Northern Flying Squirrel Mycophagy and Truffle Production in Fir Forests in Northeastern California[1]

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Abstract

In this paper we summarize the results of four studies in which we either examined the feeding habits of the northern flying squirrel (*Glaucomys sabrinus*), a mycophagous (consuming fungi) small mammal, or compared the abundance of truffles (sporocarps of hypogeous mycorrhizal fungi) among different types of fir (*Abies*) forest. The studies were conducted within the Lassen National Forest in northeastern California between 1990 and 1994. In the first study, we found that abundance of northern flying squirrels was significantly less in old-growth fir stands that had been shelterwood-logged 6 to 7 years previously than in nearby, unlogged old-growth and mature fir stands. Truffles were common in the diet of flying squirrels, truffle frequency was low in the shelterwood-logged stands compared to the unlogged old-growth and mature stands, and abundance of flying squirrels was correlated with truffle frequency across the 12 stands in which we estimated both. In the second study, we found no significant effects on total truffle frequency and biomass of truffles from commercial thinning or broadcast burning that had occurred about 10 years previously, but there were significant effects of thinning on frequencies of individual truffle genera. In the third study, we compared food preferences of captive northern flying squirrels among sporocarps of five species of fungi, two species of lichens, and fir seeds. Foods most preferred were two species of truffles, and consumption rate differed significantly among the five species of fungi. In the fourth study, we found that total truffle frequency and biomass and species richness did not differ significantly between old-growth and nearby, mature fir stands. We also observed that abundance of truffles (pooled across species) was not significantly associated with decayed wood, depth of the organic soil, or other habitat features. We collected 46 species of truffles in these floristically simple forests, however, and there was significant association between age class and frequencies of individual truffle species. Our data suggest that the effects of disturbance on truffle assemblages are species specific, and that predicting the effects of forest management on mycophagous small mammals may be difficult until more is known about the effects of disturbance on truffle production and the nutritional values of different truffle species.

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Introduction

Most species of fungi that produce hypogeous sporocarps (truffles) are ectomycorrhizal (Miller 1983; Trappe 1962, 1971), though a few species of vesicular-arbuscular mycorrhizal fungi also form macroscopic sporocarps (Janos and Sahley 1995, Maser and others 1978), Spores of hypogeous fungi are believed to be primarily dispersed by animals that eat truffles (Fogel and Trappe 1978, Maser and others 1978). Spores are viable after passage through the digestive tracts of small mammals (Cork and Kenagy 1989, Trappe and Maser 1976), and truffles are common in the diets of small mammals in temperate forests dominated by ectomycorrhizal fungi (Fogel and Trappe 1978, Hall 1991, Johnson 1994, Maser and others 1978, Taylor 1992, Tevis 1953, Ure and Maser 1982), as well as in New World tropical forests dominated by vesicular-arbuscular mycorrhizal fungi (Janos and Sahley 1995).

Forest management may affect truffle production because ectomycorrhizal fungi are dependent on their host plants for carbon (Hacskaylo 1973, Harley 1971, Last and others 1979), and both ectomycorrhizae (Harvey and others 1978, 1979) and truffles (personal observation) develop primarily in organic soil layers and the upper mineral soil where they are vulnerable to disturbance of the forest floor. Several studies have examined seasonal and annual variation in truffle production (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987, Luoma 1991, States 1985) or compared truffle production among different age classes of forest (Amaranthus and others 1994, Clarkson and Mills 1994, Luoma and others 1991, North and others 1997, O'Dell and others 1992, Vogt and others 1981). The effects of forest management, especially partial-harvesting practices, on truffle production is still poorly understood.

In this paper we summarize results of four studies conducted in the Lassen National Forest in northeastern California between 1990 and 1994. In each study, we either examined the feeding habits of the northern flying squirrel (*Glaucomys sabrinus*), a mycophagous (consuming fungi) small mammal, or compared fruiting patterns of truffles among different types of fir (*Abies*) forest. In the first study, we compared abundance of flying squirrels among three types of forest that varied in age and stand structure and evaluated the correlation between the abundance of flying squirrels and truffle frequency. In the second, we evaluated the effects of commercial thinning and broadcast burning on truffle frequency and biomass 10 years after treatment. In the third, we determined whether captive flying squirrels preferred sporocarps of certain species over others, and whether flying squirrels preferred truffles over other types of food available to them. And in the fourth, we compared truffle frequency, biomass, number of truffle species, and relative frequencies of individual species between old-growth and mature fir forests to determine whether old-growth fir forests had unique truffle communities.

Study I: Patterns of Flying Squirrel Abundance

A study of home range size and habitat use patterns of California spotted owls (*Strix occidentalis occidentalis*) in the Lassen National Forest indicated that owls selected stands with relatively dense canopy cover (Zabel and others 1992b). One of the most striking patterns of habitat use by spotted owls was a clear avoidance of old-growth forests within Swain Mountain Experimental Forest that had been shelterwood-logged in 1984-1985 (Zabel and others 1992a). Radiotelemetry positions of owls were rarely located in shelterwood-logged areas but frequently were located

in unlogged stands of old-growth and mature forest adjacent to shelterwood-logged areas. Analysis of pellets egested from spotted owls indicated that the northern flying squirrel was the owl's primary prey within the Lassen National Forest, occurring in about 80 percent of the pellets analyzed.

We hypothesized that the lack of use of the shelterwood-logged forests within Swain Mountain Experimental Forest by spotted owls could be related to prey abundance. To test this hypothesis, we compared abundance of flying squirrels in the shelterwood-logged old-growth forests and in nearby, unlogged old-growth and mature forests (Waters and Zabel 1995). We also sampled truffles within each forest type to determine whether truffle frequency was correlated with abundance of flying squirrels.

Study Area and Methods

Stands of unlogged old-growth, unlogged mature, and shelterwood-logged old-growth fir forest were located within or near Swain Mountain Experimental Forest, which is located at the southern end of the Cascade Range within the Lassen National Forest in northeastern California. Soils were well drained and derived from mafic andesite. Forests were high elevation (1,800-2,000 m) and dominated by white fir (*A. concolor)* or a mixture of white and red fir (*A. magnifica*). Scattered sugar pine (*Pinus lambertiana*), Jeffrey pine (*P. jeffreyi*), ponderosa pine (*P. ponderosa*), and lodgepole pine (*P. contorta*) occurred within some of the grids.

Unlogged old-growth forests (hereafter, old-growth forests) were characterized by multilayered canopies and large logs, stumps, and snags. Dense patches of small firs occurred in the understory, but herbaceous plants (e.g., *Pyrola picta, Viola purpurea,* and *Corallorhiza maculata*) and shrubs (primarily *Chrysolepis sempervirens*) were uncommon. The organic soil included layers of litter and humus and large pieces of buried, decayed wood. From counts of growth rings on cut stumps in adjacent shelterwood-logged areas, we estimated that the majority of codominant and dominant trees in the old-growth and shelterwood-logged forest types were 200 to 400 years old.

Unlogged mature forests (hereafter, mature forests) were characterized by even-aged stands that grew back after stand-replacement wildfires (this forest type was referred to as "young" by Waters and Zabel [1995]). These forests were in the stem-exclusion phase (Oliver and Larson 1996) of forest development. They were dense and had closed canopies, and virtually no herbaceous plants or shrubs were present in the understory. Old, dead stems on the forest floor indicated that shrubs were abundant for some period after wildfires occurred. The organic soil included well-developed layers of litter and humus. From counts of growth rings of cored trees within each stand, we estimated that most codominant and dominant trees in this forest type were 80 to 100 years old.

Shelterwood-logged old-growth forests (hereafter, shelterwood-logged forests) were located in Swain Mountain Experimental Forest. The experimental forest was dominated by old-growth fir forests until 1984-1985 when large areas were logged to study natural regeneration rates using the shelterwood silvicultural system. These timber harvests left an open stand structure of widely spaced, large-diameter trees. The ground was intentionally disturbed to expose mineral soil for natural regeneration. Tractors with brush blades were used to remove logs and disturb soils,

and slash was piled and burned or broadcast burned. At the time of our study, grasses, forbs, and low shrubs (primarily *Ceanothus cordulatus* and *Ribes roezlii*) had become established, and the little organic soil present on the forest floor was primarily characterized by undecomposed litter.

We selected four areas within each of the three forest types that were similar in elevation and tree species composition, at least 150m apart, relatively homogeneous, and sufficiently large. Within each of the 12 areas we established a 12- to 13-ha rectangular or square grid. During August or September of 1991 and 1992, we livetrapped flying squirrels during a single trapping session that was 15 to 16 nights long. Flying squirrels were captured in Tomahawk livetraps (41 x 13 x 13 cm) and individually eartagged. Fecal pellets were also collected from captured flying squirrels and analyzed to describe diet. We used the first-order jackknife estimator (Burnham and Overton 1979, Rosenberg and others 1995) to estimate population size within each grid. Abundance of flying squirrels was estimated by dividing the jackknife population estimate by the effective area trapped. The effective area trapped was estimated by adding to the area of each grid a strip equal in width to one-half the mean maximum distance moved by flying squirrels captured at least twice (Wilson and Anderson 1985).

