Response of northern flying squirrels to supplementary dens

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Abstract   The northern flying squirrel (*Glaucomys sabrinus*) is a keystone species in Pacific Northwest conifer forests, consuming and disseminating spores of ectomycorrhizal fungi essential to Pinaceae and preyed upon by different vertebrate predators. Increasing the numbers of flying squirrels has been suggested as part of a strategy to increase the population viability of the spotted owl (*Strix occidentalis*). Flying squirrel populations in second-growth forests have been hypothesized to be limited by 1) abundance of den sites, 2) quality, quantity, and diversity of food, and 3) predation. I conducted an experiment to test the null hypothesis that number and quality of dens did not affect flying squirrel population density. in 1992, I added nest boxes and tree cavities to 8 of 16 Douglas-fir (*Pseudotsuga menziesii*) stands of various management histories in the Puget Trough of Washington. Flying squirrel use of boxes increased over 5 years, predominantly by pregnant and nursing females. Proportions of adult females breeding, however, did not increase. Population sizes did not increase significantly. Dens were not the overriding factor limiting flying squirrels in second-growth Douglas-fir forest in the Puget Trough of Washington. Rather, a complex of factors seemed to be operating, and limiting management focus to one or 2 factors may not produce desirable results.

Key words   Cavities, dens, forest management, *Glaucomys sabrinus*, limiting factors, nest boxes, northern flying squirrels, predation, wildlife management

The northern flying squirrel (*Glaucomys sabrinus*) is a keystone species in Pacific Northwest forest ecosystems (Carey 2000). Flying squirrels eat the sporocarps and disseminate the spores of ectomycorrhizal fungi that are essential symbionts of dominant conifer species, including Douglas-fir (*Pseudotsuga menzieii*), and various hardwoods, including Pacific madrone (*Arbu-tus menziesii*, Maser et al. 1978, Molina et al. 1992). Northern flying squirrels also may aid in dispersing mosses and lichens (Hayward and Rosentreter 1994). Flying squirrels are a major prey of the threatened spotted owl (*Strix occidentalis*, Forsman et al. 1984), longtailed weasel (*Mustela frenata,* Wilson and Carey 1996), American marten (*Martes americana*, Verts and Carraway 1998), and other predators (Wells-Gosling and Heaney 1984). Silviculture and snag management to increase densities of flying squirrels have been proposed as part of a conservation for spotted owl (Thomas et al. 1990).

Factors suggested as limiting to flying squirrels include 1) abundance of den sites, especially cavities in trees (Maser et al. 1981, Wells-Gosling and Heaney 1984), 2) quantity and diversity of sporocarps of mycorrhizal fungi and other foods (Carey 1995, Colgan et al. 1999, Ransome and Sullivan 1997), and 3) predation (Carey et al. 1992, Zabel et al. 1995, Wilson and Carey 1996). Support for dens being limited comes from observations by naturalists that flying squirrels use cavities (Bailey 1936, Wells-Gosling and Heaney 1984), ready use of nest boxes by northern flying squirrels in eastern (Maser et al. 1981) and western Oregon (Witt 1991), limited evidence that nest boxes can increase carrying capacities of second-growth forests in western Oregon (Witt 1991), correlations between abundance of flying squirrels and abundance of

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large snags (Carey 1995), use of large snags and large, live, decadent trees as den sites in high-density populations (Carey et al. 1997), and successes in the eastern United States in increasing populations of tree squirrels (*Glaucomys volans, Sciurus carolinensis, S. niger*) with supplementary dens.

In this paper, I report the results from 8 years of a replicated, controlled experiment designed to test the hypothesis that den sites limit northern flying squirrel population size in second-growth Douglas-fir forests. I compared populations in variously treated stands in 2 types of 55- to 70-year-old second-growth forests with and without supplemental dens. The forests either had been thinned twice with removal of dead trees ≥10 years prior to my study (thinned forest) or never thinned with retention of some large, decadent, live trees and large snags from the preceding old-growth forest (legacy forest). I also report on use of supplementary dens by potential competitors of the flying squirrel (Townsend's chipmunk [*Tamias townsendii*] and Douglas' squirrel [*Tamiasciurus douglasii*]).

