth year, III = second year following the birth year, and IV = third year following the birth year.

Fecal pellets were removed from the anus of each flying squirrel that defecated upon first capture in a trapping period to avoid contamination with wind-born spores and bait, respectively. At least 50 microscope fields/pellet sample were examined at 400X to determine relative densities of spores of fungal taxa (genus for most hypogeous fungi and family for most epigeous fungi), fungal hyphae, lichens, and plant material [18, 20, 34]. Observations of feeding were recorded when flying squirrels were released after capture and during telemetry [45].

Some to all flying squirrels captured were fitted with neck-collar radio transmitters. Relocation with remote triangulation had low success because topography, large trees, tall canopies, and rapid movements by squirrels prevented routine, accurate relocation. Rugged topography and dense vegetation precluded following flying squirrels through the forest at night in southwest Oregon and on the Olympic Peninsula; thus only a few squirrels were studied with telemetry. Den sites were located during the day. In Puget Trough, study areas were relatively flat to rolling with well-developed networks of primitive roads. Again, triangulation proved unreliable. Strategically placed trails, existing roads, labeled grid points, and taking time to become familiar with large areas and squirrel movement patterns, however, allowed effective tracking of squirrels through the forest, identification of activity centers, and mapping of travelways and dens (unpublished procedures).

After pilot efforts, we attempted to place radios on all adult squirrels. All squirrels were regularly located in their dens [16]. Each night 1 observer would be assigned to track 1 randomly chosen squirrel. The observer would locate the squirrel during the day, sit near the den at dusk, and wait for the squirrel to leave. The observer would monitor the squirrel (sedentary or active) for 3-4 hours., Most squirrels would complete their nocturnal activity during that time. On a subsample of nights, squirrels were tracked all night long. As a check on the influence of observers on moving squirrels, observers would occasionally predict where a squirrel would go, based on past behavior, go to that place, and await the arrival of the squirrel uninfluenced by a person. Unlike a similar study [54], there appeared to be no undue influence of observers on squirrels; numerous nstances of squirrel resting, foraging, and social behavior were observed and squirrels followed predictable patterns of traveling and foraging.

Initial, retrospective studies of plant and wildlife communities compared natural “young” (40-70 yr), “mature” (80-200 yr), and old-growth (> 250 yr) forests [42]. When comparisons were extended to managed stands (post-clearcutting second growth, with or without subsequent manipulation), an expanded classification of stand conditions was developed to account for differences in retention of biological legacies from preceding stands, levels of decadence, degree of understory development, and stand history [7, 8]. These conditions included: competitive exclusion, understory reinitiation, developed understory, niche diversification, and old growth. In southwestern Oregon and Olympic Peninsula, 55 structural and compositional variables were measured at each of 3,400 trap stations [4, 11]. In Puget Trough, vegetation composition, cover, and structure were measured at 15 randomly selected nested plots per stand (240 total) and fungi were sampled every 6 weeks for 3 years (> 4,000 plots) [14, 15].

5. Northern Flying Squirrel Databases

In my studies, 56 stands were trapped for >500,000 trap nights and > 1,500 flying squirrels were captured > 5,000 times; 226 of these squirrels were necropsied [4, 15, 47, 52]. Also, 35 flying squirrels in southwestern Oregon, 4 squirrels on the Olympic Peninsula, and 140 squirrels in the Puget Trough were radiotracked and located in >600 dens., 6,000 times [16]. Witt [53,54] captured 165 squirrels 1,023 times in 16,000 trap nights in 2 stands and radiotracked 5 squirrels in the southern Oregon Coast Ranges. Rosenberg and Anthony [39, 40] captured 796 squirrels 1,719 times in 10 stands in the Western Cascades, Oregon. Graduate students tracked 14 squirrels in the Coast Ranges of Washington [19], 39 squirrels in the central Western Cascades [29], and 56 squirrels in the southern Western Cascades [23]. When I report means from these data, they are accompanied by standard errors.