During summer 1991, we sampled truffles and vegetation within each of the 12 grids. We used a rake to search for truffles within a 4-m^2 circular plot (1.13-m radius) located at each grid point (91-104 truffle plots/grid). We raked through the litter, humus, and upper 5 to 10 cm of mineral soil. As a measure of truffle abundance we used truffle frequency, which was the percentage of 4-m^2 plots in which we found ≥1 truffle. We sampled vegetation within circular plots at every third grid point within each grid. We measured the diameter at breast height (dbh) of trees and the length and midpoint diameter of logs within each circular plot. Size of vegetation plot differed among the three forest types because of large differences in the densities of trees. In old-growth forests, small trees (< 18 cm in dbh) were measured within a 6-m radius and larger trees and logs within a 16-m radius. In mature forests, all trees and logs were measured within a 6-m radius. In shelterwood-logged forests, all trees and logs were measured within an 18-m radius. We used a spherical densiometer to obtain a relative measure of canopy cover at each vegetation plot (we used the average of three densiometer readings taken 8 m from the plot center). Ground cover was estimated using a point-intercept method; type of ground cover was recorded at 52 points per vegetation plot (13 points per transect along four transects following cardinal directions). We also dug a small soil pit at each point in the grid and measured the depth of organic soil (combined depth of litter, humus, and buried, decayed wood).

We used repeated-measures analysis of variance (ANOVA) to compare estimates of flying squirrel abundance in 1991 and 1992 among the three forest types. If variances differed significantly among forest types, we used Welch's variance-weighted ANOVA (SAS Institute 1997) and a variance-weighted multiple comparison test (SAS Institute 1997). If variances did not differ significantly among forest types, we used traditional ANOVA tests and the Ryan-Einot-Gabriel-Welsch multiple-range test (SAS Institute Inc. 1989) to compare means following ANOVA. We considered tests significant if $\alpha < 0.05$. Spearman ranked correlation analysis was used to evaluate the correlation between abundance of flying squirrels (averaged between 1991 and 1992) and truffle frequency across the 12 grids.

Results and Discussion

Measures of vegetation structure differed greatly among the three forest types. Compared to old-growth forests, shelterwood-logged forests had significantly less basal area and canopy cover, fewer large-diameter snags, greater ground cover of forbs, less ground cover of small-diameter and large-diameter logs, and a thinner layer of organic soil (*table 1*). Also, compared to old-growth forests, mature forests had significantly greater basal area and canopy cover, more small-diameter snags and fewer large-diameter snags, and less ground cover of large-diameter logs (*table 1*). Each of the three forest types had its own characteristic distribution of diameter size classes of trees (*fig. 1*).

Table 1—*Means (x) and standard errors (SE) of variables measured in three forest types (n= 4 grids in each forest type) in northeastern California in 1991. The alpha (α) value is from an ANOVA test, and means with the same letter did not differ at an experimentwise α of 0.05.*

Variable	Old-growth		Mature		Shelterwood		
	x	*SE*	*x*	*SE*	*x*	*SE*	*α*
Basal area ≥ 5 cm dbh (m^2 ha^{-1})	72.6A	1.7	92.1B	1.5	22.6C	1.6	<0.01
Canopy cover (pct)	66.0A	0.4	78.3B	1.8	24.3C	1.7	<0.01
Snags ha^{-1} 13-52 cm in dbh	69.3A	22.5	176.1B	42.6	5.0A	1.9	0.01
Snags ha^{-1} > 52 cm in dbh	9.7A	1.4	0.7B	0.7	5.8C	1.0	<0.01
Shrub cover (pct)	0.9A	0.4	0.5A	0.3	6.3A	3.6	0.15
Grass cover (pct)	1.4A	0.8	0.0A	0.0	3.6A	1.6	0.10
Forb cover (pct)	0.4A	0.3	0.0A	0.0	2.2B	0.6	0.01
Ground cover (pct) of logs ≤52 cm in diameter	2.1A	0.4	1.3A,B	0.1	0.6B	0.1	0.01
Ground cover (pct) of logs > 52 cm in diameter	3.3A	0.3	0.0B	0.0	0.5B	0.1	<0.01
Organic soil depth (cm)	6.8A	0.3	7.9A	0.4	1.7B	0.4	<0.01

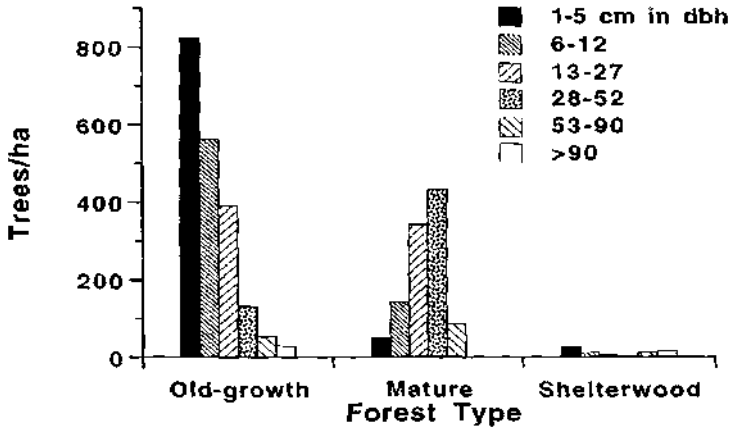

Figure 1—Mean densities of trees sampled in 1991 in old-growth (n = 4 grids), mature (n = 4), and shelterwood-logged (n = 4) fir forests in northeastern California.

Flying squirrel abundance was significantly less in shelterwood-logged forests than in old-growth and mature forests (*fig. 2*). Mean abundance was greater in old-growth forests than in mature forests in both 1991 and 1992, but in neither year was that difference significant. These results suggest that within our study area, flying squirrels were not old-growth specialists, but that their populations were negatively affected by the logging that occurred within Swain Mountain Experimental Forest.

Few studies have compared flying squirrel abundance among different forest types, and none have compared abundance among forests that were similar in composition and age to those in our study. Carey and others (1992) found that the mean density of flying squirrels in old-growth stands in Oregon and Washington was approximately twice that in managed conifer stands that were 40 to 70 years old. Rosenberg and Anthony (1992) found that densities of flying squirrels were similar in old-growth and 30- to 60-year-old stands of Douglas-fir (*Pseudotsuga menziesii*) in Oregon.

We found that truffles were common in the diet of northern flying squirrels. Truffle spores were found in each of the 165 fecal samples analyzed. Lichen, unknown vegetative matter, spores of epigeous fungi, pollen from staminate cones of conifers, and insect and seed parts were also observed. Truffles have been shown to be a primary food of flying squirrels in the northern Sierra Nevada (Hall 1991) and Oregon (Maser and others 1985, Maser and others 1986). McKeever (1960) found that the most common foods found in the stomachs of flying squirrels trapped in Swain Mountain Experimental Forest were fungi and lichens, but he did not distinguish between hypogeous and epigeous fungi.

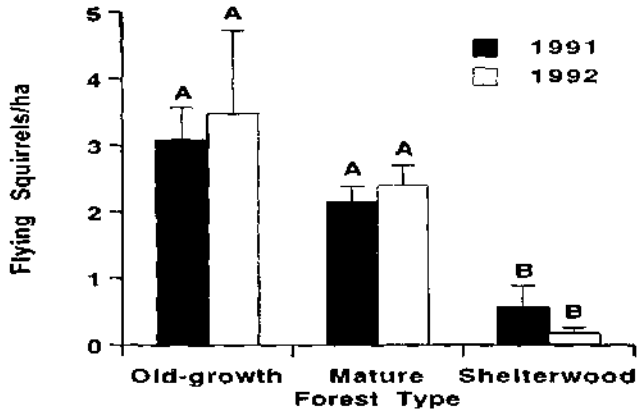

Figure 2—Mean estimates of abundance of northern flying squirrels in old-growth *(n* = 4 grids), mature *(n* = 4), and shelterwood-logged (*n* = 4) fir forests in northeastern California. Repeated-measures ANOVA indicated that abundance differed significantly among the three forest types *(F* = 20.2; d.f. = 2, 9; $\alpha < 0.01$), but not between 1991 and 1992 *(F* = 0.2; d.f. = 1, 9; $\alpha = 0.66$). Multiple comparisons were performed separately for each year; within each year, columns with the same letter did not differ at an experiment α of 0.05.

Abundance of flying squirrels was positively correlated with truffle frequency across the 12 grids ($r_s = 0.86$, $\alpha < 0.01$). Because truffles were so common in the diet of flying squirrels in our study area, the correlation between abundance of flying

squirrels and truffle frequency suggests that truffle abundance may have influenced habitat selection by flying squirrels. Other factors that we did not measure, however, undoubtedly affect the quality of habitat for flying squirrels. For example, lichens are especially common in the diets of flying squirrels during winter when conditions are harsh (Hall 1991, Maser and others 1986, Maser and others 1985, McKeever 1960), and their availability may be an important determinant of the quality of flying squirrel habitat.