Study area

I found homogeneously treated blocks of forests large enough for replication of experimental treatments on Fort Lewis Military Reservation in Thurston County, Washington. The 6,000-ha Rainier Training Area study area was south of the Nisqually River and had low relief (100-140 m), precipitation averaging 91 cm/year, minimum January temperatures that ranged from 0 to 2.5°C, and second-growth Douglas-fir stands of various management histories. Although Fort Lewis was designated as a conservation area for northern spotted owls (Lujan et al. 1992), the Rainier Training Area contained neither old-growth forests nor spotted owls (Carey et al. 1999*b*).

I chose 4 management areas ≥4 km apart and demarcated 4 13-ha stands in each, >80 m apart (Carey et al. 1999*b*). The size of these stands was similar to the mean sizes (15-18 ha) of young stands in Pacific Northwest landscapes (Carey and Peeler 1995). I set the minimum distance between experimental stands (≥80 m) at the same magnitude as the reported maximum distances (≈90 m) moved by flying squirrels between subsequent recaptures (Rosenberg and Anthony 1992, Carey 1995) to ensure independence of the squirrel populations in the stands live-trapping confirmed that few squirrels moved between stands during our study;

some males, however, roamed widely during breeding seasons (Carey 2000). The 4 stands within each management area composed a block for a randomized block experiment. The 4 blocks were in different locations, with different environmental settings and different management histories. Two (≈65 yr old) had been conventionally thinned twice ≥10 years earlier and had well-developed low vegetation (e.g.,≈90% cover of *Gaultheria shallon, Polystichum munitum, Pteridium aquilinum*, and *Rubus ursinus*). Few trees (live or dead) had been retained (<1/ha combined) during the harvest of the preceding forest, and merchantable dead and dying trees had been removed during thinnings. All the thinned stands were well-stocked (≈230 stems/ha) with Douglas-fir ≈60 cm dbh. Flying squirrel densities averaged 0.5±0.1(SE)/ha; Douglas' squirrels, 0.1 ± 0.0/ha; and Townsend's chipmunks, 0.8±0.1/ha (Carey 1999*b*).

The 2 other blocks, ≈55 years old, had not been thinned and had poorly developed understories and legacies of large snags (3.5/ha), large live trees (2.7/ha), and ≈8% cover of fallen trees from the preceding old-growth forest. Contemporary Douglas-fir in these legacy stands were small (≈43 cm dbh) and crowded (≈640 stems/ha). Flying squirrel densities averaged 1.0±0.1/ha, but Douglas' squirrels (0.1±0.0/ha) and Townsend's chipmunks (0.2± 0.1/ha) were few (Carey et al. 1999b).

The 16 stands exemplified conditions currently found in forests managed under long (>60 yr) rotations-intensive management for high-quality timber (thinned stands) and extensive management with biological legacies (live trees, snags, down wood) retained from preceding stands (legacy stands). They were past the common harvest age for industrial forests (40-50 yr) and approaching the age (>70 yr) at which public forests are commonly harvested. No stand supported the high number of squirrels (e.g., 0.4 Douglas' squirrels/ha, 2 flying squirrels/ha, and 2-5 Townsend's chipmunks/ha) characteristic of late-seral forest (Carey 1995).

Methods

Experimental design

I used a complete randomized blocks design with 4 blocks; each block had one of 2 histories of management, thinning or legacy retention with no

thinning. Each block was divided into 4 stands, with 4 treatments assigned randomly to these stands: control (no treatment), dens added, experimental thinning (mosaic), and experimental thinning with dens added (mosaic + dens). The center of each 13-ha stand was subdivided by an 8x8 sampling grid of 64 stations 40 m apart (10.2 ha). In spring 1992,1 added 32 dens to each of 8 of the 16 stands, placing a den at every other grid point (a density of 3 dens/ha). In spring 1993, 8 stands (2/block) were experimentally thinned. Thinning reduced basal area of trees by 24-30% and initially depressed flying squirrel populations in legacy stands, but populations recovered before the 5- to 6-year evaluation of supplementary dens (Carey et al. 1999*b*).

