

INFLUENCE OF THINNING OF DOUGLAS-FIR FORESTS ON POPULATION PARAMETERS AND DIET OF NORTHERN FLYING SQUIRRELS

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Abstract: We investigated the effects of thinning young (35- to 45-yr-old) Douglas-fir (*Pseudotsuga menziesii*) forests on density, survival, body mass, movements, and diets of northern flying squirrels (*Glaucomys sabrinus*) in the northern coast range of Oregon. We used a repeated measures, randomized block design with 3 treatments (control, moderate thinning, and heavy thinning) and 4 replicates to study diets and population characteristics from 1994–1997. Densities of flying squirrels were variable in space and time, but they were positively correlated to biomass and frequency of fungal sporocarps, suggesting they were responding to food resources rather than forest structure. Fungal sporocarps comprised a major portion of the squirrel's diet, and other vegetative material made up the remainder of the diet. Several fungal genera including *Gautieria*, *Geopora*, *Hymenogaster*, *Hysterangium*, *Melanogaster*, and *Rhizopogon* were found more frequently in diets than on the trapping grids and therefore appeared to be selected by the squirrels. Flying squirrel movements were negatively correlated with the frequency of occurrence of fungal sporocarps at trap stations, suggesting that squirrels traveled greater distances to find fungal sporocarps where these food items were more sparsely distributed. We hypothesized that flying squirrel densities would be relatively low in these young, structurally simple forests; however, densities on some of the grids were >1.5 squirrels/ha, which was comparable to densities described for the species in late-successional forests. Our results indicated that commercial thinning did not have measurable short-term effects on density, survival, or body mass of flying squirrels.

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Northern flying squirrels occupy conifer and mixed-conifer forests throughout most of North America (Wells-Gosling and Heaney 1984) and are among the most common arboreal rodents in the Pacific Northwest (Carey 1991). Northern flying squirrels are important disseminators of hypogeous fungi, which form symbiotic relationships with coniferous trees and are important to the health and survival of coniferous forests (Fogel and Trappe 1978; Maser et al. 1985, 1986). Flying squirrels commonly den in cavities in large snags or live trees (Weigl and Osgood 1974, Maser et al. 1981, Carey et al. 1997) or in nests built of sticks in the forest canopy (Cowan 1936, Weigl and Osgood 1974). Their high abundance in older forests and association with decadent trees (Carey et al. 1999) has led some to suggest that they are particularly sensitive to timber harvests (Carey 1991).

Northern flying squirrels are the primary prey of northern spotted owls (*Strix occidentalis caurina*) in the northern part of the owl's range (Forsman et al.

1984). It has been hypothesized that spotted owls are associated with late-successional forests (Forsman et al. 1984) because flying squirrels are more abundant in these forests as compared to younger, managed forests (Carey et al. 1992). According to Carey et al. (1992), northern flying squirrels were twice as abundant in old-growth forests as in young, managed forests in the coast range of western Oregon, and Carey (1995) suggested that flying squirrel abundance was associated with the presence of ericaceous shrubs and large snags. In contrast, other studies found no significant differences in densities of northern flying squirrels in old-growth vs. young, managed forests in the Oregon Cascades (Rosenberg and Anthony 1992) and northwestern California (Waters and Zabel 1995). Cotton and Parker (2000) found flying squirrels to inhabit sub-boreal forests with a wide range of conditions, and the habitat of flying squirrels in southeast Alaska did not reflect the properties of old-growth forests (Smith et al. 2005). These latter studies suggested that northern flying squirrels might be generalists with respect to forest succession.

Historically, the primary form of disturbance in forests of the Oregon Coast Range was wildfire

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(Spies and Franklin 1991), but clear-cut timber harvest has become the principle cause of disturbance in recent decades. Commercial thinning in combination with retention of snags and coarse woody debris has been used to accelerate development of complex forest structure in young, structurally simple stands, while maintaining a level of commodity production (Carey and Curtis 1996, Hayes et al. 1997). Commercial thinning has been proposed to accelerate old-forest characteristics in young (<80 yr) stands in late-successional reserves on federal lands under the Northwest Forest Plan (FEMAT 1993). However, recent research is beginning to shed light on the responses of animal and plant species to thinning (e.g., Bailey and Tappelliner 1998, Hayes et al. 2003, Suzuki and Hayes 2003), but substantial gaps in our understanding of the ecological implications of thinning remain for many species in general, and for flying squirrels in particular. Greater understanding of these influences will enable resource managers to evaluate the ecological consequences of thinning forests and may facilitate development of more ecologically sensitive forest management.

We investigated the short-term effects of commercial thinning on abundance, survival, movements, diets, and habitat associations of northern flying squirrels in 35- to 45-year-old forests in the northern Oregon Coast Range. These forests had few of the vegetative characteristics that are associated with flying squirrels (Carey et al. 1992, 1999) including large trees, large snags, and ericaceous shrubs. Consequently, we predicted that abundance of flying squirrels in these young, structurally simple forests would be lower than that reported in previous studies (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995). In addition, we hypothesized that thinning would reduce density and survival rates of northern flying squirrels by as much as 25% because of the associated reduction in tree canopy, their arboreal habitat. We also examined the potential effect of thinning on abundance of hypogeous fungi because of its importance in flying squirrels diets (Maser et al. 1985, Waters and Zabel 1995, Carey et al. 1999) and the potential for hypogeous fungi to limit populations of mycophagist rodents in young, managed forests (North et al. 1997).

STUDY AREA AND DESIGN

Our study area was located in the northern Oregon Coast Range on the Tillamook State Forest and adjacent Stimson Lumber Company lands in Tillamook and Washington Counties, Oregon,

USA. We chose this area for its large acreage of even-aged, closed-canopy coniferous forest. The area burned during a series of intense fires from 1933 to 1951 (Wells 1999), and few live trees remained following the fires. Most of the area was salvage logged, and many snags were cut and removed or left on the forest floor. The area was reseeded or replanted with Douglas-fir from 1949 to 1970.

Douglas-fir was the dominant tree species in the study area, and red alder (*Alnus rubra*) occurred in riparian and recently disturbed areas. Less common tree species included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and noble fir (*Abies procera*). Vine maple (*Acer circinatum*) and red huckleberry (*Vaccinium parvifolium*) were the dominant deciduous shrubs. Salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*) were the most common evergreen shrubs. This area was influenced by the maritime climate of western Oregon; with mild, wet winters and cool, dry summers (Brown and Curtis 1985).

