Management and Conservation Article

Small Mammal Mycophagy Response to Variations in Green-Tree Retention

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ABSTRACT We studied the effects of 6 green-tree retention levels and patterns on the diets of northern flying squirrels (*Glaucomys sabrinus*), Townsend's chipmunks (*Tamias townsendii*), Siskiyou chipmunks (*T. siskiyou*), western red-backed voles (*Myodes californicus*), and southern red-backed voles (*Myodes gapperi*) using fecal pellet analysis. These rodents are truffle spore dispersers and prey for forest predators such as the northern spotted owl (*Strix occidentalis caurina*). Pretreatment diets showed differences in truffle and plant consumption among genera. Tree harvesting, especially in the 15% aggregated retention pattern, reduced frequency of *Rhizopogon* spores in the diet of voles, which may reflect a reduced ability of these animals to forage for *Rhizopogon* truffles, a decreased access to these truffles, or a reduction in *Rhizopogon* truffle abundance or frequency. Habitat island effects and edge effects provide conceptual frameworks for the reduction in consumption of *Rhizopogon* truffles by voles in green-tree aggregates. Overall, small mammal consumption of truffles showed little change in response to the treatments. Animals may be compensating for a locally declining food source by altering their foraging behavior. The long-term effect of this postulated behavioral compensation on small mammal energetics and population dynamics is unknown. Forest managers may reduce the impact of tree harvesting on these key forest ecosystem components by including green-tree aggregates within a dispersed retention matrix. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1747–1755; 2008)

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In the Pacific Northwest (PNW), USA, ectomycorrhizal fungi (EMF) are an essential part of forest ecosystems, particularly in maintaining tree health and in providing food for a variety of animals (Trappe and Maser 1977, Malajczuk et al. 1987, Luoma 1988, Clarkson and Mills 1994). Ectomycorrhizal fungi form a symbiotic relationship with the feeder roots of a variety of trees, including members of Betulaceae, Fagaceae, and Pinaceae. The heterotrophic fungi receive photosynthates and the trees receive benefits such as increased water and nutrient uptake (Smith and Read 1997). Some EMF form hypogeous (underground) sporocarps, commonly known as truffles (ascomycetes) or false truffles (basidiomycetes; both hereafter truffles). Truffles are an important food source for many small mammals in the PNW (Maser et al. 1978, North et al. 1997). These mycophagous mammals disperse fungal spores in forested and nonforested habitat (Fogel and Trappe 1978) and are important prey to many predators, including the threatened northern spotted owl (*Strix occidentalis caurina*; Forsman et al. 1984). The mammal–fungus–tree and predator–prey relationships can be disrupted when humans manipulate forests for timber production (Luoma et al. 2003). Thus, the general hypothesis that maintenance of mature forest legacies in timber harvest areas is an effective ecological mitigation strategy (Franklin and Forman 1987, Franklin et al. 1997) needs specific testing with regard to small mammal mycophagy.

Historically, clearcutting has been considered an economical harvest method in Douglas fir (*Pseudotsuga menziesii*) dominated forests of the PNW (Aubry et al. 1999). However, disturbance associated with heavy logging machinery can alter habitat and soil microsite conditions, and some plant and animal species may become locally extirpated or isolated, whereas populations of other species increase (Franklin and DeBell 1973, Halpern and Spies 1995). Managed forests regenerated after clearcutting and grown on short rotations may contain fewer native and rare species and more invasive nonnative species (Halpern and Spies 1995, Halpern et al. 2005*b*). Better understanding of these effects led to the use of alternative harvest methods that mitigate forest disruption and retain some of the structure and function of mature forests. In the PNW, concerns about timber management practices and habitat loss for certain species prompted the creation of the Northwest Forest Plan, which set specific guidelines for management of late-successional and old-growth forest species on federal land, associated with the northern spotted owl (Interagency Supplemental Environmental Impact Statement Team 1994).

Green-tree retention is the practice of leaving live, structurally sound, large trees in a stand after extracting timber (Halpern et al. 1999). This management approach is designed to retain mature forest characteristics or expedite development of these characteristics in managed stands (Aubry et al. 1999, Szaro et al. 2006). The Demonstration of Ecosystem Management Options (DEMO) experiment is a long-term study designed to observe the effects of different levels and patterns of green-tree retention on multiple attributes of mature Douglas fir forests (Aubry et al. 1999).

We sought to determine those levels and patterns of green-tree retention that maintained and those that changed the fungal diets of northern flying squirrels (*Glaucomys*

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sabrinus), Townsend's chipmunks (*Tamias townsendii*), Siskiyou chipmunks (*Tamias siskiyou*), western red-backed voles (*Myodes californicus*), and southern red-backed voles (*Myodes gapperi*). Our specific objectives were to 1) document the diets of the study animals under the pretreatment conditions and 2) test for changes in cumulative number of genera consumed (richness) and in mean spore frequency of the most common truffle genera consumed (abundance). We hypothesized that 1) pretreatment diets of the studied animal genera would differ, 2) mean cumulative number of truffle genera in the diet of the study mammals (richness) would change as a result of tree harvesting, showing the most change in treatments with the least percentage of green-trees retained, and 3) mean spore frequency of the most common truffle genera (abundance) would exhibit the greatest changes in those treatments having the highest proportion of trees harvested.