Den supplementation

I supplemented natural dens by adding 16 nest boxes and 16 cavities created in trees, alternating between cavities and boxes at 80-m intervals across sampling grids. I assumed that 3 dens/ha would be sufficient to increase densities of flying squirrels by >0.5 squirrels/ha (6 dens/additional squirrel) if dens were the overriding factor limiting abundance of flying squirrels. I based this assumption on denning studies that found 1) individual squirrels used 6 dens on average, 2) several individuals used each den, and 3) ≈3 natural dens/ha already were supporting 0.5 squirrels/ha in the previously thinned stands (Carey et al. 1997). Supplementary dens were placed 6 m high in the largest tree ≥30 cm dbh, ≤5 m from the grid point, or on the nearest tree ≥30 cm dbh if no large tree was ≤5 m from the grid point. I chose a 6-m height because I wanted to 1) minimize tree breakage by removing <50% of wood in the area of cavity creation (i.e., we required a diameter of approximately 25 cm) and trees were small in legacy stands, 2) compare the attractiveness of boxes and cavities, 3) ensure that the dens were sufficiently high above the forest floor to avoid attracting predators, and 4) safely and regularly inspect the 256 dens.

Nest boxes had exterior dimensions of 20 cm wide x 22 cm deep x 22 cm tall, with a 3.8 x 3.8cm entrance in the upper left front corner of the box. Each box had a shelf (predator and heat-loss baffle) just below the entrance that extended across the interior to an entrance to the interior nest chamber in the corner opposite the outside entrance (Figure 1). The nest chamber was 16 x 17 x 16 cm (4,352 cm^3). I designed the box to be large enough to contain 2-4 flying squirrels plus net materials, but small enough to be hung securely

Figure 1. A northern flying squirrel (*Glaucomys sabrinus*) in a Flyger nest box.

in small-diameter trees. Because most nest boxes were in use by 1995 and to ensure a surplus of dens, I systematically placed 8 additional nest boxes, each 40 m away from other dens, in each stand previously treated.

Tree cavities (10 cm wide, 18 cm tall, and 15 cm deep; 2,700 cm^3) were created with a chainsaw and covered with a wooden faceplate 3.8 cm thick with a 4.5-cm-diameter (16 cm^2) entrance in the center of the upper third of the plate (Carey et al. 1999*b*). Because cavities were receiving low use after 2 years and it appeared entrances were allowing too much rain and sun to enter cavities, I replaced faceplates on 96 (75%) cavities in 1995 using corner entrances of 3.8 x 3.8 cm (14 cm^2). In 1996, in another attempt to increase attractiveness, I doubled the size of 48 of the 128 cavities by increasing the vertical dimension 15 cm, producing a volume of 5,400 cm3.

Sampling procedures

I inspected the supplementary dens once in summer and once in winter from summer 1993 to summer 1998 and recorded species, age, and gender for each captured squirrel. I trapped flying squirrels in spring 1997, fall 1997, and fall 1998 to determine whether treatments affected numbers of flying squirrels. I followed the procedures of Carey et al. (1991) and placed 2 Tomahawk 201 traps at each sampling-grid point (one on the ground and one 1.5 m high in a tree; 2,048 traps total), baited them with peanut butter, molasses, and oats, and left them open for 2 4-night periods separated by 3 nights in spring 1997, fall 1997, and fall 1998 (3 trapping

totaling 49,152 trap nights).

I used number of individual flying squirrels caught/unit effort (ICPUE) to index abundance, with effort calculated as number of total trap nights minus one-half the number of sprung-but-empty traps and traps containing animals (Nelson and Clark 1973; Carey et al. 1991, 1999a). This metric avoids multiplicative errors in estimates of density arising from mark-recapture calculations and estimates of mean maximum distances moved between subsequent recaptures (MMDM, Skalski and Robson 1992) and errors in estimating population size from simple counts that arise from reductions in trapping effort for a species due to wind, rain, and animals closing traps (Nelson and Clark 1973). With low population densities (and thus low numbers of captures), mark and recapture calculations can provide population estimates wildly divergent from the minimum number of individuals known to be alive in an area (Menkens and Anderson 1988, Carey et al. 1991). Number of individuals captured, however, is a good predictor of population size (as estimated from various mark and recapture analyses) of flying squirrels and chipmunks over a wide range of densities in the Pacific Northwest (Carey et al. 1991), with R^2=0.82, slope =1.16, and intercept= 1 .07 for flying squirrels in the baseline phase of this study. ICPUE can be misleading if a species exhibits significant differences in MMDM among sampling grids; thus, I calculated MMDM and tested for differences using 95% confidence intervals generated from marginal means estimated by a general linear model incorporating management history, experimental treatment, and history by treatment interaction. After finding no statistically significant differences ($F_{3,39}$=1.23, P= 0.314) in MMDM (O±SE=125±8 m) among treatments, I estimated overall mean densities of flying squirrels per treatment using number of individuals captured divided by area encompassed by the trapping grid and a buffer equal to one-half the distance between trap stations (10.2 ha). Even though MMDM were greater than previously reported (Carey 1995), I recorded few instances of individuals moving between grids during trapping. I used the proportion of adult female flying squirrels that bred in 1997 and 1998 as a second measure of demographic response to treatment.