We selected 4 replicates (Stimson, C-Line, Deer Diamond, Ben Smith) for study, each initially consisting of 3 35- to 45-year-old unthinned stands ranging in size from 26 to 40 ha. Initial tree densities ranged from 412 to 713 trees/ha. Stands within replicates were <0.5 km apart, with the exception of the heavy thinned stand in the Deer Diamond replicate, which was approximately 1.5 km from the other stands. We randomly assigned 1 of 3 treatments to each stand within a replicate: control with no thinning (455–680 trees/ha), moderate thinning (240–330 trees/ha) and heavy thinning (165–240 trees/ha). Moderately thinned treatments were similar to typical operational thinning currently used to achieve wood fiber production. Heavily thinned treatments were designed to increase canopy openings, accelerate growth of overstory trees, stimulate understory development, and change structural complexity (Hayes et al. 1997). Thinnings were from below (Smith 1986), in which larger, dominant trees were retained and smaller, subdominant and suppressed trees were removed. Stands were thinned in the summer and fall of 1994, following 1 season of pre-treatment sampling. Slash was stacked in piles randomly throughout the stands.

Density of medium-sized conifers ($P = 0.0001$), density of all trees ($P = 0.0001$), abundance of small snags ($P = 0.011$), and all snags ($P = 0.026$) were significantly higher in the controls than in thinned stands. Stumps ($P = 0.0003$) and slash ($P = 0.001$) were greater in the thinned stands than in the controls. There were no significant differ-

ences in the number of small and large logs (coarse woody debris) among the treatments, and few large (>50-cm diameter at breast height [DBH]) trees and snags, and ericaceous shrubs were found in all stands.

METHODS

Trapping Design and Method

We established grids in each stand with 40 m between stations. Grid arrays varied from 17 × 6 to 10 × 10 with 96–100 stations depending on the size and shape of the stand. We placed 1 Tomahawk no. 201 live-trap (41 × 13 × 13 cm) on the ground within 5 m of the station center, and we attached another trap 1.5 m off the ground on the tree closest to the station center (Rosenberg and Anthony 1992). We baited traps with a mixture of rolled oats, molasses, and peanut butter, and we supplied them with polyester-fiber batting and nest boxes to minimize exposure and trap mortalities.

We trapped northern flying squirrels during May and June for 18 consecutive days in 1994 and 21 consecutive days each year from 1995 to 1997. We also trapped squirrels for 6 days in the fall of 1996 solely to describe diets. We ear-tagged each squirrel in both ears with uniquely numbered Monel no. 1 tags (National Band and Tag Company, Newport, Kentucky, USA), and we weighed, identified to sex, and released each squirrel. Weights of flying squirrels at first capture for each season and year were used in body mass comparisons. We classified individuals with body mass >102 g as adults according to Rosenberg and Anthony (1992). Small sample size ($n = 5$) precluded statistical analyses for juveniles, so we excluded them from all analyses.

Dietary Analysis

We collected fecal pellets directly from the anus of northern flying squirrels or from clean, dirt-free surfaces where pellets fell during handling of animals. We collected fecal samples the first time an animal was captured in the spring of 1996 and 1997 and in fall 1996. We sampled flying squirrels diets and fungi during fall 1996, because fruiting of hypogeous fungi varies seasonally (Luoma et al. 1991). We stored pellets in 50% ethanol to dissolve lipid layers. We later added 4–5 drops of distilled water and allowed the samples to rehydrate for 48 hours at room temperature. Rehydrated pellets were macerated and mixed thoroughly, and we transferred 5 drops of the suspension to a microscope slide. We added 3–4 drops of Melzer's

Reagent (iodine, potassium iodine, and chloral hydrate in aqueous solution) to the suspension and covered the slide with a 22 × 50 mm cover slip. We examined each slide under 250× magnification using a compound microscope. We identified fungal spores to genus according to Castellano et al. (1989), and we recorded frequency of occurrence of plant material (e.g., seed parts, pollen, and other vegetative material).

Habitat and Fungal Sampling

We sampled habitat characteristics at every fourth trapping station to estimate abundance of potential den structures (i.e., tree cavities) and characterize habitat for flying squirrels. We sampled live trees, stumps, logs, and slash in 10-m radius plots. We recorded species, DBH, and tree height for all live trees >2 m tall and >10 cm DBH. We tallied stumps >20 cm in diameter and <2 m tall; we tallied logs >1 m long and >10 cm in diameter by size class; and we estimated dimensions of each slash pile (width, length, and height). We recorded DBH, height, and decay class (Maser et al. 1979) of each snag >2 m high and >10 cm DBH in larger (20-m radius) plots because snags were less abundant than live trees.

In the spring and fall 1996 and spring 1997, we sampled hypogeous fungal sporocarps at every fourth station on each trapping grid 1 week prior to trapping, during trapping, or within 1 week of closing traps. Sampling methods were modified from Luoma et al. (1991). We sampled sporocarps using 4-m² circular plots at random distances from 1–20 m from the station center. In the fall 1996 and spring 1997, we located a new sample point 180° from the plot originally sampled in spring 1996. We removed the litter, and topsoil was raked to a depth of 5–10 cm. All sporocarps found were dried, weighed, and identified to genus; voucher specimens were deposited in the Mycological Herbarium at Oregon State University, Corvallis, Oregon, USA. This study was approved by the Animal Care and Use Committee at Oregon State University.

Statistical Analyses

We used program CAPTURE (Otis et al. 1978, Rextad and Burnham 1991) to estimate capture probabilities and abundance (N) of northern flying squirrels. Northern flying squirrels are known to have low and heterogeneous capture probabilities, so we used the Jackknife method for estimating abundance (Rosenberg et al. 1995). For each individual captured >2 times, we calculated

the mean maximum distance moved (MMDM), and we added half MMDM to the perimeter of each grid to estimate the area effectively trapped (\hat{A} ; Wilson and Anderson 1985). We used N/\hat{A} to estimate density (D).

We estimated annual survival rates from capture-recapture data using Cormack-Jolly-Seber models for open populations (Pollock et al. 1990, Lebreton et al. 1992). Capture-recapture analysis of the flying squirrel data allowed estimation of annual survival probabilities (ϕ , probability that a squirrel alive in a particular year t , survives to the same time the following year at time $t + 1$) and recapture probabilities (p , probability that a squirrel alive in year t is captured, or recaptured). We modeled sex and treatments as group effects, and we used replicates as covariates. We evaluated models and computed estimates using program MARK (White and Burnham 1999). The general approach used to estimate apparent survival was to: (1) evaluate goodness-of-fit and estimate an overdispersion parameter (\hat{c}) for the data, if needed; (2) fit a set of models to the data with program MARK; (3) adjust the covariance matrices and Akaike's Information Criterion (AIC) values with c , if necessary, to obtain quasi-likelihood Akaike's Information Criterion (QAIC) values; and (4) select an appropriate model for inference based on AIC model selection criteria (Burnham and Anderson 1998:53). Our focus in the data analysis and model selection process was to find the model that best fit the data (i.e., the most parsimonious model). Prior to model fitting, we used program RELEASE to test the goodness-of-fit of the data set to the assumptions of the Cormack-Jolly-Seber model and to estimate overdispersion (c). The candidate models we used allowed survival and recapture probabilities to vary by time (t) or have linear (T) or quadratic (T²) trends over time. We used maximum likelihood estimation for model fitting and optimal parameter estimation. We used AIC_c (Akaike 1973) instead of QAIC_c because the overdispersion parameter was small ($\hat{c} = 1.23$).