Truffle frequency during summer 1991 differed significantly among the three forest types (F = 9.71; d.f. = 2, 9; $\alpha < 0.01$). Multiple comparisons indicated that truffle frequency did not differ significantly between old-growth forests (x = 27.8 percent, SE = 6.0) and mature forests (x = 17.5 percent, SE = 1.6), but was significantly less in shelterwood-logged forests (x = 4.2 percent, SE = 2.2). Because we sampled truffles only once, interpretations from these data are limited. The much lower frequency of truffles in shelterwood-logged forests compared to that in nearby, unlogged old-growth forests, however, suggests that the logging and/or site preparation that occurred within Swain Mountain Experimental Forest resulted in reduced truffle production.

Other species of forest rodents were abundant in shelterwood-logged forests. Mean abundance was greatest in shelterwood-logged forests for golden-mantled ground squirrels (*Spermophilus lateralis*), yellow pine chipmunks (*Tamias amoenus*), lodgepole chipmunks (*Tamias speciosus*), and deer mice (*Peromyscus maniculatus*) (Waters and Zabel [In press]). These species are known to eat truffles, but they have varied diets that also include seeds, leaves, fruit, flowers, and insects (Fogel and Trappe 1978; McKeever 1964; Nowak 1991; Sutton 1992; Tevis 1952, 1953), and are not considered to be as mycophagous as northern flying squirrels. The only other species whose abundance we compared among forest types and that is considered to be highly mycophagous is the California red-backed vole (*Clethrionomys californicus;* Maser and others 1978, Ure and Maser 1982). We captured 22 California red-backed voles in old-growth forests, four in mature forests, and none in shelterwood-logged forests (Waters and Zabel [In press]).

Study II: Effects of Thinning and Broadcast Burning on Truffle Abundance

We considered the silvicultural treatments within Swain Mountain Experimental Forest to be relatively severe, especially the site preparation techniques, which left highly disturbed soils with large areas of exposed mineral soil. To evaluate the effects of less severe silvicultural treatments on the abundance of truffles, we sampled truffles at a site (Jennie Springs) near Swain Mountain Experimental Forest that had been used by other researchers to study the effects of commercial thinning and broadcast burning on various stand conditions (Oliver and others 1981).

Study Area and Methods

The Jennie Springs site was located at an elevation of 1,860 m about 1 km south of Swain Mountain Experimental Forest. The site is characterized by an even-aged, mature (stem-exclusion phase) stand of white fir that originated after a stand-replacement wildfire.

We sampled truffles in 21 units, a subset of the units originally treated (Waters and others 1994). The 0.4-ha units were square. Seven were heavily thinned (about 70 percent of basal area removed), seven moderately thinned (about 35 percent of basal area removed), and seven not thinned. Thinning occurred in 1982. Logs were removed by horse or cable to minimize ground disturbance. Within each thin level, four of the seven units were burned, and three were not. Two of the four units were burned in the spring and two in the fall, but we pooled spring and fall burned units for these analyses. Burn intensities were light to moderate with flame lengths averaging about 0.5-1.0 m (Weatherspoon 1994).

Within each unit we established a 5 x 6 grid with 8-m spacing between grid points. In June 1992 we searched for truffles in a 4-m^2 circular plot located at each grid point (30 truffle plots/unit). In September 1992 we searched for truffles in a 4-m^2 circular plot located midway between adjacent grid points (15 truffle plots/unit). Truffles were placed in paper bags and stored in a cooler or refrigerator until they could be identified to genus, dried, and weighed. Vegetation was sampled in four systematically located 0.02-ha circular plots (8-m radius) within each unit. Within each vegetation plot we measured the dbh of all trees and snags ≥8 cm and the length and midpoint diameter for all logs ≥12 cm wide at the midpoint. We also estimated canopy cover using a spherical densiometer at three systematically located points within each vegetation plot. At 12 systematically located points within each unit, we dug a small soil pit and measured the depths of the litter and humus layers. We collected a sample from the litter, humus, and mineral soil (5 cm below the top of the mineral soil) at each of the 12 points and combined these subsamples into one composite sample for each unit. These composite samples were oven-dried, and soil moisture was determined gravimetrically for each layer. A separate composite sample (six systematically located subsamples) of mineral soil was collected from each unit. These samples were used to determine percent total nitrogen, percent total carbon, and pH by a soils laboratory at Oregon State University in Corvallis.

We tested for effects due to thinning and burning on truffle frequency (proportion of truffle plots in which we found ≥1 truffle) and biomass using two-factor ANOVA. Truffle biomass in this and following studies was the dry weight of all truffle collections found during a particular sampling interval (standing crop); we made no attempt to estimate annual production. Variables whose distribution was not normal were transformed using a log or arcsine transformation.

Results and Discussion

During the June sample period, we found truffles in 206 of the 630 plots sampled; the biomass of all truffles collected was the equivalent of 1.56 kg ha^{-1}. During the September sample period, soils were dry, and we found truffles in only 13 of the 315 plots sampled (most of those truffles appeared old); results reported here are thus only from the June sample period.

Compared to unthinned units, heavily thinned units had significantly fewer trees, less canopy cover, more undecayed logs, a thinner organic layer, and less moisture in the litter and humus layers (*table 2*). Truffle frequency and biomass did not differ significantly among the three thin levels (*fig. 3*). Truffle biomass was more variable than frequency, with mean biomass of truffles greatest in the heavily thinned units. Truffle frequency was similar among thin levels because some genera such as *Gymnomyces* (includes genus *Martellia* because we could not reliably separate these

two similar genera at the time) had significantly greater frequencies in thinned units, and others (*Hysterangium* and *Gautieria*) had significantly greater frequencies in unthinned units (*table 2*).

Table 2—*Means (x) and standard errors (SE) of variables measured at the Jennie Springs site in June 1992. For each thin level (n = 7), values were averaged across four broadcast burned units and three unburned units. The alpha (α) value is from effect due to thinning in*

Item	Thinning level						
	Heavy		Moderate		Unthinned		
	x	*SE*	*x*	*SE*	*x*	*SE*	α
Tree density (stems ha^{-1})	101.2	6.3	248.7	24.1	749.6	74.0	<0.01
Canopy cover (pct)	41.7	2.7	66.5	3.1	85.2	1.0	<0.01
Undecayed logs (m^2 ha^{-1})	417.5	57.4	435.0	61.2	160.0	36.7	<0.01
Decayed logs (m^2 ha^{-1})	59.9	13.0	91.4	23.9	79.0	17.3	0.42
Depth of organic soil (cm)	3.1	0.6	3.7	0.5	4.9	0.5	<0.01
Litter moisture (pct)[1]	4.9	0.7	8.5	1.1	15.2	1.7	<0.01
Humus moisture (pct)[1]	14.3	2.3	17.6	2.8	26.2	3.0	0.01
Mineral soil moisture (pct)[1]	22.7	1.7	25.0	1.2	24.4	0.6	0.77
Alpova frequency (pct)	1.9	1.4	3.3	1.8	4.8	2.2	0.42
Gautieria frequency (pct)	0.0	0.0	1.4	1.0	5.2	1.9	0.02
Hysterangium frequency (pct)	1.4	1.0	2.4	1.2	12.4	4.6	0.01
Gymnomyces frequency (pct)[2]	25.7	5.5	18.1	5.7	6.2	1.1	0.02
Balsamia frequency (pct)	2.4	0.6	1.9	1.0	2.4	1.2	0.61

[1] *n* = 6 units for each thin level.
[2] Includes genus *Martellia.*

Table 3—*Means (x) and standard errors (SE) of variables measured at the Jennie Springs site in 1992. For broadcast burned units (n = 12), values were averaged across four heavily thinned units, four moderately thinned units, and four unthinned units. For unburned units (n = 9), values were averaged across three heavily thinned units, three moderately thinned units, and three unthinned units. The alpha (a) value is from effect due to burning in two-factor*

Item	Burn level				
	Broadcast burned		Unburned		
	x	*SE*	*x*	*SE*	α
Tree density (stems ha^{-1})	350.2	71.2	388.2	128.9	0.48
Canopy cover (pct)	61.8	5.9	68.0	6.1	0.02
Undecayed logs (m^2 ha^{-1})	295.9	57.7	393.0	52.1	0.14
Decayed logs (m^2 ha^{-1})	64.1	13.6	93.6	16.0	0.19
Depth of organic soil (cm)	2.9	0.3	5.2	0.3	<0.01
Litter moisture (pct)[1]	8.5	1.4	11.5	2.5	0.06
Humus moisture (pct)[1]	16.2	1.7	25.6	3.5	<0.01
Mineral soil moisture (pct)[1]	23.5	1.0	25.1	0.8	0.30
Soil pH	5.87	0.03	5.72	0.05	0.03
Alpova frequency (pct)	5.0	1.6	1.1	0.6	0.10
Gautieria frequency (pct)	1.7	0.9	3.0	1.6	0.60
Hysterangium frequency (pct)	4.7	2.4	6.3	3.1	0.46
Gymnomyces frequency (pct)[2]	15.3	3.9	18.5	5.2	0.49
Balsamia frequency (pct)	2.5	0.7	1.9	0.8	0.52

[1] *n* = 12 for broadcast burned units and *n* = 6 for unburned units.
[2] Includes genus *Martellia.*

Compared to unburned units, burned units had significantly less canopy cover, a thinner organic soil layer, less moisture in the humus layer, and higher soil pH (*table 3*). Truffle frequency and biomass did not differ significantly between burned and unburned units (*fig. 3*). Unlike differences among thin levels, however, frequencies of the five most common genera did not differ significantly between burn levels (*table 3*), suggesting that thinning affected truffle frequencies more than broadcast burning.