6. Flying Squirrel Demographics

Sex ratios were 1:1 (M:F) for nestlings in nest boxes in Puget Trough and for adults in all my study areas [47]. In the Western Cascades, however, adult sex ratios were skewed towards females in young, managed stands (but not old growth); in 1 year in old growth, more male juveniles were caught than female juveniles [39]. Witt [53] found sex ratios of 1:1 for juveniles and subadults (A-I and A-II) in summer in the Oregon Coast Range, but 1.5:1 in favor of male adults in spring (possibly due to greater movements by males than by females in spring).

In fall, body mass varied but variation was not statistically significant among the widespread physiographic provinces (Table 1). In the Oregon Coast Ranges, adult mass was greatest in winter (143 ± 2 g, $n = 55$), 133 ± 3 g ($n = 165$) in fall, and lowest in spring and summer (127 ± 1 g, $n = 149$). Over all seasons, adult Puget Trough squirrels were larger than adult squirrels in southwestern Oregon in both femur length and body mass (142 ± 2 g vs. 132 ± 2 g); adult mass ranged from 105 g to 194 g. Provincial populations differed in other respects also [47]. In southwestern Oregon, females matured sexually in their second spring; in Washington, females matured in their first spring. Puget Trough A-II females gained weight more quickly than Oregon A-II females (spring masses were 129 ± 3 g and 115 ± 2 g, respectively).

Puget Trough A-11 females in the spring weighed more (153 ± 3 g), on average, than A-III males in Puget Trough (132 ± 2 g) or A-III males and females in southwestern Oregon (134 ± 3 g and 132 ± 3 g, respectively). In Washington, 90 % of A-II and A-III females were reproductively active, but only 39 % of A-II and older females in Oregon were reproductively active. But males (> 90 %) in all my study areas developed scrotal testes in their first spring.

Onset of female reproductive activity was more synchronized (late April to late May) in Washington than in Oregon (late April to early June) and termination (end of lactation) was earlier—September versus November. Some earlier and some later litters have been reported [25, 38]. Litter sizes were similar: 3.1 (range 2-4; placental scar counts) in Oregon and 2.8 (range 1-4; young/nest box) in Washington. Young of the year (A-I) comprised 21-36 % of fall populations [47], with the lowest juvenile recruitment in the Western Cascades (Table 1). In fall, A-I squirrels were 67 % (Sep-Nov 6), dropping to 9 % (7 Nov-Feb), of squirrels eaten by spotted owls [25]. No spotted owls occurred in the Puget Trough study areas and spotted owls used very large home-ranges on the Olympic Peninsula where juvenile recruitment was high and overall squirrel population densities were low; owls were relatively abundant and used relatively small home-ranges in Oregon where juvenile recruitment was low and squirrel population densities were high [10].

Survivorship was higher in southwestern Oregon old growth than in: (1) Puget Trough second-growth (A-I to A-II, 54 % vs. 30 %; A-II to A-III, 33 % vs. 22 %; A-III to A-IV, 58 % vs. 10 %), (2) southwestern Oregon second growth (7 %, 33 %, and 0 %, respectively), or (3) Western Cascades second growth and old growth (between-year recapture rates in the second year of study were 50 % and in the third year, 19 %) [39]. Between-year recapture rates in California for *G. s. flaviventris* were 12 % for adults in old growth and 9 % in "mature" forest; recaptures of juveniles (A-I to A-II) were 28 % and 18 %, respectively [49]. Both within- and among year recapture rates in the Western Cascades were low and suggestive of high turnover due to emigration and mortality [39], large numbers of transient animals, or, simply, low probabilities of capture (e.g., poor trapping technique). Maximum recorded age was 7 years in both Washington and Oregon.

Table 1

Mean (±SE) body mass, season of female sexual maturation, percent of fall population in the first year of life (A-I), and mean (±SE) population density in old-growth forests in various physiographic locations in the Pacific Northwest, USA.