We compared the effects of thinning on population density and body mass among treatments within years using ANOVA for a randomized block design and repeated measures analysis. We used orthogonal contrasts to compare population densities and body mass between pre-treatment (1994) and post-treatment sampling periods (1995–1997) for thinned vs. unthinned stands. We also tested for differences between heavy vs. moderately thinned stands to determine if response differed with thinning intensity. We conducted

analysis of body mass separately by sex because males were heavier than females (Wells-Goshing and Heany 1984).

We tested for differences among treatments for habitat variables and compared biomass (dry weight) and percent frequency of hypogeous fungi among treatments and sites for the 5 most common genera of hypogeous fungi, using ANOVA for a randomized block design. We used the same approach to compare total biomass, total frequency, and number of genera among treatments within sample periods. We used repeated measures analysis to compare total biomass, frequency (percentage of plots where hypogeous sporocarps were found), and number of genera among treatments with sample period used as the repeated factor. Variables were $\log_{10}(x + 1)$ or square-root transformed where necessary to adjust for non-normality or heterogeneous variances. We compared differences in fungal community composition among treatments with chi-square goodness-of-fit tests (Steele and Torrie 1980:529).

We compared number of genera per fecal sample and percent frequency of each genus in fecal samples among treatments within sample periods using ANOVA for a randomized block design with sample period as the repeated factor. We assessed selection of fungal taxa by flying squirrels by differences between ranks of abundance in fecal samples and in sporocarp sample plots (Johnson 1980). We chose this method of comparing use to availability for its hierarchical ordering, objectivity, and robustness.

We used linear regression (Steel and Torrie 1980) to assess the relation between densities of flying squirrels to characteristics of the hypogeous fungal community and habitat for years when we collected those data. We used multiple linear regression to evaluate the relationship between presence of sporocarps and habitat characteristics. We presented the best model chosen from the top 10 ranked using Mallows' C_p Selection Criteria (Mallows 1973), based on significance of independent variables and amount of variability explained by the model.

RESULTS

Flying Squirrel Populations

Recapture probabilities (p) varied from 0.70 to 0.99 depending on sex and study sites. Mean recapture probabilities were consistently higher for males ($p = 0.97$) than for females ($p = 0.83$) and were generally >0.90 indicating a high probability

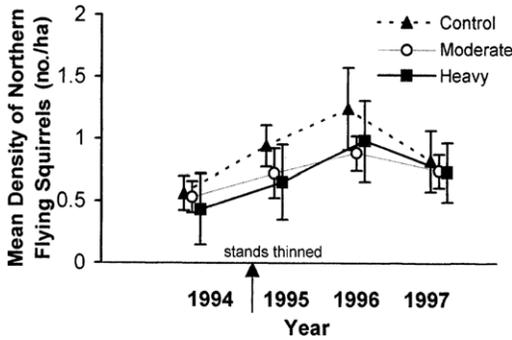


Fig. 1. Mean density estimates (N/A) of flying squirrels, in 4 control, moderately thinned, and heavily thinned stands, Oregon Coast Range, 1994–1997. Error bars represent ± 1 SE.

of capture of squirrels that were on the trapping grids. High recapture probabilities resulted in precise estimates of apparent survival and abundance; therefore, 21 days of trapping was more than sufficient to estimate these parameters.

We captured 124 flying squirrels 480 times in 1994 (10.3 flying squirrels/grid), 196 flying squirrels 934 times in 1995 (16.3 flying squirrels/grid), 306 flying squirrels 1,944 times in 1996 (25.5 flying squirrels/grid), and 240 flying squirrels 1,487 times in 1997 (20.0 flying squirrels/grid). Thinning did not significantly affect densities of flying squirrels ($F = 0.9$, $df = 1$, $P = 0.34$), nor did thinning intensity ($F = 0.4$, $df = 1$, $P = 0.51$; Fig. 1). Density of flying squirrels was variable (range = 0.1–2.2 squirrels/ha) in space and time, and it differed significantly among years ($F = 11.9$, $df = 3$, $P = 0.0001$). Density in most stands increased in 1995 and 1996, but it declined in 1997.

There was a good fit of the capture–recapture data to the Cormack-Jolly-Seber population model ($\hat{c} = 1.23$). The treatments had no detectable effect on apparent survival rates of flying squirrels; the best model with treatments (ϕ [time + treatments] p [sex]) had a $\Delta AIC = 2.4$ relative to best model (ϕ [time] p [sex]). However, there were 4 other models that had ΔAIC values < 2.0 from the best model and were considered competing models (Burnham and Anderson 1998; Table 1). Four of the 5 competing models had time or time + replicates as significant factors affecting apparent survival. One of the top models had sex as a factor, but the difference between apparent survival of males and females was not significant. All of the top models had sex or sex + replicates as important factors affecting recapture probabilities, so we report the results of the most parameterized model of the top 5 (ϕ [time + replicates] p [sex + replicates]) with a $\Delta AIC = 1.67$.

Annual survival rates of flying squirrels varied from 0.32–0.68 among years and replicates (Fig. 2). A few squirrels captured as adults in 1994 survived to 1997, indicating that they were at least 4 years old. Thinning did not significantly influence survival rates in the first 3 years following treatment. Survival rates varied significantly over time (Fig. 2), ranging from 0.46 to 0.61 during 1994–1995, 0.53 to 0.68 during 1995–1996, and 0.32 to 0.46 during 1996–1997. Survival rates were significantly lower over the last year of the study, corresponding to a decrease in densities the last year. Survival rates also varied significantly among the different study sites (Fig. 2) and were highest for the Ben Smith site, intermediate for Stimson and Deer Diamond, and lowest for C-line.

Thinning influenced movements of male and female flying squirrels between successive captures (MMDM) differently ($F = 47.9$, $df = 1$, $P = 0.0001$). The MMDM for males was 1.2 times (23.1 m) greater than females in 1994 and 1.5 times (65.4–72.2 m) greater in 1995–1997. In general, MMDM of male flying squirrels did not change in response to thinning ($F = 0.2$, $df = 1$, $P = 0.63$) or thinning intensity ($F = 1.2$, $df = 1$, $P = 0.28$; Fig. 3A); however, a gradual

Table 1. Model selection criteria for models of apparent annual survival (ϕ) and capture probabilities (p) of northern flying squirrels on 4 areas of the Oregon Coast Range, 1994–1997.