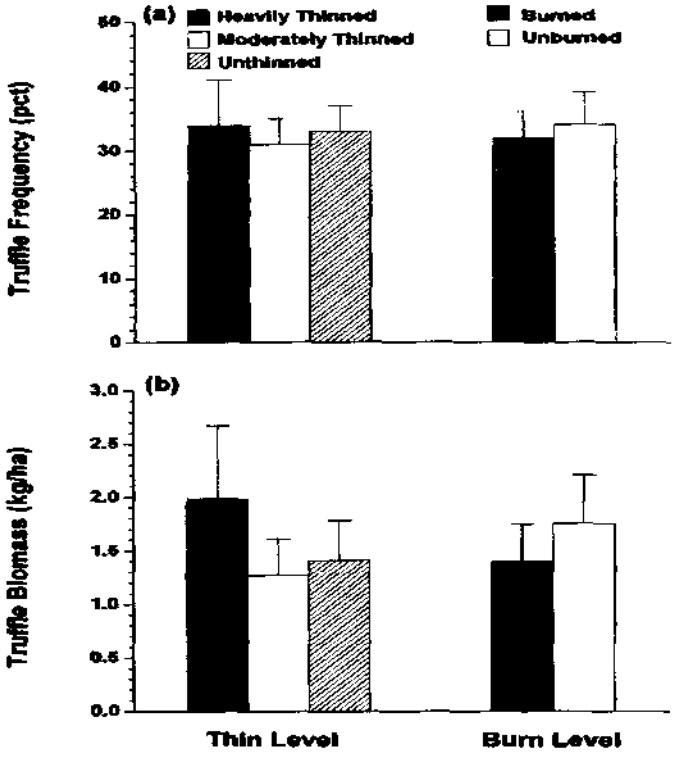

Figure 3—Means and standard errors of (a) truffle frequency and (b) truffle biomass by thin level and burn level in northeastern California in 1992. For each thin level (n = 7), values were averaged across four broadcast burned units and three unburned units. For broadcast burned units (n = 12), values were averaged across four heavily thinned units, four moderately thinned units, and four unthinned units. For unburned units (n = 9), values were averaged across three heavily thinned units, three moderately thinned units, and three unthinned units. Two-factor ANOVA indicated that for truffle frequency, neither the effect due to thinning (F = 0.04; d.f. = 2, 15; α = 0.96) nor the effect due to burning (F = 0.06; d.f. = 1, 15; α = 0.80) was significant. Similarly, for truffle biomass, neither the effect due to thinning (F = 0.11; d.f. = 2, 15; α = 0.90) nor the effect due to burning (F = 0.29; d.f. = 1, 15; α = 0.60) was significant.

Unfortunately, we were unable to continue this study, so caution must be taken in interpreting the results because of its short duration. The similarity in mean truffle frequency among thin levels and between burned and unburned units, however,

contrasts greatly with the significant difference in mean truffle frequency between shelterwood-logged old-growth forests and unlogged old-growth forests found in the previous study,

Study III: Food Preferences of Northern Flying Squirrels

Because results of the previous study suggested that thinning could lead to changes in relative frequencies of truffle species, we wanted to know whether northern flying squirrels preferred sporocarps of certain fungal species over others. We also wanted to know whether flying squirrels preferred sporocarps over other naturally occurring food types. In this study, we compared preferences of captive flying squirrels among sporocarps of five species of fungi, two species of lichens, and fir seeds (Zabel and Waters 1997). Although many studies have shown that truffles are common in the diets of small mammals, we know of no published studies comparing preferences of mycophagous small mammals among different kinds of truffles.

Methods

We captured flying squirrels in two stands of old-growth fir in Swain Mountain Experimental Forest in August 1994. Fungal sporocarps and lichens were collected in old-growth and mature fir stands, also within Swain Mountain Experimental Forest. Fir seeds (*A. concolor* and *A. magnifica*) were obtained from the USDA Forest Service Nursery in Placerville, California. Choice of fungal species was determined by availability; we used sporocarps of the five most commonly found species at the time of sampling (August 1994): *Gautieria monticola, Alpova trappei, Gymnomyces abietis, Endoptychum depressum,* and *Arcangeliella lactarioides.* All are ectomycorrhizal basidiomycetes, except *Endoptychum depressum,* which is a saprobic basidiomycete. *Endoptychum depressum* and *Arcangeliella lactarioides* are secotioid fungal species, which exhibit morphological and fruiting characteristics intermediate between those of epigeous and hypogeous fungi. The two lichen species were *Bryoria fremontii* and *Letharia vulpina,* which were common epiphytic species in fir stands within Swain Mountain Experimental Forest.

After capture, flying squirrels were transported to and housed in outdoor pens at Humboldt State University in Arcata, California. Feeding trials were conducted in two 1.2 x 1.2 x 1.0-m cages built with wood and hardware cloth. Size of food samples was standardized across foods and tests; samples were 2-3 cm in diameter. Food samples were weighed before and after each feeding trial to determine the proportion eaten. Each food sample was placed in a randomly assigned grid cell across the bottom tray of the feeding cage. The tray was filled with peat moss to a depth of about 8 cm. Truffle food samples were buried 2-3 cm, and all other food samples were placed on top of the peat moss. Peat moss was thoroughly mixed after each experiment and changed nightly. Experiments began shortly after sunset when squirrels were moved from their outdoor cages into the test rooms, which were illuminated with a red light. Flying squirrels entered the center of the feeding cage through a plastic tube (8 cm in diameter). An observer used a tape recorder and described behavior of the flying squirrels from behind a blind 1 m from the cage. Feeding trials were performed on seven male squirrels for 45 minutes each night for four consecutive nights.

We used the proportion of food samples eaten (averaged across the four nights) as a measure of food preference. We tested whether this measure varied among the eight food types using ANOVA with a randomized complete-blocks design (each squirrel was a block). Mean proportion of food eaten was compared among the eight foods following ANOVA using the Ryan-Einot-Gabriel-Welsch multiple-range test.

Results and Discussion

Mean proportion of food samples eaten varied significantly among the eight foods (*fig. 4*). Among the five species of fungi, mean proportion of food eaten ranged from 0.90 (SE = 0.05) for *Gautieria monticola* sporocarps to 0.11 (SE = 0.04) for *Arcangeliella lactarioides* sporocarps. Multiple comparisons indicated that samples of the hypogeous species *Gautieria monticola* were eaten significantly more than samples of the hypogeous species *Gymnomyces abietis,* and samples of the secotioid species *Endoptychum depressum* were eaten significantly more than samples of the secotioid species *Arcangeliella lactarioides* (*fig. 4*). North and others (1997) concluded that palatability varied greatly among truffle species in their study area because consumption rates, determined by comparing truffle biomass between open plots and exclosures, varied greatly among truffle species. The three hypogeous species used in our study were consumed more than the two secotioid species, which is consistent with results of other studies that showed truffles were more common than mushrooms in the diets of mycophagous small mammals (Maser and others 1978, 1985, 1986; North and others 1997; Taylor 1992; Ure and Maser 1982).

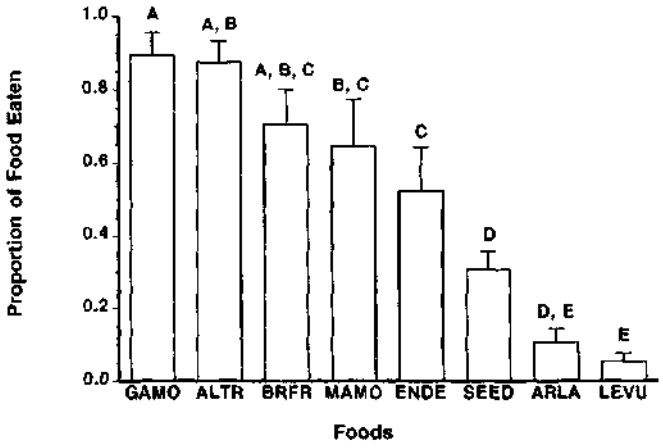

Figure 4—Means and standard errors of proportion of food sample eaten (averaged across a four-night period) by seven captive northern flying squirrels (all male) in 1994. The eight food types were *Gautieria monticola* sporocarps (GAMO), *Alpova* frappe/sporocarps (ALTR), the lichen *Bryoria fremontii* (BRFR), *Gymnomyces abietis* sporocarps (GYAB), *Endoptychum depressum* sporocarps (ENDE), fir seeds (SEED), *Arcangeliella lactarioides* sporocarps (ARLA), and the lichen *Letharia vulpina* (LEVU). Mean proportion of food eaten varied significantly among the eight foods (F = 31.75; d.f. = 7, 42; $\alpha < 0.01$). Foods with the same letter did not differ at an experiment α of 0.05.