STUDY AREA

Field work took place in the Umpqua National Forest in Oregon (Watson Falls and Dog Prairie blocks) and the Gifford Pinchot National Forest in Washington (Paradise Hills and Butte blocks). The DEMO researchers chose blocks for their accessibility and harvesting ease as well as for forest composition and environmental factors; no large streams or wetlands were included, though blocks encompassed multiple environmental gradients. The dominant tree species in each block was Douglas fir, though the composition of the remaining canopy differed among blocks. The management history of the study blocks differed. One to two decades prior to the initiation of the DEMO study, the Watson Falls block was salvage logged and the Dog Prairie block was thinned. Neither the Butte nor the Paradise Hills blocks were previously managed. Additional information on the study sites, conceptual framework, and establishment of the DEMO study may be found in Aubry et al. (1999) and Halpern et al. (1999, 2005*a*).

METHODS

The DEMO experiment employed a complete randomized block design. We studied 4 of the 6 DEMO blocks: block 1 (Watson Falls), block 4 (Dog Prairie), block 5 (Butte), and block 7 (Paradise Hills). Within each block, DEMO scientists established 6 13-hectare stands as experimental treatment units. They randomly assigned treatments to one experimental unit in each block. Each treatment consisted of a combination of green-tree retention level and pattern, ranging from 15% to 75% retention of the original basal area in a dispersed or aggregated pattern, resulting in 5 manipulated stands and a control in each block (Aubry et al. 1999). The treatments were 1) 100% retention of trees (control), 2) 75% aggregated retention of the original basal area (75% A), 3) 40% dispersed retention of the original basal area (40% D), 4) 40% aggregated retention of the original basal area (40% A), 5) 15% dispersed retention of the original basal area (15% D), and 6) 15% aggregated retention of the original basal area (15% D; Fig. 1).

Field technicians from the DEMO small mammal research group established permanent 8 × 8 or 7 × 9 sampling grids in each treatment unit. Grid points were 40 m apart with 40 m between the grid and the edge of the treatment unit; a Tomahawk 201 live-trap (Tomahawk Live Trap Co., Tomahawk, WI) for capturing arboreal rodents (chipmunks and squirrels) and a pitfall trap for small terrestrial mammals (voles) were placed at each grid point. Live-traps, which were checked daily, were set twice in the fall for 2 consecutive 4-day periods with 2 weeks between the periods, resulting in 16 trap nights per grid point (Lehmkuhl et al. 1999). Fall sampling (late Sep to early Nov) was used to estimate reproductive status, relative abundances, and consumption of fungi during peak fall sporocarp production period (Lehmkuhl et al. 1999, Luoma et al. 2004). Pitfall traps were opened for a period of 28 days in the fall and checked weekly (Institutional Animal Care and Use Protocol no. 1713, no. 2283). Technicians trapped during the 2 years prior to and the 2 years after treatment application (Gitzen et al. 2007).

We used fecal pellet analysis, which allows for examination of an animal's recent meals, to examine diets of mycophagous animals (Fogel and Trappe 1978, Maser et al. 1978, McIntire and Carey 1989). In each treatment unit, field technicians collected fecal pellets from ≤25 animals of each genus per year. They collected 1 to 10 fresh fecal pellets from each live-trapped animal as expelled, avoiding the introduction of spores from other materials onto the sample. Fecal material from each individual was placed in a vial of 70% ethanol, marked with identification and collection numbers, and sent to the laboratory. Technicians followed a similar protocol in the lab with pellets collected from pitfall-trapped animals. Fecal pellets from each animal capture constituted a sampling unit (Lehmkuhl et al. 1999).

For laboratory analysis of each individual collection, we drained the vials of ethanol and added approximately 1.0 mL of de-ionized water per pellet. We macerated the pellets with a glass rod, placing 3 to 5 droplets of the resulting solution on a glass slide. We added a drop of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) and mixed it with the samples on the slide to aid in spore identification. We evenly distributed this liquid sample on the glass slide and placed 3 cover slips (22 × 22 mm) per slide side-by-side on top of the fecal sample solution. We then examined each sample under a compound microscope.