Model	AIC _c	ΔAIC_c	No. parameters	Deviance
{ ϕ (t) p (sex)}	1710.835	0.00	5	1700.785
{ ϕ (t) p (sex + reps)}	1712.083	1.25	8	1695.962
{ ϕ (t + reps) p (sex)}	1712.162	1.33	8	1696.041
{ ϕ (t + sex) p (sex)}	1712.391	1.56	6	1700.321
{ ϕ (t + reps) p (sex + reps)}	1712.501	1.67	11	1690.279
{ ϕ (t + treat) p (sex)}	1713.232	2.40	7	1699.138
{ ϕ (t + sex + reps) p (sex)}	1713.401	2.57	9	1695.249
{ ϕ (t + sex) p (sex + reps)}	1713.691	2.86	9	1695.540
{ ϕ (t + reps) p (sex + treat)}	1714.116	3.28	10	1693.930
{ ϕ (t + sex + reps) p (sex + reps)}	1714.142	3.31	12	1689.879
{ ϕ (t + sex + treat) p (sex)}	1714.645	3.81	8	1698.524
{ ϕ (t + treat) p (sex + reps)}	1714.758	3.92	10	1694.573
{ ϕ (t + reps + treat) p (sex)}	1714.820	3.98	10	1694.635
{ ϕ (t + reps) p (reps)}	1716.187	5.35	10	1696.002
{ ϕ (t*sex*reps) p (t*sex*reps)}	1741.812	30.98	40	1658.980

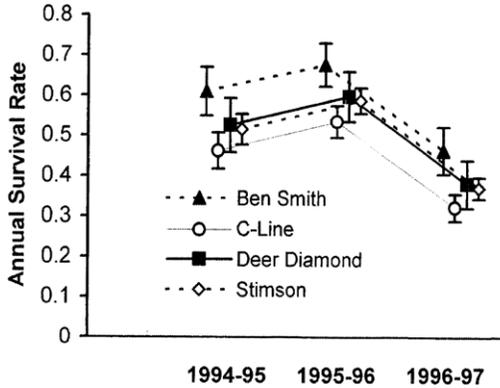


Fig. 2. Annual survival rates of flying squirrels at 4 sites in the Oregon Coast Range, 1994–1997. Error bars represent ± 1 SE.

increase in MMDM occurred in the moderately thinned stands. In addition, MMDM of males differed significantly among years ($F = 5.15$, $df = 3$, $P = 0.008$). There was no significant effect of treatments on movements of female flying squirrels due to thinning ($F = 0.1$, $df = 1$, $P = 0.77$) or thinning intensity ($F = 0.01$, $df = 1$, $P = 0.926$; Fig. 3B).

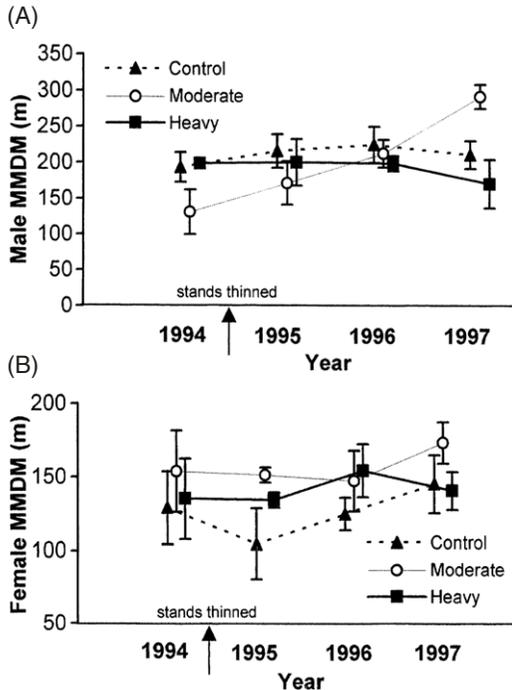


Fig. 3. Mean maximum distances moved (MMDM) of (A) male and (B) female flying squirrels in control, moderately thinned, and heavily thinned treatments, Oregon Coast Range, 1994–1997. Computed from stand means ($n = 4$); with the exception of 1994 control and 1996 heavy thin ($n = 3$), 1994 heavy thin ($n = 1$), and 1995 heavy thin ($n = 2$) for males, and 1994–1996 heavy thin ($n = 3$) for females. Error bars represent ± 1 SE.

Body mass of flying squirrels did not differ between sexes ($F = 2.3$, $df = 1$, $P = 0.13$), so we combined data for further analysis. Thinning did not affect body mass of flying squirrels ($F = 0.04$, $df = 1$, $P = 0.84$; Fig. 4), but body mass of flying squirrels differed significantly among years ($F = 8.9$, $df = 3$, $P = 0.0003$). There was some evidence that thinning intensity may have positively affected body mass ($F = 3.1$, $df = 1$, $P = 0.09$), as flying squirrels in the heavily thinned stands had slightly greater weights in post- vs. pre-treatment years.

Food Resources

We sampled a total of 3,576 m² for hypogeous fungi in 1996 and 1997, and we collected 566 hypogeous sporocarps in 17% of 894 plots on the 12 study areas. The 566 sporocarps had a dry weight of 106.2 g or a standing biomass of 0.3 kg/ha. We collected 18 genera and 34 species of sporocarps, including 7 undescribed and new species (see Gomez et al. [2003] for more detail). *Hysterangium* and *Rhizopogon* accounted for >56% of the total biomass of sporocarps on the plots (Table 2) and were most abundant in spring 1996. *Rhizopogon* and *Alpova* had the highest biomass in fall 1996, and *Hysterangium* and *Gautieria* accounted for the highest biomass in spring 1997. *Hysterangium* occurred on >24% of the plots, and *Rhizopogon* and *Tuber* were found on 18% (Table 2). We collected *Tuber* in more stands (92%) than any other genus, followed by *Rhizopogon* (75%) and *Hysterangium* (67%).

Community composition of hypogeous fungi varied among treatments (Fig. 5), as *Alpova*, *Barssia*, *Elaphomyces*, *Hydnotrya*, *Hymenogaster*, *Hysterangium*, *Truncocolumella*, and *Tuber* decreased in response to thinning. In contrast, *Endogone*, *Gautieria*, *Glomus*, *Leucangium*, and *Rhizopogon* increased in response to thinning. The difference in mean biomass of sporocarps among treatments was not significant ($P > 0.05$) for the 5 most common genera due pri-

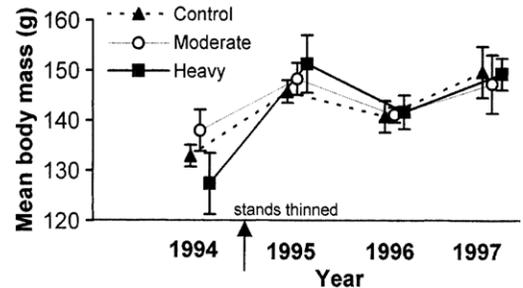


Fig. 4. Mean body masses of northern flying squirrels in 4 control, moderately thinned, and heavily thinned stands, Oregon Coast Range, 1994–1997. Error bars represent ± 1 SE.