Data analysis

Field experiments conducted outside a laboratory, such as mine, are inevitably confounded by historical and concomitant uncontrolled confounding factors and

fall in the class of quasi-experiments (Cook and Campbell 1979, Hoaglin et al.1991. Johnson 1999). I expected variation within populations in treated and untreated stands due to uncontrollable confounding factors (e.g., weather, predation, annual variation in food supply). Even though my study was large in area and number of stands studied, replicates were few (4) compared to requirements for determining normality and homoscedasticity. Therefore I analyzed my data on flying squirrel abundance with box-and-whisker plots and a repeated measures (3 sampling periods) general linear model incorporating management history and 4 treatments with ICPUE as the dependent variable but checked my results with the nonparametric Kruskal-Wallis test (no discrepancies occurred between tests). Mauchly's test of sphericity (W= 0.243, χ_2^2 =9.9, P=0.007) suggested that ICPUE data met the assumptions of normality (Norusis 1999); thus I used untransformed values. I used univariate ANOVA to test for effect of treatment on proportion of females breeding in 1997 and in 1998; Levene's test indicated no departures from homoscedasticity (P=0.20 in 1997 and 0.69 in 1998), thus I used untransformed data. I used the 95% confidence intervals around estimated mean differences to determine whether differences exceeded my *a priori* specified biologically and managerially significant differences. I used SPSS (Norusis 1999) for all analyses.

Biological, statistical, and managerial levels of significance

Flying squirrels often differ in abundance between natural and managed forests by ≥0.5 squirrels/ha (Carey 1995); on this basis, I chose 0.5 squirrels/ha as my *a priori* lower limit for biological significance. On my study area, an increase of 0.5 squirrels/ha would be an increase in population density of 50% in the legacy forest and 100% in the thinned forest. I was able to demonstrate differences in densities of <0.5 flying squirrels/ha at P<0.01 among the 4 blocks of 4 stands in a pilot study prior to treatment; thus I chose the conventional standard of P<0.05 for statistical significance of differences in flying squirrel abundance due to treatment. I set ecological and managerial significance for spotted owl recovery efforts at increases of one flying squirrel/ha because 1) spotted owl foraging can reduce flying squirrel populations by one squirrel/ha in areas where they intensively forage, 2) squirrel densities

in areas selected for intensive foraging often differ from areas avoided by one squirrel/ha, and 3) an addition of one squirrel/ha would elevate 50% of my study stands to the densities comparable to those in old-growth forests used by spotted owls (Carey et al. 1992, Carey 1995, Carey and Peeler 1995).

Results

Use of dens

Use of supplementary dens by flying squirrels, Douglas' squirrels, and chipmunks increased slowly from summer 1993 to summer 1998. Nine months after installation, only 10% of boxes and 9% of cavities contained nest materials added by squirrels; after 35 months, 80% of nest boxes and 34% of cavities contained nests. Some (9%) cavities exuded pitch and were sticky to the touch. In some instances, pitch sealed the edges of the faceplate to the tree, making a water-tight cavity in which water accumulated; these cavities were not used by squirrels. Use of nest boxes (89% vs. 70%) and artificial cavities (59% vs. 9%) was greater in the thinned forest than in the legacy forest by 1995. By 1998, use of nest boxes (80% vs. 74%) and artificial cavities (50% vs. 34%) was more equivalent in the 2 types of forest. In summers following winter cleaning of nest boxes in 1995 and 1998, 65% of nest boxes contained fresh nest material.

