NORTHERN FLYING SQUIRREL DENSITIES IN FIR FORESTS OF NORTHEASTERN CALIFORNIA

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Abstract: The northern flying squirrel (*Glaucomys sabrinus*) is the primary prey of northern spotted owls (*Strix occidentalis caurina*) and California spotted owls (*S. o. occidentalis)* throughout much of the owls' ranges. Flying squirrel abundance patterns, however, are poorly documented. Using capture-recapture techniques to estimate density, we compared flying squirrel densities among 3 types of fir (*Abies* spp.) forests in Lassen National Forest, northeastern California. We compared densities between 3 each of old and shelterwood-logged fir stands in 1990 and among 4 each of old, shelterwood, and young fir stands in 1991-92. Shelterwood stands had been logged and had undergone site preparation 5 years prior to our study. In 1990 flying squirrel density was greater in old ($\bar{x}$ = 2.76 squirrels/ha, SE = 0.55) than in shelterwood ($\bar{x}$ = 0.31 squirrels/ha, SE = 0.11) stands (P = 0.005). In 1991-92 density varied (P = 0.001) among the 3 stand types, averaging 3.29 squirrels/ha (SE = 0.63) in old, 2.28 squirrels/ha (SE = 0.18) in young, and 0.37 squirrels/ha (SE = 0.17) in shelterwood stands. Body mass of adult males and females and recapture rate did not differ (M, P = 0.438; F, P = 0.983; P = 0.218, respectively) between old and young stands, and percent juveniles captured was greater (P = 0.052) in old than in young stands. Diet analyses were consistent with other studies and indicated that sporocarps of hypogeous fungi were a common food source. Frequency of hypogeous sporocarps was correlated (r_s = 0.860, P < 0.001) with flying squirrel density, but cavity density and understory cover were not (P = 0.344 and 0.217, respectively). Flying squirrels were not old-growth specialists; however, low densities in shelterwood stands suggest that heavy logging and intensive site preparation negatively affected flying squirrel populations.

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The ecology of a predator cannot be understood without knowledge of the ecology of its primary prey. The northern flying squirrel is the primary prey of northern and California spotted owls throughout much of the owls' ranges (Forsman et al. 1984, Thomas et al. 1990, Verner et al. 1992). Few studies have examined abundance patterns of northern flying squirrels. Frequency of occurrence determined from track plates was reported for northern flying squirrels in several forest types in northwestern California (Raphael et al. 1986, Raphael 1988), but Carey and Witt (1991) found that frequency of occurrence determined from track plates was a poor index of northern flying squirrel abundance. Witt (1992) reported northern flying squirrel densities in different stand age classes in Oregon, but focused on home range size and den tree use. Carey et al. (1992) found that flying squirrel density was approximately twice as great in old stands than in young stands in Oregon and Washington, whereas Rosenberg and Anthony (1992) found that mean density in old-growth stands in Oregon was only slightly greater than in second-growth stands.

Northern flying squirrels are nocturnal and forage on sporocarps of hypogeous fungi and epiphytic lichens (McKeever 1960; Maser et al. 1978, 1986; Hall 1991). They use tree cavities for nests and dens but also use stick or leaf nests (Cowan 1936, Weigl and Osgood 1974) and trees infected with witches' broom rusts (*Chrysomyxa* spp.) (Mowrey and Zasada 1984). Amount of understory cover may influence predation risk and thus use of habitat and population levels of flying squirrels because they forage on the ground for hypogeous fungi.

Our objectives were to (1) compare northern flying squirrel density and other population characteristics (body mass, age distribution, and recapture rate) among stand types that varied in forest structure; (2) describe the diet of flying squirrels; and (3) evaluate associations between flying squirrel density and 3 habitat attributes (frequency of hypogeous sporocarps, cavity density, and understory cover). We compared population characteristics other than density among stand types to better assess potential differences in habitat quality (Van Horne 1983). We assumed body mass reflected physical condition, percent juveniles captured reflected reproductive rate, recapture rate reflected dispersal and survival rates, and each was positively associated with habitat quality.

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STUDY AREA

The study area lay at the southern tip of the Cascade Range in northeastern California and was located in Plumas County in Lassen National Forest. Stands were located in an area approximately 13 km wide that encompassed Swain Mountain Experimental Forest in its eastern half. Elevations ranged from 1,784 to 1,966 m and slopes from 10 to 40%.