Table 2. Sporocarp biomass and percent frequencies of hypogeous fungal genus in 12 Douglas-fir stands (3,576-m² total sample area) Oregon Coast Range, 1996 and 1997.

Genera ^a	No. of sporocarps	Dry wt (g)	Percent frequency in plots ^b	Percent frequency in stands ^c
<i>Alpova</i>	24	6.8	3.8	42
<i>Barssia</i>	26	3.0	3.8	33
<i>Elaphomyces</i>	5	5.2	1.5	17
<i>Endogone</i>	16	1.0	6.8	58
<i>Gautieria</i>	12	7.7	2.3	17
<i>Genea</i>	15	0.9	1.5	17
<i>Geopora</i>	2	0.4	0.8	8
<i>Glomus</i>	3	0.1	2.3	25
<i>Hydnotrya</i>	21	1.1	6.8	42
<i>Hymenogaster</i>	10	1.9	5.3	25
<i>Hysterangium</i>	231	34.9	24.8	67
<i>Leucangium</i>	2	3.4	6.0	33
<i>Leucophleps</i>	29	0.1	0.8	8
<i>Martellia</i>	1	0.7	0.8	8
<i>Melanogaster</i>	11	2.7	0.8	8
<i>Rhizopogon</i>	85	24.8	18.0	75
<i>Truncocolumella</i>	16	4.7	7.5	42
<i>Tuber</i>	54	6.8	18.8	92
Total	566	106.2		

^a Species of hypogeous fungal sporocarps collected: *Alpova diplophloeus*, *Barssia oregonensis*, *Endogone flammicorona*, *Endogone lactiflua*, *Elaphomyces granulatus*, *Gautieria monticola*, *Genea intermedia*, *Geopora cooperi*, *Glomus macrocarpum*, *Hydnotrya cubispora*, *Hydnotrya variformis*, *Hymenogaster* sp. (no. 1, 2, and 3), *Hymenogaster gilkeyae*, *Hymenogaster subillacinus*, *Hysterangium coriaceum*, *Hysterangium crassirhacis*, *Leucangium* sp., *Leucangium carthusianum*, *Leucophleps magnata*, *Martellia* sp., *Melanogaster tuberiformis*, *Rhizopogon* sp., *Rhizopogon hawkeriae*, *Rhizopogon parksii*, *Rhizopogon villosulus*, *Rhizopogon vinicolor*, *Truncocolumella citrine*, *Tuber gibbosum*, *Tuber monticola*, *Tuber murinum*, *Tuber shearii* and *Tuber* sp.

^b Percentage of total number of plots with truffles.

^c Percentage of total number of stands.

marily to large standard errors (Table 3). Mean total biomass did not differ significantly among treatments ($F_{2,6} = 0.79$, $P = 0.50$) or sample periods ($F_{2,6} = 2.01$, $P = 0.18$); however, thinning may have negatively affected total frequency of sporocarps among treatments ($F_{2,6} = 3.72$, $P = 0.09$). The difference in total frequency of sporocarps among sample periods was not significant ($F_{2,6} = 2.26$, $P = 0.15$). The average number of sporocarp species was significantly higher in controls than thinned stands ($F_{2,6} = 5.23$, $P < 0.05$), and we found more species in controls than thinned treatments in fall 1996 ($F_{2,6} = 6.09$, $P = 0.04$). The number of species of sporocarps collected was not significantly different among sample periods ($F_{2,6} = 2.20$, $P = 0.21$).

Flying Squirrel Diets

We sampled fecal pellets from 497 flying squirrels in 1996 and 1997 and found spores of 25 genera of hypogeous fungi (Table 4). Plant material

occurred in 98% of the fecal samples. *Rhizopogon* was the most common genus (73%) in squirrel diets with *Hysterangium* and *Melanogaster* the next most frequent averaging 36%. *Hymenogaster* (22%) and *Gautieria* (19%) were also common in squirrel diets. The percent frequency of *Gautieria*, *Hydnotrya*, *Hymenogaster*, *Hysterangium*, *Melanogaster*, *Picoa*, *Rhizopogon*, and *Tuber* in fecal samples was similar among treatments. *Gautieria* ($F_{2,6} = 9.23$, $P = 0.0037$), *Hydnotrya* ($F_{2,6} = 17.41$, $P = 0.0003$), *Melanogaster* ($F_{2,6} = 16.88$, $P = 0.0003$), *Rhizopogon* ($F_{2,6} = 30.34$, $P = 0.0001$), and *Tuber* ($F_{2,6} = 7.41$, $P = 0.008$) occurred more often in fecal samples in the fall than in the spring (Table 4). *Hymenogaster* ($F_{2,6} = 5.08$, $P = 0.03$) and *Picoa* ($F_{2,6} = 12.24$, $P = 0.001$) occurred more often in fecal samples in the spring. *Hymenogaster*, *Hysterangium*, *Melanogaster*, *Rhizopogon*, and *Tuber* were the only genera found in fecal samples from every stand. In addition, there was a significant interaction between season and treatment for *Hydnotrya* ($F_{4,12} = 7.19$, $P = 0.003$), and the frequencies of *Microthecium* ($F_{2,6} = 5.97$, $P = 0.04$) and *Tuber* ($F_{2,6} = 5.07$, $P = 0.05$) were significantly higher in unthinned than thinned treatments in fall 1996.

We compared the percent frequency of occurrence of 22 hypogeous fungi genera in fecal samples to the biomass of sporocarps collected in plots within the 3 sample periods. Nine genera were selectively consumed, and 9 were used less than available; the remaining 4 genera were similar in rank between sample plots and fecal samples (Fig. 6). *Gautieria*, *Geopora*, *Hymenogaster*, *Hysterangium*, *Melanogaster*, and *Rhizopogon* were the most frequently selected hypogeous sporocarps by flying squirrels (Fig. 6). *Alpova*, *Barssia*, *Endogone*, *Leucangium*, *Truncocolumella*, and *Tuber* were consumed proportionally less than their availability.