For each cover slip, we systematically selected 25 nonoverlapping fields of view and examined them at 400× magnification (5 rows of 5 fields each) for 75 fields per fecal sample (McIntire and Carey 1989). We recorded presence of each truffle genus, plant material, and spores of epigeous sporocarps for each field of view; we identified truffle spores to genus using spore morphology and reaction to Melzer's reagent according to Castellano et al. (1989). We grouped *Truncocolumella*, *Alpova*, and *Trappea* spores with *Rhizopogon* spores due to their morphological similarity. We calculated the frequency of each item as a percentage of its

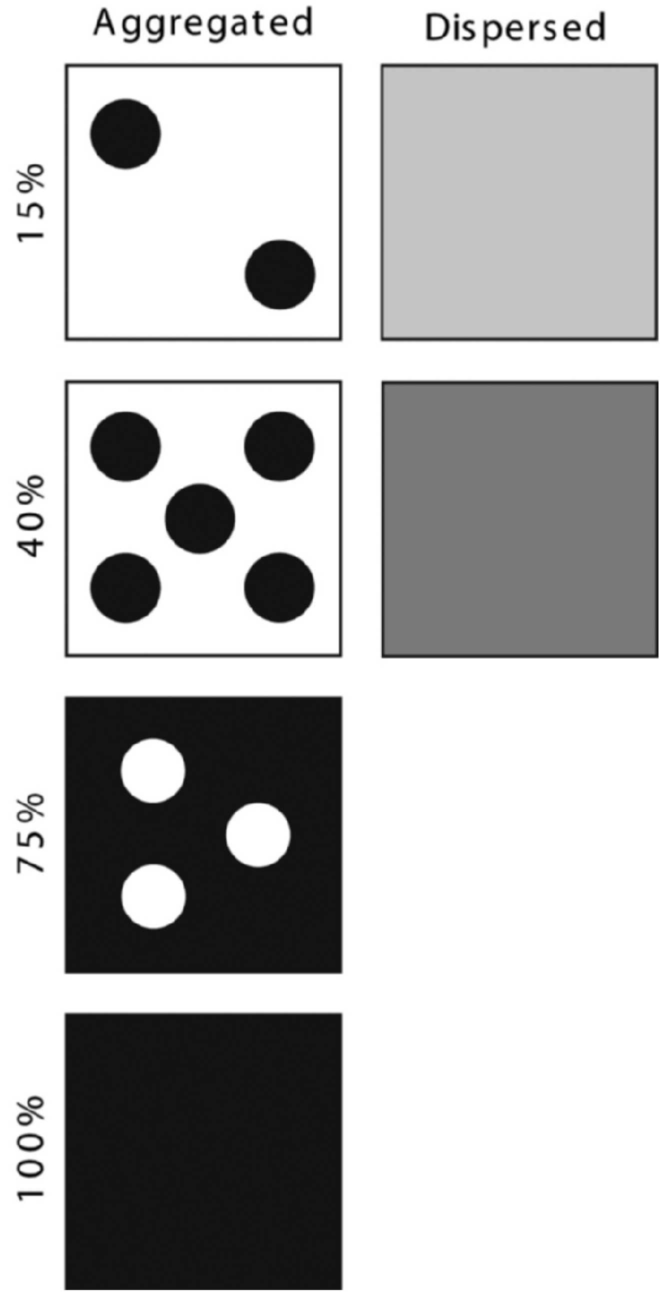

Figure 1. Schematic diagram representing levels (% basal area) and patterns (aggregated, dispersed) of green-tree retention used for the Demonstration of Ecosystem Management Options experiment in western Oregon and Washington, USA, fall 1995–2000. In the aggregated retention treatments, black areas represent trees retained, white areas were harvested. The 2 levels of dispersed retention are represented by gray tones.

occurrence in the 75 possible fields for each sample. We also recorded total number of truffle genera identified in each fecal sample. For each animal genus, we calculated pre- and posttreatment mean cumulative number of genera by summing across all samples collected in a treatment unit. We assessed mycophagy for voles across 4 blocks and for northern flying squirrels and chipmunks across 2 blocks due to low capture numbers in other blocks.

We considered the southern red-backed vole to be the ecological equivalent of the western red-backed vole in the western Cascade Mountains of Oregon and Washington. We expected both species to consume equivalent numbers of fungal genera because their habitats in our study areas were similar (Maser and Maser 1988). Likewise, the ecology and habitat of the Townsend's and Siskiyou chipmunks were similar in our study, and they were similarly mycophagous. Therefore, we also considered the feeding habits of these chipmunks to be ecologically equivalent (Maser et al. 1978, McIntire 1984).

In our dietary analyses, we treated the response variables as independent of one another. Also, we assumed that a small mammal maximized its use of a truffle before expending energy to search for another and treated each genus as an independent feeding event. Consequently, we analyzed the response of each truffle genus to each treatment independently using analysis of variance (ANOVA) at the $\alpha = 0.05$ level.

We used only pretreatment data to describe and compare diets among animal genera. We compared mean frequencies of each diet item for each animal using a one-way ANOVA at the $\alpha = 0.05$ level. All data met the assumptions of normality and constant variance.