In summers ≥1 year after installation, I found an average of 51 individual squirrels using nest boxes. Far fewer squirrels used supplementary dens in winter (Table 1). The primary use of supplementary dens was as natal dens in summer; approximately 54% of flying squirrels, 78% of chipmunks, and 94% of Douglas' squirrels using supplementary dens were mothers with young. However, addition of dens did not influence the proportion of adult female flying squirrels breeding in 1997 ($F_{3,12}$= 2.22, P=0.14, O±SE = 0.53 ± 0.07) or 1998 ($F_{3,11}$= 1.14, P=0.37, O±SE=0.51±0.08). I did not observe squirrels in cavities until 29 months after installation and then only one squirrel. Use of cavities by squirrels remained low, peaking in summer 1998, when I found 10 individual squirrels using cavities. From summer 1993 to summer 1998, I found 431 (368 during scheduled biannual checks, Table 1) squirrels in supplementary dens, 410 of them in nest boxes. Of the 410 squirrels, 66% (*n*=270) were flying squirrels, 31% were Douglas' squirrels, and 3% were Townsend's chipmunks. More squirrels were found in supplementary dens in the thinned forest (64% of individuals found in dens) than in the legacy forest (36% of individuals). For flying squirrels, I found the same 52 individuals in dens in successive inspection periods, most in the thinned forest (31 individuals). I found the same 18 flying squirrels during ≥3 scheduled inspections, including one that I caught 5 times during 7 den inspections over 6 years. I caught and ear-tagged 9 females in nest boxes as juveniles that I later found in nest boxes with young of their own. I found one litter of flying squirrels in nest boxes in 1994 and 12 litters in 1998 (with an average=5.8 litters/yr between 1994 and 1998). In all, I found 20 litters in the thinned forest and 15 litters in legacy forests. Mean litter size was 2.4 (range =1-4). Thus litters in nest boxes potentially contributed 14.5 squirrels/ year to the populations in our study areas. During the same period I found 28 litters (average = 4.7 litters/yr, range = 0-9 litters/yr) of Douglas' squirrels; 18 were in thinned forest and 10 in legacy forest. Mean litter size for Douglas' squirrels was 4.2 (range= 1-6).

Table 1. Numbers of northern flying squirrels (*Glaucomys sabrinus*), Douglas' squirrels (*Tamiasciurus douglasii*), and Townsend's chipmunks (*Tamias townsendii*) using 128 nest boxes and 128 artificial cavities in summer (S) and winter (W) in 4 stands historically managed (HM) with conventional thinning (Thinned) and 4 stands historically unthinned but with legacies of large live and dead trees (Legacy), on Fort Lewis, Washington, 1993-1998.

Species	HM	Spring						Winter					Total	Neonates
		93	94	95	96	97	98	94	95	96	97	98		
Flying squirrel	Legacy	3	10	6	16	17	25	3	3	4	0	9	96	33
	Thinned	22	18	21	25	22	18	0	7	17	2	7	158	62
Douglas' squirrel	Legacy	12	0	11	0	7	9	0	0	1	0	0	40	36
	Thinned	24	0	7	0	22	3	0	0	12	0	0	68	57
Townsend's chipmunk	Legacy	0	0	0	0	0	0	0	0	0	0	0	0	0
	Thinned	0	0	1	8	0	0	0	0	0	0	0	9	7
Total	Legacy	15	10	17	16	24	34	3	3	5	0	9	136	69
	Thinned	46	18	29	33	44	21	0	7	29	2	7	236	126

In my samples of adult flying squirrels from supplementary dens, males (*n*=135) outnumbered females (*n* = 116). There were equal numbers (*n* = 54) of male and female Douglas' squirrels and 9 female chipmunks compared to 3 male chipmunks. I found > 1 flying squirrel in a single nest box on 31 occasions. In summer, I found pairs of males (*n*= 9), females (*n* = 1), and male and female *(n=5)*. In winter I found 2-5 squirrels in individual nest boxes (males and females in 8 of occasion, I found 2 Douglas' squirrels in an artificial cavity.

Table 2. Marginal mean numbers of individuals and densities of northern flying squirrels (*Glaucomys sabrinus*) estimated by a general linear model incorporating management history (thinning vs. legacy retention), experimental treatments (control, dens, experimental thinning [EXPT], EXPT + dens), and repeated measures (spring 1997, fall 1997, fall 1998) for 4 blocks of 4 stands (16 stands total) in a complete randomized blocks experiment on Fort Lewis, Washington, 1991-1999.

	Experimental treatments			
Measure	Controls	Dens added	EXPT	EXPT + dens
Mean number of flying squirrels/stand	4.92	8.17	4.33	5.25
Standard error	0.78	1.12	0.67	0.54
Estimated density (squirrels/ha)[a]	0.48	0.80	0.42	0.51

[a] Calculated by dividing the mean number of individual captured/stand by 10.2 ha (area of the sampling grid).