Relationship between Habitat Variables and Flying Squirrel Abundance

Density of flying squirrels was positively related to total hypogeous sporocarp biomass ($D = 0.41 + 0.0012 \times$ fungal biomass; $r = 0.81$, $P = 0.001$; Fig. 7A) and with sporocarp frequency ($D = 0.25 + 1.41 \times$ sporocarp frequency; $r = 0.65$, $P = 0.02$). In addition, flying squirrel density was positively correlated with biomass of *Hysterangium* ($D = 0.48 + 0.25 \times$ *Hysterangium* biomass; $r = 0.66$, $P = 0.02$). The relation between MMDM of male ($P = 0.46$) and female ($P = 0.13$) flying squirrels and biomass of sporocarps were not significant; however, movements of females were negatively correlated with the frequency of occurrence of sporocarps at grid sta-

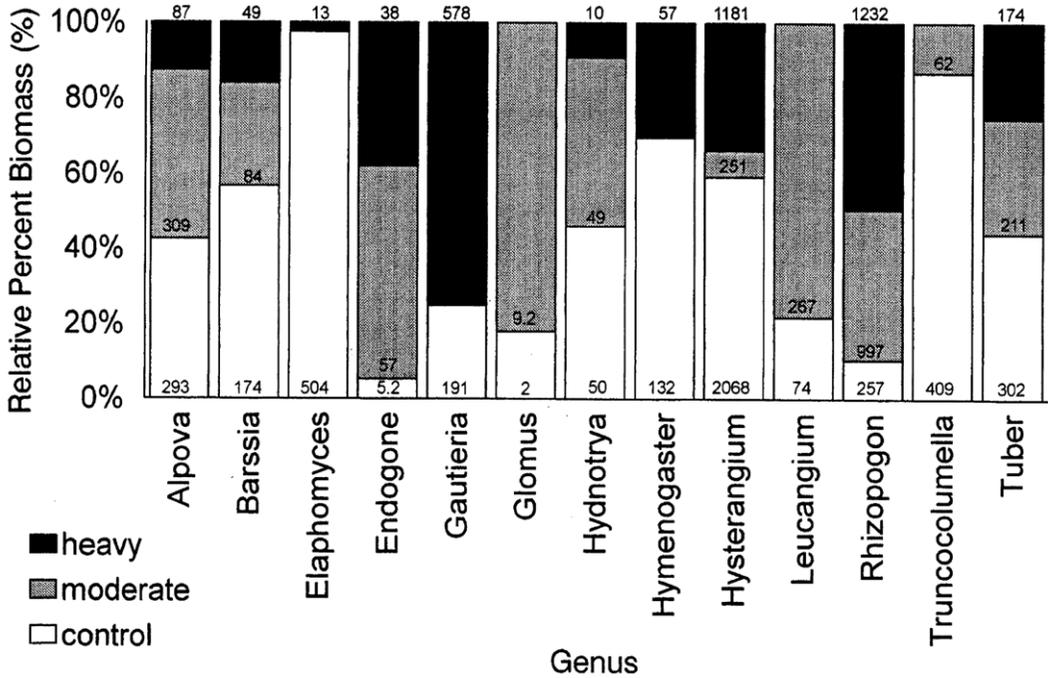


Fig. 5. Total biomass of hypogeous fungal sporocarps expressed as a percentage of genera found among control, moderately, and heavily thinned stands, Oregon Coast Range, 1996–1997. Numbers on bars represent biomass (g/ha).

tions in 1996 (MMDM = 173.5–155.4 × sporocarp frequency; $r = 0.70$, $P = 0.02$; Fig. 7B).

Flying squirrel density was significantly correlated with density of conifer trees >50-cm DBH ($r = 0.65$, $P = 0.02$), and 9 of 10 of the best multiple regression models for flying squirrel density included large conifer trees as a significant ($P < 0.05$) independent variable. Flying squirrel densities were correlated positively to density of large conifer trees and large logs ($D = -2.19 + 0.13X_1$ large conifer trees density + $1.32X_2$ large log density; $r = 0.79$, $P = 0.01$). Density of flying squirrels was not related to density of

large deciduous trees ($r = -0.48$, $P = 0.12$), snags 10- to 49-cm DBH ($r = -0.01$, $P = 0.97$) or snags >50-cm DBH ($r = 0.27$, $P = 0.40$).

DISCUSSION

Influence of Commercial Thinning

Contrary to our hypotheses, commercial thinning had no significant short-term influences (<3 yr) on population density, survival rate, or body mass of flying squirrels. The positive association between flying squirrel density and abundance of hypogeous

sporocarp in our study reflects the flying squirrel’s dependence on hypogeous fungi as a food source (Fogel and Trappe 1978; Maser et al. 1985, 1986). Consequently, the effects of thinning on abundance and richness of hypogeous fungi are likely an important factor in population response of flying squirrels.

Waters et al. (1994) compared hypogeous

Table 3. Mean biomass (g/ha) of hypogeous fungal sporocarps in 4 control, moderately, and heavily thinned stands, Oregon Coast Range, 1996 and 1997. P-values represent 2-way ANOVA for a randomized block design to test for treatment effect.

Variable	Thinning level						P-value
	Unthinned		Moderately		Heavily		
	Mean	SE	Mean	SE	Mean	SE	
Endogone	1.3	1.3	14.2	7.8	9.5	8.8	0.20 ^b
Hydnotrya	12.6	7.6	12.3	12.3	2.5	2.5	0.44 ^b
Hysterangium	517.0	408.9	62.6	39.6	295.2	271.8	0.46 ^b
Rhizopogon	64.4	28.2	248.4	137.7	308.0	209.5	0.35 ^b
Tuber	75.5	19.4	56.5	26.2	43.6	24.2	0.37 ^c
Total biomass	1124.9	417.0	603.7	177.6	934.5	512.0	0.38

^a Means computed from mean of subsamples within each stand (n = 23–28).
^b Variable was Log10 + 1 transformed.
^c Variable was square-root transformed.

Table 4. Percent frequency of occurrence of fungal genus in fecal pellets of northern flying squirrel in the Oregon Coast Range, 1994–1997.

Genera	Season			Seasons combined
	Spring 1996	Fall 1996	Spring 1997	
<i>Alpova</i>	0.5	0.0	1.2	0.6
<i>Beletaceae</i>	0.0	27.2	0.0	9.1
<i>Choiromyces</i>	0.0	0.7	0.0	0.2
<i>Coprinaceae</i>	0.0	0.0	0.3	0.1
<i>Cortinarius</i>	2.3	0.0	0.3	0.9
<i>Elaphomyces</i>	3.2	0.5	5.8	3.2
<i>Endogone</i>	3.3	1.4	2.9	2.5
<i>Gautieria</i>	9.1	41.2	6.3	18.9
<i>Genabea</i>	0.5	0.0	0.0	0.2
<i>Genea</i>	0.0	0.0	1.1	0.4
<i>Geopora</i>	14.4	12.4	12.1	13.0
<i>Glomus</i>	0.4	0.0	1.9	0.8
<i>Hydnotrya</i>	11.9	19.3	3.5	11.6
<i>Hymenogaster</i>	30.4	15.0	21.9	22.4
<i>Hysterangium</i>	46.2	48.3	13.5	36.0
<i>Leucogaster</i>	0.4	6.9	0.0	2.4
<i>Martellia</i>	5.8	12.7	5.3	7.9
<i>Melanogaster</i>	31.0	57.1	18.4	35.5
<i>Microthecium</i>	8.6	6.9	7.3	7.6
<i>Picoa</i>	15.9	2.1	2.8	6.9
Plant material	98.1	96.5	99.3	98.0
<i>Rhizopogon</i>	69.1	96.9	52.8	72.6
<i>Russulaceae</i>	0.0	18.6	0.0	6.2
<i>Sclerocystis</i>	0.5	0.0	0.0	0.2
<i>Scleroderma</i>	0.5	0.0	0.0	0.2
<i>Tuber</i>	13.5	19.9	6.9	13.4
No. of genera	20.0	17.0	18.0	
No. of samples	173.0	133.0	191.0	