We tested 6 response variables for treatment effects for each animal genus: change in mean spore frequencies for the 4 most common genera of truffles in the diets of captured animals (*Gautieria*, *Hysterangium*, *Leucogaster*, and *Rhizopogon*), change in mean frequency of plant material, and change in mean cumulative number of truffle genera. For each year and treatment unit combination, we calculated means for the frequency of each diet item and the cumulative number of genera for each animal genus. We averaged the means of the diet items from the 2 pretreatment years to calculate one pretreatment mean per diet item.

We calculated the change in frequency of each diet item for each animal genus in each treatment; for each diet item–animal genus–treatment combination, we subtracted the pretreatment mean frequency of a diet item from each posttreatment mean frequency of that diet item (e.g., posttreatment yr 1 minus pretreatment mean; posttreatment yr 2 minus pretreatment mean). We then averaged the posttreatment changes to provide one mean posttreatment value per diet item. We used this 2-step, posttreatment approach to handle instances of missing data associated with those experimental units that experienced no captures in one of the posttreatment years. When necessary to better meet assumptions of normality and constant variance (Sabin and Stafford 1990), we transformed truffle spore frequency values using a hyperbolic arcsine transformation (SAS Institute 1998). To determine the change in the mean cumulative number of truffle genera in the diet of each animal genus, we subtracted each pretreatment mean cumulative number of genera from the posttreatment mean cumulative number of genera on an experimental unit basis.

We used one-way ANOVA to detect differences in the mean change (from before to after treatment) for each response variable using StatView 5.0.1 (SAS Institute, Cary, NC). Main effects for these ANOVAs were block and

Table 1. Mean frequencies (%; ± SE) of the common truffle genera and plant material and mean number of truffle genera (± SE) in the fecal pellets of voles, flying squirrels, and chipmunks captured in 4 western Oregon and Washington, USA, Demonstration of Ecosystem Management Options study blocks, fall 1995 and 1996 (preharvest). Sample size (*n*) represents the number of fecal samples we examined.

		Diet item[a]											
		Gautieria		*Hysterangium*		*Leucogaster*		*Rhizopogon*		Plant material		Mean no. of genera	
Animal	*n*	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
Voles	458	16.7 B	2.8	11.4 AB	2.9	4.9 B	1.1	97.7	0.9	36.2 B	2.9	2.2 B	0.1
Flying squirrels	278	54.7 A	4.9	16.6 A	2.7	29.1 A	4.2	99.3	0.6	28.1 C	1.7	3.3 A	0.1
Chipmunks	143	0.9 C	0.6	4.2 B	1.5	9.2 B	3.6	98.3	0.9	49.8 A	1.8	1.9 B	0.2

[a] Values within a column followed by different letters are significantly different between animals by Fisher's protected least significant difference, $P \leq 0.05$.

treatment. For each animal genus and diet item combination, we compared response variables among treatments when ANOVA showed an overall significant treatment difference at the $\alpha = 0.05$ level. We used Fisher's protected least significant difference to determine significant differences among treatments at the $\alpha = 0.05$ level.

Using EstimateS version 5.0.1 (Colwell 1997), we constructed genus accumulation curves for each block and treatment combination for each animal genus to determine adequacy of sampling for the cumulative number of genera in the diet analysis. We used 50 randomized data runs to construct each curve. If the curve for a block-by-treatment combination did not approach the asymptote, we considered it to have an unacceptable number of trapped animals to capture most of the genera available to be eaten by the population.

Table 2. Constancy[a] of truffle genera found in the fecal pellets of voles, flying squirrels, and chipmunks from 4 western Oregon and Washington, USA, Demonstration of Ecosystem Management Options blocks, combined pre- and posttreatment data, fall 1995 through fall 2000. Sample size (*n*) represents the number of fecal samples examined.

Fungal genus	Voles ($n = 1{,}185$)	Northern flying squirrels ($n = 442$)	Chipmunks ($n = 569$)
Balsamia	3.8	17.2	9.7
Choiromyces	0.2	0	0
Elaphomyces	1.6	1.8	0.7
Endogone	0.7	0	0.4
Gautieria	42.4	79.4	21.0
Genabea	0.7	0	0.4
Geopora	1.0	1.1	1.2
Glomus	1.3	0.5	1.6
Hymenogaster	1.2	1.8	0.5
Hysterangium	25.0	62.4	32.7
Leucangium	0.7	0	0.4
Leucogaster	17.7	67.2	44.6
Leucophleps	1.8	3.2	8.8
Gymnomyces	3.6	12.7	3.9
Melanogaster	8.0	7.0	1.6
Octaviania	0	0.2	0
Radiigera	0.7	14.0	0
Rhizopogon	99.6	100	99.8
Thaxterogaster	1.7	2.7	3.3
Tuber	2.6	0.9	3.7
Total no. of genera	19	16	17

[a] % of fecal samples with the truffle genus present.