The relatively high preference for the lichen *Bryoria fremontii* is consistent with dietary studies, which have shown that lichens were a common food of northern flying squirrels (Hall 1991, Maser and others 1985, 1986; McKeever 1960). These studies, however, showed that lichens were less common in the summer diets of flying squirrels than in the winter diets, suggesting that lichens were eaten more when other foods like truffles were unavailable. The low preference for fir seeds is also consistent with dietary studies, which have not found conifer seeds to be common in the diets of northern flying squirrels.

We showed that preference varied significantly among the eight foods tested, but we do not know how the nutritional values of these foods varied. Cork and Kenagy (1989) found that the nutritional value of one truffle, *Elaphomyces granulatus,* was low for the ground squirrel *Spermophilus saturatus* because digestibility of the sporocarps was low. They hypothesized that truffles generally have relatively low nutritional value for small mammals but are commonly consumed because they are seasonally abundant and highly detectable because of the strong odors they develop when mature. Claridge and Cork (1994), however, found that the nutritional values of two truffle species were high for a forest-dwelling marsupial (*Potorous tridactylus*) in Australia. Because of their high water content, fungal sporocarps may be important during certain periods or in certain areas as a source of water (Fogel and Trappe 1978).

Study IV: Truffle Production in Old-Growth and Mature Forests

Great concern has been expressed over the potential loss of biodiversity due to logging of remaining old-growth forests in the western United States. The Forest Ecosystem Management Team (FEMAT) identified more species of fungi (527 species, 80 of which were truffles) as being closely associated with late-successional and old-growth forests in the Pacific Northwest than any other group of organisms evaluated (arthropod associations were not evaluated; FEMAT 1993). Large decayed logs are considered to be important habitat features of late-successional forests (Harmon and others 1986, Perry and Amaranthus 1997), and at least two published studies have shown that truffle production was positively associated with decayed wood (Amaranthus and others 1994, Clarkson and Mills 1994). We wanted to know whether truffle production and number of truffle species were greater in old-growth fir forests than in younger forests. We also wanted to know whether truffle presence was associated with habitat features such as decayed logs and organic soil depth. In this study, we compared truffle fruiting patterns between old-growth and nearby, mature fir forests, and evaluated associations between truffle abundance and measures of habitat structure and composition within those forests (Waters and others 1997).

Study Area and Methods

We located four areas in which a stand of old-growth fir forest was located near a stand of mature (stem-exclusion phase) fir forest. The old-growth and mature stand within each of these four areas were similar in elevation, slope, aspect, and tree species composition (*table 4*). Within each of the eight stands we established a 6 x 6 grid with 10-m spacing between grid points (0.25 ha). In three of the pairs, the two

grids were less than 0.4 km apart and in the fourth, the two grids were 0.7 km apart. The eight grids were located in Swain Mountain Experimental Forest and were within stands of similar age, structure, and composition to old-growth and mature stands used in Study I.

In 1993, we measured vegetation characteristics within 50.3-m^2 circular plots (4-m radius) centered at each grid point. Within each of these vegetation plots, we measured the dbh of all trees ≥12 cm in dbh and tallied trees 1-5 cm and 6-11 cm in dbh. We also determined decay class (Maser and others 1979) and measured the length and mid-point diameter of portions of all logs within the vegetation plot with a mid-point diameter ≥10 cm.

Table 4—*Stand information for old-growth and paired, mature stands. Percent red fir was the percentage of total basal area.*

Pair	Stand type	Elevation m	Aspect	Slope pct	Red fir pct
1	Old-growth	1988	NW	9	90
	Mature	2003	NW	11	99
2	Old-growth	1796	SE	16	41
	Mature	1811	NE	18	10
3	Old-growth	1799	SE	19	60
	Mature	1823	SE	19	19
4	Old-growth	1945	NE	16	87
	Mature	1954	NE	14	100

Truffles were collected within a 4-m^2 circular plot positioned systematically near each of the 36 grid points. In 1993, truffles were collected during four sample periods; the four truffle plots were clustered around each grid point (total of 144 truffle plots per grid). In 1994, truffles were collected during three sample periods, and the three truffle plots were clustered around each of 36 points offset from the 1993 points (total of 108 plots per grid). Plots were never located on previously sampled areas. The fourth sample period in 1994 was canceled because soils were dry and we found few truffles. We also measured the length and diameter of portions of decayed logs (classes 4-5; Maser and others 1979) within the 4-m^2 truffle plot (decayed logs were soft and elliptical to flat in cross-sectional shape) and the depth of the organic soil layer at three systematically positioned points within each truffle plot. Decayed logs and organic soil depth were measured within truffle plots in all sample periods except the first sample period of 1993.

We used repeated-measures ANOVA (sample period was the repeated factor) with a randomized-blocks design (each pair of grids was a block) to test whether truffle frequency and biomass and number of truffle species differed significantly between the two age classes in 1993 and 1994. We also compared frequencies of truffle species between old-growth and mature forests using a contingency table to test the null hypothesis of no association between age class and frequencies of the 10 most common truffle species; numbers of truffle collections were pooled across sample periods and years for this test.

We used two methods to evaluate potential associations between truffle abundance and measures of habitat structure and composition. First, we evaluated

Spearman ranked correlations across the eight grids between truffle abundance (truffle frequency and biomass pooled across sample periods and years for each grid) and eight habitat measures (we used the mean value from the 36 vegetation plots sampled in each grid). The eight habitat measures were basal area of white fir, basal area of red fir, basal area of snags, number of fir stems 1-5 cm in dbh, number of fir stems 6-11 cm in dbh, surface area of undecayed logs, surface area of decayed logs, and average organic soil depth. We performed multiple regressions to evaluate the association between truffle abundance in 1993 within the area of the 50-m^2 vegetation plots and the same eight habitat variables used above. We were able to perform this analysis for the 1993 data only because the four truffle plots sampled in 1993 were located within the 4-m-radius vegetation plots, but the truffle plots sampled in 1994 were not. We performed two multiple regressions. In one, the dependent variable was the number of truffle plots at each grid point in which ≥1 truffle collection was found (values ranged from 0 to 4) and in the other, the dependent variable was the sum of the dry weights of truffle collections found in the four truffle plots at each grid point. We pooled across forest type (n = 288 vegetation plots) for each multiple regression.

We also evaluated associations between truffle presence and (1) presence of decayed wood and (2) organic soil depth within the 4-m^2 truffle plots. We used a 2 x 2 contingency table to test for association between truffle presence (plots with ≥1 truffle and plots with no truffles) and presence of decayed wood (plots with at least some decayed wood and plots with no decayed wood). We used the Wilcoxon rank-sum test (SAS Institute 1989) to compare organic soil depth values between plots with truffles and plots without truffles. Tests were performed separately for three sample periods in 1993 and three sample periods in 1994.

Results and Discussion

We sampled 8,064 m^2 over 2 years and found truffles in 30.4 percent of the 2,016 plots; truffle biomass was equivalent to 2.43 kg/ha. A total of 46 species were found. Truffle frequency (*fig. 5*) and biomass (*fig. 6*) did not differ significantly between the two age classes in 1993 or 1994. Number of truffle species also did not differ significantly between age classes in 1993 (F = 0.74, d.f. = 1, 3, α = 0.45) or 1994 (F = 0.l6, d.f. = 1, 3, α = 0.72). A total of 38 species were found in old-growth forests and 38 in mature forests. There was significant association between age class and frequencies of the 10 most common species (*fig. 7*). Frequencies of *Gautieria monticola, Gymnomyces abietis, Thaxterogaster pingue,* and *Leucophelps spinispora* were similar between old-growth and mature forests, but frequencies of *Hysterangium crassirhachis* and *Hysterangium coriaceum* were greater in mature forests, and frequencies of *Alpova trappei, Rhizopogon evadens, Melanogaster varigatus,* and *Hymenogaster sublilacinus* were greater in old-growth forests.

None of the correlations between the eight habitat measures and truffle frequency were significant (α > 0.31), nor were any of the correlations with truffle biomass (α > 0.13). Also, little of the variation in either measure of truffle abundance within the 288 50-m^2 circular areas was explained by the eight habitat measures. R^2 was only 0.06 for the multiple regression using number of truffle plots with ≥1 truffle collection as the dependent variable, and 0.02 using the total dry weight of truffles as the dependent variable.