sporocarp production in true fir forests in northern California that were unthinned or subject to 1 of 2 thinning intensities. They found some hypogeous sporocarps (*Gautieria*, *Hysterangium*, and *Alpova*) were significantly more abundant in unthinned than thinned forests, and *Gymnomyces* was the most dominant genus in the thinned stands 10 years after commercial thinning. Relative frequency and biomass of hypogeous sporocarps were similar between treatments in their study because of overall dominance of *Gymnomyces*. We found greater biomass of *Rhizopogon* in moderately and heavily thinned stands and *Hysterangium* in the unthinned stands. We collected the most *Gautieria* in heavily thinned stands during the fall. These 3 genera were highly selected by flying squirrels in our study, which supports the studies by Zabel and Waters (1997) who found these genera highly preferred in feeding trials. *Hysterangium* and *Hymenogaster* were highly selected by flying squirrels in our study and were most abundant in the unthinned stands. Most of the genera of hypogeous fungi in diets of flying squirrels in our

study were similar to those in the Oregon Coast Range and Olympic Peninsula (Carey 1995); therefore, the above genera are likely to be the most important ones for flying squirrel diets.

Although thinning may have had some influence on movements and diets of flying squirrels, any negative effects were not profound and may have been minimized by the presence of large logs and moderately large trees on the study sites. We suspect that increased distances moved by male flying squirrels in moderately thinned stands were in response to low availability of patches of hypogeous fungal sporocarps. Although we did not find the immediate impact of thinning on densities and composition of fungi to be statistically significant, the influence of hypogeous sporocarps on flying squirrel abundance was significant. Thus, effects of thinning on hypogeous sporocarps is an important indicator of how flying squirrel populations may be influenced by future thinning. We believe that future monitoring of fungal abundance and flying squirrel populations on our study areas, would improve understanding of the long-term (10–30 yr) effects of thinning and the relation between abundance of sporocarps and flying squirrels.

Factors Influencing Flying Squirrel Abundance

We predicted that abundance of northern flying squirrels would be lower than that found in other studies (Carey et al. 1992, Rosenberg and Anthony 1992, Waters and Zabel 1995) because our study sites were in young, structurally simple stands of Douglas-fir that had low densities of large trees and large downed logs. Although low densities (<0.5 squirrels/ha) of flying squirrels occurred in some of our stands, densities in several stands exceeded 1.5 squirrels/ha and were comparable to densities documented for older forests in the Pacific Northwest (see Smith et al. [2003:184] for a list of flying squirrel densities). Our results raise a number of questions about the factors that influence abundance of flying squirrels because other studies (Carey et al. 1992, 1999) characterized the species as being most abundant in late-seral forests. Our results indicate that components of old-growth forests (i.e. large downed logs, large trees) are influential, but may not be the most important factors in determining flying squirrel abundance. We found that abundance of hypogeous fungi was an important factor in determining flying squirrel abundance and other factors, such as downed logs and large conifers may be correlated with the abundance of hypogeous fungi. This is consistent with North et al.'s (1997) observations that abundance of hypo-

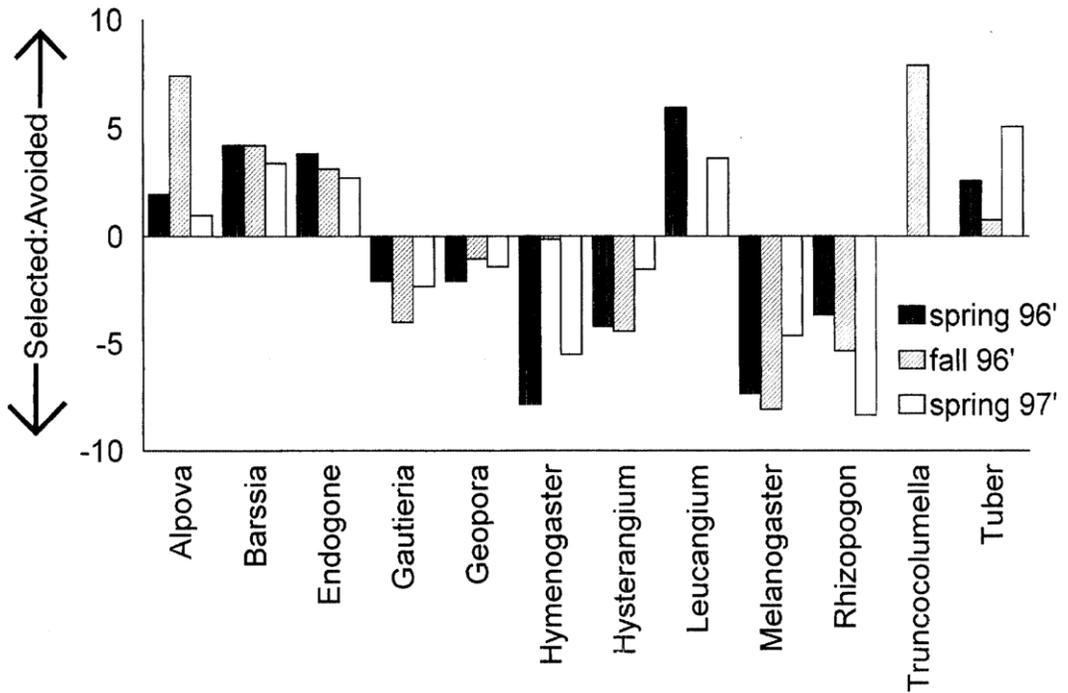


Fig. 6. Average differences between ranks of hypogeous fungal genera usage (from fecal pellets of Northern flying squirrels) and availability (from 4-m² sample plots in the field) in 3 seasons from 12 stands, Oregon Coast Range, 1996–1997.

geous fungi may limit populations of mycophagists in young, managed forests. Although previous studies (Rosenberg and Anthony 1992, Waters and Zabel 1995, Cotton and Parker 2000, Smith et al. 2005) indicate that northern flying squirrels are not old-forest specialists, we hypothesize that forest management that emphasizes the retention of large trees and downed logs will result in greater abundance of hypogeous fungi and higher densities of northern flying squirrels.