Physiographic location	Fall body mass (g)	Maturation (season)	Fall A-I (%)	Density (no./ha)
Northern Cascade Range, Washington	128 ± 5	—	—	0.2 ± 0.1
Olympic Peninsula, Washington	136 ± 3	1st spring	34	0.5 ± 0.2
Puget Trough, Washington	141 ± 3	1st spring	36	—
Central Cascade Range, Oregon	132 ± 1	—	21	2.3 ± 0.2
Southwestern Oregon	128 ± 3	2nd spring	29	1.9 ± 0.2

Thus, it is apparent that demographics varied not only among populations in various physiographic provinces but also between managed and natural forests, particularly in southwestern Oregon where survivorship in A-I and A-III and older age classes and population densities were markedly lower in managed stands (Table 1). On the Olympic Peninsula, populations in old growth differed from populations in managed competitive-exclusion and understory reinitiation forests in adult mass (136 ± 4 g vs. 128 ± 5 g), percentage of individuals that were reproductively active females (31 % vs. 29 %), percentage of individuals that were A-I or A-II in fall (25 % vs. 46 %), and population density (0.5 ± 0.2/ha vs. 0.2 ± 0.1/ha).

7. Patterns of Abundance

Densities of flying squirrels increase from north to south in the Pacific Northwest (Table 1, [4]). Ransome (pers. comm.), however, has found high densities (2-3/ha) in western hemlock forests in coastal British Columbia. East of the Cascade Range in British Columbia, densities of *G. s. columbiensis* in old (> 120 yr) spruce-fir (*Picea-Pseudotsuga-Abies* spp.) were 0.4-1.0/ha [37], similar to densities of *G. s. oregonensis* in northwestern Washington. Highest reported average densities (2.8-3.5/ha, *G. s. flaviventris*) are from northeastern California true fir (*Abies* spp.) forest > 200 years old [49]. Maximum densities in old growth in my southwestern Oregon study areas were 3.0-3.7 *G. s. oregonensis*/ha, but the overall mean density was 1.9/ha [4]. The high densities in California may be due to extended trapping periods (15-16 nights vs. 6-8 nights in southwestern Oregon), sampling open populations, low capture probabilities, and use of a jacknife estimator (vs. a modified Lincoln-Peterson estimator) [6].

Most studies of northern flying squirrels in the Pacific Northwest have compared natural forest > 250 years old (old growth) with 40-80-year-old managed forest [4, 10, 39, 54]. A principal focus of these investigations has been to address hypotheses about why spotted owls use so much old growth. Study areas differed physiographically and biogeographically. Old-growth study sites differed markedly in recent history of foraging by spotted owls that can reduce population size [10, 39, 49]. Managed stands differed markedly: (1) in retention of biological legacies (coarse woody debris, large snags, large live trees, shrubs, and soil organic matter) from the previous old-growth stand, (2) age and history of silvicultural treatments including planting (vs. natural regeneration from seed), herbicide applications, fertilizer application, precommercial thinning, commercial thinning, and partial cuttings, and (3) stand character (e.g. coarse woody debris, snags, understory composition and development, and midstory development). Despite differences, most managed and natural stands < 150 years old were categorized as “young”. Meta-analyses [3, 4, 49] concluded that, in general, flying squirrel densities in managed forests were 40-65 % of those in old growth. Equivocal results were found for *G. s. columbiensis* in eastern British Columbia in 2 naturally-regenerated (following clear-cutting), thinned and fertilized, 20-28-year-old lodgepole pine (*Pines contorta*) stands and 2 lodgepole pine stands > 120 years old (stand structure not described) [37]. Densities were 0.6- and 0.7 squirrels/ha in the managed stands and 0.4- and 1.0 squirrels/ha in the natural stands.

Across the Pacific Northwest, some old-growth stands had low densities of flying squirrels in some seasons (sometimes following documented intensive predation and sometimes not); a few had low densities in most sampling periods [4]. Still, variation in flying squirrel densities seems greater in young (40-70 yr), managed stands than in old growth [3]. Some young, managed stands (especially those with understory development, coarse woody debris, and snags) have high densities of flying squirrels. Flying squirrels may be more abundant in niche-diversification (90-150 yr old with substantial legacies form old growth) than in old growth > 350 years old [11]. In general, flying squirrel densities increase in abundance from absence or near absence in competitive-exclusion stands (closed canopy, little understory, and suppression mortality) without legacies through understory-reinitiation and developed-understory to niche-diversification stands (developed understory and midstory, diverse vegetation site types, large coarse woody debris cover > 10 %, large snags, large variation in tree dbh, > 70 yr old) with densities of > 3 squirrels/ha.