RESULTS

In comparing pretreatment diets among the animal genera, we found *Rhizopogon* spores with similar abundance in all pretreatment fecal samples ($P = 0.98$), occurring in >97% of the fields for all animal genera. Mean frequency of *Gautieria* spores in the diet of northern flying squirrels was approximately 3.3 to 61 times greater than in the other 2 animal genera ($P = 0.048$; Table 1). Plant material was approximately 1.8 times more common in the diet of the chipmunk species than in the diet of northern flying squirrels and 1.4 times more common than in the diet of voles ($P = 0.026$ and $P = 0.040$, respectively). Plant material was the second most common diet component in vole samples; whereas it ranked fourth in the diet of northern flying squirrels (Table 1). Mean frequency of *Hysterangium* spores was 4 times greater in the diet of northern flying squirrels than the chipmunk species ($P = 0.014$; Table 1). Only northern flying squirrels had a high frequency of *Leucogaster* spores in the pretreatment fecal samples (29.1%; Table 1). Pretreatment fecal samples from northern flying squirrels contained an average of 1.4 more truffle genera per fecal sample than those of chipmunks ($P \leq 0.001$) and 1.1 more genera than voles ($P \leq 0.001$; Table 1). Maximum number of genera counted in one pretreatment fecal sample for northern flying squirrels was 10, chipmunks 8, and voles 5.

We pooled pretreatment and posttreatment data for a count of the total number of truffle genera in the diet of each animal genus, identifying 19 truffle genera from 1,185 vole samples, 17 genera from 569 chipmunk samples, and 16 genera from 442 northern flying squirrel samples (Table 2). Fecal samples from each of these animal genera also contained minor amounts of spores of the mushroom genus *Laccaria* as well as mushroom spores identified to the families Boletaceae, Cortinariaceae, Entolomataceae, and Russulaceae. We also occasionally found spores of epigeous Ascomycota.

We identified treatment effects on spore frequency in the diets of voles only for the genus *Rhizopogon* ($P = 0.032$; Table 3). A posttreatment decrease in frequency of *Rhizopogon* spores in vole fecal pellets occurred in all treatments (Table 3). We found that only the decreases in *Rhizopogon* spore frequency of 4% and 11% observed in 40% A ($P = 0.028$) and 15% A ($P = 0.004$) treatments, respectively, differed from the change observed in the control.

Table 3. Change in mean frequency (%; ± SE) of diet items and in the mean cumulative number of genera (± SE) in fecal samples of western red-backed and southern red-backed voles by diet item and retention treatment with analysis of variance (ANOVA) results from 4 blocks of the Demonstration of Ecosystem Management Options study, western Oregon and Washington, USA, fall 1995–2000.

	Retention treatment[a]												
	100%		75% A		40% D		40% A		15% D		15% A		
Diet item	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	Overall ANOVA *P* value
Gautieria	−1.7	8.3	−3.4	4.1	−5.4	6.5	−2.2	5.7	1.8	4.1	1.7	6.1	0.989
Hysterangium	0.6	1.3	−1.6	1.3	−3.5	7.1	−0.5	0.6	−6.3	3.8	−1.0	2.8	0.833
Leucogaster	4.4	6.5	0.3	0.9	10.8	16.1	−1.4	3.2	7.8	4.9	−0.7	3.5	0.917
Rhizopogon[b]	0.0 A	2.4	−3.2 ABC	2.6	−4.5 AB	4.5	−4.2 BC	1.9	−4.9 AB	9.3	−11.3 C	3.6	0.032
Plant material	4.0	7.7	−1.3	7.4	8.5	4.9	−1.0	7.4	3.6	4.5	7.3	2.9	0.407
Cumulative no. of genera[b]	2.8 AC	0.9	2.0 ABC	1.1	−1.0 B	0.7	4.8 C	1.3	0.3 AB	0.9	1.0 AB	1.7	0.029

[a] A, aggregated retention; D, dispersed retention.

[b] Diet item change values that are followed by different letters are significantly different between treatments by Fisher's protected least significant difference ($P \leq 0.05$) based on transformed values, when necessary.

We also detected a treatment effect for the change in mean cumulative number of truffle genera in the diet of voles ($P = 0.029$; Table 3). The 40% D treatment declined relative to the control ($P = 0.028$) and its response contrasted with the 40% A treatment ($P = 0.002$), which showed an increase. The 40% D treatment also differed from the changes in the 15% D ($P = 0.011$) and 15% A ($P = 0.028$) treatments. Posttreatment, the randomized genera accumulation curves did not approach the asymptote in the Watson Falls 15% D treatment, nor in the Dog Prairie 15% A treatment due to low capture numbers.