Old, shelterwood, and young stands were dominated by white (*A. concolor*) and red (*A. magnifica*) fir; we grouped the 2 species into a single fir category. Jeffrey pine (*Pinus jeffreyi*) and sugar pine (*P. lambertiana*) occurred in most stands but composed < 10% of trees sampled.

Old stands (>200 yr old) were multilayered, with firs dominating all layers. We counted growth rings on 20 large cut stumps located in shelterwood stands adjacent to old stands; mean age was 250 years (range 188-370). Other than fir seedlings, only scattered herbaceous plants (e.g., *Pyrola picta*, *Viola purpurea*, and *Corallorhiza maculata*) and occasional shrubs (primarily *Chrysolepis sempervirens*) grew in the understory.

Shelterwood stands were old stands (>200 yr old) that had been harvested in 1984-85. Harvest levels were high, leaving a parklike stand structure dominated by widely spaced, large trees (39-60 trees/ha). After harvest, logging slash was piled by tractor and burned or broadcast burned to clear a mineral soil bed for natural regeneration. Much organic matter was removed or displaced during site preparation. Low shrubs (*Ceanothus cordulatus, Ribes roezlii*) and various herbaceous plants, including grasses and thistle (*Cirsium* sp.), were common in the understory of shelterwood stands.

Young stands regenerated naturally following stand-replacement wildfires. Stands were dense, even aged, and homogeneous in composition and structure. Few residual logs, snags, or trees were found in any young stands. Because stands had closed canopies, virtually no herbaceous plants occurred in the understory. We estimated these stands were 75-95 years old because mean age at breast height of 26 randomly selected trees was 64 years (range 47-83), and red and white fir took about 20 years to grow to breast height at a nearby site (Oliver 1988).

METHODS

Stand Selection

We identified potential study stands from aerial photos. We looked for stands that had high within-stand and within-type homogeneity in tree species composition and stand structure. Stands also had to be large enough to fit a trapping grid and buffer strip of similar forest ≥40 m wide (total area of about 19 ha). These criteria limited potential stands such that we selected 4 stands that best met the above criteria within each stand type. Because we did not randomly select stands, caution should be taken in making inferences beyond the stands we studied.

Vegetation Sampling

Within each stand we established a rectangular to square grid (7 X 13, 8 X 13, 8 X 12, 9 X 11, or 10 X 10) with 40-m spacing that was used for sampling vegetation and fungi and live-trapping flying squirrels. We sampled vegetation at every third grid point during summer 1991. Because tree densities varied among stand types, we used different-sized vegetation plots among the 3 stand types to improve sampling efficiency. In shelterwood stands we took all measurements within an 18-m radius (0.10 ha).

In old stands we measured small-diameter trees (<18-cm diam at breast height [dbh]) within a 6-m radius (0.01 ha) and all other measurements within a 16-m radius (0.08 ha). In young stands we took all measurements within a 6-m radius. We recorded species and dbh for each tree or snag ≥5-cm dbh. We also scanned trees and snags in each vegetation plot for cavities and recorded estimated numbers of natural and woodpecker-excavated cavities. We assumed that these estimates provided an index of actual cavity numbers. We tallied trees and snags <5-cm dbh. For logs ≥12 cm at midpoint diameter, we measured the length within the sample plot and the midpoint diameter and determined decay class (Maser et al. 1979). We used the area formula for a rectangle to compute percent ground cover of undecayed and decayed logs. Undecayed logs were circular in cross section, and decayed logs were elliptical to flat in cross section. Stumps ≥24 cm in diameter were tallied. We used a spherical densiometer to estimate canopy cover (Lemmon 1956).

Trapping

At each grid point we placed 2 livetraps (41 x 13 x 13 cm): 1 on the ground and 1 attached at breast height to the nearest large tree (≤5 m from grid points in old and young stands and ≤10 m in shelterwood stands). We baited traps with a mixture of rolled oats, peanut butter, and molasses. In 1990 we trapped in 3 old stands and 3 shelterwood stands. In 1991-92 we trapped in these same stands, 1 additional old stand, 1 additional shelterwood stand, and in 4 young stands. We simultaneously trapped in 2 old, 2 young, and 2 shelterwood stands during 2 trapping sessions each year. During each session we trapped for 15-16 nights. In 1990 we began trapping in mid-July, and in 1991 and 1992 we began in early August. We followed an animal welfare protocol approved by the Humboldt State University Institutional Animal Care and Use Committee.