7.1 Effects of Predation

Three reports [10, 39, 49] allude to the possibility that intensive foraging by spotted owls in old growth may reduce squirrel densities. Carey [10] presented graphs of population size before, during, and after periods of intense predation and average densities following 3 different levels of predation; it appeared that heavy predation could reduce population size by 50 % and that the effects of intensive predation could last 1-3 years. Carey and Peeler [12] illustrated how the spotted owl's behavior seems oriented to tracking prey population sizes and avoiding depletion or areas of depletion. Spotted owls are not the only predators seeking out flying squirrels. Long tailed weasels (*Mustela frenata*) killed up to 32 % of radiocollared flying squirrels in 1 season in the Puget Trough [6]. Other owls (e.g., *Bubo virginianus* and *S. varia*) and mustelids (*Martes americana* and *Martes pennanti*) seek out flying squirrels [2, 7, 8, 11]. It appears from my review of demographics in this paper that population age structure and recruitment may be affected by predation and that, perhaps, life-history strategy may vary with both carrying capacity (implying density dependence) and predation.

7.2 Effects of Silvicultural Systems

Waters and Zabel [49] found densities of *G. s. flaviventris* in mixed fir (*A. concolor* and *A. magnifica*) and pine (*P. jeffreyi* and *P. lambertiana*) forest averaged 0.2-0.6 squirrels/ha in 5-year-old shelterwood cuttings compared to 2.8-3.5/ha in old growth and 2.2-2.4 /ha in naturally (wildfire) regenerated stands 75-95 years old (inappropriately labeled "young"). Broadcast burning and thinning had no effects on flying squirrel populations [48]. Abundance of *G. s. oregonensis* on the Olympic Peninsula increased in stands developing after clearcutting and natural seeding from 0/ha in 44-year-old competitive-exclusion western hemlock to 0.4/ha in 57-year-old Douglas-fir with understory development (particularly ericaceous shrubs); highest densities in managed stands were in stands with 3-5 large residual snags/ha with abundant understory [4].

Carey et al. [15] compared 2 management strategies in Douglas-fir monocultures in the Puget Trough: intensive management (clearcutting, intensive site preparation including removal of coarse woody debris, and two commercial thinnings before 65 yr) and legacy management (clearcutting with retention of large live trees, coarse woody debris, and snags, with no further treatment for 55 yr). Densities of flying squirrels in intensively managed, understory reinitiation stand with < 1 % cover of coarse woody debris were 0.3 ± 0.0 squirrels/ha, similar to the average for stands managed for timber on the nearby Olympic Peninsula (0.2 ± 0.1 squirrels/ha), but much less than stands managed for legacies (0.6 ± 0.1 squirrels/ha) or for old growth on the Olympic Peninsula (0.5 ± 0.2 squirrels/ha). Experimental thinning depressed both fungal populations and squirrel populations in both legacy and intensively managed stands in the short-term, with greatest effects in the legacy stands [14, 15, unpublished data].

Considering all the studies to date, significant potential exists for accelerating development of managed stands through silvicultural manipulations, but only when combined with legacy management and with special attention to ecological scale [7, 8, 11]. Variable-density thinning (varying spacing among 0.2-0.5-ha patches) should be heavy enough to promote understory development but not to have undue impacts on fungal communities, canopy connectivity, and vulnerability to windthrow [4, 5, 8, 11]. Short-term results of intermediate cuttings, however, are likely to be negative [15].

7.3 Effects of Nest Boxes

Den sites, particularly secure maternal den sites, may be limiting to flying squirrels in second-growth forests [16]. Testing hypotheses about dens as limiting factors is complex; interactions with food supply and predation are likely. Nest boxes have been used successfully to increase populations of *Sciurus* and *Glaucomys* [9, 13]. Nest boxes added to competitive-exclusion (legacy management) and understory-reinitiation (intensively managed for wood) stands in Puget Trough eventually were used fully, including use as maternal den sites. Population density, however, did not increase during the first 5 years after installation [15].