Effects of supplementary dens on flying squirrel abundance

Box-and-whisker plots suggested that den supplementation had positive effects on flying squirrel abundance in stands not treated with experimental thinning (Figure 2). General linear model analysis, however, found no significant effect due to management history ($F_{1,8}$ =1.30, P=0.29), treatment ($F_{3,8}$ =2.55, P=0.13), or history-treatment interaction ($F_{3,8}$=0.69, P=0.58). Nonparametric Kruskal-Wallis tests confirmed the nonsignificant general linear model results for spring 1997 (χ^2_3 =6.7, P= 0.08), fall 1997 (χ^2_3 =6.6, P=0.09), and fall 1998 (χ^2_3 = 1.9, P = 0.59). Thus I failed to reject
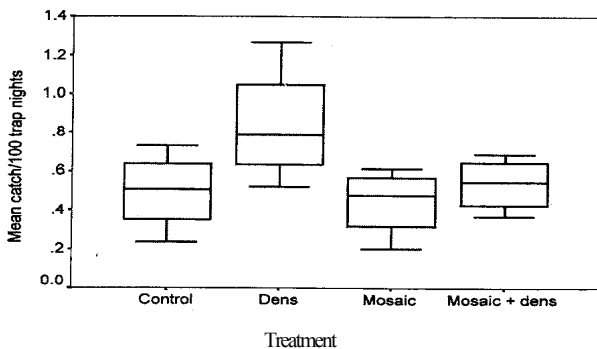

Figure 2. Box-and-whisker plots (boxes show medians and quartiles, whiskers show ranges) of numbers of individual northern flying squirrels (*Glaucomys sabrinus*) caught per 100 trap nights in experimental stands with 1) no treatment (Controls), 2) supplementary nest boxes and cavities created in trees (Dens), 3) variable-density thinning to create a vegetation mosaic (Mosaic), and 4) variable density thinning with supplementary dens (Mosaic + dens) on Fort Lewis, Washington, 1997-1998.

the null hypothesis of no differences in flying squirrel abundance due to treatment (including dens). Because of the few (4) replicates, my tests may have had low power and choice of a liberal level of significance (i.e., *P*<0.10 or *P*<0.16) would have resulted in rejection of the null hypothesis of no difference due to treatment. Thus I examined marginal means estimated by my general linear model (Table 2) and found that the difference (O± SE = 0.347 ± 0.059) between controls and dens treatment was >0, but nonsignificant by my *a priori* criteria (t_1=0.59, *P*= 0.06), equivalent to 0.32 squirrels/ha, significantly less (upper 95% confidence level of 0.43 squirrels/ha) than my *a priori* standards of 0.5 squirrels/ha for biological significance and 1.0 squirrel/ha for ecological and managerial significance. Therefore, even though there may have been a difference due to treatment that might have become statistically significant with higher number of replicates, the magnitude of the differences were not significant biologically, ecologically, or managerially by my *a priori* criteria.

Discussion

Use of dens

Prior to this experiment, there had been no reports of systematic investigation of den use by northern flying squirrels. Northern flying squirrels were known to use cavities in trees and nests of sticks, moss, and lichen on tree branches, but cavities were thought to be especially important as winter dens (Wells-Gosling and Heaney 1984). Most authors seemed to agree that cavities were preferred over nests on branches in winter (Carey et al. 1997). Animals that use cavities in trees benefit from increased

protection from precipitation, wind, cold temperatures, and predators relative to stick nests; thus cavities seem particularly important to warm-blooded vertebrates that do not migrate or hibernate (Collias 1964, Short 1979, Stapp et al. 1991). As a result, providing cavities in trees, or trees in which animals may excavate cavities, has received considerable attention in wildlife management (McComb and Lindemnayer 1999).

Denning in groups in cavities provides additional conservation of metabolic heat and was known to be common for many tree squirrels, but not for northern flying squirrels (Stapp et al. 1991, Layne and Raymond 1994). Although few cavity-using mammals are obligate cavity users, quality of habitat, as measured by population density, may be related to abundance of cavities. Carey et al. (1997) found that 40% of natural dens in legacy forest and 60% of natural dens in thinned forest were in cavities. Group denning was common, as in southern flying squirrels (Stapp et al. 1991, Layne and Raymond 1994). I found, however, that supplementary dens were used infrequently in winter, and Carey et al. (1997) found that the most common natural dens were stick nests in small-diameter, live trees in the dominant age cohort in the stands (48%) of dens in legacy forest and 33% of dens in thinned forests).

Northern flying squirrel at a natural den entrance.