We marked animals on first capture with aluminum ear tags, and determined body mass, sex, and age class. We used pelage characteristics to determine age class (Wells-Gosling 1985): juveniles had a gray coat, whereas the tips of guard hairs on adults were reddish brown.

Diet Analysis

We examined fecal pellets of individuals captured in 1991-92 to describe flying squirrel diet. Fecal samples consisted of 1-5 fecal pellets, and we collected only 1 sample from an individual squirrel. We mixed fecal samples with 90% ethyl alcohol and prepared 3 slides from each sample. On each slide we examined 25 systematically located fields of view (400x) for 75 fields of view/fecal sample. Results are reported as the percentage of fecal samples that contained evidence of a particular food type on ≥1 of the 75 fields of view.

Fungi Sampling

During summer 1991 we systematically sampled each stand for sporocarps of hypogeous fungi. We sampled shelterwood stands from 21 to 24 June and old and young stands from 8 to 18 July. Snow melted and soil temperatures increased earlier in shelterwood stands than in the other stands because they were more open. At each grid point (91-104 points/grid) we searched for sporocarps in a 4-m^2 circular plot (1.13-m radius). We first dug a small pit in the center of each plot and measured the depth of the organic layer. To search for sporocarps we used 4-tined rakes to rake through the organic layer and upper 5-10 cm of mineral soil within each plot. We identified sporocarp collections to genus (Castellano et al. 1989).

Analyses

We used principal components analysis as an ordination technique (Gauch 1982, Pielou 1984) to graphically display how vegetation varied among the 12 stands and 3 stand types. We used 11 variables (Table 1) that described stand structure for this analysis.

We used the first-order jackknife estimator (Burnham and Overton 1979) calculated by program CAPTURE (Rexstad and Burnham 1991) to estimate flying squirrel population size ($\hat{N}$). Rosenberg et al. (1995) found that the first-order jackknife estimator provided reliable population estimates when capture probabilities were low and heterogeneous among individuals, which was typical of flying squirrel capture probabilities in our study. To estimate effective area trapped ($\hat{A}$), we added 50% of the mean maximum distance moved (MMDM) to the perimeter of the grid by animals captured ≥2 times (Wilson and Anderson 1985). We estimated density ($\hat{D}$) as $\hat{N} / \hat{A}$.

Using a *t*-test we compared density estimates from 1990 between old and shelterwood stands. We used repeated measures analysis of variance

Table 1. Factor loadings for the first 2 principal components and means and standard errors for vegetation variables measured in 3 types of fir stands (*n* = 4 stands for each stand type) in 1991 in Lassen National Forest, California. Old stands were >200 years old, young stands were 75-95 years old, and shelterwood stands were stands >200 years old that had been shelterwood-logged in 1984-85.

	Factor loading (component)		Old		Young		Shelterwood	
Variable	1	2	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
No. trees/ha <5-cm dbh	0.33	0.17	1,735.0	580.5	71.8	15.5	105.0	39.1
No. firs/ha 5-27-cm dbh	0.23	0.38	855.4	159.4	482.8	50.1	19.1	4.2
No. firs/ha 28-90-cm dbh	-0.21	0.41	181.9	7.7	517.9	27.0	13.1	1.4
No. firs/ha >90-cm dbh	0.40	-0.13	30.2	2.4	1.5	0.8	17.3	1.3
No. snags/ha 13-52-cm dbh	-0.26	0.35	57.0	20.1	368.3	65.6	7.0	2.4
No. snags/ha >52-cm dbh	0.38	-0.13	9.8	1.5	0.7	0.7	5.8	1.0
% canopy cover	-0.02	0.47	66.0	0.4	78.3	1.8	24.3	1.7
% ground cover of undecayed logs	0.41	0.03	2.2	0.2	0.5	0.1	0.9	0.1
% ground cover of decayed logs	0.39	0.15	3.1	0.2	0.1	0.1	0.1	0.0
Organic soil depth (cm)	0.01	0.47	6.8	0.3	7.9	0.4	1.7	0.4
No. stumps/ha	0.33	0.21	22.2	4.6	9.2	1.5	6.7	2.1

(ANOVA) to compare density estimates from 1991 and 1992 among old, young, and shelterwood stands. We used the Ryan-Einot-Gabriel-Welsch multiple-range test (SAS Inst. Inc. 1988: 598) to compare means following ANOVA; this is a stepwise unplanned multiple comparison that controls Type I experiment-wise error rate. We performed the multiple comparison test separately for 1991 and 1992 data. To improve homogeneity of variances, we log transformed density prior to analyses.