8. Use of Dens

Northern flying squirrels use a variety of dens, both inside cavities in trees and outside of protective enclosures [2, 51]. In the Pacific Northwest, den sites include: (1) cavities in live and in dead old-growth trees, (2) cavities, stick nests, and moss-lichen nests in small (10-50 cm dbh) second-growth trees, (3) cavities in branches of fallen trees, (4) nests in decayed stumps of felled old-growth trees and suppressed young trees [16] and, as in Alaska [36], (5) witches brooms formed by mistletoe infections [23]. Intensive study revealed unexpected competition for dens from Douglas' squirrels (*Tamiasciurus douglasii*) and possibly other animals [2, 16]. In forests of the Olympic Peninsula, Washington Coast Ranges, southern Western Cascades of Oregon, and southwestern Oregon, squirrels tended to den in cavities in large live or large dead conifers in both naturally old stands and young managed stands (i.e., residual trees); live trees used as dens had deformities indicative of past damage and top rot [16, 19, 23]. In the central Western Cascades, flying squirrels used large, live trees in old growth and small, live trees in 40-year-old intensively managed plantations [29]. In Puget Trough, flying squirrels commonly used stick nests in live trees in competitive exclusion stands and cavities in live trees in intensively managed understory reinitiation stands [16]. Cavities were lined with moss, lichen, bark, and leaves.

Dens were occupied by several squirrels of the same or opposite sex. Individual squirrels used multiple (1-27, commonly 3-6, dens/season) dens, switching dens, on average, every 2 weeks. Groups of squirrels often changed den sites simultaneously, with some or all occupants moving to a single, new den [16, 23]. Sometimes changes in dens were accompanied by changes in cohabitants. In Puget Trough second growth, dens of males were 211 ± 7 m apart and dens of females were 108 ± 4 m apart. In southwestern Oregon old growth, dens of males were only 114 ± 28 m apart and dens of females were 86 ± 14 m apart. In Puget Trough, females selected cavities in low, often fragile, structures (e.g., fallen trees, stumps) as maternal dens and occupied these dens only with their young. In the nearby Willapa Hills (Washington Coast Ranges), 2 nests of females were found in stumps (1 in summer, 1 in winter) [19]. When nest boxes were provided in Puget Trough, many females chose nest boxes as maternal dens.

Denning by northern flying squirrels, as with nest building by birds [21, 43], is a complex social phenomenon seemingly geared at: (1) energy conservation through multiple occupancy, use of plant material as insulative lining, and thermal insulation by shelter materials (wood in tree cavities, sticks in external nests, and witches brooms) [28, 43], (2) isolation and protection of young from other flying squirrels, (3) protection from nest-raiding predators (e.g., mammalian predators in the genera *Martes*, *Mustela*, *Frocyon*, and *Didelphis* [2, 51]) with use of secure shelters such as cavities in trees with sound sapwood [13] or well-constructed nest boxes [9] or less secure shelters with multiple exits (e.g., stick nests), (4) avoidance of predation (e.g., by owls) by regular changes in den sites, and, possibly, (5) improved access to widely-separated foraging areas or food sources, and, for males, (6) improved access to numerous, distant, potential mates.

Actual den use, then, would reflect: (1) climate and seasonal extremes in precipitation and temperature, (2) stand structure as it influences microclimates within the stand, (3) abundance (density) and distribution of types of dens (e.g., natural or woodpecker-created cavities of appropriate size for multiple occupancy and sound condition for protection from predators and weather vs. stick nests vs. cavities in rotten stumps), not necessarily the supporting structure (e.g., a dead tree of some specified minimum size), (4) total density and overall distribution of dens, (5) types, abundance, and distribution of competitors for dens, (6) density of flying squirrels, (7) types, abundance, and distribution of food, and (8) type and abundance of predators. For example, in my study areas with: (1) high densities of flying squirrels (southwestern Oregon old growth), large, live, old trees with cavities, moss covered branches, and heavy loads of lichen were the most commonly used structure, (2) moderate densities (southwest Oregon and Olympic Peninsula second growth), medium-dbh live trees with deformities indicative of top rot and residual old-growth moderately-decayed snags were most commonly used, and (3) low densities (Puget Trough), stick nests in small-dbh trees, cavities in small, suppressed deciduous trees, and stumps were most commonly used.