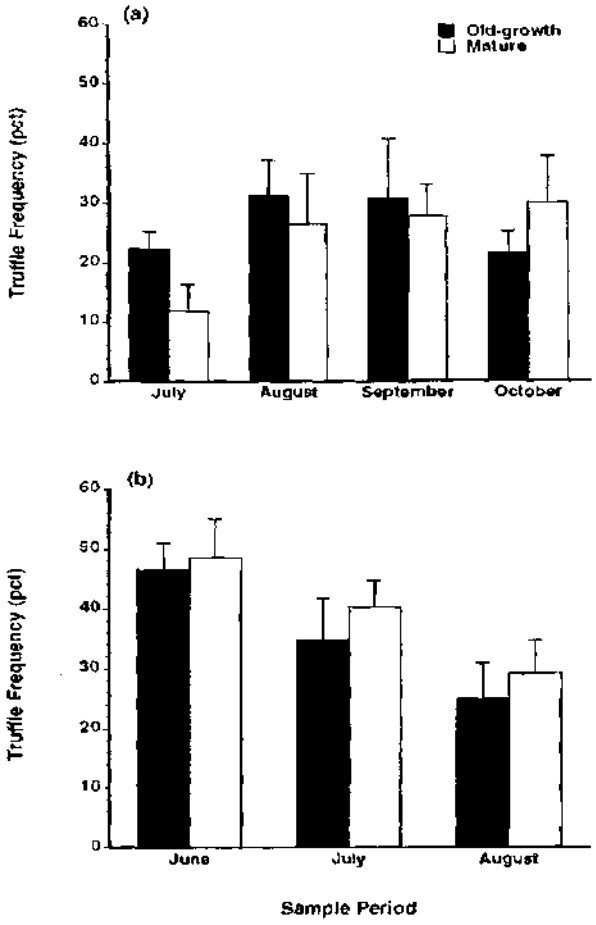

Figure 5—Means and standard errors of truffle frequency in four old-growth and four mature fir stands in northeastern California during (a) four sample periods in 1993 and (b) three sample periods in 1994. Repeated-measures ANOVA (sample period was repeated measure) indicated effect of age class was not significant in 1993 (F = 0.10; d.f. = 1, 3; α = 0.78) or 1994 (F = 0.62; d.f. = 1, 3; α = 0.49). Sample period effect was nearly significant in 1993 (F= 3.32; d.f. = 3, 9; α = 0.07) and significant in 1994 (F= 13.39; d.f. = 2, 6; α = 0.01).

Not only were decayed wood and organic soil depth not good predictors of truffle abundance among grids or among vegetation plots, they were not good predictors of truffle presence among 4-m^2 truffle plots. We found a significant association between presence of decayed wood and presence of truffles in only one of six tests (*fig. 8*). Association was greatest in both years during the last sample period, however, when soils were dry. Decayed logs retain large amounts of water and may influence truffle production most when soils are driest (Amaranthus and others 1994). Mean values of organic soil depth were greater in plots with truffles than in plots without truffles in each sample period, but ranked values were only marginally significant in one of six tests (*fig. 9*).

Truffle production has been shown to be low in young (< 30 years) conifer stands after stand-replacement events like clearcutting (Amaranthus and others 1994,

Clarkson and Mills 1994, Vogt and others 1981). North and others (1997) found that 60-year-old stands that had originated after clearcutting in Washington had significantly lower truffle biomass than old-growth (≥300-year-old) stands, but that truffle biomass did not differ significantly between old-growth and natural, mature stands (stands that developed after windstorms in the early part of the century and that were dominated by trees about 70 years old). Luoma and others (1991) did not statistically compare truffle biomass among stand age classes, but found that standing crop biomass of truffles was greater in mesic, mature stands (80 to 199 years old) of Douglas-fir in Oregon than in mesic, old-growth stands (≥200 years old).

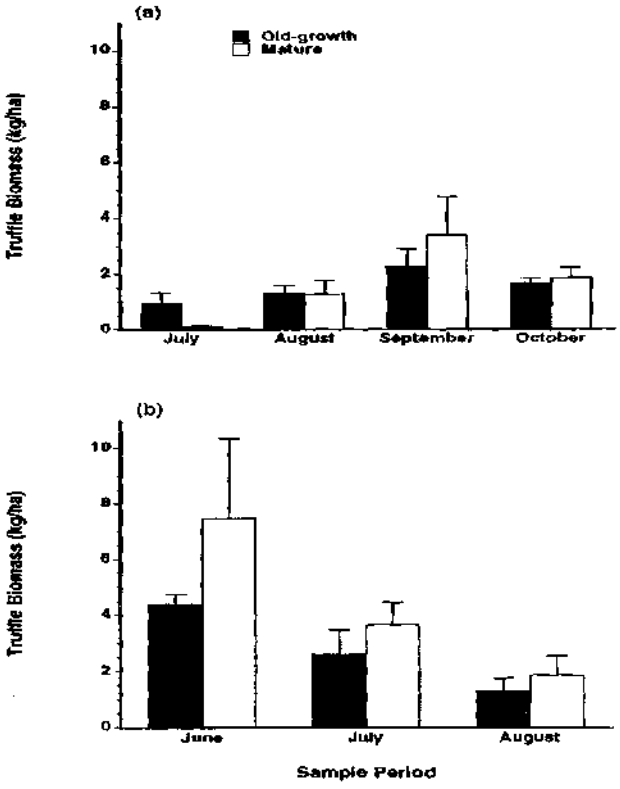

Figure 6—Means and standard errors of truffle biomass in four old-growth and four mature fir stands in northeastern California during (a) four sample periods in 1993 and (b) three sample periods in 1994. Repeated-measures ANOVA indicated effect of age class was not significant in 1993 (F = 3.38; d.f. = 1, 3; α = 0.16) or 1994 (F = 0.68; d.f. = 1, 3; α = 0.47). Sample period effect was significant in 1993 (F = 23.17; d.f. = 3, 9; α < 0.01) and 1994 (F= 8.14; d.f. = 2, 6; α = 0.02).

The lack of significant associations between truffle abundance and habitat measures suggests that truffle collections (pooled across species) were more or less randomly distributed within the stands in which we sampled. Each of these stands, however, was densely stocked, unmanaged, and relatively homogeneous. Associations may be greater in more disturbed or heterogeneous stands.

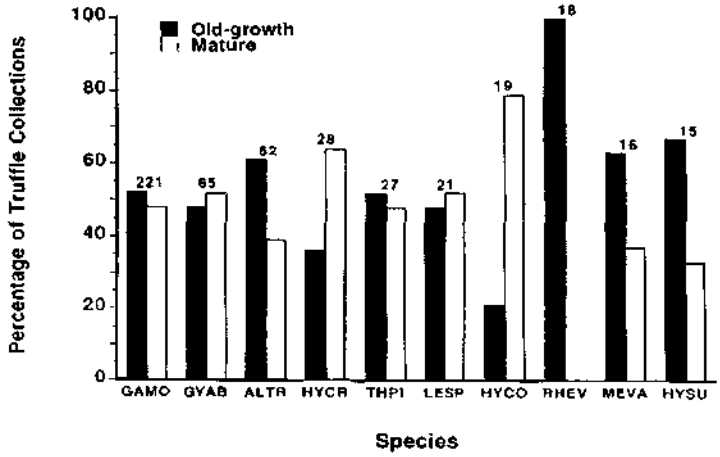

Figure 7—Percentages of truffle collections found in four old-growth and four mature fir stands in northeastern California. Total number of collections found in 1993 and 1994 for each species is listed above bars. Contingency table analysis indicated significant association between age class and numbers of collections of 10 most common truffle species (X^2= 31.58, d.f. = 9, α < 0.01). Ten species were *Gautier/a monticola* (GAMO), *Gymnomyces abietis* (GYAB), *Alpova trappei* (ALTR), *Hysterangium crassirhachis* (HYCR), *Thaxterogaster pingue* (THPI), *Leucophelps spinispora* (LESP), *Hysterangium coriaceum* (HYCO), *Rhizopogon evadens* (RHEV), *Melanogaster varigatus* (MEVA), and *Hymenogaster sublilacinus* (HYSU).

Conclusions

We began our research with the goal of trying to understand patterns of spotted owl habitat use observed in and around Swain Mountain Experimental Forest in the Lassen National Forest. We tested the hypothesis that abundance of the owl's primary prey was lower in old-growth forests that had been shelterwood-logged 6 to 7 years previously (where owls were rarely detected) than in nearby, unlogged old-growth forests (where owls were frequently detected). Abundance of flying squirrels was significantly less in shelterwood-logged old-growth forests than in unlogged old-growth and mature forests. Spotted owls may have avoided the open, shelterwood-logged forests for additional reasons, but low abundance of flying squirrels made these forests poor foraging habitat for the owl.

Consistent with other studies, dietary analysis showed that truffles were a common food of flying squirrels in our study area. The food preference study showed that the foods most preferred by captive squirrels were two species of truffles, although the lichen *Bryoria fremontii* was also readily eaten. Truffle frequency was correlated with abundance of flying squirrels across the 12 grids in which we sampled, suggesting that truffle availability may have influenced habitat selection by flying squirrels.