We were able to compare demographic characteristics other than density only between old and young stands because we captured so few squirrels in shelterwood stands. We used repeated measures ANOVA to compare body mass of adult males and females, sex ratio, and percent juveniles captured between stand types. We compared sex ratio between stand types because it was a potential confounding factor in comparisons of percent juveniles captured and recapture rate between stand types. We analyzed recapture rate, the percentage of individuals captured in 1991 that was recaptured in 1992, using a 2-factor ANOVA; the 2 factors were stand type (old and young) and age class (juv and ad). We tested the significance of the interaction term to determine whether age class was a confounding factor in the comparison of recapture rate between stand types.

We compared frequencies of occurrence of the same foods between old and young stands to determine if flying squirrels had similar overall diets. We used the absolute value of the Spearman rank correlation coefficient as an index of similarity in diet. Because digestibility differs among foods, differences in frequencies of occurrence among foods found in fecal samples do not necessarily reflect differences in the diet.

To evaluate associations between flying squirrel density and frequency of hypogeous sporocarps, cavity density, and understory cover, we first compared each measure among stand types using ANOVA. We then evaluated the correlation between each habitat measure and flying squirrel density using Spearman rank correlation analysis. We averaged flying squirrel density across 1991-92. Frequency of hypogeous sporocarps was the percentage of plots in which we found ≥ 1 hypogeous sporocarp. Cavity density was the combined density of natural and woodpecker-excavated cavities counted during vegetation sampling. Because small firs were dominant in the forest understory, we used number of trees/ha <5-cm dbh as the measure of understory cover. We reduced skewness and improved homogeneity of variances prior to ANOVA by log transforming cavity density and understory cover.

RESULTS

Vegetation Characteristics

Ordination of the 12 stands showed how distinct vegetation structure was among the 3 stand types (Fig. 1). The first principal component explained 50% of the total variation, the second explained 39%, and the third explained 5%. Component 1 primarily distinguished between old and young stands. Compared with young stands, old stands had greater amounts of un-

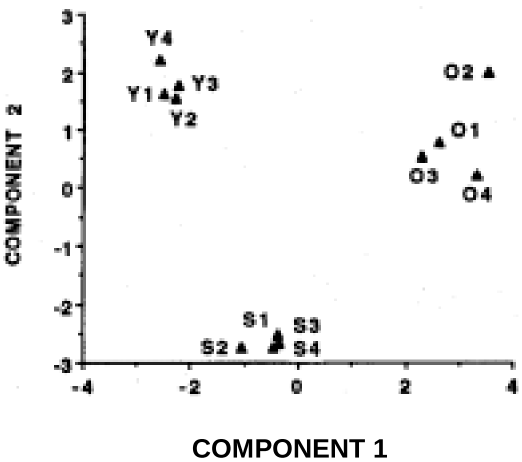

Fig. 1. Principal component scores of the 4 old (01-04), 4 young (Y1-Y4), and 4 shelterwood (S1-.S4) grids on the first 2 principal components from an analysis of 11 vegetational variables measured in 1991 in Lassen National Forest, California. Variables with greatest factor loadings on Component 1 were percent ground cover undecayed logs, number of firs/ha >90-cm dbh, percent ground cover decayed logs, number of snags/ha >52-cm dbh, number of trees/ha <5-cm dbh, and number stumps/ha. Variables with greatest factor loadings on Component 2 were percent canopy cover, organic soil depth, number firs/ha 28-90-cm dbh, number firs/ha 5-27-cm dbh, and number snags/ha 13-52-cm dbh.

decayed and decayed logs, and more firs >90-cm dbh, snags >52-cm dbh, stumps, and trees <5-cm dbh (Fig. 1 and Table 1). Component 2 primarily distinguished shelterwood stands from old and young stands. Compared with old and young stands, shelterwood stands had thinner organic soil layers, less canopy cover, and fewer firs 28-90-cm dbh, firs 5-27-cm dbh, and snags 13-52-cm dbh.