Comparison of use versus availability within any given area, particularly when based solely on supporting structures [19, 23, 29], provides potentially misleading information when applied to other areas or to the biology of the squirrel in general. Squirrels do not select dens independently of availability and other environmental factors. The most important results of studies of den use seem to be: (1) there is a relationship between den types used and population density, (2) secure maternal dens seem particularly lacking in areas of low population density, and (3) den types are varied and distribution and abundance of types of dens is not very predictable.

9. Food Habits

Abundance of sporocarps of hypogeous fungi and mushrooms and nuts and seeds of woody plants is 1 of 3 factors (food, dens, predation) potentially limiting abundance of northern flying squirrels in the Pacific Northwest [2]. Food habits of northern flying squirrels have been extensively documented in the Pacific Northwest [4, 11, 14, 15, 24, 31, 32, 33, 34, 45] and nearby areas [26, 33, 35, 41, 49]. Early studies pointed to strict mycophagy (of hypogeous fungi - truffles - with some consumption of lichens) in the Pacific Northwest but broader diets (still dominated by fungi) in northeastern California, eastern Oregon, and Idaho. Fungal dietary diversity appeared to increase N-S [2, 4, 10]. It now appears nonfungal food items are significant constituents of diets in the Pacific Northwest too, composing 10-30 % of fecal pellets [4, 11, 45].

Direct observations of feeding have confirmed use of diverse mycorrhizal and saprophytic epigeous fungi (e.g., mushrooms), seeds of bigleaf maple (*Acer macrophyllum*), salal (*Gaultheria shallon*) berries, black cottonwood (*Populus trichocarpa*) leaf buds and staminate catkins, and, on 1 occasion, Douglas-fir seed [45]. Fungi appear to be the dietary mainstay. Sporocarps of hypogeous fungi, however, are of marginal dietary sufficiency to squirrels, and even small amounts of high quality foods (fruits, seeds, and nuts) are nutritionally significant [22].

Dietary fungal production and flying squirrel foraging are associated with coarse woody debris in Oregon [11] and northeastern California [49]. In Puget Trough in spring and fall, flying squirrels consumed 16 of 21 genera and 40 of 51 species of mycorrhizal fungi found in the soil with intensive year-round sampling [14]; 11 genera were consumed on the Olympic Peninsula [4] and 27 genera in southwestern Oregon [11]. *Rhizopogon*, *Gautieria*, *Hymenogaster*, *Hysterangium*, *Leucogaster*, *Leucophleps*, and *Melanogaster* are commonly consumed hypogeous fungi in the Northwest. Mushrooms (*Russula*, *Peziza*, Agricaceae, and Boletaceae) are common in diets also, particularly in Washington.

Dietary analyses suggest that efforts to promote fungal diversity through retention of coarse woody debris, maintenance of soil mycelial networks through retention of some live trees and ericaceous shrubs during harvests, and managing for diverse trees species, including some evergreen hardwoods such as Pacific madrone (*Arbutus menziesii*), would help ensure a consistent and abundant supply of truffles for flying squirrels and other animals [11]. Managing for understory and midstory shrubs and trees, particularly vine maple (*A. circinatum*), bigleaf maple, and other fruit and nut-bearing shrubs and trees, could help provide supplemental high quality foods [8, 11, 45]. Flying squirrel density in a bigleaf maple-mixed conifer stand in Puget Trough was substantially higher than densities in 16 Douglas-fir monocultures. In British Columbia, supplemental food (sunflower seed) increased population sizes of *G. s. columbiensis* two-fold in second-growth lodgepole pine forests [37]. Flying squirrels repeatedly visited feeding stations I put out for them in Washington-up to 8 squirrels visited 1 feeder at 1 time; a variety of foods were consumed, especially dried corn and black-oil sunflower seed [unpublished data].