We identified treatment effects on the mean change in frequency of *Hysterangium* spores in the diet of northern flying squirrels, which decreased in the 40% D treatment ($P = 0.004$; Table 4), and *Gautieria* spores ($P = 0.01$). Posttreatment, *Gautieria* spores increased by a frequency of nearly 29% in the 40% D treatment ($P = 0.023$; Table 4) and decreased by 17% in the 40% A treatment ($P = 0.016$; Table 4). These changes were significant not only when compared to the control, but were also different from one another ($P = 0.002$; Table 4). No flying squirrels were trapped in the 15% D posttreatment in the Butte block, thus we removed it from analysis.

We detected no change in the mean cumulative number of truffle genera in the diet of northern flying squirrels ($P = 0.191$). The posttreatment genera accumulation curves for northern flying squirrels did not approach the asymptote in the 40% A, 40% D, and 15% A treatments in the Watson Falls block nor the 40% D treatment in the Butte block due to low capture numbers.

We detected no treatment effects for the change in mean frequency of diet items or in mean cumulative number of truffle genera in the diet of the chipmunk species (Table 5). Technicians captured no chipmunks pretreatment in the 40% D treatment in the Watson Falls block; thus we removed this treatment from analysis. The randomized genera accumulation curves for the chipmunk species did not approach the asymptote for several treatments in the Watson Falls block.

DISCUSSION

Pretreatment Diets

Our research emphasized that the animals we studied are important truffle spore dispersers, although the abundance and number of truffle genera and amount of plant material in the diet differed among these animal groups. One truffle genus, *Rhizopogon*, occurred most commonly in the pretreatment fecal samples, appearing in >97% of the

Table 4. Change in mean frequency (%; ± SE) of diet items and in the mean cumulative number of genera (± SE) in fecal samples of northern flying squirrels by diet item and retention treatment with analysis of variance (ANOVA) results from 2 blocks of the Demonstration of Ecosystem Management Options study, western Oregon and Washington, USA, fall 1995–2000.

	Retention treatment[a]										
	100%		75% A		40% D		40% A		15% A		
Diet item	%	SE	%	SE	%	SE	%	SE	%	SE	Overall ANOVA *P* value
Gautieria[b]	4.8 A	2.1	3.2 A	6.2	28.9 B	7.2	−17.0 C	8.5	−7.0 AC	2.8	0.010
Hysterangium	22.3 A	15.1	9.5 A	2.6	−1.4 B	0.7	20.9 A	2.3	49.6 A	17.2	0.004
Leucogaster	12.5	0.3	31.8	3.8	40.0	34.8	1.4	3.2	17.5	12.3	0.338
Rhizopogon	0.3	0.3	0	0	0	0	1.7	5.9	0.03	0.03	0.999
Plant material	8.0	9.6	4.3	9.2	15.1	0.3	7.7	1.6	23.0	2.3	0.169
Cumulative no. of genera	2.5	0.5	2.5	2.5	−3.5	0.5	3.5	3.5	−2.0	3.0	0.191

[a] A, aggregated retention; D, dispersed retention.

[b] Diet item change values that are followed by different letters are significantly different between treatments by Fisher's protected least significant difference ($P \leq 0.05$) based on transformed values, when necessary.

Table 5. Change in mean frequency (%; ± SE) of diet items and in the mean cumulative number of genera (± SE) in fecal samples of Townsend's and Siskiyou chipmunks by diet item and retention treatment with analysis of variance (ANOVA) results from 2 blocks of the Demonstration of Ecosystem Management Options study, western Oregon and Washington, USA, fall 1995–2000.

	Retention treatment[a]										
	100%		75% A		40% A		15% D		15% A		
Diet item	%	SE	%	SE	%	SE	%	SE	%	SE	Overall ANOVA *P* value
Gautieria	7.7	0.2	1.7	0.2	7.9	0.7	3.9	1.3	7.4	5.4	0.356
Hysterangium	16.6	2.4	−1.2	2.4	15.6	11.9	4.7	6.4	12.3	9.7	0.144
Leucogaster	18.9	5.6	−7.1	14.1	1.2	1.7	21.5	2.0	15.3	11.4	0.561
Rhizopogon	1.7	2.1	−0.1	0.2	−1.9	1.0	−2.0	2.0	2.8	2.8	0.465
Plant material	−10.6	3.9	−13.1	5.5	−5.0	12.3	−8.8	1.9	−3.4	4.5	0.867
Cumulative no. of genera	4.5	1.5	5.0	0	6.0	2.0	6.0	2.0	4.5	1.5	0.666

[a] A, aggregated retention; D, dispersed retention.

fields for all animal genera (Table 1). *Rhizopogon* sporocarps were also the dominant truffles found in the study blocks (Luoma et al. 2004). We speculate that much of the observed diet composition was driven by the relative abundance of *Rhizopogon*.