Population Characteristics

Density.-The MMDM did not differ between old and young stands ($F = 0.05$; 1, 6 df; $P = 0.824$) but did differ between 1991 and 1992 ($F = 5.05$; 1, 6 df; $P = 0.066$). We therefore averaged MMDM across stands for each year to estimate effective area trapped. In 1990 mean flying squirrel density was greater in old stands than in shelterwood stands ($t = 5.753$, 4 df, $P = 0.005$) (Table 2). In 1991-92 mean density varied among old, young, and shelterwood stands ($F = 20.16$; 2, 9 df; $P = 0.001$) but not between years ($F = 0.20$;1, 9 df; $P = 0.662$). Mean density was greatest in old stands and lowest in shelterwood stands (Table 2). Density estimates were most variable in old stands, especially in 1992. Mean densities did not differ between old and young stands in either year (Table 2).

Body Mass.-Pooled across years and stand types, adult females ($x = 128.8$ g, $n = 156$, SE = 1.05) weighed more than adult males ($x = 117.9$ g, $n = 155$, SE = 0.76) ($t = 8.41$, 309 df, $P < 0.001$). Body mass of adult males did not differ between stand types ($F = 0.69$; 1, 6 df; $P = 0.438$) but did differ between years ($F = 6.75$; 1, 6 df; $P = 0.041$); males weighed more in 1992 than in 1991 (Table 3). Body mass of adult females did not differ between stand types ($F = 0.00$; 1, 6 df; $P = 0.983$) or years ($F = 1.27$; 1, 6 df; $P = 0.302$).

Sex Ratio *and Age Distribution*.-Sex ratio was similar between stand types ($F = 0.52$; 1, 6 df; $P = 0.497$) and years ($F = 0.61$; 1, 6 df; $P = 0.464$) (Table 3). Percent juveniles captured was greater in old than in young stands in 1992 but similar between stand types in 1991 (Table 3). Effects due to stand type ($F = 5.83$; 1, 6 df; $P = 0.052$), year ($F = 4.70$; 1, 6 df; $P = 0.073$), and the interaction between stand type and year ($F = 5.02$; 1, 6 df; $P = 0.066$) were marginally significant.

Recapture Rate.-Recapture rate was greater for juveniles than adults ($F = 5.70$; 1, 12 df; $P = 0:034$) but not different between old and young stands ($F = 1.69$; 1, 12 df; $P = 0.218$) (Table 3). There was no interaction between stand type and age class ($F = 0.43$; 1, 12 df; $P = 0.525$).

Table 2. Means and standard errors of northern flying squirrel density estimates (squirrels/ha) in 3 types of fir stands in Lassen National Forest, California. Old stands were >200 years old, young stands were 75-95 years old, and shelterwood stands were stands >200 years old that had been shelterwood logged in 1984-85.

	Old			Young			Shelterwood		
Year	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
1990	3	2.76	0.55				3	0.31	0.11
1991	4	3.09A[a]	0.48	4	2.15A	0.24	4	0.57B	0.32
1992	4	3.48A	1.25	4	2.40A	0.30	4	0.18B	0.08

[a] Row means with same letter were not different ($P > 0.05$).

Table 3. Means and standard errors for body mass, sex ratio (M:F), percent juveniles captured, and recapture rate of northern flying squirrels captured in 2 types of fir stands in Lassen National Forest, California. Old stands were >200 years old, and young stands were 75-95 years old.

		Old			Young		
Year	Population characteristic	n^a	$\bar{x}$	SE	n	$\bar{x}$	SE
1991	M body mass (g)	33	116.8	1.63	21	114.7	2.26
	F body mass (g)	36	130.8	2.36	30	132.4	2.65
	Sex ratio	4	1.02	0.21	4	1.01	0.07
	% juv	4	48.4	3.77	4	45.9	4.67
1992	M body mass (g)	50	120.2	1.36	41	117.3	1.06
	F body mass (g)	41	127.6	1.56	41	126.1	2.07
	Sex ratio	4	1.07	0.24	4	1.34	0.29
	% juv	4	48.6	3.07	4	31.9	2.45
1991-92	Recapture rate (%)						
	Juv	4	27.7	7.85	4	17.7	2.62
	Ad	4	12.2	4.88	4	8.9	3.49

[a] n = no. of individuals for M and F body mass and no. of stands for sex ratio, % juv, and recapture rate.