10. Movements

Mean maximum distances moved between subsequent recaptures within 6-21 day trapping periods generally are 80-100 m [6]. When trapping technique and squirrel behavior produced high probabilities of recapture, mean maximum distances moved were less in old growth (84-89 m) than in second growth (102156 m) [3, 4]. In high-density populations, maximum distances moved were 6076 m. However, in second growth, distances were probably underestimated—occasional very long-distance movements (> 300 m) were observed between16-ha trapping grids [4, 6, 54]. In old growth, distances moved were asymptotic when 16-ha grids were compared with larger grids up to 36 ha (1 grid) and 50 ha (2 adjacent grids). Foraging patch sizes (clusters of adjacent recaptures) based on the inclusive boundary method were 0.79 ± 0.06 ha in niche-diversification, 0.85 ± 0.05 ha in old-growth, and 0.94 ± 0.04 ha in second-growth competitive-exclusion and early understory-reinitiation stands in southwestern Oregon [11]. Home-range size based on using the approximate median (90 m) of mean maximum distances moved as a radius was 2.5 ha. Home-ranges based on repeated sampling and minimum convex polygon encompassing recapture points were 2.1-2.5 ha, whereas the inclusive boundary home-ranges were 3.7-4.2 ha [54]. Range sizes for both methods, however, reached asymptotes after 48 captures, far more than would be obtained in 6-21 days of trapping. Independent estimates of home-range in old growth based on minimum convex polygons encompassing radiotelemetry relocations and close observations of squirrels were 3.4-3.9 ha; combined trapping and telemetry data produced estimates of 3.4-4.9 ha [54].

In studies with low probabilities of recapture, differences in distances moved were not found among markedly different environmental conditions [39, 49], perhaps because mean maximum distances moved were commonly based on 1 recapture per animal recaptured. Home-ranges based on adaptive kernel analysis of remote simultaneous telemetric bearings by 2 observers also detected—no difference between movements in stands of markedly different character in the central Western Cascades; home-ranges averaged 3.9 ± 0.4 ha for females and 5.9 ± 0.8 ha for males [29]. The reliability of these results, however, is suspect because: (1) bearings > 300 m from either observer were deleted [29], (2) flying squirrels can move quickly and simultaneous bearings would not be possible much of the time, (3) much foraging activity is on the ground where even minor differences in relief could preclude accurate bearings-thus the majority of bearings would be to squirrels at dens or other stationary activities in trees, (4) the choice of a 95% utilization distribution is entirely arbitrary and further truncates estimates of home range, and (5) there is no evidence that squirrels follow a 2-dimensional utilization distribution.

In a multiscale study (2,000 trap stations in 19 stands in 4 seral stages) of flying squirrel responses to environmental factors in coniferous forests in southwestern Oregon [11], 5 extracted factors described the plant communities: crown-class differentiation, decadence, canopy stratification, understory development, and a complex moisture- temperature gradient representing vegetation site types (also expressed as habitat breadth). Factors were more effective than habitat elements in predicting abundance of flying squirrels. Flying squirrels used only 59 % of the available habitat space. Decadence and canopy stratification were most influential in discriminating between used and unused points. Foraging activity was best described by decadence and habitat breadth (50 % of variance explained). Stand carrying capacity for flying squirrels was best explained (70 %) by decadence, habitat breadth, and position on the moisture-temperature gradient.

A review of studies illustrated that the best predictors varied among studies just as the dimensions of habitat space varied among studies. For example, coarse woody debris cover on the Olympic Peninsula averaged 8-13 % (vs. 49 % in southwestern Oregon) and areas of heavy shrub cover occupied < 39 of stand areas (vs. 40-65 % in southwestern Oregon); accordingly, shrubs were a better predictor in Washington, coarse woody debris in Oregon. The analyses also suggested that not only is animal abundance multifactoral but that multifactor interactions resulted in synergistic effects as forests developed over time. Studies on the Olympic Peninsula [4], Puget Trough [14, 15], and south-western Oregon [11] provided convincing evidence that abundance of flying squirrels in coniferous forests is deterministic (related to plausible variables related to food, den sites, and protective cover), not independent of environmental conditions as suggested by Rosenberg and Anthony [39]. Abundance appears to be a good measure of habitat quality and is correlated with other demographic measures, especially age-related survivorship. Age of onset of first breeding and proportion of females breeding may be density dependent. These studies provide a basis for formulating ecosystem management prescriptions.