In our study, abundance of truffle spores in the feces of southern and western red-backed voles emphasizes the importance of truffles in their diets as well as their potential role as spore dispersers in forests and open areas. Our findings reinforce those of Maser and Maser (1988), who found a diverse array of truffle genera in the diets of southern and western red-backed voles. Although vole feces contained the highest number of truffle genera, this result may be an artifact of sample size rather than evidence that voles eat a more diverse array of truffles than the other animal genera.

We found that northern flying squirrel fecal samples consistently contained high mean frequencies for several fungal genera; spores of the most common truffle genera were more frequent in northern flying squirrel samples than in chipmunk or vole samples. Our findings support the description of the northern flying squirrel as a fungal specialist that utilizes a diverse array of fungi for most of its diet (Maser et al. 1986, Carey et al. 1999). Diets of northern flying squirrels tend towards higher fungal diversity than diets of chipmunks or voles (Maser et al. 1978). In support of this conclusion, we found that northern flying squirrel samples had the highest number of genera in one fecal sample and the highest mean number of truffle genera.

Our evidence suggests that northern flying squirrels consume more *Gautieria* truffles than the other animal genera we studied (Table 1). A high frequency of *Gautieria* spores was present in the diet of northern flying squirrels compared to the low frequency in the diets of the vole and chipmunk species. Our results are supportive of food trial research conducted by Zabel and Waters (1997), which showed that of the truffle genera offered to northern flying squirrels, *Gautieria* sporocarps were most commonly eaten. Colgan et al. (1997) and Cázares et al. (1999) reported that *Gautieria* spores were rare or even absent in the diets of voles and chipmunks in locations where *Gautieria* spores were common in northern flying squirrel samples. Carey et al. (2002) detailed that *Gautieria* spores occurred with greater rank frequency in northern flying squirrel diets than the rank of sporocarp frequency in the squirrels' habitat. *Gautieria* sporocarps emit strong odors that may make them easier to detect than other truffles; however, other small mammals consume *Gautieria* less frequently than northern flying squirrels. Cumulative evidence suggests that the northern flying squirrel utilizes *Gautieria* for a greater proportion of its diet as compared to other small mammals.

Maser et al. (1986) compared fluctuation in spore frequencies in the feces of northern flying squirrels with previously measured, not concurrently measured, fruiting patterns of the truffle genera found in the area. Maser et al. (1986) described the northern flying squirrel as consuming an assortment of truffle species with no preference for specific truffle genera. Without direct comparison of truffle consumption versus available biomass, the conclusion of Maser et al. (1986) that the northern flying squirrel does not select certain truffle genera is tenuous, and more recent lines of evidence contradict that conclusion.

Based on low presence of truffle genera other than *Rhizopogon* in chipmunk fecal samples, these chipmunks do not appear to rely on a highly varied fungal diet. More truffle genera were consistently found in the diets of both northern flying squirrels and vole species than in the diets of chipmunks in our study. McIntire (1984) found *Rhizopogon* to be the most frequently represented truffle genus in the feces of Siskiyou chipmunks. In our study, plant material was the second most common diet item for the chipmunk species, implying a lesser dependence on a varied fungal diet than voles or flying squirrels. Tevis (1952) noted that chipmunks utilized truffles but consumed a variety of plant materials too. Colgan et al. (1997) also found plant material to be heavily represented in the diet of Townsend's chipmunks, ranking second in dietary importance. Our results, along with those from other studies, support the depiction of this chipmunk by Maser et al. (1978:805) as an "avid mycophagist," rather than a fungal specialist.

An earlier study of mycophagy in the Watson Falls block of the DEMO experiment showed that *Leucogaster* spores were more frequent in the diet of Siskiyou chipmunks than in western red-backed voles (Cázares et al. 1999). In our study, frequency of *Leucogaster* spores in the diets of the chipmunk and vole species did not differ; only northern flying squirrels had a high frequency of *Leucogaster* spores. Luoma et al. (1991) documented effects of season and habitat on *Leucogaster* sporocarp production; thus the discrepancy in these results is likely due to temporal and between-block differences, including different seasonal phenologies that affect sporocarp abundance, because Cázares et al. (1999) examined only one block during a different time frame. The pretreatment chipmunk fecal samples from the Watson Falls block in this study had twice the frequency of *Leucogaster* spores, as did samples from the Butte block. Pretreatment *Leucogaster* sporocarp biomass averaged 6 times more in the Watson Falls block compared to the Butte block (D. Luoma, Oregon State University, unpublished data).

The overall high diversity of fungal genera in the diets of the small mammals that we studied emphasizes the importance of mycophagy as a potential spore dispersal mechanism for truffle fungi. In the PNW, mycophagy as a form of dispersal enhances the establishment of truffle fungi, as compared to wind-dispersed mushrooms (Luoma et al. 2004). Parks (1919) noted the positive association of truffle abundance with woodrat (*Neotoma* sp.) abundance and proposed an important role for woodrats in spore dispersal. Truffle fungi are disproportionately successful as ectomycorrhiza-formers in relation to their proportion of species richness (Luoma and Eberhart 2005). Retaining adequate populations and diversity of both small mammals and mycorrhizal fungi to promote forest health and biodiversity will contribute to forest ecosystem resilience.