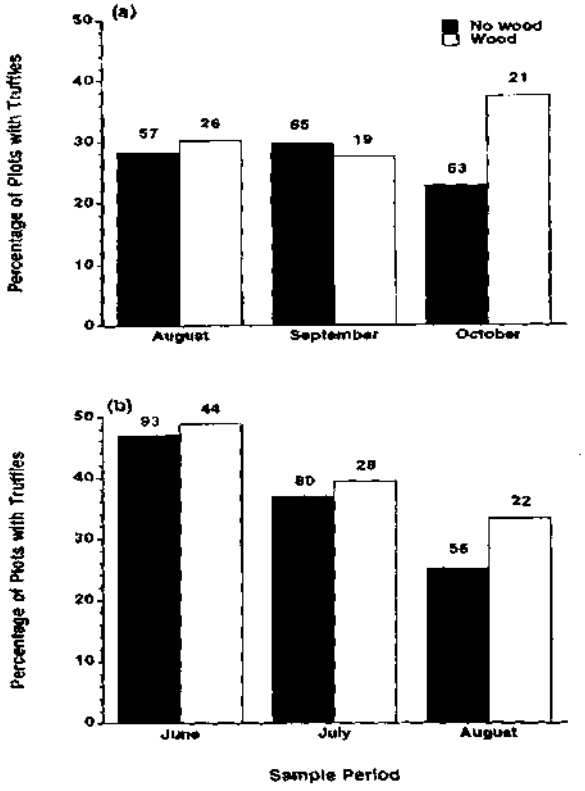

Figure 8—Percentages of 4-m^2 truffle plots (pooled across four grids in old-growth stands and four grids in mature stands) in (a) 1993 and (b) 1994 without decayed wood and with at least some decayed wood that had ≥ 1 truffle collection (n = 288 truffle plots for each sample period). Number of plots with truffles is listed above each bar. The α values from 2 x 2 contingency tables (d.f. = 1) testing for association between truffle presence and presence of decayed wood were 0.73 in August 1993, 0.73 in September 1993, 0.02 in October 1993, 0.76 in June 1994, 0.70 in July 1994, and 0.19 in August 1994.

Low truffle frequency in shelterwood-logged forests suggests that silvicultural treatments within Swain Mountain Experimental Forest negatively affected truffle production. Our study was not designed to determine the relative impacts of harvest level and ground disturbance. We note, however, that harvest level in the shelterwood-logged forests (where mean basal area in the four grids was about 30 percent of that in the four grids in old-growth forests) was roughly similar to harvest level in the heavily thinned units at the Jennie Springs site, but in that study, truffle frequency and biomass were not significantly less in heavily thinned units than in unthinned units. Unlike disturbance to the forest floor in the shelterwood-logged forests, disturbance to the forest floor was minimized at the Jennie Springs site, suggesting that the ground disturbance associated with site preparation in Swain Mountain Experimental Forest may have had a greater effect on truffle production than harvest level. Longer-term studies specifically designed to determine the relative impacts of tree harvest and ground disturbance on sporocarp production would provide useful information for forest managers.

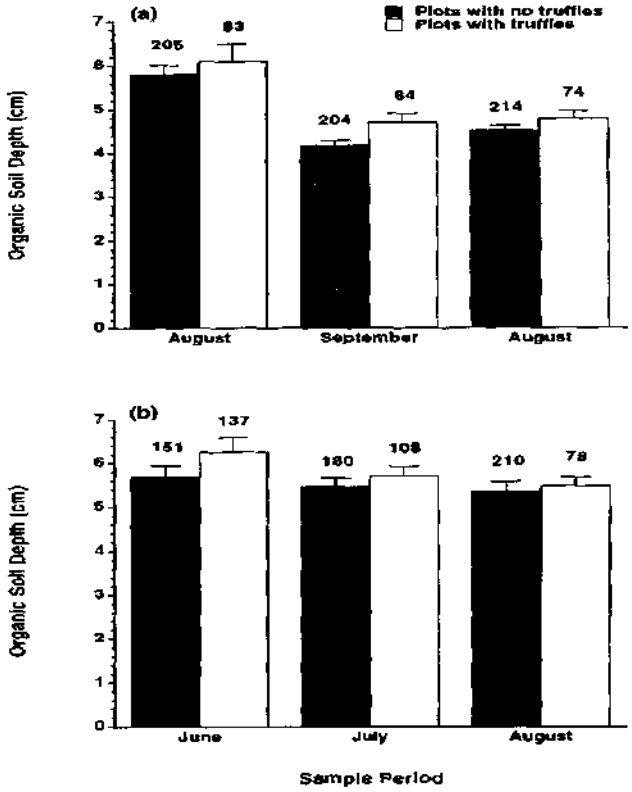

Figure 9—Means and standard errors for organic soil depth in (a) 1993 and (b) 1994 within 4-m^2 truffle plots with no truffles and plots with ≥ 1 truffle collection (pooled across four grids in old-growth stands and four grids in mature stands). Number of truffle plots is listed above each bar. The α values from Wilcoxon rank-sum tests comparing ranked values between plots without truffles and plots with truffles were 0.45 in August 1993, 0.06 in September 1993, 0.33 in October 1993, 0.35 in June 1994, 0.49 in July 1994, and 0.10 in August 1994.

We found that by the stem-exclusion phase of forest development, truffle production and species richness were similar to that found in old-growth forests. Thus, we found no evidence indicating that old-growth fir forests in the Lassen National Forest were unique in truffle production or diversity of truffle species. Even though the old-growth and mature forests we sampled were floristically simple, 46 species of hypogeous ectomycorrhizal fungi were found in 2 years, and we do not know how many epigeous ectomycorrhizal species were present. The functional significance of this high diversity of mycorrhizal fungi is poorly understood. Even though truffle frequency (pooled across truffle species) did not differ significantly among thinning levels or between old-growth and mature forests, frequencies of individual taxa did. This suggests that the effects of forest management on truffle production and assemblages of mycorrhizal fungi are species specific and complex. Different species may perform different functions and be adapted to different environmental, substrate, and host conditions (Perry and Amaranthus 1997, Trappe 1977). It may be difficult to make predictions or generalizations until we have more information on species-specific effects of disturbance. Similar disturbances may have

different overall effects in areas with different assemblages of truffle species, and the same species may react differently under different environmental conditions. This implies that the effects of forest management on mycophagous mammals are also complex, especially because our food preference study and other studies suggest that different truffle species have different payabilities, and so little is known about the nutritional values of different truffle species. Acknowledgment of the complexities of forest ecosystems and the limitations of current knowledge argues for an adaptive approach to forest management (Kohm and Franklin 1997),

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References

Amaranthus, Michael; Trappe, James M.; Bednar, Larry; Arthur, David 1994. **Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy.** Canadian Journal of Forest Research 24: 2157-2165.

Burnham, K.P.; Overton, W.S. 1979. **Robust estimation of population size when capture probabilities vary among animals.** Ecology 60: 927-936.

Carey, Andrew B.; Horton, Scott P.; Biswell, Brian L. 1992. **Northern spotted owls: influence of prey base and landscape character.** Ecological Monographs 62: 223-250.

Claridge, A.W.; Cork, S.J. 1994. **Nutritional value of hypogeal fungal sporocarps for the long-nosed potoroo (*Potorous tridactylus*), a forest-dwelling mycophagous marsupial.** Australian Journal of Zoology 42: 701-710.

Clarkson, David A.; Mills, L. Scott 1994. **Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon.** Northwest Science 68: 259-265.

Cork, S.J.; Kenagy, G.J. 1989. **Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel.** Ecology 70: 577-586.

FEMAT. 1993. **Forest ecosystem management: an ecological, economic, and social assessment.** Report of the Forest Ecosystem Management Assessment Team. Washington, DC: Government Printing Office.

Fogel, Robert 1976. **Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand.** Canadian Journal of Botany 54: 1152-1162.

Fogel, Robert; Trappe, James M. 1978. **Fungus consumption (mycophagy) by small animals.** Northwest Science 52: 1-31.

Fogel, Robert M.; Hunt, Gary A. 1979. **Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover.** Canadian Journal of Forest Research 9: 245-256.

Hacskaylo, Edward 1973. **Carbohydrate physiology of ectomycorrhizae.** In: Marks, G.C.; Kozlowski, T.T., eds. Ectomycorrhizae: their ecology and physiology. New York: Academic Press; 207-230.

Hall, Darrell S. 1991. **Diet of the northern flying squirrel at Sagehen Creek, California.** Journal of Mammalogy 72: 615-617.

Harley, J. L. 1971. **Fungi in ecosystems.** Journal of Ecology 59: 653-668.