12. Niche

The northern flying squirrel is a member of the arboreal rodent community that includes the Douglas' squirrel, Townsend's chipmunk (*Tamias townsendii*), Western gray squirrel (*Sciurus griseus*), and, in Oregon, the Red tree vole (*Arborimus longicaudus*), Bushy-tailed woodrat (*Neotoma cinerea*), and Dusky-footed woodrat (*N. fuscipes*). These species use much of the same habitat space, some overlap extensively in diet and den sites, and together with juvenile lagomorphs, are prey that are especially attractive to raptors, owls (*Strix* and *Bubo*), weasels (*M. frenata* and *M. erminea*), marten, fisher, canids, and felids. The role of competition among arboreal rodents in the Pacific Northwest is unknown. I have observed interspecific agonistic interactions, including a Bushy-tailed woodrat killing a Northern flying squirrel and dusky-footed woodrat in captivity. But all these species coexist, and apparently thrive, in complexly structured late-seral forests. It does appear that predators may switch foraging emphasis among the various species and one might hypothesize that species demographics could vary depending upon arboreal rodent community composition under moderate predation pressure.

Flying squirrels are important components of prey bases for many predators associated with late-seral forests in the Pacific Northwest. Given its wide movements, the Northern flying squirrel may be the best disseminator of spores of hypogeous and epigeous ectomycorrhizal fungi essential to many of the conifers in the Pacific Northwest. Its dissemination of fungi and bacteria may contribute to diversity in soil food webs that are foundations for ecosystem resiliency [11, 14, 15]. Flying squirrels may also play important roles in the dissemination of lichens and mosses they transport through the forest for nest materials (5, 41]. Thus, the Northern flying squirrel is a keystone species in Pacific Northwest coniferous forests.

13. Conclusions

Much information on *G. s. oregonensis* has accumulated in the last 10 years. The emerging picture is one of an animal adapted to exploiting abundant low quality food (truffles) in complex, relatively stable, late-seral forests that provide tree cavities as shelters for communal denning (and the resultant energy conservation) and a variety of high-quality foods in low abundance (e.g., bigleaf maple seed). The squirrel has evolutionary adaptations. Nocturnality is, presumably, to avoid detection by predators and to partition its niche temporally from those of tree squirrels and chipmunks. Gliding is presumably to escape from predators and an adptation to cross gaps in the forest canopy—most travel is arboreal through the canopy—and reduce exposure to terrestrial predators. Its size, however, makes it especially attractive to the medium-sized predators in the Pacific Northwest, especially to spotted owls, whose tactic of sit-and-wait nocturnal foraging is well-matched to the squirrels' nocturnality and noisy landings after gliding. It seems reasonable that the squirrel's routine switching of dens and rapid arboreal travel to scattered foraging areas is aimed at evading both terrestrial mammalian predators (weasels) and nocturnal avian sit-and-wait predators that could key in on repetitive use of communal den structures and foraging that follows a simple utilization distribution.

The Northern flying squirrel is providing guidance on how to manage for biodiversity in second-growth forests [3, 4, 5, 7, 8, 11, 14, 15]. There is not agreement, however, among the various students of the Northern flying squirrel [3, 8, 40, 48, 49]. The sources of disagreement are varied: loose use of jargon; poorly defined ecological terms and concepts; differences in methods; differences among study areas and subspecies; differences in culture, world views, and disciplinary belief systems of authors; and, simply, competitive contrariness. I hope this review will clarify what is known about *G. s. oregonensis*, contribute to a synthesis of that knowledge, and illustrate the relevance of that knowledge to ecosystem management and conservation of biodiversity.

Additional research is needed on the northern flying squirrel. Studies of genetics and kinship will be necessary to more fully interpret movement and denning behavior. Reliable information on space use by flying squirrels in natural, old forests is lacking. Statistical methods for describing and comparing space use are lacking. Studies in the southern Washington Cascade Range would add another geographic replicate for determining generalizability of implications for ecosystem management. Formal prospective experimental tests of management hypotheses based on ecological correlations derived from retrospective studies are needed. These experiments could help clarify factors limiting flying squirrel populations and can help test the utility of using flying squirrels as indicators of forest ecosystem function.

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