Greater abundance of flying squirrels was reported for late-seral vs. young forests in the Oregon Coast Range, and abundance was related to presence of large snags and shrub cover (Carey et al. 1992). Flying squirrel populations may be limited by the availability of cavities in trees for den sites (Carey 1991); however, we found no association between snags and flying squirrel density, even though availability of potential dens was low. Food availability, predation, and competition with other species, rather than structural components of forests, may limit abundance of flying squirrels (Rosenberg and Anthony 1992). Our results indicated that food availability was an important determinant of flying squirrel abundance in young stands in the northern Oregon Coast Range. Although we found a positive association between fly-

ing squirrels and large conifer densities, decreases in densities of trees and snags resulting from thinning (Hayes et al. 1997, this study) did not have a measurable impact on densities of northern flying squirrels in the short term. However, the effects of thinning on populations could be manifested over longer periods because flying squirrels have relatively small home ranges (Martin and Anthony 1999) and are relatively long-lived (this study) based on the survival rates and longevity in our study.

We found nonrandom distributions of sporocarps at the plot and grid scales, and strong associations between total sporocarp abundance and density of large logs, indicating that hypogeous sporocarps were clumped in distribution similar to results of Waters et al. (1997). Flying squirrels traveled greater distances to find these clumps of sporocarps as indicated by the negative association between movements and frequency of occurrence of sporocarps. Amaranthus et al. (1994) and Clarkson and Mills (1994) found truffle production associated with the presence of decayed logs, and Amaranthus et al. (1994) suggested that coarse woody debris (CWD) is especially important for hypogeous sporocarp production in the dry, summer months in mature (180-year-old) forest fragments. Clear-cuts in their study had significantly

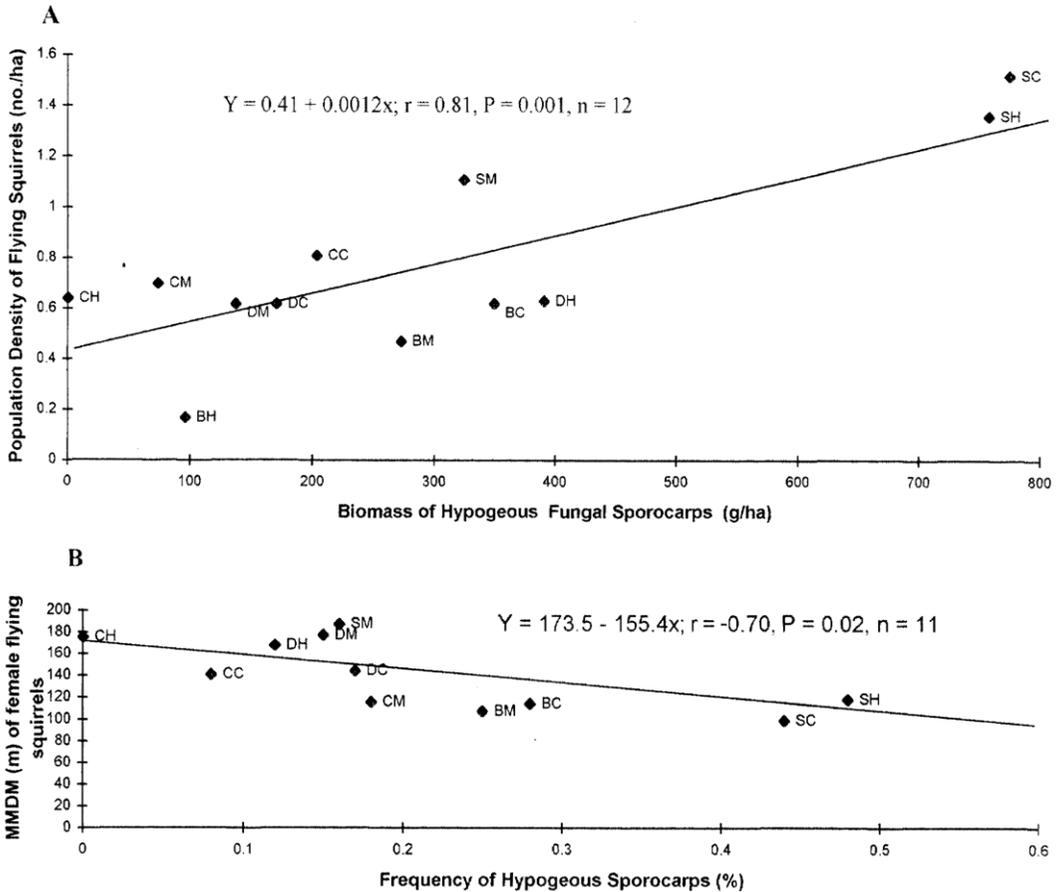


Fig. 7. Relation between (A) population density of flying squirrels (no./ha) and biomass of hypogeous fungal sporocarps (g/ha), and (B) female flying squirrel movements (MMDM) and percent frequency of hypogeous fungal sporocarps, Oregon Coast Range, 1996 and 1997. Point labels indicate stands (SC = Stimson control, SM = Stimson moderate, SH = Stimson heavy, CC = C-line control, CM = C-line moderate, CH = C-line heavy, DC = Deer Diamond control, DM = Deer Diamond moderate, DH = Deer Diamond heavy, BC = Ben Smith control, BM = Ben Smith moderate, BH = Ben Smith heavy).

fewer hypogeous sporocarps, and there was no association between CWD and sporocarp presence. The positive correlation between density of large logs and sporocarp abundance in our study may explain why flying squirrel density was associated with the prevalence of large logs.

Apparent Survival

Although Villa et al. (1999) provide some empirical estimates of survival of northern flying squirrels, our study is the first to estimate annual survival rates of the species from capture-recapture data and open population models. Our results indicate that survival rates were variable, spatially and temporally, ranging annually from 0.32–0.68. Some adult squirrels captured in spring 1994 were alive in spring of 1997, indicating longevity of at least 4 years.

Management Implications

We hypothesize that thinning of young Douglas-fir forests in western Oregon to tree densities similar to those in our study will have neutral or positive influences on northern flying squirrels over longer periods of time because of the structural changes created by thinning. Thinning reduces competition among remaining trees, which accelerates growth of trees (Marshall et al. 1992, Barbour et al. 1997), and density of hypogeous sporocarps is positively associated with proximity to large trees (Fogel 1976, Johnson 1994). Thinning also increases light penetration to the forest floor which stimulates growth of herbaceous and shrubby vegetation. Northern flying squirrels are likely to respond positively to these changes, if stands are not harvested prior to development of these characteristics. This is an important topic for future research and management.

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