Diet Change

Our results are most pertinent to the season of sampling (fall) and to the immediate postdisturbance (tree harvest) time period. The posttreatment decrease of *Rhizopogon* frequency in vole samples represents a substantially larger proportional change in *Rhizopogon* consumption as compared to other truffle genera due to the saturation effect in subsamples (Williams 1987). Pretreatment vole fecal samples were saturated with *Rhizopogon* spores, typically being abundant in 100% of the microscope fields examined. In the sample plots, the genus *Rhizopogon* produced the most truffle biomass pre- and posttreatment (Luoma et al. 2004). Our observed decrease in *Rhizopogon* consumption might be explained by 1) habitat change, such as the removal of trees, which would reduce ready access to *Rhizopogon* truffles or 2) a large decrease in *Rhizopogon* truffle abundance within a treatment unit.

Recently harvested clearcuts are generally considered unsuitable habitat for voles (Gashwiler 1970). In the DEMO aggregated retention treatments, vole captures were strongly associated with tree aggregates, suggesting that aggregates act as refugia. Voles in the aggregates would have to cross an expanse of open ground in order to reach another aggregate or forest edge, especially in the 15% A treatment. Therefore, movement of these animals may have been restricted, creating a green-tree aggregate island effect.

Mills (1995) found a strong negative edge effect on both vole numbers and truffle abundance. Both decreased with decreasing distance to edge in 0.6- to 2.5-ha forest remnants. The DEMO aggregates were 1.0 ha and would be expected to show a strong negative edge effect. Thus, not only are voles restricted in traveling as compared to a continuous forest, their movements may be concentrated towards the center of the aggregates due to edge effects. We speculate that movement of voles in the aggregated treatments was restricted, thereby limiting access to alternate sources of *Rhizopogon* truffles, and when combined with reduced truffle production due to edge effects, the opportunity for individual voles to encounter *Rhizopogon* truffles was lowered. If voles compensated by eating increased amounts of other truffles or plant material (such as seeds), we were unable to detect that change with our data. The animals may simply have been getting less food with subsequent changes in population dynamics.

Gautieria truffles appear to be a preferred food of northern flying squirrels (Zabel and Waters 1997); therefore the changes in *Gautieria* spore frequency we found may reflect important ecological responses. However, low capture numbers from certain treatments and the removal of the 15% D treatment from analysis reduce our ability to ascribe particular effects to treatments. The ability of northern flying squirrels to travel outside treatment units, truffle abundance, and within-treatment competition for truffles will influence consumption of *Gautieria* truffles by northern flying squirrels, but we identified no readily discernable relationships.

Chipmunks, like northern flying squirrels, were rare and in some cases we captured as few as 2 animals in a specific posttreatment experimental unit. Additionally, chipmunk data from only one pretreatment year were available for the 75% A treatment. No statistically significant changes in the mean frequency of diet items were evident from our research. Low capture numbers from certain treatments and the removal of the 40% D treatment from analysis may have reduced our ability to assess treatment effects.

Cumulative Number of Genera

Genera accumulation curves indicated that a minimum of 8 animals was generally necessary to observe most of the truffle genera consumed by study animals. This number is similar to that determined by Carey et al. (1999; ≥ 7 samples) as adequate to estimate genus richness in the diets of flying squirrels and chipmunks. Low capture numbers for northern flying squirrels and chipmunks preclude broad conclusions from our study because genera accumulation curves did not reach an asymptote in several treatments.

There is no clear biological interpretation for the decrease in mean cumulative number of genera in the diets of voles in the 40% D retention treatment. Local interactions of predator–prey relationships and animal population dynamics not measured in this study have potential to influence this result.

MANAGEMENT IMPLICATIONS

In Douglas fir–dominated forests of the PNW, forest managers could expect that management for isolated green-tree retention aggregates will locally reduce consumption of *Rhizopogon* in the diets of western and southern red-backed voles. Forest managers may reduce the impact of tree harvesting on these key forest ecosystem components by including green-tree aggregates within a dispersed retention matrix. Our research indicates that including dispersed retention around green-tree aggregates may maintain *Rhizopogon* as a food source. A decline in *Rhizopogon* spore frequency in the diets of voles may reflect a large decrease in the availability or accessibility of *Rhizopogon* truffles. Future research could explore the possibility of cascading effects over time, such as lowered *Rhizopogon* truffle availability and abundance, as a result of reduced spore dispersal, producing a decline in the abundance of small mammals. Additionally, future research that encompasses longer time periods and samples across seasons will expand the scope of inference for which the results are applicable.

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