Evidently the dense canopies in the legacy forest provided a sheltered microclimate, within the mild, lowland climate of the Puget Trough, in which stick nests provided adequate dens, whereas the open canopies in the thinned forests promoted proportionally greater use of cavities, primarily in dead and dying suppressed hardwoods and conifers and later in supplementary dens. Cavity trees were rare in the thinned forest (Carey et al. 1997), and population sizes there were one-half those in the legacy forests. In summer, adult females sought out low structures (stumps of various sizes and fallen trees) to use as natal dens. In contrast, in managed and old forest with population densities considerably higher than in the experimental stands, flying squirrels used large, old, live trees without visible stick nests and did not use low structures as natal dens (Carey et al. 1997). Carey et al. (1997) predicted the first use of supplementary den sites would be by nursing females. This prediction proved correct. Their data suggested that use of supplementary den sites would be higher in the thinned forest than in the legacy forest because of open canopies, and it was.

Population responses to supplementary dens

Carey et al. (1997) concluded that denning by northern flying squirrels was a complex behavior that included social, energetic, predator-avoidance, parasite-avoidance, and foraging elements as well as behavioral preferences, availability of den sites of different types, and density-dependent social requirements. They suggested that conclusions about dens (types and abundances) as a factor limiting population density must await experimental evaluation that demonstrated that 1) squirrels found and used supplementary dens, 2) food-den and understory-den (cover from predation) interactions were not important, and 3) demographic responses did or did not result.

During live-trapping in fall (1993-1998) following nest-box checks, Carey (2001) recorded 426 individual flying squirrels, 253 in the legacy forest and 173 in the thinned forest. I found more squirrels used supplementary dens in the thinned forest (64% of individuals) than in the legacy forest (36% of individuals). Most individuals living in the thinned forest were using artificial dens, whereas about 40% of the flying squirrels living in the legacy forest were using artificial dens. Thus, supplementary dens were acceptable as dens to flying squirrels and were used by a substantial percentage of the population, and criterion

1 (Carey et al. 1997) was met. In addition, the 256 supplementary dens (later 320 dens) provided in this study were a significant addition to the 490 known natural dens discovered by Carey et al,. (1997). Overall, litters born in this study were a significant addition to the 490 known natural dens discovered by Carey et al. (1997). Overall, litters born in supplementary dens potentially were contributing 14.5 individuals/year to populations averaging 56 individuals. Nevertheless, observed changes in population density were not statistically significant.

Diversity and standing-crop biomass of sporocarps of hypogeous ectomycorrhizal fungi (the primary food of flying squirrels) did not differ between the legacy and thinned forests, but biomass was much less than reported for old-growth forests (Colgan et al. 1999). Ancillary high-quality foods (e.g., seed of bigleaf maple [*Acer macrophyllum*]) were rare in both forests (Carey et al. 1999*b*). Predation on northern flying squirrels was high, with up to 32% of radio-collared squirrels killed by weasels (*Mustela frenata* and *M. erminea*) during winter (Wilson and Carey 1996). Great horned owls (*Bubo virginianus*) also were observed preying on flying squirrels in the experimental stands (Carey et al. 1999*b*). Flying squirrels in the experimental stands had lower survivorship in all age classes than flying squirrels in old-growth forests (Villa et al. 1999). Thus, there was potential for negative effects on flying squirrels due to poor-quality natal dens, paucity of food, and heavy predation (Carey 2000, 2001, this study) that can not be separated from the consequences of inadequate dens *per se*. Thus, criterion 2 for assessing den availability (Carey et al. 1997) was not met.

Factors limiting populations may change from place to place and season to season (Fretwell 1972). Shelford's Law of Tolerance (Odum 1971) suggests that as > 1 factor approaches values that might limit population size or growth, the negative effects may become multiplicatively negative. Such a situation may have existed in this study, especially the thinned stands. The flip side of Shelford's Law is the concept of emergent properties of ecosystems (Odum 1969); as components are added and subsystems interact, positive multiplicative effects (synergy) occur and new properties accrue to the system. In old-growth forests in the Pacific Northwest, biocomplexity may lead to emergent properties such as simultaneously high populations of flying squirrels, Douglas' squirrels, Townsend's chipmunks, and, sometimes, other species of arboreal rodents and terrestrial prey that markedly increase carrying capacity for vertebrate predators (Carey 2000).