Harmon, M. E.; Franklin, J. F.; Swanson, F. J.; Sollins, P.; Gregory, S. V.; Lattin, J. D.; Anderson, N. H.; Cline, S. P.; Aumen, N. G.; Sedell, J. R.; Lienkaemper, G. W.; Cromack, K., Jr.; Cummins, K. W. 1986. **Ecology of coarse woody debris in temperate ecosystems.** Advances in Ecological Research 15: 133-302.

Harvey, A.E.; Jurgensen, M.F.; Larsen, M.J. 1978. **Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana.**
Forest Science 24: 203-208,

Harvey, A.E.; Larsen, M.J.; Jurgensen, M.F. 1979. **Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types.** Forest Science 25: 350-358.

Hunt, Gary A.; Trappe, James M. 1987. **Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand.** Canadian Journal of Botany 65: 438-445.

Janos, David P.; Sahley, Catherine T. 1995. **Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru.** Ecology 76: 1852-1858.

Johnson, C.N. 1994. **Nutritional ecology of a mycophagous marsupial in relation to production of hypogeous fungi.** Ecology 75: 2015-2021.

Kohm, Kathryn A.; Franklin, Jerry F. 1997. **Introduction.** In: Kohm, Kathryn A.; Franklin, Jerry F., eds. Creating a forestry for the 21st century: the science of ecosystem management. Washington, DC: Island Press; 1-5.

Last, F.T.; Pelham, J.; Mason, P.A.; Ingleby, K. 1979. **Influence of leaves on sporophore production by fungi forming sheathing mycorrhizas with *Betula* spp.** Nature 280: 168-169.

Luoma, Daniel L. 1991. **Annual changes in seasonal production of hypogeous sporocarps in Oregon Douglas-fir forests.** In: Ruggiero, Leonard F.; Aubry, Keith B.; Carey, Andrew B.; Huff, Mark H., technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 83-89.

Luoma, Daniel L.; Frenkel, Robert E.; Trappe, James M. 1991. **Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation.** Mycologia 83: 335-353.

Maser, Chris; Anderson, Ralph G.; Cromack, Kermit, Jr.; Williams, Jerry T.; Martin, Robert E. 1979. **Dead and down woody material.** In: Thomas, Jack Ward, ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Hand. 553. Washington, DC: Forest Service, U.S. Department of Agriculture; 78-95.

Maser, Chris; Maser, Zane; Witt, Joseph W.; Hunt, Gary 1986. **The northern flying squirrel: a mycophagist in southwestern Oregon.** Canadian Journal of Zoology 64: 2086-2089.

Maser, Chris; Trappe, James M.; Nussbaum, Ronald A. 1978. **Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests.** Ecology 59: 799-809.

Maser, Zane; Maser, Chris; Trappe, James M. 1985. **Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon.** Canadian Journal of Zoology 63: 1084-1088.

McKeever, Sturgis 1960. **Food of the northern flying squirrel in northeastern California.** Journal of Mammalogy 41: 270-271.

McKeever, Sturgis 1964. **The biology of the golden-mantled ground squirrel, *Citellus lateralis*.** Ecological Monographs 34: 383-401.

Miller, Orson K., Jr. 1983. **Ectomycorrhizae in the Agaricales and Gasteromycetes.** Canadian Journal of Botany 61: 909-916.

North, Malcom; Trappe, James; Franklin, Jerry 1997. **Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests.** Ecology 78: 1543-1554.

Nowak, Ronald M. 1991. **Walker's mammals of the world.** 5th ed. Baltimore, MD: The Johns Hopkins University Press, 1: 642 p.

O'Dell, Thomas E.; Luoma, Daniel L.; Molina, Randolph J. 1992. **Ectomycorrhizal fungal communities in young, managed, and old-growth Douglas-fir stands.** Northwest Environmental Journal 8: 166-168.

Oliver, Chadwick D.; Larson, Bruce C. 1996. **Forest stand dynamics.** Update edition. New York: John Wiley & Sons, Inc.; 520 p.

Oliver, W.W.; Powers, R.F.; Weatherspoon, C.P.; Laacke, R.J. 1981. **Effects of intensive silviculture on growth, fire hazard reduction, and nutrient cycling in a young white fir sawtimber ecosystem.** Unpublished study plan supplied by authors.

Perry, David A.; Amaranthus, Michael P. 1997. **Disturbance, recovery, and stability.** In: Kohm, Kathryn A.; Franklin, Jerry F., eds. Creating a forestry for the 21st century: the science of ecosystem management. Washington, DC: Island Press; 31-56.

Rosenberg, Daniel K.; Anthony, Robert G. 1992. **Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon.** Canadian Journal of Zoology 70: 161-166.

Rosenberg, Daniel K.; Overton, W. Scott; Anthony, Robert G. 1995. **Estimation of animal abundance when capture probabilities are low and heterogeneous.** The Journal of Wildlife Management 59: 252-261.

SAS Institute. 1989. **SAS/STAT user's guide.** Version 6, 4th ed. vol. 2. Cary, NC: SAS Institute Inc.; 846 p.

SAS Institute. 1997. **SAS/STAT software: changes and enhancements through release 6.12.** Cary, NC: SAS Institute, Inc.; 1162 p.

States, J. 1985. **Hypogeous, mycorrhizal fungi associated with ponderosa pine: sporocarp phenology.** In: Molina, R., ed. Proceedings of the 6th North American conference on mycorrhizae. Corvallis: Oregon State University; 271 p.

Sutton, Dallas A. 1992. ***Tamias amoenus*.** Mammalian Species 390: 1-8.

Taylor, Robert J. 1992. **Seasonal changes in the diet of the Tasmanian Bettong (*Bettongia gaimardi*), a mycophagous marsupial.** Journal of Mammalogy 73: 408-414.

Tevis, Lloyd, Jr. 1952. **Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada.** Journal of Mammalogy 33: 198-205.

Tevis, Lloyd, Jr. 1953. **Stomach contents of chipmunks and mantled squirrels in northeastern California.** Journal of Mammalogy 34: 316-324.

Trappe, James M. 1962. **Fungus associates of ectotrophic mycorrhizae.** The Botanical Review 28: 538-606.

Trappe, James M. 1971. **Mycorrhiza-forming Ascomycetes. In: Hacskaylo, Edward, ed. Mycorrhiza-forming Ascomycetes.** Miscellaneous Publication 1189. Washington, DC: Forest Service, U.S. Department of Agriculture; 19-37.

Trappe, James M. 1977. **Selection of fungi for ectomycorrhizal inoculation in nurseries.** Annual Review of Phytopathology 15: 203-222.

Trappe, James M., Maser, Chris 1976. **Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract.** Mycologia 68: 433-436.

Ure, Douglas C.; Maser, Chris 1982. **Mycophagy of red-backed voles in Oregon and Washington.** Canadian Journal of Zoology 60: 3307-3315.

Vogt, Kristiina A.; Edmonds, Robert L.; Grier, Charles C. 1981. **Biomass and nutrient concentrations of sporocarps produced by mycorrhizal and decomposer fungi in *Abies amabilis* stands.** Oecologia 50: 170-175.

Waters, Jeffrey R.; McKelvey, Kevin S.; Luoma, Daniel L.; Zabel, Cynthia J. 1997. **Truffle production in old-growth and mature fir stands in northeastern California.** Forest Ecology and Management 96: 155-166.

Waters, Jeffrey R.; McKelvey, Kevin S.; Zabel, Cynthia J.; Oliver, William W. 1994. **The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi.** Canadian Journal of Forest Research 24: 1516-1522.

Waters, Jeffrey R.; Zabel, Cynthia J. 1995. **Northern flying squirrel densities in fir forests of northeastern California.** Journal of Wildlife Management 59: 858-866.

Waters, Jeffrey R.; Zabel, Cynthia J. [In press]. **Abundances of small mammals in fir forests in northeastern California.** Journal of Mammalogy.

Weatherspoon, C. Phillip, Research Forester, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. [Telephone conversation with Jeffrey R. Waters]. 1994.

Wilson, Kenneth R.; Anderson, David R. 1985. **Evaluation of two density estimators of small mammal population size.** Journal of Mammalogy 66: 13-21.

Zabel, Cynthia J.; McKelvey, Kevin S.; Johnston, James D. 1992a. **Patterns of habitat use by California spotted owls in logged forests of the northern Sierra Nevada.** In: Verner, Jared; McKelvey, Kevin S.; Noon, Barry R.; Gutierrez, R. J.; Gould, Gordon I., Jr.; Beck; Thomas W., technical coordinators. The California spotted owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 165-174.

Zabel, Cynthia J.; Steger, George N.; McKelvey, Kevin S.; Eberlein, Gary P.; Noon, Barry R.; Verner, Jared 1992b. **Home-range size and habitat-use patterns of California spotted owls in the Sierra Nevada.** In: Verner, Jared; McKelvey, Kevin S.; Noon, Barry R.; Gutierrez, R. J.; Gould, Gordon I., Jr.; Beck, Thomas W., technical coordinators. The California spotted owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 149-163.

Zabel, Cynthia J.; Waters, Jeffrey R. 1997. **Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California.** Northwest Science 71: 103-107,