Diet Analysis

Every fecal sample contained spores of hypogeous fungi (Table 4). Other foods observed were lichen, unknown vegetational matter, spores of epigeous fungi, pollen from staminate cones of conifers, insect parts, and seed parts. The 7 foods ranked similarly between old and young stands (1991, $r_s = 0.964$; 1992, $r_s = 0.991$), suggesting squirrels had similar overall diets.

Density and Habitat Attributes

Sporocarps were found most frequently in old stands and least frequently in shelterwood stands ($F = 9.71$; 2, 9 df; $P = 0.006$) (Table 5). Sporocarp frequency was correlated with mean flying squirrel density ($r_s = 0.860$, $n = 12$, $P < 0.001$).

Cavity density varied among stand types and was greatest in old stands and least in young stands ($F = 5.95$; 2, 9 df; P =, 0.023) (Table 5). There was no correlation between cavity density and mean flying squirrel density ($r_s = 0.300$, $n = 12$, $P = 0.344$).

Understory cover varied among stand types, with density of trees <5 cm dbh greatest in old stands and least in young stands ($F = 25.01$; 2, 9 df; $P < 0.001$) (Table 5). There was no correlation between understory cover and mean flying squirrel density ($r_s = 0.385$, $n = 12$, $P = 0.217$).

DISCUSSION

The difference in mean flying squirrel density between old and young stand types was intermediate between differences reported by Carey et al. (1992) and Rosenberg and Anthony (1992). Carey et al. (1992) reported mean densities in old stands twice as great as those in young stands (40-70 yr old). Rosenberg and Anthony (1992) reported mean densities in old-growth stands that were only 15-21% greater than those in 30-60-year-old second-growth stands. In our study, mean density in old stands was 44% greater in

Table 4. Percent frequencies of various food types found in fecal samples (n) of northern flying squirrels captured in 2 types of fir stands in Lassen National Forest, California. Old stands were >200 years old, and young stands were 75-95 years old.

			Food type						
Year	Stand type	n	Hypogeous fungi[a]	Epigeous fungi[a]	Lichen	Unknown vegetational matter	Seeds	Conifer staminate cones[b]	Insects
1991	Old	41	100	29	85	63	5	10	15
	Young	34	100	41	82	65	6	32	9
1992	Old	47	100	11	57	68	2	19	26
	Young	33	100	15	36	64	0	18	18

[a] Determined by presence of spores.

[b] Determined by presence of pollen.

Table 5. Means and standard errors of 3 habitat attributes measured in 3 types of fir stands in Lassen National Forest, California, 1991. Old stands were >200 years old, young stands were 75-95 years old, and shelterwood stands were stands >200 years old that had been shelterwood logged in 1984-85.

Habitat attributes	Old		Young		Shelterwood	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Frequency of hypogeous sporocarps (%)	27.8A[a]	6.0	17.5A	1.6	4.2B	2.2
No. cavities/ha	5.4A	0.7	1.5B	1.5	4.1A	0.8
No. trees/ha <5-cm dbh	1,735.0A	580.5	71.8B	15.5	105.0B	39.1

[a] Row means with same letter were not different ($P > 0.05$).

1991 and 45% greater in 1992 than mean density in young stands. Young stands sampled by Carey et al. (1992) and Rosenberg and Anthony (1992) regenerated following clear-cut logging, whereas young stands sampled in this study regenerated naturally after wildfire. Young stands sampled in this study were older than those sampled by Rosenberg and Anthony (1992) and Carey et al. (1992) but, unlike the second-growth stands used by Rosenberg and Anthony (1992), lacked residual logs, trees, and snags.

Comparisons of population characteristics between old and young stands were consistent with comparison of density. Mean values for male body mass, percent juveniles captured, and recapture rate were greater for old stands than young stands, but tests were either not significant or marginally significant. We interpret these results to suggest that old stands in our study area provided slightly greater but not significantly greater habitat quality than did young stands for flying squirrels. The power of our comparisons was clearly limited with sample sizes of 4. The low densities in shelterwood stands, however, suggest that these stands provided poor quality habitat for flying squirrels.