Abundance of dens as a limiting factor

Abundance of dens was not the overriding factor limiting flying squirrel abundance in second-growth Douglas-fir forest in the Puget Trough. Rather, a complex of factors, including quality of natal den sites, abundance and quality of food, and predation seem to be in operation. In harsher climates, lack of cavities could be more influential than in the mild climate of the Puget Trough. In old-growth forests, spotted owls join weasels as major predators of flying squirrels and may have significant negative impacts on population densities (Carey et al. 1992, Wilson and Carey 1996). Nevertheless, flying squirrel densities in the thinned stands were among the lowest reported to date (Carey 2001). Densities in legacy stands were low for forests dominated by Douglas-fir, despite the retention of large snags and large live trees from the preceding old-growth forest.

Spatial heterogeneity in vegetation and structural complexity in old forests seem to be important in providing relatively abundant and diverse foods for flying squirrels and for ameliorating predation and competition (Carey et al. 1999*a*). Large live and dead trees in old forests provide dens far above the forest floor, away from terrestrial predators, in well-developed and well-connected canopies that provide shelter and travel ways (Carey et al. 1997). In contrast, canopy foliage in the experimental second-growth stands was well separated from understory foliage; midstory trees were absent. Canopy trees of a single species were distributed evenly as a result of commercial thinning or self-thinning. Understories were homogeneous (Carey et al. 1999*b*). Biocomplexity in old forests apparently results from basic stand-structuring processes (crown class differentiation, decadence, canopy stratification, and understory development) and a higher-order process of development of habitat breadth that arises from spatial heterogeneity produced by these 4 fundamental processes (Carey et al. 1999a). The end result is preinteractive niche diversification (Hutchinson 1978) that promotes high-density coexisting species that otherwise might be in competition for food and den sites, e.g., northern flying squirrels, Douglas' squirrels, and Townsend's chipmunks. Thus, management for biocomplexity might be the key to maintaining high populations of flying squirrels and other small mammals (Carey et al. 1999a). Silviculture is well developed for most North American forests (see Curtis et al. 1998 for a review for Douglas-fir), but current strategies for managing

forests as complex ecosystems are lacking in efficacy (Carey 2001). New approaches incorporating stand and landscape management have been developed, but proven methods for the management of decadence, including the formation of cavities for wildlife, are lacking (Carey et al. 1999*a*, McComb and Lindenmayer 1999).

Management implications

The results of this study and its sister studies (e.g., Wilson and Carey 1996, Carey et al. 1997, Colgan et al. 1999, Carey 2001) suggest that management limited in focus to providing a few structural features in a forest (e.g., large trees for lumber, snags for woodpeckers, and cavity trees for squirrels) may not only fail to meet societal demand for conserving biodiversity and maintaining sustainability (e.g., Ray 1996, Kennett 1998), but also may have long-term deleterious consequences on species like the spotted owl and for invasion by exotic species of plants such as wall lettuce (*Mycelis muralis*), stinking willy (*Senecio jacobaea*), English holly (*Ilex aquifolium*), and 15 other species previously established on our conventionally thinned sites (Thysell and Carey 2000). Sophisticated, active, highly intentional management may be required to meet the growing demands of the human population for a variety of economic goods (e.g., timber, floral plants, and mushrooms are eagerly sought in Puget Sound forests) and ecological services (e.g., forests on Ft. Lewis provide open space for military training and outdoor recreation, extract carbon dioxide from the air, serve as a watershed for adjacent municipalities, and contribute to the maintenance of viable populations of a number of sensitive species, including anadromous salmonids in the very developed and growing Seattle-Tacoma-Olympia corridor in Washington, USA). Intentional management has potential to meet these demands, but is based on as yet experimentally unproven concepts of biocomplexity and emergent properties of self-organizing systems (Carey et al. 1999*a*, Carey 2001).
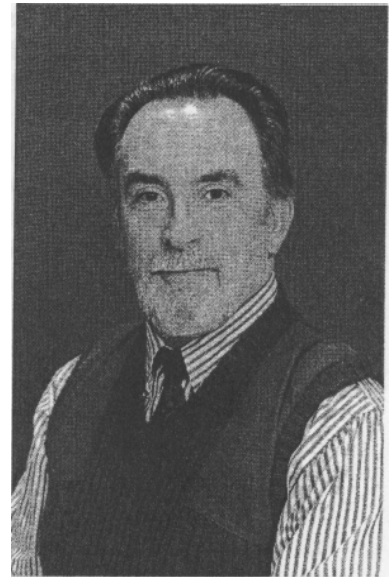
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