Spotted owl predation may have affected flying squirrel abundance in 1 trapping grid. The only grid in which a spotted owl pair successfully nested nearby had a low density estimate and recapture rate. In 1992 this owl pair fledged 3 young from a nest located 170 m from 1 old stand. On several occasions, members of this owl family were observed within the trapping grid (J. A. Blakesley, U.S. For. Serv., Arcata, Calif., pers. commun.). The 1992 flying squirrel density estimate for this grid was only 0.81 squirrels/ha, a 74% decrease from the 1991 density estimate of 3.09 squirrels/ha. The recapture rate for this stand was 2.9%, whereas the mean recapture rate was 25.1% (SE = 4.1) for the other 3 old stands and 12.5% (SE = 2.4) for the 4 young stands. Flying squirrels are the primary prey of spotted owls in Lassen National Forest, occurring in 78% of regurgitated pellets collected between 1990 and 1992 (J. A. Blakesley and B. R. Noon, U.S. For. Serv., Arcata, Calif., unpubl. data). Carey et al. (1992) and Rosenberg and Anthony (1992) also found evidence that spotted owl predation may have negatively affected flying squirrel densities.

The correlation between flying squirrel density and sporocarp frequency suggests that abundance of hypogeous sporocarps may have been a factor influencing flying squirrel density. Given an array of naturally occurring foods including sporocarps of hypogeous and epigeous fungi, fir seeds, and lichen, flying squirrels that were trapped on our grids preferred hypogeous fungi in captivity (Zabel and Waters, unpubl. data). McKeever (1960), who examined stomach contents of flying squirrels trapped at the same locality where we trapped, noted that the diet consisted entirely of fungi during .summer and fungi and lichen during winter. Similar results were found in the central Sierra Nevada (Hall 1991) and in Oregon (Maser et al. 1978, 1986; Maser et al. 1985). Hall (1991) assumed that flying squirrels cached sporocarps during snow-free months because spores of hypogeous fungi were found in fecal samples of squirrels trapped throughout winter when snow cover would have prevented ground foraging.

The hypothesis that flying squirrel densities are limited by availability of den cavities (Carey 1991, Carey et al. 1992) was not supported by our data. Although tree densities were low, large snags and cavities were relatively abundant in shelterwood stands because snags with cavities or broken tops had been marked and not harvested. The low density of cavities in young stands reflected the lack of residual trees and snags in these stands. We suspect that flying squirrels primarily used stick nests in these stands.

Most flying squirrel nests found by Martin (1994) in second-growth stands in the Oregon Cascades were stick nests.

We found no support for the hypothesis that understory cover is an important factor influencing flying squirrel density. Carey (1995) found that prevalence of ericaceous shrubs was positively associated with flying squirrel density. He suggested that abundance and diversity of ericaceous shrubs could influence the diversity and abundance of mycorrhizal fungi. The only habitat characteristic Rosenberg and Anthony (1992) found to be correlated with flying squirrel density was deciduous shrub cover, but they concluded the correlation may have been spurious because there was a correlation in only 1 of *2* years. Understory cover was a poor indicator of suitable habitat for populations of northern flying squirrels in the southern Appalachian Mountains (Payne et al. 1989).

MANAGEMENT IMPLICATIONS

Northern flying squirrels in our study area were not old-growth specialists, as indicated by the relatively high densities in young stands. Low densities in shelterwood stands, however, suggest that heavy logging and intensive site preparation negatively affected flying squirrel populations. Flying squirrel density also was associated with frequency of hypogeous sporocarps. Although we found few hypogeous sporocarps in shelterwood stands, we do not suggest that silvicultural practices necessarily adversely affect sporocarp production of hypogeous fungi. At a nearby site we found no difference in sporocarp production of hypogeous fungi among units that had been heavily thinned, moderately thinned, and not thinned and between units that had been broadcast burned and units left unburned (Waters et al. 1994). Thinning and broadcast-burning treatments at this site were less severe than silvicultural treatments in shelterwood stands at Swain Mountain Experimental Forest. Despite prevalence of hypogeous fungi in diets of flying squirrels and other small mammals (Fogel and Trappe 1978), little is known about the effects of silvicultural practices on sporocarp production of hypogeous fungi.

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